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# ROAD-KILLS IN NEW ZEALAND: LONG-TERM EFFECTS TRACK POPULATION CHANGES AND REVEAL COLOUR BLINDNESS

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*Abstract.*

*Road-kills were recorded at random throughout New Zealand, on 96359 km of roads, avoiding towns and busy motorways, from 1963-2018. Traffic increase from 1.04 m to 4.33 million vehicles during the study had little effect on mortality, even at the greater traffic density in the North Island. Seasonal changes measured on 8435 km (151 trips) between Lower Hutt and Otaki from 1985-2015 showed lowest mortality in winter. Major differences in species identification between two independent observers on the same route, from 2009-2014, resulted from one being red/green colourblind. Possum (*Trichosurus vulpecula*) numbers dipped briefly in the 1970s, peaked in the 1990s, and have declined since then where there has been widespread poisoning to protect trees, birds, and limit bovine TB. Rabbits (*Oryctolagus cuniculus*) increased steadily after control was lifted in the 1980s and now dominate the road-kills; the effect of RHD, introduced in 1997, does not register, probably because it causes short-term local oscillations. Hedgehog (*Erinaceus europaeus*) numbers show no clear trend and, unlike the other species, North and South Island patterns differ; the lower numbers in the South may reflect the cooler climate. Brown hares (*Lepus europaeus*) remain relatively stable, with a doubling in numbers since the 1980s in parallel with rabbits. The predators, cats (*Felis catus*) and mustelids (*Mustela furo, M.erminea, M. nivalis*), followed their prey increase until the 1990s when extensive predator control began; they then declined, although rabbit and rat (*Rattus rattus, R. norvegicus*) numbers continued to rise. In the 1950-60s, far more live mammals were being seen on and from roads, and adaptations to traffic have evolved. These historical records may be useful to assess future changes in road-kill following the adoption of silent electric cars, driverless vehicles, and public transport.*

*Key words: bird, hare, hedgehog, mustelid, possum, rabbit, road-kill*

## Introduction

Road-killed animals have been scientifically recorded since the mid1920s (Stoner 1925, Dreyer 1935, Barnes 1936), and the increasing numbers of roads, vehicles, and deaths are worrying. At least 25,000,000 km of additional roads are expected by 2050, and peer-reviewed publications on road-kill have proliferated, from one a year in 2000 to 50 by 2019 (Schwartz et al.2020). As Coffin (2007) points out, growing interest in the effects of roads has now resulted in an emerging science of "Road Ecology." Even insect mortality is being carefully measured (Rao & Girish 2007). Austria set up an international citizen science road-kill scheme with the unexpected benefit of allowing academics to teach larger classes computer skills (Heigl & Zaller 2014). Australia has introduced a nation-wide database (Englefield et al. 2020) with the aim of monitoring and minimising road-kill. New Zealand, in contrast, aims to maximise road-kill to get rid of introduced pests: "The utility, therefore, of roads in the management of invasive species might also be a novel perspective in road ecology not yet developed but a potentially valuable adaptation..." (Sadleir & Linklater 2016). Current conservation emphasis on the enormous numbers of animals killed on roads may be misplaced: relatively few species are rare, and these are confined naturally to small areas, where special road signs are warranted (Grilo et al. 2020). However, there is growing public awareness of the ethical implications involved: in a remarkably wide review of all aspects of American road-kill, Corrigan (2021) suggests "a civilization should be measured by how it treats the most vulnerable creatures that share the planet's ultimate gift of life".

In New Zealand road-kill counts were started by Dr K. Wodzicki and R. H. Taylor in 1949 (an earlier count on 30 December 1948 for five miles cycled near Taupo recorded 18 rabbits, 2 hares and 1 cat, but no dead animals). From Taylor's notebooks, the first counts (10 January – 30 August 1949) totalled 7 possums, 85 hedgehogs, 4 hares, and 2 stoats on 1474 km of roads between Wellington and Napier. On 180 km from Havelock North to Taupo on 24 November 1949, the tally was 1 hedgehog and 7 rabbits; plus 13 live rabbits, 7 hares, 10 wild horses and 1 deer. The return trip on 30 November listed 2 hedgehogs, 6 rabbits and 3 hares; plus 34 live rabbits and 2 wild horses. The only other noteworthy road-kill tallies were on 193 km from National Park to Palmerston North on 1 April 1950 (2 possums, 2 hedgehogs, 1 rabbit, 1 hare and 1 stoat); from Palmerston North to Wellington, 142 km, on 26 April 1950 (1 possum, 13 hedgehogs, 1 hare, 1 rat and 1 magpie (*Gymnorhina tibicen*)); and from 28 January – 10 February 1955 on 711 km around central North Island (7 possums, 15 hedgehogs, and 1 hare).

Early figures are remarkable for the abundance of hedgehogs (discussed by Brockie 1960) and of live animals seen: on 26 October 1960 Flux drove 650 km from Auckland to Lower Hutt without seeing any live wild mammals. However, in the South Island over 2975 km in January 1964, there were 18 live and 19 dead hares, 2 live and 15 dead rabbits, 1 live and 90 dead possums, 1 live and 202 dead hedgehogs, 3 live and 2 dead stoats and 1 dead rat on the roadway; but a similar tour in May 1978 gave only 8 dead hares and 5 dead rabbits (other road-kills were not counted, but there were no live animals). There has been a marked change away from diurnal behaviour, and it is rare to see any live mammals now, even in adjacent fields.

Brockie et al. (2009) provide a comprehensive overview of the rationale and problems associated with counting mammalian road-kills in New Zealand and overseas. Their main conclusions, based on three 1600 km trips the length of the North Island, from Lower Hutt to Kaitaia, were that possum numbers rose 80% between 1984 and 1994, but declined 60% by 2005; a "possible irruption of hedgehogs" in 1988-89, followed by an 82% decline between 1994 and 2005; and an increase in rabbits of 59% between 1994 and 2005.

The first author of this paper (John EC Flux) counted road-kills in a less systematic way, but more frequently, and over a longer distance (96359 km) since 1963. These counts give some support to two of their conclusions, oppose the third, and present an independent picture of probable population changes in some mammals during the past 50 years. We do not consider road-kill counts an accurate measure of the numbers killed for any species, nor a way to assess densities, but they provide an index of major changes in distribution and abundance, and ratios between the species are useful. There is also concern that ever-increasing road construction and vehicle numbers may cause local extinctions: even 20 years ago "an estimated 15-20% of the United States is ecologically impacted by roads" (Forman & Alexander 1998), and a recent review found rare primates were also at risk (Hetman et al. 2019). In view of proposals to eliminate all mammalian pests from New Zealand by 2050 (Russell et al. 2015), the introduction of silent, or driverless electric vehicles (Tryjanowski et al. 2021), and the growth of "citizen science" as a monitoring tool (Olson et al. 2014, Vercayie & Herremans 2015), historical records may become of interest as a base-line for future ecological comparisons; and the 2016-18 counts provide a reasonably robust view of the present status throughout New Zealand. The adoption of a standard international protocol, as recommended by Collinson et al. (2014), seems premature; the aims and faunal diversity differ too widely between countries. However, the list of factors to record and techniques to make best comparative use of the results, given by Erritzoe et al. (2003) is an extremely valuable beginning.

## Methods

The first author (John E.C. Flux) recorded road-kills at random, preferably driving 150 m behind a slow truck, or being driven at speeds up to 100 kph. Collinson et al. (2014) found no difference in the counts, whether the observer was driving or in the passenger seat. Counts were done when viewing conditions were suitable, avoiding sun glare, rain, busy motorways and towns. "Random" here means starting and ending at pre-determined points, not when an interesting kill was seen or unusually high numbers were encountered. Hence the only road-kill kiwi (*Apteryx australis*) seen, near National Park at a sign saying "Beware, kiwi crossing", was not included.

Unlike Brockie et al. (2009) there was no attempt to repeat set routes. Early analyses showed clearly that a single count was not representative: road-kill numbers varied too much, according to weather (rain the previous night might increase the number of hedgehogs foraging snails on the road, but decrease possums which avoid rain); scavenger activity and technique (counts on 38000 km in East Africa in 1967-68 yielded only 11 hares, 4 jackals, 3 mongoose, 3 hedgehogs, 1 cat, 1 ground squirrel, 1 bat, and 15 bird road-kills – Flux unpublished data) and see Fig. 1A, B ; traffic speed and intensity (which

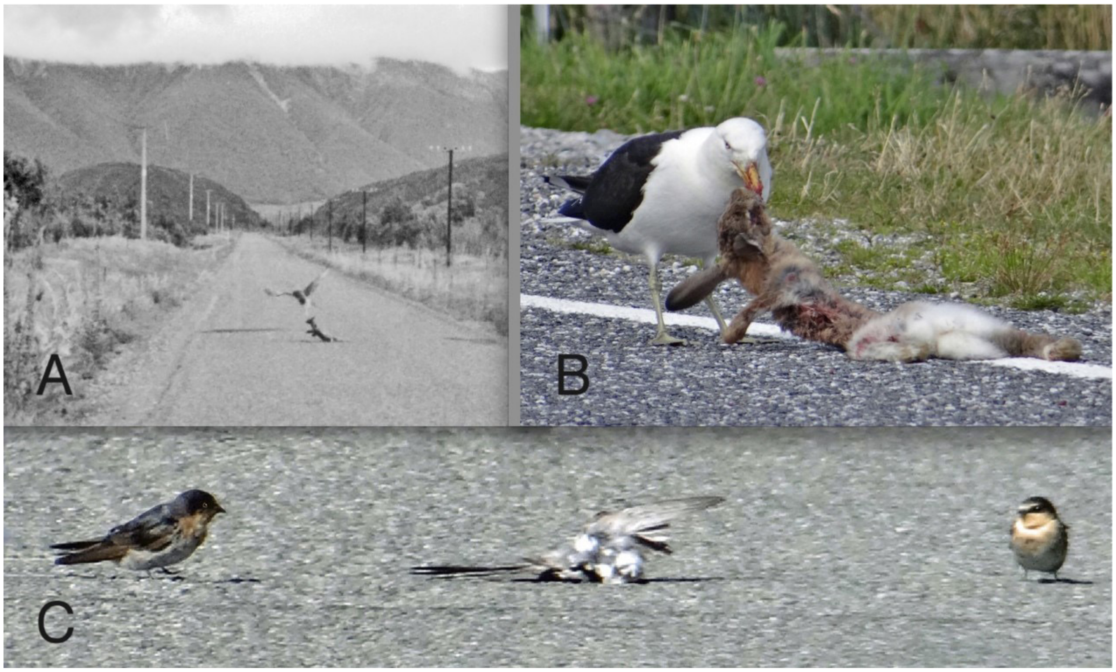


**Figure 1.** A. Harrier removing dead hare from road, St Arnaud, 1964. Harriers are often seen in fields alongside roads, eating such prey; B. Black-backed gull pulling corpse off road; C. Swallows (*Hirundo neoxena*) inspecting dead swallow.

can have positive or negative effects on kill rates and the duration carcases last); body size and colour – 3 kg possums are easier to see than rats, but bright tan-coloured weasels are hard to miss; patchy distribution (wallabies only occur near Rotorua (*Notamacropus eugenii*) and Waimate (*Notamacropus rufogriseus*)); and attraction to dead conspecifics (Fig. 1C). In Spain, Santos et al. (2011) found "Most animal carcasses persisted on the road for the first day only." In Brazil, 89% disappeared within 24 hours (Ratton et al. 2014). Even in temperate areas scavengers may have a marked effect: in Wales, Slater (2002) measured the removal of carcases, chiefly by cats, at 12 to 16 times the number left on the road the following morning; and all 178 toads were removed by scavengers within an hour of sunrise. In Norway, a careful study showed small birds lasted less than a day; large ones averaged six days (Husby 2016). Human interference cannot be excluded: during the 2016 counts we met five separate artists removing road-kill for their work. Collection of edible animals may explain our total lack of deer, a common road-kill in Europe and America (Seiler et al. 2004, Corrigan 2021), although we did record four dead sheep in the North Island and two in South Island.

Repeated counts, made a few days apart over the same stretches of road, illustrate the variability. On 30 May 2014, from Lower Hutt to Turangi, (with the return trip values two days later in brackets) there were 5 (17) possums, 4 (2) hedgehogs, 10 (9) rabbits, 3 (2) hares and 7 (5) birds, with the addition of one rat and a stoat on the return trip. On 10 March 2012, from Lower Hutt to Oakune, (with the return trip values four days later in brackets) there were 9 (14) possums, 2 (2) hedgehogs, 13 (7) rabbits, 2 (0) hares, 1 (0) stoat and 3 (4) birds.

Some of these differences will have been due to real changes (fresh or removed corpses) but observer error is undoubtedly present; an example of this was a count from Lower Hutt to Otaki (60 km) on 20 March 2014, when an unusually high total of 39 rabbits was recorded. To check, a re-count on the return one hour later tallied 50 rabbits and two hares; and the latter, in grass at the left-hand verge, were not new kills, even if some of the rabbits could have been. Another example was on 17 August 2009, when 3 rabbits and 6 birds were recorded from Lower Hutt to Otaki, but 1 possum, 4 rabbits, 2 hares, 1 rat and 2 birds on the return trip 3 hours later.

Numbers of the commoner species, possums, rabbits, hedgehogs, and hares, appeared to be reaching stability at 2-3000 km, so counts were accumulated for about 4000 km to compare relative numbers over time. (Far longer distances would be needed for rarer species such as mustelids.) Fewer trips were made to the South Island (total 35830 km), and the

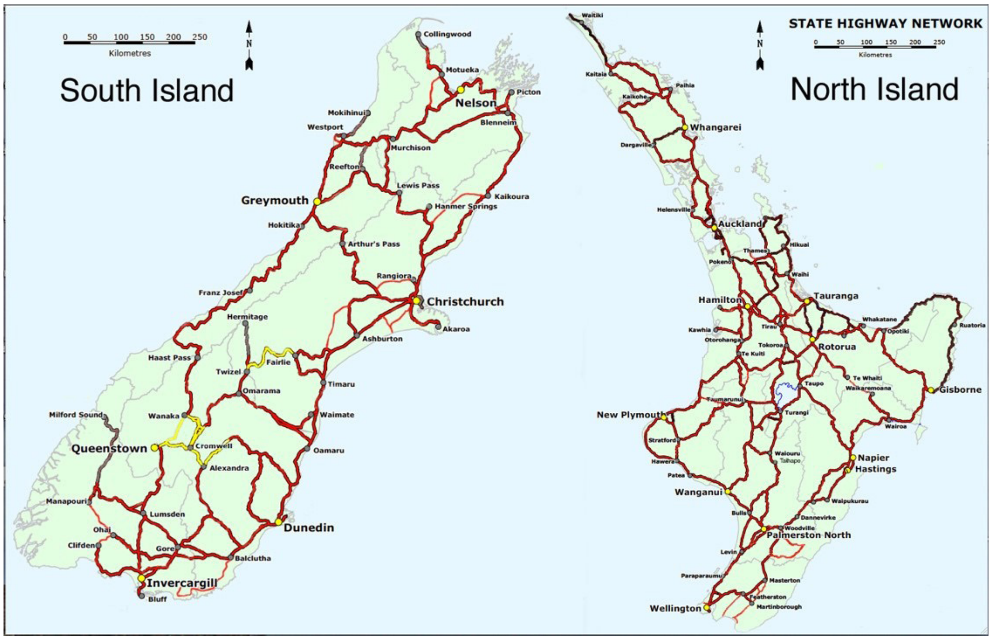

**Figure 2.** Main roads counted, red with black border; those not counted, black; side-roads red; rabbit problem area, yellow.

intervals of time are consequently longer than for the North Island (total 60529 km). Since the totals are data points, they have no statistical margin of error, but can be assessed by chi-square. Seasonal variation was measured by comparing monthly totals from 151 trips (8435 km) between Lower Hutt and Otaki collected from 1985 to 2015. These trips were so numerous they would have biased the North Island counts, so they were only included when they formed part of a longer count.

Quite by chance, and unknown to either of us, Dr Richard Sadleir was recording road-kills on the same route between 2009 and 2014 (Sadleir & Linklater 2016), and the subset 2009-2014 of our data can be directly compared to measure observer differences.

The 2016-18 counts were not random collections of trips; they were specifically designed to cover the whole country uniformly: North Island, 7473 km, 1 November 2016 to 20 January 2017: South Island, 9292 km, 11 February to 18 September 2018 (Fig. 2). This allowed an overall view of the current position, and some regional comparisons.

Birds were initially identified and counted also, but it became clear that few species except harriers (*Circus approximans*) reached meaningful totals for analysis, and these have been reported separately (Flux 2019). All have been lumped as "birds" for a seasonal comparison of road-kills in this paper. Being mainly diurnal, there are far more efficient ways of assessing most bird distributions and numbers than by road-kills, and they are not included in the inter-island tables.

The effect of traffic volume on road-kills is complex, and overseas results conflict. In New Zealand the vehicle fleet rose from 1.04 to 4.33 million during the study, appearing to increase mortality until cars reached 2 million, then decreasing, but the changes were not statistically significant. Mortality was higher in North Island where there are more cars, but the milder climate, allowing increased populations, may be responsible.

## Data Processing and Analyses

Data on the animal mortality recorded in subsequent years of the study are presented as the annual number of individuals killed per 100 km of the roads studied. We checked for possible differences in the overall mortality between islands, and differences in the mortality of the species identified, controlling for the island effect. Separate analyses were performed for the total number of animals killed and for the identified species using the Generalized Linear Models (GLZ) with Poisson distribution and log link function.

To investigate changes in mortality throughout the study period, data from individual years was assigned to the following decades. The analysis was performed using the GLZ with Poisson distribution and log link function, where an overall mortality in a given year was the dependent variable, and the factors were decade and island. Furthermore, we checked whether there was a correlation between the overall number of registered cars, as they increased over the years of study, and the overall summarised mortality recorded on both islands in each year studied. For this purpose, we used data from the years (n = 26) when research was conducted simultaneously on both islands in a given year, and the Spearman correlation was applied.

The calculations were performed using STATISTICA (TIBCO Software Inc., 2017). Throughout the text, mean values are presented with 95% confidence limits (95% CL).

## Results

### General overview

Overall, the mean annual mortality of the animals recorded over the whole study period was 19.2 individuals per 100 km (CL: 16.3 – 22.3) and ranged from 2.6 to 72.4. Recorded mortality was higher in the North Island than in the South Island (GLZ, Wald chi-square = 33.04, df =1, p < 0.001, Fig. 3).

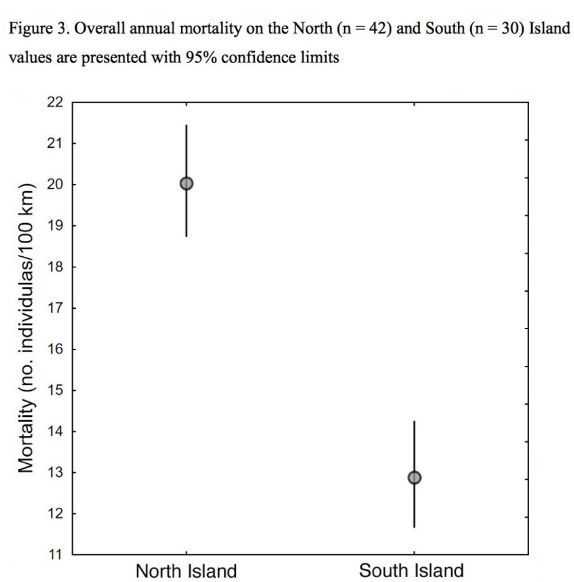


**Figure 3**. Mean annual mortality over the whole study, in North and South Islands.

Furthermore, we recorded differences in mortality between the compared animal species, which were similar in the case of both islands (GLZ, species: Wald chi-square = 651.83, df =8, p < 0.001; species*island: Wald chi-square = 10.52, df = 8, p = 0.231, Fig. 4).

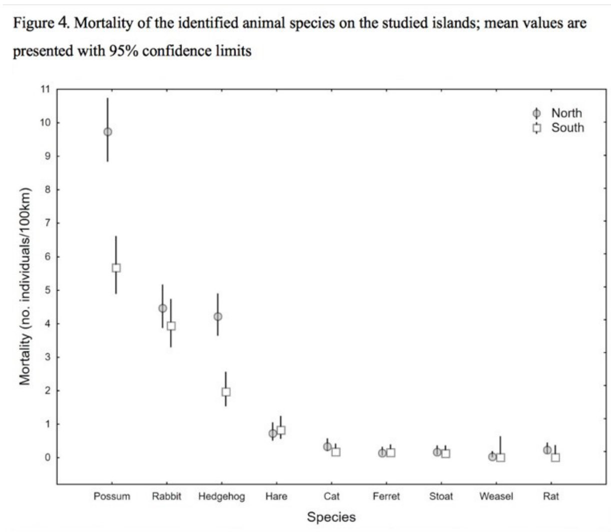


**Figure 4**. Individual species killed per 100km in North and South Islands.

Moreover, the overall mortality differed between the decades of study and shaped differently within the studied islands (GLZ, decade: Wald chi-square = 125.38, df = 5, p < 0.001; decade*island: Wald chi-square = 56.41, df = 5, p < 0.001; Fig. 5).

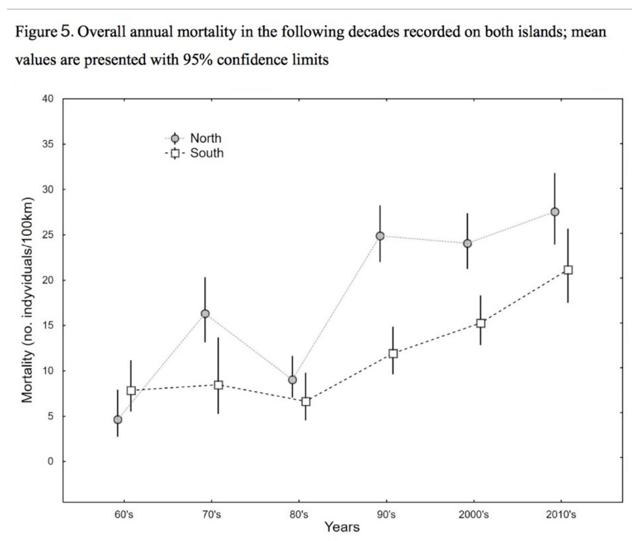


**Figure 5**. Mortality (individuals/100 km) per decade in North and South Islands.

In addition, the overall mortality recorded in a given year on both islands was positively correlated with the number of cars being registered in a given year in New Zealand (Spearman correlation, r = 0.57, n = 26, p < 0.002, Fig.6).

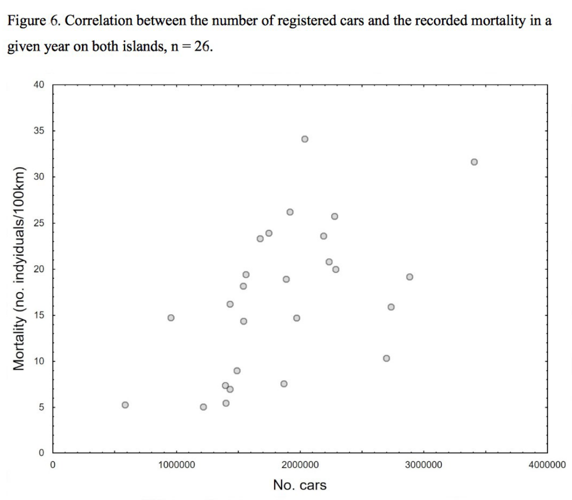


**Figure 6**. Mortality (individuals/100 km) with increasing traffic.

## Observer identifications

A completely blind comparison between observers independently identifying road-kills showed alarming disparities. Sadleir's counts (Sadleir & Linklater 2016) were made on 92 trips totalling 5814 km in 2009-2014, and the Flux 2009-2014 counts were of 59 trips (3715 km) extracted from a longer 1985-2015 series to match. Both routes were identical, as was the weather selected. Per 4000 km, counts agreed on the total mammals recorded (Sadleir 957, Flux 991; $P = 0.51$), but the species totals all differed significantly (chi square, two-tail with Yates' correction, $P < 0.0001$) except for ferrets ($P = 0.23$), stoats ($P = 0.001$), weasels ($P = 0.014$), and rats ($P = 0.007$). Looking at the totals for each year gave more similar patterns for the three dominant mammals. Possums were fairly level apart from our higher numbers in 2010 and 2011; our hedgehogs showed the same peaks in 2010 and 2013, but at far lower amplitude; and rabbits differed only in our higher value in 2010.

## Seasonal variation

Table 1 lists the actual numbers of road-kills for each species of mammal encountered, and "birds", accumulated from 1985 to 2015 between Lower Hutt and Otaki. Winter counts (June to September), being fewer, averaged 390 km per month, compared with 859 km for other months of the year. All species declined in winter compared with the other seasons of the year in the following ratios: possum 1:6.2, hedgehog 1:15.1, rabbit 1:7.3, hare 1:4.6, cat 1:3.9, ferret 1:2.8, stoat 1:13.0, weasel 1:3.3, rat 1:2.5, and birds 1:3.7. Hibernating hedgehogs show the greatest fall in winter, but possums, rabbits, hares, stoats and birds all declined markedly.

## Variation with time

The Lower Hutt to Otaki counts are too short and variable to track temporal changes accurately, but accumulating counts from 1985 to 2007, and from 2008 to 2015, gave total distances of 4225 and 4210 km respectively. Per 4000 km, possums declined from 599 to 265 (56%), hedgehogs from 251 to 154 (39%); rabbits increased from 325 to 468 (44%), and hares from 37 to 48 (30%); cats declined from 24 to 9 (63%), ferrets from 12 to 0 (100%), stoats from 16 to 10 (38%), weasels from 6 to 5 (17%); rats increased from 23 to 35 (52%) and birds from 460 to 513 (12%).

**Table 1.** Total monthly road-kill counts between Lower Hutt and Otaki, 1985-2015.

| Species | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Possum | 72 | 91 | 193 | 131 | 33 | 18 | 9 | 22 | 20 | 85 | 139 | 108 | 921 |
| Hedgehog | 35 | 37 | 99 | 40 | 22 | 6 | 4 | 2 | 5 | 40 | 65 | 76 | 431 |
| Rabbit | 55 | 103 | 232 | 100 | 34 | 16 | 4 | 25 | 9 | 93 | 97 | 73 | 841 |
| Hare | 16 | 9 | 18 | 6 | 5 | 2 | 1 | 5 | 1 | 12 | 9 | 7 | 91 |
| Cat | 1 | 1 | 8 | 6 | 2 | 1 | 1 | 2 | 0 | 2 | 7 | 4 | 35 |
| Ferret | 0 | 0 | 2 | 3 | 1 | 0 | 1 | 1 | 0 | 1 | 3 | 1 | 13 |
| Stoat | 2 | 2 | 7 | 0 | 2 | 0 | 1 | 0 | 0 | 1 | 5 | 7 | 27 |
| Weasel | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 4 | 2 | 11 |
| Rat | 1 | 3 | 13 | 1 | 9 | 3 | 0 | 4 | 3 | 10 | 10 | 2 | 59 |
| Bird | 98 | 86 | 145 | 75 | 34 | 26 | 21 | 57 | 20 | 128 | 210 | 133 | 1033 |
| Dist. (km) | 600 | 745 | 1245 | 735 | 520 | 410 | 300 | 540 | 310 | 940 | 1230 | 860 | 8435 |

**Table 2.** North Island accumulated road-kills per 4000 km.

| Species | 1966-70 | 71-78 | 83-86 | 87-90 | 91-95 | 96-98 | 99-01 | 02-05 | 06-09 | 10-11 | 12-15 | 16-17 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Possum | 318 | 100 | 400 | 258 | 601 | 586 | 582 | 430 | 347 | 337 | 152 | 552 |
| Hedgehog | 196 | 139 | 162 | 145 | 162 | 195 | 140 | 193 | 146 | 67 | 124 | 285 |
| Rabbit | 28 | 11 | 37 | 50 | 154 | 268 | 162 | 288 | 267 | 251 | 389 | 276 |
| Hare | 34 | 16 | 21 | 6 | 26 | 26 | 28 | 33 | 47 | 26 | 42 | 32 |
| Cat | 8 | 4 | 28 | 18 | 20 | 13 | 13 | 21 | 5 | 7 | 7 | 12 |
| Ferret | 8 | 0 | 2 | 3 | 9 | 7 | 5 | 3 | 5 | 2 | 1 | 3 |
| Stoat | 1 | 8 | 1 | 3 | 7 | 9 | 5 | 11 | 18 | 5 | 8 | 9 |
| Weasel | 1 | 2 | 0 | 0 | 0 | 1 | 2 | 1 | 4 | 1 | 3 | 1 |
| Rat | 0 | 0 | 1 | 2 | 5 | 7 | 5 | 14 | 20 | 18 | 18 | 22 |
| Actual km | 3650 | 2270 | 3450 | 3550 | 4250 | 4115 | 5111 | 4610 | 4907 | 4584 | 4124 | 7473 |

**Table 3.** South Island accumulated road-kills per 4000 km.

| Species | 1963-64 | 72-78 | 83-84 | 87-90 | 91-97 | 98-01 | 02-15 | 17-18 |
|---|---|---|---|---|---|---|---|---|
| Possum | 176 | 62 | 223 | 144 | 412 | 231 | 188 | 345 |
| Hedgehog | 186 | 34 | 38 | 14 | 63 | 124 | 72 | 246 |
| Rabbit | 14 | 26 | 18 | 65 | 129 | 343 | 350 | 518 |
| Hare | 18 | 9 | 24 | 14 | 15 | 35 | 49 | 53 |
| Cat | 1 | 8 | 3 | 13 | 21 | 8 | 4 | 8 |
| Ferret | 0 | 1 | 5 | 4 | 13 | 15 | 6 | 38 |
| Stoat | 2 | 1 | 0 | 3 | 5 | 6 | 10 | 6 |
| Weasel | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| Rat | 1 | 0 | 0 | 0 | 1 | 3 | 0 | 3 |
| Actual km | 4700 | 3600 | 2650 | 4250 | 3005 | 4183 | 4150 | 9292 |

North Island and South Island totals per 4000 km are shown in Tables 2 and 3. The key changes in pest management were the formation of the Rabbit Destruction Council in 1947; its enlargement as the Agricultural Pests Destruction Council (APDC) in 1964, to include possums, wallabies, and other pests; the pegging of its funding in 1981-84; and its disbandment in 1989 in favour of far less efficient regional control (Gibb & Williams 1994). In effect, national rabbit control was lifted in 1987.

Possum numbers show a brief decline in both islands in the 1970s (64% in the South Island (Chi sq = 72.7, P<0.0001), 69% in the North Island (Chi sq = 113.7, P<0.0001)), possibly associated with APDC shooting along roads. They show a highly significant decline (P<0.0001) since 1994, following greatly increased control to reduce bovine TB. The 2016-17 increase is due to high numbers north of Taihape (815/4137 km) compared to Wellington -Taihape (149/3142 km) (P < 0.0001). In the South Island numbers are higher to the east of a line from Murchison to Queenstown (774/7385 km) than to the west (45/1907 km)(P< 0.0001).

Separate tallies for the predators, cats, ferrets, stoats and weasels, are shown in Tables 1-3, but numbers are too low for confidence in specific trends. Combined, and grouped in decades, they follow the increase in their main prey, rabbits and rats, until the 1990s when predator control expanded rapidly throughout New Zealand (see Discussion).

In the 2016-18 counts, one Dama wallaby was found near Rotorua, and ten Bennett's wallabies in the Waimate area. All were in places where isolated populations are known to be expanding (Latham et al. 2018) and illustrate the potential for road-kills to monitor population boundaries and spread.

## Discussion

A recent review of the value of monitoring road-kill (Schwartz et al. 2020) suggests five ecological topics merit investigation: numbers, distribution, population trends, animal behaviour, and contaminants/disease. By chance, we cover four of those, but ignored contaminants/disease as a specialist field, of lesser interest in New Zealand where all mammals are introduced pests. We would add the behaviour of motorists (in New Zealand most aim to kill possums, while in Australia they avoid them), and the need to check observer identifications.

Traffic quadrupled from 1.04 to 4.33 million registrations during this study, 1963-2018 (Motor Industry Association 2019), and appears to have had little effect. Although Fig. 6 shows a significant increase with increasing traffic, this may be caused by South Island having both low traffic and low populations; neither island gives a significant correlation with increasing traffic on its own, or combined in relation to time. At most, road-kill may have doubled, and much of the increase is due to possums, which were still expanding in range in the 1980s, and the rabbit increase following the lack of efficient control after 1987-89. This unexpected result might be due to fear of crossing busy roads, or reflect a constant proportion of the animals present on roads being at greater risk: juveniles; sick, wounded, or stupid individuals. Once these are weeded out, no more are killed. An additional possibility is that evolution (cultural and genetic) has fostered adaptations to the increase in traffic, e.g. becoming nocturnal, when there are fewer cars (discussed below - Changes in behaviour).

Holisova & Obrtel (1986) found no difference in road-kill comparing 15768 km of motorway and 40701 km of roads in Czechoslovakia. In the UK "We found no correlation between changes in traffic flow and road counts of hedgehog or rabbit" (Bright et al. 2015), although George et al. (2011) found a negative correlation, with fewer rabbits killed as traffic density increased. Grilo et al. (2015), working in Portugal, agree with the negative correlation, but with different thresholds for rabbits and hedgehogs. In Canada, Clevenger et al. (2003) also found a consistently higher bird and mammal road-kill on roads with lower traffic volume and speed. On the other hand, Orlowski & Nowak (2006) found road-kill (including hedgehogs but not rabbits) increased sevenfold from traffic flows of about 400 to 10000 vehicles per day in Poland. A general review of bird road-kill in Europe (Erritzoe et al. 2003) found more were killed on high-speed roads, but a careful three-year study in Finland came to the opposite conclusion (Husby 2016).

For New Zealand roads, Brockie et al. (2009) found a slight increase in corpses per 100 km, from 21 at 1- 2000 vehicles per day, to 30 at 16-17000 vehicles per day; but, with intermediate traffic volumes ranging from 9 to 49 corpses per day, the correlation is insignificant compared to other sources of variation. Sadlier & Linklater (2016) confirmed a positive relationship with traffic, but made no allowance for busy roads being wider, thus increasing the area counted, or speed of traffic.

How representative road-kills are of the population present depends on the species; those with patchy distributions and low densities require more effort to reach a stable figure, and that figure relates to the fraction of the population at risk on the road. For magpies and rabbits the summer peaks are of inexperienced juveniles, as can be seen from their colour and size respectively, but many hares and pukeko (*Porphyrio porphyrio*) are adults on aggressive or mating chases. Starlings are the commonest species searching roads and verges for insects but are traffic-wise and even juveniles are seldom hit by cars. In New Zealand only 1% of 309 birds killed were starlings (Flux 2019).

Many papers calculate how long an animal would take to cross a road, ignoring the fact that birds and hedgehogs are often there to feed on insects killed by cars, and others, including mustelids, cats, birds and hedgehogs, are scavenging road-kills (Fig. 1a). In New Zealand only the herbivores (possums, rabbits and hares), normally cross roads directly to get to food on the other side. Individuals attempting to establish a home range with a road down the middle probably die young; and high numbers are killed crossing a newly opened motorway (JECF personal observations, and see also Havlin (1987)). On the first day a new 17 km motorway near Wellington was opened, six pukeko were hit (Dr B Brockie pers. comm. 31 February 2022), 18 times more than the average on the main road it replaced (Sadlier & Linklater 2016).

Even for a species like humans, where the road-kill is completely accurate, it is not possible to calculate the population of a town from these statistics. The accuracy of counts varies between species: possums are obviously easier to see than rats because they are larger, but the distinctive chestnut colour of weasels makes them far more conspicuous than rats, although they are smaller. Bias in the proportions identified should be reasonably constant for a single observer, and could be measured by cycling or walking the same route; but motoring is the simplest way to amass data. Cars do not distinguish between species (subject to presumably constant specific avoidance behaviour) so road-kills offer a useful index of the relative proportions of species present, and any major changes with time.

### Reliability of road-kill counts

The key to reliability is repeatability, but even for a single observer the variability was very high. Since the mammals were mainly nocturnal, counts would be expected to be at a maximum at dawn, and decline during the day as bodies were removed by scavengers; birds should show the reverse pattern as more are killed during the day. The mammalian scavengers (cats, mustelids, rats and hedgehogs) hunt mostly by night, as does the morepork owl (*Ninox novaeseelandiae*); the other birds, harriers (*Circus approximans*) and black-backed gulls (*Larus dominicanus*) only by day. As shown above, counts were so variable that no confidence could be placed on individual journeys, so we chose to accumulate high mileage. Brockie et al. (2009) obviously encountered the same problem in hedgehogs: "Between 1998 and February 1990 (sic!) the mean number rose suddenly to 11.5 ... range 1-31." They had the opportunity to measure repeatability on the 398 km of road (Lower Hutt – Waiouru, and Hamilton – Albany) counted in both directions, but do not report this.

Having more than one observer would increase variability. Brockie et al. (2009) claim to measure "the performance of different observers" by comparing their own 1984 counts of hedgehogs from Awanui to Lower Hutt with those of Morris & Morris (1988), made in 1987 on the same route (their Table 3). Both were single journeys, and knowing the 1-31 range quoted above for 35 km, they still assume that similar numbers would be available to be counted on a single trip three years later. The different totals (116 and 135) they attempt to explain by "a genuine, exceptionally large increase in population density in this area". Which area is not specified; but by removing it from the analysis "the general correlation between the two different observers' sets of figures rises to r = 0.84." If the area was Taupo to Waiouru, where they recorded one hedgehog, and wrongly quote Morris & Morris (1988) as nine in mistake for zero, removal is required; and the respective totals become 116 and 126. Morris & Morris's (1988) version is that they found fewer, not more, hedgehogs than "R.M. Sadleir and R.E. Brockie (unpublished data)" on this route.

We suggest that the performance of different observers can be better assessed by having them in separate cars doing the same route 100 m apart, thus ensuring they are attempting to count the same things; and having observers on foot, to check what the correct answer is. Perhaps the most accurate and practical system was designed by Hansen (1982) who covered 23,299 km in Denmark between 1957-1981 on a moped, stopping to remove every corpse as it was identified: mice were the most common mammals.

The recent paper by Sadleir & Linklater (2016) provides a remarkable check on observer bias. Unknown to us, Sadleir had recorded road-kills on 92 trips between Lower Hutt and Otaki, between 2009 and 2014, a time range spanned by our counts on the same road. The results overall are close: Per 4000 km, with ours in brackets, 957 (991) mammals, of which 93.4% (90.3%) were hedgehogs, rabbits and possums, and 338 (456) birds. However, the disparity in species identified is disturbing: hedgehogs 465 (103), rabbits 276 (493), possums 153 (287), cats 39 (9), and hares 2 (51). Flux is confident that the 51 hares recorded is a minimum, having stopped to sex, age, and measure them all (only two were small enough to be mistaken as rabbits), leaving the bodies at the side of the road; and it agrees with the 32-56 range over the rest of New Zealand in recent years. Hence Sadleir's count of two seems a result of misidentification as cats, since hares are the same size, and it would explain his remarkably high cat numbers. Sadleir & Linklater (2016) realised their hare numbers were lower than Brockie et al. (2009) had found, and suggest this was because of "reduced distances through farmland" which is clearly untenable from our counts. A more likely explanation, that Sadleir was red/green colourblind, as found in 8% of men, was confirmed by Dr A Moeed (pers. comm. 2019). This would render tawny species (hares, stoats, and weasels) grey/brown, resulting in hares boosting cat numbers; and explain the low proportion of mustelids (2 v.10). It might also explain the high hedgehog: rabbit ratio if Sadleir was unable to see the chestnut/tan colour on the back of rabbit's necks and counted baby rabbits as hedgehogs. On the other hand, it is hard to understand the difference in possums (here averaging 2.5 kg). Both of us have long experience in doing road counts (cf. Collinson et al. 2014), so such major discrepancies are alarming. It demonstrates the importance of blind trials, and of recognising the effects of colour blindness, especially as New Zealand has far fewer species to identify compared with other countries (cf. Israel, with three species of hedgehogs, four small cats and 33 rodents (Ferguson 2002)).

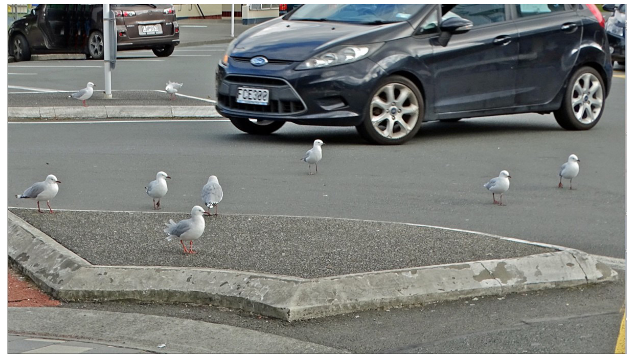

**Figure 7.** Red-billed gulls have learned to walk among moving cars, use traffic islands, and seldom have to fly.

### Seasonal variation

There is a clear decline in road-kills in winter, as expected because most species will be at their lowest population levels then, although the longer night might be expected to increase mammal vulnerability. The dip in midsummer is probably real, and matches almost exactly the pattern Haigh (2012) found in road-killed mammals (predominantly rabbits) surveyed monthly for three years (total 45815 km) in Ireland. Her suggestion that the first (summer) peak coincides with breeding, and the second (autumn) one with dispersal of young, seems applicable here, and holds for most birds and mammals surveyed recently in Britain (Raymond et al. 2021).

### Impact of road-kill on populations

In New Zealand there has been little concern about the effect of road-kills, because most are of introduced mammalian pests and exotic birds. Indeed, Sadleir & Linklater (2016) suggest roads could assist in reducing pest numbers, form boundaries around cleared areas, and be used to monitor re-invasion. At present there is no population, even of the commonest road-kills (possums and rabbits), that appears to be adversely affected.

Harriers are the most likely native bird to be threatened: except for the breeding season when they are restricted to a home range of about 900 ha (Seaton et al. 2013), all of the population would have access to road-kill, which makes up a large part of the diet. At present, the benefits appear to outweigh the risks (Flux 2019).

### Changes in behaviour

The few road counts in the 1950s by Dr K Wodzicki, and our earliest 1960s counts, included large numbers of live animals (see Introduction). This pattern is backed up by a questionnaire circulated in December 1960 to Rabbit Boards; Agriculture Stock Instructors; Internal Affairs, National Park, and Forest Service rangers; and Acclimatisation societies, to establish the distribution and status of mustelids following 10 years of intensive rabbit control (Marshall 1963). One question asked "How many of each species have you seen in the last six months?", "Alive" and "Dead on the road". This data was not analysed, and is worth recording. In the North Island 106 respondents answered the question, and 130 in the South Island, so the following totals are per 100 replies: North Island, ferrets 194 live, 101 dead; stoats 475 live, 88 dead; weasels 148 live, 26 dead. South Island, ferrets 453 live, 178 dead; stoats 415 live, 85 dead; weasels 54 live, 4 dead. Clearly stoats were evenly spread over both islands, ferrets commoner in the South Island, and weasels commoner in the North Island. The proportions of road-kills increase with body size, but far more live animals were being seen than in later years.

Apart from the apparently innate ability of starlings to avoid cars, some species are able to learn. This is clearly demonstrated by about 20 red-billed gulls (*Larus novaehollandiae*) fed from cars in Waterloo, Lower Hutt (Fig. 7). At this busy intersection, they look carefully before walking across the road and make use of "islands" where they are safe from vehicles driving at up to 50 kph. Only two were found hit by cars in the past five years. Several other species are adapting to urban life – even European hares are now resident in many German and Danish cities (Kohler 2013, Mayer & Sunde 2020).

## Conclusions

Road-kills offer a convenient index of changes in distribution, relative numbers, and behaviour of nocturnal mammals over wide areas, hard to obtain in any other way. However, attempts to translate such counts to population estimates, or extrapolations to calculate total numbers killed by cars per year, are dangerous. Slater (2002) found scavengers (mainly cats) remove 12-16 times the number of corpses left to be counted, a timely reminder of how little we know of what is happening on our roads. (These cats, of course, are blamed for killing the animals when they carry them home (Flux 2017)). In the UK, 24 different organisations are assessing the status and distribution of mammal populations, some using road-kill data (Battersby 2005), others demonstrating fascinating results from six years of "citizen science"

(Raymond et al. 2021). Bil et al. (2020) review national wildlife road-kill reporting systems operating in Europe. Pest monitoring is recommended as an integral part of pest control in New Zealand (Ruffell et al. 2015). With so few species to identify, road counts could be an ideal topic for expanding along the lines suggested by Brockie et al. (2009), using a "citizen science" network to provide useful ecological data, and a pest monitoring system independent of the usual trap/tracking indices. However, the discrepancy between our results and those of equally experienced professional zoologists (Sadleir & Linklater 2016) demonstrates the importance of checking the accuracy of identifications, possibly using smart-phones as Vercayie & Herremans (2015) suggest.


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