

COMPENSATORY RESPONSE OF ARTIFICIALLY CONTROLLED MAMMAL POPULATIONS

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INTRODUCTION

Ecology contributes to management of animal pests in two ways: by defining the precise damage done by the suspect and finding efficient methods of reducing the population to numbers compatible with land use. The latter is the most sought-after service because it concerns development and evaluation of efficient control methods; and herein lies, perhaps, the great bogey of pest control, for this elementary requirement usually amounts to an extremely formidable technical problem. The degree of reduction of numbers, amelioration of the pest's effects, the rate at which survivors increase to reassert their status, and the costs and benefits of control, have all to be taken account of in the evaluation of a technique.

Of these, the rate of increase of animals has, outside the context of control, received much attention from ecologists because it impinges on the much wider problem of homeostasis of populations.

Compensatory response is one aspect of homeostasis. In population ecology it is defined in terms of changes of birth rates and death rates (Errington 1945; Andrewartha and Birch 1954, pp. 636-40; Lack 1954, pp. 67-70) which tend to raise the rate of increase when numbers are low, and depress it when numbers are high (Errington's "inverse density law"). When applied to the context of artificial control, the law suggests that the rate of increase of survivors of a control programme will tend toward the maximum possible for the species, to cancel out the reduction of numbers.

Evidence has been set out for a number of instances in New Zealand which are said to exemplify this: Bull (1956) suggested that survivors of a rabbit population reduced by arsenic poisoning included a high proportion of females and that this was symptomatic of "an unusually high potential to make good the loss during the following breeding season". Gibb (1967) made a general statement relating to rabbit control: "When held at low density by our control, rabbits are usually in

specially good condition . . . large . . . and have a long and intense breeding season". The high productive potential in such artificially suppressed populations "explains why we find it harder to reduce the number of rabbits the lower we get them". Similarly, control of ungulate populations is thought to have improved physical condition or stimulated higher birth rates (Anderson and Henderson 1961; Howard 1965, p. 52; Riney 1955; Riney *et al.* 1959, p. 34).

However, some information has already been published showing this does not always occur. Daniel (1966) records that an excessive ratio (3.2:1) of adult female to male fallow deer (*Dama dama*) were killed by poisoning in one area. Douglas (1967) has suggested that poisoning kills proportionally more young thar (*Hemitragus jemlahicus*). Both these results show that the ability of a population to increase may be impaired by the kind of control technique employed.

This paper develops the same theme, particularly in regard to the dampening of recovery of controlled populations through effects on behaviour of survivors. This common denominator—the effect of certain control techniques on behaviour—suggests an explanation which unifies a number of puzzling observations made in connexion with control campaigns during the past few years, and which may be put as a simple hypothesis: When the control technique disrupts the ability of survivors to use favoured or essential components of the habitat, the effects of reduction of numbers are reinforced by suppression of compensating response mechanisms.

RESULTS OF CONTROL CAMPAIGNS ON WHICH THE HYPOTHESIS IS BASED

Deer and chamois control in the Harper-Avooca catchment

A campaign against red deer (*Cervus elaphus*) and chamois (*Rupicapra rupicapra*) in this catchment was the first intensive trial in New Zealand in which increasing numbers of hunters were employed the year-round to try to determine the

pressure necessary to obtain a measurable reduction in the population (Logan 1956). To some extent this objective was set because Riney (1956) had shown that, formerly, most effort had been expended on deer control in areas where most deer could be killed, rather than in areas where a nominated density was required and hunting persevered with until that was obtained.

Some features of the campaign have been evaluated by Batcheler and Logan (1963). In 1955–56, an increase in the number of man-days spent hunting was accompanied by a rise in the number of deer and chamois shot. Then, from 1957 on, with further effort, the number of deer killed per season and counts of faecal pellet groups both fell, making it altogether evident that hunting had reduced the population significantly. But the number of chamois killed continued to increase.

The degree of reduction of deer could not be determined accurately from existing data. The numbers killed per man-day fell by about 80%, but this was probably a generous estimate because the animals gradually became more wary and difficult to hunt. On the other hand, pellet group density dropped by about 38%, which was undoubtedly a conservative estimate because of the time-lapse relationship between change of population and change of faeces density.* It therefore seems reasonable to place the reduction between 50–70%.

Progressively more chamois were killed throughout the campaign which suggested, as did a lack of any significant change of pellet density, that their numbers were not being significantly reduced. (The progressive increase in kill was believed by field staff to have been partly caused by movement of chamois into the Avoca River headwaters from the Wilberforce Valley which lies to the southwest.)

Despite cropping of the population, the ratio of fawns and yearlings per 100 hinds did not rise as would have been expected from the hypothesis of compensatory response (Fig. 1). The fawns:100

* This will be clear from an example. Suppose a stable population is removed in a very short period, prior to which decay of faeces occurs at a constant rate (c), as proposed by Taylor and Williams (1956). If n_1 pellet groups are present at t_1 , when the population is removed, n_2 , the number remaining at a later time (t_2) will be $n_2/n_1 = e^{-c(t_1-t_2)}$, where (t_1-t_2) is the interval of time in units of the mean "life" of pellet groups. If mean life is 2 years, 65% will be present one year after the population is removed, and 10% will be present after about 5.7 years.

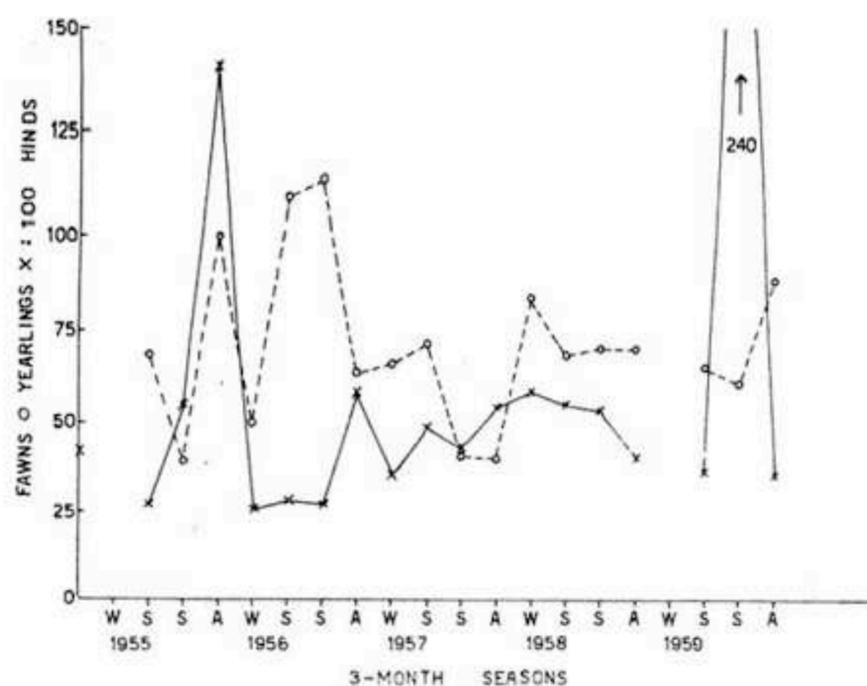


FIGURE 1. Trend lines of fawns:100 hinds and yearlings:100 hinds shot in the Harper-Avoca, 1955–59. Downward trend of the fawn ratio is significant ($b_{yx} = -3.004$, $P < .01$) and yearling proportion remained about the same ($b_{yx} = +0.106$, $P > .50$). The yearling peaks in summer-autumn follow ejection from family groups, when they are relatively easy to hunt.

hinds ratio fell significantly ($P < .01$), and the yearlings:100 hinds figure remained about the same ($P > .50$). The physical condition of the animals did not appear to respond either. Riney (1955) sampled the same population in 1952–53 and established a seasonal trend for the kidney fat index (Fig. 2) and P. C. Logan reported (pers.

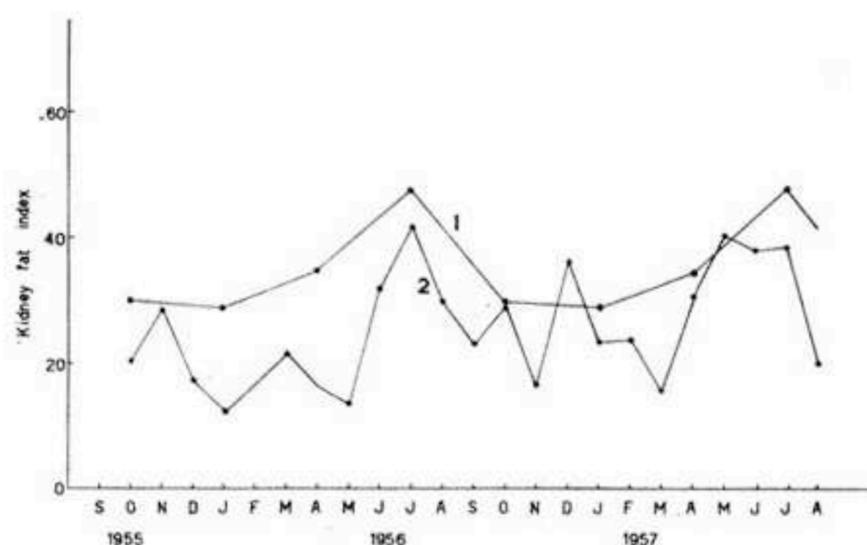


FIGURE 2. Fat reserves of hinds in the Harper-Avoca as measured by kidney fat index. Line (1) is redrawn from Riney (1955, Fig. 7). Line (2) is the corresponding line for the period of the campaign, and shows fat reserves were persistently lower than before numbers were reduced.

comm.) that some very fat animals were taken during that period. More measurements were taken from September 1955 to August 1957 and, contrary to expectation, the kidney fat indices were persistently lower than those recorded by Riney, and did not improve during these two years ($P > .10$). Unfortunately, measurements were not taken during the last two years of the campaign.

The ratios of chamois kids:100 nannies and yearlings:100 nannies killed also declined during the campaign (Fig. 3, $P < .01$ for both kids and yearlings).

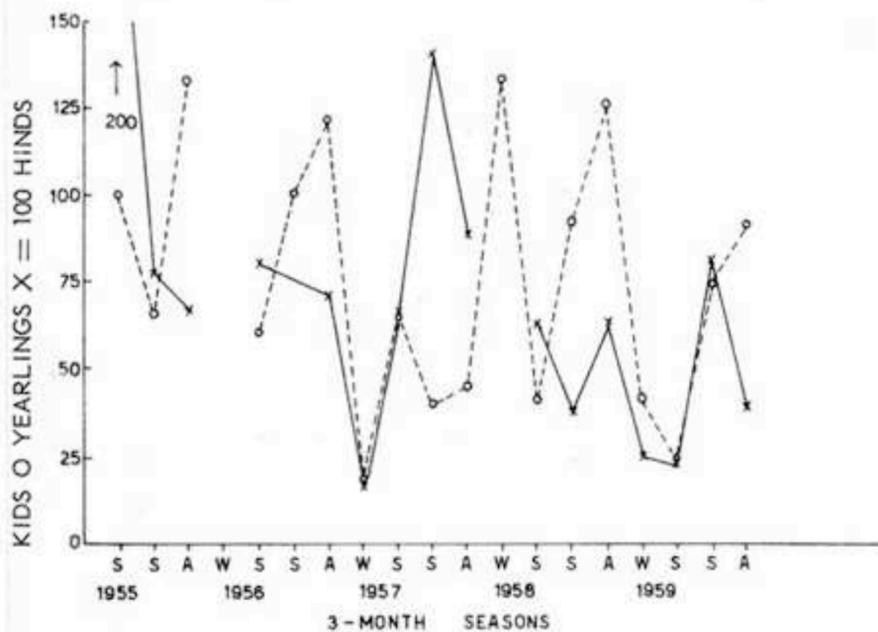


FIGURE 3. Trend lines of juvenile chamois: 100 nannies shot in the Harper-Avooca. Incidence of both kids and yearlings declined significantly (kids $b_{yx} = -7.34$, $P < .01$; yearlings $b_{yx} = -11.9$, $P < .01$).

What is the explanation for these results?

As noted earlier, deer became extremely wary during the campaign. Batcheler and Logan (1963) deduced from their changed distribution and density of faeces that their numbers dropped most in areas which, at the beginning of the campaign, had been most heavily occupied; the survivors taking refuge in the dense timber-line scrub. As hunting pressure mounted they grazed, only at night, in grasslands away from the bush; and these secretive habits were retained for at least two years after cessation of hunting (M. J. W. Douglas, pers. comm.). Chamois took refuge in forested bluff systems which included timber-line scrub and contiguous grassland and hunters found that they stayed in these throughout winter, whereas formerly they moved on to the warmer hill faces.

These points suggest that the characteristics of compensatory response were suppressed because the survivors were forced to occupy habitats which

formerly they did not prefer. The food resources of the timber-line scrub and bluff systems are relatively poor and, referring particularly to chamois, confinement to the bluffs may have increased the likelihood of accidental death among young animals, especially during icy conditions.

Control of deer in the Kokatahi catchment, Westland

Very large numbers of deer were shot in the late 1940s and early 1950s by contract hunters operating over large blocks of the Hokitika River system, including the Kokatahi catchment. Since about 1958 hunting effort has been concentrated into high priority catchments such as the Kokatahi and, as more huts have been built, tracks developed and more hunters deployed, total tallies and numbers killed per man-day have declined.

TABLE 1. Ratios of fawns and yearlings to hinds as indicated by kill records (M. R. O'Reilly, pers. comm.).

	NOS. KILLED		PROPORTIONS (%)	
	Hinds	Yearlings Fawns	Yearlings	Fawns
1.4.60-31.3.61	94	92 58	98	62
1.4.61-30.4.62	101	59 63	58	62
1.11.62-24.3.63	39	8 12	21	31
1.4.63-31.3.64	30	23 13	77	43
1.4.64-31.3.65	168	60 51	36	30

Decline of the Kokatahi deer population in recent years has been accompanied by decline of the proportions of fawns and yearlings per 100 hinds killed (Table 1). The data for fawns are particularly interesting. In 1959-60, 62 fawns per 100 hinds were recorded, but by 1965-66 only 30:100 — a decline of about 50%. This proportion of fawns is very low. It is about 6% lower than autumn fawn:hind counts recorded for any South Island population by Riney (1956) and is within only the lower quartile of the 90% confidence range of the estimate for the South Westland population, 35 ± 13.5 . Consistent with this, M. R. O'Reilly recently reported (pers. comm., 1965) "an observation . . . made on quite a number of occasions by hunters and staff of . . . a fair percentage of barren hinds appearing in the Kokatahi".

Changes in behaviour because of disturbance by hunting appear to have contributed to this effect. The forested levels of the catchment are rough, in many parts precipitous, and, at least before occupation by introduced mammals, the forests were very dense (Travers 1964; Holloway 1966). The

alpine grasslands above are on generally easier slopes (Wraight 1960). Before protracted shooting was begun, most deer occupied the alpine grassland and forest clearings, and spread into the forest relatively slowly (Holloway 1959), probably in the same way as described for red deer in the Tararua Range (Davidson and Kean 1960).

Hunting pushed them into the forest (Travers 1964) and as it progressed, many of these forest deer were noted to be older, smaller hinds with their yearlings and fawns, somewhat greyer than the typically rufous red deer living in open country.

Collectively, these observations are consistent with the hypothesis, insofar as lower fawn numbers and older smaller hinds were seen once the facility of the survivors to use preferred parts of the habitat was reduced by the control technique.

Control of opossums by poisoning with sodium monofluoroacetate ("1080")

The poison "1080" is considered to be outstanding for control of mammalian pests (McIntosh 1958). It is tasteless, odourless, readily soluble in water, and there is always a delay between ingestion and onset of symptoms (Kean 1956; McIntosh 1959). Mr J. Bell, Department of Agriculture (pers. comm.) found that up to 34 hours elapsed between ingestion and death at doses ranging from one to 2.5 times LD_{50} (0.7 mg./kg.); the shortest time was $3\frac{1}{2}$ hours. (On average, it was less than $18\frac{1}{2}$ hours, but an accurate figure could not be obtained because poisoned animals were not under continuous observation.)

The delay before onset of illness has been considered undesirable (Gilmore 1967) because it permits ingestion of much more than a lethal quantity of bait (McIntosh 1959; Daniel 1966; Batcheler and Pracy 1962). However, it may be extremely valuable for, as shown below, it enables poisoned animals to return to a nest before death, and this may radically alter the pattern of use of the habitat by survivors.

A "1080" poison campaign was carried out against opossums in the Arahura catchment, on the north flank of the Hokitika River system in Westland in June–July 1963. Carrot bait containing about 2 lb. of "1080" per ton was distributed throughout more heavily infested areas by aircraft, and observations before and after the poison was laid indicated the campaign was fairly successful (M. R. O'Reilly, pers. comm.).

During earlier poison trials in which "1080" had been used, especially at Mt Bruce and Aorangi (see Batcheler, Darwin and Pracy 1967), control officers had gained the impression that deaths continued to occur for some months after poisoning. The circumstances precluded any possibility that they had taken toxic remnants of bait; and, since a sub-lethal dose of "1080" is metabolised, it seemed extremely unlikely that it could be any direct consequence of consuming the poison (McIntosh *et al.* 1959). Therefore, in the Arahura area, a particular lookout was kept for dying animals during subsequent inspections.

L. T. Pracy (unpubl. report) recorded an inspection made in December with M. R. O'Reilly, when the latter considered opossum sign was even less common than in July. Animals were found in December which had recently died, and others were "nearly dead, and in a condition where death was [probable within] a matter of days. Fur condition was good, body condition poor, mites present on recently and nearly dead opossums". Further, "Though the cause of the mortality is not known it is suggested it could be the result of an efficient and quick kill over a wide area by aerial poisoning with consequent disruption of habitat, scent-posting, tracks, and contamination of nests. . . ."

Occurrence of deaths in the nests would be extremely important if (a), as Pracy and some others suggest, survivors generally avoid them during putrefaction of the poisoned animals and (b) if alternative nests used by survivors provide inadequate shelter. However, we can only speculate at present whether these suggestions are correct.

The qualities of a preferred nest doubtless affect many aspects of the ecology of opossums and include dryness, warmth, and sufficient depth to prevent attack by blowflies during the day (L. T. Pracy, pers. comm.). Such nests should also be suitably distributed in the habitat as far as food, trails and other facilities are concerned. And it would follow that if poisoned animals seek shelter in these, contamination would have very extensive repercussions on the habitat available to survivors.

The point made concerning disruption of other social factors is equally interesting, though indirect. Kean (1967) suggests *Trichosurus* is not a particularly social mammal. Apart from the female-kitten unit, individuals in a population are essentially solitary except when involved in mating.

Aggregations are consequences of chance meetings, dispersion of limited quantities of food, or local shelter. This interpretation tends to imply that survivors would not be greatly influenced by death of a large proportion of a population.

Nonetheless, a population may require facilities which develop only by repeated, though not necessarily co-ordinated, use. Besides nests—which may be solitary or communal—a lattice of clear trails is the most obvious example because these are necessary to facilitate movement between nests and food in wet forests (Kean and Pracy 1949; Batcheler *et al.* 1967). Territorial marks and scent posts of other opossums are also features of the habitat which opossums recognise (Kean 1967). Repeated use of such facilities may lead to a degree of organisation beyond the social needs of individual animals.

It may therefore be contended that death of a large portion of a population incurs deterioration of the habitat for survivors and so could account for delayed deaths after poisoning. On the other hand, decline of facilities must accompany reduction of numbers regardless of how reduction is effected; whereas, with the possible exception of a decline of an opossum population on Kawau Island after poisoning with cyanide on flour baits (R. I. Kean, pers. comm.), delayed deaths after poisoning of the kind described have been associated by control officers only with use of "1080". This tends to weigh the argument in favour of the ecological features of the reduction—i.e. death in nests—rather than the numbers which die.

DISCUSSION

The hypothesis provides for predicting the sequence of events which will occur even though the circumstances under which control campaigns are carried out may differ widely. But it must be stressed that evidence for it is controversial because interpretation of the results of killing pests involves the analysis of a vast amount of information: Norms and trends of dynamics, environmental ecology, behaviour, pathology, toxicology, nutrition and population density are all involved. Nonetheless, the hypothesis emphasises the importance of the connexion between behaviour and control technology and, specifically, it draws attention to the need for knowledge of the mechanisms of survival from control operations. With reference to opossums, for example, it is possible that the

distribution of deaths may be as important in controlling a population as the proportion killed. Speculating further, it would be interesting to know whether death in burrows of rabbits poisoned with "1080" ultimately causes death among survivors. Or, in general: Is the slow action of "1080" a key attribute for controlling nesting species in habitats which have few available nest sites?

The hypothesis also suggests that comparison of the efficiency of poisoning with that of hunting as a means of controlling ungulate populations must involve consideration of the extent to which the techniques disturb survivors. It might be argued that if it costs about the same amount to remove equal proportions of populations by poisoning as by hunting, hunting will be more efficient where the food resources within refuges is poor. This condition, and the intensity of hunting required to achieve it, may be adequately established by measuring the trend of reproductivity and physical condition of survivors.

SUMMARY

Results of some control campaigns suggest that the characteristic features of response to reduction of numbers (improved physical conditions, higher reproductive rates) are suppressed when the control technique disrupts the ability of survivors to exploit preferred components of the habitat.

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