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LONG-TERM TRENDS IN POSSUM NUMBERS AT PARARAKI: EVIDENCE OF AN IRRUPTIVE FLUCTUATION

Summary: We examined possum trapping data collected from 1945 to 1989 in the Pararaki catchment to assess whether there was any evidence for a major natural decline in possum numbers several decades after colonisation and whether the population has subsequently shown any long-term trend in abundance. The catchment was probably colonised by possums around 1915-20. We found evidence for a major decline *(c.* 80%) in possum numbers between 1945 and 1965. There was no significant trend in our trap catches from 1965 to 1976, but in 1977 there was a further abrupt decline. The next decade was characterised by a progressive increase in possum numbers, which by 1989 reached a level slightly below that during the stable period 1965-76. We suggest that the population now experiences irregular fluctuations around a more-or-less stable equilibrium abundance. Our data thus support cautious application of the irruptive fluctuation model *(sensu* Riney, 1964) to possums, which have some of the demographic characteristics of larger ungulate herbivores.

Keywords: *Trichosurus vulpecula;* brushtail possums; population dynamics; population density.

Introduction

When large herbivores are introduced into previously unoccupied habitat and are undisturbed, they typically increase to a peak density and then crash steeply to a considerably lower level (Caughley, 1976). Riney (1964) termed this an "eruptive oscillation", although "irruptive" is a more appropriate term *(c.f.* Leader-Williams, Walton and Prince, 1989). Irruptive oscillations are thought to be the consequence of time-lags in the adjustment process between a herbivore population and its food supply, in that herbivore numbers overshoot the ecological carrying capacity of the habitat and consequently suffer markedly decreased fecundity and/or increased mortality (Caughley, 1976; Hanks, 1981). Irruptive fluctuations are associated with populations regulated primarily by extrinsic factors (e.g., food) rather than intrinsic factors (e.g., behavioral interactions). Theoretical analysis suggests that extrinsic regulation will be most pronounced among large herbivores (>30 kg body weight) that have a relatively low intrinsic rate of increase (<0.45 per annum) (Caughley and Krebs, 1983).

Population growth of brushtail possums *(Trichosurus vulpecula* Kerr) after their liberation in many parts of New Zealand in the early 20th century has been commonly interpreted by the irruptive fluctuation model (e.g., Bamford, 1972; Fraser, 1979; Pekelharing, 1979; Pracy, 1981). However, possums are relatively small (2.2 - 3.5 kg mean body weight; Cowan, 1990) and their populations appear to be influenced by intrinsic factors - spacing behaviour and social interactions (Green, 1984). On theoretical grounds, therefore, the validity of applying the irruptive fluctuation model to possums is questionable (M. Efford, *pers. comm.)*.

A key prediction of the irruptive fluctuation model is that a major natural decline in possum abundance should occur several decades after colonisation of new forest habitat. Subsequently, the population should experience lesser fluctuations about the ecological carrying capacity (= equilibrium density, *sensu* Clout and Barlow, 1982). Unfortunately, there is almost no quantitative evidence for major natural declines in possum numbers anywhere in New Zealand. It is also unclear whether supposedly "post-peak" populations are now fluctuating around a stable equilibrium density or whether they are showing a progressive downward trend in density (Pracy, 1981) as possums continue to modify the forest species' composition (Campbell, 1990).

In this paper we estimate changes in possum numbers in the Pararaki catchment, in the southeastern Wairarapa, over the period 1945-89 to test the prediction that there should have been a major natural decline in possum abundance several decades after colonisation and, if so, to determine whether there has been any subsequent long-term trend in possum numbers. The analysis is based on kill-trapping data collected in the Pararaki catchment. Kill-trapping began in 1945 and continued sporadically over the next 20 years as one of us (L.T.P.) recorded possum catches on a trap line originally established for commercial fur harvesting. Annual population surveys on adjacent lines were carried out by L.T.P. from 1965 to 1974 for the New Zealand Forest Service, and were continued by M.D.T. and J.D.C. from 1975.

Detailed demographic information on the population collected since 1975 is to be presented in a subsequent paper.

Study Area

The study area comprises the forested hills of the upper Pararaki catchment, Haurangi State Forest Park, Wairarapa (NZMS 260, S28, 034653; Fig. 1), and has low but steep relief ranging from 200 to 700 m a.s.l. The forest, described by Wardle (1967), is dominated at low altitude (<600 m) by mahoe *(Melicytus ramiflorus* Forst. et Forst. f.), hinau *(Elaeocarpus dentatus* Forst. et Forst. f.), and rewarewa *(Knightia excelsa* R. Br.), above an understorey mainly of silver fern *(Cyathea dealbata* Forst. f.), pigeonwood *(Hedycarya arborea* Forst. et Forst. f.), and hookgrass *(Uncinia* spp.). On the higher slopes black and silver beech *(Nothofagus solandri* var. *solandri* Hook. f. and *N. menziesii* Hook. f.) are dominant above an understorey of tree ferns *(Cyathea* spp.), small-leaved coprosmas *(Coprosma* spp.), and pepperwood *(Pseudowintera colorata* Raoul). The forest canopy is generally intact, although windthrow, particularly from the Wahine storm in April 1967, is common at higher altitude. The understorey is considerably denser now than between 1940 and 1960 when red deer *(Cervus elaphus* Lannberg), goats *(Capra hircus* Linnaeus), and wild sheep *(Ovis aries* Linnaeus) were common in the catchment (Jane and Pracy, 1974).

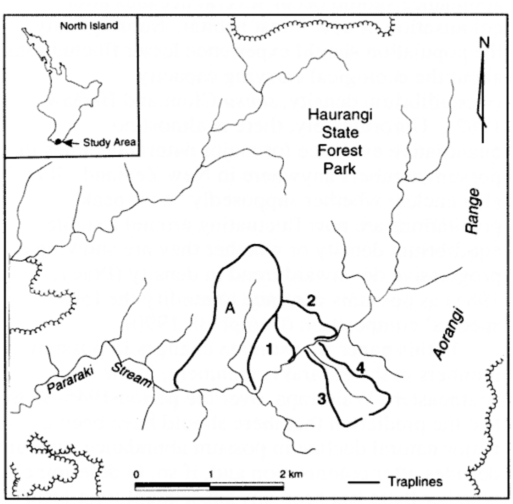

Figure 1: *The Pararaki catchment. Haurangi State Forest Park, with locations of the five trap lines.*

Possums (both black and grey) were liberated at Bull Hill, 12 km north of the study area, in 1908 (probably only two animals) and 1921, at Hurapi *(sic)* Valley 6 km away in 1920, and at Mt Barton 13 km away in 1912 (Pracy, 1962). The study area has been closed to commercial harvesting since 1965, but limited private trapping before this and a small-scale aerial baiting trial in 1957 may have altered possum abundance.

Methods

Possum abundance was assessed from the catches recorded on five permanently marked kill-trap lines. Line A formed a loop on the northern side of the valley (Fig. 1) and consisted of 56 traps at about 60-m spacings. Traps on this line were set unlured for 6-20 nights in 1945, 1951, 1965, 1969, 1975, 1981, and 1986 at the same trap sites. This line was named line I in Batcheler, Darwin and Pracy (1967); a second line referred to in that paper was not trapped after 1951 and has been excluded from this analysis. Four additional lines (1-4) were established in 1965 and have been trapped annually since (except for 1979 and 1987). Each of these lines extended from valley floor to ridge crest (Fig. 1) and consisted of 20 permanently sited traps spaced at about 60 m intervals. These were sited on good possum "sign" present in 1965 and were set unlured for three consecutive fine nights each winter (usually in July).

Very high catches on Line A in 1945 and 1951 meant that traps were then close to being saturated with possums, and 5-10 nights trapping were required before the nightly catch began to decrease. We calculated a crude estimate of the number of trappable possums around line A during each survey using the generalised removal method described by Otis *et al.* (1978) and implemented in their programme CAPTURE. Data from later surveys were not analysed in this way because the short trapping periods in those surveys did not cause sufficient declines in catch for the removal method to be reliable. Instead for lines 1-4, the total catch over three nights was used as a simple index of possum abundance. Annual variation in catch was partly caused by variation in trappability of possums between years because of weather, so we were unable to use more sophisticated trapping indices. Instead we used Analysis of Covariance (ANCOVA) to assess trends in catch over this period and the consistency of trends between lines.

Results

A major decline?

Estimates of the trappable possums around line A (Table 1) suggest that there was a substantial decrease in possum abundance in the area from 1945 to 1951, which continued into the 1960s. Although the 1945 estimate has a substantial confidence interval, we note that mote than 1400 possums were actually caught in this survey (Batcheler *et* al., 1967) so that the estimated total (1785) does not seem unrealistic. The 1969 data provided a good fit to the removal model and the estimate had relatively tight confidence limits;

Table 1. *Total number of trappable possums around line A for the four surveys conducted* 1945-69, *estimated using CAPTURE (see text).*

Year	No. of trappable possums	95% C.I.
1945	1787	1100 - 2474
1951	839	289 - 1380
1965	381	129 - 633
1969	238	198 - 279

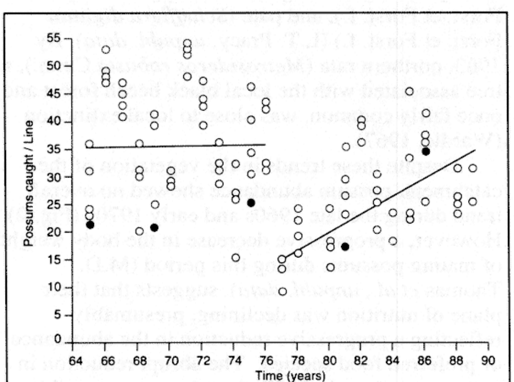

Figure 2: *Possum population trends* 1965-89, *based on* 3-night *catch data on lines* 1-4 (_) *and line* A (_). *Catches on line* A *were corrected for the greater number of traps on this line (see text).*

comparisons with the 1945 estimate suggests that possum abundance declined by c. 80% (±15% as a 95% CI) over the two decades. Observations in the study area during the late 1940s suggested that the possum population reached peak density in 1948 and 1949. The following marked reduction in numbers was due, at least in part, to starvation of adult possums. Possums were observed feeding during daylight hours, were found dead in nest sites and were observed feeding on deer carcasses (LT. Pracy, *pers. com.).*

A subsequent equilibrium?

Possum catches on lines 1-4 showed an overall downward trend from 1965 to 1989, but this was strongly influenced by a marked decline in catches in 1977. This sudden decline in possum abundance appeared to be a result of starvation as possums in an emaciated condition were found dead in traps (J.D. Coleman and LT. Pracy, *pers. obs.).* Demographic data collected at that time showed possums had low mean body weights, very low levels of fat, few pouch young, and low numbers in the l-year-old cohort showing poor survival of yearlings (M.D. Thomas, *unpubl. data).*

Based on this ecological evidence for a discontinuity in the population trend, we consequently analysed the trends in possum catch separately for the periods 1965-76 and 1977-89. Possum numbers did not vary significantly over the first period *(P*=0.45*)*. After the sudden reduction in catch in 1977 there was a highly significant linear increase in catch over time during the next decade *(P*=O.OO2*),* so that by 1989 it was similar to that in the stable period 1965-76. This linear trend was consistent across all lines *(P*=0.92), and in neither period were there significant differences in catches between lines *(P*=0.97*,* P=0.49 respectively).

When the 1965-89 catches on line A are adjusted so that catches are the equivalent per proportion of traps on lines 1-4 (i.e., by multiplying the catch over the first three nights by 20/56 to correct for the different number of traps), it is apparent that they have been within the range of variation for the other lines (Fig. 2) and have shown similar trends over time.

Discussion

A major natural decline?

Assuming that colonising possums were present in the Pararaki catchment by 1915-20, it took 25-30 years to reach the high catches in 1945. Similar times from colonisation to peak density have been proposed for possums in Westland National Park (25-30 years; Pekelharing and Reynolds, 1983) and slightly longer in the Hokitika catchment (35-40 years; Boersma, 1974).

The high catches in 1945 had declined by about 80% by 1965. Possums were observed to be at peak densities in 1948 and 1949 and this was followed by a marked reduction in numbers due to starvation, (L.T. Pracy, *pers. comm.)*. Possums were observed feeding during daylight hours in winter and were found dead in nest sites and were also seen feeding on deer carcasses. Our removal trapping could have influenced the *speed* of this decline but would not seem to have influenced its extent (as catches on line A were subsequently similar to those on lines 1-4, which were not trapped in the earlier surveys).

These data support the hypothesis that the Pararaki possum population experienced an irruptive oscillation broadly similar to that reported for large herbivores such as red deer (c. *elaphus;* Leader-Williams *et al.,* 1989) and Himalayan thar *(Hemitragus jemlahicus;* Caughley, 1970). Thus a possum may have some of the demographic characteristics of a "large" herbivore. Possums have low fecundity (a maximum of two offspring per season; Cowan, 1990) compared with other mammals of similar size, and realistic estimates of possum intrinsic rate of increase (0.3, Clout and Barlow, 1982; 0.22, Hickling and Pekelharing, 1989) are consequently on the "large herbivore" side of the 0.45 threshold identified by Caughley and Krebs (1983). We therefore propose that possum population growth can be considered extrinsically limited - by the food supply - at least during the initial decades after colonisation (see below).

A subsequent equilibrium?

For possums the concept of an equilibrium population size invokes a tendency for a population to move towards that size after it has been altered by such factors as abnormally severe weather, poisoning operations, lack of food, high population densities or sudden immigration. The equilibrium size could fluctuate with time, and could also show a consistent trend (for example, if possum browsing were causing long-term changes in forest species' composition). Equilibrium size remains a theoretical concept, albeit a useful one, because in practice it is not possible to separate a fluctuation in population size about the equilibrium from a fluctuation in the equilibrium value itself (Wolda, 1989). Furthermore, most mammal populations - including those in their native habitats - show marked fluctuations in population size (e.g., Ostfeld, 1988) and it is important to distinguish this variation from systematic trends. Possums are no exception. The Orongorongo Valley possum population is stable by mammalian standards, but despite this some years show increases or decreases in population size of up to 50% (M.G. Efford, *pers. comm.)*.

The sampling variation associated with our trapping methods means we cannot usefully interpret any but the most major between-year changes in catch (e.g., 1976-77). We therefore confine the following discussion to the broad trends in catch in the Pararaki catchment in the decades since the major natural decline described for 1945-69.

Possum populations can cause substantial modification of natural forest composition as they become established in an area. Defoliation and killing of preferred canopy and sub-canopy tree species on a large scale at times of high possum densities have been reported for Westland (see Pekelharing, 1979; Batcheler 1983; Payton, 1988; Leutert, 1988). Similar changes in forest structure occurred in the Pararaki catchment, where widespread canopy damage in 1948 was coincident with high possum mortality (L.T. Pracy, *pers. obs.)*. By 1957, the highly palatable and previously common kotukutuku *(Fuchsia excorticata)* had been locally eliminated and many less palatable species had been depleted, e.g., kamahi *(Weinmannia racemosa* Linn. 0, lacebark *(Hoheria sexstylosa* Col.), kowhai *(Sophora microphylla* Ait.), five-finger *(Pseudopanax arboreus* (Murray) Philipson), raukawa *(P. edgerleyi* (Hook. f.) K. Koch), haumakaroa *(P. simplex* var. *sinclairii* (Hook. 0 Edgar), rangiora *(Brachyglottis repanda* Forst. et Forst. f.), and pate *(Schefflera digitata* Forst. et Forst. f.) (L.T. Pracy, *unpubl. data)*. By 1963, northern rata *(Metrosideros robusta* Cunn.), a tree associated with the local black beech forest and once fairly common, was close to local extinction (Wardle, 1967).

Despite these trends in the vegetation of the catchment, possum abundance showed no overall trend during the late 1960s and early 1970s (Fig. 2). However, a progressive decrease in the body weight of mature possums during this period (M.D. Thomas *et al., unpubl. data),* suggests that their plane of nutrition was declining, presumably reflecting a progressive reduction in the abundance of preferred food species. The abrupt reduction in possum numbers in 1977, therefore, was possibly triggered by severe weather impinging on a population in poor condition.

Possums numbers have increased progressively since 1977 and are now similar to the number present before the mid 1970s crash. Thus the variation in catches over the period 1965-89 may represent irregular fluctuations around an equilibrium density that has remained more-or-less constant over the past 3 decades. A similar conclusion has been reached by M.G. Efford *(pers. comm.),* who found no overall trend in density of possums in the Orongorongo Valley between 1966 and 1987, despite the increases or decreases of up to 50% mentioned above.

It is difficult to predict future trends in the size of this population. A continued gradual deterioration of the habitat's carrying capacity as a result of natural and possum-induced mortality of palatable canopy species seems likely in the absence of possum control. The reduction of preferred species and their gradual replacement by less palatable species suggests a forest able to support fewer possums, although this may be offset to some extent by the reduction in browsing pressure by ungulates in the 1960s, which has allowed increased regeneration of some palatable species. The possum population appeared to be close to its mean density for the period 1966-87, but mean adult body weight continues to decrease (M.D. Thomas *et al*., *unpubl. data).* If the population remains uncontrolled, we predict that another rapid population decline similar to that recorded in 1977 may occur at Pararaki during the mid 1990s.

Clear evidence of food-limitation among present-day possum populations is lacking, and it has been suggested that spacing-related (intrinsic) mechanisms may be important in regulating possum population size (Green, 1984). We suggest that social mechanisms may have increased in importance in New Zealand possum populations over time. The pressure of rapid population growth in the first decades after colonisation could have exceeded any regulatory ability of partially-established intrinsic mechanisms in some habitats, leading to irruptive oscillations in such populations.

Such an hypothesis highlights our current lack of knowledge about the relative importance of extrinsic and intrinsic regulation of possum abundance in New Zealand.

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References

Bamford, J.M. 1972 (unpublished). *The dynamics of possum* (Trichosurus vulpecula *Kerr) populations controlled* by *aerial poisoning*. Ph.D. thesis, University of Canterbury, Christchurch, N.Z. 158 pp.

Batcheler, C.L.; Darwin, J.H.; Pracy, L.T. 1967. Estimation of opossum *(Trichosurus vulpecula)* populations and results of poison trials from trapping data. New *Zealand Journal of Science 10:* 97-114.

Batcheler, C.L. 1983. The possum and rata-kamahi dieback in New Zealand: A review. *Pacific Science* 37: 415-426.

Boersma, A. 1974. Opossums in the Hokitika River catchment. New *Zealand Journal of Forestry Science 4*: 64-75.

Campbell, D.J. 1990. Changes in structure and composition of a New Zealand lowland forest inhabited by brushtail possums. *Pacific Science 44*: 277-296.

Caughley, G. 1970. Eruption of ungulate populations, with emphasis on himalayan thar in New Zealand. *Ecology 51:* 53-71.

Caughley, G. 1976. Wildlife management and the dynamics of ungulate populations. *Applied Biology 1:* 183-246.

Caughley, G.; Krebs, C.J. 1983. Are big mammals simply little mammals writ large? *Oecologia 59*: 7-17.

Clout, M.N.; Barlow, N.D. 1982. Exploitation of brushtail possum populations in theory and practice. *New Zealand Journal of Ecology 5*: 29-35.

Cowan P.E. 1990. Brushtail possum. *In:* King, C.M. (Editor), *The handbook of* New *Zealand mammals,* pp. 68-98. Oxford University Press, Auckland, NZ. 600 pp.

Fraser, K.W. 1979. Dynamics and condition of opossum *(Trichosurus vulpecula* Kerr) populations in the Copland Valley, Westland, New Zealand. *Mauri Ora 7*: 117-137.

Green, W.Q. 1984. A review of ecological studies relevant to management of the common brushtail possum. *In:* Smith, A.P.; Hume, I.D. (Editors), *Possums* and *gliders,* pp. 483-499. Surrey Beatty, NSW, Australia. 598 pp.

Hanks, *J*. 1981. Characterisation of population condition. *In:* Fowler, C.W.; Smith, T.D. (Editors), Dynamics *of large mammal populations,* pp. 47-73. Wiley, New York, USA. 477 pp.

Hickling, G.J.; Pekelharing, C.J. 1989. Intrinsic rate of increase for a brushtail possum population in rata/kamahi forest, Westland. New *Zealand Journal of Ecology 12:* 117-120.

Jane, G.T.; Pracy LT. 1974. Observations on two animal exclosures in Haurangi Forest over a period of twenty years (1951-1971). *New Zealand Journal of Forestry 19*: 102-113.

Leader-Williams, N.; Walton, D.W.H.; Prince, P.A. 1989. Introduced reindeer on South Georgia- A management dilemma. *Biological Conservation 47*: 1-11.

Leutert, A. 1988. Mortality, foliage loss, and possum browsing in southern rata *(Metrosideros umbellata)* in Westland, New Zealand. *New Zealand Journal of Botany 26*: 7-20.

Ostfeld, R.S. 1988. Fluctuations and constancy in populations of small rodents. *American Naturalist 131*: 445-452.

Otis, D.L; Burnham, K.P.; White, G.C.; Anderson, D.R. 1978. *Statistical inference for capture data on closed animal populations*. Wildlife Monographs No. 62, The Wildlife Society, University of Louisville, Louisville, Kentucky, U.S.A. 134 pp.

Payton, I.J. 1988. Canopy closure, a factor in rata *(Metrosideros)* - kamahi *(Weinmannia)* forest dieback in Westland, New Zealand. *New Zealand Journal of Ecology 11*: 39-50.

Pekelharing, C.J. 1979. Fluctuation in opossum populations along the north bank of the Taramakau catchment and its effect on the forest canopy. *New Zealand Journal of Forestry Science 9*: 212-224.

Pekelharing, C.J.; Reynolds, R.N. 1983. Distribution and abundance of browsing mammals in Westland National Park in 1978, and some observations on their impact on the vegetation. *New Zealand Journal of Forestry Science 13*: 247-65.

Pracy, L.T. 1962. *Introduction and liberation of the opossum* (Trichosurus vulpecula) *into New Zealand*. New Zealand Forest Service Information Series No 45, N.Z. Forest Service, Wellington, N.Z. 28 pp.

Pracy, LT. 1981. Opossum survey. *Counterpest 5*: 5-15.

Riney, T. 1964. The impact of introductions of large herbivores on the tropical environment. 9th technical meeting Nairobi. *IUCN Publications New Series No.4:* 261-273.

Wardle, J. 1967. Vegetation of the Aorangi Range, southern Wairarapa. *New Zealand Journal of Botany* 5: 22-48.

Wolda, H. 1989. The equilibrium concept and density dependence tests: what does it all mean? *Oecologia 81*: 430-432.