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ERUPTION OF UNGULATE POPULATIONS, WITH EMPHASIS ON HIMALAYAN THAR IN NEW ZEALAND

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Abstract. An eruptive fluctuation is defined operationally as an increase in numbers over at least two generations, followed by a marked decline. Reported eruptions in ungulates suggest that the upswing is initiated by a change in food or habitat and is terminated by overgrazing. An apparent exception—the Kaibab eruption—probably also fits this pattern. The interpretation causally linking reduction of predators on the plateau with increase of deer is an overstatement of evidence. Eruption of established populations is essentially the same process as the buildup of populations initiated by liberation, with the difference that in the second case a zone of high density migrates radially from the point of liberation.

Eruption of thar (a goat-like bovid) after liberation in New Zealand was studied by sampling populations at different distances from the point of liberation. The aim was to determine trend of demographic statistics across an eruptive fluctuation that spans 50 years. Although fecundity varied across the eruption, the major influence on rate of increase was traced to variation in death rate. The major component of this variation was the rate of mortality over the first year of life. Trend in death rate, and hence in rate of increase, was associated with trends in other population statistics that are easier to measure. The most useful correlative of rate of increase is probably the level of fat reserves.

While we do not know whether trends in population statistics of thar reflect those of other ungulates during an eruptive fluctuation, the generality of the reported trends may usefully serve as a testable hypothesis.

REVIEW OF UNGULATE ERUPTIONS

The purpose of this study is to examine records of ungulate eruptions in an attempt to generalize the process and its causes, and to examine against this background the eruption of Himalayan thar (*Hemitragus jemlahicus*) in New Zealand.

No ungulate population yet studied has remained constant in numbers over a period of years. A. S. Leopold et al. (1951), for instance, suggested that a mule deer population tends to fluctuate between years by 5–10%. Minor fluctuations of this kind are difficult to study because the standard error of most census estimates is usually greater than 10% of the mean.

Yearly fluctuation of numbers would be expected in the fluctuating environments to which ungulate populations are subjected. Yearly variability of weather influences food supply and the condition of the animals, thereby affecting rates of fecundity and mortality. This is a primary effect. Any change in these rates has a secondary effect of changing the age distribution. In automatic consequence there is a change in rates of birth and death. A favorable season resulting in atypically high survival over the first year of life will produce a decreased birth rate the following year even when age-specific rates of mortality and fecundity return to their mean values. In this

instance the drop in birth rate reflects no more than the temporary increase in proportion of animals below breeding age.

Ungulate populations are also prone to occasional massive fluctuations that are inexplicable in terms of essentially random annual variation in conditions of life. These eruptive fluctuations can be defined operationally as a steady rise in numbers over at least two generations, followed by a marked decline. Such fluctuations occur both in well-established populations and in populations that have recently been established by liberation (i.e., artificial introduction into previously uninhabited territory). Riney (1964) developed the thesis that “introduced populations of large herbivores, if undisturbed, normally follow a pattern of adjustment to the new environment which consists of a single eruptive oscillation.” He considered that this sequence of events does not differ in kind from eruptions occurring in well-established ungulate populations and that it is triggered by the same circumstance: “a large discrepancy between the number of animals the environment can carry, and the number of animals actually present.”

Eruption of established populations

A. Leopold, Sows, and Spencer (1947) estimated that about 100 odocoileid deer herds in the United States entered an eruptive fluctuation be-

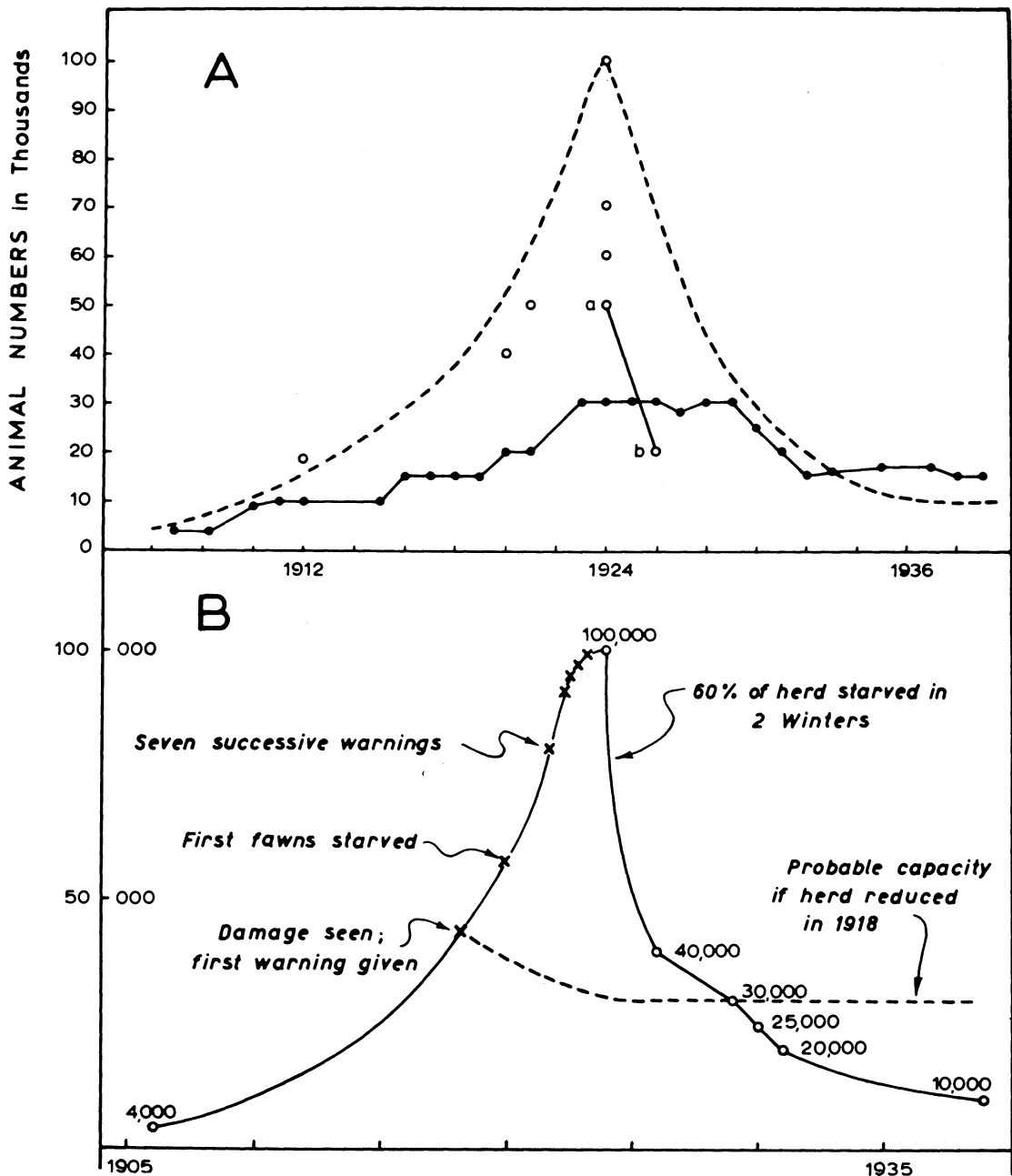
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tween 1900 and 1945. Banfield (1949) recorded an eruption of wapiti (*Cervus canadensis*), and Martin and Krefting (1953) did the same for a population of white-tailed deer. Each of these eruptions was suspected or shown to be checked by depletion of food.

In most cases a change in the vegetative habitat was postulated as the cause of initial increase. An exception is the eruption of mule deer (*Odocoileus hemionus*) on the Kaibab North Plateau. As this case is often treated as the type example of an eruptive fluctuation, it will be examined in detail.

The interpretation of the Kaibab eruption to be

found in most text books (e.g. Allee et al. 1949, Lack 1954, Andrewartha and Birch 1954, Odum 1959, Browning 1963) is: as a consequence of the removal of predators the deer population rose from 4,000 in 1906 to 100,000 in 1924. Having depleted its food supply the population was in no condition to withstand the following two harsh winters and 60% died. The decline continued for about 14 years to a population level of about 10,000. Leopold (1943) is usually quoted as the source of these data but he has given only a generalized interpretation of estimates presented by Rasmussen (1941).



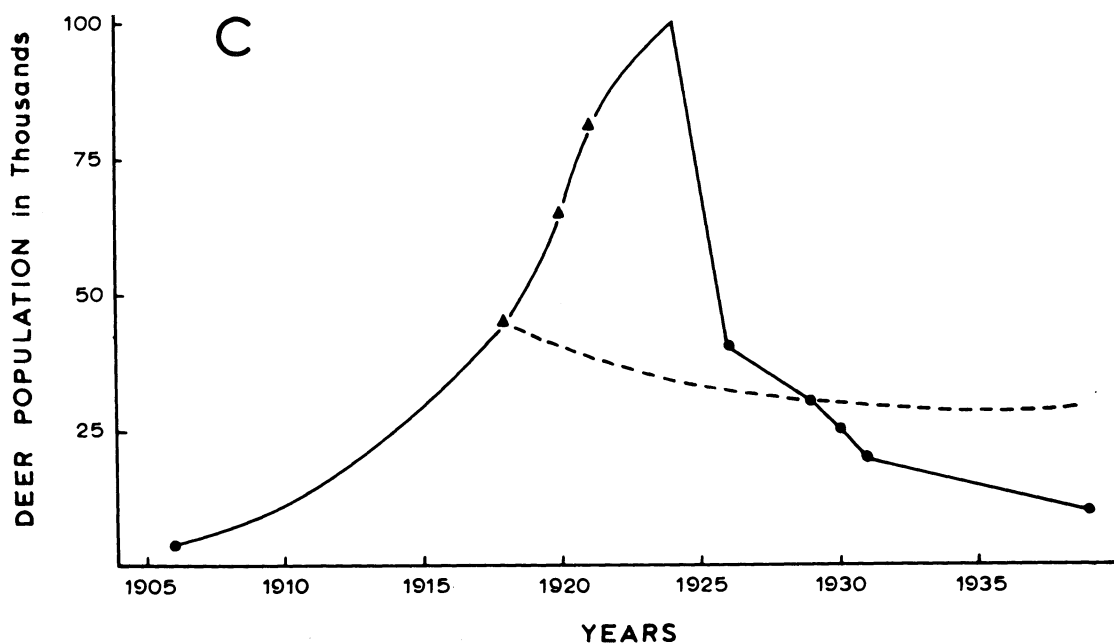


FIG. 1. Evolution of the Kaibab deer herd eruption.

A. Population estimate of the Kaibab deer herd, copied from Rasmussen (1941). Linked solid circles are the forest supervisor's estimates; circles give estimates of other persons, those labelled a and b being those of Mr. B. Swapp; and the dashed line is Rasmussen's own estimate of trend.

B. A copy of Leopold's (1943) interpretation of trend.

C. A copy of trend given by Davis and Golley (1963), after Allee et al. (1949), after Leopold (1943) from Rasmussen (1941).

Figure 1 summarizes the evolution of the Kaibab account. It reproduces Rasmussen's (1941) graph (A), Leopold's (1943) interpretation of it (B), and Davis and Golley's (1963) version (C) after Allee et al. (1949).

Rasmussen gave three sets of population estimates. The most comprehensive comprised the forest supervisor's estimates made each year, apart from a few gaps not exceeding 2 years. His second set consisted of eight estimates made between 1912 and 1926, taken from "reports of men visiting the Kaibab Plateau to make observations on deer." The third was Rasmussen's own estimate of trend. It was based on four points: the forest supervisor's estimate of 4,000 in 1906, Mann and Locke's (1931, in Russo 1964) estimate of 100,000 in 1924, the forest supervisor's estimate of 20,000 in 1931, and an undocumented estimate of "less than 10,000" in 1939. Rasmussen sketched an exponential trend of increase from 1906 to 1924 and a mirror-image declining exponential from that date to 1939.

The three sets of estimates recorded by Rasmussen show little correlation. For instance, the population in 1924 was variously estimated as 100,000, 70,000, 60,000, 50,000 and 30,000.

Figure 1B shows Leopold's (1943) adaptation of Rasmussen's graph. It is compiled as follows:

1904–1926 roughly followed Rasmussen's exponential trend with the difference that the trend was modified to an asymmetrical sigmoid; 1924–26 showed a decline from 100,000 in 1924 to 40,000 in 1926, based on U.S. Forest Service Ranger B. Swapp's estimate that a 60% decline occurred over this period (note that Swapp's own estimate was of a drop from 50,000 to 20,000 and that the forest supervisor estimated a population stable at 30,000 over the period of the postulated decline); 1926–1929 was a linear interpolation to the forest supervisor's estimate for 1929; 1930–1931 followed the supervisor's estimates for these years; and 1932–1939 left the supervisor's trend and reverted to Rasmussen's declining exponential. On the upswing section of the graph are seven crosses that are not population estimates but represent times at which warnings were given that the number of deer was too high for the carrying capacity of the plateau.

Allee et al. (1949) reproduced Leopold's graph with little modification and discussed it as if it were accurate. Subsequently Lack (1954) and Davis and Golley (1963) produced slightly simplified versions of the graph presented by Allee et al. Davis and Golley captioned their figure (reproduced here as Figure 1C): "The rise and fall of a Kaibab deer herd (redrawn from Allee

et al. 1949)," and left symbols undefined. They apparently mistook as population estimates three of the symbols representing warnings of overpopulation, because they cited the trend between 1906 and 1924 as evidence that the population passed through a regime of sigmoidal growth over that period. But this entire section of the graph is an interpolation between two dubious estimates of population size. The figured sigmoidal trend results from Leopold's arbitrary modification of Rasmussen's arbitrary exponential trend.

The inconsistency of the original population estimates presented by Rasmussen (1941) suggests that it would be unwise to place much reliance on the interpretive trends presented subsequently. Little can be gleaned from the original records beyond the suggestion that the population began a decline sometime in the period 1924–1930, and that this decline was probably preceded by a period of increase. Any further conclusion is speculative.

The cause of the eruption is more doubtful than the literature suggests. Increase in deer numbers was certainly concomitant with reduction of pumas and coyotes (Mann and Locke 1931, in Russo 1964) but it also coincided with a reduction of sheep and cattle. A reported total of 200,000 sheep grazing on the plateau in 1889 had by 1908 decreased to a total of 5,000 (Russo 1964). Lauckhart (1961) and Howard (1965a p. 483) considered that the increase of deer was a consequence of habitat being altered by fire and grazing, and that the reduction of predators was of minor influence.

Data on the Kaibab deer herd in the period 1906–1939 are unreliable and inconsistent, and the factors that may have resulted in an upsurge of deer are hopelessly confounded. The study is unlikely to teach us much about eruption of ungulate populations.

Eruptions following liberation

Scheffer (1951) outlined the events following liberation of reindeer on two of the Pribilof Islands. Both populations increased for a period and then declined, but the peak was reached 11 years after liberation on St. George Island and 27 years after liberation on St. Paul Island. The declines were associated by Scheffer with depletion of a lichen that was an important food during winter.

Klein (1968) presented another account of the fortunes of a reindeer population originated by liberation. Twenty-nine animals liberated on St. Matthew Island in 1944 had by 1963 given rise to about 6,000. The subsequent die-off reduced the population to below 50 animals. Klein indicated

shortage of food interacting with bad weather as the cause of the crash.

Woodgerd (1964) described the growth of a population of bighorn sheep liberated on a small island in 1939. The population rose to a peak of 137 animals in 1959 and the density remained almost constant in the following 4 years.

Mech (1966) drew together records on the establishment by natural dispersal of moose on Isle Royale in Lake Superior, U.S.A. From establishment in the early 1900's, the population peaked sometime in the period 1921–32. It subsequently declined sharply and appeared to stabilize at a density well below the peak. The decline was associated with malnutrition resultant on overgrazing.

Although no precise census data are available, indirect evidence indicates that many red deer populations in New Zealand have gone through an eruptive fluctuation (Holloway 1950, Elder 1956, McKelvey 1959, Riney et al. 1959, Wardle 1961, Riney 1964, Howard 1965b). In each case, both in New Zealand and elsewhere, declines following high numbers were shown or suspected to result from depletion of food supply by overgrazing.

Two recorded eruptions do not fit easily into the postliberation category. Mohler, Wampole, and Fichter (1951) described the rise of a mule deer population after a forestry planting program was begun on 36,000 ha in 1903. Deer were previously absent from the area or very uncommon. By 1941 depletion of forage was evident, and to alleviate the damage 361 deer were shot in 1945 from a population estimated at that time to number about 850. The population may well have declined without assistance had the shooting campaign not disrupted the normal trend.

Andersen (1953, 1962) described the almost complete eradication of roe deer from a Danish game estate in 1950 and the growth of a new population initiated by 24 roe deer of a different strain released in 1951. Mark-recapture estimates suggested that by 1956 the numbers had risen to the former level. Andersen considered that immigration was probably a component of this increase. By 1959 (the final year reported by Andersen) numbers were 25% higher than the total preceding eradication. This case differs from the others in that the animals were liberated into an area utilized by the same species a short time previously.

Figure 2 shows Riney's (1964) model of the events following the liberation of an ungulate. The sequence is pictured as a progressive increase in numbers, a leveling off, a decline, and finally a phase of relative stability. By the model, the same

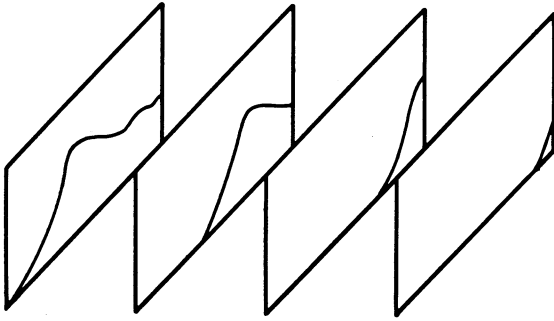


FIG. 2. The first graph shows numbers on the vertical axis against time on the horizontal axis indicating an eruptive fluctuation followed by postdecline stability. Graphs to the right represent the same process occurring in similar habitat, but at later dates, as the nucleus population spreads into areas progressively more remote from the point of liberation. Modified from Riney (1964).

sequence of events occurs in areas to which the animals disperse. At the dispersal front density is increasing; further back into the range the density is at a peak; and nearer the point of liberation the population attains relative stability at a lower density. These zones move outward from the center like the expanding wave generated by a stone thrown into a lake. The sequence following liberation (or introduction by dispersal) can, by hypothesis, be observed both at one point over a range of time, and at one time over a range of distance.

Causes of eruptive fluctuations

Riney (1964) contended that eruptive fluctuation of established populations does not differ in kind from eruptive fluctuation of populations initiated by liberation. His conclusion is supported by the meagre evidence cited here. In both cases a population increases in response to favorable conditions until its food supply is depleted. It then usually declines before leveling out at a lower density.

Although Klein (1968) indicated shortage of food as the proximate cause of reindeer crashing on St. Matthew Island, he suggested that the ultimate cause was "the limited development of ecosystems and the associated deficiency of potential population-regulating factors on islands." But eruptive fluctuations are not limited to islands nor to areas of low plant diversity, and they occur both where predators are present and where they are absent. I think an appeal to lack of regulatory mechanisms multiplies explanations beyond necessity.

The conclusion that populations increase in response to favorable conditions and decline when shortage of food intervenes tells nothing about the population processes involved. Fluctuations in

numbers and rate of increase are relatively easy to observe and measure, but they simply reflect changes in the population's composition and the life history of its members. In themselves they do not reveal the nature of these changes. Rate of increase is a function of age distribution, sex ratio, fecundity and survivorship, and the population's size reflects the history of these. But we are largely ignorant of the changes in these parameters resulting in the upswinging phase of a fluctuation, and the cause, in terms of changes in these parameters, of a decline in numbers.

Only Klein (1968) has previously investigated demographic characteristics of an ungulate eruptive fluctuation. The study to be reported here aims at exploiting the situation provided by the liberation of thar in New Zealand, to furnish a case history on an eruption in terms of changes in fecundity, mortality and fat reserves.

ERUPTION OF THAR

The thar is a goat-like ungulate of the Himalaya. In 1904 the species was liberated in New Zealand and spread to occupy a present breeding range of 3,600 km² in the Southern Alps. The history of dispersal and colonization is summarized by Caughley (1970a) and an account of ecology is provided by Anderson and Henderson (1961).

Of all the ungulates established in New Zealand, this species is probably the most appropriate for testing Riney's model and for investigating population characteristics at different stages of the fluctuation. Specimens can be aged by growth rings on the horns (Caughley 1965); estimation of parameters is simplified by a season of births with low variance and an extremely low frequency of multiple births; and most important, the pattern of spread is not confused by overlapping distributions originating from several points of liberation.

Investigational design and hypotheses

Both Riney (1964) and Howard (1965b) divided the postulated fluctuation following liberation into four arbitrary stages. Their stages are defined partly by attributes of the population and partly by changes in vegetation. The two classifications are not congruent, and although each has merits in itself, neither is entirely satisfactory for the purpose of this study. To this end I will erect four hypothetical stages defined only by attributes of the population:

1) "initial increase" stage covers the period between the population's establishment and the attainment of the initial peak,

- 2) "initial stabilization" stage continues until the population commences a significant decline,
- 3) "decline" stage covers the period of this decline, and
- 4) "postdecline" stage refers to the period thereafter.

This classification is not advanced as an alternative to those of Riney and of Howard, but as a means of circumventing, for purposes of investigation, the causal connotations of their systems.

If Riney's model is correct, these stages should be sampled in sequence along any transect from the current boundary of breeding range to the point of liberation. Dispersal rates have fluctuated least in the quadrant represented by the eastern flank of the Southern Alps north of the point of liberation (Caughley 1970a) and the study was

therefore concentrated in this region. Areas were selected within it (Fig. 3) that should, by hypothesis, contain the four population stages.

The postulated "increasing" population (stage 1) was sampled a little inside the breeding range of the species. One sample of 253 thar ("Rangitata 1") was shot between November 1964 and February 1965 in the Rakaia Valley and the Clyde and Lawrence branches of the Rangitata Valley. A second sample of 115 ("Rangitata 2") was shot the following summer in the latter two branches during November, December and the first half of January. The pooled sample of 368 autopsies will be referred to as the "Rangitata sample."

Stage 4, the "postdecline population," was assumed to occupy the area around the point of liberation because this is the only area from which

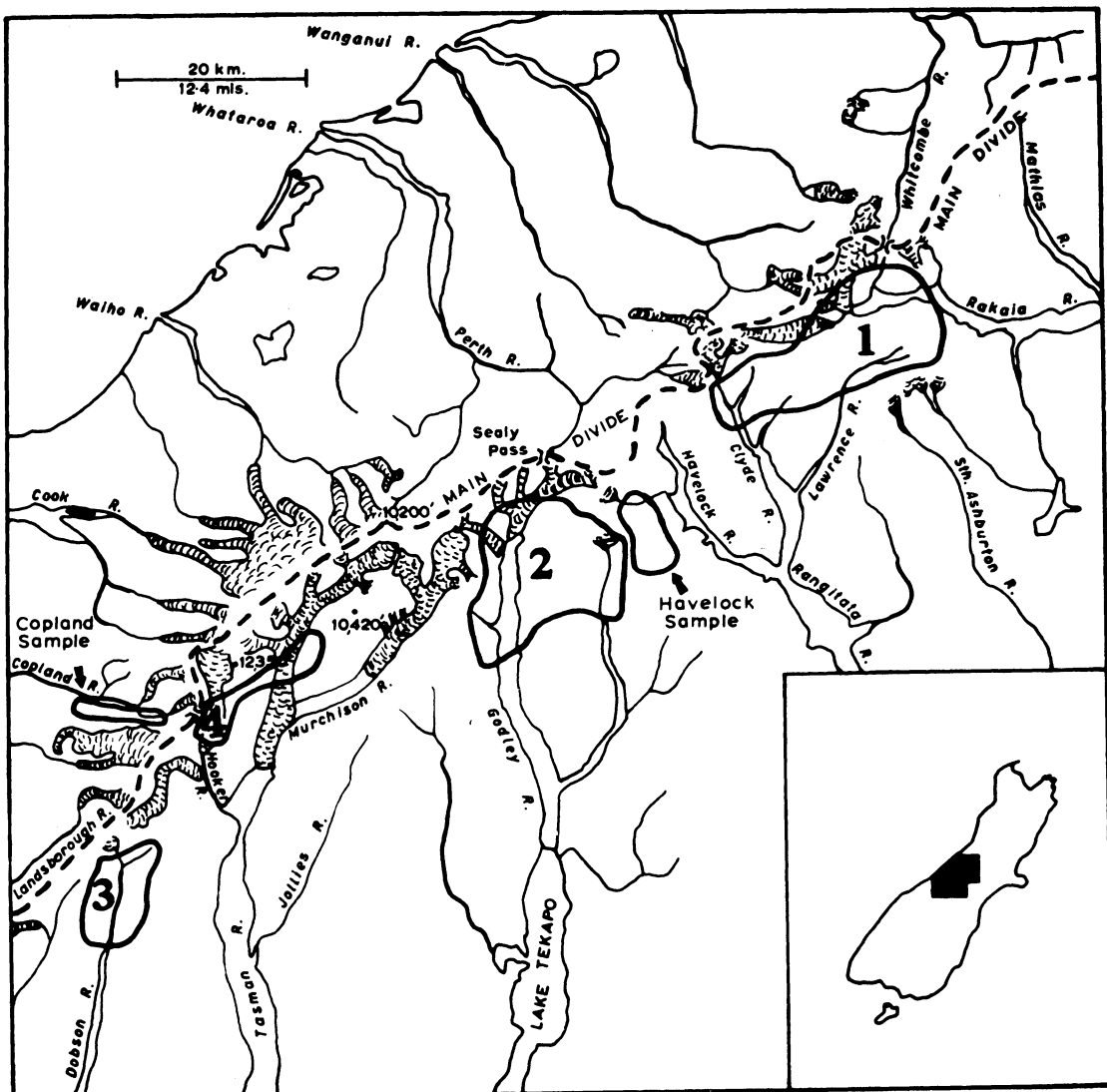


FIG. 3. Areas from which samples were taken numbered according to the population stage predicted by hypothesis to be present.

there is clear independent evidence of a previous decline in numbers (Anderson and Henderson 1961). Thar were liberated near the mouth of the Hooker Valley, and would probably have first colonized this valley, and the Tasman Valley of which the Hooker is a branch, before spreading further. In January and February 1965 a sample was shot in the Hooker Valley, and augmented by a few shot in the Tasman Valley over the same period. The combined sample of 72 animals will be termed the "Hooker sample."

The model predicts that stage 2, the "initial stabilization" stage, will be found about midway between the dispersal front and the area containing a stage-4 population. The Godley and Macaulay Valleys are in the appropriate area and 1,090 thar were shot in these valleys between November 1963 and February 1964. Most of the animals came from the Godley Valley and consequently the total sample, which by hypothesis represents a stage-2 population, is termed the "Godley sample."

It follows from the model that a stage-3 "declining population" should occupy an area between those containing stage 2 and stage 4 populations. For logistical reasons this area was inconvenient to hunt. A sample was therefore taken the same distance south-west rather than north-east of the point of liberation. These two populations should be at about the same stage and they inhabit similar terrain. A sample of 162 animals from a postulated stage-3 population was shot in November and December 1964 in the Dobson Valley.

A test of Riney's model depends principally on the Dobson and Godley samples. The Rangitata sample comes from a population obviously increasing, while the Hooker sample represents a population that has declined. These states are assumed to represent stages 1 and 4, and the areas for stages 2 and 3 were chosen entirely on their geographic relationship to the areas representing the other two stages. Riney's model will be considered vindicated if the data gathered from the Godley and Dobson Valleys appear respectively to come from stationary and declining populations.

In theory these tests could best be carried out by studying change in numbers over a few years, but in practice this method poses large problems. Difficulties of topography, different degrees of private and government shooting, differential degrees of wariness, and a failure to establish a density index based on counts of fecal pellets, all militated against measuring density to the required accuracy. The investigation was therefore limited to indices of the populations' general wellbeing. By hypothesis, rate of increase of the Rangitata population should be positive, rates for the Godley

and Hooker populations should be zero and close to zero respectively, and the Dobson rate should be negative. A corollary of these hypothesized rates is that such statistics as fecundity, survival and fat reserves should be highest for the Rangitata population and lowest for the Dobson population, with those for the Hooker and Godley populations falling somewhere between. Much of the study is based on population statistics of this kind.

Riney's model predicts a decrease in food supply along a transect from the dispersal front to the range center. This was investigated by measurement of plant cover in each of the four study areas. The experimental design and hypotheses will be elaborated in the appropriate section but, in brief, the expected relationship is a decline in snow tussocks and concomitant increase in turf-forming short grasses.

Government campaigns to kill thar by shooting and poisoning, and shooting by private hunters, could have resulted in artefacts in the estimated population statistics. I am reasonably confident that shooting in the Godley and Rangitata areas has not been heavy enough to perturb population trends, but shooting and poisoning in the Hooker and Dobson areas has been heavy and sustained. This could have introduced deviations from the trend that population statistics would have taken in the absence of disturbance.

A second possible source of perturbation is the presence of chamois, red deer and domestic sheep within the thar range. The last two probably have negligible influence because their habitat seldom overlaps with that of thar. The chamois' habitat requirements are closer to those of thar, but differ enough to suggest that there is little interaction between the two species, either socially or in the utilization of forage.

FAT RESERVES OF THAR

Riney (1955) investigated several indices of fat reserves for red deer and suggested that the best was provided by the weight of kidney fat. The index was calculated as a hundred times the weight of fat surrounding the kidney, divided by the weight of the kidney. In this way the absolute weight of the kidney fat is corrected for the size of the animal, allowing comparison of fat reserves between animals of varying sizes. To avoid inclusion of mesenteric fat, fat extending beyond the ends of the kidney is not weighed.

Caughley (1970b) examined the applicability of the kidney-fat index to measurement of fat reserves in thar and concluded that, despite several shortcomings, it was a useful field technique. All female age classes other than the yearling class

TABLE 1. Female fat indices^a

Statistic	Population			
	Rangitata (stage 1?)	Godley (stage 2?)	Dobson (stage 3?)	Hooker (stage 4?)
Mean	26.97	18.47	17.07	26.43
Standard error	2.04	0.55	1.99	3.39
Standard deviation	18.24	11.86	10.34	16.24
Sample size	80	469	27	23

^aThe "female fat index" is calculated from females of ages 0-10 years, excluding age 1, shot December to February inclusive.

were shown to have a common seasonal trend of fat reserves—high in winter and low in summer. In contrast, the seasonal trend of male indices is a function of age. Females other than yearlings, shot during December, January and February, provide the largest subset of age and season that yields homogeneous indices. Comparison between samples will therefore be made only in terms of this category.

No significant difference in variance or mean could be demonstrated between the Rangitata-1 sample (mean = 28.03, standard deviation = 18.89, sample size = 68) and the Rangitata-2 sample (21.00, 12.23, 12). They were therefore pooled for the comparison between areas.

Table 1 gives means of female fat indices for the four study populations, together with the statistics necessary to examine differences between them. Analysis of variance indicated that the differences were larger than could be explained by sampling variation ($F_{3,595} = 12.13$, $P = 0.001$). The means are in accord with what would be expected by Riney's model. They suggest, if the model is valid, that the female fat index is highest at the stage of increasing numbers, lower when numbers stabilize for the first time, lower still when the population begins to decline, followed by a rebound of fat reserves when the decline is checked.

FECUNDITY OF THAR

Age-specific fecundity rate is measured as the mean number of female births per female at each age. Where the population breeds seasonally the ages can be limited to whole numbers of years. In this study a female is considered to have produced a kid if she was pregnant or lactating during the season of births.

The conversion of pregnancy and lactation rates to fecundity rates entails an assumption on the sex ratio at birth because the production of kids inferred from lactation of females cannot be presented as separate frequencies for each sex. The sex ratio of kids and fetuses collected November–February was 151 ♂♂ : 134 ♀♀, which does not differ significantly from an expected ratio of unity

TABLE 2. The number of breeding and nonbreeding females, by age, in samples shot during the 1964–5 and 1965–6 summers in the Rangitata area

Age	1964-65			1965-66		
	Total	Breeding	Non-breeding	Total	Breeding	Non-breeding
1	21	0	21	4	0	4
2	13	8	5	5	4	1
3	13	11	2	5	3	2
4	15	15	0	4	4	0
5	9	9	0	2	2	0
6	6	5	1	6	6	0
7	6	5	1	2	2	0
8	2	2	0	0	0	0
9	2	2	0	1	1	0
10	3	2	1	1	0	1
>10	2	2	0	3	3	0

($\chi^2 = 1.014$, $P = 0.3$). The frequency of female kids is therefore expressed as half the calculated total frequency.

Variability between years

Table 2 shows for the Rangitata sample the frequency of females 1 year of age or older that were pregnant or lactating, and those that did not produce a kid for the season. The sample is divided into Rangitata 1 and Rangitata 2 subsamples to give this information for each of the summers 1964–5 and 1965–6. These figures were examined for evidence of a difference in fecundity between years. Because no female in either sample was breeding at an age of 1 year, this class was discarded. The remainder was grouped into age classes 2–3 years and greater than 3 years to provide frequencies large enough for testing. The ratios of breeding to nonbreeding females were tested between years for the two age classes in two 2×2 contingency tables. They provided values respectively of $\chi^2 = 0.951$ and 0.096. Taken separately or in combination, neither value necessitates rejection of the null hypothesis. The result is consistent with the assumption, necessary for comparing populations, that the age-specific fecundity of a population does not fluctuate greatly between years. The two Rangitata samples were therefore pooled.

Variability between populations

Accurate measurement of age-specific fecundity requires large samples. Only the Godley and Rangitata samples are large enough for this purpose and they will first be examined to establish the general trend of fecundity rate with age. The Dobson and Hooker samples will then be compared with this trend.

Godley and Rangitata samples.—Table 3 shows the age-specific fecundity rates (i.e. the m_x series) for these two samples and the frequencies of breed-

TABLE 3. Estimated age-specific fecundity (m_x) for the Rangitata (R) and Godley (G) samples, and the frequency of breeding and nonbreeding females by age

Age (yr)	Number		Breeding		Non-breeding		m_x	
	R	G	R	G	R	G	R	G
1	25	94	0	1	25	93	0.000	0.005
2	18	97	12	26	6	71	0.333	0.135
3	18	107	14	94	4	13	0.389	0.440
4	19	68	19	57	0	11	0.500	0.420
5	11	70	11	65	0	5	0.500	0.465
6	12	47	11	40	1	7	0.458	0.425
7	8	37	7	34	1	3	0.437	0.460
8	2	35	2	34	0	1	0.500	0.486
9	3	24	3	24	0	0	0.500	0.500
10	4	16	2	16	2	0	0.250	0.500
>10	5	28	5	23	0	5	0.500	0.411
>2	82	432	74	387	8	45	0.451	0.448

ing and nonbreeding females on which these rates are based. These ratios were tested between populations by $2 \times 2\chi^2$ incorporating Yates' correction. To increase low frequencies beyond an age of 3 years they were pooled into two age classes: 4–7 years and > 7 years. The difference in fecundity rates at 1 year of age was tested by the exact probability method. These tests indicated that the observed difference in fecundity rate at 2 years of age was most unlikely to be an artefact of sampling ($\chi^2 = 9.19$, $P = 0.005$), but that no significant difference between populations could be demonstrated for any other age class.

Fecundity rates for ages greater than 2 years show little variation. This apparent homogeneity was tested by combining the Godley and Rangitata samples and testing by $2 \times 9\chi^2$ for differences between ages in the ratio of breeding to nonbreeding females. A nonsignificant result of 10.22 indicated that fecundity rates can be considered constant from an age of 3 years. A weighted mean annual fecundity rate, common to the two populations from 3 years of age forward, was calculated as $(461 \times 0.5)/514 = 0.448$.

The only significant difference discovered between fecundity rates of the Godley and Rangitata populations was at an age of 2 years. In the Rangitata, 67% of females produced their first kid at this age, in contrast to 27% in the Godley. Thereafter about 90% of females in both populations produce a kid in any one year. In only one case was a female aged 1 year found pregnant or lactating. It was shot in the Godley. No similar case was discovered in any other area, but the low frequency and small samples do not allow any useful conclusion on whether the Godley population differs in this respect.

Dobson and Hooker samples.—Table 4 shows the age-specific fecundity rates, and the data from

TABLE 4. Estimated age-specific fecundity (m_x) for the Dobson (D) and Hooker (H) samples, and the frequencies of breeding and nonbreeding females by age

Age (yr)	Number		Breeding		Non-breeding		m_x	
	D	H	D	H	D	H	D	H
1	9	2	0	0	9	2	0.000	0.000
2	11	7	7	3	4	4	0.318	0.214
3	6	2	4	2	2	0	0.333	0.500
4	6	1	5	1	1	0	0.417	0.500
5	8	1	8	1	0	0	0.500	0.500
6	8	3	6	3	2	0	0.375	0.500
7	3	3	2	3	1	0	0.333	0.500
8	1	1	1	1	0	0	0.500	0.500
9	4	2	2	2	2	0	0.250	0.500
10	4	1	4	1	0	0	0.500	0.500
>10	7	1	5	1	2	0	0.357	0.500
>2	48	18	36	18	12	0	0.375	0.500

which they were derived, for the Dobson and Hooker samples. As these data are few, the rates cannot be assigned much reliability in themselves, but they can be tested against the Godley and Rangitata samples.

Although observed fecundity rates at an age of 2 years are higher in both cases than for the Godley sample no significant difference can be shown at this age between the Godley and Dobson ($\chi^2 = 0.09$) or the Godley and Hooker ($\chi^2 = 0.23$). The samples are too small to show a difference if one exists and consequently the question is left open.

It has previously been shown that the ratios of breeding to nonbreeding females could be pooled for the Rangitata and Godley samples from an age of 3 years, and that the age classes from this age on could be pooled to give a single estimate of "adult" fecundity. This pooled ratio was tested against the analogous Hooker data to provide a nonsignificant result ($\chi^2 = 1.05$). Adult fecundity ratios were then pooled for the Godley, Rangitata and Hooker samples and tested against that of the Dobson sample. A χ^2 value of 10.00 ($P < 0.005$) indicated that adult fecundity in the Dobson is lower than in the other areas. The Dobson population had an estimated mean m_x ($x > 2$ years) of $(36 \times 0.5)/48 = 0.375$ compared with $(479 \times 0.5)/532 = 0.450$ for the other samples pooled.

Twinning

The only case of twinning found during this study was in the Lawrence Tributary of the Rangitata. A female carrying full-term twin male fetuses was examined in November 1965. Because she lost both horns as she fell, her age cannot be established with precision, but the amount

of wear on three recovered teeth suggests an age between 5 and 7 years.

The only other record of twinning in thar from New Zealand came from the Havelock Tributary of the Rangitata in 1956–57. However, thar are potentially capable of producing twins with much greater frequency: the proportion of twin births in the Gardens of the Zoological Society of London is about 8% (Zuckerman 1953). The incidence of twinning in thar, as in sheep, is probably influenced by the plane of nutrition of the bearing females. Coop (1962) reported a close association between weights of sheep and the production of multiple births. Significantly, the one case of twinning recorded during this study was from near the front of dispersal, as was the Havelock Valley at the time a case of twinning was recorded there. These records suggest the hypothesis that the more abundant food near the front of dispersal, where thar have not been established long enough to modify the vegetation, can occasionally result in the production of twins, but that the food supply is not great enough there to result in twinning at a genetically controlled potential rate.

The observed scarcity of twinning is unlikely to be a result of resorption or abortion, as suggested by data from *Ovis canadensis*. Spalding (1966) found that 4 from a sample of 11 pregnant females killed by cars were bearing twins, although very few twin births have been recorded for this species. To check for such an effect, 37 pregnant females were shot in the Godley Valley during August 1965, 3 months before the median date of birth. None bore twins.

Discussion

The reported fecundity rates are consistent with Riney's model. The postulated "increasing" and "initial stabilization" populations had a difference in fecundity at an age of 2 years, and adult fecundity of the "declining" population showed a drop. The level of adult fecundity for the "postdecline" population had returned to that of the "predecline" population.

MORTALITY OF THAR

Estimation of mortality rates from sampled age distributions requires that the samples be free of bias. Caughley (1966) tested the largest sample (Godley) for shooting bias with respect to age, and for deviation of the age distribution from the stationary form. Results were negative.

In the same paper a life table for Godley females was constructed. It depended from 1 year of age on an empirical smoothing of age frequencies, the regression taking the form

$$\log f_x = a + bx + cx^2,$$

where f_x is the sampled frequency of age x , and the other letters are constants. The fit was tolerable but the equation is not general enough to describe most nonstationary age distributions. A more general equation was therefore devised to track age frequencies from a base age of 1 year for populations with varying rates of increase. The equation takes the form:

$$\text{Probit}(kf_x e^{rx}) = a + bx^i$$

where

f_x = frequency of age x in sample,

$k = f_x/f_1$

r = exponential rate of increase,

a = regression intercept on probit scale,

b = slope, and also reciprocal of standard deviation of x^i ,

x = age, and

i = a function of skew.

It follows from the algebra of probit transformation that the median age of adult death M is given by

$$M = \left\{ \frac{5-a}{b} \right\}^{1/i}$$

and the standard deviation s of ages of adult death is approximated by

$$s = 1/2 \left[\left\{ \frac{4-a}{b} \right\}^{1/i} - \left\{ \frac{6-a}{b} \right\}^{1/i} \right]$$

The direction of skew and some idea of its magnitude is given by $-\log_e i$, which will be termed z . These three statistics allow comparison between populations in terms of the distribution of adult deaths in a cohort, as measured from the adult age distribution.

When applied to the Godley female sample the probit regression gave a fractionally better fit than the log-polynomial and also extrapolated rather better beyond the ages used to calculate the constants. The log-polynomial predicted 7.3 females beyond 12 years of age whereas the probit equation predicted 13.1. The sample contains 11 females in this class.

In the interests of standardization, statistics of the Godley sample have been recalculated by the probit regression to allow comparison with those of the nonstationary Rangitata sample analyzed in the same way. The resultant life table differs only in detail from that published previously.

Analysis

Godley females.—A probit curve was fitted to age frequencies (Table 3) between 1 and 12 years. The first three frequencies ascend to give proportions of unity or greater relative to the first frequency. They cannot

therefore be converted to probits as they stand, but any correction is arbitrary. For the purpose of curve fitting, but not for testing the curve's goodness of fit, they were replaced by the equivalent values of the log-polynomial regression (Caughley 1966) applied to the same data. All frequencies were then multiplied by 0.0104 such that $f_{x=1} = 1$ to give an l_x series from a base age of 1 year. Those in the age interval 2, 12 years were converted to empirical probits (Finney 1947). Linear regressions of probit on age were then calculated for varying values of i and each regression was tested for deviation of the observed l_x values from the regression, for ages of the interval 1, 12 years. The aim was to find the value of i resulting in the smallest mean squared deviation. This iterative process gave a value of $i = 0.3$ to an accuracy of one decimal place, and a regression formula of

$$\text{Probit } (0.0104 f_x) = 11.72 - 3.887x^{0.3}.$$

Juvenile mortality rate was calculated as $1 - (f_1/f_0)$ where f_1 is estimated from the probit curve.

Rangitata females.—The Rangitata female sample (Table 3) was assumed to come from an increasing population with a stable age distribution. The first assumption rests on observational evidence that the population has been increasing. The second assumption was investigated by computer models (Fig. 4 and Table 5) that showed a fluctuating environment is unlikely to dislocate severely a stable age distribution when the exponential rate of increase has no systematic time trend. The first assumption is safe. The second is more doubtful but should be valid as an approximation.

Before a probit curve can be fitted, the age frequencies must each be multiplied by e^{rx} where r is the population's exponential rate of increase. Although r cannot be calculated exactly, it is possible to calculate its range of probable values. The lower limit was fixed by assuming that the mean age of adult death is higher in this increasing population than in the stationary Godley population. This seems a safe assumption. The minimum value of $r = 0.08$ satisfies this requirement. An upper limit of r was estimated by calculating the series $f_x e^{rx}$ for ascending values of r until the series no longer held to a declining trend. By $r = 0.15$ the values of $f_x e^{rx}$ came close to violating the minimum criteria for a kl_x series and with $r = 0.16$ they made biological nonsense. The value of r was therefore assumed to lie in the interval 0.08, 0.16, and in the absence of more refined criteria it was taken as the midpoint, 0.12.

Age frequencies in the range 1, 10 years were multiplied by $e^{0.12x}$ to form a kl_x series, and then by 0.0355 to give the series a base age of 1 year. The values were then converted to empirical probits with the exception of that for age 1 (it has an infinite probit by definition). The estimated survivorship of 1.089 for age 4 was assigned a maximum working probit by taking its expected probit as the average of l_x for ages 3 and 5 years. Curve fitting proceeded as for the Godley sample to give a regression equation of

$$\text{Probit } (0.0355 f_x e^{0.12x}) = 6.94 - 0.242x^{1.0}.$$

The extrapolating power of the equation was tested by calculating the number of females age 11, ∞ to be expected in a sample of this size. The equation predicted 4.39 as compared with the observed number of 5.

Juvenile mortality rate was calculated as

$$1 - (f_1 e^{0.12}/f_0).$$

Dobson females.—This sample has been shown to have a lower adult fecundity than the Godley sample, and a lower mean level of fat reserves. These strongly suggest that the population had commenced a decline. Because

the population is unlikely to have been decreasing for several years, its age distribution will not have reached a stable form. For this reason the age distribution cannot be treated in the same way as for the Rangitata sample.

Although adult mortality rates cannot be estimated, the minimum rate of juvenile mortality is provided by $1 - (f_1/f_0)$. It gives an unbiased estimate if the age distribution is stationary and an underestimate when the population is decreasing.

Hooker females.—The same problems arise here as for the Dobson sample. The population is unlikely to have a stable age distribution because of recent changes in rate of increase, and even the actual age distribution is difficult to estimate because of the small sample. It contains only 24 females aged 1 year or greater and an estimated 9 females of 0 age. An attempt to investigate the adult mortality pattern would be irresponsible in these circumstances.

In theory a juvenile mortality rate could be calculated, but it would have a bias of unknown size and direction. Equally disturbing, the first three age frequencies are low and erratic. An estimated rate could not be guaranteed as even a tenuous approximation to fact and no calculation was made.

Results and discussion

Table 6 gives life tables for Rangitata and Godley females as estimated from probit regressions,

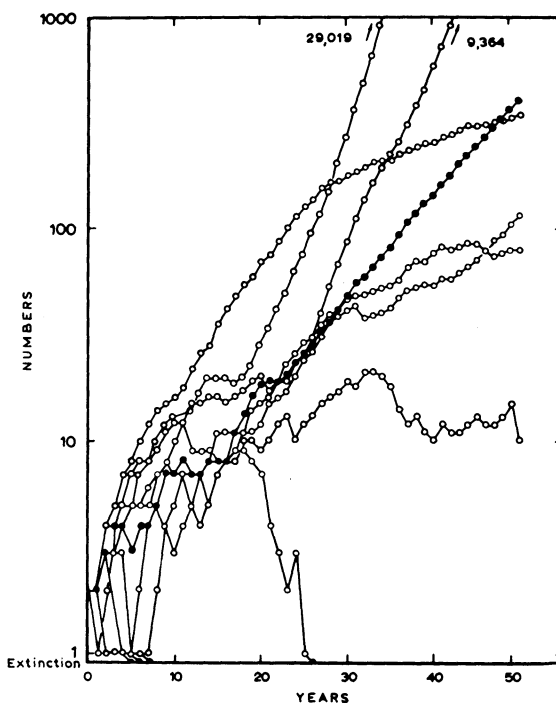


FIG. 4. Growth of 10 replicate computer populations with the same schedules of age-specific mortality and fecundity. They are subjected to a fluctuating environment with the same mean and variance whose effect is to perturbate the age-specific values by a coefficient of variation 2.5% of their means. Individual populations fluctuate almost at random when below a total of 10, and therefore are not separated in the diagram. Solid circles show a biologically identical population whose environment does not fluctuate.

TABLE 5. Female age distribution, relative to age 0, of the replicate model populations in Figure 4, when each contained approximately 100 females younger than age 9. Only 4 of the 10 replicates grew to this size

Age in years								
0	1	2	3	4	5	6	7	8
1.00	0.59	0.48	0.41	0.38	0.28	0.24	0.10	0.10
1.00	0.54	0.50	0.38	0.31	0.23	0.15	0.19	0.12
1.00	0.54	0.46	0.39	0.32	0.25	0.25	0.17	0.11
1.00	0.57	0.46	0.39	0.32	0.21	0.21	0.17	0.14

TABLE 6. Life tables for females of the Rangitata population and the Godley population

Age (yr)	Rangitata (increasing)			Godley (stationary)		
	l_x	d_x	q_x	l_x	d_x	q_x
0.....	1.000	0.374	0.374	1.000	0.533	0.533
1.....	0.626	0.018	0.029	0.467	0.011	0.024
2.....	0.608	0.027	0.044	0.456	0.031	0.068
3.....	0.581	0.035	0.060	0.425	0.055	0.129
4.....	0.546	0.043	0.079	0.370	0.059	0.159
5.....	0.503	0.052	0.103	0.311	0.065	0.209
6.....	0.451	0.059	0.131	0.246	0.058	0.236
7.....	0.392	0.065	0.166	0.188	0.049	0.260
8.....	0.327	0.062	0.190	0.139	0.039	0.281
9.....	0.265	0.058	0.219	0.100	0.030	0.300
10.....	0.207	0.050	0.242	0.070	0.022	0.314
11.....	0.157	0.045	0.287	0.048	0.016	0.333
12.....	0.112			0.032		

TABLE 7. Mortality statistics for female thar and sheep

Population	First year mortality rate	Median age of adult deaths (yr)	Standard deviation of adult deaths (yr)	Skew function z of adult deaths ($z = -\log e_i$)
Dobson.....	>0.59	—	—	—
Godley.....	0.53	6.20	3.10	1.2
Rangitata.....	0.37	8.02	4.13	0.0
Sheep ^a	0.16	7.85	2.35	-0.6

^aData from Hickey (1960, 1963)

and Table 7 gives selected mortality statistics. The age distributions of the Hooker and Dobson female samples are available in Table 4, should someone wish to analyze them for mortality statistics.

The presentation of mortality statistics in the form given in Table 7 is probably more illuminating than presentation as life tables. The latter have the advantage of showing a mortality pattern in detail, but the detail itself makes for difficulties of comparison. It is easy to show that two life tables differ, but deciding what the difference implies in terms of the total mortality patterns, and what the difference means, is no facile problem. The weakness of life tables lies in the mutual biological dependence of their age-specific statistics, even though the calculated values may be independent statistically. Any change in mortality rate of a given age will affect a large number of entries in the table. Life tables fragment by age a process

that, in my opinion, is best treated as an entity. The summary of life tables in terms of juvenile mortality rate, and of median, standard deviation and skew of adult mortality, allows pinpointing of meaningful differences between mortality patterns. This is not possible by simple inspection of life tables.

Juvenile (0,1 years) mortality was highest for the hypothesized decreasing population, lower for the stationary Godley population, and still lower for the increasing Rangitata population. Juvenile mortality of 0.16 for farm sheep (Hickey 1960, 1963) is much lower than for any thar population. It gives an indication of how low the rate might fall for thar in nearly optimal conditions. Juvenile mortality rates are consistent with expectation when the samples are considered to come from different points on an eruptive fluctuation.

No comparison is valid between median ages of adult (1, ∞ years) death in the Godley and Rangitata populations because analysis was based on the assumption that it is lower in the Godley. This restraint is not imperative when comparing between populations the skew and standard deviation of adult ages at death. The main changes in the mortality pattern with declining rate of increase are (i) a rise in juvenile mortality, (ii) a decrease in standard deviation of adult ages at death, and (iii) a skew of adult deaths in the positive direction.

Variability between years

An assumption of the previous analyses is that variability of mortality between population stages in any one year is greater than within a single stage between years. The only information available on between-year variability comes from an out-of-season snowfall in November 1967 that coincided with the season of births. No heavier late-spring snowfall had ever been recorded east of the Southern Alps. Its effect on the domestic sheep along the eastern flank of the mountains can be described only as catastrophic: 60,000 died as a direct result and lamb mortality rose to 30% above average (Hughes 1969). In the area most affected, lamb mortality rose 65%.

The storm had less effect on survival of thar kids. The proportion of females still suckling kids in January 1968 was compared with that of January 1964. Both samples were taken from the Godley Valley, where the blanketing of snow was one of the deepest reported. The comparison was restricted to females 3 years of age or older because this set has a common rate of fecundity and hence the result is independent of differences in age distribution. The ratio of females lactating to those not lactating was 175/19 in 1964 and 21/10

in 1968. These differ significantly ($\chi^2 = 12.0$). Whereas the "control" sample of 1964 had a lactation rate of 90%, the postsnowfall rate in 1968 was 68%. On these figures, the mortality rate of kids between birth and 1½ months of age was 24% higher for the year in which the population was hit by a heavy snowfall during the season of births.

I stress that this comparison does not measure typical between-year variation in mortality but provides what is probably close to an extreme range of variation. The average variation will be very much lower.

POPULATION STATISTICS OF THAR

The preceding two sections summarized age-specific fecundity and mortality. These results are combined in this section to provide estimates of birth rate, death rate, and cohort generation length. Statistics of each sampled population are summarized and examined for consistency with Riney's model. The extent to which these statistics discriminate between population stages is tested on thar sampled west of the main divide.

Caughley (1967) gave definitions and mathematical justification for statistics used in this section. These are specifically designed for seasonally breeding populations and are more relevant to thar populations than the commonly used statistics that imply no seasonal trend in birth rate.

Exponential birth rate as used here is the rate at which a population with a stable age distribution would start to increase if deaths ceased. The exponential death rate is the initial rate of decline when births cease. Birth rate b minus death rate d gives the population's exponential rate of increase r . It can be positive or negative.

Because the younger age classes contribute most to rates of birth and death, the tail of the l_x series can be ignored in their calculation without much loss of accuracy. Table 8 gives b and d for the Rangitata and Godley populations, calculated from survivorships between birth and 12 years by equations 8 and 13 of Caughley (1967).

Apparently the change from "initial increase" to "initial stabilization" is not brought about by a shift in birth rate. Birth rates are about the same in the two populations. This might appear strange insofar as the fecundity rate of juveniles is higher in the Rangitata population. However, birth rate is not a direct function of age-specific fecundity rates, but of these rates interacting with the age distribution. Almost all the difference in rate of increase is traceable to a difference in death rate.

Values of r in Table 8 were calculated as $b - d$. They are not independent estimates of this statistic but simply echo the values of r presented in the

TABLE 8. Rate of birth, death, and exponential increase

Population	birth rate (b)	death rate (d)	rate of increase ($r = b - d$)
Rangitata (increasing)	0.306	0.178	0.128
Godley (stationary)	0.300	0.290	0.010

previous section and fed into the analysis. The tabulated values are within 0.01 of the input values and thereby provide a check on the calculation of b and d . The small anomaly is produced by rounding errors and the discarding of l_x values beyond 12 years.

Dobson and Hooker samples, coming from age distributions that are not stable, allow no estimate of birth rate and death rate. However, the effect on the Dobson population of reduced adult fecundity can be investigated in a general way by substituting this rate in age-specific statistics of the Godley population. In solving the composite statistics for rate of increase we can find how much this rate would be depressed if adult fecundity of the Godley population dropped to the Dobson level. The resultant $r = -0.04$ is a relatively minor drop from $r = 0.00$. A sharp decline in population numbers as observed around the point of liberation in the mid 1950s (Anderson and Henderson 1961) is therefore more likely to reflect a marked rise in death rate than a large decrease in fecundity. The calculated $r = -0.04$ can safely be taken as a maximum rate of increase for the Dobson population.

Cohort generation length T_c is the mean interval between the birth of a female and the mean date of birth of her offspring. Its calculation (Caughley 1967, equation 20) is limited by lack of data to the Godley and Rangitata populations. Estimates based on fecundity rates (Table 3) and survivorships (Table 6) gave $T_c = 5.75$ years for the Rangitata population and $T_c = 5.37$ years for the Godley population. Consequently there is no evidence from these data that the shift from increase to stationarity is brought about by a lengthening of the interval between cohort generations.

Validity of Riney's model

Table 9 summarizes by populations all statistics given previously. As explained previously, the test of Riney's model rests with the Godley and Dobson samples. The Godley population must be shown as stationary and the Dobson population as decreasing. A test of stationarity for the Godley population has been published (Caughley 1966). It showed that the data were consistent with a

TABLE 9. Summary of population statistics for the four putative population stages

Statistic	Hypothetical population stage ^a			
	1	2	3	4
Fat index ♀	26.97	18.47	17.07	26.43
Fecundity rate, age 2	0.333	0.135	—	—
Fecundity rate, age > 2	0.448	0.451	0.375	0.500
Mortality rate, 0-1 ♀	0.37	0.53	>0.59	—
Mortality median, adult ♀ (yr)	8.02 ^b	6.20	—	—
Mort. st. dev., adult ♀ (yr)	4.13	3.10	—	—
Mort. skew index z, adult ♀	1.2	0.0	—	—
Birth rate ♀	0.306	0.300	—	—
Death rate ♀	0.178	0.290	—	—
Generation length ♀ (yr)	5.75	5.37	—	—
Exponential increase rate	0.12	0.00	< -0.04	—

^aStages: 1 = Rangitata, 2 = Godley, 3 = Dobson, 4 = Hooker

^bSee text for qualification

stationary age distribution. A rough check is provided by comparison of the Godley statistics with those of the Rangitata sample. The latter are from a population known to be increasing. Each pair of statistics compared between the two populations suggests that the Godley population has a lower rate of increase than the Rangitata population. Two apparent anomalies, adult fecundity rate and cohort generation length, are misleading. Although sampled adult fecundity is slightly higher in the Godley, the difference does not survive statistical testing. One might expect the interval between cohort generations to be shorter when a population is increasing, but it is estimated as slightly higher for the Rangitata population. The expectation does not reflect a logical necessity: longer generation length of the Rangitata population is simply a byproduct of adult survivorship higher than that of the Godley population.

All available evidence suggests that the Godley population has a rate of increase close to zero and is in the stage of "initial stabilization."

Accepting the Godley population as consistent with stage 2 of an eruptive fluctuation, Godley statistics can be used as a control for investigating the applicability of stage 3 to the Dobson population. Of those statistics estimated for both population, the values for fat reserves, adult fecundity and juvenile survival were all lower for the Dobson population, indicating a strong likelihood that rate of increase was also lower. As rate of increase of the Godley population was shown as close to zero, the Dobson rate must be negative; i.e. the population must have been declining at time of sampling and hence is consistent with stage 3.

Riney's model is supported by these findings and consequently the population stages used in this report can be accepted as real.

Discriminance of population statistics

The population stages will have little practical importance unless they can be identified from field data. A sample of 15 females was collected November 1965–February 1966 in the Copland Valley west of the divide (see Fig. 3) to determine whether the population stage could be identified. Prior to sampling little was known of the Copland population. A hurried inspection in March 1965 confirmed that thar were present, but distribution, density and age structure were not investigated. At this time I had no reason to question Christie and Andrews' (1964) map which showed continuous distribution of thar on the western flank of the Southern Alps.

Data from the Copland Valley were too few to estimate the full range of population statistics. Calculation only of female fat index and fecundity were justified by the sample size. These are presented in Table 10 and can be compared with those from the "type" stages in Table 9.

The results were unexpected. Each statistic was as high or higher than any from the type populations. They implied a rate of increase consistent with a population at the dispersal front, a conclusion conflicting with the distribution mapped by Christie and Andrews (1964). The problem was resolved by reexamining the distribution of thar in this part of Westland. The survey (Caughley 1970a) confirmed that the Copland Valley was the northern limit of breeding for a population whose geometric center lay 10 miles to the south, and that there was a gap in breeding range on the western flank of the main divide opposite Mt. Cook.

The Copland population was a straightforward case and a small sample sufficed to indicate its stage. More subtle cases would require a larger volume of data. The most difficult problem is differentiation of an increasing, postdecline popu-

TABLE 10. Statistics of the Copland thar population

Statistic	Mean	Standard deviation	Sample size
Fat index ♀	33.67	18.99	9
Fecundity rate, age 2	0.5	—	2
Fecundity rate, age > 2	0.5	—	6

iation from one that, although not newly established, is still in the stage of initial increase. But the ambiguity can be resolved by checking whether the population lies near the dispersal front or well inside the breeding range.

AVAILABILITY OF FOOD FOR THAR

It is one thing to describe differences in demography, fat reserves and growth rates between populations but quite another to find out why the differences exist. Climate, topography and rock type do not vary greatly between the areas containing the four study populations and this suggests that population differences are related to induced changes in habitat, or changes of behavior with increasing density.

No overt behavioral differences were noted between populations at high and low density, but considerable differences in the vegetation of their respective areas were apparent. The most conspicuous difference was in the density of snow tussocks (*Chionochloa* spp.) which often formed an almost continuous cover where thar were absent (e.g. Fox Valley) but were invariably scattered or uncommon where thar were numerous (e.g. Douglas Valley). The presence of dead stumps of snow tussock in these depleted areas argued that tussock had previously been more abundant there. Depleted areas were usually dominated by a turf of *Poa colensoi*, a short grass often found as scattered plants within alpine snow-tussock swards (Connor 1964). The marked differences in snow tussock cover probably reflect a similar difference in the composition of the short grass and herb communities, because reduction of the tussock canopy alters the climate near the ground.

I would expect the reduction of tussock cover to affect the thar's plane of nutrition in late winter. The blanket of snow over the thar range at this season buries many of the smaller grasses and herbs. Snow tussocks probably become an important source of food at this time because many of the species utilized in summer are no longer accessible. That the second half of winter is critical for the animals is suggested by the steep decline of fat reserves over this period (Caughley in press, b).

From these observations and reasoning I reached the tentative conclusion that availability of tussocks was likely to be an important influence on thar, and that differences in tussock cover might explain much of the demographic difference between populations. I would not expect availability of tussocks to account for all variation between thar populations but it is my nomination as the probable source of a large component of this variability, particularly between stage 1 and the other stages. Differences in behavior (e.g. emigration and sociality), summer food supply, disease, and stochastic effects are further possible sources, but I think they are less likely to be important.

If the casual observations relating to the effect of grazing on snow tussocks are accurate, they suggest a relationship between percentage cover and length of time thar have been present in an area. The following hypothesis was erected: on a transect from the edge of breeding range to the point of liberation the density of snow tussocks should decrease, the decline being steepest between the area where thar have recently established and the area holding a population in the stage of initial stabilization. A corollary of this hypothesis is that *Poa colensoi* and other turf-forming species should show a reverse trend providing that there is no serious erosion of soil from the site.

The species to be considered are *Chionochloa flavescentis*, *C. pallens* and *C. rigida*, three snow tussocks that normally grow to a height of about 90 cm. Wraight (1964), in describing the alpine grassland west of the divide, considered that the first two are dominant on slopes greater than 30° where the snow-free growing season is 5 months or more. *C. rigida* has a greater altitudinal range than the other two, but most snowgrass swards between 1,300 and 1,400 m east of the divide are a mixture of two or three of these species. While each species has a different range of habitat requirements, these requirements overlap considerably.

C. rigida is the only one of these species that has been studied in any detail but some of the findings from it probably can be extrapolated with caution to the others.

Mark (1965b) studied growth rates of *C. rigida* and fortuitously provided an insight into the reaction of this plant to grazing. He measured regrowth of leaves after clipping and found this method unsatisfactory for his purpose because it altered the normal pattern of growth. He reported (p. 99) that "an increasing number of tillers failed to recover each year and by the end of the third season a large proportion of tillers were dead. Repetition of this treatment for only a few more seasons would probably have been suffi-

cient to kill what were initially vigorous tussocks." He concluded (p. 102): "the severe deterioration of tussock vigor which follows annual reclipping indicates that the narrow-leaved snow tussock is ill-adapted to tolerate severe grazing for any length of time."

Chionochloa is a genus of evergreen perennial grasses. *C. rigida* flowers approximately every 3 years (Connor 1966) and produces around 2.5 tillers per 10 normal tillers each year (Mark 1965a) by vegetative reproduction. Seeds may remain dormant in the soil for several years (Mark 1965b).

Experimental design

An index of percentage cover of grasses and herbs normally growing above 30 cm was calculated over April and May 1967 for each area containing one of the four study populations east of the divide. Five sites per area each contained three parallel lines oriented in the direction of fall, measuring 40 m and separated by 7.6 m. On each line the extreme intercepts of each plant were measured as a distance from one end and these were converted to percentages of the total line subtended by each species or pooled group of species. Variances were homogenized by transforming the percentages to arc-sines. Each species or group was sampled in four areas, on five sites within each area, and on three lines within each site. A hierarchical analysis of variance was performed on measurements of each sampled species or group to test variance of lines within sites against variance of sites within areas, and the variance of sites within areas against variance between areas. The primary aim was to determine whether the difference between areas was of a greater order than the variability of sites within them.

Because random sampling across a region of this scale poses practical difficulties, sampling was restricted to one stratum of the habitat. It was arbitrarily circumscribed as follows:

Altitude: 1,220–1,460 m
Aspect: 300° Mag.–40° Mag.
Slope: 30°–40°

Special conditions:

- a) the site is used by thar in winter,
- b) it has no recent history of burning,
- c) each line contains less than 10% bare rock, and
- d) the vegetation is predominantly grassland.

Short grasses and herbs were measured as present or absent on fifty 15-cm-diameter plots per line, circle centers being 80 cm apart. These observations were expressed as per cent frequency

per line, converted to arc-sines, and analyzed in the same way as were the other data.

Field methods

When sampling points are not chosen at random, there is a danger that the choice will be influenced by the operator's preconception of what the results should be. The danger is heightened when the operator knows the country well. He is then in a position to choose a set of sampling points that would support any hypothesis he cares to erect, while being firmly convinced that his selection is unbiased. Criteria for choice of sites were therefore made as tight as possible.

On a map of each sampling area I circled a number (generally eight) of possible sampling locations that I knew from experience would probably contain several sites conforming to the prescribed criteria. These were handed to J. S. Holloway (N.Z. Forest Service) who made the final selection of sites in each area. His choice of five of my mapped locations in each area was dictated largely by closeness to his line of march and by flooded rivers restricting the number of locations that could be reached by his party. On reaching a location marked by me on his map he selected one site within the specified altitudinal zone, it being the first encountered site that conformed to the other criteria. By this system we hoped to minimize bias in the choice of sites.

Results

Table 11 gives a summary of analyses of variance on five species or groups normally growing above 30 cm in height. Only species giving mean percentages above 0.1% for at least three of the four areas are included. Mean percentage cover is shown for each area but the analyses were performed on percentages transformed to arc-sines. Analysis-of-variance *F* ratios and their probabilities are given for site and area.

The first species in the table has an *F* ratio of 13.11 for "site," indicating that, on the average, sites within an area were about 13 times more variable than the lines within a single site. Even with this considerable variability within areas, *F* ratio for "area" shows that the variability between areas is greater by a factor of 15 than the average variability between sites within one area. The probability of this *F* ratio indicates that the sampled variability between areas has less than 1 chance in 1,000 of being due to sampling variation.

Table 11 shows that all species or groups had significant variation between sites within areas, but that only the snow tussocks and *Poa colensoi* could be shown as differing significantly between areas.

TABLE 11. Percentage cover of grasses and herbs normally growing above 30 cm in the absence of grazing. Only those species returning means of greater than 0.1% in at least three areas are included. *Poa colensoi*, a short grass postulated to increase in the presence of grazing, is measured as percentage frequency. *F* ratios are for area per sites within areas, and sites within areas per lines within sites

Species	Rangitata	Godley	Dobson	Hooker	Site		Area	
					<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<i>Chionochloa flavescens</i>	30.0	1.1	12.6	0.0	13.11	0.001	15.55	0.001
<i>C. pallens/rigida</i>	26.0	3.0	2.9	0.0	6.85	0.001	16.85	0.001
<i>Celmisia lyallii</i>	1.3	8.1	4.2	15.9	21.07	0.001	1.59	n.s.
<i>Celmisia</i> spp.....	0.5	3.9	0.1	0.0	22.02	0.001	0.99	n.s.
<i>Schoenus pauciflorus</i>	0.8	0.0	2.3	4.4	6.39	0.001	2.99	n.s.
<i>Poa colensoi</i>	19.1	29.1	65.5	67.7	22.46	0.001	5.17	0.01

The snow tussocks conformed to hypothesis by exhibiting a trend of decreasing per cent cover from the edge of the range to its center. *Poa colensoi* also conformed to hypothesis with a trend in the opposite direction.

A further 15 species or species groups of short grasses and herbs returned per cent frequencies above 0.1 for 3 or more areas and showed a significant difference between areas. They were: *Notodanthomia setifolia*, *Cyathodes fraseri*, *Pratia macrodon*, *Epilobium* spp., *Euphrasia* spp., *Geum geranium*, *Scleranthus biflorus*, *Columbanthus* spp., *Anisotome aromatica*, *Rumex* spp., *Pimelea pseudolyalli*, *Drapetes laxus*, *Celmisia petiolata*, *Helichrysum bellidioides*, and *Coprosma pumila*. Only the last four showed an apparent trend, in each case a general rise from the edge of the thar range to its center. None of these four is known to be regularly eaten by thar.

The Hooker Valley is relatively small and contains little country falling within the limits set by the plot prescription. To avoid cramping the sites, plots 2 and 3 were placed at 1,450 m, whereas all other plots in the Hooker Valley and other areas were below 1,370 m. As this could result in bias, the results were checked by a second analysis on the species listed in Table 11, with plots 2 and 3 excluded from each area. A similar result was obtained: those species differing between areas by the first analysis gave significant *F* ratios by the second, and those nonsignificant by the first analysis remained nonsignificant.

Discussion

Results of the vegetation survey were in general accord with the hypothesis. A large component of the marked decrease in percentage cover of snow tussocks between areas containing population stages 1 and 2 is probably referable to grazing by thar, and the shift from the first population stage to the second is likely to be causally related to this change in vegetation. Decrease in tussock density is associated with a rise in death rate whose

major component is an increase of first-year mortality. The decreasing winter food per head brought about by the increasing density of thar and the related decreasing density of snow tussocks, is probably the major influence on rate of increase as it moves from positive to zero.

Table 11 provides little evidence that initiation of stages 3 and 4 are related to a further change in tussock density. More detailed studies will probably show that the marked decrease of tussocks reflects a more subtle decrease in density of other food species, the decrease continuing beyond the point when tussocks become relatively uncommon. Shrub species in particular are utilized as winter forage during stage 2, and patches of scrub that appear to have been killed by browsing are common in areas of high thar density (e.g. Landsborough, Douglas and Carneys Valleys). Decline of a thar population after stage 2 is likely to reflect decreased availability of plants other than snow tussocks.

As a survey of availability of food, this study can be considered little more than a pilot trial. To establish close relationships between food supply and population dynamics the study should be extended to several other habitat strata and combined with a study of stomach contents.

Neither J. S. Holloway who made the final selection of sites, nor I who mapped possible site localities, is completely satisfied that his selection was free of bias. I would like to see our observations checked, preferably by someone skeptical of the hypothesis.

CONCLUSIONS

The eruptive fluctuation of thar described here is a composite of population stages at varying distances from the point of liberation. Only the population at this point has passed through all four stages. Those further away are at earlier stages in the sequence, and the time each takes to reach stage 4 is loosely correlated with distance from the liberation point. Thus the state termed

stage 2 will migrate radially, preceded by stage 1 and leaving a stage-4 state behind it. The process can be pictured as a wave forming the circumference of a circle, the crest representing high density of stage 2 with lower densities of stages 1 and 4 on either side. In reality the circle is highly distorted, but information on rates of dispersal (Caughley 1970a) suggests that the velocity of the wave is relatively constant on any "radius" extending through thar habitat.

Figure 5 gives a schematic interpretation of changes in a thar population as it grows from a nucleus of liberated animals. Tables 8, 9 and 10 give the statistics on which it is based. The figured trend of density is not accurate. It was deduced partly from the trend of the other statistics, but mainly from subjective impressions of relative density along the sampling transect. These subjective impressions are based on several inspections of each valley in both summer and winter. While being unwilling to mount a spirited defense of this kind of estimate I am reasonably satisfied that the sketched trend is not grossly in error.

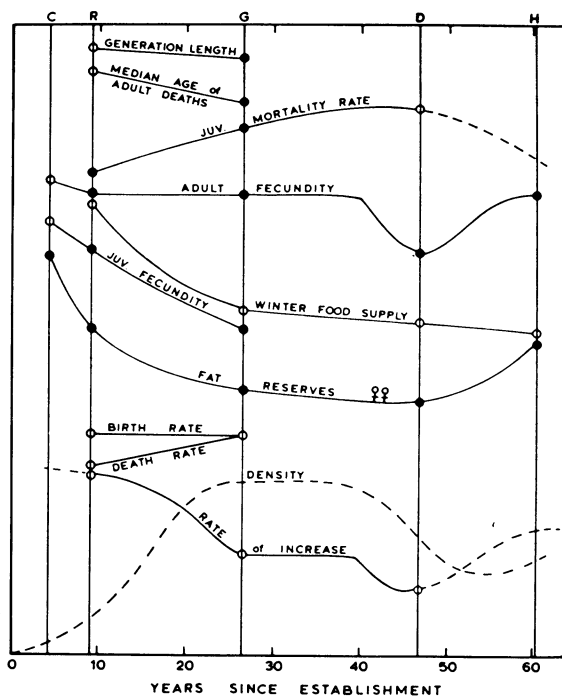


FIG. 5. Schematic representation of changes in a thar population and its food supply during an eruptive fluctuation following liberation. Vertical axis is a scale of magnitude but the scale and origin for each variable is separate. Solid circles indicate estimates that should be reasonably accurate, open circles indicate estimates presented with lesser confidence, and broken lines are extrapolations inferred from the trend of the other statistics. Vertical lines show the estimated positions on the fluctuation of five sampled populations: C = Copland, R = Rangitata, G = Godley, D = Dobson and H = Hooker.

The first half of the eruptive fluctuation provides the most reliable data. These indicate that the change from positive to zero rate of increase is brought about chiefly by a rise in death rate. Analysis tempered by a couple of mild assumptions suggested that a further rise in death rate initiated the stage-3 decline. Changes in birth rate appear, in comparison, to be of minor importance.

The difficulty of measuring death rate and rate of increase emphasizes the necessity for finding easily calculated statistics that correlate with them and which therefore serve as their indices. Female fat reserves in summer provided the most promising index in this study, but the exact form of the nonlinear relationships between fat reserves and death rate and between fat reserves and rate of increase has yet to be determined.

This study suggests, but does not prove, that the thar population's rate of increase is influenced by food supply, and that progression along the sequence of an eruptive fluctuation reflects progressive depletion of forage by the animals themselves. Fat reserves and adult fecundity of the Hooker sample (stage 4) imply that at time of sampling this population had a positive rate of increase, suggesting that its previous decline halted at a density where the available food per head was greater than before. This population is probably in the upswing of a second fluctuation that will level off at a density below that characterizing stage 2.

Riney's (1964) model picturing an eruption after liberation as a rolling wave of density, is an adequate description of the history of thar in New Zealand. His further contention that eruption of ungulates is a response to a change in conditions of life, and that the eruption is terminated by modification of habitat by the animals themselves, applies equally well to eruption following liberation and eruption of established populations. His contention that these two processes are essentially the same appears valid.

The easily observable characteristics of an eruptive fluctuation do not differ much between thar and the other ungulates discussed previously. By extrapolation, the reported trends in population statistics over the fluctuation may not be unique to thar but may mirror the essential features of eruptive fluctuations in other species. While the generality of the pattern should not be accepted uncritically, it may be useful as a hypothesis to be tested further.

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