A POPULATION STUDY OF FERAL GOATS (*CAPRA HIRCUS* L.), FROM MACAULEY ISLAND, NEW ZEALAND

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SUMMARY: In August 1966, the entire population of hitherto undisturbed feral goats on Macauley Island, Kermadec Group, New Zealand, was destroyed. Of 3,200 animals (4/acre) 1,047 were examined after death. Primary coat colours were black (37.8%), tan (11.9%) and white (0.7%). Horns were mostly of the twisted 'prisca' type, maximum lengths being 20.3 in. for males and 9.5 in. for females. Of 118 mandibles 8% showed a range of abnormalities including localised excessive wear, diseased alveolar bone and loss of teeth. Life expectancy at birth was 4.5 years.

22% of females over two years old were simultaneously pregnant and lactating and twins occurred in 39% of pregnancies. Corresponding figures in females under two years old were 1.4% and 2.0% respectively. Mortality of kids between birth and six months was estimated to be between 34% and 57%. A minimum estimate of pre-natal mortality was 33%. Some females bred twice yearly in two ill-defined seasons with peaks probably in August and March.

In the absence of predation, hunting or emigration the population appeared to be regulated by suppression of first year breeding, pre-natal mortality and high mortality of kids up to six months old.

INTRODUCTION

During the last 200 years the descendants of goats released by early explorers and settlers have become feral throughout the mainland of New Zealand and many of its off-shore islands (Thompson 1922, Wodzicki 1950). With other introduced mammals they have destroyed much native forest (Howard 1965) and are now shot in great numbers each year under the provisions of the Noxious Animals Act. Hitherto, the opportunities for obtaining and analysing large samples of the goat populations by means of these shooting programmes have not been taken. This paper presents an analysis of material obtained during the extermination of an island population.

Between 28 July and 21 August 1966 officers of the New Zealand Wildlife Service visited Macauley Island (which is uninhabited) to eliminate the goats. The limitations of time imposed by this priority, and the rugged terrain, restricted the range of biological information which could be gathered. Nevertheless, about one third of the total population was examined after death.

DESCRIPTION OF THE ISLAND AND HISTORY OF THE POPULATION

Macauley (30° 13′ S., 178° 33′ W.), the second largest island of the Kermadec Group, lies approximately 500 miles N.N.E. of East Cape, North Island and about 65 miles S.S.W. of Raoul Island. It is roughly rectangular, 1.25 miles long and just over one mile wide, with an area of approximately 800 acres. Its highest point, Mt. Haszard, is 780 feet above sea level (see Fig. 1).

The island is an extinct basalt volcano composed of very gently dipping flows and breccias. The last rocks formed were basaltic scoria and, on the lower north-eastern parts, the surface of the land cuts through acid pumice tuff (Brothers and Martin, pers. comm.). Earlier accounts of the geology may be found in Smith (1887) and Oliver (1909).

Perpendicular or near perpendicular cliffs ring the island and these are lowest, about 200 feet high, at Windy Head in the north-east. Except at Sandy Bay, which is a dangerous beach approximately 150 yards long, the coast is of lava shelves, rock walls and enormous boulders and reefs. Above the cliffs (which may be readily ascended at only two

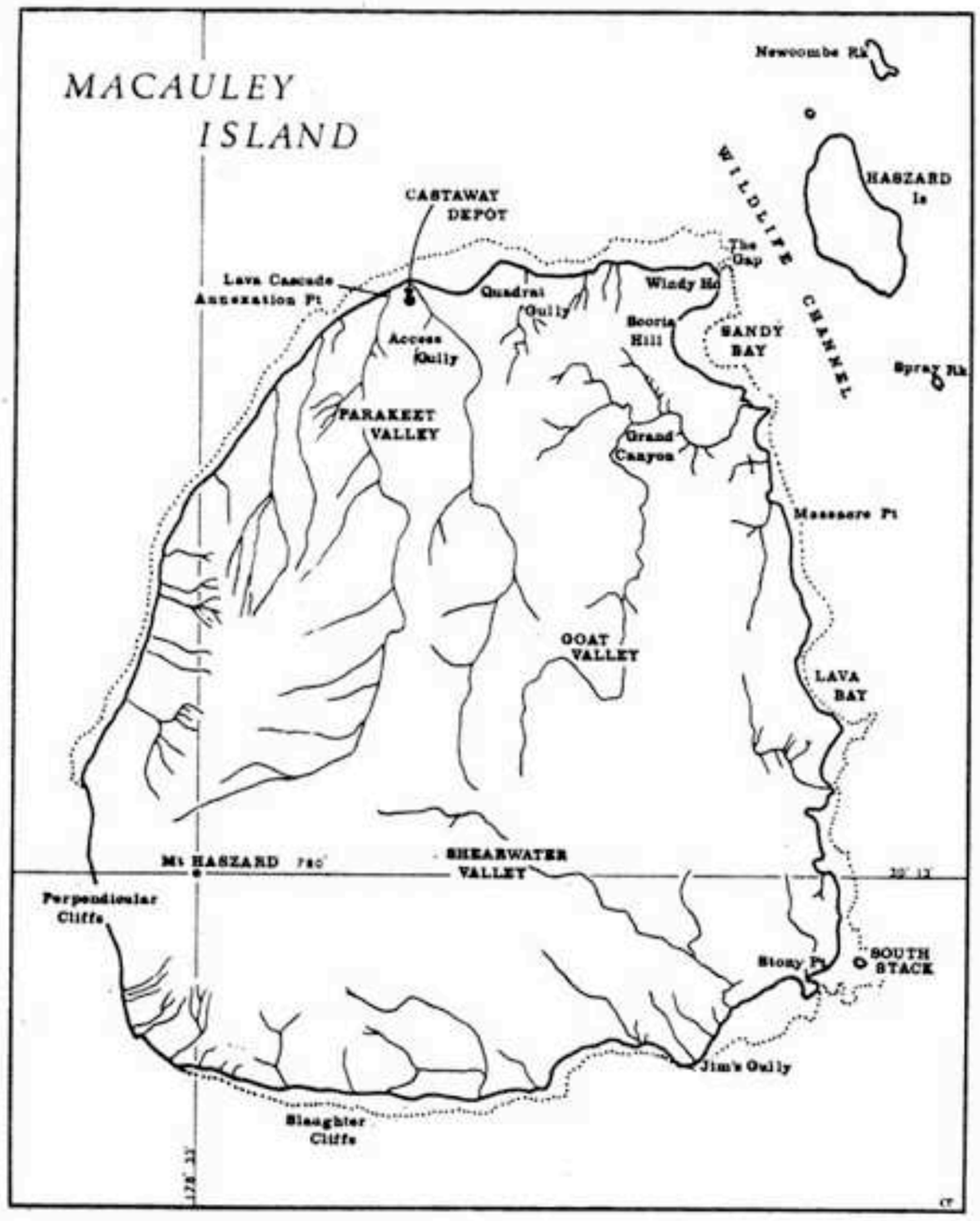

FIGURE 1. *Place names, except Mt. Haszard, Haszard, I., Annexation Point, Sandy Bay, Lava Cascade, and Perpendicular Cliffs, were bestowed by members of the 1966 expedition.*

points—Access Gully and Jim's Gully) the land slopes gently upward as a dissected plateau towards the south-west and Mt. Haszard. There are numerous very deep erosion gullies, inaccessible in places; the largest, Grand Canyon, is up to about 150 feet deep and 300 feet wide and discharges through vertically-walled channels about 50 feet above Sandy Bay. It is significant that the earliest accounts (Bowes 1788–1789 and Watts 1789) do not mention such gullies and that Smith refers to them only as "shallow". Access Gully, which is now the easiest and most obvious way to the top, cannot have existed as such until relatively recently because earlier visitors reached the plateau by climbing the Lava Cascade nearby.

Haszard Island lies about 300 yards off Windy Head and is approximately 500 yards long and 250 yards wide. Its cliffs, though lower than those of the main island, appear even more formidable; it has no goats and we had no opportunity to land upon it.

The nearest weather station is at Raoul Island and there is no reason to believe that the climate at Macauley is very different from that at Raoul: the annual rainfall of about 60 inches is fairly evenly distributed, with a winter maximum. There are about 2,100 hours of sunshine a year; the mean temperature in February is 72° F. (22° C.) and 61° F. (19° C.) in August; the mean daily maximum in February is 77° F. (25° C.) and the mean daily minimum in August 56° F. (12° C.). South-easterly and easterly winds predominate in summer, north- westerlies at other seasons.

Except during and immediately after rain there is no standing or running fresh water on Macauley; what falls drains away rapidly through the scoriaceous soil or is contaminated in the rock pools by the sea.

When the island was discovered on 31 May 1788 and landed upon on the following day, it was covered with trees, shrubs and grass and "the sandy soil was mixed with a litter of rotten leaves and bird droppings" (Bowes). Watts remarked that the trees were mangroves, but they were almost certainly Kermadec ngaios (*Myoporum obscurum*). In 1827, according to D'Urville (1832), Macauley was "tapissée seulement de pelouses ou de broussailles sans un seul arbre". However, he passed the island at some distance, so his description would be expected to lack detail. Rhodes landed in 1836 (Straubel 1954) and reported "a few stunted trees and a little wild parsley and other herbage on the most elevated part". Pigs (not reported since and now absent) and goats had already been introduced, apparently some years beforehand, and the island may have been burnt at about that time to supply forage as layers of charcoal underlie the present vegetation.

There appear to be no more accounts of Macauley for 50 years until the visit of Cheeseman and Smith in August 1887. They found the island well grassed and observed "the charred stumps of some ngaios of a good size". Cheeseman (1887) recorded only 33 species of plants and Smith saw "over a hundred" goats (almost certainly an underestimate), "very few kids" and a dog in good condition which was left behind. In his opinon the dog was responsible for the shortage of kids. The state of the vegetation and the number of goats support the supposition that burning and stocking had occurred a considerable time previously.

Oliver (1909) found the vegetation in a similar state 21 years later and it was still, presumably, much the same in 1966, when there was a fine

sward, mainly of rice grass (*Microlaena stipoides*) and, where this was less dense, the introduced *Vulpia bromoides*. Other plants were *Notodanthonia racemosa*, *Cyperus ustulatus* (probably the "coarse grass" of 1788), *Scirpus nodosus*, etc.; and, out of reach of the goats, a few Kermadec ngaios. (For a fuller account of the botany, see Sykes, 1969, to whom we are indebted for this information).

A careful tally was made of the goats as they were killed and the final total, to the nearest round number, was 3,200. The presumed last survivor was found after a considerable search and shot about 24 hours before the party left the island.

COLLECTION OF DATA

Material was collected in three ways:

1. Horns (165) were taken — as found — from skeletons of animals which had died from natural causes prior to the arrival of the expedition. Another 95 horns were similarly taken from animals which were killed.
2. Mandibles (118) were also collected from skeletons, but as they usually came from animals other than those from which the horns were taken they constituted a virtually independent sample. Only left mandibles were taken to ensure that, in the event of any subsequent expedition, the remains of this population would be distinguishable from the one that was destroyed. The mandibles were used to assess the mortality pattern in the undisturbed population.
3. As both manpower and time were limited it was impossible to perform an autopsy on all animals killed. Furthermore, many fell from the cliffs into the sea or other inaccessible places. The party operated as several independent teams each undertaking to examine part of its kill. Animals were killed unselectively and examined where they fell with no distinction as to sex or size. The sample is thus considered representative of the population as a whole. Every effort was made to maintain consistency and accuracy between the records of each team.

The following data were obtained: Sex, age-group (roughly estimated from body size), reproductive condition of females, and the numbers, sex and size of embryos. The colour and major pattern of the coat were recorded as in Table 1; minor markings of the face and legs were ignored. Body weights and external measurements were not taken, neither was any parasite collection made.

In the absence of structures that could be accurately aged the field estimates of age could not be checked later and some are almost certainly suspect. For this reason only the least ambiguous age groups have been used in the following analyses.

RESULTS

NATURAL HISTORY

Since Macaulay Island is very rarely visited (the last recorded visit was Oliver's in 1908), we have little knowledge of previous population densities. Rhodes' statement (Straubel 1954) that goats were already "abounding" in 1836, Smith's rough estimate of "over a hundred" in 1887 and Oliver's of

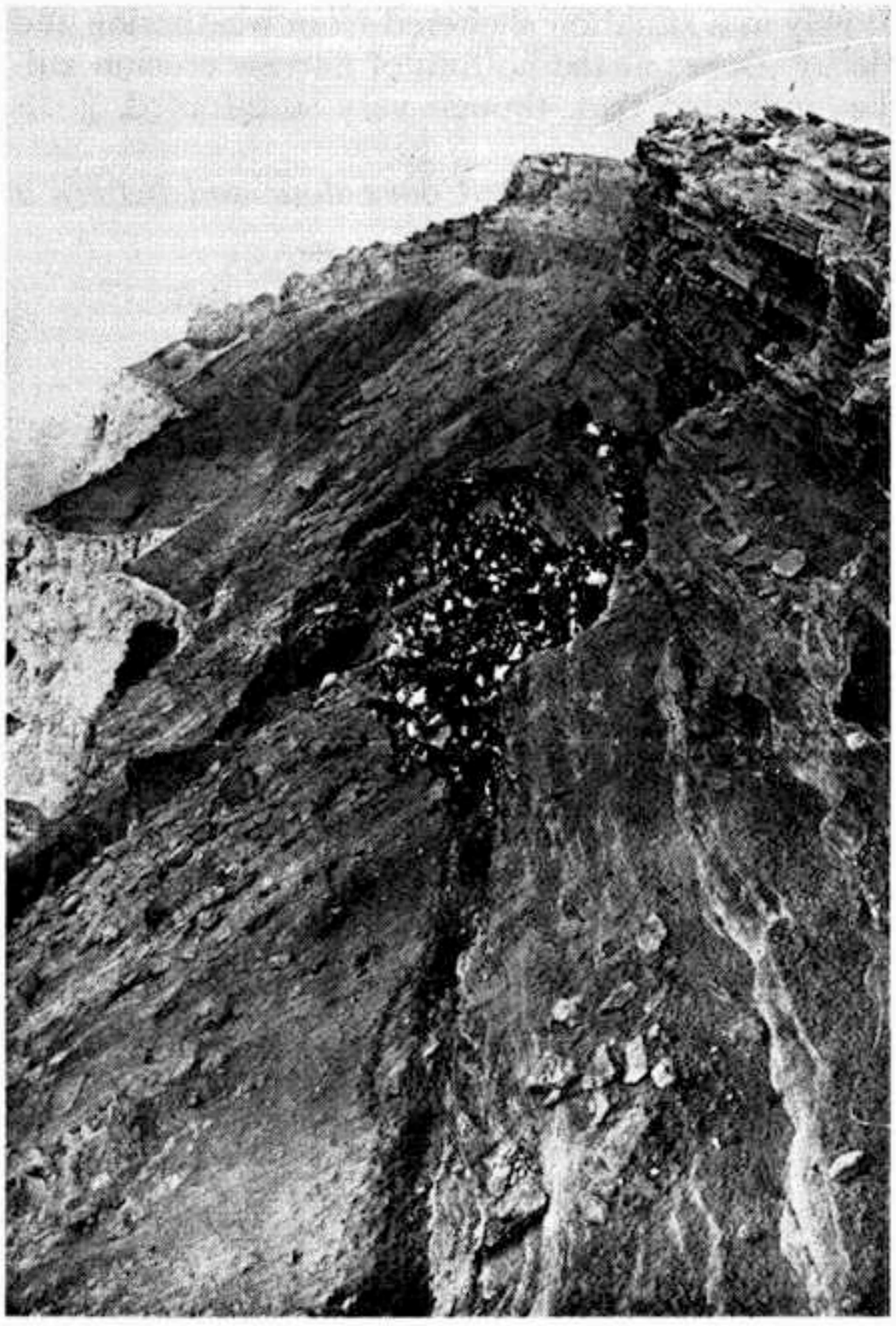

FIGURE 2. *A herd of goats on the western cliffs of Macauley Island. (Photo taken by R. B. Oliver in late 1908).*

"thousands" in 1908 are the only data available. No accurate count was made before shooting began in 1966 since the plan was to count the animals as they were being killed; but the upper estimate of 3,000 was close to the final tally of 3,200.

Brief observation indicated that the goats covered the island as one diffuse herd with perhaps some sub-groups within it. Few were seen on the shore or cliffs. Many young kids were present and were often seen sheltering in the eroded, enlarged entrances to petrel burrows (mainly those of *Puffinus* and *Pterodroma* spp., Williams, unpubl.). Animals of all ages were found in caves in the cliffs which, in the absence of trees or shrubs, afforded almost the only protection from the elements.

Skeletons were scattered all over the island. Piles of them in the caves probably had accumulated slowly in a situation sheltered from weathering and decay. Bones at the bottom of narrow erosion gullies indicated that, though very sure-footed, goats occasionally fell to their death or got into places from which they were unable to escape. A pile of skulls at one place was interpreted as evidence of hunting by a ship's party. Such events are not likely to have been common in recent times, as passing ships need no longer resort to such ways of obtaining fresh meat.

DESCRIPTION OF THE ANIMALS

Pelage and colour pattern: All animals were smooth-coated, though males were noticeably shaggier than females and bore larger beards. In females these were often no more than whispy tufts. The throat toggles commonly present in domesticated goats were absent.

The most frequent coat patterns in both sexes (Table 1) were white or brown markings upon a black base (87% ♂, 83% ♀). In males, black with a white flank spot was most frequent (32%) followed by all-black (26%). In females this order

TABLE *1: Coat colour and pattern in 1,047 feral goats from Macauley Island.*

COLOUR COMBINATIONS	MALES N	MALES %	FEMALES N	FEMALES %
Black (with tan and white equally)	8	2.3	20	3.7
Black with tan, white spot	38	11.0	44	8.1
Black with tan	71	20.6	123	22.7
Black with white	29	8.4	43	7.9
Black with white spot	109	31.6	129	23.8
Black only	90	26.1	183	33.8
Totals	345		542	
Tan with white	0	0	3	2.8
Tan (with black and white equally)	1	2.1	3	2.8
Tan with black, white spot	12	25.5	23	21.3
Tan with black	16	34.0	38	35.2
Tan with white spot	1	2.1	2	1.8
Tan only	17	36.2	39	36.1
Totals	47		108	
White with tan	0	0	1	0
White with black	3	0	0	0
Totals	3	0	1	0
Grand totals	395		651 (+1 unstated)	
Black as primary colour		87.3		83.1
Tan as primary colour		11.9		16.5
White as primary colour		0.7		0.5

was reversed (24% and 34% respectively) but all other patterns were equally common in each sex. With patterns based upon brown as main colour (12% ♂, 16% ♀) the three leading combinations were the same in each sex. White as main colour was found in less than 1% of animals. Male coats were not significantly darker than those of females.

Horns: These were carried by all adult animals and showed marked sexual dimorphism in size and shape (Table 2 and Figs. 3 and 4). In males they were sharply keeled anteriorly and elliptical in basal section. They rose up and back from the head with, in adults, a variable degree of twist and divergence. Only five of the 103 collected were so strongly curved as to bring their tips to face forward. The horns of females were more slender, rounded in basal section and curved back at the tips with less divergence and twist than in males. Departures from this form in the 157 female horns included four with excessive backward curvature (Fig. 4), six with excessive lateral curvature (Fig. 5) and three with re-curved tips.

As the horn-ring method of age determination (Pino 1952, Leonti and Bontempo 1955) has not yet been shown to hold for New Zealand feral goats, the horns were divided into broad age classes on the basis of known growth forms (Rudge unpubl.). In each age class the dimensions of male horns were about twice those of the females (Table 2). Maximum length for a male horn was 20.3 in. (51.5 cm.) and of a female horn, 9.5 in. (24.1 cm.).

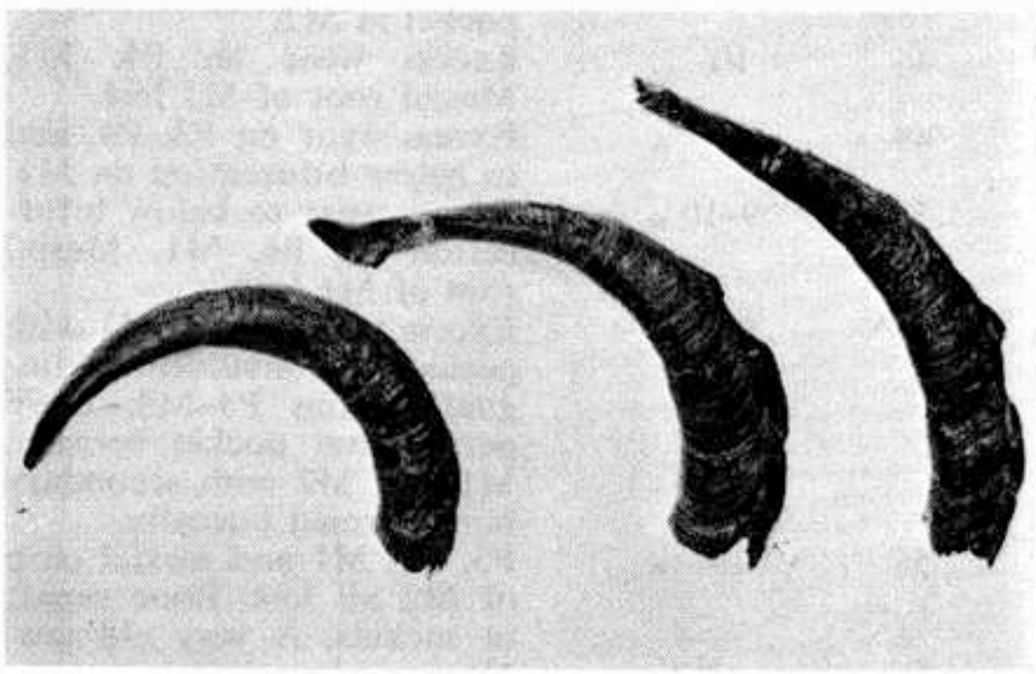

FIGURE 3. *Horns of Macauley Island male goats (side view). Typical "prisca" form in centre, excess currvature on the left, "erect" form on the right. (Right-hand horn, 17.5 in.)*

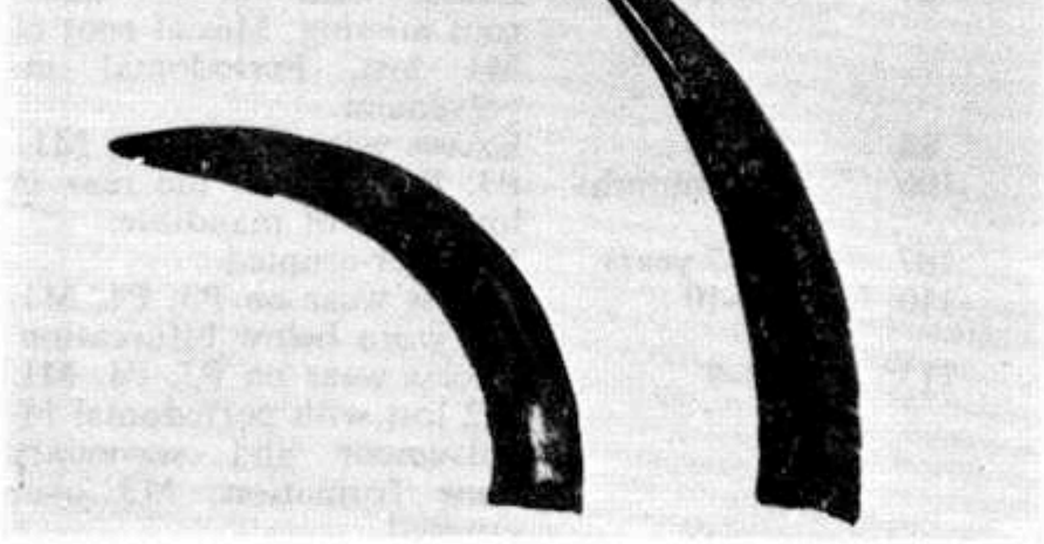

FIGURE 4. *Horns of Macauley Island female goats (side view). Excess backwards curvature compared with typical "erect" form (Right-hand horn, 8.0 in.)*

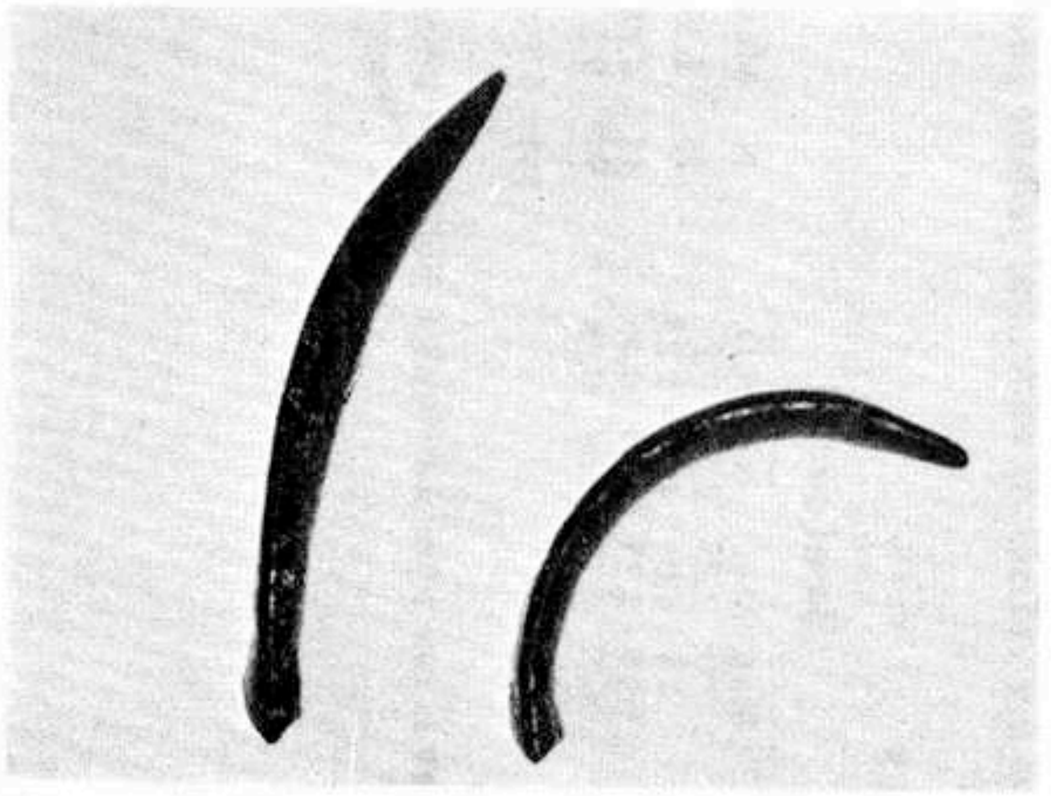

FIGURE 5. *Horns of Macauley Island female goats (front view). Excess lateral curvature compared with typical form. (Left-hand horn, 8.25 in.)*

Diseases and abnormalities: The health and general condition of the animals seemed good and most carried extensive deposits of body fat. (In 1836 Rhodes commented that the seven he took for food were "miserably poor".) No instances of foot-rot or ringworm, both of which may afflict mainland goats, were seen. Two females were affected by mastitis.

A number of abnormalities were found in the mandibles collected from the skeletons (Tables 3 and 4). The data do not include incisor teeth as these had dropped out after death. Age estimates are based on tooth succession and wear (Habermehl 1961 and Leonti and Bontempo 1955).

TABLE 2. *Horn dimensions (in inches) in four age classes of male and female feral goats from Macauley Island*

Age Group	N	MALES Length Max.	Min.	$\bar{x}$	S.D.	Basal circ. Max.	Min.	$\bar{x}$	S.D.	N	FEMALES Length Max.	Min.	$\bar{x}$	S.D.	Basal circ. Max.	Min.	$\bar{x}$	S.D.
Kids (<6 months)	8	2.75	2.0	2.29	0.3	3.0	2.25	2.59	0.2	15	2.25	1.63	2.12	0.2	2.75	1.25	2.32	0.5
Kid to <1 year	7	6.75	4.25	5.35	0.3	4.5	4.0	4.25	0.25	48	4.88	2.75	3.78	0.2	2.88	2.25	2.64	0.2
1 year <2 years	31	8.25	5.75	7.35	0.7	6.5	4.25	5.15	0.46	94*	9.5	3.0	6.19	1.5	3.75	2.12	2.9	0.22
Older than 2 years	57	20.3	7.88	11.9	3.4	6.5	4.75	5.68	0.38	157*								
Totals	103																	

* N for length=94 as one horn was broken but N for circumference=95.

TABLE 3. *Nature of the abnormalities in 23 of a sample of 118 feral goat mandibles from Macauley Island.*

MANDIBLE NUMBER	ESTIMATED AGE	CONDITION
7	10 years	Excess wear on P3, P4, M1. M1 worn below bifurcation and roots free.
36	10 ,,	Excess wear on M2. Buccal face of mesial cusp broken off.
37	6–7 ,,	Excess wear on P4, M1.
40*	8–9 ,,	Buccal tilt to P3, P4, M1. Periodontal involvement.
42*	9–10 ,,	Excess wear on P2, P3, P4, M1. P4, M1 worn below bifurcation, and roots remain as loose pegs. Periodontal pocket between M2 and M3 accentuated by migration of these teeth.
44*	9–10 ,,	Wear to below bifurcation on M1. Buccal periodontal pocket at M2.
46	10 ,,	Excess wear on P4, M1. Mesial root of M1 lost.
49	10 ,,	Excess wear on P3, P4, and to below bifurcation on M1.
50	9–10 ,,	Excess wear to below bifurcation on P4, M1. Mesial root of M1 lost.
55*	8–9 ,,	Excess wear on P4, M1 with periodontal involvement lingually from P3–M3. Deep periodontal pocket between M1 and M2 with secondary bone formed buccally.
56	10 ,,	P3, P4, M1 and mesial cusp of M2 all lost. Bone repair in sockets. A very old jaw. No periodontal disease.
60*	20 months	Exostosis on buccal side of P3, P4.
75	8–9 years	P2, P3, P4, over-erupted Excess wear on M1.
77*	8–9 ,,	M1 lost with peridontal involvement extending along M2.
80	9–10 ,,	Excess wear on P3 and P4, mesial half of M1 lost.
81*	9–10 ,,	Excess wear on P3, distal root missing. Mesial root of M1 lost. Periodontal involvement.
84	9–10 ,,	Excess wear on P3, P4, M1.
100	18 months	P3, P4 tilted to the rear in long axis of mandible.
107	6–7 years	M3 over-erupted.
110	9–10 ,,	Excess wear on P3, P4, M1. M1 worn below bifurcation.
113*	8–9 ,,	Excess wear on P3, P4, M1. M2 lost with periodontal involvement and secondary bone formation. M3 over erupted.
115*	9–10 ,,	Excess wear on P4, M1. Periodontal erosion lingual to M2.
116	6–7 ,,	Excess wear on P3, P4, M1.

* Pathological condition present.

The 23 abnormal mandibles included nine with disease of the supporting bone. This mainly consisted of erosion of the socket rim alongside a row of teeth or of more localised erosion forming a small diastema between adjacent teeth. The commonest non-pathological condition was excessive wear of one or several teeth in the row involving particularly premolar 4 (P4) and molar 1 (M1).*

TABLE 4. *Frequency of occurrence of abnormalities in 118 feral goat mandibles (summarising data in Table 3).*

ABNORMALITY	TEETH INVOLVED	NO. OF OCCURRENCES	% FREQUENCY OF OCCURRENCE
Pathological	n.a.	9	7.6
Non-pathological			
Excess wear	P2	1	0.8
	P3	9	7.6
	P4	13	11.0
	M1	14	11.9
	M2	1	0.8
Wear extending below root bifurcation	P4	2	1.7
	M1	6	5.1
Loss of all or part of a tooth	P3	2	1.7
	P4	1	0.8
	M1	6	5.1
	M2	3	2.5
Over-eruption	P2	1	0.8
	P3	1	0.8
	P4	1	0.8
	M3	2	1.7
Displacement	P3	2	1.7
	P4	2	1.7
	M1	1	0.8
	M2	1	0.8
	M3	1	0.8
Broken	M2	1	0.8

In particular, the wear on M1 in 26% of mandibles extended below the root bifurcation. This left the roots free to drop out during life and would account for some of the gaps in the row. Although skulls were not examined, occasional loss of teeth from the maxilla was inferred from over-eruption of P2, P3, P4 and M3 in the mandible.

Marked unevenness of wear began at about six years of age and the most extreme reduction of teeth was associated with advanced age. Mandible 56, for instance, retained but one and one-third of its original six cheek teeth. Unequal wear should be distinguished from extreme but even wear. Several mandibles estimated to be over seven years old showed extensive wear along the row but without the deep trough at P3–M1. This pattern probably had its main cause in the extreme abrasiveness of the volcanic dust ingested with the food. As the tooth crowns wore down, food and grit impacting on the exposed gums would cause lesions which would deepen, reach the alveolar bone and lead to periodontitis. (Colyer 1947). A more detailed analysis of this effect is being made in comparison with mandibles from the mainland. (Rudge, in prep.).

POPULATION STRUCTURE

Sex: Of 1,047 animals examined (Table 5) 395 were males and 652 were females a sex ratio of 1: 1.65 (significantly different from unity at $p = 0.01$). The change in sex ratio from 1: 1 at birth to 1: 1.8 at two years shows a heavier mortality amongst young males than young females.

TABLE 5. *Total numbers, age composition and sex ratios of the goats from Macauley Island.*

AGE	MALES	FEMALES	SEX RATIO
0 <1 week	45	46	1:1
1 week <1 month	6	2	1:1
1 month <2 months	0	4	1:1
2 months <6 months	95	120	1:1.26
6 months <1 year	14	12	1:2.5
1 year <2 years	22	78	
Older than 2 years	213	390	1:1.8
Totals	395	652	1:1.65
Number of females older than 1 year	468		
Number of young of less than 6 months (kids)	318		
Ratio of adult females to kids	1:0.66		

Age: Although the sample of mandibles is rather small it may be used to construct at least a provisional life table for the undisturbed population. Age determination based on tooth eruption and wear is tolerably accurate up to three years of age but beyond that depends on subjective estimation. The unequal wear already described greatly influences such estimates particularly in the 3–5 year and 6–8 year groups in which wear on M1 and M2 respectively is a key criterion. Mandibles have not been separated into age classes beyond ten years.

In preparing the life table two assumptions have been made: (i) the sample represents the frequencies of ages at death and (ii) the population had a stationary age distribution. Each of these assump-

* Terminology is based on the phylogenetic dental formula

$$I=\frac{0}{3};\ C=\frac{0}{1};\ P=\frac{4}{4};\ M=\frac{3}{3}\ \text{(Winge 1942)}$$

tions deserves comment: (i) the youngest age groups are probably under-represented since their mandibles would decay more quickly than those of adults; (ii) as the goats had been isolated on Macauley for a minimum of 130 years and had apparently been "in thousands" since at least 1908 a stationary age distribution is a reasonable assumption.

TABLE 6. *A composite-dynamic life table for feral goats based on 118 mandibles from Macauley Island.*

Age in years (x)	d_x	l_x	q_x	E_x	% deviation of each age from mean E_x
0–1	33	118	0.280	4.58	−100.0
1–2	11	85	0.129	5.17	− 78.2
2–3	4	74	0.051	4.86	− 56.3
3–4	8	70	0.114	4.11	− 34.5
4–5	1	62	0.016	3.58	− 12.7
5–6	13	61	0.213	2.63	+ 9.2
6–7	21	48	0.438	2.21	+ 31.0
7–8	2	27	0.074	2.54	+ 52.8
8–9	6	25	0.240	1.70	+ 74.7
9–10	8	19	0.421	1.08	+ 96.5
10+	11	11			

Weighted mean annual mortality=19.7%.

Table 6 presents the resultant d_x series and the q_x series calculated from it. After a rate of 28% in the first year, mortality dropped until the sixth year, after which it climbed towards extinction at about ten years. The mean expectation of life at birth was 4.5 years.

REPRODUCTION

Reproductive state of females: Females less than one year old showed no signs of reproductive activity (Table 7). Those older were divided into two age groups, '1–2 years' and 'two years plus'. Within these age-groups only 7.6% showed no reproductive activity, 28.6% were pregnant only, 18.6% pregnant and lactating and 45.1% lactating only.

Fewer females were in non-breeding condition in the two-year-plus class (4.0%) than in the 1–2 year class (27%). Simultaneous pregnancy and lactation was almost entirely confined to the older females.

Although no female less than one year of age was pregnant, the 1–2 year class contained seven which were lactating and one pregnant and lactating. This suggests that they could have conceived in their first year. Conception may occur at six months in both domestic (Asdell 1964) and feral goats (Yocom 1967) but the complete absence of pregnancies in the 0–1 year age class indicates that it was very infrequent in the Macauley Island population.

Analysis of pregnancies: The proportion of *single embryos* was greater in the 1–2 year class (98%) than in the two-year-plus class (61%) (Table 8). In pregnant-only females of both age groups the sex ratio of embryos did not differ significantly from unity. By contrast, the ratio in pregnant-lactating females showed a bias (though not significant at $p < 0.05$) towards females.

Twins occurred in 39% of females older than two years but in only 2% of younger females (Table 8). Within the older age-group (Table 9) twins were significantly more common in pregnant-lactating than in pregnant-only females. ($X^2 = 23.5$, $p < 0.001$ with 1 d.f.). Of the twin pregnancies, 40% were all male, so raising the sex ratio to 1: 0.64 which differed significantly from unity at $<0.05>$ 0.025. However, the final sex ratio

TABLE 7. *Reproductive states of 614 female goats from Macauley Island.*

Age	No.	Preg only No.	Preg only %	Preg./lact No.	Preg./lact %	Lact. only No.	Lact. only %	Neither preg. nor lact. No.	Neither preg. nor lact. %
0<6 months	172	0	0	0	0	0	0	172	100
6 <12 months	12	0	0	0	0	0	0	12	100
1<2 years	70	45	64.3	1	1.4	7	10.0	17	24.3
2 years plus	360	78	21.7	79	21.9	187	51.9	16	4.5
Total	614	123	20.0	80	13.0	194	31.6	217	35.3
Pregnancies as % of females older than 1 year	430	123	28.6	80	18.6	194	45.1	33	7.7

TABLE 8. *Distribution of single and twin conceptions between the two groups of breeding-age female goats from Macauley Island.*

	Single conceptions		Twin conceptions		Total embryos		Sex ratio	Ratio of pregnant females: embryos
	N	%	N	%	M	F		
1–2 years	45	97.8	1	2.2	26	21	1:0.81	1:1 (46:47)
2 years or more	96	61.2	61	38.9	112	100	1:0.89	1:1.4 (157:217*)
Totals	141	69.5	62	30.5	138	121	1:0.88	1:1.3 (203:264*)

* Includes embryos of unstated sex.

TABLE 9. *Distribution of single and twin conceptions between pregnant females and pregnant-lactating females in the two breeding age-groups from Macauley Island.*

		SINGLE CONCEPTIONS				TWIN CONCEPTIONS						
	Condition	Total embryos	Male	Female	% Male	Total embryos	All male	All Female	Mixed	% all male	% all female	% mixed
Less than 2 years old	Pregnant only	44	24	20	55.6	1	0	0	1	—	—	—
	Pregnant — lactating	1	1	0		0	—	—	—	—	—	—
More than 2 years old	Pregnant only	60	29	31	48.4	15	4	4	7	26.6	26.6	46.6
	Pregnant — lactating	32	13	19	40.6	45	18	8	19	40.0	17.7	42.2

from all embryos was close to 1: 1 (138 ♂, 121 ♀) which was also the ratio for newly-born kids (Table 5).

(c) *Age distribution of embryos and prenatal mortality:* Embryos were assigned to size classes and their probable ages estimated later from the data of Eaton (1952) for domestic goats (Table 10). The size range showed that breeding extended at least from the end of March up to August (the time of sampling) and possibly even the year round. The presence of many young kids in the herd suggests a peak of births in about August and pregnant-lactating females carrying small embryos must have mated shortly after parturition. As gestation is about five months (150 days, according to Asdell 1964) each female was potentially able to give birth twice in a year.

Prenatal mortality was estimated by subtracting birth rate from conception rate. Conception rate was calculated by comparing the number of females bearing early embryos (78) with the number of early embryos (115), a ratio of 1: 1.5; and birth rate by comparing the number of females with full-term embryos (34) with the number of full-term embryos (35), a ratio of 1: 1. The difference between the two ratios showed a post-implantation loss of 33%.

DISCUSSION

The measurements of population density on Macauley Island (4/acre) are the best yet available for feral goats. When another population was exterminated on Cuvier Island, Atkinson (1964) arrived at an estimate of density of less than one per acre. The density of Macauley Island goats was twenty times greater than that of the free-living ungulates in the Nairobi National Park (Foster and Coe 1968). Expressed as biomass, however, the two areas supported 3,400 kg./sq.

TABLE 10. *Sizes and estimated ages of embryos in pregnant-only and pregnant-lactating females from Macauley Island.*

Size of embryo	Estimated age	N. females preg. only	N. embryos	N. twin conceptions	N. females preg./lact.	N. embryos	N. twin conceptions
0–4 in.	2 months	23	27	4	55	88	33
5–7 in.	3 months	20	25	5	6	10	4
8–10 in.	4 months	23	24	1	1	1	0
Near term	5 months	28	29	1	6	6	0
Unstated		27	32	5	12	15	3
Totals		121	137	16	80	120	40

km.* and 5,687 kg./sq. km. respectively. If, as a final comparison, the Macauley density is expressed as ewe equivalents (3.5/acre), it approaches that of non-intensive New Zealand sheep range (Dept. of Agriculture, pers. comm.).

Macauley goats, with their dark parti-coloured coats, were probably derived from the unimproved 'English' breed type (Pegler 1929). Similar markings occur in feral populations in Hawaii (Yocom 1967) and British Columbia (Geist 1960), though the latter seem to be mixed breeds. Horns corresponded generally to the twisted form ('prisca'-type of Zeuner 1963) characteristic of domesticated goats of European origin. No exaggeratedly twisted 'Angora'-type horns were seen such as may occur amongst feral herds on the New Zealand mainland. Some other feral populations, notably those in Britain, differ greatly in both body markings and horn shape from those of Macauley, Hawaii or British Columbia. Black and white in various proportions seem to predominate in British goats and their horns are of the erect, sweeping, 'bezoar'-type — up to 4 ft. long, (Boyd–Watt 1937, Tegner 1965, Milner Goodier and Crook 1968). Whether such characteristics represent an original state or a reversion to an ancestral condition amongst long-feral stock is not clear (Grieg, *in litt.* 1968).

Domesticated goats in the northern hemisphere are polyoestrus within seasonal breeding periods (Asdell 1964). The same seems largely true of feral goats in Britain (Boyd–Watt 1937, Milner *et al.* 1968), Hawaii (Yocom 1967), Japan (Asahi 1960) and British Columbia (Geist 1960). However, both Geist and Yocom noted that, despite an increase in births during summer, a few kids may be born in any month of the year. According to Wodzicki (1950), feral goats breed throughout the year in parts of New Zealand. Present work largely substantiates this (Rudge, unpubl.) with some indication of two main seasons about six months apart. On Macauley Island, the reproductive season was well-spread and possibly bimodal. Apparently, upon transfer across the equator, goats have not reversed their breeding seasons as completely as have, for example, red deer. (Marshall, 1937).

Goats on Macauley differed very little from domestic goats in the frequency of twinning (Villegas 1939, Tantawy and Ahmed 1960, Lyngset 1966, Moulick *et al.* 1966, Sacker and Trail 1966) or in the increase of fertility with age (Asdell 1964). However, females failed to reproduce in their first year, unlike domestic goats (Asdell 1964) and feral goats in Hawaii (Yocom 1967) and on the New Zealand mainland (Rudge unpubl.). Furthermore, there is a significantly greater frequency of twin conceptions in pregnant-lactating females than in pregnant-only females. An increased fertility of females inseminated *post-partum* is indicated but this may well be because these would necessarily be the older females.

The population of goats on Macauley was a closed system in which an annual recruitment of 1.7* kids per female per year was balanced by natural mortality. Apart from the pigs recorded by Rhodes in 1836 and the dog seen in 1887, no predators were present. Emigration was impossible, hunting very rare and any explosive stage of colonisation would long since have passed.

There seems to have been a high death rate between birth and six months of age and three

* This estimate is calculated from the live weights of feral goats from the mainland (Rudge, unpubl.).

* Each breeding age female is capable of producing at least one kid per year. A further 70% (the proportion pregnant and lactating) would produce another kid in that year, raising the overall birth rate to 1.7 kids/female/year.

estimates of this are available: Firstly, a rate of 28% is derived from the life table based on mandibles; this is a certain underestimate. Secondly, a rate of 34% is derived from the ratio of females of breeding-age to kids (1: 0.66 in Table 6). Finally, if the number of kids (0–6 months) in the shot sample (318) is subtracted from the theoretical number of 739 born (calculated from 435 breeding females x 1.7 kids/female/year), a loss of 421 or 57%, is obtained. However, this may be an overestimate arising from inadequacies in the age groupings. But, as losses of up to 34% occur even amongst husbanded goats (Lall and Singh 1949, Ahmed and Tantawy 1960), losses on Macauley Island could well have been between 34% and 57%. An important factor in the mortality of kids may have been the scarcity of water in all but the brief periods after rain. Such dry conditions could have imposed severe stresses on nursing females, particularly those with twins.

Fecundity (at the ovum stage) and fertility were both high; but the failure of females to breed in their first year and a partial pre-natal mortality of 33%, both presumably aggravated by the high population density and by the rigours of the climate, reduced the production of young. Recruitment is much higher and kid survival better on the New Zealand mainland than on Macauley (Rudge, unpubl.).

Although no detailed search was made for disease the animals seemed healthy. Only the mandibles were examined in detail and the abnormalities in them were not considered extensive enough to affect survival in the way that Murie (1944) found for dall sheep (*Ovis dalli*). Animals could survive to about ten years with a very depleted dentition (see mandible 56. Table 3). Probably only a few animals were killed by falling into gullies.

In summary, our evidence suggests that the population of goats on Macauley Island was regulated largely by suppression of breeding in the first year, by pre-natal mortality and by a high mortality in the first six months of life.

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REFERENCES

AHMED, I. A. and TANTAWY, A. O., 1960. Studies on Egyptian baladi goats. 2, Some factors affecting mortality rate. *Emp. J. Exp. Agric.* 28: 104–8

ASAHI, M. 1960. On the free ranging herd of Tokara goats in Tomagasima Island. *Physiol. and Ecol.* 9: 44–53.

ASDELL, S. A. 1964. *Patterns of mammalian reproduction.* (2nd edition). Comstock Publ. Co. N.Y.

ATKINSON, I. A. E. 1964. Relations between feral goats and vegetation in New Zealand. *Proc. N.Z. Ecol. Soc.* 11: 39-44.

BOWES, A. 1787–1789. *Journal of Arthur Bowes in the Lady Penrhyn . . . MS. Diary*, Mitchell Library, Sydney.

BOYD-WATT, H. 1937. On the wild goat in Scotland. *J. Anim. Ecol.* 6: 15-20.

CHEESEMAN, T. F. 1887. On the flora of the Kermadec Islands; with notes on the fauna. *Trans. N.Z. Inst.* 20: 151–181.

COLYER, F. C. 1947. Dental diseases in animals (paradontal). *Brit. Dent. J.* 82: 31–35.

D'URVILLE, M. J. DUMONT, 1832. *Voyage de la corvette l'Astrolabe . . . Histoire du voyage.* Vol. 4. J. Tastu (Ed.), Paris.

EATON, O. N. 1952. Weight and length measurements of fetuses of Karakul sheep and of goats. *Growth* 16: 175–187.

FOSTER, J. B. and COE, M. J. 1968. The biomass of game animals in Nairobi National Park, 1960–66. *J. Zool. Lond.* 155: 413–425.

GEIST, V. 1960. Feral goats in British Columbia. *Murrelet* 41: 34–40.

HABERMEHL, K. H. 1961. *Alterbestimmung bei Haustieren, Peltztieren und beim jagdbaren Wild.* Paul Parey, Berlin.

HOWARD, W. E. 1965. Control of introduced mammals in New Zealand. *N.Z. Dept. Sci. Industr. Res., Information Series.* 45.

LALL, H. K. and SINGH, J. 1949. Some observations on mortality in goats. *Ind. J. Vet. Sci.* 19: 261–73.

LYNGSET, O. 1966. Studies on the reproductive organs of the female goat. A preliminary report. *Nord. Vet. Med.* 18: 34–37.

LEONTI, F. and BONTEMPO, C. 1955. I cerchi cornei nella diagnosi dell'eta dei Caprini ed osservazioni sulla loro dentizione comparata a quella degli ovino (Contributo casistico) [Horn rings in determining the age of goats and observations on their dentition compared with that of sheep (Case histories)]. *Agric. Ital.* 55: 1–12.

MASHALL, F. H. A. 1937. On the changeover in the oestrus cycle in animals after transference across the equator, with further observations on the incidence of the breeding seasons and the factors controlling sexual periodicity. *Proc. Roy. Soc. Lond.* 122B: 413–428.

MILNER, C., GOODIER, R. and CROOK, I. G. 1968. Feral goats. *Nature in Wales* 11: 3–11.

MOULICK, S. K., GUHA, H., GUPTA, S., MITRA, D. K. and BHATTACHARYA, S. 1966. Factors affecting multiple birth in black Bengal goats. *Ind. J. Vet. Sci.* 36: 154–163.

MURIE, A. 1944. The wolves of Mount McKinley. *Fauna of the National Parks of the U.S. Fauna series* 5.

OLIVER, R. B. 1909. The vegetation of the Kermadec Islands. *Trans. N.Z. Inst.* 42: 118–175.

PEGLER, H. S. H. 1929. *The book of the goat.* Billing and Son Ltd., Guildford.

PINO, N. 1952. Il valore eteologico dei cerchi cornei nei Caprini (Contributo alla cognoscenza dell'eta in *Capra hircus*). [The etiological value of horn rings in goats. (Contribution to knowledge of the age in *Capra hircus*)] *Zootec. e Vet.* 7: 1–11.

SACKER, G. D. and TRAIL, J. C. M. 1966. Production characteristics of a herd of East African mubende goats. *Trop. Agric. (Trinidad)*, 43: 43–51.

SMITH, S. Percy. 1887. *The Kermadec Islands: their capabilities and extent.* Govt. Printer, Wellington.

STRAUBEL, C. R. 1954. *The whaling journal of Captain W. B. Rhodes: barque "Australian" of Sydney, 1836–1838.* Whitcombe & Tombs, Wellington.

SYKES, W. R. 1969. The effect of goats on the vegetation of the Kermadec Islands. *Proc. N.Z. Ecol. Soc.* 16: 13–16.

TANTAWY, A. O. and AHMED, I. A. 1960. Studies on Egyptian baladi goats. I. Frequency of multiple births and sex ratios. *Emp. J. exp. Agric.* 28: 73–82.

TEGNER, J. 1965. Wild goats of Britain. *Scottish Field.* Feb. 1965: 70–71.

THOMSON, G. M. 1922. *The naturalisation of animals and plants in New Zealand.* Cambridge University Press.

VILLEGAS, V. 1939. Multiple births in goats and sheep. *Philippine Agric.* 28: 5–14.

WATTS, Lieutenant. 1789. *The voyage of Governor Phillip to Botany Bay . . .* Printed for John Stockdale, London.

WINGE, M. 1942. *The inter-relationships of the mammalian genera. III, Ungulata, Cetaceae.* Copenhagen.

WODZICKI, K. A. 1950. Introduced mammals of New Zealand. *N.Z. Dept. Sci. Industr. Res. Bull.* 98.

YOCOM, C. F. C. 1967. Ecology of feral goats in Haleakala National Park, Maui, Hawaii. *Amer. Midl. Nat.* 77: 418–451.

ZEUNER, F. E. 1963. *A history of domesticated animals.* Hutchinson and Co., London.