

## Predator indices from artificial nests and tracking tunnels: do they tell the same story?

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**Abstract:** Artificial nests and tracking tunnels are alternative predator encounter devices that can be used to predict predation risk to native species. Tracking tunnels are used ubiquitously in New Zealand, whereas artificial nests are used extensively overseas. To assess whether these devices give similar information about predation risk, we compared tracking tunnel and artificial nest data from 16 native forest fragments in the central North Island over two summers. The fragments were expected to vary in predation risk due to rat control in some fragments, and possibly due to habitat differences caused by stock grazing. We modelled the ‘survival’ of both types of devices, where ‘survival’ is defined as the probability of not being tracked or bitten by a rat over a set period (possum bites were also considered to indicate nest failure, but were rare). We used a Bayesian hierarchical framework that allowed for random effects of individual devices as well as fragments, and random time effects. Data from both devices showed clear effects of rat control, but otherwise gave different results. Tracking tunnel survival varied greatly among fragments in the absence of control, with survival generally higher in grazed than ungrazed fragments, whereas no such pattern occurred in artificial nest survival. Different habitat variables explained variation in survival at both site and fragment level; understorey density was the only useful predictor of tracking tunnel survival, whereas artificial nest survival was correlated with canopy cover, vegetation cover at 1.5 m, and supplejack presence. When both data types were modelled simultaneously, the tracking tunnel data improved capacity to explain the artificial nest data whereas the reverse was not true. Consequently, while it is unknown whether the additional inter-fragment variation detected by tracking tunnels indicates real variation in predation risk, we currently see no reason to prefer the more labour-intensive artificial nests.

**Keywords:** artificial nest; exotic predator; index; *Rattus rattus*; survival; tracking tunnel

### Introduction

Introduced mammalian predators have decimated much of New Zealand’s native flora and fauna (King 1984; Towns & Daugherty 1994; Innes et al. 2010), leading to a proliferation of predator control programmes to restore native populations (Saunders & Norton 2001). A key component of these programmes is the ongoing monitoring of the targeted mammal populations to assess the effectiveness of control. This monitoring is done through a set of indices thought to provide useful information on the risk levels posed by the predator populations (e.g. Ward-Smith et al. 2004; Moorcroft et al. 2010).

In New Zealand, rodents and mustelids are usually monitored using footprint tracking tunnels to assess effectiveness of predator control (King & Edgar 1977; Innes et al. 1995; Blackwell et al. 2002). Tracking tunnel data are easy to collect, and standard protocols have been developed for their use (Gillies & Williams 2001). Rat tracking rates were found to be a useful predictor of nest success in North Island kōkako (*Callaeas cinerea wilsoni*; Innes et al. 1999), and subsequent mainland island projects have typically aimed for <5% tracking based on that study. Recent research has also shown rat tracking rates to be a good predictor of survival, reproduction and nest success of North Island robins (*Petroica longipes*) (Armstrong et al. 2006; Parlato & Armstrong 2012).

Outside of New Zealand, tracking tunnels are rarely used, and predation risk to birds is commonly indexed using artificial nests (King et al. 1999; Buler & Hamilton 2000; Zanette & Jenkins 2000). Like tracking tunnels, artificial nests

allow data to be collected fairly quickly, and allow risk from different predators to be indexed due to distinguishing marks left on artificial eggs. Because artificial nests can be used to index predation by birds, they have been widely used to assess edge effects and other habitat-related changes in nest success thought to be caused by predatory birds (Batáry & Báldi 2004; Moore & Robinson 2004; McKinnon et al. 2010). However, use of artificial nests could potentially be advantageous in any situation where nest success is the key parameter of interest, as the index is designed to closely mimic real nest predation. In addition, extensive international literature can be drawn on when planning and interpreting artificial nest studies. Consequently, artificial nests have recently been used to index predation risk in several New Zealand studies (Whyte et al. 2005; Smith et al. 2008; van Heezik et al. 2008; Lewis et al. 2009). Lewis et al. (2009) compared survival of artificial nests and North Island robin (*Petroica longipes*) nests among nine sites around the North Island of New Zealand, where ‘survival’ of an artificial nest means its eggs were not bitten by a predator over a set time period. They found artificial nest survival estimates based on rat and possum (*Trichosurus vulpecula*) tooth marks explained 64% of the variation in robin nest survival among sites.

At present it is unknown whether tracking tunnels or artificial nests are more effective for predicting predation risk in New Zealand. Although intuition suggests artificial nests would be best for predicting nest success of native birds, this is not necessarily the case. Tracking tunnels and artificial nests are alternative types of predator encounter devices, and the probability of a device not being encountered (e.g.

tracked or bitten) is akin to the probability of a prey animal surviving some period among a predator population (Leslie & Davis 1939). The 'survival' probability of a predator encounter device will be inversely related to predator density and activity, and is therefore expected to predict several demographic rates of prey populations reflecting survival processes, e.g. nest survival, productivity, adult survival or population growth rate. In principle, it would be useful to compare the performance of tracking tunnels and artificial nests at predicting multiple demographic rates of different prey species in different scenarios. However, a simpler first step is to compare the patterns of predation risk over space or time as suggested by the two indices (Blackwell et al. 2002). If the patterns are concordant, then it is sensible to simply use the index that gives greater precision for less effort. Only if the indices suggest different patterns of variation is it then necessary to assess which pattern is better correlated with the population parameters of interest.

We compared tracking tunnel and artificial nest survival among a set of forest fragments expected to vary in predation risk due to rat control and possibly due to differences in habitat modification caused by stock grazing. Our study aimed to (1) estimate variation among forest fragments in survival of both tracking tunnels and artificial nests, including effects of rat control, (2) assess the concordance in this among-fragment variation between the two indices, and (3) assess whether variation among fragments could be explained by environmental variables thought to be associated with habitat suitability for rats, and whether the performance of these predictor variables was similar for tracking tunnels and artificial nests.

## Methods

### Study area and sampling design

We collected data from 16 native forest fragments ranging from 2 to 56 ha (Table 1) scattered over 15 000 ha of pastoral landscape near the town of Benneydale in the central North Island (see Boulton et al. (2008) for map of the landscape). These fragments all have mature regenerated podocarp-broadleaf forest dominated by tawa (*Beilschmiedia tawa*). However, they vary greatly in understorey density due to stock access, and can be divided into 'grazed' and 'ungrazed' fragments except for two fragments that have both grazed and ungrazed portions due to being partially fenced (Table 1). Rats were controlled in some fragments each year as part of a larger research programme. This control involved kill trapping over 10 consecutive nights starting in late August, followed by poison baiting with bromodialone cereal blocks until March. These cereal blocks were placed in bait stations at 50-m intervals throughout the selected fragment. All rats trapped in these fragments (>500) have been ship rats (*Rattus rattus*), suggesting this is the only rat species present. The 16 fragments for this study were chosen to represent a range of habitat types in terms of vegetation and topography, while including fragments with and without rat control. Previous research had shown that in the absence of rat control, rat tracking tends to be much lower in grazed than ungrazed fragments (Boulton 2006).

Sampling occurred over summer in both 2009/10 (December–February) and 2011/12 (November–January). Fourteen of the 16 fragments were sampled both summers, and the other two fragments sampled in one summer each

(Table 1). The reason for one fragment being replaced in 2011/12 is that it was subject to a new rat control regime as part of another project.

Tracking tunnels and artificial nests were both placed near permanent grid points. There is one grid per fragment, except for the two partially grazed fragments, which have separate grids in the grazed and ungrazed portions. Grid points were 50 m apart, with each grid having either 16 points (4 × 4), 9 points (3 × 3) or 5 points (cross) as space permitted (Table 1). This gave a total of 190 sampling sites among the 17 grids in each of the two summers.

The construction, placement and monitoring of artificial nests followed protocols developed by Lewis et al. (2009), who constructed the nests and eggs to mimic those of North Island robins. Latex gloves were worn by fieldworkers during all construction and handling of nests and eggs to avoid transferring human odour that might attract or deter predators. The nests were made of leaf litter and moss held together with a plastic cup and bird netting, and the two eggs per nest were made of Sculpey™ odourless modelling clay shaped with a silicon mould. Eggs were tied into nests to prevent predators from removing them. All nests were made of fresh material in 2009/10, whereas about two-thirds (131/190) of nests were reused in 2011/12 and the remainder made fresh (the reused nests were kept indoors for the interim 2 years). The proportion of reused nests was approximately equal in all fragments, and nest age was included as a factor in our analysis. All eggs were made from new clay in both years. At the start of each sampling period, a nest was tied in place in a tree fork or tree fern crown 1–2 m from the ground at a distance of 2–10 m from each grid point.

Standard tracking tunnels were placed within 2 m of each grid point following New Zealand Department of Conservation protocols (Gillies & Williams 2001), and had been in place for at least 3 years when the present study commenced. Tunnels were baited at both ends with peanut butter, and tracking papers with a central ink pad were placed inside the tunnels to record tracks.

We scored seven habitat variables (see below) in the 15-m radius around each grid point, deliberately choosing variables that we believed might be useful predictors of rat activity based on previous experience at the study site and other studies (Christie et al. 2006, 2009).

### Data collection

Artificial nests were checked every 7 days for up to 4 weeks, with these checks taking place over a 3-day period on each occasion. We recorded whether the nest had 'survived' the week or 'failed' on each occasion, and discontinued checks once failure had occurred. Following Lewis et al. (2009), nest failure meant one or both eggs had rat or possum tooth marks. Although possum tooth marks are obvious, it was often unclear in the field whether marks were from rats. If it was unclear whether eggs had been marked by rats, the eggs were removed for later checking in the laboratory, and replaced by new eggs that were checked in subsequent weeks. If the marks turned out to be from rats, the nest was considered to have failed when the marks were found, and the data from subsequent checks were discarded. To avoid potential biases when eggs were checked in the laboratory, the observers were unaware of which fragments the eggs came from when they did these checks. Although it was usually clear under the dissecting microscope whether marks were from rats, incisor imprints were measured using vernier callipers to distinguish rat and mouse imprints. These

**Table 1.** Characteristics of forest fragments, number of sampling stations where tracking tunnels and artificial nests were placed, and whether rats were controlled each year of sampling.

Fragment	Area (ha)	Grazed	Stations	Rat control	
				2009/10	2011/12
12 <sup>th</sup>	2	Y	5	N	N
Dennis	13	N	16	Y	Y
Dizzy <sup>1</sup>	56	Y	9	N	N
		N	9	N	N
Fatty <sup>1</sup>	14	Y	5	N	N
		N	16	N	N
Flag	8	Y	9	N	N
Jacks <sup>2</sup>	19	N	16	Y	-
Little Tutu	2	N	5	N	Y
Lucky	6	Y	9	N	N
Mangaruhe1 <sup>2</sup>	34	N	16	-	N
Skinny	39	N	16	N	N
T91	18	N	16	N	N
Te Hape Iti	9	Y	16	N	N
Te Hape Toru	9	Y	9	Y	N
Teds	6	N	9	N	N
Tutu	5	N	16	N	Y
Twisted	6	N	9	Y	N

<sup>1</sup> These two fragments had grazed and ungrazed portions due to partial fencing, so these portions were sampled separately.

<sup>2</sup> The fragment 'Jacks' was involved in a separate project in 2011/12, so was replaced with Mangaruhe1 in the second year.

were compared to measured imprints from lab mice, skulls of wild mice, and from rats visiting tracking tunnels (eggs were placed in tracking tunnels to distinguish whether it was a rat or mouse that bit the egg, and this was done at a different time from when tracking data were collected).

Tracking tunnels were run on two occasions in both field seasons, once before the artificial nests were put out and once after the artificial nest experiments were completed. The rationale for this design was to avoid putting peanut butter out during the artificial nest monitoring period, as this lure may have confounded the artificial nest data. On each occasion we left the tunnels out for one night in all fragments simultaneously, and recorded whether each tunnel was tracked by a rat. There was no rainfall on these nights.

The seven habitat variables scored at each grid point were: (1) presence of supplejack (*Ripogonum scandens*) within 15 m; (2) presence of a stream within 15 m; (3) dead tree fern cover at ground level; (4) vegetation cover at 1.5 m from the ground; (5) canopy cover; (6) understorey density; and (7) canopy height. Variables 1–2 are dichotomous (0 or 1), variables 3–5 were scored subjectively as proportions from 0 to 1, and variables 6–7 were scored subjectively into three classes (0, 0.5, 1). The three canopy-height classes were approximately 0–5 m (0), 5–15 m (0.5), and >15 m (1). The subjective variables (3–7) were scored independently by two observers (KS, ABH) and averaged.

### Analysis

Artificial nests and tracking data were fitted to generalised linear mixed models using the Bayesian updating software WinBUGS 1.4 (Spiegelhalter et al. 2003). In both cases the dependent variable was binary, and indicated whether or not a nest or tunnel had survived each interval (one week or one night respectively). We used a log(-log) link function to model survival because this function is theoretically sensible for the indices (Appendix 1). In addition, preliminary analyses showed it gave a better fit to the data than the standard logit

**Table 2.** Parameters for survival of tracking tunnels and artificial nests in forest fragments near Benneydale, central North Island. A tracking tunnel is considered to 'survive' if not tracked by a rat and an artificial nest is considered to 'survive' if eggs are not bitten by a rat or possum. a = average log(-log) probability of a tunnel surviving one night or an artificial nest surviving one week without rat control, b.cont = effect of rat control, b.old = effect of using an old nest rather than fresh nest, s.grid = SD (standard deviation) among grids (usually one per fragment; Table 1), s.site = SD among individual tunnels or artificial nests, and s.time = SD among sampling times (nights for tracking tunnels, weeks for artificial nests).

Data	Node	Mean	SE	2.5%	Median	97.5%
Tracking tunnels	a	1.05	0.83	-0.81	1.10	2.67
	b.cont	2.97	0.49	2.08	2.94	3.99
	s.grid	1.24	0.33	0.75	1.19	2.00
	s.site	0.59	0.16	0.30	0.59	0.90
	s.time	1.58	1.35	0.51	1.23	4.75
Artificial nests	a	1.99	0.35	1.30	1.99	2.68
	b.cont	1.24	0.34	0.57	1.24	1.92
	b.old	-0.59	0.24	-1.09	-0.58	-0.13
	s.grid	0.49	0.17	0.21	0.47	0.88
	s.site	0.54	0.21	0.14	0.54	0.93
	s.time	0.70	0.30	0.31	0.64	1.48

**Table 3.** Parameter estimates for effects of habitat variables on log(-log) probability of a tunnel surviving one night or an artificial nest surviving one week. All variables ranged from 0 to 1, so the means shown are the estimated effects of a variable changing from its minimum to maximum. Variables were added one at a time to the models shown in Table 2, and the effect on the predictive value assessed using  $\Delta$ DIC (change in Deviance Information Criterion, where a negative value shows an improvement in the model). Variables with suffix ‘site’ apply to the 15-m radius around individual grid points where tunnels and nests were placed, whereas ‘ave’ refers to the average for the grid. Density = understory density score, cancover = canopy cover, vegcover = cover of green vegetation at 1.5 m height, pongacover = cover of dead tree fern fronds at ground level, canht = canopy height score, supplejack = supplejack present, stream = stream present within 15 m.

Data	Variable	Mean	SE	2.5%	Median	97.5%	$\Delta$ DIC
Tracking tunnels	density.site	-1.13	0.41	-1.97	-1.12	-0.35	-3.80
	density.ave	-2.41	1.30	-4.98	-2.40	0.21	-1.66
	cancover.site	1.29	0.66	-0.03	1.30	2.58	-1.11
	stream.site	0.29	0.25	-0.19	0.29	0.77	-0.50
	vegcover.ave	-2.86	3.04	-9.75	-2.56	2.58	-0.31
	canht.site	0.52	0.27	-0.01	0.52	1.07	-0.09
	pongacover.site	0.12	0.52	-0.87	0.11	1.17	0.33
	vegcover.site	-0.43	0.41	-1.28	-0.42	0.35	0.34
	pongacover.ave	-2.50	2.53	-7.59	-2.49	2.37	0.36
	stream.ave	-1.48	1.34	-4.34	-1.45	1.14	0.44
	supplejack.ave	-0.49	0.94	-2.34	-0.51	1.45	0.47
	canht.ave.site	2.52	1.26	0.14	2.48	5.05	0.76
	supplejack.site	0.12	0.28	-0.46	0.12	0.65	2.26
	cancover.ave	-1.29	3.83	-9.42	-1.35	6.46	2.36
Artificial nests	cancover.ave	5.14	2.40	-0.01	5.26	9.76	-3.14
	vegcover.ave	-3.95	1.25	-6.64	-3.87	-1.75	-3.11
	supplejack.site	-0.43	0.27	-0.97	-0.42	0.08	-2.62
	stream.ave	1.25	0.64	-0.06	1.26	2.49	-1.26
	density.site	-0.57	0.35	-1.27	-0.57	0.13	0.18
	stream.site	0.33	0.24	-0.13	0.33	0.80	0.29
	supplejack.ave	0.63	0.45	-0.24	0.61	1.54	0.44
	density.ave	-0.83	0.68	-2.17	-0.84	0.59	0.60
	pongacover.ave	-0.72	1.45	-3.49	-0.74	2.26	0.62
	pongacover.site	0.62	0.52	-0.36	0.61	1.66	1.14
	vegcover.site	-0.63	0.42	-1.48	-0.63	0.16	1.44
	canht.ave	0.87	0.69	-0.48	0.87	2.26	1.50
	canht.site	0.30	0.27	-0.22	0.29	0.82	2.65
	cancover.site	-0.82	0.63	-2.11	-0.82	0.37	3.11

link function, as indicated by lower DIC (Deviance Information Criterion; Spiegelhalter et al. 2002).

We first modelled the two data types separately to assess the effects of rat control, grid, individual tunnel or nest, and time (sampling occasion). For artificial nests we also assessed the effect of using old nests rather than fresh nests (Table 2). Rat control and nest age were dichotomous fixed effects, whereas the other variables were treated as normally-distributed random effects. We also fitted models with grid and time as fixed effects, but the random-effect models had lower DIC. We also initially used fragment rather than grid as a factor, including a distinction between grazed and ungrazed grids (Table 1), but found that using grid as a factor lowered DIC.

We then did an exploratory analysis with both types of data to assess whether variation in survival among fragments could be explained by any of the seven habitat variables. This meant assessing whether DIC was reduced by adding the habitat variable (Table 3). We considered each habitat variable in two forms: (1) the original site-specific measurements to reflect habitat variation around individual artificial nests and tracking tunnels; and (2) the average scores for the grid to reflect wider-scale habitat quality.

Finally, we modelled the artificial nest and tracking tunnel data simultaneously to assess the concordance between the two indices both at the whole-grid scale and individual-sampling-site scale. This involved fitting models of the form

$$\log(-\log(s_{an})) = k + \log(-\log(s_{tt}))$$

where  $s_{an}$  is the probability of an artificial nest surviving one week,  $s_{tt}$  is the probability of a tracking tunnel surviving one day, and  $k$  is a parameter reflecting the different time intervals and different predator encounter rates for these devices (see Appendix 1 for theoretical basis of this relationship). We considered models where this relationship applied to both grid and site effects, or grid effects only, and compared these to the null model where survival of artificial nests and tracking tunnels was assumed to be independent (Table 4).

Uninformative priors were used for all parameters. Priors for fixed effects were normally distributed with mean 0 and precision  $1.0E-6$ , and priors for standard deviations of random effects were uniformly distributed from 0 to 1. All models were run with a burn-in of at least 4000 samples, with two chains used to check convergence, then at least 30 000 samples used to obtain posterior distributions.

**Table 4.** Comparison of models for the relationship between tracking tunnel and artificial nest survival among grids in forest fragments near Benneydale, central North Island. ‘Independent’ means that tracking tunnel and artificial nest data were modelled independently (parameter estimates shown in Table 2), ‘shared grid effects’ mean the random grid effects were the same for the two data types, and ‘shared grid+site effects’ means random effects of individual grid points were also taken to be the same for the two data types.  $\bar{D}$  = posterior mean of the deviance,  $\hat{D}$  = deviance with parameters set at posterior means,  $pD$  = effective number of parameters, DIC = Deviance Information Criterion (lower is better).

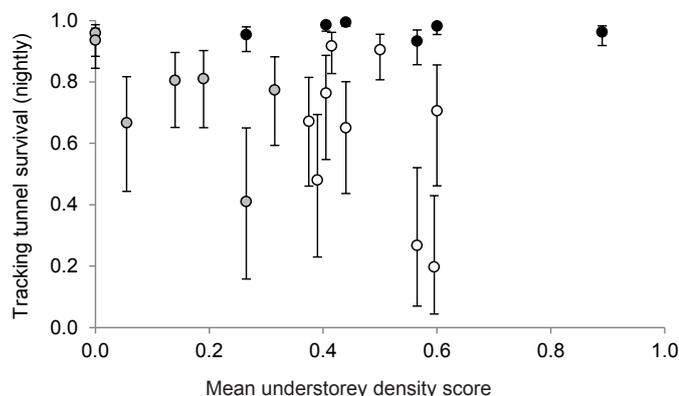
Model	Data	$\bar{D}$	$\hat{D}$	$pD$	DIC
Independent	Artificial nests	808.62	754.86	53.76	862.38
	Tracking tunnels	601.59	540.58	61.01	662.60
	Total	1410.21	1295.44	114.77	1524.98
Shared grid effects	Artificial nests	777.19	699.98	77.21	854.41
	Tracking tunnels	630.62	581.24	49.38	680.00
	Total	1407.81	1281.22	126.59	1534.41
Shared grid+site effects	Artificial nests	825.00	785.98	39.03	864.03
	Tracking tunnels	642.95	600.95	42.00	684.95
	Total	1467.95	1386.93	81.03	1548.98

## Results

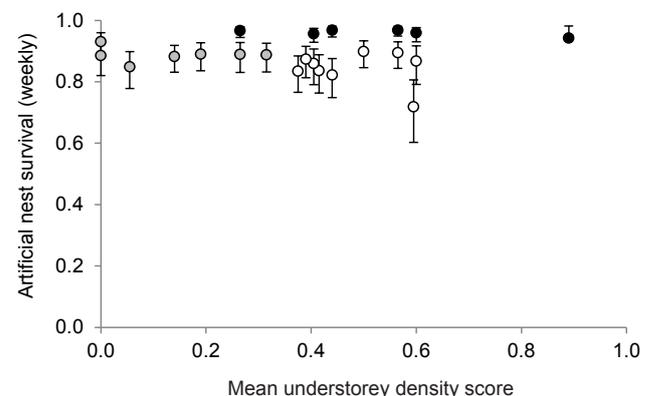
Overall, 52% (198/380) of artificial nests ‘survived’ for 4 weeks (i.e. eggs were not bitten by a rat or possum) in the 16 fragments over the 2 years, with a weekly survival probability of 0.83. Of the 182 failures, 170 (94%) were due to rats and 12 to possums. In comparison, 69% of tracking tunnels ‘survived’ the night (i.e. were not tracked by a rat) over the four sampling occasions over the 2 years.

Survival of artificial nests and tracking tunnels were significantly affected by all factors considered in the initial models (Table 2). That is, the posterior distributions of the fixed effects do not overlap zero, the posterior distributions for the random effects do not approach zero, and removing any of these factors resulted in an increase in DIC. Rat control

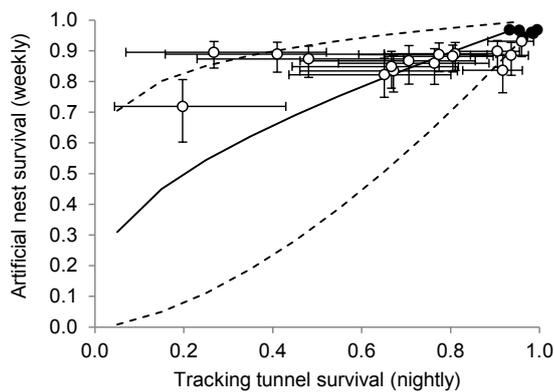
had the strongest effect, as survival of both devices was consistently high in fragments with rat control (Fig. 1, Fig. 2). For artificial nests, reused nests had lower survival than fresh nests. There was clear temporal variation in survival of both devices, but there were no clear patterns in terms of yearly or seasonal variation. There was also clear spatial variation, both among grids and among individual tracking tunnels and artificial nests. However, the relative variation at these two spatial scales differed between the two devices. Tracking tunnels showed much greater variability among whole grids than individual tunnels, whereas artificial nests showed similar variation at these two scales (Table 2). Consequently, there is much clearer variation among grids (and therefore forest fragments) for tracking tunnel survival than artificial nest survival (Fig. 1, Fig. 2).



**Figure 1.** Estimated probabilities of a tracking tunnel surviving one night (not being tracked by a rat) in forest fragments near Benneydale, central North Island, based on a generalised linear mixed model fitted to the data (Table 2). Two fragments were partly fenced from livestock, so had separate sampling grids in the grazed and ungrazed portions. Grey and white dots show grazed and ungrazed grids respectively, and black dots show fragments with rat control. Four fragments were sampled both with and without control, hence there are 22 points shown for the 18 grids. Error bars show standard errors.



**Figure 2.** Estimated probabilities of an artificial nest surviving one week (eggs not bitten by a rat or possum) in forest fragments near Benneydale, central North Island, based on a generalised linear mixed model fitted to the data (Table 2). These estimates assume fresh nests rather than reused nests. Other conventions as for Fig. 1.



**Figure 3.** Relationship between tracking tunnel and artificial nest survival, based on estimates shown in Figures 1–2. The lines show the mean and 95% credible intervals for the model  $\log(-\log(s_{an})) = k + \log(-\log(s_{tt}))$  fitted to the data where random grid effects are taken to be independent for tracking tunnels and artificial nests (Table 4). Black dots show fragments with rat control.

Some of the measured habitat variables appeared to be useful predictors of variation among grids, but these variables differed for tracking tunnels and artificial nests. The understorey density score at grid points was the only habitat variable that clearly helped explain variation in tracking tunnel survival, with survival tending to be lower at denser sites; this can be seen by the negative  $\Delta\text{DIC}$  value (Table 3). All other models with habitat variables added were within two DIC units of the models excluding them, meaning the effects can be considered ambiguous. However, the average density per fragment was an almost equally good predictor, and explains a reasonable proportion of the variation in tracking among grids (Fig. 1). In contrast, the habitat variables explaining variation in artificial nest survival were average canopy cover, average vegetation cover, and supplejack presence, and understorey density was not a useful predictor (Table 3).

There was some correlation between the two indices, both because survival was consistently highest where rats were controlled and because the same fragment ('T91') had the lowest survival of both tracking tunnels and artificial nests (Fig. 3). However, excluding those points, there was no significant variation in artificial nest survival among grids (Fig. 3) and therefore no correlation with tracking tunnel survival. There appeared to be no relationship whatsoever ( $r^2 = 0.05$ ) between the estimated random effects of tracking tunnels and artificial nests at individual grid points. Consequently, when tracking tunnel and artificial nest data were modelled simultaneously, the model with shared random effects for individual grid points had very poor support (Table 4). The best model overall (lowest total DIC) was the one where tracking tunnel and artificial nest data survival were assumed to be independent (Table 4). However, the model with shared random grid effects had the lowest DIC for the artificial nest data (Table 4). This means that the tracking tunnel data improved predictions about artificial nest survival whereas the artificial nest data impaired predictions about tracking tunnel survival, suggesting the tracking tunnel data have much greater power.

## Discussion

Tracking tunnels and artificial eggs do not convey the same information regarding predation risk. Although both indices

suggested rat control reduced predation risk to low levels, there was otherwise little correlation between them, with tracking tunnels suggesting substantial variation among fragments that was not detected by artificial nests. The habitat variables that explained variation among fragments also differed for the two indices.

Although artificial nests mimic reality more closely if the aim is to predict nest success, our results suggest that tracking tunnels are a more sensitive measure of variation in predation risk among habitats. It is currently unknown whether the variation detected is correlated with real nest success or other survival measures, and it is possible that the variation reflects habitat-related differences in predator behaviour that are unrelated to predation risk (Blackwell et al. 2002). However, it is notable that the tracking tunnel data improved capacity to predict artificial nest survival, whereas the reverse was not the case, suggesting the tracking tunnel data were more powerful. This partly reflects the higher predator encounter rates with tracking tunnels, probably because of the scent lure from the peanut butter. The fact that nightly tracking tunnel survival (average 69%) gave better differentiation than weekly artificial nest survival (average 83%) results in the tracking tunnel data being more powerful despite being collected over two nights per season rather than 4 weeks.

The finding that old (reused) nests had significantly lower survival than freshly made nests suggests that artificial nest data could be made more powerful by using artificial nests that have been left to dry before use. However, the difference was fairly small, with old nests having 78% weekly survival on average compared with 86% for fresh nests. It is unknown why old nests were more attractive to predators, but it is possible that the dryness of the leaf litter makes them stand out as novel objects, or alternatively that dried nests mimicked real bird nests more effectively because they are generally built in locations sheltered from the rain. A key finding of previous artificial nest studies is that they tend to give the best predictions of real nest success when the artificial nests effectively mimic real bird nests (Moore & Robinson 2004).

It is not surprising that high understorey density was associated with low tracking tunnel survival (i.e. high rat tracking rates), as ship rats are known to prefer denser habitat (King et al. 1996). It is also not surprising that high vegetation cover at 1.5 m and supplejack presence were associated with low artificial nest survival, as these are also indicators of dense habitat. The positive association between canopy cover and artificial nest survival is less easy to interpret, but could potentially reflect differences in visibility associated with light levels. It is not obvious why understorey density predicted survival of tracking tunnels (ground level) whereas vegetation cover and supplejack presence predicted survival of artificial nests (1.5–2 m up), as these measures seemed to apply equally well to both heights.

The choice of index will partly depend on the main predators likely to affect the survival parameters of interest. In our study the artificial nest index included 'predation' by possums as well as rats, following Lewis et al. (2009), whereas tracking tunnels do not record possums because they are too large to fit through the tunnels. This made little difference because most (94%) artificial nest failures were due to rats; we found that reanalysis of the data with possum predation excluded gave very similar results. However, artificial nests could provide a more useful index if possums were the dominant predator (Whyte et al. 2005), or if birds were the main predators as is typically the case in overseas studies

where artificial nests are used (Moore & Robinson 2004). Although stoat tooth marks were not recorded in this study, stoat (*Mustela erminea*) predation has been monitored with both artificial nests (Smith et al. 2008) and tracking tunnels (Gillies & Williams 2001). The choice of index could also reflect the seasonality of threats, as artificial nests would seem to be most applicable during avian breeding seasons whereas tracking tunnels may be equally applicable any time of year.

The main reason for using indices of predation is that they require less effort, and therefore less cost, than directly estimating population parameters such as abundance, survival, or reproduction (Caughley 1977). In choosing between indices, their relative costs must be considered as well as any differences in bias or precision. Indexing predation using tracking tunnels is far more time efficient than using artificial nests. Tracking tunnels are quick to build, and once set up, rodent tracking can be done over 2 days (one day to set up and one day to collect papers or cards). In contrast, construction of artificial nests and eggs takes about 30 minutes per nest, and we found that leaving artificial nests out for 4 weeks gave less powerful data than leaving tracking tunnels out for two nights. Given that artificial nests did not detect any variation among fragments that was not detected by tracking tunnels, we do not see any reason to prefer artificial nests as an index of predation risk if ship rats are the main predator. However, it would be useful to assess whether the additional variation among fragments detected by tracking tunnels translates into real differences in predation risk. Blackwell et al. (2002) emphasised the need to assess relationships between indices and predator densities, but it is equally valuable to assess relationships of indices to survival and reproduction of native prey.

A key finding of our study is that there was a high level of variation in survival among individual tracking tunnels and artificial nests despite care being taken to be as consistent as possible in the placement of these devices (e.g. placing tracking tunnels near logs or other cover when available rather than in the open). Such individual variation will confound comparisons over time or space unless it is taken into account, so we discourage the use of raw tracking rates or similar indices that assume all devices are similar. Previous research (e.g. Christie et al. 2006, 2009) has identified microhabitat variables correlated with trapping success, and we have also identified variables at individual sampling sites correlated with survival of tracking tunnels (understorey density) and artificial nests (supplejack presence). However, these variables accounted for only a small portion of the individual variation. Consequently, we recommend the use of hierarchical models accounting for random individual variation when making any inferences from predator detection devices such as tracking tunnels or artificial nests.

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#### Appendix 1. Modelling the relationship between artificial nest success and predator tracking rate.

Indices based on predator encounter devices such as artificial nests or tracking tunnels are akin to survival processes (Leslie & Davis 1939). That is, the index reflects the probability of a device being encountered (e.g. marked, bitten) by one or more predators over a defined time interval, and the probability of not being encountered is the ‘survival probability’. This survival probability is expected to be inversely related to the density of predators in the environment. Under the simplest scenario, survival probability of encounter devices is expected to show a power relationship with both the predator density and the time interval. That is, the relationship will take the form

$$p = \alpha^{id}$$

where  $p$  is the probability of surviving an interval of length  $i$ ,  $d$  is predator density, and  $\alpha$  is probability of surviving one time unit if  $d = 1$ . Applying a  $\log(-\log)$  transformation gives the linear model

$$\log(-\log(p)) = \log(-\log(\alpha)) + \log(i_1) + \log(d).$$

As well as being linear and theoretically plausible, this form of the relationship constrains survival probability to be between 0 and 1 regardless of the parameter values on the right-hand side of the equation. It is therefore sensible to consider a  $\log(-\log)$  link function when modelling survival of predator encounter devices.

If there are two types of encounter devices (e.g. tracking tunnels and artificial nests), these devices will probably have inherently different survival probabilities, i.e.  $\alpha_1 \neq \alpha_2$ , and the time intervals between checks may be different, i.e.  $i_1 \neq i_2$ . The probabilities of these different devices surviving their respective intervals will then be

$$\log(-\log(p_1)) = \log(-\log(\alpha_1)) + \log(i_1) + \log(d)$$

and

$$\log(-\log(p_2)) = \log(-\log(\alpha_2)) + \log(i_2) + \log(d).$$

Solving both equations for  $\log(d)$  shows that

$$\log(-\log(\alpha_1)) + \log(i_1) - \log(-\log(p_1)) = \log(-\log(\alpha_2)) + \log(i_2) - \log(-\log(p_2)).$$

This equation can then be rearranged to show that the expected relationship between the survival probabilities for the two devices is the linear model

$$\log(-\log(p_2)) = \log [i_2 \log(\alpha_2) / i_1 \log(\alpha_1)] + \log(-\log(p_1))$$

where the term to the right of the equals sign is a constant (see term  $k$  in text). It is therefore sensible to consider a linear relationship with  $\log(-\log)$  transformations of survival probabilities when assessing the similarity of trends shown by two types of predator encounter device.