Geospatial and temporal patterns of stoat (*Mustela erminea*) activity in Tongariro Forest, central North Island, New Zealand.

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Abstract

Spatial and temporal characteristics of stoat (*Mustela erminea*) activity in Tongariro Forest were quantified using two well documented monitoring methodologies : i) radio telemetry using motion sensitive radio collars provided high detail measurement of individual activity of a number of stoats, and ii) footprint tracking tunnels provided measurement of population-level tendencies in activity, abundance and habitat use. The specific objectives were to identify predictable times of high and low stoat activity, and identify habitat types and specific locations within Tongariro Forest where stoat visitation to a control station is likely to be especially high and low. Prior to field data collection the radio transmitters were assessed and calibrated using captive stoats and video equipment to compare telemetry signals with actual behaviour. Two motion sensitivities where tested (fine and coarse), and the fine sensitivity transmitter was identified as most suitable for a field study. Estimates of locomotor activity derived from telemetry data correlated with directly observed behaviours at hourly and greater time scale, and verified suitability of activity transmitters for field study of stoat activity. Eleven stoats were tagged with motion-sensitive radio transmitters and monitored in the field in Tongariro Forest to quantify temporal patterns in wild stoat activity. Four monitoring 'seasons' representing early and late summer, autumn and spring seasons of the year, provided a total of 896 hours of stoat activity. On average, stoats were active 28% of the 24-hour day (seasonal range 16-41%). Both the total time spent active per day and the partitioning of this activity through the day varied between seasons. Tracking tunnel visitation indices obtained in subsequent years showed similar seasonal patterns to the data obtained using telemetry, except during early summer when tracking rates were lower than the equivalent locomotor activity estimate. Most radio-tagged stoats were predominantly diurnal in all seasons. Winter and spring had the largest proportions of daytime activity even though daytime was on average about 4 hours shorter during these seasons than in summer. Crepuscular peaks in activity were apparent in all seasons but particularly so during late summer. Activity was least structured in early summer, when it was spread more or less evenly throughout the 24 hours of the day. Active periods usually lasted at least 40 min, and up to 43% of activity was maintained continuously for >3 hours. Variability in activity between and within stoats was high, but variability in spring was marginally lower than in the other seasons. Temperature had some influence on activity at an hourly timescale, and the correlation between activity and temperature strengthened with increasing timescale. Autumn activity comprised more extended bouts of movement so might represent a time of year when stoats are ranging further, or exploring or searching within their ranges more intensively. This suggests that stoat control and monitoring devices might be most effective in autumn. Habitat use by stoats was quantified using a Geographical Information System (GIS) approach and statistical modelling with multi-year tracking tunnel records to data-mine for terrain variables that predict stoat visitation to stations in a New Zealand indigenous forest. Spatial analysis scale was found to be important for modelling outcomes, and an optimal model equation was derived using model selection techniques assessing at a range of relevant scales. The sensitivity of the model to different terrain parameters was tested by systematically substituting each variable and calculating the difference this made to the model derived estimates of stoat visitation. The most dominant terrain predictors influencing stoat visitation were proximity to tracks, altitude, northerly and easterly aspect, mean curvature, topographical position and slope. Proximity to tracks and mean curvature were the most sensitive variables to analysis scale. Indices of mouse and rat activity, which are known prey of stoats, and autocorrelation factors for previous and nearby stoat visitation, significantly improved the model and reduced the effects of terrain. Visitation to tracking tunnels was negatively correlated with rat visitation suggesting possible prey aversion of predators. Mouse visitation had no detectable effect on stoat tracking rates. Relevance for management and fit with known stoat ecology are discussed.

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Chapter 1. Introduction - background, study plan and objectives.

1. Introduction

This thesis arises from the conservation needs of a central North Island kiwi sanctuary. Tongariro Forest hosts one of five nationally significant kiwi (*Apteryx* spp.) protection areas (Robertson 2006), and one of four priority blue duck (whio, *Hymenolaimus malacorhynchos*) recovery areas (Glaser *et al.* 2010). In this multispecies protection area, stoats (*Mustela erminea*) are the key threat to the remnant populations of both kiwi and blue duck, and intensive pest control is the key to protection of these populations. Ongoing kiwi protection in Tongariro Forest began in 1994 when lines of Fenn traps were deployed across 250 hectares, and whio protection in 2008 when substantial numbers of DOC 200 traps were deployed. Since stoat control came into full effect there have been good years and bad years in terms of adult and chick survival from stoat predation, both for kiwi and whio. The greatest gains have been made following aerial sodium monofluoroacetate (1080) operations designed for possum control (Martin and Poutu 2007, Hood *et al.* 2009). However, these operations take place only every 5-7 years, and the resulting secondary poisoning effect on the stoat population only lasts for one or two years following the aerial poisoning. In years between aerial 1080 operations stoat trapping is conducted for whio protection, and kiwi management reverts to reliance upon removing eggs for hatching and raising in captivity until the chicks are of a stoat-proof size (‘Operation Nest Egg’, Colbourne 2005).

2. Stoats

2.1. Brief history of stoats in Tongariro Forest.

Stoats are small carnivorous predators indigenous to Northern Europe and North America, originating from Europe and reaching North America during the Pleistocene period (King and Murphy 2005). Stoats were introduced to New Zealand in 1884 by colonising Europeans who sought a natural control for plague rabbit populations which threatened pastoral farming. At this time stoats were released at sites across North and South Islands of New Zealand and there are indications that stoats became widespread across New Zealand mainland by the turn of the 20th century (King and Murphy 2005). Stoats have likely been present in Tongariro Forest since that time, with their presence confirmed in 1950 (Wodzicki 1950). The first modern record of stoats in Tongariro

Forest is from 1994 when stoats were caught in Fenn traps installed specifically to assess stoat numbers and what they were feeding on (Miles 1997). From late 1994 onwards structured trapping was instigated across *c.*250 ha of forest with the aim of quantifying the relative abundance of mustelid species, and seasonal and annual variability in their numbers (Keys and Speedy 1996, Martin *et al.* 1999). Trapping confirmed that stoats are widespread in the forest, that the population is persistent between years, and that the stoat is the predominant mustelid species in the forest. Further, after resident territory-holding adult stoats are removed by trapping, the majority of stoats captured are juvenile.

Stoat trapping was discontinued in Tongariro Forest in 1999 after interventional chick rearing (‘Operation Nest Egg’) was identified as the primary management option for recovery of the kiwi population. It is likely that stoats also had a major role in the decline of blue ducks and kaka (*Nestor meridionalis*) in Tongariro Forest, with both being susceptible to predation of eggs, chicks and adults while nesting (Bristol *et al.* 2008).

2.2. Stoat biology and ecology

Stoat biology and ecology are well documented in world literature, a reflection of the long history of stoats impacting on human interests as a conservation threat, a pest of game or food species, and also as a protected native species (King and Moors 1979, Alterio and Moller 1997, King and Murphy 2005, McDonald and Lariviere 2001, McDonald and Harris 1999, Sidorovich and Solovej 2007). This chapter does not attempt to review exhaustively the massive body of literature on stoats but rather aims to summarise key factors of relevance to pest management for kiwi protection and to the overall aims of this thesis.

Stoats are specialist predators evolved to hunt rodents in the Northern hemisphere (King and Murphy 2005, Raymond *et al.* 1990, Erlinge 1981, Erlinge 1983). They are bold, fast-moving and effective hunters both on the ground and in trees, and are capable of catching and killing prey several times their own size (Moors 1983b, McLennan *et al.* 1996, Polkanov 2000), Whitehead *et al.* 2008, O’Donnel 1996, McDonald 2000, Dilks *et al.* 2003, Moorehouse *et al*. 2003). Stoats eat a range of prey including birds, rodents, possums, lagomorphs (rabbits and hares) and invertebrates, with composition varying seasonally and with location (King and Murphy *et al* 2005). At some sites stoats can have a diet that includes a large proportion of native birds and invertebrates (Murphy and Dowding 1994, Purdy *et al.* 2004); for instance, native birds and invertebrates made up at least 64% of dietary items identified in stoat gut samples collected in Tongariro Forest (Miles *et al.* 1997). Elsewhere, threatened New Zealand native species have been reported as only minor components of the diet, with rodents and lagomorphs being the primary prey (Moors 1983b, Murphy *et al.* 1998, Murphy *et al.* 1999, King *et al.* 2003a, White and King 2006). Stoats are 'surplus killers' (Oksanen *et al.* 1985) which means that their intrinsic rate of killing is based on their rate of interception of prey and is independent of hunger. As a result their rate of predation can be higher than their metabolic requirements (McDonald and Larivierre 2001).

Stoats are strongly territorial (Erlinge 1977, Sandel 1995, Robitaille and Raymond 1995) and typically maintain large home ranges in New Zealand (Moller and Alterio 1999, Murphy and Dowding 1991). Transient juveniles and non-territory holding adults can move across the landscape rapidly covering significant distances (King and McMillan 1982, Murphy and Dowding 1994, Murphy and Dowding 1995). Often these can overlap multiple home ranges of native prey species (Dilks *et al.* 2003, Gibbs and Clout 2003).

Stoats have evolved a strongly r-selected reproductive strategy, meaning they have evolved to maximise population growth more through fecundity than through parental investment into survival and quality of young (Erlinge 1983, McDonald 2000). Stoats are rapid breeders, with mean fecundity of around ten embryos per year (range 3-20) (King and Moody 1982, McDonald and Larivierre 2001). Reproductive output in terms of emergent juveniles is not necessarily related to fecundity as complex factors influence completion and success of litters. Stoats are one of a relatively rare set of *c.*100 mammal species capable of delayed implantation (Renfree and Shaw 2000). After ovulation and fertilisation, females hold 8-10 blastocysts in embryonic diapause in the uterus for 9-10 months until either embryos implant and develop, or partial or full re-absorption of embryos takes place. Implantation is determined by food availability during the spring (King 2002, Thom *et al.* 2004, Powell 1985, King and White 2004). As a consequence, reproductive output is optimised to available food resources and stoat populations are able to respond very quickly to increasing prey numbers (Johnson *et al.* 2000, Blackwell *et al.* 2003). At some sites, particularly in beech forest where mice are numerous and breed quickly in response to mast seeding events, stoats can periodically irrupt into substantial numbers in response to increased prey availability (McDonald and Lariviere 2001, Ruscoe *et al.* 2003, King *et al.* 2003a, King and Powell 2011). At times of stoat population irruption, populations of threatened native species can be heavily impacted through predation and nest disruption (Lawrence 1997, Wilson *et al.* 1998).

2.3. Impacts on species and ecosystem

Predation by stoats has been identified as a major factor in the decline of many of New Zealand's threatened fauna. Native species are particularly vulnerable to stoat predation due to the evolutionary origins of New Zealand species. Having evolved in the absence of indigenous mammalian ground predators, New Zealand native species have insufficient anti-predatory defence mechanisms to avoid or repel stoats (Dilks *et al.* 2003, Moors 1983a, Gibbs and Clout 2003). Many New Zealand species are conspicuous, noisy, and nest in overt locations. Flightless species such as kiwi and yellow-eyed penguin are vulnerable to stoat predation, particularly while they are young (McLennan *et al.* 1996, McLennan 1997, Basse *et al.* 1999, Gibbs and Clout 2003, Ratz and Murphy 1999). Adult female whio (blue ducks) and their chicks are vulnerable to predation while on the nest, and even if they are not killed, nest disturbance and harassment can result in reproductive failure (Whitehead *et al.* 2008, Glaser *et al.* 2010). Kaka, mohua and other hole-nesting birds are vulnerable to stoat predation as adults and chicks while on nests, even when high up in trees (O'Donnell *et al.* 1996, Wilson *et al.* 1998, Dilks *et al.* 2003). Ground-nesting sea birds such as shearwaters and dotterels also fall prey to stoats (Dowding 1998, Cuthbert *et al.* 2000, Norbury and Heyward 2008). Stoats also prey heavily on many common forest birds (Moors 1981, Moors 1983a, Moors 1983b, Murphy *et al.* 1998, Elliot *et al.* 2010, Etheridge and Powlesland 2001), and in places invertebrate species are under threat (Smith *et al.* 2005, Wilson *et al.* 2006). For several species, local extinction is inevitable for populations that do not receive on-going intensive management (McLennan and Potter 1992, O'Donnell 1996). Stoat predation impact across the entire ecosystem (e.g., Kelly *et al.* 2005) although stoats prey upon rodents which also have ecosystem-level impacts; the intricacies of these interactions are not yet fully understood. Impacts on native prey species can be exacerbated at times when the stoat population has been elevated by high numbers of a non-native primary prey (rodents and/or lagomorphs), followed by removal of the supporting prey population through predation suppression or from large scale control of that prey. Prey switching has been identified as a significant risk in these situations (Parkes and Murphy 2004, Murphy *et al.* 1999, Smith *et al.* 2010, Moors 1983b).

2.4. Stoat control and monitoring

Stoat control methods currently used in New Zealand are variants of either kill-trapping, typically using snap traps, or poisoning by application in bait stations or with poisoned whole eggs (Dilks and Lawrence 2000, Lawrence and Dilks 2000, Brown 2003, Parkes and Murphy 2004). More recently, efficiencies have been gained by deploying the vertebrate pest control poison sodium monofluoroacetate (1080) from helicopters. This has proven increasingly effective in controlling stoats via a secondary poisoning pathway through rodents and possums (Murphy *et al.* 1999, Sutton *et al.* 2007, Martin and Poutu 2007, Hood *et al.* 2009). However, for some sites manual trapping and ground poisoning with stations arranged in grids or lines, are the only feasible or politically allowable control options. Ground control options are labour intensive and expensive to set up and maintain (Brown 2003).

Nationally, numerous control operations target stoats to protect vulnerable or flagship species, or are conducted as part of integrated ecosystem-focused restoration programmes (Saunders 2000, Christie *et al.* 2004). Most stoat control operations are run by the Department of Conservation (Brown 2003, Glaser *et al.* 2010), but an increasing number of projects are being initiated and administered by local community groups (e.g., Pukawa Trust, Kuaoutunu Kiwi Sanctuary, Maungatautari Ecological Island Trust).

Trapping

Stoat trapping in New Zealand originally relied on the Fenn trap (Figure 1), a large spring loaded kill trap (King and Edgar 1977). Intensive trapping has been successful at a number of sites, relieving predation impact sufficiently to allow population recovery, but even then results have been variable (Keedwell *et al.* 2002; Dilks, *et al.* 2003; Gaze 2003). Trapping efficacy has been achieved over the past two decades through improvements to baits and lures (King and Murphy 2005, Miller 2003), trap and bait station placement and spacing (Dilks *et al.* 1996), and the frequency of trap servicing (Brown 2003) including using environmental queues to optimise this (Choquenot 2006).

Changes in animal welfare regulations necessitated that traps kill quickly, especially since many traps are not checked each day (National Animal Welfare Advisory Committee (NAWAC) regulations, Murphy and Fechney 2003). Several new trap designs were tested and failed to meet animal welfare regulations under which traps can left set in place long term (Poutu and Warburton 2003, Poutu and Warburton 2005a). One trap design (the ‘DOC150 and DOC200’ traps, *Curtis Metal Products Ltd*) was developed that passed a humane-kill test (Poutu and Warburton 2005b). These traps are now a ‘best practice’ standard for trap-based stoat control.

Figure 1. Stoat in fenn trap. Photo Ross Martin

Stoats are highly mobile yet their defended home ranges are large, so the chance of stoats intercepting a trap station remains a rare and variable occurrence (King and McMillans 1982, King *et al.* 2003, Watkins *et al.* 2009). Distribution of stoats and their prey is patchy (Watkins *et al.* 2010). The efficacy of a stoat control layout relies on deploying tunnels at sufficient density to place at least one trap per stoat home range and to be able to intercept dispersing transient adults and juveniles moving though the site from outside of the control area. Typically traps are now deployed on lines or grids with 100-300 m spacing between traps depending on the species being protected (King and Murphy 2005, Whitehead *et al.* 2008) and the maximum home range size for stoats at a site (Miller *et al.* 2001).

Ground Poisoning

Direct poisoning of stoats has only been successful using eggs injected with sodium monofluoroacetate (1080), brodifacoum (Talon) or diphacinone (Spur and Phillipson

1995, Spur 2000). Secondary poisoning has been successful by targeting rats for poison delivery using bait stations, upon which stoats feed and die from ingested toxin (Alterio *et al.* 1997, Brown et al 1998, Alterio and Moller 2000), albeit with mixed results so a careful baiting strategy is required (Gillies and Pierce 1999). New toxins have been identified for direct poisoning of stoats, and one in particular, p-aminopropio-phenone shows potential for successful application in pest control operations (O'Connor 2002, Eason *et al.* 2002, Fisher *et al.* 2005).

Aerial poisoning

Secondary poisoning by aerial deployment of an acute rodent toxin (1080) has been proven effective for killing stoats and delivering benefits for threatened species over very large areas too great to consider for ground-based control. All thirteen radio-tagged stoats died after an aerial 1080 operation across Pureora Forest in 1997 and no stoats were tracked or trapped for three months following the operation (Murphy *et al.* 1999). In Tongariro Forest stoat footprint tracking indices dropped to zero following an aerial 1080 operation and remained at near-zero levels for several months (Martin and Poutu 2007).

Monitoring

Currently the only accepted non-kill method for assessing pre- and post-control stoat abundance is the footprint tracking tunnel system (King and Edgar 1977). Tracking tunnels (Figure 2) provide a coarse index of relative abundance (Gillies and Williams 2001). Tracking indices have been shown to correlate with trap catch in one report (Gillies and Dilks 2003). When deployed strategically using a standard design, they can provide a coarse but useful measure of stoat activity and abundance, allowing managers to monitor pest numbers and measure the response of a target population to control. Tracking tunnel indices have been shown to correlate with stoat density (Gillies and Dilks 2003). It is poorly understood how tracking indices relate to absolute stoat numbers, especially at low abundance, and to what degree the activity of individuals over time influence tracking data.

Figure 2. Footprint tracking tunnel

Photo Ross Martin

3. Study Area

3.1. Site description

The study area comprised ~20,000 ha of contiguous forest to the West of Tongariro National Park that includes Tongariro Forest, Pukepoto Forest, Maungakatote (New Zealand TOPO50 tile AH34 - see Figure 3). Altitude ranges from 280 m in the Whanganui River trench to 1076 m a.s.l. and the landscape is dissected by rivers and streams of various sizes.

Tongariro Forest was logged for native timber up until 1972, so the vegetation today consists of small fragments of un-logged podocarp/broadleaf forest restricted to the deep valleys or inaccessible ridges, surrounded by vegetation at various stages of regeneration. Most ridge-tops are covered in large expanses of toetoe (*Cortaderia toetoe*), often traversed by derelict roads and logging skid sites. Unlogged vegetation predominantly comprises stands of rimu (*Dacrydium cupressinum*), montane totara (*Podocarpus cunninghamii*), miro (*Prumnopitys ferruginea*), matai (*Prumnopitys taxifolia*), and tawa (*Beilschmieda tawa*) trees, with dense sub-canopy vegetation (Figure 4.). River valleys are steep, often with small sheer-sided gorges at the river's edge.

Whanganui River forms a significant valley trench that bisects the local landscape. To the north of this Tongariro Forest becomes Pukepoto Forest, although vegetation type is the same on both sides of the river. Wainoe Stream further dissects the landscape, forming a large mountain scarp to the west that forms a major highpoint in the Forest, named Taurewa (830 m). The Whakapapa River borders the forest margin to the west and south, presenting in a deep river trench that runs west then north. Both the Whanganui and Whakapapa Rivers are subject to minimum flow regulation due to water extraction for hydroelectric power generation off-site.

3.2. Kiwi recovery

Tongariro Forest is one of five nationally designated kiwi sanctuaries (Robertson 2004, Holzapfel *et al.* 2008). Management for kiwi protection commenced in 1996 with small scale investigative predator trapping in a central core area that ran until 1998 (Martin *et al.* 1999). Kiwi management then reverted to nest manipulation and ex-situ rearing of eggs and chicks (Colbourne 2005) until 2001 when the site was designated a Kiwi Sanctuary (Figure 5).

Management then diverted to experimental assessment of the value of aerially deployed 1080 poison for kiwi protection via secondary poisoning of stoats (Etheridge 2002, Sutton *et al*. 2007). Tongariro Forest south of the Wanganui River became a treatment area for a BACI-styled trial design (Before After Control Impact, Green 1979) that received 1080 deployment in 2001 and 2006 (Westbrooke *et al.* 2003), and the large forest fragments north of Wanganui river (Pukepoto to Maungakatote) were used as an experimental non-treatment control.

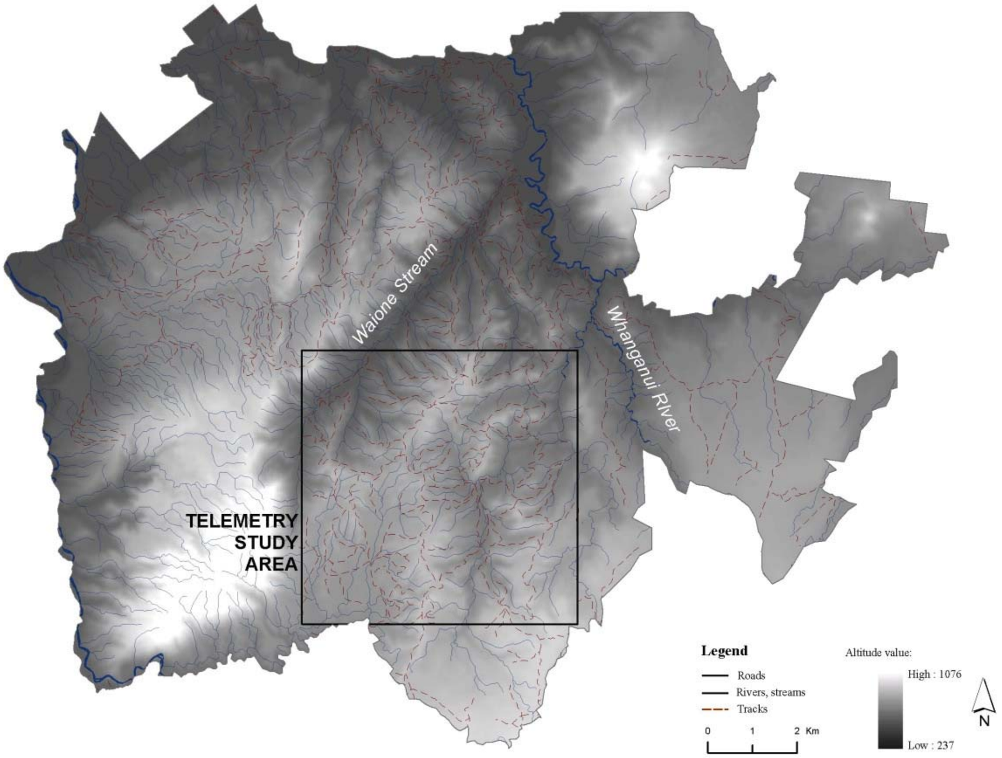

Figure 3. Study area topography with major rivers and roads and tracks. Hill-shade is based on a northerly sun, and brighter general shading denotes increased elevation

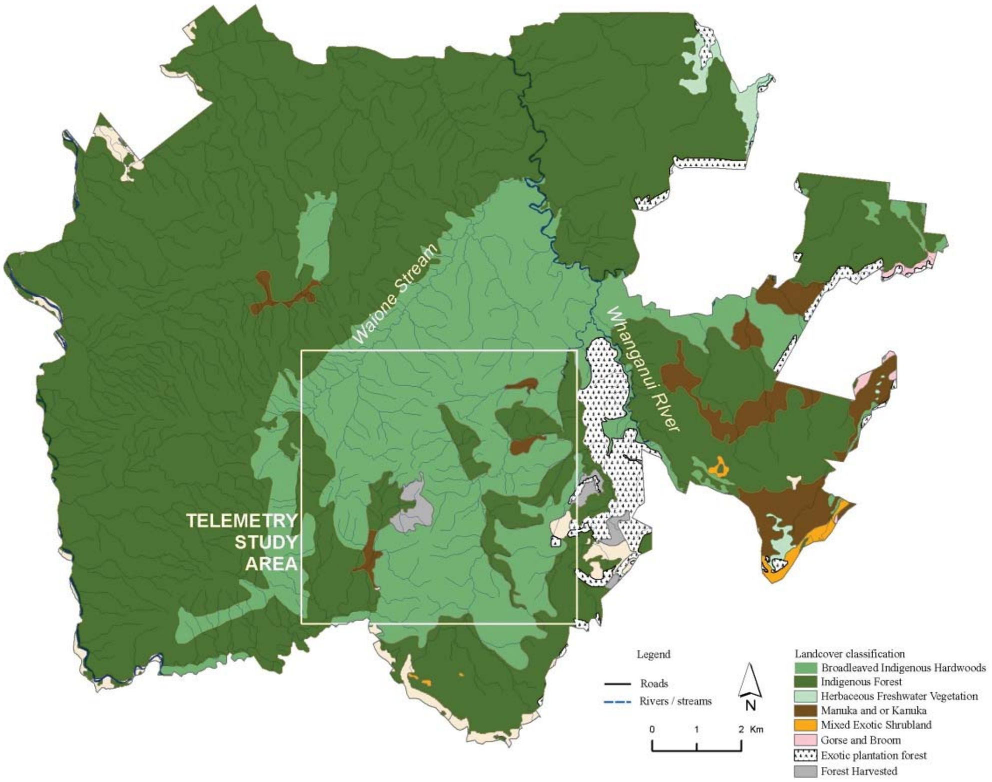

Figure 4. Broad land cover classification extracted from the Landcover Database 2 (LCDB2) spatial data layer.

3.3. Other flora and fauna

Tongariro Forest contains a multitude of threatened or special plant and animal species. The forest contains regionally significant vegetation types including Halls totara (*Podpcarpus halli*), kaikawaka (*Libocederus bidwilli*), and kahikatea (*Dacrycarpus dacrydioides*) on alluvial river terraces. The forest contains nationally significant population of woodrose (*Dactylanthus taylorii*) and Turner's kohuhu (*Pittosporum turneri*) which are subjects of threatened species recovery investment. The forest contains a nationally significant population of whio/blue ducks (*Hymenolaimus malacorhynchos*), which are subject to intensive management (Glaser *et al.* 2010). Also present are North Island falcon (*Falco novaeseelandiae*), North Island kaka (*Nestor meridionalis*), long tailed cuckoo (*Eudynamys taitensis*), North Island fern bird (*Bowdleria punctata vealeae*), yellow-crowned kakariki (*Cyanoramphus auriceps*), kereru (*Hemiphaga novaeseelandiae*) and both short and long tailed bats (*Mystacina tuberculata* and *Chalinolobus tuberculata* respectively), as well as common notable invertebrate species such as cave weta (Family Rhaphidophoridae) (Figure 6).

Figure 5. (left) Northern brown kiwi with northern white male.

Figure 6. (right) Cave weta.

Photos Ross Martin

3.4. Tracking tunnel network

Three hundred tracking tunnels were deployed by Department of Conservation staff at the time of an aerial 1080 operation in September 2001, to track the recovery of affected small mammal pest populations. Tunnels were deployed according to a Department of Conservation protocol for best practice (Gillies and Williams 2001). The tracking tunnels used were 600 mm long by 100 mm wide and high, made of black plastic, and contained a central ink pad with two removable pieces of paper either side (King and

Edgar 1977). Bait is placed in the tunnel - rabbit for mustelids (stoats, ferrets and weasels) and peanut butter for rodents - to lure animals to walk across the assembly and leave discernible footprints. The tracking tunnels were deployed in lines of ten tunnels at ~50 m station spacing on 450-m-long transect lines located on the landscape using a semi-random stratified design as described in Gillies and Williams 2001. Tracking tunnel monitoring was structured into five-day sessions run four times a year at key times relative to stoat and kiwi annual cycles. Under this protocol, on the first day of a 5-day session tunnels receive fresh papers and ink and peanut butter bait to capture a one-night numerical snapshot of rodent numbers. On day two, the bait is swapped to rabbit and old papers are collected and replaced with new papers which were left out for three more nights to index mustelid visitation, but only using every second tunnel. This best practice methodology is generally considered an acceptable trade-off between exposure time required to detect the rare event of a nearby mustelid visiting a tunnel, the potential ink congestion from receiving too many rat prints in high density areas, and the independence requirements for tunnels based on the different home range and bait preference characteristics of mustelids and rodents (Gillies and Williams 2001).

The tunnels in the treatment area have been run continuously since 2001 to the present, and non-treatment tunnels were only decommissioned in late 2007, around one year following the 2006 repeat of the 1080 operation. Reductions in small mammal numbers following each 1080 operation lasted around 12 months before pest populations showed signs of recovery. Data were only used for the alternating tunnels used for collecting mustelid tracks (i.e., only 150 tunnels out of 300 were used) and only for the times when rabbit bait was in place. Although the one-night monitoring sets targeting rodents would have been better for collecting data on rodents due to their affinity to peanut butter, we wanted to eliminate as much as possible any potential between-night difference in probability of visitation (e.g., due to weather, temperature, prey activity and any compounding influence of previous visits by rats). Thus, only data from surveys that monitored mustelids and rats at the same time were used.

4. Habitat use modelling and GIS

Geographical Information Systems (GIS) and modern spatial analysis techniques have been in use now for several decades for geostatistical predictive habitat modelling (Palmeirim 1988, Pereira and Itami 1991). GIS is the integration of cartography and mathematical and statistical analysis, managed within a relational database framework

(Church 2002). The programmability of current GIS and statistical software coupled with increasing computer processing power has opened up a range of different data-mining approaches for predictive spatial modelling. The benefit of using GIS is that multiple spatial data layers describing terrain form or geographic features can be rapidly processed or recalculated to generate ecologically meaningful test data, for assessing driving factors behind the abundance and distribution of animals and plants. A multitude of statistical methods exist to derive models with value for making spatial predictions on population distribution based on environmental measures (Haefner 1996, Guisan and Zimmermann 2000). A conventional approach to modelling is to test a range of potential predictors based on biologically or ecologically sensible combinations of environmental variables. Variables can be considered as direct i.e., empirical measures of environmental conditions (e.g., altitude, temperature) or indirect i.e., constructs of direct variables interacting spatially (e.g., soil moisture, land cover) (Guisan and Zimmermann 2000). Logistic regression modelling is the statistics of binomial observations (e.g., present / absent), and is a common approach for describing how species occurrence patterns are shaped by environmental and habitat characteristics based on presence absence data (Pereira and Itami 1991, Austin *et al.* 1996, Bian and West 1997, De la Ville *et al.* 1997, Osborne *et al.* 2001, Wintle *et al.* 2005, Newton-Cross *et al.* 2007, Coulon *et al.* 2008, Syartinilia and Tsuyuki 2008).

Model selection is a progressive process of model enhancement that involves reduction of the number of candidate predictor variables to an optimal subset of significant ones, a process called term reduction or shrinkage (Burnham and Anderson 2002). Popular heuristic model selection methods include variants of forwards, backward and stepwise term reduction processes (e.g. Shtatland 2001, Guisan and Zimmerman 2000). In forward selection, variables are added one by one in sequence of model fit (forwards selection) until an optimal model is attained. In backwards selection, terms are removed one by one from a full set of potential predictors until an optimal model fit is attained. Stepwise selection is similar to forward selection except terms can be both added and removed during steps, based on thresholds for insertion and retention in the model. In performance trials, stepwise selection was shown to reflect the true model better than forward and backward selection, but it has been argued that stepwise selection can be sensitive to input data and produce regression coefficients that are biased high (Wanga *et al.* 2008).

In many ecology studies finding causal relationships and empirical drivers of ecological processes is of principal interest, and careful choice of predictor combinations and analysis scale becomes important (Austin 2007). But if the goal of analysis to simply to predict a system for management application, then the focus can shift towards finding variables (direct or indirect) that most accurately and consistently predict the system mathematically, perhaps at the expense of know empirical relationships. There has been debate as to whether automated data mining necessarily provides accurate or useful predictive models compared to more subjective assembly of variable sets compiled by researchers familiar with their sites and able to filter choices with ecologically sensible parameters. However, many indirect variables can be closely related by the underlying direct variables from which they are comprised (e.g., soil moisture and proximity to rivers are a function of a sites terrain model). This can result in collinearity between variables that duplicates the influence of more fundamental drivers in a model assessment, and so is another potential source of bias. Methods to eliminate or account for collinearity effects on statistical inference have been explored previously, and include exclusion of collinear terms, and orthogonal transformations (Mason and Perreault 1991, Chatterjee and Yilmaz 1992). In general there is a trade-off when building models, between exclusion of collinearity to minimize model bias, and inclusion of as many significant variables as required to maximize predictive power and explain variability. Models that preserve collinearity tend to have stronger predictive value but individual parameter estimates for variables tend to be less accurate and more sensitive to observed value in a sampled data set. However, models that ruthlessly exclude collinear variables risk losing explanatory power in the model. In habitat modelling it is also desirable to explore multiple models and validate the choice of a final model against independent field data or using cross-validation or re-sampling techniques (Guisan and Zimmerman 2000). User choice of validation techniques can also affect modelling outcomes and impact on interpretation. A rigorous modelling process applied to assessing key animal habitat use would include testing multiple modelling approaches and a range of spatial analysis scales to look for strong habitat predictors that consistently turned up as being drivers of activity/presence.

There are a number of modelling approaches in common use for investigating habitat use depending on the data structure and factorial design. One-way analysis if variance (ANOVA) is modelling with a single categorical predictor variable. Main effect ANOVA uses separate one-way ANOVA designs for assessing multiple effects.

Factorial ANOVA is used when the experimenter wants to examine interaction effects between multiple dependant variables. Multiple regression models first order effects in a single linear regression equation. Factorial regression models first order effects with some or all possible products of effects (i.e., interactions) in a single linear equation. Polynomial regression models higher order effects e.g., quadratic relationships. Response surface regression is the modelling of first and higher order effects with interactions. Mixture surface regression is the modelling of first and second effects, but without an intercept, where mixture factors add to a constant value. Mixed model is appropriate in situations when there are factors that have random effects associated with them (e.g., individual stoats and their preferences), or where there is non-consistent covariance structure to the 'fixed effect' parameters. Mixed modelling is also appropriate when modelling both categorical and continuous parameters (e.g., day/night vs. temperature). Logistic regression approach is applicable for dichotomous data (presence or absence of stoats at a location).

Habitat use by stoats has been assessed previously at a coarse scale using radio tracking data (Gibbs and Clout 2003; Murphy and Dowding 1995; Smith and Jamieson 2003; Smith *et al.* 2007), and the performance of individual trapping stations has been modelled against both microhabitat factors and GIS-derived predictors (Kliskey and Byrom 2004, Christie *et al.* 2006, Lough 2006, Christie *et al.* 2009). In these studies significant environmental drivers of stoat activity were identified, but there were marked differences between sites in both the significance level and direction of response to environmental factors. This means that an investigation into predictive activity drivers needs to take into account site specific habitat preferences and ecology differences.

5. Objectives

This thesis sets out to quantify the ecology of stoats in Tongariro Forest in terms of activity and habitat use, and to provide information that might allow improvement in the efficacy and cost-efficiency of stoat control methods. The overarching theme is a search for ways to predict the visitation (both in space and time) of stoats to control stations, to guide management optimisation of stoat control.

The specific objectives were:

1. To identify predictable times of high and low stoat activity where they exist.

2. To identify habitat types and specific locations within Tongariro Forest where stoat visitation to a control station is likely to be especially high and low.

3. To understand limitations of results.

6. Thesis plan:

Chapter one. General Introduction.

In chapter one, current knowledge and established theory is reviewed to set the scene for this research. Three main fields are covered – i) stoat behavioural ecology and species management in Tongariro Forest, ii) quantifying animal activity in the field, and iii) modelling habitat use. This chapter also describes the study area Tongariro Forest, its history, fauna and flora.

Chapter two. Calibration of transmitters

Chapter two develops methods for use in chapter 3 which presents a field study assessing activity of wild stoats using activity-sensitive radio transmitters in the field. Although radio transmitters have been used extensively in the field to track the location stoats, activity transmitters have only been used a few times to quantify stoat activity, and there no literature could be found that attempts to calibrate the transmitter-generated data against real behaviour. So, this chapter compares activity transmitter telemetry signal and video observations of behaviour, recorded simultaneously using wild stoats brought into a captive filming arena, to quantify accuracy and consistency, and to aid in making some decisions about methodology. This chapter verifies that a field study of stoat activity using these transmitters is valid and will provide accurate information.

Chapter three. Calibration of activity transmitters

Chapter three investigates the activity of stoats, caught in Tongariro Forest, and tagged with activity sensitive radio transmitters. Computer processing of this information enabled construction of daily activity budgets for multiple stoats monitored in four representative monitoring ‘seasons’. These were 1-2 week sessions of data collection timed for important stages in the forest year. This chapter also presents footprint tracking tunnel visitation data, collected during later years, that provide complementary insight into seasonal patterns of activity in stoats.

Chapter four. Sensitivity of GIS derived terrain variables at multiple scales for modelling stoat activity.

Chapter four critically examines the application of an established method of habitat use assessment to describe stoat habitat use. This chapter develops a method that is used in chapter five. Geographical information systems (GIS) and logistic regression modelling are integrated to quantify the influence of terrain effects on stoat visitation to footprint tracking tunnels. The impact of user-defined geospatial scale on model outputs is assessed in order to choose an optimal equation for stoat activity using terrain variables. This chapter is formatted for journal presentation, and is already published in an international journal (Martin *et al.* 2011).

Chapter five. Terrain and prey effects on stoat activity

In chapter five, the optimal terrain model derived in chapter four is extended to assess how prey species influence stoat activity, and to quantify autocorrelation in the data. Findings are framed in terms of stoat ecology, and the limitations of the method are discussed.

Chapter six. Synthesis and conclusion.

In chapter six, findings are brought together to summarise new knowledge about stoat activity in Tongariro Forest. The fit of these new findings to established ecological theory are discussed, as well as how they relate to other stoat research in New Zealand and to New Zealand conservation in general. Finally, recommendations are made for threatened species management and future research direction.

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Appendix 1.. Colour-enhanced satellite aerial photo of study area (SPOTMAP 2008). Darker shades of green withint the study extent depict unlogged or late regeneration forest age, and lighter shades of green depict early regeneration or seral vegetation.

Chapter 2. Calibration of activity transmitters using captive stoats.

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Abstract.

Activity-sensitive radio transmitters were assessed and calibrated using captive stoats and video equipment to compare telemetry signals with actual behaviour. The transmitters emit two different radio pulse rates depending on whether the transmitters experience motion above a certain activation threshold. Activation is determined by an internal microcontroller and mercury tilt switch. The telemetry received from the transmitters allowed distinction between locomotor activity and non-locomotor or nest-bound activity (grooming, feeding, stillness and sleeping). Two motion sensitivities where tested (fine and coarse) by varying the angle of the linear mercury tilt switch inside the transmitter and comparing their telemetric responses to a range of stoat behaviours. Overall, the fine sensitivity transmitter produced activity estimates that better depicted observed behaviours, for both timescales tested (hourly and quarter-day). Correlation of telemetry against videoed activity was strongest at quarter-day rather than hourly time scale. Removal of the timeout period from time records made no discernible difference to the correlation of telemetry with recorded video activity, but reduced overestimation inherent in the raw telemetry data. Removal of blocks of activity of less than five minutes resulted in a dataset that more accurately depicted activity outside of the nest box. Variability was observed between stoats both in terms of observed activity budget and transmitter performance. This paper concludes that activity-sensitive transmitters with a binary response can accurately describe relative stoat locomotor activity patterns at different in captivity via monitoring the telemetry signal, and presents parameters for applying the method for field telemetry. However the findings also indicate that there is potential for overestimation in absolute activity estimates, and that orientation of the mercury tilt switch has important effect on telemetry accuracy.

Keywords: Stoat, activity, captive, telemetry, calibration, video.

1. Introduction.

Radio telemetry is a widely used method for quantifying the activity of animals in the wild (Kenward 1987, Casper 2009). Radio transmitters can be attached to the outside of animals or implanted under the skin or within the viscera. As a general guideline animals can tolerate carrying a radio transmitter to a maximum of around 5% of their body weight for terrestrial small mammals, 3.5% for flying birds, and 4% for bats, before incurring significant energetic or behavioural costs (American Society of Mammalogists 1998, Casper 2009). Modern microcontroller technology allows for encoding of the raw telemetry radio signal with information. For large animals (e.g. dogs, ungulates, albatrosses) the 5% body weight encumbrance limit allows still for moderately complex instrumentation to be packaged into animal-borne attachments (e.g. Moll et al 2009) along with long range radio transmission and long term battery life. However, for smaller animals there persists a challenging trade-off between functionality, transmission power, battery life and durability, as even the smallest batteries and other components amount to an encumbering weight when higher transmission power is required.

Increasing miniaturisation of electronic components means that inclusion of programmable integrated circuit boards and motion sensitive components (e.g. mercury tilt switches and strain/inertia sensors) is possible into even very small transmitter packages (Schregadus et al 2006, Hassal et al 2001). The stoat (*Mustela erminea*) is a small terrestrial hunting predator, highly mobile, and known to have daily activity structured in short bursts of locomotion interceded with periods of rest (King and Murphy 2005). The timing and duration of activity during the day varies geographically and with time of year. Body weights of adult stoats in Tongariro Forest were found to range from 240 to 470 g (Miles *et al*. 1997). This means the maximum transmitter weight allowable (i.e. no more than 5% of body mass) for a field study of randomly caught adults is around 12 g if stoat tagging is restricted to stoats weighing more than 240 g. Captive assessment of the effects of radio tags on weasels suggests that stoats should be able to bear a transmitter of this length with acceptable cost (Gehring and Swihart 2000). Stoat home ranges can be several kilometres in width and overlap considerably (Murphy and Dowding 1994, Murphy and Dowding 1995). While many stoats defend a stable territory, there is also a large proportion of the population dispersing to find a territory. These stoats can cross many kilometres in a few hours or days (Murphy and Dowding 1994, Murphy and Dowding 1995) so there is a minimum transmitter power output required in order to maintain radio contact with a stoat from a fixed station. Field-based studies of stoat activity using motion-sensitive radio telemetry require transmitters with a consistent detection range of 1-2 km if they are to reliably detect territorial stoats throughout their range as well as transient individuals. The practical limitations of live trapping, radio-tagging and monitoring a moderate sample size of stoats for long enough to gain a representative measure of activity requires transmitters to run continuously for at least several weeks. Stoats can be highly energetic in their mobility, pursue prey in tight burrows and vegetation, and are vigorous groomers (Robertaille and Baron 1987). Transmitters thus need to be packaged in a robust housing with a strong attachment. One effective attachment system devised for stoat radio tracking is a neck collar, with the electronics encased in acrylic resin, and a metal collar forming a closed loop antenna for radio transmission. With this requirement for radio power output and battery/housing longevity, the bulk of the weight of the 12 g transmitter allocation has to be battery, so only a simple microcontroller and motion sensitivity is currently possible.

No published literature was found on tilt-switch-based continuous activity transmitters that either verifies that the transmitters are reliable in the field, or guides interpretation of the data they generate. A number of studies have reported on aspects of stoat behaviour in captivity (Robertaille and Baron 1987), and other field-based studies have provided insight into the dynamics of how the movements of stoats in the wild can be detected by telemetry. Most studies distinguished stationary from locomotor activity by detection of fluctuating changes in signal strength (Alterio and Moller 1997). Detection of activity in this way is made under the assumption that i) when the stoats are moving, the transmitter radio field is consistently modified by surrounding trees and small scale terrain features or by field pole rotation (the transmitters have an electrostatic dipole-shaped radio field with marked difference in transmission power output with radial direction), and ii) when stoats are in their nest box/den there is no activity that causes field pole rotation.

However, situations could certainly occur when active animals produce steady signals; for example, when engaged in small-scale hunting and exploration, underground exploration, and when the signal is long-distance or attenuated by obscuring terrain features. Consideration of these factors may be important for telemetric studies of stoats as a large component of their prey acquisition can involve small-scale movements as they hunt for prey in ground cover and underground (Moors 1983, King and Murphy 2005). In such situations the radio signal characteristics may not be dissimilar to the signal attained when a stoat is grooming or feeding. Extended bouts of feeding or grooming activity, which typically occur in a nest/roost situation, make up a substantial component of daily activity (Robertaille and Baron 1987). As a stoat's neck and body can change in orientation considerably while grooming, there could be movement of the asymmetrical radio field that could result in extended periods of highly fluctuating transmitted signal. The fluctuating signal method has been widely used on stoats (Erlinge 1980, Sampson and Raymond 1995, Alterio and Moller 1997). A current scan of the literature was unable to find published studies that quantify how accurately this 'fluctuating signal' method depicts actual activity. Studies into effectiveness of triangulation based on radio-transmitter signal direction have identified terrain effects on radio signal (Garrott *et al.*1986, Parker *et al.* 1996). Tilt-switch based transmitters provide an alternative to this method that is independent of terrain or pole orientation.

Typically the telemetry signals produced by readily available tilt-switch-based activity transmitters are encoded combinations of short radio pulses emitted at varying intervals. Converting radio signal feeds into accurate and useful measures of animal behaviour requires careful sample design and interpretation of the data. Calibration of the telemetry system requires comparison of the signal feed with observed behaviour of animals to ensure it is possible to derive an accurate measure of activity from telemetry data. For large conspicuous or easily accessible animals, direct observation in the animals' wild habitat is plausible (Gillingham 1985). For small cryptic or highly mobile animals it can be necessary to bring animals into captivity in order to collect behaviour data sufficient to calibrate a field telemetry method and quantify the precision and variability of the system.

The purpose of this study was to calibrate the activity telemetry signal of Sirtrack 12-g activity/mortality radio collars against video footage of wild-caught stoats held in captivity. The specific objectives were to i) assess whether locomotor activity (defined here as time spent mobile outside of the nest box or den) could reliably be identified from the radio signal distinct from other behaviours that can activate the transmitter; ii) ascertain optimal technical parameters for use of radio collars in measuring stoat activity in the field; and iii) provide information to refine data processing and interpretation.

2. Methods.

2.1. Overview

Wild stoats were captured in Tongariro Forest, fitted with radio collars and transferred to indoor enclosures for two weeks of video monitoring. Video recording equipment and infra-red illumination was set up simultaneously in each stoat's enclosure and associated nest box enabling observation of all of their activity and behaviours. Telemetry information from each stoat was recorded onto the soundtrack of the video tape as the footage was being recorded, thereby providing a continuous synchronised record of stoat and transmitter activity. Two transmitter tilt switch orientations were tested. Data were analysed to compare activity budget profiles at an hourly time scale between the telemetry signal and the actual observed behaviours. Hourly activity indices were averaged to produce quarter-day activity indices to nominally represent hours surrounding dawn, midday, dusk and midnight.

Activity transmitters.

Sirtrack 2-stage activity/mortality radio tags, packaged in a standard 12 g stoat radio collar (Sirtrack N.Z. Ltd., Havelock North) were used in this study. The transmitters contained small mercury tilt switches to provide motion-sensitivity. Transmitter micro-controllers were programmed to produce one of three different radio signal pulse rates dependant on stimulus received from the mercury tilt-switch. The transmitters produced a base inactive pulse rate of 20 pulses per minute (ppm) when no stimulus was received from the tilt switch. The pulse rate changed to an 'active' pulse rate (55 ppm) upon receiving tilt switch signal, and only returned to the inactive pulse rate after a 10 second 'timeout period' with no tilt switch stimulus. The purpose of this timeout period was to make short duration activity more obvious to the observer in the field. Short bursts of activity of only a few seconds could otherwise be missed in noisy environments. The transmitters produced a third 'mortality' pulse rate after 8 hours of inactivity, indicating that the stoat had died or the transmitter had been shed.

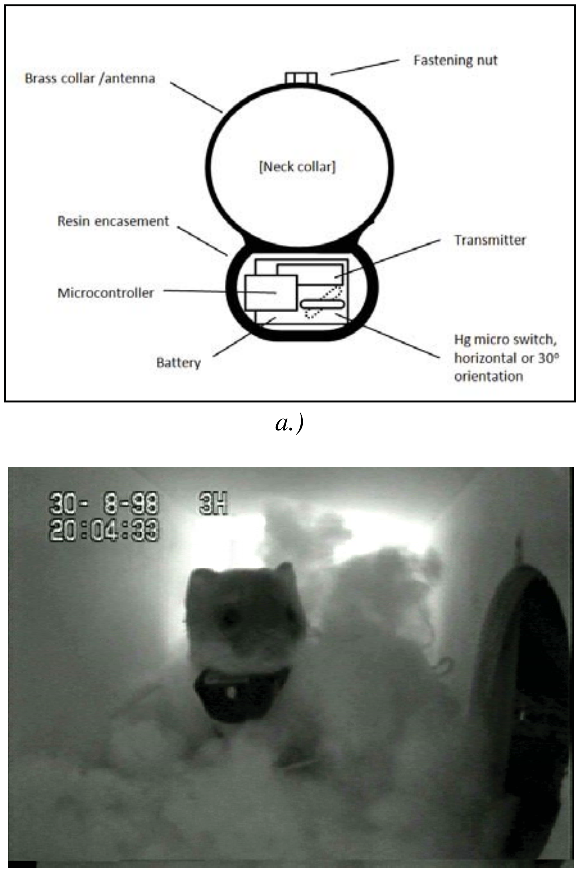
Two different transmitters that were identical in construction except for the vertical angle of the mercury tilt-switches, and hence levels of motion-sensitivity, were assessed (see Figure 1). With the transmitter hanging below the neck of the stoat, the tilt switches were oriented parallel to the shoulder-to-shoulder axis. Along this axis the switch was mounted at 0° inclination (level with horizontal) for the fine sensitivity transmitter, and 30° for the coarse setting.

2.2. Stoat capture and radio tagging.

Four stoats (three males and one female) were live-captured in Tongariro Forest, Central North Island, New Zealand using wooden tilt-ramp live capture traps (King and Edgar 1977). Stoat details are given in Table 1. Two video enclosures were available, so stoats were videoed in two sessions with trapping coordinated to catch stoats two weeks prior to each session. Following capture, the stoats were held overnight in an indoor holding cage (dimensions 2 m x 1 m x 0.5 m, with a 150 x 150 x 300 mm wooden nest box), then transported in their nest box to the Massey University small animal facility in Palmerston North where they were held in duplicate holding cages until they were released into the main video enclosures. Prior to being released into the video enclosures the stoats were radio tagged with one of the two randomly allocated radio transmitters (fine and coarse sensitivity settings). Anaesthesia was achieved using halothane (Fluothane) administered at up to 4% saturation in 1 L per minute oxygen, and delivered into a sealed acrylic gas chamber via a Bain's circuit (Dr. Paul Chambers, Massey University, pers. comm.). After induction of anaesthesia, the patient end of the circuit was placed over the stoat's nose and the halothane reduced to 1% saturation to maintain anaesthesia while it was fitted with the radio collar.

Table 1. Details of stoats held in captivity for filming.

Label	Sex	Mass at capture g	Capture date	Date of 1st radio-tagging/ release	First TX assignment (sensitivity)	Date of 2nd radio-tagging/ release	Second TX assignment
11	f	195	17/8/98	18/8/98	Coarse	25/8/98	Fine
12	m	242	17/8/98	18/8/98	Fine	25/8/98	Coarse
21	m	260	29/8/98	31/8/98	Coarse	7/9/98	
22	m	290	29/8/98	31/8/98	Fine	7/9/98	Coarse



a.)

b.)

Figure 1. *a.)* Transmitter tilt switch orientations. *b.)* Stoat in nest box wearing transmitter

2.3. Captive enclosures and video set-up.

Two adjacent triangular indoor enclosures were constructed by dividing a rectangular room in half diagonally with plywood (see Figure 2). The floors of the enclosures were covered with hay plus several patches of higher vegetation to provide cover for the stoats.

Wooden nest boxes (dimensions 150 x 150 x 300 mm) containing polyester fibre and straw for nesting material were placed against the walls furthest from the external camera mounts. Captive stoats were provided with surplus food (day old chicks) and water.

The temperature of the enclosures was maintained between 12^{o}-15^{o} and lighting was timer-controlled to turn on and off at 7:00 am and 6:00 pm, equivalent to sunrise and sunset times at that time of year in Tongariro Forest.

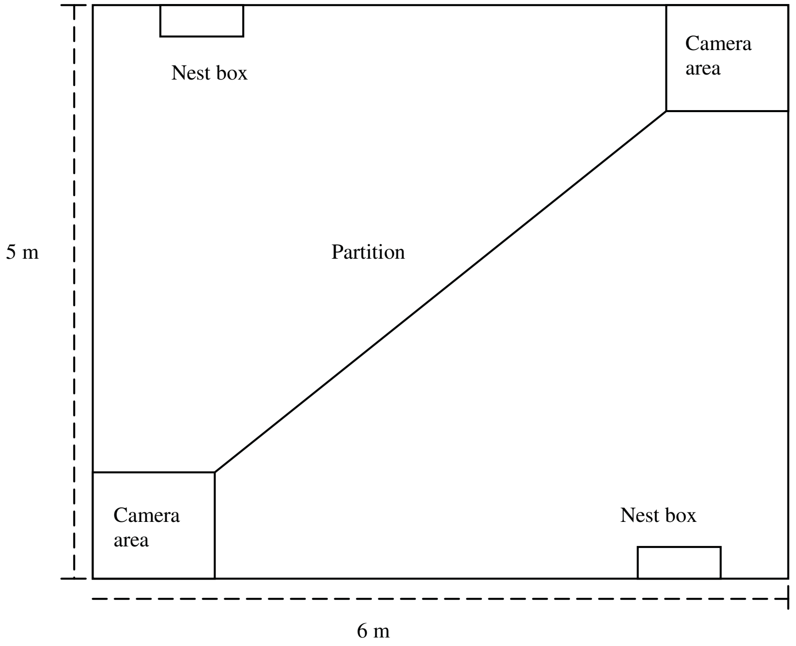


Figure 2. Captive enclosure setup.

Stoat activity outside of the nest box was videoed using a camcorder with high gain night time recording. The cameras were erected on 2-m high tripods and placed at one corner of each enclosure such that the entire enclosure was within the field of view except for a 1 m^2 blind spot directly underneath and in front of each camera.

Activity within the nest boxes was recorded using infra-red (IR) video camera modules with IR emitting diode arrays in a 120 mm wide PVC tubular housing. The nest boxes were fitted with a camera coupling such that the camera formed one wall at the end of the box nearest to the single entrance hole. Video footage from the nest box was recorded onto a VHS time-lapse video recorder set to 5-fold time compression.

Following recovery from anaesthesia, each stoat was released into one of the two enclosures. Videoing and telemetric recording commenced six hours after release and continued for one week. Following this, the stoats were removed from the enclosures, radio-tagged with the alternate transmitter using the same anaesthetic protocol, and released back into the alternate enclosure for a second week of monitoring that, once again, commenced six hours after release to avoid residual anaesthetic effects.

This sampling strategy was chosen so that each stoat was observed wearing both transmitter types, and so that each stoat and transmitter combination experienced similar experimental conditions (i.e., total duration held in captivity, duration in holding cages until radio-tagging and release, video duration until transmitter change-over, exposure to unfamiliar surroundings upon release with a new transmitter type). One stoat fell sick and was withdrawn from the trial during the second week of monitoring so one stoat-transmitter combination was not available for analysis.

2.4. Activity data collection

Stoat activity was reviewed by VHS tape playback under the frame control of a video jog/shuttle wheel. Stoat footage was processed into a time series with consecutive blocks of activity categorised as either nest-box or external activity (based on location of the hind limbs relative to the nest box opening). External activity was then categorised into ten behaviour-types, which were then classed as either stationary activity or locomotor activity (see Table 2 for definitions). Concurrent telemetry data were collected by recording the times that the transmitter signal changed between active and inactive pulse-rates, from which the duration of each bout of activity was calculated.

The rare occasions that stoats moved out of sight of the camera were accepted as being a continuation of the preceding locomotor behaviour bout if i) the duration spent out of sight was less than three minutes duration and less than half of the total combined duration and ii) the radio transmitter signal was active during this time. The area of the blind spot (1 m^2) was too small for prolonged locomotor activity, so most activity in this area was likely escape behaviour (attempts at digging or climbing), and this was verified in part by direct observation from the enclosure window.

Continuous behaviour logs from video-derived activity time series were converted into a data set quantifying the duration of each activity bout. Bouts were labelled according to classes given in Table 2. Time series were also re-processed giving bouts of stationary and locomotor activity. A corresponding data set of bout durations for stationary and locomotor activity was produced. “Digging” behaviour was entirely digging, chewing, gnawing and scraping at doors, floor and plywood partitions associated with escape attempts.

This behaviour was eliminated from the record base, as escape behaviour was deemed entirely related to the captive conditions and not representative of typical behaviour in free-living stoats. It should be noted though that digging behaviour should be factored back into the data set if used to assess the full captive energy budget of the stoats, as some stoats spent a lot of time and effort trying to escape.

Hourly indices of locomotor activity were generated by computing the time spent engaged in locomotor activity per hour. Hourly indices derived from less than 30 minutes of observation time per hour were excluded from this data set. Note that over 85% of hourly indices were derived from 60 minutes continuous observation per hour. The hourly index of activity was chosen as the temporal resolution for this study so as to meet the minimum resolution required by the subsequent field study.

Continuous telemetry time series were processed to remove the nine-second timeout period from all active to inactive transmitter state changes. Durations were calculated for telemetry-derived bouts of activity. Hourly, day/night and daily activity indices were formed in the same way as the respective indices for video-derived locomotor activity. The resulting data set comprised paired activity indices for video (actual) and telemetry locomotor activity.

Table 2. Behaviour categories and groups.

Location of activity	Behaviours	Code	Definition of behaviours	Activity classes
External	Walking	W	Step-by-step movement (walking, creeping, crawling), and including carrying food to nest box.	Locomotor
	Bounding	B	Use of back arch and back leg-thrust for locomotion (running, bounding).	
	Jumping	J	Vertical leaping with thrust from hind legs from a stationary position. Jumps less than 3 s apart were treated as being part of the same jumping bout.	
	Climbing	C	Scaling of vertical objects; typically seams between plywood panels, electrical cabling and wall joints.	
	Stationary	S	Sitting or standing for greater than 3 s, (mainly looking around, staring into space), but not including feeding and grooming..	Stationary
	Nesting	N	Preparation/manipulation of nesting material (straw, Dacron) or exploring the straw substrate from a stationary position (moving material with head movements). Similar body action to grooming.	
	Feeding	F	Tearing, chewing, licking, and other manipulation of food, but not carrying of food to nest box.	
	Grooming	G	Scratching, washing, and preening of body/fur with head and feet.	
	Out of sight	OOS	Unknown behaviour occurring in the 1m^2 area out of the field of view of the cameras. Mostly escape behaviour.	
	Digging	D	Lying on back or sides with head on ground chewing at the bottom of the plywood partitions (escape behaviour). As this is a behaviour specific to this captive situation and non-applicable to activity in the wild, digging data were excluded from the total data set.	
Nest Box	Inside the nest box	NB	All time spent inside the nest box.	

2.5. Data analysis

Data were analysed according to a four step process: *i*) characterisation of stoat activity in captivity and assessment of behaviour captured for valid analysis; ii) comparison of 24-h activity budget profiles between video and telemetry measures of activity for the two transmitter types; iii) assessment of impact of transmitter timeout period from telemetry data; iv) identification of locomotor activity from active telemetry bout characteristics. All analyses were performed using SAS System 9.1.3 statistical analysis software.

2.5.1. Stoats in captivity

The total active time outside of the nest box engaged in each behaviour was summed for each stoat then standardised against the number of active hours videoed. The calculated activity budgets describe the proportion of time outside of the nest box spent engaged in each behaviour. Differences between stoats in the proportion of active time spent in behaviour classes was assessed using Kruskal-Wallis non-parametric analysis of variance. The mean duration of all bouts was calculated for each behaviour class, and histograms were produced to characterise each behaviour and assess any detectable differences in the time spent engaged in each activity. Data were partitioned according to the transmitter type worn by the stoat to assess whether the transmitters were exposed to the same activities.

2.5.2. Comparison of transmitter types

The accuracy with which each transmitter type quantified stoat locomotor activity was assessed by comparing the hourly activity budget constructed from observed video behaviour with the equivalent hourly budget of activity measured simultaneously by each transmitter. Accuracy was measured by degree of correlation. The transmitter with the highest correlation coefficient was deemed the more accurate transmitter. Correlations were assessed using SAS 9.1 PROCCORR. Any correlation coefficient greater than 0.7 was considered a satisfactory minimum standard for measuring locomotor activity in the field. Because the transmitters were sampling different activities, the validity of a between-transmitter comparison was assessed by *i*) assessing difference between transmitters in the characteristics of observed video–derived activity budget, and *ii*) constructing a 1-way ANOVA in SAS PROCANOVA to test for difference in mean hourly activity.

2.5.3. Assessment of timeout removal

The correlation in the previous section was repeated using telemetry data that had the transmitters' programmed nine-second timeout period removed. Correlation of telemetry activity with video-derived locomotor activity budgets was inspected for each transmitter with and without timeout removal to identify whether removal of the timeout period improved accuracy.

2.5.4. Refinement of the data set for estimating locomotor activity.

Potential for improvement to the data set for estimating locomotor activity was investigated by removing bouts of activity of less than a nominal 5 minutes duration. The impact of this removal on accuracy of activity measures was assessed by the strength of correlation between the hourly activity indices before and after removal for equivalent telemetry and video data.

3. Results

The stoats were active nest-builders and formed dense nest structures from the available straw and Dacron fibre. This meant around half of their activity inside of the nest-box was obscured from the view of the camera. Due to the unreliability of nest-box observations this study does not report on videoed activity within the nest-box. However, the nest-box video footage was used to verify when the stoats exited from and returned to the nest-box, and what stoats were doing during brief visits to the nest box during external bouts of activity.

Total video footage collected for each stoat ranged from 28 to 141 h (total 234.4 h – see Table 3). Considerably more video footage was collected for stoat 22 than for the other three stoats as more video recording equipment was available to record activity once stoat 21 was removed from the trials. All stoats spent a minor proportion of time 'digging' to attempt escape from their enclosures, except for stoat 21 that spent most of its time outside of the nest-box 'digging' to escape (Table 3).

3.1. Stoat behaviour in captivity

On average the stoats spent 13% of each day outside of the nest box. Stoats 11, 12 and 22 spent similar proportions of time outside of the nest box (8%, 7% and 10%

respectively) in contrast to stoat 21 that spent 27% of each day outside of its nest box (see Table 3).

Bouts of external activity (i.e., from leaving to returning to the nest box) ranged in duration from 10 s to 3.3 h, with a mean duration for all stoats of 21 min. Stoat 21 was active in longer bouts than the other three stoats (Table 4). Although most external bouts were less than 20 min duration, these bouts only accounted for a small proportion of total external activity. Over half of the total external time was spent in bouts lasting more than 80 min.

Table 3. Summary of video footage collected for behaviour analysis.

Stoat	Total footage (h)	Total time (h)		Proportion of time external	Total external activity observed (h)	Proportion of total external time observed on camera	Proportion of observed activity spent digging
		Internal	External				
11	39.7	36.5	3.2	0.08	1.7	0.58	0.04
12	49.8	46.3	3.5	0.07	2.0	0.59	0.01
21	33.2	24.2	9.0	0.27	3.3	0.37	0.71
22	141.0	127.4	13.6	0.10	13.2	0.97	0.39
			Mean =	0.13			

Table 4. Characteristics of excursions outside of the nest box.

Stoat	Average duration of excursions (min)	Total footage, min (hour)	Number of excursions	95% cl for duration (lower)	95% cl for duration (upper)
11	6.8	176 (2.9)	26	3.9	9.7
12	15.8	253 (4.2)	16	3.7	27.8
21	54.4	544 (9.0)	10	4.5	104.3
22	25.5	280 (4.7)	32	11.5	39.5

External activity typically consisted of alternating short bouts of walking/bounding or climbing and short or long bouts of standing/sitting still. Most locomotor activity produced continuously active transmitter signal, with fewer inactive breaks in between active bouts. The majority of the stationary activity produced an active transmitter signal, often with multiple inactive breaks.

Sustained bouts of locomotor activity were uncommon, largely due to the small travel distance within the enclosure. Even with breaks in locomotor movements, the stoats were often still sufficiently active to produce continuous activity in the telemetry feed.

Walking mostly took place in bouts of less than 5 min, and less than 3 min for bounding (Figure 3). There were many very short bouts of walking and bounding with short rests in between, or walking interspersed with brief periods of running, but these did not amount to a large proportion of total activity in that behaviour class.

Most climbing activity occurred as either short (>3 min) or extended (12 and 31 min) bouts. These long bouts of climbing were both done by a single stoat (stoat 22). Feeding activity tended to be in bouts greater than 5 min.

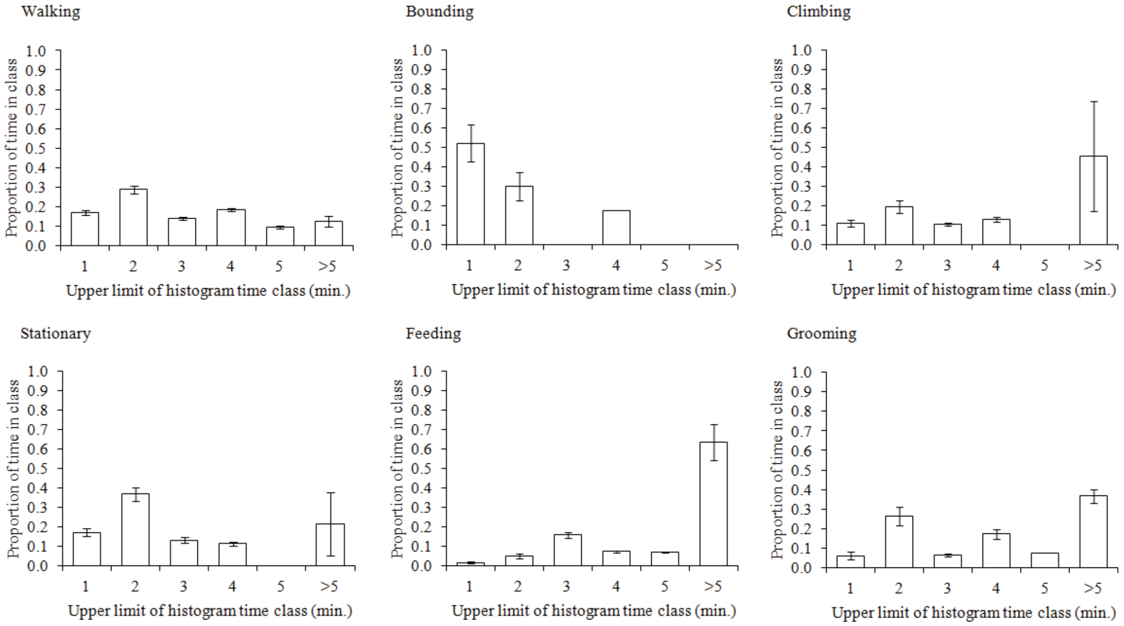


Figure 3. Characteristics of stoat activity outside of the nest box. Histograms show the relative duration of active bouts of each behaviour type as a proportion (score out of 1) of total time for each behaviour. Error bars show 95% confidence limits.

The proportion of external time stoats spent in each behaviour category was similar for stoats 11, 12, and 22, with most non-escape activity occurring as walking, feeding or standing (Table 5a). After adjusting for time spent digging and gnawing at the enclosure walls, the proportion of time spent walking, feeding or standing was 39%, 22% and 13% respectively (Table 5b). Stoat 21 differed markedly in behaviour from the other stoats, with most of its time outside of the nest box spent trying to escape (71% of external activity) or walking between points on the enclosure wall where the stoat chewed at the walls. Only stoat 11 (female) engaged in nesting behaviour (transport of Dacron or hay into the nest box and manipulation into nest lining).

All stoats except stoat 21 fed outside of the nest box in short and long bouts ranging from ten seconds to eleven minutes in duration. No external feeding behaviour was recorded for stoat 21 as all external behaviour with respect to food involved running out of the nest box to grab food and returning (with haste) back to the nest box, which was classified as walking or bounding behaviour. The other stoats spent most feeding time at or near the feeding bowl, and occasionally carried remaining food back to the nest box.

Table 5. Proportion (%) of total time stoats spent outside of their nest box engaged in each behaviour category a) including digging activity and (b) excluding digging activity. Results report on version (b) which eliminated digging data from the record base, as escape behaviour was deemed only related to the captive conditions and not representative of wild condition. Key: walking (W), bounding (B), jumping (J), climbing (C), stationary (S), nesting (N), feeding (F), grooming (G), brief excursion into nest-box (NB) and digging (D).

(a)

Stoat	Total external footage (h)	Behaviours									
		W	B	J	C	S	N	F	G	NB	D
11	1.7	33	5	1	4	15	9	24	1	3	4
12	2.0	30	2	0	11	16	0	35	0	5	1
21	3.3	22	1	0	3	1	0	0	0	2	71
22	13.2	23	1	>1	9	8	0	12	6	1	39
Overall mean		27	2	>1	7	10	2	18	2	3	29

(b)

Stoat	Behaviours								
	W	B	J	C	S	N	F	G	NB
11	34	6	1	4	16	9	25	2	3
12	30	2	0	12	16	0	35	0	5
21	77	2	0	10	4	0	0	0	7
22	38	1	1	15	13	0	21	10	2
Overall mean	39	3	1	12	13	2	22	6	3

In the initial days after radio tagging and release into the enclosures, the stoats all spend considerable time grooming, scratching and rubbing against structures in effort to remove the radio collars, both inside and outside of the nest box. This irregular behaviour largely ceased for all stoats after three days. Subsequently, external grooming behaviour was uncommon, with grooming observed outside of the nest box only for stoats 11 and 22. 95% of these grooming bouts lasted less than 4 min, and 50% less than 2.5 min.

Bouts of activity in the nest box determined from the telemetry feed, ranged from instantaneous movements (twitches) that trigger transmitter activity, to 20 min duration. Most activity occurred as short bouts. Longer bouts of activity were likely nest manipulation, grooming or feeding judging from the behaviours observed in the nest box video footage. Stoats spent a lot of time moving and shaping Dacron nest material into enclosed cavities, and re-arranged the nest box interior several times during a week of recording (unquantifiable due to obscured view).

On average, the four stoats spent 61% + 11% (SE) of time outside of the nest-box engaged in locomotor activity (Table 6). The proportions of external time spent in locomotor activity were similar for stoats 11, 12 and 22 (53% + 3% SE), with external time divided evenly between locomotor and stationary activity. Stoat 21 was exceptional with locomotor activity constituting 96% of external time, which was significantly different from the mean proportion of locomotor activity for data excluding stoat 21 (‘Tukey's studentised range test’, SAS system 9.1; all pair-wise comparisons between stoat 21 and each other stoat were significant at α=0.05).

Aggregation of component behaviours into continuous bouts of either stationary or locomotor behaviour (walking, running etc.) produced a profile of alternating stationary and locomotor activity. Both stationary and locomotor bouts outside of the nest-box took place mostly in bouts < ~2 min (Figure 4) and up to 33 min duration. There was little distinction between the characteristics of locomotor and stationary activity in terms of the proportion of total activity that took place in different size classes for bout duration.

Table 6. Proportion of total observable (i.e., captured by video) time outside of the nest box that was spent engaged in each behaviour class. Behaviour proportions show the proportion of time spent active as a fraction of the total time videoed. Key: S= stationary activity, L= locomotor activity, D=digging/chewing (escape) behaviour.

	% of total external activity (±SE)			% of total external activity excluding escape behaviour (±SE)	
Stoat	S	L	D	S	L
11	49	47	4	51	49
12	53	45	2	54	46
21	1	28	71	4	96
22	27	34	39	44	56
Overall	32 (12)	38 (5)	30 (16)	39 (11)	61 (11)
Overall excluding st-21	43 (8)	42 (4)	15 (12)	51 (3)	49 (3)

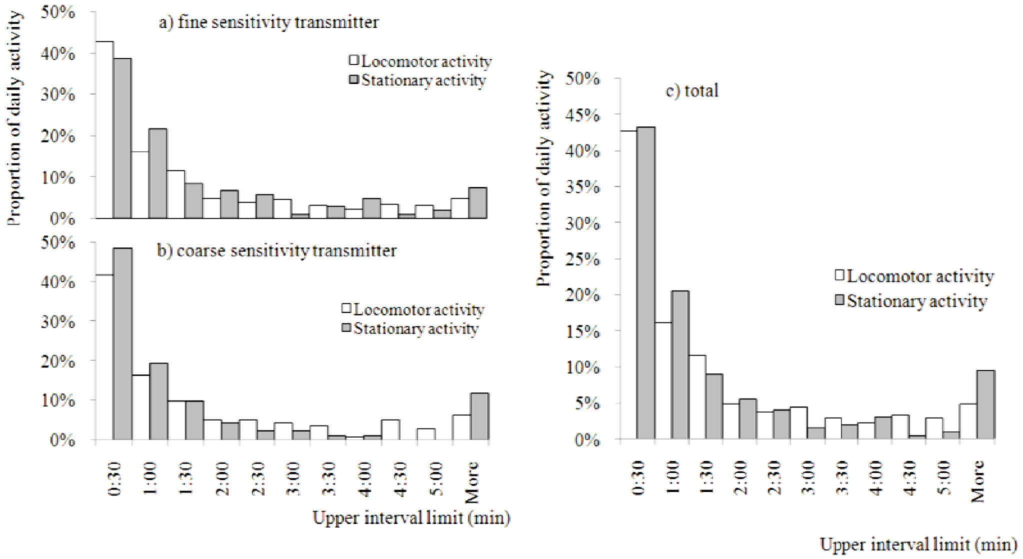


Figure 4. Characteristics of stoat activity outside of the nest box, comparing bout duration for continuous locomotor and stationary activity outside of the nest box for a.) the fine sensitivity transmitter b.) the coarse transmitter and c.) data from both transmitters pooled.

3.2. Comparison of transmitters.

3.2.1. Equivalence of behaviours experienced by the transmitters.

Each transmitter experienced a different subset of total stoat activity so could potentially have been subjected to a different proportions of each behaviour. This potential source of bias was examined in several ways. Both transmitters experienced similar activity in terms of duration of active bouts (refer to Figure 4). Analysis of variance of mean hourly indices for locomotor activity found no difference in mean activity between the coarse and fine transmitter data-sets for any of the three stoats for which there was both data available for both transmitters. Similarly, the Kruskal-Wallis test failed to find statistically significant difference in locomotor bout length between each transmitters' data-set when examined for all stoats pooled and for each stoat individually. This means that effectively the transmitters experienced equivalent behaviour regimes in terms of transmitter excitation and movement.

3.2.2. Transmitter performance.

Both transmitter types were superficially able to create 24-h activity budgets that resembled the video-derived 24-h activity profile (Figure 5). Both transmitters roughly described the same peaks in activity in the early morning, evening and around the middle of the day as the video derived 24-h profile, and the same low levels of activity between peaks.

The fine-sensitivity transmitter was consistently a better estimator of locomotor activity than the coarse-sensitivity transmitter, both for each stoat individually, and with all stoat data pooled (Table 7a). This was the case at hourly and 6-hourly (quarter-day blocks spanning sunrise, midday, sunset and midnight) time scales (tables 7a and b respectively). The fine sensitivity transmitter also performed better than the coarse transmitter in its ability to distinguish between internal (nest box) and external activity (Table 8).

Table 7 Correlation coefficients for comparison of transmitter activity indices (unadjusted and time-out adjusted data sets) with video-derived records of locomotor activity for the two transmitter types, for a) hourly timescale, b) quarter day timescale.

a). Hourly timescale correlation between video and telemetry

Data subsets		**Correlation coefficients (p>|r|)**		
Stoat	Transmitter	Unadjusted	Time-out adjusted	N (obs)
All Stoats	Fine	0.79 (<0.01)	0.80 (<0.01)	124
	Coarse	0.40 (0.01)	0.41 (0.01)	111
Stoat 11	Fine	0.56 (0.19)	0.535 (0.22)	20
	Coarse	0.49 (0.51)	0.517 (0.48)	11
Stoat 12	Fine	0.69 (0.08)	0.694 (0.08)	22
	Coarse	-0.14 (0.82)	-0.135 (0.83)	21
Stoat 21	Fine	-	-	-
	Coarse	0.102 (0.90)	0.328 (0.67)	20
Stoat 22	Fine	0.834 (<0.01)	0.853 (<0.01)	82
	Coarse	0.422 (0.04)	0.414 (0.04)	59

b.) Correlation coefficients at quarter-day time scale (3-hourly time divisions centered on sunrise, midday, sunset, midnight centred 3-hour blocks) between video and telemetry data. Numbers in brackets are p>|r|.

	Unadjusted (p-value)	**Timeout adjusted (p-value)**
Fine sensitivity	0.73 (<0.01)	0.75 (<0.01)
Coarse sensitivity	0.51 (<0.01)	0.51 (<0.01)

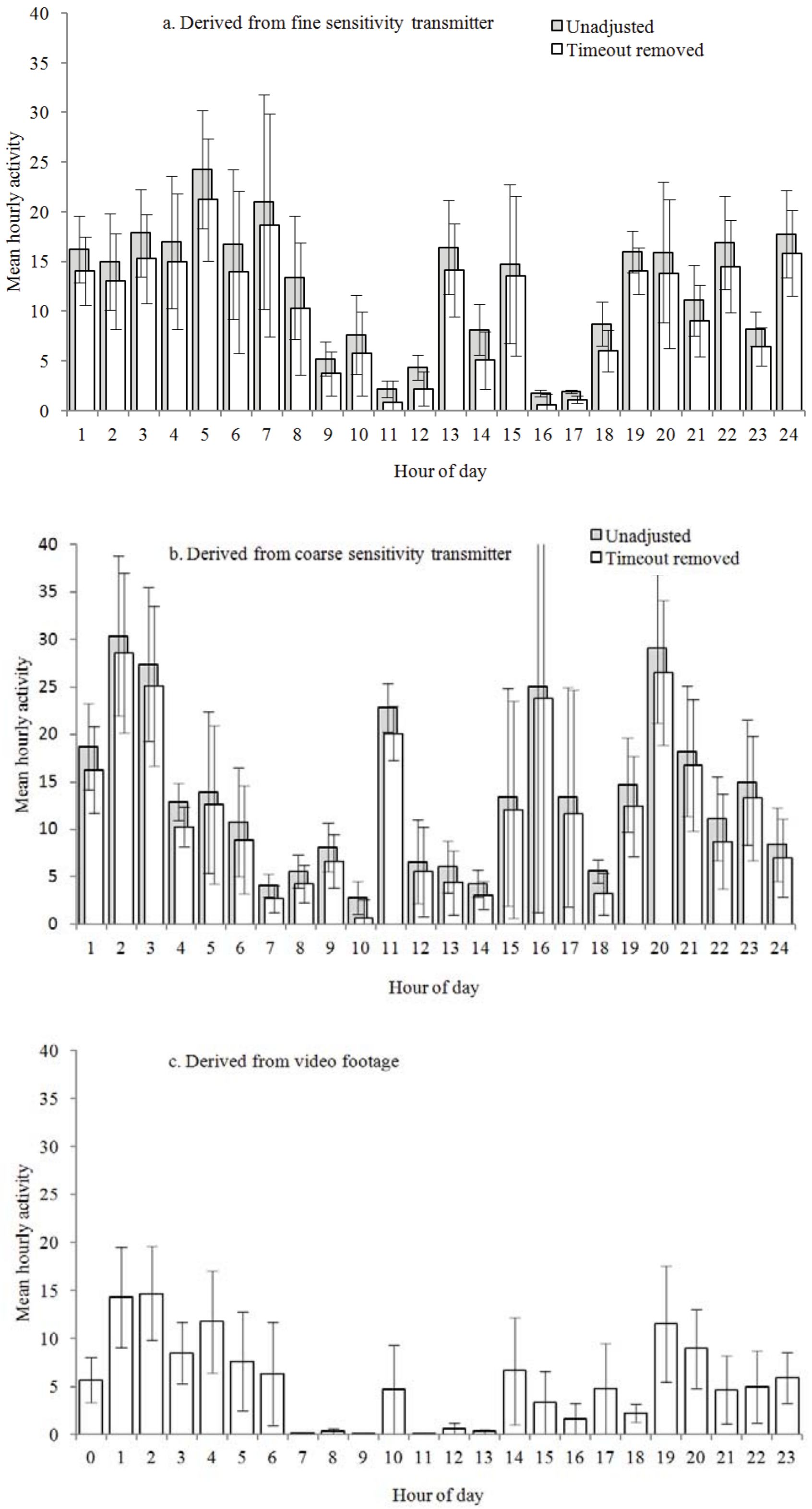


Figure 5. Mean (± SE) hourly activity patterns across the 24 h of the day. a) video-derived activity budget; b) telemetry-derived data for fine transmitter type; and c) telemetry-derived data for coarse transmitter type.

Table 8. Percentile values for duration of transmitter activity bouts, for fine and coarse transmitter types.

	Percentile			
	50%	**90%**	**95%**	
(a) Fine sensitivity transmitter				
Nest box	1.09	6.35	7.52	
External	10.55	40.80	50.35	*
(b) Coarse sensitivity transmitter				
Nest box	1.53	10.36	21.14	
External	6.89	15.32	15.56	

**note 64% of external bouts recorded by the fine transmitter were longer in duration than the 95th percentile for next box bouts (i.e., ~36% overlap), compared to near-complete overlap of coarse transmitter*

3.3. Factors influencing interpretation of data

3.3.1. *Variability in activity between stoats.*

Understanding variability in observed behaviours and derived activity measures is important for assessing applicability of this calibration study for use on wild stoats. Distinct variability was observed for stoats in a number of key ways. There was variability between stoats in terms of observed behaviour classes (Table 5), day and night activity levels (Figures 6 and 7), time spent outside the nest-box (Figure 5), proportion of locomotor activity (Table 6), and in the ways that the extent of correlation between video and telemetry hour activity indices.

However, the key outcome for this study was that the pooled activity data produced an hourly activity profile for at least one of the transmitters (fine sensitivity) that correlated significantly with observe locomotor activity levels. With a larger sample size of stoats to pool behaviour, a more confident measure of mean stoat activity would be expected to emerge.

3.3.2. *Timeout period.*

Timeout period amounted to 19% of unadjusted activity data (Table 9). The removal of transmitter time-out error made negligible difference to the correlation between transmitter and video derived locomotor activity levels (Table 9).

Unadjusted activity data consistently overestimated time-out adjusted data by 23 ± 3% (SE) when all stoat data was combined (Table 9). There was variability in this over-estimation between stoats (Table 10).

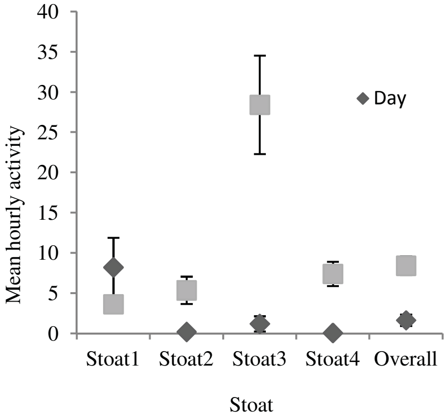


Figure 6 Day and night activity levels outside of the nest box

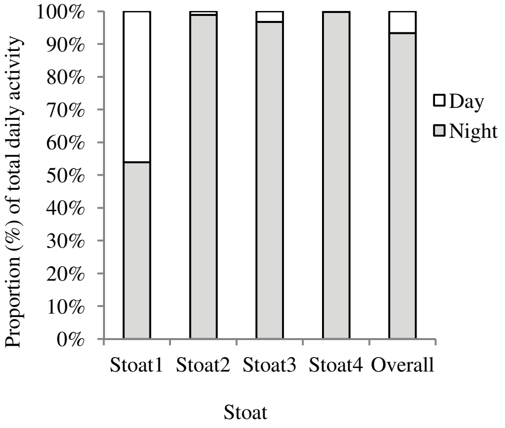


Figure 7 Day and night activity levels as proportion of daily activity

Table 9. Total timeout error component and degree of overestimation in activity data.

	Fine sensitivity	**Coarse sensitivity**	**Both Combined**
Timeout Component	19%	19%	19%
Overestimation	23%	23%	23%
Standard Error	13%	10%	8%

Table 10. Timeout overestimation in activity data for individual stoats.

Stoat	**Fine transmitter % Overestimation**	**Coarse transmitter % Overestimation**
1	19%	19%
2	23%	43%
3		26%
4	24%	20%

3.3.3. Overestimation of activity by transmitters.

Both transmitters overestimated real activity when assessed at hourly timescale partitioning of activity data. The fine-sensitivity transmitter overestimated locomotor activity more than the coarse transmitter (see Table 11). Overestimation of activity was markedly less when assessed in terms of total time outside of the nest-box (rather than only the locomotor component of time outside of the nest-box). The fine transmitter overestimated activity more than the coarse transmitter for both locomotor activity estimates and time spend outside of the next box. Overestimation was less after short bouts of activity were removed from the data that were below a 5 minute elimination threshold. The telemetry data became under-representative in its estimation of observed activity with an exclusion threshold greater than 5 minutes duration.

Removal of activity taking place in bouts of less than 5 min duration resulted in improved correlation at the hourly timescale between telemetry data and video observations of time spent outside of the nest box for the fine sensitivity transmitter but not so for the coarse sensitivity transmitter (Table 12). Correlation for the fine sensitivity transmitter was significant before and after removal of activity bouts <5 min, but the coarse sensitivity transmitter was not significant in either treatment.

Table 11. Comparison of transmitter performance in terms of the degree that the telemetry data overestimated actual observed activity.

Exclusion threshold (min)	**Transmitter type**	**Locomotor**	**External**
0	Fine sensitivity	667%	204%
	Coarse sensitivity	469%	157%
1	Fine sensitivity	466%	168%
	Coarse sensitivity	512%	123%
2	Fine sensitivity	700%	209%
	Coarse sensitivity	268%	104%
5	Fine sensitivity	278%	101%
	Coarse sensitivity	241%	91%

Table 12. Correlation coefficients for correlation between telemetry-based measures of hourly activity and video-based measures of times spent outside of the next box, with removal of active transmitter bouts of 5 minutes or less in duration (activity indices at hourly time scale). Numbers in brackets are p>|r|

	Unadjusted (p-value)	**Removal of blocks <5 min.** (p-value)
Fine sensitivity	0.71 (<0.01)	0.83 (<0.01)
Coarse sensitivity	0.51 (<0.01)	0.45 (0.01)

4. Discussion

The activity transmitters trialled here provided a telemetric measure of activity in captive-held stoats that was accurate both in terms of total activity taking place and activity structure over a 24-h day at two scales of analysis. Conclusions from this study were, however, based on just four individual stoats, one of which showed very different activity patterns compared with the other three, and the assumption needs to be made that other stoats in a population would wield a transmitter in the same way as these sample stoats. Although there were differences between stoats in their behaviours and activity levels, pooling of all stoats activity correlated strongly with the aggregated video observations for the fine transmitter, but not so for the coarse transmitter. The characteristics of stationary and locomotor activity sampled by coarse and fine transmitters were consistent between fine and coarse transmitter types, indicating that both transmitter types were experiencing the same kinds of activity. Comparisons of transmitter performance are therefore valid in terms the transmitters sampling from equivalent subsets of captive behaviour. An assumption was made based on manufacturer assurance that transmitters of each technical specification would perform the same so long as tilt switch orientation was consistent.

While useful correlation was found between video and telemetry measures of activity, the absolute structure of activity patterns in these captive stoats may not be representative of stoats in the wild as daily rhythms may be the result of entrainment into feeding and cleaning patterns of staff, and other inescapable noises associated with running the trails in a university building complex. While efforts were made to minimise noise, complete elimination was not possible. No effort was made to randomise feeding times or avoid human-induced patterns as the objective of the trial was to compare transmitter telemetry data with observed video footage. These data should not be used to compare to stoat activity budgets acquired in the field.

Direct comparison between the accuracy of the telemetry data obtained from the two transmitters would be most valid if both transmitters were sampling the same activity, which would require stoats to be tagged with both transmitters at the same time. This approach was not possible as tagging each stoat with two transmitters or building a transmitter combining both circuitries (a significantly larger collar package) would have encumbered the stoats unacceptably, and invalidated use for telemetry testing of a standard collar. However, the data obtained indicated that both transmitters experienced the same total locomotor activity over the two week-long trials.

The unadjusted data overestimates locomotor activity by nine seconds for every inactive transmitter change. The nine second timeout error made negligible difference to conclusions about patterns of structure in daily activity, but overestimated activity compared to actual activity observed. Both adjusted and unadjusted data sets overestimated observed activity by 1.5 to 7 –fold. It is likely that the impact of the nine second timeout error would be greater in a captive situation than in the field as the restrictive environment for locomotor activity would increase the frequency of inactive transmitter events (i.e., disjunctions in locomotor activity). The reasoning follows that because frequency of longer bouts of transmitter activity with increasing bout-size of locomotor activity, the data should have fewer breaks in activity with longer stoat ranging and hunting behaviour. So timeout error would diminish markedly in application of activity transmitters to stoat field-telemetry. Removal of shorter bouts of activity below a set exclusion threshold reduced the overestimation and improved correlation between telemetry and observed data sets. However at 5-minutes threshold the removal of activity began to cause underestimation of activity. So this study identified 5 minutes as an optimal approximate exclusion threshold for refinement of the telemetry data.

Stoats in their natural range are highly mobile, covering large distances quickly (Murphy and Dowding 1994), and they spend considerable components of their active time in extended bouts of locomotor activity (Erlinge 1980, Samson and Raymond 1995). The captive enclosures in this study were only 6 m across the long-axis, a ten-second journey for a walking stoat, and a two second sprint. In addition, with inanimate food provided in surplus, the stoats would lack the opportunity and stimulus to engage in activity equivalent to searching and acquiring prey. It is likely that the locomotor activity of these captive stoats was suppressed and disjointed compared to what it might have been in the wild. If this is the case then the activity transmitters would become a better estimator of locomotor activity in a field study because it is likely that bouts of locomotor activity would be more energetic and sustained.

No data were collected specifically to assess the effects of wearing the radio transmitters on the energetic cost, mobility and survival of stoats. We can report that after observing 234 hours of video footage there was no overt evidence of encumbrance or impairment to comfort behaviours or to feeding on the food provided. No comment can be made on the impact of the transmitters on the hunting ability of stoats as all food items were dead. Stoats were able to explore the enclosure, climb structures and manipulate material in the captive enclosure without any obvious impairment. It was clear though that stoats found the radio transmitters uncomfortable or irritating to wear initially and went to great effort to remove the collars when first attached. This behaviour largely ceased within three days. It is therefore recommended that any field study only commences data collection after a three day conditioning period.

Radio-tracking studies infrequently quantify the energetic and encumbrance effects of radio transmitters on stoats (Godfrey and Bryant 2003). In studies that address effects of radio transmitters on animals, mammals had the highest proportion of tests indicating a significant tag effect (Godfrey and Bryant 2003). Studies assessing effects of radio transmitters on small mammals are rare, and the only study found with similarity to this stoat telemetry study, documented that for captive weasels (*Mustela nivalis*), radio collars weighing around 4-5% of body weight did not affect weasel mobility or reproduction (Gehring and Swihart 2000). A review of effects of radio collars on black footed ferrets, a mustelid predator of similar morphometry but around twice the body mass of stoats, failed to find significant impact of radio collars on the ferrets, in terms of movement, survival and reproduction, across multiple study sites (Biggins *et al*. 2006).

While this study concludes that a 12 g Sirtrack activity mortality transmitter can be used to quantify stoat locomotor activity in the field, observations highlight an issue for transmitter accuracy during the first days after radio tagging when the stoats engaged in extensive efforts to removed the collars. This behaviour was largely gone after 3 days for all stoats. We therefore recommend that telemetry data from these transmitters are not included in activity analysis that take place within the first three days after radio-tagging. In the future as telemetry technology allows for further miniaturisation, it may be possible to have more complex and sensitive activity sensor capability, and onboard processing to better identify activity in-situ.

5. Conclusion

The purpose of this study was to calibrate the activity telemetry signal of Sirtrack 12 g activity/mortality radio collars against video footage of wild stoats in held captivity. The specific objectives were to: i) assess whether locomotor activity could reliably be identified from the telemetry feed; ii) ascertain optimal technical parameters for application in the field; and iii) refine data interpretation.

In this study activity transmitters were shown to accurately describe the locomotor activity of a sample population of stoats. Using these transmitters, locomotor activity can be discriminated from stationary activity in a telemetry signal feed in the field. The better choice out of the two transmitters tested for accuracy in estimating animal activity was the fine sensitivity transmitter. Transmitters with a mercury tilt switch oriented horizontally with respect to the stoats' shoulder axis (fine sensitivity) achieved better correlation with observed external activity and the locomotor component of that external activity, than the coarse sensitivity transmitter. This was the case at both hourly and quarter-day (3-hourly) time scales. However, the fine transmitter over-estimated activity by a greater degree, potentially requiring some correction to be applied.

Removal of the timeout component conveyed no benefit in terms of measuring the activity budget structure across the day, however its removal did decrease the degree of over-estimation compared to behaviour observed in video footage. Removal of short bouts of activity from the telemetry data set, as an estimation of nest-bound activity, reduced the intrinsic overestimation and improved concordance between telemetry and observed data sets. Five-minutes was identified as an optimal approximate exclusion threshold for removing over estimation. Future studies might look to quantify the overestimation (if any) with respect to activity in the field given dynamics of activity are likely different in an environment where stoats have access to 100 ha or greater home ranges and live prey.

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Chapter 3. Seasonal patterns in stoat (*Mustela erminea*) activity.

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Abstract

Eleven stoats (*Mustela erminea*) were tagged with motion-sensitive radio transmitters and monitored in Tongariro Forest during 1999 to quantify temporal patterns in stoat activity. Four monitoring 'seasons' representing early and late summer, autumn and spring seasons of the year, provided a total of 896 hours of stoat activity. On average, stoats were active 28% of the 24-hour day (seasonal range 16-41%). The total time spent active per day varied between seasons, and the partitioning of this activity through the day also varied considerably between seasons. Tracking tunnel visitation indices obtained in subsequent years showed similar seasonal patterns to the telemetry, except during early summer when tracking rates were lower than the equivalent locomotor activity estimate. Most radio-tagged stoats were predominantly diurnal in all seasons. Winter and spring had the largest proportions of daytime activity even though daytime was on average about 4 hours shorter during these seasons than in summer. Crepuscular peaks in activity were apparent in all seasons but particularly so during late summer. Activity was least structured in early summer, when activity was spread more or less evenly throughout the 24 hours of the day. Active periods usually lasted at least 40 min, and up to 43% of activity was maintained continuously for >3 hours. Variability in activity between and within stoats was high, but variability in spring was marginally lower than in the other seasons. Temperature had some influence on activity at an hourly timescale, and the correlation between activity and temperature strengthened with increasing timescale. Autumn activity comprised more extended bouts of movement so might represent a time of year when stoats are ranging further, or exploring or searching within their ranges more intensively. This suggests that stoat control and monitoring devices might be most effective in autumn.

Key words: stoats, daily rhythms, activity patterns, radio telemetry.

1. Introduction

Stoats (*Mustela erminea*) remain a significant threat to many New Zealand native fauna (Murphy and Fechney 2003). Numerous studies have documented direct effects of stoat predation on sensitive indigenous species such as mohua (*Mohoua ochrocephala*), kaka (*Nestor meridionalis*), brown kiwi (*Apteryx australis*) and yellow-eyed penguin (*Megadyptes antipodes*) (McLennan *et al* 1996; Wilson *et al.* 1998; Ratz and Murphy 1999; Dilks *et al.* 2003). Population modelling studies identify stoats as a significant extinction threat to some species if their predation impact is left unchecked (McLennan and Potter 1992; O'Donnell 1996). Nationally, numerous control operations target stoats to protect vulnerable or flagship species, or are conducted as part of integrated ecosystem-focused restoration programmes (Saunders 2000; Christie *et al.* 2004). Most are run by the Department of Conservation, but an increasing number of projects are being initiated and administered by local community groups.

Stoat control methods currently used in New Zealand are all variants of either kill-trapping, or poisoning via bait stations or with poisoned whole eggs (Dilks *et al.* 1996; Dilks and Lawrence 2000; Lawrence and Dilks 2000; Brown 2003; Parkes and Murphy 2004; Poutu and Warburton 2005). The efficacy of stoat control operations has increased over the past two decades through improvements to baits and lures (King and Murphy 2005; Miller 2003), trap and bait station placement and spacing (Dilks *et al.* 1996), and use of environmental queues to optimise pest control outcomes from management investment (Choquenot 2006, Brown 2003). Despite this, intensive trapping has in only a few locations reduced predation enough to allow population recovery, and even then results have been variable through time (Keedwell *et al.* 2002; Dilks *et al.* 2003; Gaze 2003; Moorhouse *et al.* 2003).

Difficulties in developing a reliable and affordable method of monitoring changes in stoat abundance in response to management have confounded the refinement of control methods. Having a precise monitoring system is critical both for accurately assessing the scale of the threat posed by stoats to various fauna within a management site, and for quantifying the operational performance of pest control (Brown and Miller 1998). A protocol for monitoring stoats based on footprint tracking tunnels has been shown to produce data consistent with monitoring by live-trapping, except at low density (Gillies and Williams 2001; Dowding and Elliott 2003; Gillies and Dilks 2003). Visitation to a network of tracking tunnels is a function of both the abundance of animals in an area and their ranging activity. The variability in stoat activity, both for individual stoats, and between individuals in a local population, over the typical 3-day timeframe of a tracking tunnel monitoring operation (Gillies and Williams 2001) or the 1-2 week timeframe of a trap service regime, is largely unknown and may vary between habitats.

While the activity rhythms of stoats have been studied in the northern hemisphere (Erlinge 1980; Debrot *et al.* 1985; Samson and Raymond 1995), less is known about stoat activity patterns in New Zealand. What is known has come from South Island beech forest and grassland habitats (Murphy and Dowding 1991; Alterio and Moller 1997), and has relied on detecting changes in radio transmitter signal intensity to distinguish between locomotor activity and rest. Activity sampled from only a few and usually brief periods per day, provides only a coarse picture of stoat activity.

The purpose of this research was to quantify in detail the temporal patterns and variability in the activity budgets of radio-tagged stoats in a central North Island podocarp forest, across a range of different timescales meaningful to current monitoring and control techniques.

2. Methods

2.1. Research overview

There were two components to this investigation into stoat activity; one using telemetry data from stoats radiotagged during 1999 to quantify fine-scale predictability in stoat locomotor activity, and the other using footprint tracking data collected between 2001 and 2008 to quantify patterns in stoat visitation to tracking tunnels.

The telemetry study involved radio-tagging stoats with motion-sensitive radio transmitters and continuously monitoring the radio signals from the stoats to derive 24-h activity budget information. Multiple radio-tagged stoats were monitored at the same time over 1-3 week periods on four occasions during the year corresponding to late summer, winter, spring and early summer (see Table 1). All reference in this report to ‘seasons’ and ‘seasonal patterns’ refer to these four monitoring periods. Five telemetry stations were set up at high-points across the study area, each equipped with a radio receiver (Telonics TR4) and a fixed three-element Yagi antenna mounted upon a 6 or 12 m mast. Teams of field workers camped at each station, achieved up to 24-h continuous activity data collection during rostered monitoring-shifts. The listening stations were positioned to allow continuous radio reception from individual or multiple stoats, although there were times when stoats moved out of range of the listening stations. The goal was to collect activity data from up to five stoats monitored simultaneously and continuously over approximately five days in four 'seasons' throughout the year. Logistical problems that included terrain-related radio reception issues, premature transmitter failure, and stoat dispersal from the study area, resulted in more intermittent radio monitoring of a variable number of stoats.

The footprint tracking tunnel analysis involved processing tracking data for stoats, rats and mice to assess seasonal and temperature-related variation in tunnel visitation. A network of tracking tunnels was installed and serviced four times per year since 2001 as part of kiwi sanctuary management. Stoat visitation data records from 2001 to 2008 comprised fifteen lines spanning Tongariro Forest (Figure 1), positioned on semi-random transects. Each line consisted of ten tunnels positioned at 50 m spacing, but only five odd-numbered tunnels were baited with rabbit and used for assessing stoat visitation (see Martin *et al* 2011 for full method description).

2.2. Study Area

This study was undertaken between January and December 1999 in Tongariro Forest, central North Island, New Zealand. A core study area of *c.*800 ha on the eastern side of Tongariro Forest was the focus of the telemetry component of the study, centred on a major ridge system running eastward from the Waione Stream to the head of the Okupata Stream (Figure 1), and ranged in altitude from 520 to 830 m a.s.l.

A secondary study area, Pukepoto Forest, lying to east of Whanganui River, was used to assess the repeatability of tracking results by comparing with a nearby site of similar climate, terrain form and nearby vegetation composition. Tongariro Forest was logged for timber up until 1972, so the vegetation today consists of small fragments of un-logged podocarp/broadleaf forest restricted to the deep valleys or inaccessible ridges, surrounded by vegetation at various stages of regeneration.

Most ridge-tops in Tongariro Forest are currently covered in large expanses of toetoe (*Cortaderia toetoe*), often traversed by derelict roads and logging skid sites. Unlogged vegetation comprises stands of rimu (*Dacrydium cupressinum*), montane totara (*Podocarpus cunninghamii*), miro (*Prumnopitys ferruginea*), matai (*Prumnopitys taxifolia*), and tawa (*Beilschmieda tawa*) trees, with dense sub-canopy vegetation. Stoats were known to be widespread throughout the 20,000 ha extent of Tongariro Forest at the time of this study (Martin *et al.* 1999).

Tongariro Forest is one of five nationally designated kiwi sanctuaries (Robertson 2004, Holzapfel *et al.* 2008). Management for kiwi protection commenced in 1996 with small scale investigative predator trapping in a central core area that ran until 1998 (Martin *et al.* 1999). Kiwi management then reverted to nest manipulation and ex-situ rearing of eggs and chicks (Colbourne 2005) until 2001 when the site was designated a national Kiwi Sanctuary. Management then diverted to experimental assessment of the value of aerially deployed 1080 poison for kiwi protection via secondary poisoning of stoats (Etheridge 2002, Sutton *et al.* 2007). Tongariro Forest south of Whanganui River became a treatment area for a BACI-styled trial design to test efficacy of aerially deployed 1080 poison applied in 2001 and 2006 for stoat control outcomes (Westbrooke *et al.* 2003). Pukepoto Forest was the experimental non-treatment control area. Data collected within the 12 months following aerial pest control operations in the forest were deleted from the data set prior to analysis for both Tongariro Forest and Pukepoto Forest to avoid potentially confounding pest control effects.

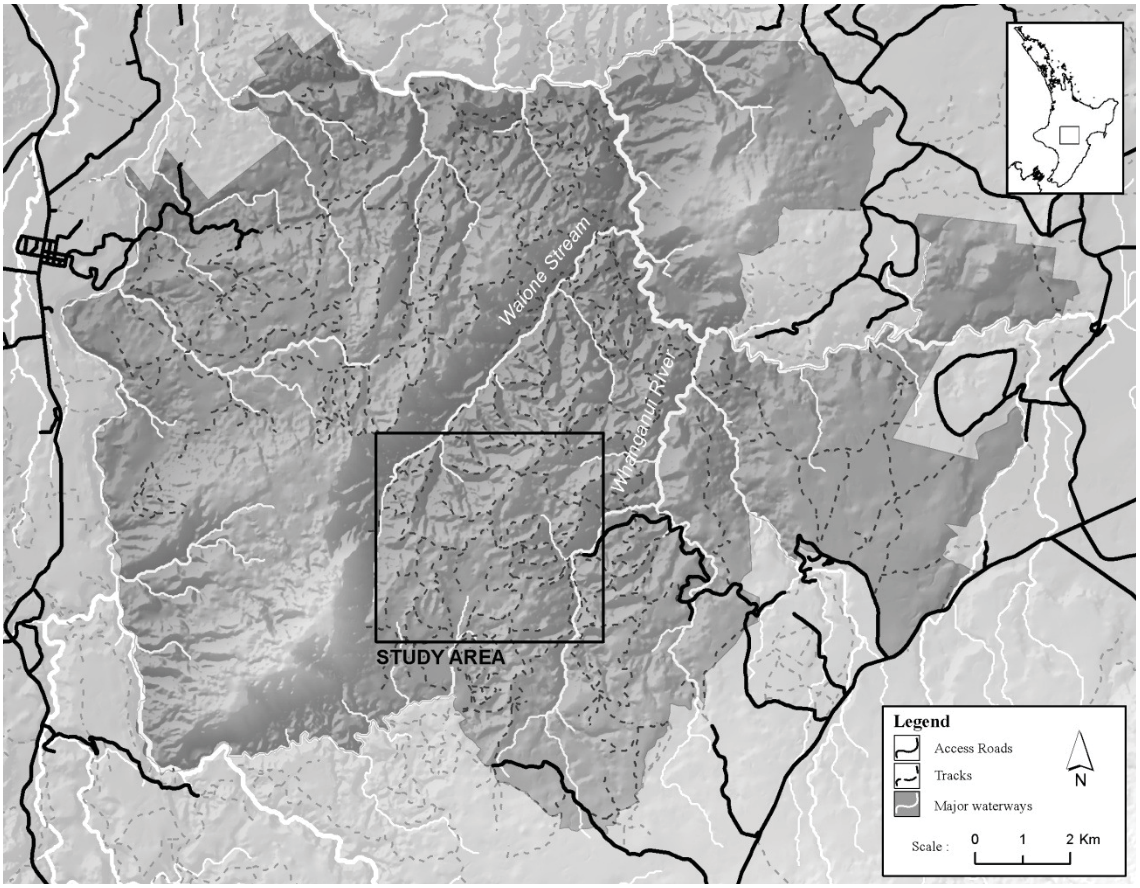

Figure 1. Location of study area, Tongariro Forest park boundary (darker grey shading) and study area (solid line).

2.3. Capture and tagging.

Stoats were trapped in wooden live capture “tippee” traps (King 1973) along a 5 km stretch of road running through the centre of the study area. Most of the 40 traps (40 in total) were placed within 20 m of roads, and were pre-baited with hen eggs for two weeks (traps locked open), then baited with dead day-old-chicks or mice whilst set. Only adult stoats were radio tagged as determined by observing scrotal testes (males) or visible nipples (females). Captured stoats were immobilised at a nearby field base using portable halothane aspirator equipment constructed for this study.

All stoats were kept in holding cages until they had taken food and water, and then released at their points of capture. Activity data collection for each stoat did not commence until at least three days after release to allow stoats to adjust to wearing the transmitters.

2.4. Activity transmitter function and settings

The activity transmitters used in this study (Sirtrack New Zealand Ltd., Havelock North) were micro-processor controlled and contained small mercury tilt switches to detect stoat movement. The tilt switch position aligned with the shoulder-to-shoulder axis of the animal when the collar was fitted correctly. The micro-controller was programmed to produce one of two different radio pulse-rates depending on whether the stoats were active or inactive. The active pulse rate (55 ppm) engaged as soon the transmitter sensed motion whilst the inactive pulse rate (20 ppm) engaged after ten seconds of inactivity (i.e., each transmitter activity bout was at least nine seconds longer than the animal was actually active). The purpose of this ten second ‘timeout period’ was to make successive rapid short bursts of movement (typical of locomotor activity) appear as one continuous bout of activity, thereby making it easier to distinguish periods of locomotor activity from non-locomotor activity. However, this has potential for overestimation of total activity (Martin and Potter unpubl. data).

2.5. Data collection and processing

Telemetry data were collected in the field by continuously listening to the radio signal from each individual stoat and recording the time of day when the radio transmitter changed between the active and inactive pulse-rates. The timeout period component was removed from the data by subtracting nine seconds from each time entered for when the transmitters went inactive. The duration of each active bout was calculated from the start and stop times of transmitter activity. Bouts of activity lasting less than a nominal 5 min were labelled as ‘den’ activity and removed from the data. This threshold was chosen following a pilot study of captive stoats, sourced from Tongariro Forest and tagged with the same transmitters (Martin and Potter unpubl. data.), which found improved estimation of activity after removal of blocks of transmitter activity of less than 5 min duration. Based on the activity characteristics of captive stoats, this was assumed to be activity taking place in the stoat’s den before emerging to hunt. The data remaining after removal of bouts of less than 5 min duration were considered as being representative of locomotor activity.

Hourly indices of activity were generated from telemetry recordings, calculated as the sum of the number of seconds the transmitters were active during each hour of monitoring, but expressed in units of minutes of activity per hour (for simplicity in interpreting data).

Tracking tunnel visitation data were processed to calculate percent visitation per season. Stoat home ranges may span several kilometres (Moller and Alterio 1999, Murphy and Dowding 1994), and it is generally considered that stations need to be at least 1 km apart for statistically independent (Gillies and Williams 2001, Brown and Miller 1998). Consequently there can be multiple tunnels tracked by a single stoat on any one line during a monitoring session and current operational best practice requires that only presence/absence for each line is considered. Consequently, tracking tunnel visitation data were reduced to the presence or absence of mustelids on a tracking tunnel line during a monitoring session. The mean line-tracking rate per season was calculated by pooling data from both years.

Daily maximum and minimum temperatures for the 2001 and 2008 tracking tunnel datasets were obtained from an automatic weather station situated in Taumarunui approximately 20 km north of the study area.

Temperature data were collected from two sources. During the 1999 telemetry study two “Tiny-Tag” temperature data loggers (Gemini Data Loggers, UK) were deployed; one on a ridge-top high point (“Red Clearing”), the other on the river flats of the predominant river valley in the forest (“Waione Stream”).

The temperature loggers were programmed to take a temperature reading every hour, and temperature data were joined to respective hourly activity records using look-up functions in MS Excel. Stoat activity data were also compared against the temperature recorded two hours prior to the activity; this is termed ‘templag’ in the model. This allowed assessment of the effects of both ambient temperature and recent past temperature on stoat hourly activity.

2.6. Statistical analyses

Tracking tunnel data were analysed using a general linear modelling approach. Seasonal patterns in tracking tunnel visitation activity were assessed using PROC GLM (The SAS System v. 9.1). Tracking tunnel indices for rats and mice were based on the proportion of tunnels tracked on each line. Seasonal mean estimates and corresponding standard errors were estimated using the LSMEANS statement within the PROC GLM procedure.

Tracking tunnel visitation by stoats was analysed using the same procedure except that the sampling unit was visitation to a line rather than visitation to a tunnel. The ANOVA model statement was set to treat individual tunnels as subjects of repeat measurement, and the model equation was fitted with ‘year’ and ‘season’ model terms to factor variability arising from these temporal effects.

Telemetry data contained random effects from differences between individual stoats that could not be controlled due to the random nature of live-capture, and because different stoats were monitored in different seasons. Consequently, these data were analysed using the PROC MIXED procedure (The SAS System v. 9.1). Hourly activity indices were arcsine transformed to normalise the data. This transformation is common for proportion data that ranges from -1 to 1 (Zar 1996).

General linear (REML) models were constructed in PROC MIXED to assess the strength of model factors on activity patterns, and to determine seasonal differences in these patterns. Stoat activity patterns were assessed at three time scales (hourly, daytime vs. night-time, and quarter-day divisions), and seasonal means and model effects at the different time scales were all recalculated derived from the hourly dataset. Day and night activity was categorised according to sunrise and sunset times. The ratios of daylight:night hours were 15:9 and 11:13 for the warm and cold seasons respectively, and model outputs for the day/night timescale were standardised for these differences in hours of light. Equal daylight and night activity estimates would indicate that activity was random or taking place in proportion to the number of daylight/night hours for that season.

Quarter-day classes were assessed with activity data sorted into four equal 6-hour classes bounded by 0300, 0900, 1500 and 2100 hours representing midnight, dawn, midday, and dusk activity. The relative influence of seasonal, timescale and temperature effects were assessed by examining different combinations of main effects in several parallel mixed models.

Akaike information criterion (AIC) values were used as a measure the relative strength of each candidate model, and AIC weights were calculated to assess the relevance of differences between AIC values relative to the lowest (best) AIC value (Burham and Anderson 2002). Correlation between hourly activity and temperature and corresponding significance level were calculated using PROC CORR.

Activity means presented for the various time classes were derived from weighted least squared means estimates generated from the PROC MIXED model outputs. During the two seasons when females were present, observed differences between male and female activity raised the question of whether it was appropriate to pool male and female data. Differences in mean activity between males and females were assessed by introducing a ‘sex’ term in the same SAS mixed model statement.

3. Results

From the eleven stoats (9 males and 2 females) caught and radio tagged during the four seasons, a total of 896 hours of telemetry observations were recorded (Table 1). Stoats were monitored in continuous sessions ranging in length from 4 to 98 h.

Five of the eleven stoats were radio-tracked across two seasons. During the late summer and autumn monitoring periods, stoat and telemetry sample sizes were small due to premature transmitter failure and loss of tagged individuals from the study area.

3.1. Locomotor activity component

Raw activity data contained at least 6% timeout error, and 11-28% of resulting total activity was designated as non-locomotor activity (see Table 2). Both components were subtracted from the data to generate the stoat activity components that follow.

3.2. Duration of active bouts

Telemetry data were converted into a time-series of activity bouts (see Figure 2). Active bouts ranged in duration from the five-minute cut-off threshold to over five hours (Table 3). Stoat activity typically occurred in bouts of 40-50 min with both short (<20 min) and long (>6 h) rests between bouts.

Table 1. Identity of stoats and monitoring achieved in each season.

Season	Stoat (eartag ID)	Sex	Total monitoring achieved (h)	Longest period of continuous monitoring (h)
Late summer: 21 Jan.-10 Feb. 1999	H493	m	20.0	12.5
	H495	m	40.5	13.5
	H497	f	17.0	10.0
	H499	m	18.0	7.0
		Total	95.5	
Autumn: 17-30 April 1999.	H484	f	33.5	9.0
	H493	m	49.0	26.0
		Total	82.5	
Spring: 17 Aug.-3 Sept 1999.	H488	m	6.5	6.5
	H489	m	39.5	39.5
	H490	m	119.0	98.0
	H491	m	41.0	27.9
	H492	m	158.0	41.5
		Total	364.0	
Early summer: 27 Nov.- 3 Dec. 1999.	H448	m	56.0	56.0
	H488	m	90.0	53.5
	H489	m	87.5	87.5
	H490	m	24.5	24.5
	H492	m	96.0	62.0
		Total	354.0	
Grand total			896.0	

Table 2. Timeout error and den activity components (% of activity from the original data set that is due to the 9 second timeout error, or that has been identified as den activity), with standard error in brackets

Monitoring period	Minimum timeout error component (±SE), %	Est. den activity component (±SE), %
Late summer	4.9 (0.8)	13.2 (3.5)
Autumn	9.9 (2.6)	27.7 (8.5)
Spring	6.6 (0.9)	16.9 (2.5)
Early summer	4.2 (0.6)	11.1 (1.7)
Mean	6.1 (0.6)	16.4 (2.1)

All stoats in all seasons engaged in activity bouts of greater than two hours duration and at least some continuous bouts of activity exceeding four hours were recorded in all seasons. During the late summer and autumn monitoring periods, when females as well as males were monitored, females were also active for long periods. There was no detectable difference between sexes in mean bout length (Wilcoxin test scores 172 (p=0.17) and 357 (p=0.19) for late summer and autumn periods respectively).

Three quarters of daily stoat activity occurred in bouts lasting more than 42 min, and up to 43% of total seasonal activity occurred in bouts of more than 3 hours duration (see Table 3). All monitoring periods except Autumn were similar in the distribution of the length of active bouts (see Appendix 1). During the autumn period activity occurred in longer bouts, with half of the total activity occurring in bouts longer than 2½ hours.

Table 3. Transmitter-active bout size distribution, and the proportion of total seasonal activity occurring in bout classes.

		Frequency distribution of active bouts.			Active bout size for quartiles of of total seasonal activity*.			Proportion of total seasonal activity occurring in bouts >3 hours.
Season	Number of bouts	Mean (h:min)	75%-ile (h:min)	Max (h:min)	25% (h:min)	50% (h:min)	75% (h:min)	
Late summer	49	0:41	0:45	4:52	0:39*	1:38	2:13	24%
Autumn	36	0:49	0:52	4:59	0:52	2:28	3:50	43%
Spring	154	0:38	0:31	5:10	0:32	1:29	2:28	17%
Early summer	152	0:46	1:11	4:13	0:50	1:25	2:09	16%

* For example, should be read as '25% of total seasonal activity occurred in bouts less than 0:39 h:mm.

3.3. Seasonal changes in daily activity

On average stoats were active 28% of the time recorded, ranging between 16% and 41% across the four seasons (Figure 3). The apparent differences in mean activity between the monitoring periods in Figure 3 were all non-significant due to within-season variability. Data for males and females were combined for the late summer and autumn periods, as there was no significant difference in mean daily activity between sexes, and no difference in the pattern of distribution of active bouts between the males and females.

Seasonal mean stoat locomotor activity correlated significantly with seasonal mean daytime temperature (r^2=0.80), and appeared similar in profile (Figure 3). Seasonal mean tracking tunnel visitation rates for stoats also correlated strongly with equivalent temperature records taken during the tracking tunnel monitoring sessions of 2001 to 2008 (r^2=0.63).

There was no correlation between mean temperature and both mean rat and mouse seasonal tracking rates (r2=0.12 and 0.05 respectively) – see Figure 3. Tongariro Forest (1999) and Taumarunui (2001-2008) seasonal mean temperatures were very similar and the seasonal pattern was significantly correlated (r^2=0.96), confirming relevance of using temperature data from this location off site in tracking rate analyses.

Mean tracking rates for each season corresponded with equivalent telemetry-based seasonal estimates for late summer, spring and autumn, both in terms of magnitude and seasonal profile of relative change. However, the tunnel tracking rate was proportionally higher during early summer compared to the telemetry activity rate. Early and late summer tracking tunnel visitation rates were higher than autumn and spring visitation rates.

Variability between stoats in their individual seasonal activity was high. In all seasons there were individuals with both high and low daily activity, and day-night activity (refer Appendix 2) noting however that Autumn stoat sample size was inadequate to fully assess the characteristics of activity within that season (n=2 stoats). Spring was the time of year with the least variability both between and within the activity of individual stoats.

The seasonal pattern of tracking rates in Tongariro Forest was similar to that within Pukepoto Forest, although absolute tracking rates were higher in Pukepoto Forest.

3.4. Seasonal changes in day and night activity

Stoats were typically diurnal throughout the year with between 65% and 83% of the recorded daily activity taking place during daylight hours (see Table 4). Stoats were more diurnal during autumn and spring than during the summer periods, both with and without adjustment for the longer daylight hours at the respective times of year, but were similarly active day and night during early and late summer (Figure 4). This was also the case when seasonal differences in daylight hours were accounted for (Appendix 2).

Table 4. Mean day and night activity with SE in brackets, and the proportion (%) of daily activity taking place during daylight and night hours. Mean activity indices are a proportion ranging from 0 (not active at all) to 1 (active all of the time).

Season	Mean daylight activity	Mean night activity	% of total daily activity during daylight hours	% of total daily activity during night hours
Late Summer	0.38 (0.04)	0.34 (0.06)	65%	35%
Autumn	0.54 (0.12)	0.09 (0.07)	83%	17%
Spring	0.45 (0.07)	0.12 (0.04)	76%	24%
Early Summer	0.43 (0.11)	0.39 (0.11)	65%	35%

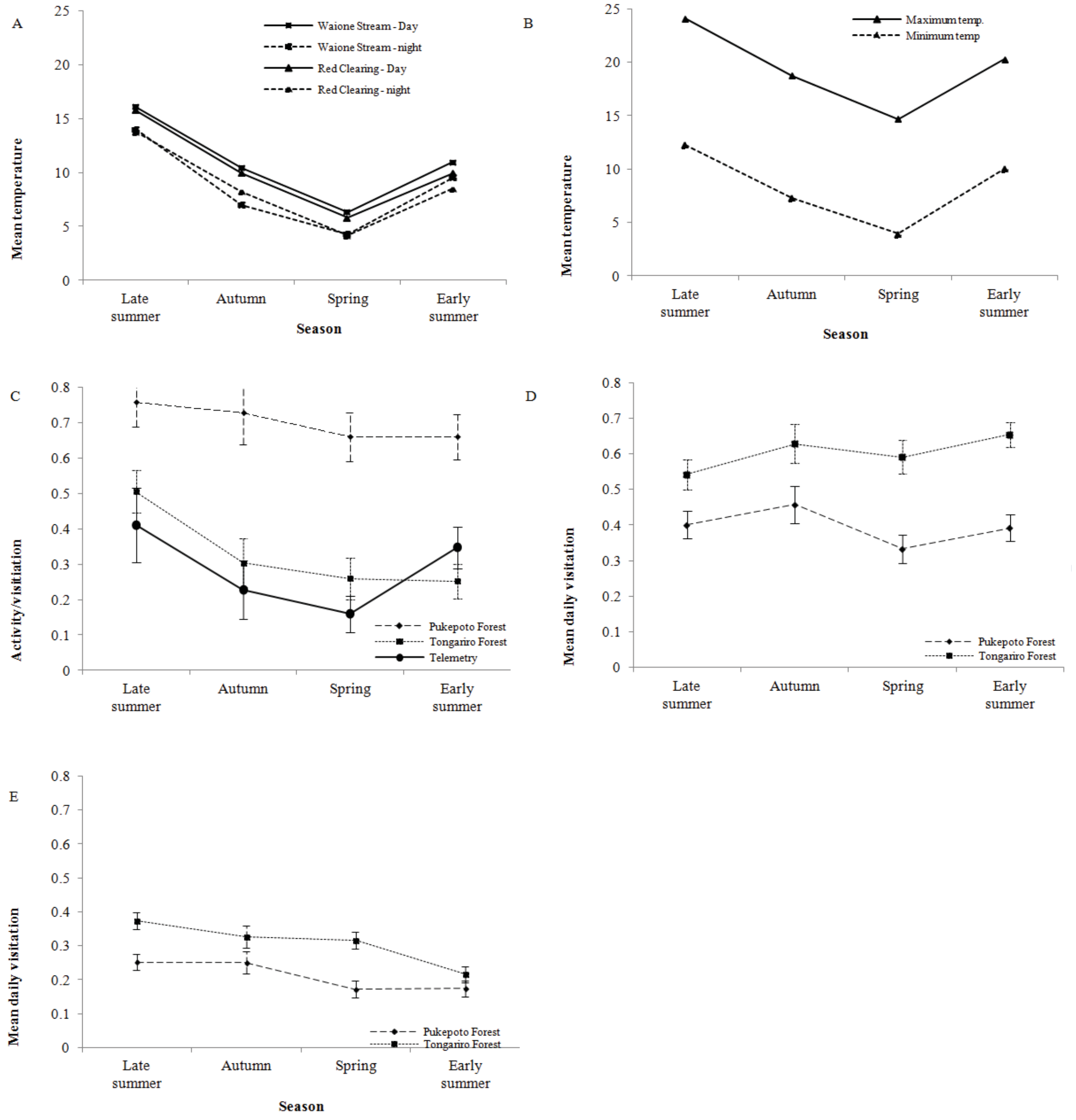

Figure 3. Seasonal change in visitation to footprint tracking tunnels and radio-telemetry-based activity estimates for Tongariro Forest and Pukepoto Forest and corresponding temperature profiles. a.) Mean daylight and night temperatures for two temperature probes situated on a ridge-top (Red clearing) and in a deep valley floor (Waione Stream during 1999; b.) Seasonal mean temperatures from a nearby weather station (Taumarunui) taken during the tracking tunnel monitoring periods of 2001 - 2008. c.) stoat visitation and equivalent locomotor activity profile; d.) rat visitation; e.) mouse visitation; Error bars denote standard error. Charts c, d and e comprise seasonal means derived from GLM/LSMEANS estimates. Charts a and b are arithmetic mean temperatures. Standard errors in mean temperatures were too small to display as temperature was consistent between and within days.

3.5. Seasonal changes in dawn, midday, dusk and midnight partitioned activity

Stoat activity assessed at a quarter-day timescale (dawn, midday, dusk, and midnight intervals) was weakly structured (Figure 5), and confirmed the observations made at day/night and hourly timescales. During the late summer, activity was most often recorded during dawn and dusk quarters, with little activity across the middle of the day. In contrast, in autumn 84% of the whole day's activity took place in 12 out of the 24 hours (dawn and midday quarters), including 57% of the total during the midday quarter. Early summer activity was spread more evenly throughout the day. However, despite apparent structure in daily activity, the variability in activity within seasons and between individual stoats was so large that no within-season differences in activity during quarter-day time classes were significant, except midday and midnight activity during spring (p=0.03, 10 d.f.).

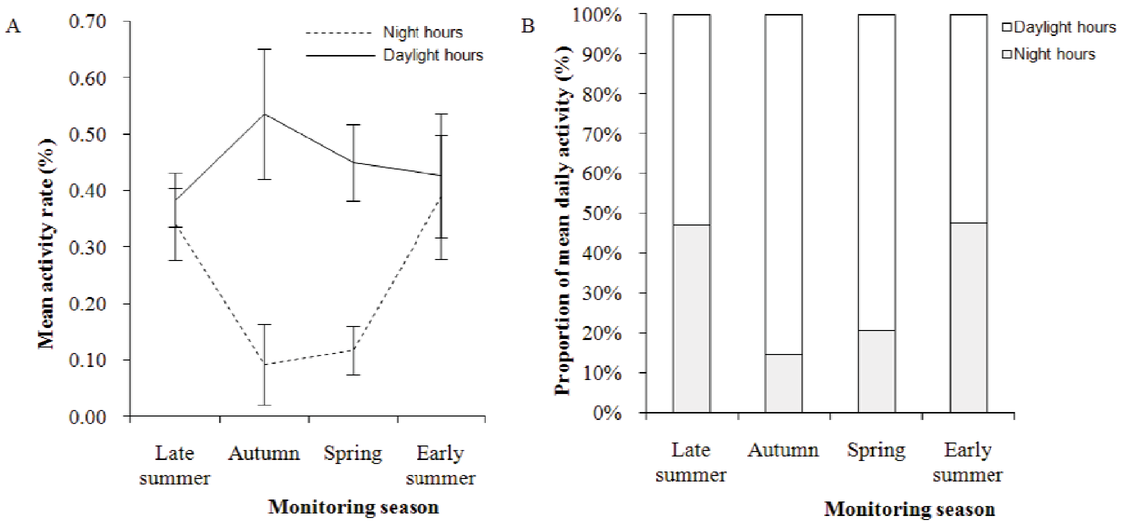

Figure 4. Seasonal changes in the day and night activity budget of stoats: a.) Day and night activity rates standardised for seasonal differences in day length (classes bounded by sunrise/set) with standard error bars, and b.) day and night components of the total activity of each season.

3.6. Seasonal changes in 24-hour activity patterns

Stoats were active at any time of the day in all seasons, although they seemed to avoid going out during the hottest hours of the day during late summer, irrespective of cloud cover (radio tracking observation). Twenty-four hour activity profiles varied significantly with season (Figure 6). Stoats were partially crepuscular in all seasons, especially during the late summer, although they were active almost any time during early summer. Autumn and spring activity was largely diurnal, and long continuous activity pulses often commenced along with the sunrise (radio-tracking observation).

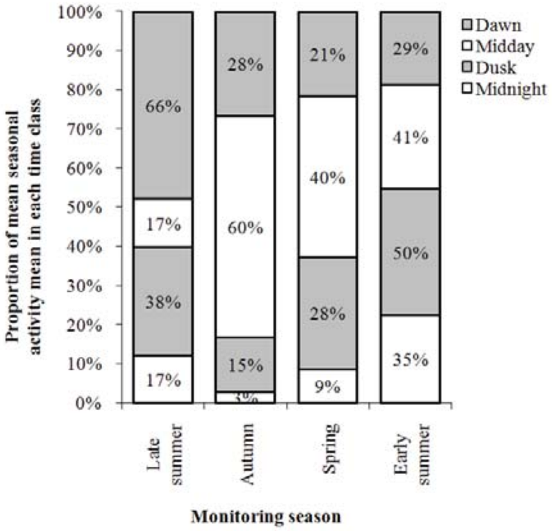

Figure 5. Seasonal changes in the activity budget of stoats: relative proportions of each seasons activity during four equal sub-day divisions (classes partitioned by the times 0300, 0900, 1500, 2100 h) representing dawn, midday, dusk and midnight activity, with data values printed within columns.

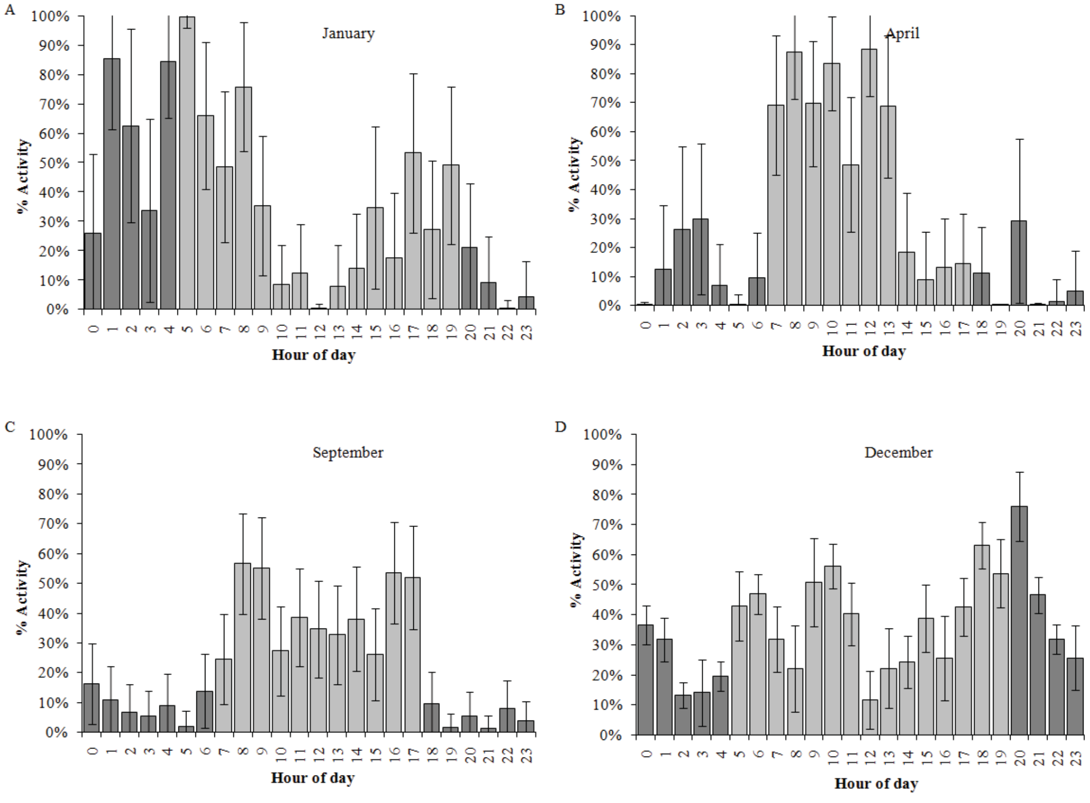

Figure 6. Seasonal changes in 24 h activity patterns. Error bars refer to standard error. Light and dark bars show day and night hours (respectively) in relation to sunrise and sunset times. X-axis labels refer to low bound of each hourly interval.

3.7. ANOVA model effects

Four iterations of a mixed linear model were run with variation in timescale and temperature terms to assess the relative strength of main effects (see Appendix 3 for ANOVA outputs). Model fit was best at the hourly timescale but AIC differences were minor so there was no particular benefit of one model over another in terms of model selection. Seasonal effect was statistically significant in all models. There was no detectable difference between males and females at any time scale.

The effect of temperature on stoat activity was only marginally significant at hourly time scale, and likewise for the temperature two hours previous to the activity bout. However, the importance of temperature increased in significance when examined at longer time divisions throughout the day (i.e. at the quarter-day and day-night temporal scale). There was little discernible difference between statistical effects of temperature and the 2-hour-lagged temperature on hourly activity. In all seasons day time activity was lower at times of higher temperature (Table 5). Conversely night time temperature was consistently positively correlated except for during the autumn monitoring season. However, there was little significance in night time correlation coefficients.

Table 5. Correlation between day and night mean activity estimates and mean temperature for the corresponding hourly activity data used to generate the mean activity.

Season	**Mean activity %**	**Mean temp. (°C)**	**Day/night class**	**Pearson correlation coefficient**	***p***
Late summer	34%	16.08	Night	0.14	0.43
	38%	16.15	Day	-0.39	0.001
Autumn	9%	6.93	Night	-0.10	0.57
	54%	10.70	Day	-0.22	0.1
Spring	12%	3.91	Night	0.05	0.55
	45%	6.21	Day	-0.19	0.01
Early summer	39%	7.80	Night	0.16	0.08
	43%	10.23	Day	-0.12	0.08

4. Discussion

Stoats in Tongariro Forest were active at all times of the day, and there was discernible variation across seasons, although not statistically significant due to variability in a small sample size and noting the fact that seasonal data were not replicated between years. Seasonal patterns in both telemetry based activity estimates and tracking results agree with high December and January, and low April and September trap catch results from Fenn-trapping done in the Tongariro Forest at an earlier time (Martin *et al.* 1999). In all seasons there was more daytime activity than night-time activity, particularly during April and September. Generally there was a daily cycle in activity, but the pattern varied across seasons. During late summer activity was concentrated around dawn and dusk, but in autumn and spring most activity was during the day. This is likely due to of the seasonal pattern of nesting activity of birds with the summer increase in the number of chicks on nests perhaps motivating stoats to spend more time hunting in trees. Indeed one of the radio-tagged stoats was found dead up a tree during late summer, apparently having fallen from a high place. Early summer activity was the least structured, and during that season stoats could be out of their dens virtually any time.

These findings suggest that there is no especial time to focus trapping intensity for adult stoats based on their activity levels alone. A possible exception might be during autumn (April monitoring) when a considerably larger proportion of activity comprised extended bouts of movement. This might represent a time of year when stoats are ranging further, or exploring or searching within their ranges more intensively, in which case they would be more likely to intercept a control or monitoring device at this time of year. If it could be established that this behavioural change was a response to a diminishing food resource, then stoats might be more trappable, and more inclined to respond to baits and lures during this season than at other times of the year. Autumn might also be a time when poisoning operations achieve a higher degree of secondary poisoning of adult stoats than other seasons. Variability in stoat activity within and between individuals was high, but September was the time of year with least variability. Thus long term abundance monitoring using tracking tunnel might be marginally less confounded by individual activity patterns in September than in the other months. The data also suggest that stoat activity patterns during early summer might make them less likely to encounter traps. This means that trapping intensity should be increased during early summer, perhaps by increasing trap density or service frequency, in order to maintain interception rates and thus stoat population control; alternatively, trapping might be discontinued during early summer and effort directed towards trapping during periods of the year when stoats are more active and hence more likely to encounter tunnels.

The seasonal rates of footprint tracking tunnel visitation were similar in pattern to mean activity rates based on radio telemetry of individual stoats. Furthermore, the single-year data set of the telemetry monitoring agreed in pattern and scale with the multi-year tracking tunnel data set. So although the seasonal telemetry trends were not replicated between years, there is strong indication that the results are valid and representative. The two activity monitoring methods measure different quantities. The radio telemetry measured the activity patterns of a few individual stoats in high detail, but across only one year. The tracking tunnel monitoring provides a coarse measure of activity across a population. By pooling data from many tunnels across many years, this data set is of sufficient magnitude to estimate an intrinsic seasonal pattern for visitation at the site. However, chance of tracking tunnel visitation is due to a combination of both how many animals are near a tunnel (stoat territory density and dispersal rate of transient individuals) and the intrinsic activity the those animals. The absolute values of the two seasonal activity profiles cannot immediately be compared due to this fundamental difference in the data. But relative quantity (or season rank) can be compared for coarse tendency. The similarity in seasonal patterns in the tracking tunnel and telemetry datasets is consistent with a general model where intrinsic activity (and possibly prey availability) operates as a key influence for tracking tunnel visitation at a station rather than abundance. However, the early summer tracking rates increased markedly from winter levels compared to the equivalent telemetry activity measures, suggesting that abundance has a stronger influence at this time of year than activity. This is consistent with an ecological argument that at times of year when stoat numbers are reasonably stable (e.g. winter and spring), chance of visitation would be influenced by individual activity (and therefore prey availability). Juvenile stoats and cryptic females irrupt from spring dens during late spring and early summer, which explains the increase in tracking visitation observed in the data from winter to early summer. The decrease in intrinsic individual activity during early summer may be due to reduced hunting effort at a time of year when prey availability (rodents, birds and invertebrates) increases with spring productivity. The tracking tunnel seasonal visitation profile in Pukepoto Forest was the same as that in Tongariro Forest, providing replication of the result in a nearby alternative site.

A study of stoat daily activity patterns in the South Island New Zealand (Alterio and Moller 1997) found that in coastal grassland stoats were more active by day in spring, which agrees with our findings. However, they also recorded equal activity day and night in autumn, which differs from the strong diurnal pattern we recorded in Tongariro Forest. These studies may not, however, be comparable, as Alterio and Moller (1997) sampled activity using a markedly different telemetric method than ours, using variations in signal volume to distinguish between locomotor activity and rest. Also, on most occasions they recorded just one or two radio fixes per animal by day or night in each 24 h sampling period. In contrast, our data were sourced from transmitters that changed pulse rate when movement started, so activity patterns were derived from continuous monitoring of individual stoats for up to 98 h at a time. In South Island beech forest stoats were more active during night time that during daytime (Murphy and Dowding 1991), but again this study used fluctuations in signal intensity to determine activity. They were, however, able to establish that spot checks of activity using this method produced comparable results to activity measures derived from stoats that were followed continuously.

Samson and Raymond (1995), using methods similar to ours, studied time budgets of stoats in forest habitat in southern Quebec during summer under similar day length conditions (i.e., 16L:8D light and dark hours), and monitored individual stoats for continuous periods of up to 36 h. They found, as did we, that stoats had predominantly diurnal activity rhythms characterised by short bouts lasting less than 40 min in most cases. However, the stoats in this study were active on average for only about 5 h per 24 h period (21%) compared with the 8.4-9.8 h activity per 24 hour period (35-41%) we recorded during summer. Erlinge (1980) reported active periods of 6.5 (27%) and 8 (33%) h respectively for two males in the northern hemisphere spring (Sweden). The comparable average activity level for male stoats during spring in our study was markedly lower at 3.8 h (16%). In a South Island beech forest, stoats were found to be active 52% of the time during summer, and 31% of the time during autumn (Murphy and Dowding 1991). These differences in activity will certainly depend heavily on regional differences in the type and density of prey, since when food is scarce, hunting trips have to be longer. In a captive study of weasels (Price 1971), an animal similar in form and physiology to the stoat, locomotor activity rate in a fixed enclosure size was found to increase with food deprivation, suggesting a physiological basis to the intensity of activity.

The extent that stoats occupy and defend a home range or territory varies with age, social status and time of year. Sub-adults tend towards dispersing movements, while adults are residents or transients according to age and experience (Sandell 1986). Territoriality and home range size varies cyclically with season; large summer and autumn home ranges contract approaching winter, then in spring there is a shift towards extended ranging in search of mates (Sandell and Liberg 1992), with increasing overlap in territory (Erlinge and Sandell 1986). Most stoats in this study were probably resident adults with stable home ranges within each monitoring period (Martin and Potter, unpublished radio tracking observations). In a long term predator control programme most resident animals would be removed during the early stages of the control operation, so an important part of improving the efficacy of a sustained predator control campaign is to understand the behaviour of transient adults and dispersing juveniles that are likely to reinvade a site (Barlow and Norbury 2001).

The influence of temperature on stoat activity was dependent on temporal scale. At an hourly scale of examination there was only weak influence on stoat activity. Generally stoats became more active with decreasing temperature during the day time, and stoats were equally influenced by temperature two hours prior to activity. At night time stoat activity tended to increase as temperature became warmer. At the larger temporal scale the temperature effect became more significant. The effect of temperature increased in significance when examined at longer time divisions throughout the day (i.e. at the quarter-day and day-night temporal scale). Daily activity and seasonal activity levels were positively correlated with seasonal mean temperature, and the same tendency was found in the seasonal tracking tunnel visitation rates. This means that activity and temperature had a strong relationship at larger time scale, but perhaps had less influence on the smaller scale activity decisions made by stoats. The difference in activity response to temperature between day (negative correlation) and night (positive correlation) requires further investigation, but may be related to times when their prey are active and corresponding hourly structure in the stoat daily activity pattern. For example there is evidence in our data of stoats becoming active around dawn, probably in response to the dawn chorus that is frequent in Tongariro Forest. These dawn hours tend to be colder. Once stoats have fed at this time there will likely be a tendency to rest as the birds become less vocal, so activity would be expected to decrease as the morning temperature rises.

Duration and daily frequency of weasel activity was found to be influenced by ambient temperature in Poland (Jedrzejewski *et al.*2000). However, decisions may be related to prey activity response to temperature. For some of the stoats prey species activity is known to be influenced by temperature. Mouse (*Mus domesticus*) activity was found to be strongly correlated with temperature in south-east Australia (Twigg and Kay 1994) and likewise dormouse (*Muscardinus avellanarius*) activity in southern England (Bright *et al.* 1996). While the strong correlation between stoat activity and temperature has predictive value, and intuitively this result appears to have an energetic basis, to establish whether this is an ecologically causal relationship would require other important factors to be modelled at the same time. For example, the autumn and spring seasons, when rainfall, soil moisture and vegetation saturation are greater, may be times when stoats are less successful at detecting and taking down prey, so avoid being active at these times to conserve energy. April activity shows some sign of this possibility as this was a season with fewer but markedly longer bouts of locomotor activity. In another study temperature was found to influence stoat habitat use (Christie *et al.* 2009), and mean geographic ambient temperature was found to influence body growth (Yom-Tov *et al.* 2010), so results of this study align with current knowledge about the influence of temperature on stoat activity.

Activity transmitters of the type used here are highly sensitive to motion and provide a precise measure of stoat movement. By recording the time when the transmitters change between active and inactive modes during continuous monitoring of the signal, stoat activity is measurable to a precision equal to the pulse rate of the transmitters i.e., 1 or 3 sec for the transmitter settings used in the study. Activity budget information derived from these data provides an accurate description of when the collared stoats are active and when they are at rest. However, these transmitters do not provide information about the intensity of the activity, nor whether the activity is locomotor or stationary (e.g. grooming, eating). This study estimated locomotor activity by excluding data that were likely to be den activity, based on a separate study which calibrated the transmitters using captive stoats (Martin and Potter unpubl. data). Removal of these data made little difference to the observed temporal patterns in daily activity and to the statistical conclusions made, suggesting that these activity transmitters, with the data processed as in this study, provide a reasonable estimate of locomotor activity.

Key recommendations for pest management that arise from our findings are that i) summer and autumn are marginally better times of year than spring to intercept stoats with monitoring or control devices; ii) spring is a marginally more accurate time of year for annual population monitoring as abundance indices are least confounded by the activity of individuals; iii) trapping operations would benefit from servicing lines with minimal disturbance during early morning and late afternoon, especially during autumn, to avoid human disturbance at these highly active times of day and iv) high variability in the activity of individual stoats means one particular trap layout and service regime will not necessary be optimal for all stoats.

This study has found patterns in stoat locomotor activity that add to our understanding of stoat activity in New Zealand, but we caution that the findings may not be valid for all habitats or management sites across New Zealand. Seasonal conditions and activity trends have been estimated from short monitoring periods, but these may not account for all parts of stoat annual activity profile. Conclusions made in this study are most valid for adult stoats in sites with similar prey availability and land cover conditions to Tongariro Forest.

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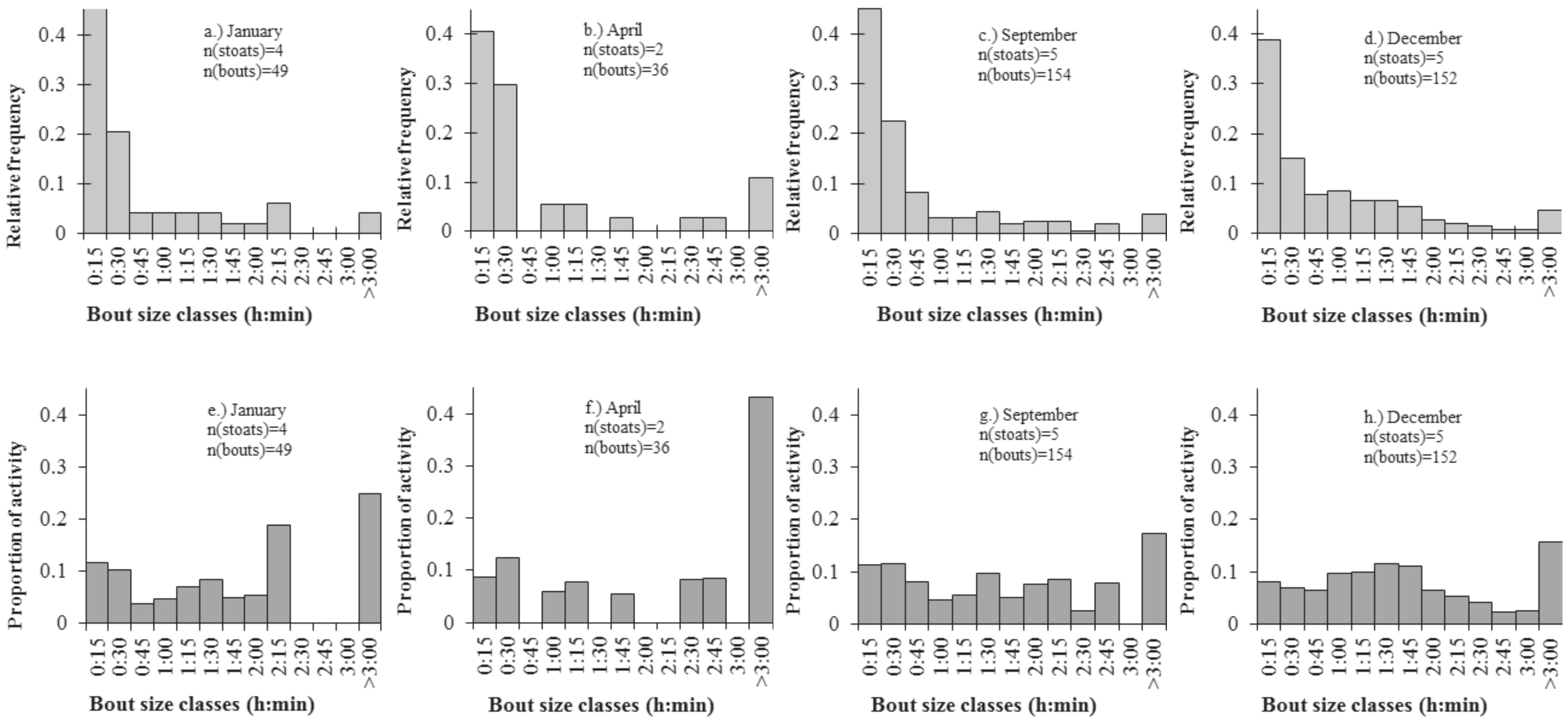
Appendix 1. Relative frequency distribution of locomotor bouts in different size [i.e., duration] classes, for each monitoring period (a-d), and the proportion of the total active time for each season taking place in each class (e-h) for each season. Bouts greater than 3 hours duration are grouped into a single class. x-axis labels refer to the upper bound of each class. Sample sizes refer to the total number of bouts in each class.



Appendix 2. Daily and day-night activity for stoat individuals in each season.

Season	ID	Mean % activity for season (±SE)	Day % activity*	Night % activity*
1	493	36 (9)	35 (0.13)	36 (12)
	495	39 (7)	40 (0.09)	38 (10)
	497	23 (12)	35 (0.12)	13 (13)
	499**	78 (27)	41 (0.11)	*99 (10)*
2	484	26 (7)	40 (0.12)	13 (9)
	493	31 (7)	64 (0.10)	7 (6)
3	488**	69 (14)	99 (10)	41 (11)
	489	16 (5)	21 (7)	12 (5)
	490	34 (3)	56 (5)	16 (4)
	491	15 (5)	31 (7)	4 (4)
	492	30 (4)	49 (6)	13 (4)
4	448**	67 (8)	44 (10)	*87 (8)*
	488	28 (6)	31 (7)	26 (9)
	489	36 (6)	55 (8)	20 (7)
	490	54 (11)	57 (13)	52 (15)
	492	25 (5)	33 (7)	17 (7)

*note day and night activity adjusted for seasonal difference in daylight hours.
**activity data collected for stoat 448, 488 and 499 in these seasons were inadequate to provide a representative estimate – the observed high activity estimates are partly an artefact of sampling bias for these stoats that were in best radio reception when running around, but poor reception when inactive.

Appendix 3 a. Model outputs from PROC MIXED analysis of variance. Boldface p values were significant at alpha=0.05; b. AIC value table from respective models.

Effect	***d.f.***	***f***	**p > f**
Season	3	3.62	**0.013**
Sex	1	0.51	0.4737
Hour	23	1.76	**0.0151**
Temp	1	3.21	0.0735
Season*Hour	69	2.14	**<0.0001**
Season	3	3.63	**0.0127**
Sex	1	0.55	0.4592
Hour	23	1.5	0.0626
TempLag	1	3.36	0.0671
Season*Hour	69	2.16	**<0.0001**
Season	3	4.7	**0.0029**
Sex	1	0.65	0.4187
Qday	3	6.86	**0.0001**
Temp	1	7.02	**0.0082**
Season*Qday	9	6.95	**<0.0001**
Season	3	6.78	**0.0002**
Sex	1	1.06	0.3038
DN	1	34.8	**<0.0001**
Temp	1	15.9	**<0.0001**
Season*DN	3	14.35	**<0.0001**

Appendix 3 b. Model fit statistics for outputs above. Akaike weights (w_i *(AIC)*) can be interpreted as the probability the model is the best model given the candidate models (Burnham and Anderson 2002).

Model main effect set	**AIC**	**Δ_i (AIC)**	**w_i (AIC)**
Season, sex, hour, temp, season*hour	1394.3	0.2	0.47
Season, sex, hour, templag, season*hour	1394.1	0	0.52
Season, sex, qday, temp, season*qday	1417.3	23.2	0.00
Season, sex, dn, temp, season*dn	1400.7	6.6	0.02

Chapter 4. Sensitivity of GIS derived terrain variables at multiple scales for modelling stoat (*Mustela erminea*) activity.

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Abstract

This research combines automated Geographical Information Systems (GIS) and iterative logistic regression scripting to data-mine for terrain variables that predict stoat (*Mustela erminea*) visitation to stations in a New Zealand indigenous forest, and explore the impact of spatial analysis scale on modelling outcomes. Variables such as curvature and density of tracks are dependent on the scale of the analysis window used to compute the values. With automated GIS analysis it is possible to derive a large number of terrain parameters that vary in computational scale. It is common for analysts to make nominal choices regarding the size and type of analysis windows, when calculating these derived variables, without testing the statistical validity of that choice. Stoats are a significant pest in New Zealand and threaten extinction for a number of vulnerable native species. Field data on stoat activity, based on footprint tracking tunnels, were used to develop an Akaike Information Criterion (AIC) optimized predictive model applying step-wise model selection. Once the optimal model was determined, the sensitivity of the model to different terrain parameters was tested by systematically substituting each variable and calculating the difference this made to the model equation. The most dominant terrain predictors influencing stoat visitation were proximity to tracks, altitude, northerly and easterly aspect, mean curvature, and topographical position and slope. Proximity to tracks and mean curvature were the most sensitive variables to analysis scale. This paper demonstrates the importance of considering scale in developing predictive models and the need to test many ecologically sensible analysis scales in order to find the best predictive variables. The paper concludes that GIS-based spatial data extraction, combined with automated statistical data-mining methods, has an important role in developing accurate animal activity models.

Keywords: Terrain, Predictors, Scale, Sensitivity, GIS, Regression, Habitat

1. Introduction

Geographical Information Systems (GIS) provide a powerful platform for geostatistical predictive habitat modelling (Palmeirim 1988, Pereira and Itami 1991). The programmability of current GIS and statistical software and increasing computer processing power have made a range of different data mining approaches more accessible for spatial modelling. The benefit of using GIS is that multiple spatial data layers describing terrain form or geographic features can be rapidly processed or recalculated to generate ecologically meaningful test data for assessing driving factors that determine animal abundance. A range of analytical approaches exist to derive models which make spatial predictions on animal distribution based upon environmental measures (Haefner 1996, Guisan and Zimmermann 2000, Skidmore 2002, Wintle *et al.* 2005). Logistic regression modelling is a statistical framework for analysing binomial observations such as the presence or absence of a species. This form of modelling has been applied in many ecological fields to predict animal distribution (Pereira and Itami 1991, Austin *et al.* 1996, Bian and West 1997, De la Ville *et al.* 1997, Osborne *et al.* 2001, Wintle *et al.* 2005, Newton-Cross *et al.* 2007, Belongie 2008, Coulon *et al.* 2008, Syartinilia and Tsuyuki 2008). With logistical regression modelling, a set of potential predictor variables are assessed to quantify how each predictor influences the observed response data and thereby derive predictive or causal relationships. Using conventional methods, the selection of candidate variables for regression analysis was limited to familiar or ecologically sensible combinations of environmental descriptors chosen by the researcher (Scott *et al.* 2009, Skidmore 2002). Modern model selection techniques allow for a broader exploratory approach indentifying subsets of predictor variables that best fit response data (Burnham and Anderson 2002).

A spatial analyst building a logistic regression model has to make a series of choices regarding not only how to analyse data from a set of spatial predictors, but what scale and calculation to use when transforming geospatial data layers into derived descriptors of landscape/terrain condition. For example, common terrain descriptors such as slope, curvature, and topographical position are each calculated from a digital elevation raster data layer, entering user-specified programme parameters including the size and shape of analysis window (Lo 2007). The choice of window size introduces user bias that propagates through the analysis to affect modelling inference (Behrens *et al.* 2009).

Variables can be considered as direct, i.e. empirical measures of environmental conditions (e.g. altitude, temperature) or indirect i.e. constructs of direct variables interacting spatially (e.g. soil moisture, land cover) (Guisan and Zimmermann 2000). Using automated GIS, based on scripts (e.g. Arc Marco Language) or graphical model interfaces (e.g. ArcGIS Model Builder), a large number of derived topographical variables can be generated that vary in content and scale. The rapidly increasing suite of vector and raster analysis functions available in GIS, plus the increasing availability of spatial data sets, means a large number of indirect spatial variables could be derived as candidates for habitat modelling. When this geoprocessing capability is combined with automated statistical analysis that identifies variables that have the best predictive performance, then there is a potentially powerful tool for building predictive spatial models for a range of species.

Data mining is a systematic process of selecting, transforming and analysing large volumes of data to extract unknown or unexpected information (Foody 2003). Data mining as applied to habitat modelling traditionally relies on some prior knowledge of the ecological system and careful consideration of scale and accuracy of the source data (Foody 2003, Austin 2007, Mennis and Guo 2009). However, data mining using automated computer search routines has potential for deriving predictive equations with accuracy beyond what can be achieved based on a researcher's intuition alone, as hidden or non-intuitive variables can be brought together to form statistically optimised predictor variable sets. To develop the most predictive model possible, many spatial and computational forms of derived variable can be tested. This automation has the usual issues associated with statistics and GIS such as uncertainty, collinearity, model performance, and computational efficiency (Ofir and Kuri 1986, Mason and Perreault 1991, Foody 2003, Brambilla *et al.* 2009, Zhang and Wu 2010).

This paper uses a simple semi automated data mining framework to explore the impacts of spatial analysis scale on modelling the activity of stoats (*Mustela erminea*), which are a significant conservation pest in New Zealand. A large set of monitoring data quantifying presence/absence of stoats at stations across a threatened species management site was made available for analysis. This data set was combined with derived topographical layers to develop a predictive model describing likelihood of stoat visitation across an extensive forested mountainous area. The model development involved three main steps: (1) characterising the environments using GIS at a range of analysis scales; (2) logistic regression modelling to determine the best predictive equation from a set of readily available spatial data layers; (3) sensitivity analysis to demonstrate the impact of analysis scale on model outcomes.

2. Methods

2.1. Study area and monitoring data

The study area comprised approximately 20,000 ha of contiguous forest to the west of Tongariro National Park, in the central volcanic plateau of the North Island, New Zealand (Figure 1). Altitude ranges from 300 m to 830 m and the landscape is dissected by streams and four-wheel-drive access tracks. Tongariro Forest is one of five nationally-designated kiwi sanctuaries (Robertson 2004). Stoats are a key threat for kiwi recovery (McLennan et al. 1996) and kiwi management in the sanctuary focuses on regular stoat population control.

Footprint tracking tunnels are a common method for monitoring small mammalian pest species in New Zealand (*Jones et al.* 2004). The tracking tunnels used here were 600 mm long, 100 mm wide black plastic tunnels containing an ink pad with two removable papers secured either side (King *et al.* 1994).

Rabbit bait placed in the centre of the tunnel lures animals to walk across the ink pad and leave discernible footprints. One hundred and fifty tracking tunnels located on 30 permanent transects (5 tunnels per line at 100 m spacing) have been in operation monitoring stoats in the study area since 2001 using a standardised protocol (Gillies and Williams 2001).

Tracking tunnel sites were located by handheld GPS to ~10 m estimated positional error (Burrows 2000). The mean tracking rate for each tracking tunnel was calculated from presence/absence data pooled across the four seasonal inspections each year.

Figure 1. Study area, and location of tracking tunnels (black dots) on lines within the Tongariro Forest Kiwi Sanctuary operational boundary.

The tracking tunnel data used here were obtained over seven years (2001-2008), but two pest poisoning operations occurred during this period so data collected during the 12 months following these operations were deleted in order to minimise any confounding influence from the resulting artificial change in population makeup. The resulting data set comprised ~22 repeat measurements at quarter-year intervals of the presence or absence of mustelid footprints pooled for the 150 uniquely labelled tunnels.

2.2. Terrain data, GIS and data processing

Terrain data used here were derived from a 25 m resolution Digital Elevation Model (DEM) sourced from Landcare Research (Baringer *et al.* 2002), LINZ-NZ260 feature layers, and Department of Conservation file records (see Table 1). Mean annual temperature (MAT) and mean solar radiation (MAS) were sourced from the Land Environments of New Zealand (LENZ) data set with 25m resolution. The base data-sets were converted into a range of terrain indices using geoprocessing functions in ARCGIS 9.3. Values were extracted from these terrain indices and appended as attribute information to each tracking tunnel within the point feature data layer. The resulting spatial data file (the .dbf component of a shapefile) was immediately accessible to statistics software for data analysis.

Fourteen terrain indices were selected to provide a range of empirical predictors covering altitude, aspect, landform, wetness and proximity to tracks and rivers, as well as exploring scale variants within predictor types (Table 1). All data layers were clipped from national data-sets to the Tongariro Forest boundary, in order to increase processing speed. All raster layers were processed at 25-m cell size, corresponding to the cell size of the DEM supplied. Altitude values were sourced directly cell by cell from the grid of the DEM. Slope was calculated from the DEM using the SLOPE function set with a single cell circular analysis window. Each cell in the slope raster represented the maximum rate of change of altitude with respect to neighbouring cell. A large value denotes a steep landform and values approaching zero denote flat land. Curvature was calculated using the CURVE function, with each calculated cell value providing an index of maximum rate of change of slope. Large positive values represent ridge-like (convex) features, large negative values represent valleys or depressions (concave surface), and values approaching zero denote constant angle. A compound terrain index (CTI) was formed using an established algorithm (Evans 2004, Gessler *et al.* 1995). The CTI gives a standardised relative index that is proportional to the drainage area of land uphill from each grid cell and is related to ground wetness. Relative altitude was calculated for each cell by dividing the altitude value by the mean altitude value of a particular analysis window size. Cells with large values represent sites that are higher than the average surroundings and vice versa for low values. A coarse Topographical Position Index (TPI) was adapted from Jenness (2006) by averaging the relative altitude calculated by circular neighbourhood function for three different-sized calculation windows (50 m, 200 m, 400 m). TPI is a measure of position on the terrain form at macro- rather than micro-habitat scale, and has been shown to influence animal activity and vegetation composition (Clinton and Boring 1994, Dickson and Beier 2007). The means of slope, curvature, altitude, and topographical position were calculated as the average of cell values within a further circular MEAN neighbourhood function analysis window.

Proximity to rivers was calculated using two different measures: i.) linear distance to the closest river pixel (ARCGIS 9.3 EUCLIDIAN DISTANCE) and ii.) a kernel density function that sums river abundance within a test radius from each cell, providing an inverse distance weighted index of proximity to all nearby river habitat (ARCGIS 9.3 KERNEL DENSITY function). The kernel density function, based on a quadratic kernel density estimation (Silverman 1986), calculates the magnitude per unit area of specified surrounding features (rivers and tracks in this case). A larger value denotes a location with a high presence of nearby target features.

Three different analysis window sizes (100 m, 200 m and 400 m focal radii) were used to derive test variables of varying scale. The same calculation was applied for tracks and roads, but these two features were processed as one feature layer on the premise that tracks and roads in Tongariro Forest have similar morphology and effect on stoat activity. Note that river proximity and closest river were alternate variables for the same terrain feature (likewise for tracks).

Sensitivity analysis for spatial variants of the six predictors mean slope, mean curvature, relative altitude, topographical position, river proximity and track proximity was performed to assess how the choice of a computational (focal) window radius affects the performance of the predictors in each model. These terrain indices are illustrated as rasters in Figure 2. This initial predictor set was selected for this study, from the many terrain indices that are possible, so as to provide a simple analysis environment for assessing effect of scale on model outcomes. Terrain conditions were chosen for which existing GIS data layers were accessible, and that are commonly considered in stoat and other similar small mammal habitat use studies (Christie *et al.* 2006, Christie 2009, Good 2001, King *et al.* 1996, Klar *et al.* 2008).

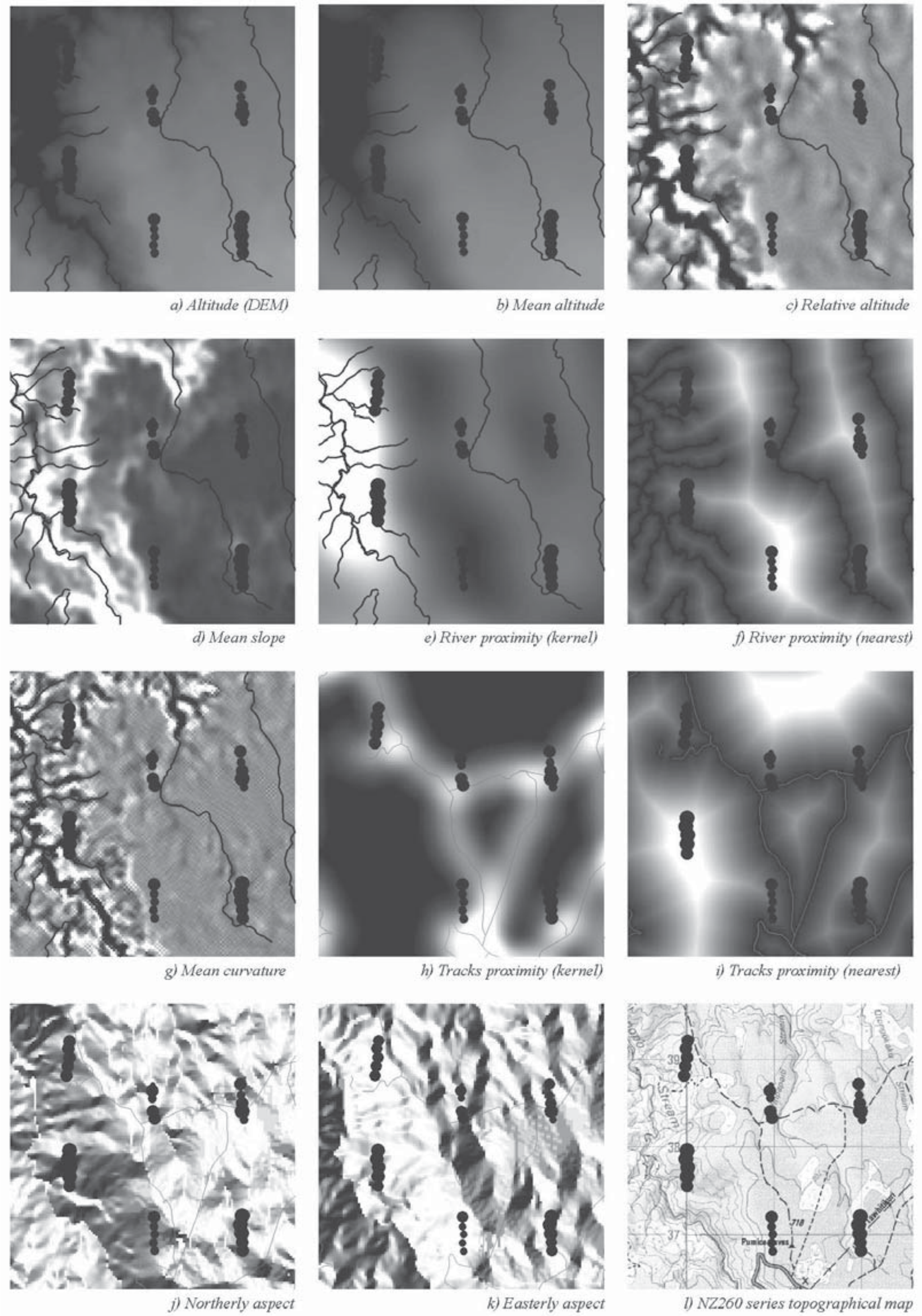

Figure 2. Example illustrations of GIS-generated terrain variable layers. Light shading denotes a large value. Rivers and roads are shown for scale and context (tones vary for each frame for contrast). The topological map (bottom right) is provided for reference (1 km grid squares).

Table 1. Source and description of response and predictor variables used for logistic regression modelling.

Predictor name	Source	Spatial variants	Best set from spatial variants	Final candidate set	Final model
Response variable					
Mustelid visitation	Department of Conservation tracking tunnel monitoring records 2001-2008				
Predictor variables					
LENZ mean annual temperature	LENZ MAT 25 m	Not varied	yes	collinear with MALT; eliminated	yes
LENZ mean annual solar radiation	LENZ MAS 25 m	Not varied	yes	yes	yes
Northerly aspect	Landcare DEM	Not varied	yes	yes	yes
Easterly aspect	Landcare DEM	Not varied	yes	yes	yes
Mean slope	Landcare DEM	**50 m, 100 m, 200 m**	yes	yes	yes
Mean curvature	Landcare DEM	**50 m, 100 m, 200 m**	yes	yes	yes
Mean altitude	Landcare DEM	**50 m, 100 m, 200 m**	yes	yes	
Relative altitude	Landcare DEM	**50 m, 100 m, 200 m**	yes	yes	failed model selection
Topographical position index	Landcare DEM	**50 m, 100 m, 200 m**	yes	yes	yes
Compound terrain (wetness) index	Landcare DEM	Not varied	yes	collinear with MSL; eliminated	
River proximity*	NZ260 Rivers	**100 m, 200 m, 400 m, 800 m**	yes	yes	
Closest river*	NZ260 Rivers	**Euclidian Dist.**			yes
Tracks proximity*	NZ260 Tracks+Roads	**100 m, 200 m, 400 m, 800 m**		yes	yes
Closest track*	NZ260 Tracks+Roads	**Euclidian Dist.**	yes		

*Closest river and river proximity were alternative indices used to characterise river environment (likewise for tracks).

** Boldface lines show spatial variants used in the sensitivity analysis

2.3. Statistical analysis

The relative influence of the 12 candidate terrain predictor variables on observed stoat visitation was assessed by logistic regression modelling using PROC LOGISTIC in SAS v.9.1 and related SAS output delivery functions. As the tracking tunnel data set was binary (presence/absence), the 'event/trial' format for the PROC LOGISTIC model statement was used. The model building process had three steps: i.) term reduction by selection of the best spatial variants for entry into model selection and reduction of collinear terms to minimize over-fitting, ii.) stepwise selection of model terms to a best subset using AIC as selection criteria, and iii.) an assessment of sensitivity of model predictions to spatial analysis scale.

2.3.1. Term reduction

Spatial variants for the six varied predictors were systematically replaced in repeats of logistic regression analysis using a base model of 12 predictors (i.e., 6 varied and 6 non-varied predictors – see Table 1). The relative strength of the models was compared using Akaike Information Criterion (AIC) scores as the measure of model fit. AIC is an extension of a regression log-likelihood measure that penalises for over-complexity in a model (Burnham and Anderson 2002). Statistical processing was done using iterative scripting in SAS Macro Language to run one logistic regression routine for every combination of all variants of the six predictors. AIC values for each model were computed and compiled into a data output table along with identifiers for the predictor variants used in each iteration. The list of model fit statistics was reverse-ranked based on AIC score. For the top 5% best-performing models from this list, a sum of rank was calculated for each variant. Terms consistently appearing in the best models scored a higher sum than terms appearing in lesser models.

Many derived variables can be closely related because of the underlying direct variables from which they are comprised e.g., both soil moisture and proximity to river habitat are a function of a site's terrain (altitude) model. This collinearity between variables can overestimate the influence of more fundamental drivers in a model assessment (Ofir and Kuri 1986). Models that preserve collinearity can result in equations that appear to fit observed data well, but individual parameter estimates tend to be less accurate and more sensitive to observed values in a data set. However, models which exclude collinear variables risk losing explanatory power and overlooking important predictive factors

(Mason and Perreault 1991). In this analysis we minimised collinearity by identifying collinear pairs of variables with $r \geq 0.7$, then eliminating the variables with the least effect in a test regression model with all candidate variables fitted. Elimination was based on regression chi-square score and associated p-value (see Appendix B).

2.3.2. Model selection

An AIC-optimized subset of the candidate predictor variables was chosen by stepwise selection, with threshold for entry into the model set to 0.157 and threshold for removal set at 0.3 based on criteria used by (Shtatland *et al.* 2001). The resulting subset was considered an optimal model to which sensitivity analysis outputs were compared.

A probability surface for estimated likelihood of stoat interception was visualised by computing the linear equation of the optimal model, cell by cell onto a 25x25-m raster grid. The resulting grid was classified based on the quartile value for stoat visitation, and labelled as *very good*, *good*, *moderate* and *poor* likelihood of visitation.

2.3.3. Sensitivity analysis

The sensitivity of terrain predictors to choice of analysis window size (scale) was assessed by observing how the probability surface changed when terrain predictors were systematically replaced one term at a time with their scale alternatives. A predictor variable would be considered sensitive to user choice if different analysis window sizes resulted in important differences in the magnitude of model predictions. Conversely, if predictions changed markedly with analysis scale, then the predictor can be considered sensitive to user choice of scale. Each iteration involved a complete model selection process, to produce the best linear equation for that candidate set. Each linear equation generated was automatically imported into a table to enable stoat activity predictions to be computed for a set of tracking tunnel locations. However, in order to test this using a different set of points from the input data, a new spatial data set of 300 randomly chosen locations within the study area were generated (ARCGIS 9.3 CREATE RANDOM POINTS function, 500 m minimum separation). A stoat activity estimate was calculated for each point in the set of random locations by applying each alternate linear model equation generated above. Point by point, alternate predictions were compared to that of the optimal model generated in section 2.3.2. Specifically, the proportion of the 300 test locations that changed in predicted stoat activity by more than 10% and 50% for each alternate model was calculated, as was the proportion of tunnels that changed in classification for *very good*, *good*, *moderate* and *poor* likelihood of stoat visitation as described earlier.

3. Results

3.1. Term reduction

The relative performance of the spatial variants of predictor variables tested, is shown in Table 2. Mean slope, curvature, and altitude predictors performed best when derived from the smallest analysis window size tested. Conversely, relative altitude performed best at the largest window size tested. There was little difference in performance between window sizes for the Topographical Position Index. River proximity performed best when calculated as Euclidean distance (i.e., distance to closest river pixel) rather than using a kernel function. Proximity to tracks only appeared in the best 5% of models when calculated using a 400-m kernel analysis window. The best performing spatial variants were selected for further modelling (boldface figures Table 2). The least significant of collinear variables were dropped from the candidate list as per Table 1 (also see Appendix B). Mean annual temperature was strongly collinear with mean altitude (2-cell radius) but was dropped from the selection list even though its effect was negligibly stronger in the model. Preference was given to mean altitude as a subject for subsequent sensitivity analysis, as it was a less derived variable than mean annual temperature.

Table 2. Performance of different spatial variants of terrain predictors based on the top 5% of the 3888 model iterations tested. Figures are unit-less sums of inverse ranking where the higher the figure, the better each variant performed in the models. Boldface figures were used in subsequent analyses. Euclid = Euclidian Distance.

Predictor variable	**50 m**	**100 m**	**200 m**	**400 m**	**Euclid**
Mean slope	**12002**	5090	2018	-	-
Mean curvature	**15527**	2280	1303	-	-
Mean altitude	**10659**	8082	369	-	-
Relative altitude	3060	6243	**9807**	-	-
Topographical position index	**7176**	5225	6709	-	-
Rivers	-	3234	6037	1243	**8596**
Tracks	-	0	0	**19110**	0

3.2. Model selection

The stepwise model selection procedure identified an AIC-minimised linear equation with nine significant predictor variables (Table 3.). In general, stoat visitation increased with mean solar radiation, easterly aspect and curvature and decreased with northerly aspect, mean slope, topographical position, and proximity to both tracks and rivers. Reliability of the model was 75% (area under the ROC curve).

Table 3. Parameter estimates and test statistics output from the selected logistic regression model.

Description (spatial variant in brackets)	Coefficient.	Std Err.	Chi Square	P > ChiSq
Intercept	-140.000	16.695	70.28	<0.0001
Mean annual solar rad.	0.968	0.117	68.11	<0.0001
Northerly aspect	-0.156	0.072	4.66	0.03
Easterly aspect	0.355	0.075	22.66	<0.0001
Mean slope (50 m)	-0.014	0.007	4.03	0.04
Mean curvature (50 m)	0.655	0.193	11.50	< 0.01
Mean altitude (50 m)	0.006	0.001	101.17	<0.0001
Topographic position (50 m)	-0.409	0.198	4.27	0.04
Closest river	-0.0012	0.0004	8.44	< 0.01
Track proximity (800 m)	-341.300	32.953	107.26	<0.0001

The resulting probability surface, mapped using the optimal model equation onto a 25-m raster grid (Figure 3), reveals distinct regions of high and low probability for stoat visitation across the Kiwi Sanctuary. Classification of the raster grid based on the quartile limits observed in the mustelid tracking tunnel data demarcates the landscape into regions of *very good*, *good*, *moderate* and *poor* likelihood of stoat interception (see Figure 4).

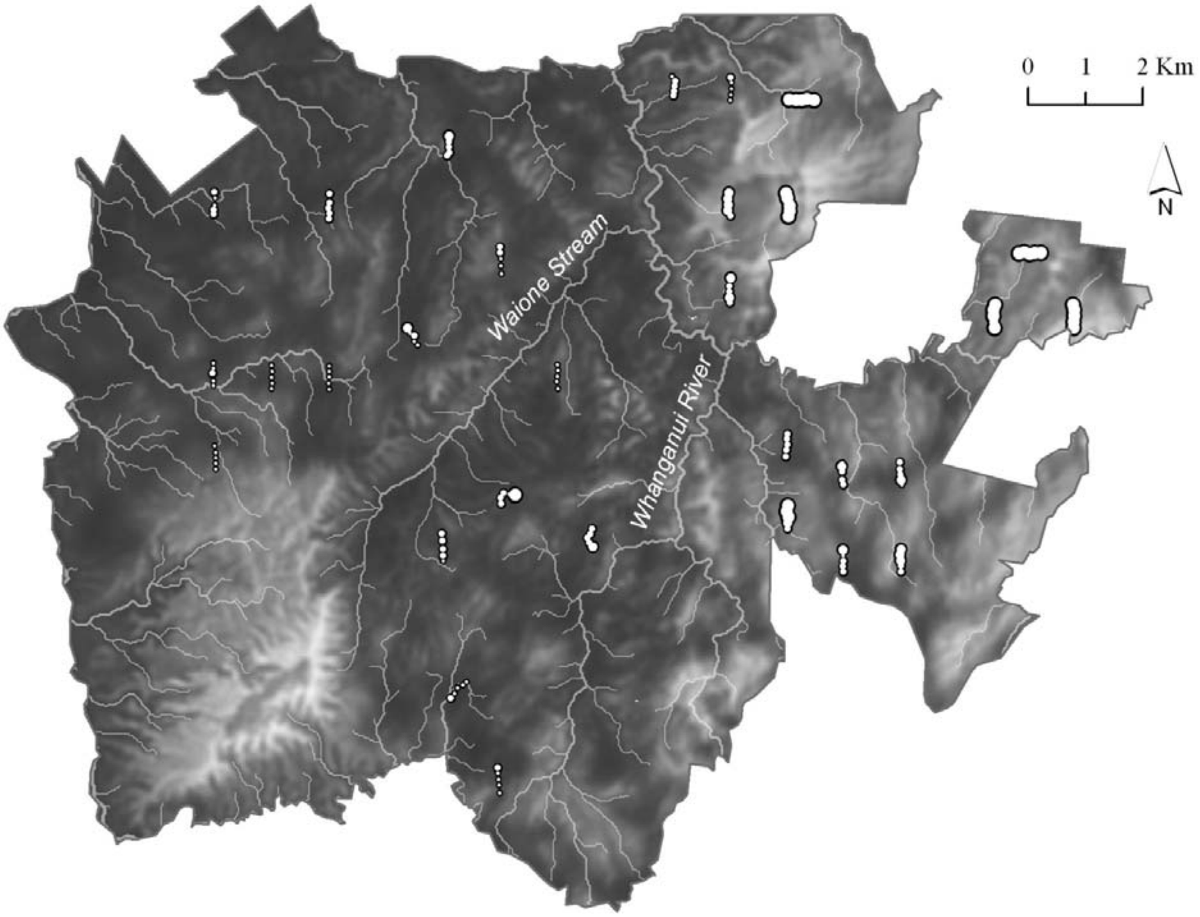

Figure 3. Predicted probability surface for likelihood of stoat visitation based on optimal linear regression equation. The shading denotes a continuous linear graduation from minimum (p~0) to maximum predicted value (P~1). Lighter shading denotes higher likelihood of visitation. White circles symbolise the magnitude of mean tracking rate at the tunnels averaged over the duration of the data collection (larger circles correspond to higher mean tracking rates).

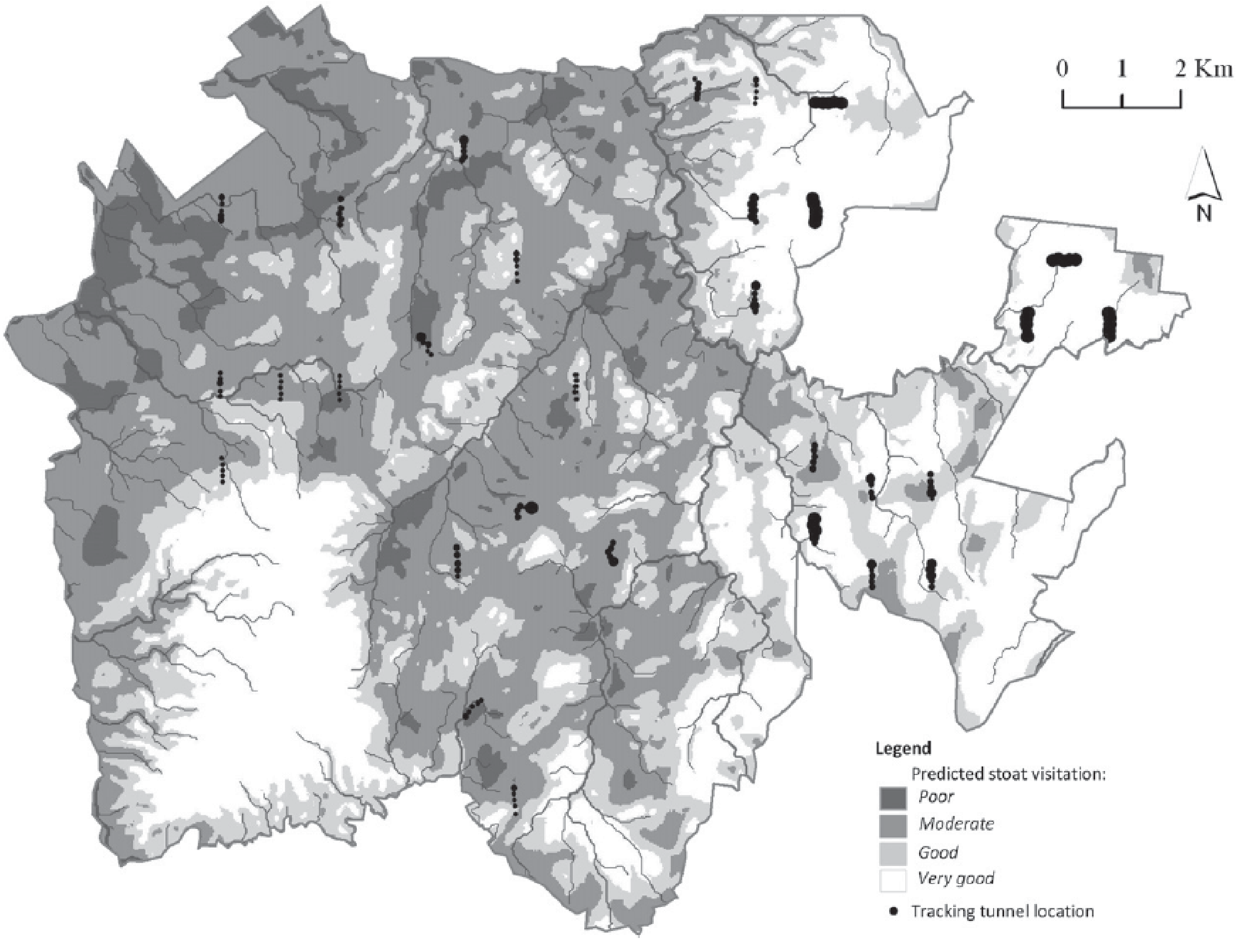

Figure 4. Predicted probability surface (from Figure 3) classified into categories of *very good*, *good*, *moderate* or *poor* likelihood of stoat visitation. Black circles show the magnitude of mean tracking rate at the tunnels averaged over the duration of the data collection (larger circles correspond to higher mean tracking rates).

Table 4. Proportion (%) of 300 randomly sampled test-locations for which predicted stoat activity changed more than *a.)* 10% and *b.)* 50% compared to the optimal model generated in section 3.2. A third measure of sensitivity *c.)* is provided in terms of how changing analysis window size deflected model predictions out of the classification made in 3.2 and in Figure 4 (i.e., *very good*, *good*, *moderate* or *poor* predicted visitation to a site). "*Opt.Mod.*" denotes variables that appeared in the optimal model. Dashed values were not tested. A large number indicates that there has been a large deflection in the mean tracking rate predicted across the site by that alternative model tested.

	Analysis window size				
Predictors	**50 m***	**100 m***	**200 m***	**400 m***	**Closest point****
a.) 10% deviation					
Mean slope	*Opt. Mod.*	1	12	-	-
Mean curvature	*Opt. Mod.*	29	43	-	-
Mean altitude	*Opt. Mod.*	9	10	-	-
Relative altitude	17	13	*Opt. Mod.*	-	-
Rivers	-	25	9	32	*Opt. Mod.*
Tracks	-	81	60	*Opt. Mod.*	86
b.) 50% deviation					
Mean slope	*Opt. Mod.*	0	0	-	-
Mean curvature	*Opt. Mod.*	0	1	-	-
Mean altitude	*Opt. Mod.*	0	0	-	-
Relative altitude	0	0	*Opt. Mod.*	-	-
Rivers	-	0	0	1	*Opt. Mod.*
Tracks	-	19	8	*Opt. Mod.*	14
c.) Proportion that changed in classification for likelihood of stoat visitation					
Mean slope	*Opt. Mod.*	2	5	-	-
Mean curvature	*Opt. Mod.*	9	12	-	-
Mean altitude	*Opt. Mod.*	3	5	-	-
Relative altitude	6	4	*Opt. Mod.*	-	-
Rivers	-	8	6	10	*Opt. Mod.*
Tracks	-	30	19	*Opt. Mod.*	32

** based on kernel density function (proximity of feature) ** based on Euclidian distance (closest point)*

3.3. Sensitivity

Variation of analysis window size had a measurable impact on stoat predictions when applying the predictive regression equations to the 300 randomly generated test-locations, as compared to the benchmark optimal model derived in section 3.2. Predicted stoat visitation deflected markedly with changing analysis window size for the variable track proximity, and for mean curvature and river proximity (refer Table 4).

The calculation of track and river proximity also had an effect on the model prediction, especially comparing the inverse-kernel based proximity calculation to the Euclidean distance. Other predictors were relatively stable with changing window size, for the model outputs generated. This tendency was consistent for all three measures of sensitivity examined (Table 4).

4. Discussion

In this study, the choice of analysis scales was found to affect the impact of terrain predictor variables in a logistic regression modelling analysis. The extent to which explanatory variables are subject to analysis scale will depend on the complexity of the landscape and the mobility of the animal being studied (Johnson and Gillingham 2005). Stoats are highly mobile animals with large but varying home ranges (Erlinge 1977, McDonald and Larivière 2001, King and Murphy 2005). Mobility varies predictably with time of year (Sandell 1986, Alterio 1997). In general, winter is characterised by localised foraging in a contracted home range, whereas spring and summer see adults ranging more widely, with activity augmented by an irruption of juveniles dispersing during the summer (Erlinge 1980, Erlinge and Sandel 1986, O'Donnell *et al.* 1996, King and Murphy 2005,). Stoats are capable of travelling several kilometres in a day within established home ranges, or further while dispersing as juveniles (King and McMillan 1982, Samson and Raymond 1998). The Tongariro Forest landscape is dissected by ridge/valley features spaced roughly 100-500 m apart through much of the forest. During a day's mobility stoats would likely traverse in and out of many different terrain forms and habitat types. Computational scale variants were chosen to span this approximate range, and an optimal scale was identified for stoats in Tongariro Forest. The influence of these terrain predictors, however, may be specific to this site's landform. An alternative site with different landscape character may reveal a different optimal scale for explanatory variables. For example, at stoat control sites in the South Island (e.g., Dilks *et al.* 2003) terrain is dominated by large ranges intersected by glacial valleys. Major landforms can occur on a markedly greater scale than in Tongariro Forest. Due to this, a stoat may traverse a more limited range of terrain forms during daily locomotor activity at this site than in the Tongariro Forest. Accordingly, stoats will less frequently traverse the full range of terrain types. Consequently, different terrain variables may become more or less influential upon stoat activity and differ in the optimal analysis scale for the best fit model. In addition, some predictors can have greatest explanatory power at landscape scale and others at site-scale (Murray *et al.* 2008). Given that information on optimal scale is rarely available without great expense, exploratory data mining to identify optimal modelling parameters should be routine to maximise predictive utility of a model.

An index for river and track proximity was used, based on a kernel density calculation, to contrast the more commonly used measure of Euclidian distance to closest river or track location. A marked difference was demonstrated between these measures both in terms of model fit and predictions made post hoc. Comparison of model fit revealed no clear rule. Euclidian distance was more important in the model for the river proximity, and kernel density was more important for tracks. The kernel density function provides an index of the relative density of nearby features (rivers and tracks in this case) where nearby features have greater weighting than more distant ones. Setting a finite window size for the analysis creates an artificial cut-off in the continuous kernel density field. This in effect assumes that the influence of kernel density variables on stoat activity stops beyond this nominal distance.

River and track indices had strongest influence on stoat activity at the largest scale tested (400 m), suggesting that stoats may be making movement decisions based on cues at this larger scale of landform. However, in Tongariro Forest, land cover generally varies with distance from rivers and tracks with typically ~10-50 m scale transition of seral vegetation from the river/track edge to the uniform more mature forest interior. So the superior fit of these predictors at the larger kernel size is not intuitively explained by observed vegetation patterns in the forest. A possible explanation may be that stoats are cueing into terrain forms that only correlate with proximity to tracks and rivers, or are pursuing prey sensitive to these factors where coarser gradients in distribution or activity are involved.

5. Conclusion

This research demonstrates that choice of computational scale can be important for some predictor variables of stoat activity, with potential to impact on modelling outcomes in terms of both finding best-fit equations and deriving outcome predictions. Investigating a range of scales for developing the model was valuable as the scales of best fit may not necessarily have been chosen by intuitive selection. The use of automated GIS analysis to derive explanatory variables at a range of scales, combined with automated statistical analysis to identify the predictive capability of the derived variables, provide a powerful system for developing predictive models. This approach can be used to predict the potential habitat of a range of species.

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Appendices

Appendix A. Performance of different spatial variants of terrain predictors based on all 3888 model iterations tested. Numbers are unit-less sums of (inverse) ranking where the higher the figure, the better each variant performed in the models. This table complements Table 2, which presents the top 5% of 3888 model iterations. Actual numbers are x1000.

Predictor variable	**50 m**	**100 m**	**200 m**	**400 m**	**Euclid.**
Mean slope	2665	2470	2425	-	-
Mean curvature	2910	2370	2280	-	-
Mean altitude	2721	2445	2395	-	-
Relative altitude	2387	2575	2598	-	-
Topographical position index	2452	2560	2548	-	-
Rivers	-	1794	1910	1712	2144
Tracks	-	692	2363	3307	1199

Appendix B. Reduction of collinearity

a.) Correlation matrix between predictor variables. Numbers tabulated are Pearson correlation coefficients (r) for correlation between predictor values for each tunnel location. Boldface numbers highlight predictor variable pairs that were considered collinear (i.e., r>0.7).

Predictor variable	LENZMAT	LENZMAS	MCTI	ASPECT0	ASPECT90	MSL2	MCURV2	MALT2	RALT8	TPI2	EUCDISTR	TRKRDK16
Mean annual temperature	-	-0.44	0.00	0.00	-0.04	-0.10	0.05	**1.00**	-0.23	0.12	0.04	0.09
Mean annual solar radiation	-0.44	-	0.00	-0.02	-0.09	0.15	0.06	-0.40	0.13	-0.12	-0.24	0.33
Compound terrain index	0.00	0.00	-	0.11	0.02	**0.73**	-0.07	0.01	0.21	0.49	-0.19	-0.14
Northerly aspect	0.00	-0.02	0.11	-	0.13	0.16	0.02	-0.01	-0.10	0.17	0.12	-0.13
Easterly aspect	-0.04	-0.09	0.02	0.13	-	-0.01	0.00	-0.04	-0.09	0.06	-0.02	-0.17
Mean slope (50 m)	-0.10	0.15	**0.73**	0.16	-0.01	-	-0.11	-0.09	0.19	0.38	0.04	0.02
Mean curvature (50 m)	0.05	0.06	-0.07	0.02	0.00	-0.11	-	0.05	-0.68	-0.43	0.11	0.01
Mean altitude (50 m)	**1.00**	-0.40	0.01	-0.01	-0.04	-0.09	0.05	-	-0.24	0.12	0.03	0.10
Relative altitude (400 m)	-0.23	0.13	0.21	-0.10	-0.09	0.19	-0.68	-0.24	-	0.13	-0.23	-0.13
Topographical pos. index (50 m)	0.12	-0.12	0.49	0.17	0.06	0.38	-0.43	0.12	0.13	-	-0.06	0.01
Closest river	0.04	-0.24	-0.19	0.12	-0.02	0.04	0.11	0.03	-0.23	-0.06	-	0.04
Track proximity (800 m)	0.09	0.33	-0.14	-0.13	-0.17	0.02	0.01	0.10	-0.13	0.01	0.04	-

b.) Model output for a logistic regression routine with all terms fitted. Significant collinearity is marked in the last column with numbers designating each collinear pair, and which variable in the pair was eliminated from the proceeding analysis based on having lower chi square score and associated p-value. "*Elim*" refers to variables eliminate from each pair.

Term name	Coefficient	Std Err.	Chi Square	P > ChiSq	Collinearity
Track proximity (800 m)	-308.30	33.443	84.959	0.0001	
Mean altitude (50 m)	0.0515	0.0076	46.052	0.0001	1
Mean annual temperature	0.7961	0.1309	37.016	0.0001	1 (elim)
Mean annual solar radiation	0.5952	0.1316	20.465	0.0001	
Easterly aspect	0.3435	0.0763	20.291	0.0001	
Mean curvature (50 m)	1.0151	0.3319	9.352	0.0022	3
MSL2	-0.0270	0.0102	7.073	0.0078	2
Relative altitude (400 m)	-21.384	8.0707	7.021	0.0081	3 (elim)
Northerly aspect	-0.1528	0.0741	4.251	0.0392	
Closest river	-0.0009	0.0004	4.201	0.0404	
Topographical pos. index (50 m)	-0.3532	0.2326	2.307	0.1288	
Compound terrain index	-0.0672	0.0645	1.084	0.2978	2 (elim)

Chapter 5. The influence of mice and rats on stoat (*Mustela erminea*) activity.

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Abstract

Stoats (*Mustela erminea*) are a widespread invasive pest in New Zealand and there are ongoing efforts to improve the efficacy and cost-effectiveness of trap-based stoat control for species protection. Geographical Information Systems (GIS) combined with spatial analysis techniques provide an important tool for developing models of stoat habitat preference. In previous research we derived an optimal predictive habitat-use model based on readily available GIS-derived data layers such as terrain and landcover. This research extends this model by including indices of mouse and rat activity, which are known prey of stoats. The addition of indices of prey species activity and autocorrelation in stoat visitation to tracking tunnels significantly improved the model and reduced the effects of terrain. Thus, when prey activity and intraspecific interaction information is available, this should be included in predictive habitat-use models for stoats.

Keywords: Stoat; habitat use; GIS; model; autocorrelation; Tongariro Forest

1. Introduction.

Stoats (*Mustela erminea*) are a widespread invasive pest in New Zealand and threaten numerous native bird species through predation and nest disruption, including kiwi (*Apteryx mantelli*) (McLennan *et al.* 1996), blue ducks (whio, *Hymenolaimus malacorhynchos*) (Whitehead *et al.* 2008; Glaser *et al.* 2010), hole nesting birds like kaka and mohua (Dilks *et al.* 2003; Green *et al.* 2004), various invertebrates (e.g., Wilson *et al.* 2006) and many shorebirds (Dowding and Murphy 2001). Stoats have been the target of intensive pest control for several decades (King and Murphy 2005). Successful control has been achieved using traps and ground poisoning (e.g., Dilks *et al.* 2003; Gillies *et al.* 2003; Whitehead *et al.* 2008), but to protect a population of a threatened species from predation requires an intensive and expensive control network sustained across a large enough area to mitigate for the large home ranges of both stoats and many of the threatened species (Basse and McLennan 2003). Furthermore, many projects operate at the fringe of required efficacy and so can only deliver effective species protection in some years (Dilks *et al.* 2003).

The difficulty in controlling stoats arises from a number of compounding issues. Stoats have large home ranges and are highly mobile such that reinvasion from outside of a control area can be rapid (Murphy and Dowding 1994, MacDonald and Lariviere 2001). Stoats also have distinct periods of high mobility and rapid, large-scale, juvenile dispersion (Murphy and Dowding 1994; Murphy and Dowding 1995; MacDonald and Lariviere 2001). This enables stoats to quickly re-colonise a controlled area (Choquenot *et al.* 2001; McLennan 2006), and the timing often corresponds with periods when native prey species are highly vulnerability to predation (e.g., McLennan *et al.* 2004). Trapping is most effective, in terms of threatened species protection outcomes, when trapped areas are large (Basse and McLennan 2003). Even for large control sites, the probability of an individual stoat intercepting a trap site is still very low (King and McMillan 1982; King *et al.* 2003). The interception rate is related to the density and spread of traps relative to home range size (Brown and Miller 1998; Lawrence 1999), which varies between locations (King 2005). Trapping is expensive to set up and maintain, especially at mountainous or remote sites where access is limited. This often results in a trade-off between the size of the protection area, trap density and service frequency.

Guidelines have been developed for optimising trap placement (Dilks *et al.* 1996; Cameron *et al.* 2005), station design (Hamilton 2004) and station density (Brown and Miller 1998; Lawrence 1999; Miller *et al.* 2001), and there is an increasing body of knowledge now describing stoat habitat use at various sites (King *et al.* 1996; Christie *et al.* 2009). However, many species protection areas are heterogeneous in terrain form and vegetation, which significantly affects stoat home range size. There is the potential to improve the potency of each trap investment if improved predictability can be found in the chance of stoat interception. Each major protection site could potentially benefit from investigation into optimal trapping layout specific to the site. Such research though can be expensive, so efficacy gains would need to be justified in terms of cost-benefit for research investment versus increased investment in the trap network. Many stoat control sites conduct long-term stoat population monitoring on semi-randomised lines, particularly using footprint tracking tunnels (Gillies and Williams 2001; King 2004), with data spanning many years (e.g., Robertson 2004; Glaser *et al.* 2010). Many trapping sites too have collected very large data sets for location and time of trapping events. There is potential to extract useful information from these data sets to enable site-specific optimisation of trap deployment.

Geographical information systems (GIS) provide a useful and proven data management and analysis framework within which to extract useful information within existing data sets (Clark *et al.* 2008). GIS has been used for modelling differential habitat use for numerous species (Gough and Rushton 2000; Delaville *et al.* 2005; Dickson and Beier 2006; Estes *et al.* 2008; Klar *et al.* 2008), and has provided useful information for steering species management direction internationally (Johnson and Gillingham 2005; Wintle *et al.* 2005; Lurz *et al.* 2008) and in New Zealand (Clark *et al.* 2008; Scott *et al.* 2009). Many geospatial layers are in common use in numerous land management agencies, describing terrain and landcover condition. These layers can easily be processed using spatial analysis techniques to generate indices of ground condition at various scales, thereby characterising the land surrounding a control station for use in statistical habitat-use modelling.

Martin *et al.* (2011) developed a predictive model for stoats using GIS terrain and topographic layers that are available nationally in New Zealand. The model used the following explanatory variables selected using logistic regression: mean annual solar radiation, northerly aspect, easterly aspect, mean slope, mean curvature, mean altitude, topo-graphical position index, nearness to river and track proximity. This research also investigated the effects of scale on these explanatory variables. The advantage of this model is that it could be applied to any part of New Zealand, because the data from which these variables were derived are available throughout New Zealand. The intention of this modelling approach is that with further adjustment, testing and validation, a tool could be made available to optimise the location of traps.

Stoat populations are heavily influenced by fluctuations in rodent numbers (King 1983; Blackwell *et al.* 2000; Klisky and Byrom 2004). A surge in rodent numbers can trigger a breeding response in stoats that significantly increases the population of stoats (Murphy and Dowding 1995). Such an increase in stoat numbers can overwhelm a control network inflicting damage to a protected species population (McLennan 1997a; McLennan 1997b). Stoats have a complex interaction with their prey, both in terms of population dynamics (King 1983; Murphy and Dowding 1995; Blackwell *et al.* 2003; King *et al.* 2003; Purdey *et al.* 2004; Barlow and Baron 2005) and known variability in habitat preference (Christie *et al.* 2009). Although data on the distribution of rats and mice are not widely available, this study explores the interaction of rodents, terrain, and topography on stoat distribution.

Another confounding and potentially misleading factor for habitat modelling is the presence and effect of autocorrelation in the data (Otis and White 2001; Betts *et al.* 2006). Spatial autocorrelation exists when events (e.g. visitation by a stoat to a tracking tunnel) have been influence by a nearby event (e.g., visitation of the same or different stoat to a nearby tracking tunnel) (Koenig 1999). Likewise, temporal autocorrelation exists in data when events have been influenced by a previous event at the same place. If the degree of autocorrelation in a data set is large enough, false inference can be made due to the over representation of one or more statistical predictor variables in the model (Guisan and Zimmerman 2000; Betts *et al.* 2006; Austin 2007). The presence and significance of autocorrelation can be modelled by factoring in simple indices of proximity to nearby or recent events as a predictor variable in a modelling process.

The purpose of this study was to take an existing predictive habitat-use model, based on extrapolation from readily available GIS-derived data layers, and factor indices of prey activity and autocorrelation to improve the performance of the model, understand its limitations, and further describe the complex interaction of rodents, terrain, and topography on stoat distribution.

2. Methods

2.1. Study Area

The study area comprised approximately 20,000 ha of contiguous forest to the west of Tongariro National Park, in the central volcanic plateau of the North Island, New Zealand (Figure 1). Altitude ranges from 300 m to 830 m and the landscape is dissected by streams and four-wheel-drive access tracks. Tongariro Forest is one of five nationally-designated kiwi sanctuaries (Robertson 2004). Stoats are a key threat for kiwi recovery (McLennan *et al.* 1996) and kiwi management in the sanctuary focuses on regular stoat population control.

Footprint tracking tunnels are a common method for monitoring small mammalian pest species in New Zealand (Gillies and Williams 2001; Jones *et al.* 2004). The tracking tunnels used here were 600 mm long, 100 mm wide black plastic tunnels containing an ink pad with two removable papers secured either side (King *et al.* 1994). Rabbit bait placed in the centre of the tunnel lures animals to walk across the ink pad and leave discernible footprints. One hundred and fifty tracking tunnels located on 30 permanent transects (5 tunnels per line at 100 m spacing) have been in operation monitoring stoats in the study area since 2001 using a standardised protocol (Gillies and Williams 2001).

Tracking tunnel sites were located by handheld GPS to ~10 m estimated positional error (Burrows 2000). The mean tracking rate for each tracking tunnel was calculated for mustelids, rats and mice from presence/absence data pooled across the four seasonal inspections each year. The tracking tunnel data were obtained over seven years (2001-2008), but two pest poisoning operations occurred during this period so data collected during the 12 months following these operations were deleted in order to minimise any confounding influence from the resulting artificial change in population makeup. The resulting data set comprised ~22 repeat measurements at quarter-year intervals of the presence or absence of mustelid, rat and stoat footprints aggregated for the 150 uniquely labelled tunnels.

2.2. Source Data

Terrain data used were derived from a 25 m resolution Digital Elevation Model (DEM) sourced from Landcare Research (Baringer *et al.* 2002), LINZ-NZ260 feature layers, and Department of Conservation file records (see Table 1). Mean annual temperature (MAT) and mean solar radiation (MAS) were sourced from the Land Environments of New Zealand (LENZ) data set with 25 m spatial resolution. The base data-sets were converted into a range of terrain indices using geoprocessing functions in ESRI ARCGIS. Values were extracted from these terrain indices and appended as attribute information to each tracking tunnel within the point feature data layer. The resulting spatial data file (the .dbf component of a shapefile) was immediately accessible to statistics software for data analysis.

Nine scale-specific terrain indices were selected based on previous model selection and sensitivity analysis (Martin *et al.* 2011) covering a range of terrain conditions such as altitude, aspect, landform, wetness and nearness to tracks and rivers (Table 1). All raster layers were processed at 25-m cell size, corresponding to the cell size of the DEM supplied.

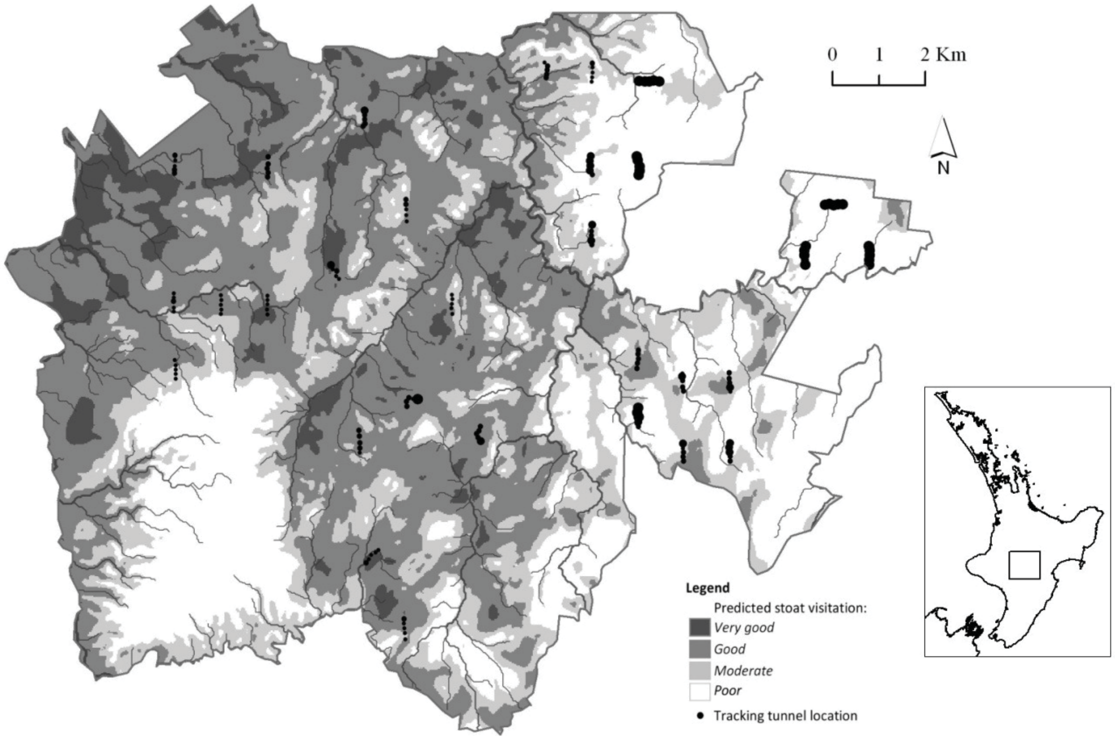

Figure 1. Study area, and location of tracking tunnels (black dots) on lines within the Tongariro Forest Kiwi Sanctuary operational boundary. Shading denotes the 4-way classified probability surface resulting from the optimal predictive terrain model in Martin et al. 2011. Tracking tunnel locations are denoted by black dots and the size of the dots are proportional to the mean tracking rate calculated for each tunnel for data from 2001 to 2007.

Altitude values were sourced directly cell by cell from the grid of the DEM. Slope was calculated from the DEM using the SLOPE function set with a single cell circular analysis window. Curvature was calculated using the CURVE function, with each calculated cell value providing an index of maximum rate of change of slope. Large positive values represent ridge-like (convex) features, large negative values represent valleys or depressions (concave surface), and values approaching zero denote constant angle. A compound terrain index (CTI) was formed using an established algorithm (Gessler *et al.* 1995, Evans 2004). The CTI gives a standardised relative index that is proportional to the drainage area of land uphill from each grid cell and is related to ground wetness. A coarse Topographical Position Index (TPI) was adapted from Jenness (2006) by averaging the relative altitude calculated by circular neighbourhood function for three different-sized calculation windows (50 m, 200 m, 400 m). TPI is a measure of the elevation position on a landform (lowland, midway, upland) and is measured at macro- rather than micro scale. TPI has been shown to influence animal activity and vegetation composition (Dixon and Beier 2007). The means of slope, curvature, altitude, and topographical position were calculated as the average of cell values within a further circular MEAN neighbourhood function analysis window.

Nearness to rivers was calculated for each raster cell as linear distance to the closest river pixel (ARCGIS 9.3 EUCLIDIAN DISTANCE). Proximity to tracks was derived for each raster cell using a kernel density function that sums track abundance within a 400 m circular test radius from each cell, providing an inverse distance weighted sum of the magnitude of per unit area of nearby tracks (ARCGIS 9.3 KERNEL DENSITY function). Model selection of these particular calculations of track and river proximity is described in Martin *et al.* (2011). A larger value of track proximity denotes a location with a high presence of nearby track features.

Mustelid, rat and mouse presence at each tunnel and service visit was recorded as a binomial record of presence/absence alongside the stoat records denoted by a 1 or zero respectively. Spatial autocorrelation was measured by attributing a 1 or 0 to a tunnel service visit depending on presence/absence of a stoat at an adjacent tunnel during the same monitoring visit. Temporal autocorrelation was attributed a 1 or 0 depending on whether a stoat was tracked in the same tunnel during the preceding tunnel service visit (Betts *et al.* 2006). These measures constitute a coarse index of autocorrelation at the smallest small spatial and temporal scale reasonably allowed by the data. The existence of autocorrelation in the data at higher spatial scale (e.g., mustelid visitation at more distant tunnels during the same visit) and temporal scale (e.g., mustelids visiting in earlier monitoring periods) was not assessed in this study.

2.3. Statistical Analysis

Four PROC LOGISTIC regression models using SAS 9.1 statistical software were compared in this study. First the optimal predictor model comprising terrain and topographical factors used in Martin et al. 2011 was reconstructed as a reference model to compare variations of this model against. A second model was run that varied from the reference model by addition of rat and mouse indices based on presence/absence data to the base predictors. A third variant of the reference model was run by addition of temporal and spatial autocorrelation factors. The final variant of the reference model, both the rat / mouse indices and the temporal / spatial autocorrelation indices were added to the base predictors. Akaike information criterion (AIC) values were used to assess relative fit of each alternative model, and Area under ROC curve ("c" values) were used to assess reliability of the models in the absolute sense.

3. Results

Addition of species and then autocorrelation factors each improved the model as measured by AIC and area under ROC curve, and so added value to the model in terms of understanding variability in the data.

The base set of terrain based predictor variables were all significant as derived from an existing model optimisation (Table 1). Addition of rat and mouse factors strengthened the model, however although rats had a significant effect on stoat visitation, the mouse effect was not significant so was dropped as a candidate predictor variable upon addition of spatial autocorrelation factors. Addition of the species factors caused slope to drop out of significance (at 95% confidence). There was a negative response effect of rats on stoat visitation.

Table 1. Individual parameter estimates from each model output showing relative strength and significance of influence of each factor in the models.

Parameter	**Co-efficient**	**Standard error**	**Chi square score**	**Pr > chi sq**
a.) Base set				
Intercept	-140.000	16.69	70.28	<0.0001
Mean annual solar radiation	0.968	0.11	68.11	**<0.0001**
Northerly aspect	-0.156	0.07	4.66	**0.0308**
Easterly aspect	0.355	0.07	22.66	**<0.0001**
Mean slope	-0.014	0.01	4.03	**0.0446**
Mean curvature	0.655	0.19	11.50	**0.0007**
Mean altitude	0.006	0.00	101.17	**<0.0001**
Topographical position index	-0.409	0.20	4.27	**0.0387**
Nearness to river	-0.001	0.00	8.44	**0.0037**
Track proximity	-341.300	32.95	107.26	**<0.0001**
b.) Base set, rat, mouse				
Intercept	-117.500	17.87	43.23	**<.0001**
Rat index	-0.764	0.20	13.00	**0.0002**
Mouse index	-0.451	0.40	1.27	0.2589
Mean annual solar radiation	0.814	0.13	42.32	**<0.0001**
Northerly aspect	-0.152	0.07	4.367	**0.0366**
Easterly aspect	0.328	0.07	18.13	**<0.0001**
Mean slope	-0.012	0.01	2.79	0.0948
Mean curvature	0.689	0.20	12.21	**0.0005**
Mean altitude	0.005	0.01	65.13	**<0.0001**

Topographical position index	-0.441	0.20	4.96	**0.026**
Nearness to river	-0.001	0.00	5.89	**0.0153**
Track proximity	-323.700	32.58	98.72	**<0.0001**
c.) Base set, Temporal, Spatial**				
Intercept	-68.463	18.37	13.89	**0.0002**
Mean annual solar radiation	0.472	0.13	13.37	**0.0003**
Northerly aspect	-0.026	0.08	0.11	0.7445
Easterly aspect	-0.049	0.08	0.33	0.5655
Mean slope	-0.005	0.01	0.41	0.5219
Mean curvature	0.503	0.21	5.77	**0.0163**
Mean altitude	0.000	0.01	0.19	0.6654
Topographical position index	-0.132	0.21	0.39	0.5344
Nearness to river	-0.000	0.00	0.12	0.7314
Track proximity	-39.693	36.15	1.21	0.2722
Temporal autocorrelation	4.972	0.38	168.15	**<.0001**
Spatial autocorrelation	0.625	0.28	4.84	0.0278
d.) Base set, rat, temporal, spatial				
Intercept	-62.135	19.17	10.51	**0.0012**
Rat index	-0.260	0.22	1.45	0.2286
Mean annual solar radiation	0.429	0.13	10.19	**0.0014**
Northerly aspect	-0.026	0.08	0.11	0.7457
Easterly aspect	-0.059	0.09	0.48	0.4907
Mean slope	-0.0037	0.00	0.23	0.63
Mean curvature	0.517	0.21	6.01	**0.0142**
Mean altitude	0.000048	0.01	0.00	0.9439
Topographical position index	-0.1406	0.21	0.44	0.5094
Nearness to river	-0.00009	0.00	0.03	0.8531
Track proximity	-42.0241	35.93	1.37	0.2422
Temporal autocorrelation	4.865	0.39	155.10	**<.0001**
Spatial autocorrelation	0.6671	0.29	5.46	**0.0195**

Both spatial and temporal autocorrelation factors had a significant effect in the model, and effected a marked change in the significance of terrain variables (Table 2). All terrain factors dropped out of significance (at 95% confidence) except for mean curvature and mean annual solar radiation. Temporal autocorrelation was notably strong in the model (chi square score = 155, p(chisq) = <0.0001).

Table 2. Alternative models tested with combinations of rat, mouse, and spatial and/temporal autocorrelation factors.

Model	**AIC**	**Holsmer-Lemeshaw**	**c**
Base set*	2950	0.001	0.75
Base set, Rat, Mouse	2939	0.001	0.75
Base set, Temporal, Spatial**	2657	0.0012	0.81
Base set, Rat, Temporal, Spatial	2658	0.0015	0.81

* Base set refers to Mean annual solar radiation, northerly aspect, easterly aspect, mean slope, mean curvature, mean altitude, topographical position index, nearness to river and track proximity

**Temporal and Spatial refer to autocorrelation components.

4. Discussion

In this analysis stoat visitation to tracking tunnels was found to be influenced strongly by a number of key terrain conditions, in particular mean annual solar radiation, easterly aspect, mean curvature, mean altitude, nearness to rivers, and the proximity to tracks. For the purpose of guiding management and optimising pest control, the optimal model equation can be used to distinguish areas of high likelihood of interception from areas of low likelihood with moderate accuracy. However, addition of indices of prey species activity and autocorrelation in stoat visitation significantly improved the model although this also had the effect of reducing the significance of terrain effects. Two predictors, mean curvature and mean solar radiation, remained significant after rodents and autocorrelation were fitted into the model. Visitation tended to be higher at locations with higher positive land curvature i.e., ridge and hill tops as opposed to flat lands and valley. This finding is seen at other sites. Trapping was found to be more successful at sites on ridge tops at a number of sites across New Zealand (Brown 2002; Christie 2009) which aligns with our findings of increased visitation with altitude. Slope influences stoat visitation in a number of studies with response consistently tending to decrease activity on steeper surfaces (Christie *et al.* 2006; Christie *et al.* 2009).

Our study found a significant relationship between stoat visitation and altitude, with higher visitation rates on higher locations. This is counterintuitive when considering the energetic cost of operating in a colder more expose environment with often steeper terrain. Other studies, however, have found higher stoat activity at high altitude (Martin 2000; Smith *et al.* 2007; Christie 2009). The graduation of vegetation type across the site from post-clearance regeneration in the south to mature podocarp forest in the north of the site may confound inference that altitude is a causal factor. There are other factors too that may change with altitude in Tongariro Forest such as ground moisture and shelter from weather, both of which diminish with altitude.

Aspect was also an important factor in this study for predicting stoat visitation. Both northerly and easterly aspects were examined concurrently as separate factors in the regression model. Northerly aspect correlates with increased solar energy incidence during colder times of the day or during non-summer months in New Zealand. As such, a positive correlation is expected between northerly aspect and plant productivity and associated increased abundance of invertebrates, birds and rodents at these times of year. Increased vegetation productivity has been demonstrated for northerly aspect in a number of locations. Northerly aspect has been found important for Samba deer (Forsyth *et al.* 2009). Studies reviewed by these authors found preference for northerly aspect related to the thermal benefits of the higher levels of solar radiation. However, their own study found that southerly aspects were in fact preferred due to the thermal protection of more stable temperature range. So intuitive models based on energetic arguments can be wrong and habitat direction of response to terrain types can vary depending on the particular macroclimatic characteristics of a site.

In this study stoat visitation was found to decrease when close to track and river features. This contrasts with studies which have found improved trapping success or habitat use when close to rivers (Samson and Raymond 1998; Brown 2002). Some studies have found that stoats similarly show a preference for roads (Murphy and Dowding 1994) and for forest margin habitat (Murphy and Dowding 1994; King and McMillan 1982) but others have found a negative relation between stoat visitation and closeness to rivers or track/road features (Murphy and Dowding 1994; Christie *et al.* 2006). Locations close to rivers are intrinsically sites of high moisture content and low water deficit due to uphill drainage area. Differences between sites may be due to differences in habitat characteristics between sites for stream and track features. Tracks have a linear shift in vegetation type with distance from a track, road or in some cases river edge consistent with ecotonal changes at a vegetation gap edge. In Tongariro Forest tracks tend to have remnant patterns of low stature or open vegetation resulting from earlier native timber logging. Stoat activity has been found to be habitat specific with low movement between major vegetation types (Smith and Jamieson 2011). Stoats are known in places to avoid open areas (Murphy and Dowding 1994) and it is likely that this is a predator avoidance strategy evolved in Europe where raptors and other aerial predators are prevalent (MacDonald and Lariviere 2001).

Deriving predictive rules to aid management decision-making only requires model equations with high correlation and low residuals, but forming an ecologically meaningful habitat model is complex and requires a rigorous examination of the interrelationship between potentially predictive factors. True causal mechanisms in stoat activity are largely intangible for most studies. Strong correlative relationships are still useful, indeed essential for management. However, it needs to be demonstrated that predictor variables are consistent with time before a model output can have applicability in management. Inference of causal rather than a correlative relationship between stoat visitation and terrain variables requires understanding of other potential driving factors, and the activity of stoat prey is an obvious factor that should be modelled in the equation.

In this study, stoat visitation at tunnels was found to correlate negatively with rat visitation during the same monitoring period. When a rat factor was built into the model, many of the terrain variables dropped out of significance. Intuitively stoats should be cueing into rat presence to some extent as rodents are known major prey-items (e.g., Cuthbert and Sommer 2002), and a positive relationship between stoat and rat visitation rates would be expected under this scenario. However a negative relationship was observed. This may be evidence of predator avoidance behaviour in the rats either by direct avoidance of stoat scent and sign, or by tending towards habitat that allows more protection or concealment from stoats. Another possible explanation is that stoat interest in tracking tunnels may decrease in habitat with higher prey numbers due to alternative attractions. There is some evidence of this from trapping studies (King and White 2004).

Many terrain responses can be the same for rats and stoats (Christie *et al.* 2006; King *et al.* 1996). The distribution of rats can be driven by food availability (Blackwell *et al.* 2000) and available vegetation type (Christie *et al.* 2006). Our research suggests that terrain factors certainly influence stoat spacing across a landscape with distinct areas of high and low predicted visitation across (Martin *et al.* 2011), but also that prey activity strongly influences patterns of occurrence. Our findings are in concordance with findings from a stoat habitat use assessment in the MacKenzie basin (South Island New Zealand) where key predictors identified from a set of candidates were indices of prey availability, average predator presence and habitat structure (Kliskey and Byrom 2004). Spatial patterns in stoat abundance can also be influenced by a combination of age-related social organisation (Erlinge and Sandell 1986), intersexual attraction and mate search (Alterio 1998), intra-sexual avoidance and territorial defence (Alterio 1998; Erlinge *et al.* 1982).

This study demonstrates that stoat activity can be predicted with reasonable accuracy from GIS-extrapolated terrain data without need to measure at each activity monitoring location microhabitat factors. However, while an optimal predictive terrain model can be derived using terrain factors alone, factoring rat visitation, and nearby or recent stoat visitation to the same tunnel significantly strengthened the model and many terrain factors appeared less important for predicting stoats. Also this modelling approach provides a first statistical investigation of an existing data-set using a conventional logistic regression modelling approach, and without factoring in other important environmental drivers such as season, vegetation type and microhabitat conditions such as visibility of tunnels and ground cover. There are also ecological complexities in terms of prey activity and conspecific interactions which require better understanding. It is clear there is strong autocorrelation present in the data that requires some correction. Spatial autocorrelation can result in underestimation of standard errors and overrepresentation of predictor variable effect in a model (Wintle *et al.* 2005; Guisan and Zimmermann 2000). A statistical resampling approach might provide a degree of control over autocorrelation effects in the model (Guisan and Zimmermann 2000). We identified rat activity as being important to the dynamics of stoat visitation, however in Tongariro Forest invertebrates and birds constitute the majority of diet items (Miles 1997), and a logical next step in this analysis would be to undertake a more complex habitat analysis using a model that factors prey activity and habitat preference, seasonal variability, and controls for spatial and temporal autocorrelation. Even so, the resulting model had an estimated accuracy of 75% using terrain predictors alone, and the resulting probability surface (Chapter 3, Figure 3) was able to provide a coarse land classification of value to managers. With more rigorous modelling it is expected that a predictive map with high accuracy could be developed to maximise the effectiveness of stoat control on threatened species recovery site.

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Chapter 6. Synthesis, conclusion and discussion

1. Introduction

This thesis investigates the spatial and temporal characteristics of stoat (*Mustela erminea*) activity in Tongariro Forest using two recognised and well documented monitoring techniques. Radio telemetry provided high detail measurement of individual activity of a number of stoats, and footprint tracking tunnels provided measurement of population level tendencies in activity and abundance. The overarching theme of the thesis was to search for ways to predict the visitation of stoats to control stations in space and time, to guide management optimisation of stoat control network.

The specific objects were as follows:

Objective 1. Identify predictable times of high and low stoat activity where they exist.

Objective 2. Identify habitat types and specific locations within Tongariro Forest where stoat visitation to a control station is likely to be especially high and low.

Objective 3. Understand relevance and limitations of results.

This chapter provides a summary of main findings across the four previous investigative chapters (chapters 2-5) and brings the findings together into a synthesis in terms of stoat behavioural ecology and wildlife management. Finally key recommendations are outlined as well as priority research directions.

2. Main findings

2.1. Objective 1. Identify predictable times of high and low stoat activity where they exist.

Temporal patterns in stoat activity were quantified using motion sensitive radio collars that provided high detail measurement of individual activity of a number of stoats. Prior to field data collection the radio transmitters were assessed and calibrated using captive stoats and video equipment to compare telemetry signals with actual behaviour. Two motion sensitivities where tested (fine and coarse), and the fine sensitivity transmitter was identified as most suitable for a field study. Estimates of locomotor activity derived from telemetry data correlated with directly observed behaviours at hourly and greater time scale, and verified suitability of activity transmitters for field study of stoat activity. In the field, 11 stoats were tagged with motion-sensitive radio transmitters and monitored in the field to quantify temporal patterns in wild stoat activity. Four monitoring 'seasons' representing early and late summer, autumn and spring seasons of the year, provided a total of 896 hours of stoat activity. On average, stoats were active 28% of the 24-hour day (seasonal range 16-41%). The total time spent active per day varied between seasons, and the partitioning of this activity through the day also varied considerably between seasons. Tracking tunnel visitation indices obtained in subsequent years showed similar seasonal patterns to the telemetry, except during early summer when tracking rates were lower than the equivalent locomotor activity estimate. Most radio-tagged stoats were predominantly diurnal in all seasons. Winter and spring had the largest proportions of daytime activity even though daytime was on average about 4 hours shorter during these seasons than in summer. Crepuscular peaks in activity were apparent in all seasons but particularly so during late summer. Activity was least structured in early summer, when activity was spread more or less evenly throughout the 24 hours of the day. Active periods usually lasted at least 40 min, and up to 43% of activity was maintained continuously for >3 hours. Variability in activity between and within stoats was high, but variability in spring was marginally lower than in the other seasons. Temperature had some influence on activity at an hourly timescale, and the correlation between activity and temperature strengthened with increasing timescale. Autumn activity comprised more extended bouts of movement so might represent a time of year when stoats are ranging further, or exploring or searching within their ranges more intensively. This suggests that stoat control and monitoring devices might be most effective in autumn.

2.2. Objective 2. Identify habitat types and specific locations within Tongariro Forest where stoat visitation to a control station is likely to be especially high and low.

Habitat use of stoats was quantified using Geographical Information System (GIS) software and statistical modelling to identify terrain variables that predict stoat visitation to stations. Spatial analysis scale was found to be important for modelling outcomes, and an optimal model equation was derived using model selection techniques that factored in a range of relevant analysis scales. The sensitivity of the model to different terrain parameters was tested by systematically substituting each variable and calculating the difference this made to the model derived estimates of stoat visitation. The most dominant terrain predictors influencing stoat visitation were proximity to tracks, altitude, northerly and easterly aspect, mean curvature, and topographical position and slope. Proximity to tracks and mean curvature were variables particularly sensitive to analysis scale. Indices of mouse and rat activity, which are known prey of stoats, and autocorrelation factors for previous and nearby stoat visitation, significantly improved the model, but reduced the statistical significance of many of the terrain factors that were previously important. When a rat factor was built into the model, many of the terrain variables dropped out of significance. This intuitively suggests that stoats may be cueing into rat presence to some extent, the distribution of which can largely be driven by rodent food availability (Blackwell *et al.* 2000) and available vegetation type (Christie *et al.* 2006). Other studies also show stoat activity related to prey presence (Cuthbert and Sommer 2002). However, counter-intuitively, in this study rat visitation to tracking tunnels was negatively correlated with stoat visitation. A possible explanation for this is that stoat interest in tracking tunnels may decrease in areas with higher prey numbers due to alternative attractions, and there is some evidence of this from trapping studies (King and White 2004). Another explanation is that rats avoid places where stoats are prevalent. Mouse visitation had no detectable effect on stoat tracking rates when factored along with terrain variables.

In a modelling environment variables are interrelated and interconnected to some extent or another. For example, the layout of where steep or curved parts of the landscape are situated is related to where water flows as these are geological constructs of water erosion. The geomorphology of the landscape determines patterns in terrain predictors such as CTI, mean temperature, means solar radiation, aspect and other biogeographical distributions. Measurements of one predictor variable may therefore have probabilistic components of other terrain predictors that may influence or have been influenced by that variable. The statistical consequence of this collinearity between model variables creates potential for information loss, bias towards variables that have influence on other predictors in the model, and masking of the influence of weaker variables in the model (Burnham and Anderson 2002). Collinearity is an intrinsic part of any natural system. Waldo Tobler propounded the first law of geography that states ‘everything is related to everything else, but near things are more related than distant things’ (Tobler 1970). Terrain modelling in this study set out to minimise collinearity by identifying predictor pairs that were significantly correlated, and excluding variables based on maximising

2.3. Objective 3. Understand relevance and limitations of results.

Activity transmitters provided a means to quantify locomotor activity, and significant correlation with actual activity was demonstrated. However, there was also a tendency for overestimation of activity using these transmitters based on the timeout period programmed into the micro-controller logic. The timeout period is a common feature supplied with the transmitters, and is essential for identifying activity during radio-tracking studies and for detecting mortality. However, removal of timeout overestimation is required to accurately quantify stoat activity in the field. The captive calibration study in Chapter Two indicated that removal of activity of less than 5 minutes duration would provide a measure of activity that is representative of time out of the den or sleeping location. The activity estimates derived from the field study are representative of time stoats are hunting or engaged in locomotor activity on the assumption that there are not large components of this activity engaged in non-locomotor activity. There is potential for re-examination of the data to improve interpretation and the precision of the telemetry activity estimates. A nominal 5-minute removal threshold, estimating bouts of nest-bound or stationary activity, was applied to reduce the total telemetry activity data set to a subset limited to locomotor activity bouts. This threshold could have a more complex elimination logic tested where inclusion of smaller bouts of telemetry are included or excluded based on chronological-proximity to larger bouts of activity. For example a short bout of activity during a sleeping time could be treated differently to the same activity bout amid longer bouts (e.g. short breaks in activity while hunting). The sequence of telemetry activity could also potentially be used to identify specific behaviour of the stoats taking place for each block, by applying a heuristic (pattern recognition) modelling approach (Nieddu and Patrizi 2000).

Footprint tracking tunnels have been shown to produce data consistent with monitoring by live-trapping, but not so well at low density (Gillies and Williams 2001; Dowding and Elliott 2003). The probability of a tunnel (or trap) intercepting a stoat is a function of the abundance of stoats in an area, their ranging activity (which is largely a function of density), and social structure which all vary throughout the year (King and Murphy

2005). Seasonal changes in food abundance are likely to also influence both the stoats search effort and attraction/aversion to entering a novel object like a tunnel or trapping device. The 300 tunnel layout was designed to give a coarse relative abundance measure with useful precision at a seasonal-annual time scale, but this frequency of tunnels and lines was based on having no prior understanding of mustelid likelihood across the landscape. There is immediate value in using predictions from this study to further refine tracking tunnel layout for long term or operational monitoring. However, tracking tunnel-derived predictive models have most value if the results can also be applied to large scale or localized trapping operations, or for species protection/research purposes. Overlap in footprint size at the extremes of the size range for stoats, weasels and ferrets means that tracking tunnel monitoring does not perfectly distinguish the three mustelid species present in New Zealand. However, stoats are by far the most numerous of these species in Tongariro Forest, as revealed by earlier kill-trapping done in the same area. Stoats were found to be 70 times more abundant than ferrets in the core of the forest, and six times more abundant than weasels (DOC Ruapehu File Records 1994-1997). Therefore, it is reasonable to make direct inference about stoats for this site. This may not be the case for other sites where the relative abundance of the predator guild and their impact on prey species differs from Tongariro Forest, so the value of tracking tunnel data for making predictions on stoat visitation should be considered site specific.

The New Zealand Landcover Cover Database (LCDB2, Landcare Research New Zealand) was considered for inclusion in the predictor variable list as vegetation cover is an important variable for modelling habitat use, but was omitted upon inspection of aerial photographs as coarse resolution of demarcation of vegetation classes did not seem to correspond with the highly variable vegetation on the ground. Also, the random tracking tunnel deployment didn't sample the LCDB2 cover classes in a stratified way (ratio of 23:6:1 lines of tunnels in 'indigenous forest', 'indigenous hardwood' and 'manuka/kanuka' categories respectively). Stoats were predicted to have higher visitation in certain parts of the forest than others. There are distinct habitat characteristics that change across the site. At a course terrain scale, the Tongariro Forest landscape changes from lower altitude deeply cut river valleys to several high plateaus with distinct peaks. There is also a broad transition of vegetation type from largely intact podocarp forest in the south, to mid-regeneration forest in the west, to largely seral and low-stature vegetation in the east, and mature podocarp forest in the north. This arrangement was likely the result of the sequence of clear-fell logging that took place up to 1972 and degree of regeneration. Unmodified forests in NZ can have a vegetation distribution that is related in predictable ways to terrain characteristics (Wardle 1991; Leathwick *et al.* 2003). As a result, landcover features would be expected to correlate with some terrain features. However, Tongariro Forest, like many North Island native forests, is highly modified. Hence landcover patterns will not necessarily correlate to the biological influence from land form, but instead may be related to human derived patterns related to the efficiencies of effective timber extraction.

There are limitations to the kind of interference on habitat use that can be drawn from tracking tunnel data of this kind. Tracking tunnel data forms an index of visitation that includes components of habitat use/preference, individual activity levels, local population density and interspecific factors like prey abundance and landcover. Significant terrain effects were detected in the data, but when prey species and autocorrelation terms were fitted to the model, terrain effects became much less significant suggesting a more complex interaction is taking place. Future analysis would need to disentangle multivariate relationships between terrain effects and other drivers of activity in the environment. Also, the predictive of the model is uncertain without field validation. In this modelling, proximity to tracks, mean annual temperature, terrain curvature and easterly aspect were strong drivers of visitation, and slope, northerly aspect, topographical position to a lesser extent.

This study has found patterns in stoat locomotor activity that add to our understanding of stoat activity in New Zealand, but we caution that the findings may not be valid for all habitats or management sites across New Zealand. Stoat habitat preference was found to differ between similar but geographically distant sites with no consistent factor stoat activity (Christie *et al.* 2009).

Seasonal conditions and activity trends have been estimated from short monitoring periods, but these may not account for all parts of stoat annual activity profile. Conclusions made in this study are most valid for adult stoats in sites with similar prey availability and land cover conditions to Tongariro Forest.

3. Fit with ecological theory

Stoats were found to be active all times of the day with some variation in mean activity across seasons. Activity was intrinsically high during the summer and mobility high during the autumn. During the summer the activity was greater by day than night, even factoring the longer daylight hours. This is a time when stoats are likely to be on the surface pursuing prey. This also means this is a time when stoats are likely to be exploring their home ranges and be accessible to tracking tunnels or trapping stations. The findings suggest that there is no particular optimal time to trap or poison adult stoats based on activity level alone. A possible exception is the observation that, during autumn (April monitoring), a considerably larger proportion of activity comprised extended bouts of movement. This might represent a time of year when stoats are ranging further, or exploring or searching within their ranges more intensively, in which case they would be more likely to intercept a control or monitoring device at this time of year.

Optimal foraging theory is the study of how and why species evolve specific preference for prey species type as a subset of the full range of potential prey species. Modelling of foraging economics centres on the relative magnitude of energy reward from a prey item compared to the energy exerted and time lost in capturing the item (i.e. profitability), and factoring the risk of the pursuit and the lost opportunity by engaging in pursuit. The breadth of diet and likelihood of pursuit is related to the average energy profitability. Tracking tunnel visitation rates were high during the early summer even though measured locomotor activity levels were at their lowest. The low activity rates can be explained by the increased food availability at this time of year: when prey densities are high, prey search and acquisition times reduce. Daily food requirements at this time of year become easier to catch as there are greater numbers of nesting chicks, naïve juveniles and nest-bound adults that require less energy to acquire. Stoats in Tongariro Forest predominantly eat birds and invertebrates during the winter and spring (Miles 1997). During this time stoats engaged in shorter activity bouts, supporting a model of more frequent prey acquisitions. But later in summer, the duration of activity bouts lengthened, which is consistent with the expected decline in prey and dilution of available prey across a larger competing stoat population. Likewise the increased locomotor activity during autumn can be explained by the same decreasing food availability and catchability approaching winter. As food density decreases and distance between food items expands, average hunting effort for each prey acquisition increases (Zielinski 1986; Zielinski 1988; Price 1971). By winter, rat numbers decline rapidly (Efford *et al.* 2006), so energetic cost of food acquisition would be expected to increase at this time while food becomes more scarce and riskier to catch, or sustained pursuit becomes necessary. In a laboratory prey choice experiment using Y-tubes and based on rodent odour, hunting by weasels was greatest for the species presented most frequently, and there was some preference for one species over another when presented together (Sundell *et al.* 2003). This verifies that weasels have instinctive affinity for prey species, but not so much selectivity that food intake becomes insufficient to meet energy requirements. This is likely the same for stoats, and there are documented examples of prey switching to secondary prey species at times of low abundance of the stoats primary food (Parkes and Murphy 2004, Murphy *et al*. 1999, Smith *et al*. 2005, Moors 1983).

Stoats have evolved surplus killing as part of their foraging strategy. The basic theory on the evolution of this, in terms of small mammal foraging ecology, is that for species that evolve in *i)* an environment of uncertain resource availability, or *ii)* where prey resource is indefensible, or *iii)* when prey live in highly heterogeneous habitat where prey can escape into habitat that favours evasion from predators, the energy return from daily activity is maximised and chance of starvation minimised by killing prey when in optimal habitat, even when not hungry (Oksanen *et al.* 1985). Surplus killing has been documented in stoats and other similar mustelids (Sundell *et al.* 2003; Jedrzejewska and Jedrzejewski 1989; Jedrzejewski *et al.* 1992). Maintenance of positive energy balance depends on energetically favourable microhabitat and efficient foraging strategy (Chappell 1980). In least weasels (*Mustela nivalis nivalis*), a morphologically and metabolically similar animal to stoats, daily energy expenditure during winter was high due to thermoregulatory cost (Zub *et al.* 2009). In small mammals adapted to cold, daily energy budget must be a trade-off between changes in daily activity, basal metabolic rate (body temperature) and use of nesting/denning behaviour to conserve energy (Humphries *et al.* 2005, Gilbert *et al.* 2009, Zub *et al.* 2009). Stoats and weasels have evolved relatively long and thin body morphology in order to be able to explore narrow tunnels and den produced by their small rodent prey. The correspondingly higher surface-area to volume ratio necessitates a higher thermal loss in cold environments compared to ‘normal’ shaped animals of similar size. This was quantified in a metabolic study where weasels metabolised at a greater rate than woodrats (*Neotoma spp.*), a species of similar size and mass, but rounder shaped body morphology (Brown and Lasiewski 1972).

4. Recommendations and Future Direction

Results from this study provide a useful insight about which predictive factors drive stoat activity and habitat use in Tongariro Forest, and add to the collective knowledge-base for stoats relevant to control. The work further details what is possible within their ecology. There are several levels of replication required before these results can be established as being representative of seasonal tendency, for this site, other sites of the same habitat type and other habitat types. The first level is to replicate this study at Tongariro Forest across several more years to quantify inter-annual variability. This was partially achieved in that tracking tunnel component of the data spanned years from 2001 to 2008. The telemetry, however, only took place within one year. The second is to replicate at another site of similar habitat-type (mixed broadleaf / podocarp indigenous forest) to establish if the results are consistent for that habitat type. This was done in part by comparing tracking visitation rates between Pukepoto and Tongariro forest. The third is to replicate at sites of habitat type different from Tongariro Forest to look for nationally consistent drivers of stoat activity. Multiple-study reviews can potentially pull together common predictive factors and contrast differences found by different authors, but common relationships in activity and habitat use are difficult to compare unless the methodology and data-structure are consistent (e.g., Christie *et al.* 2009).

Habitat modelling should ideally factor in a field validation survey to test the accuracy of the derived model for predicting visitation to a new random set of locations (Rykiel 1996). If this is not possible for funding or logistic reasons, a pseudo-validation can be achieved by use split-sample or re-sampling validation techniques such as cross-validation, jack-knife and bootstrapping (Efron and Gong 1983). In these methods a subsample of the data set is randomly partitioned off to form a training set with which to develop and optimal equation, and the remainder a test-set for assessing accuracy of the derived model. This was not possible within the scope of the study.

An important finding of this study is that inclusion of rat activity in the terrain as a predictor variable markedly changed the significance of other terrain variables in the model, suggesting that there is a statistical relationship between prey habitat-preference, stoat habitat preference and visitation rates. Findings on spatial and temporal autocorrelation also indicate the stoats' nearby and previous activity should be carefully accounted for in the modelling. It is fair to consider that rat and mouse visitation may also be auto-correlated. The next logical step in further analysis of these data therefore is to apply a multivariate modelling approach, with stoats rats and mice as covariates, with a sample design that either quantifies or eliminates spatial and temporal autocorrelation.

Application of a predictive habitat model to guide management would require greater model accuracy in terms of internal measure of fit. This study used a set of readily available geospatial terrain data layers to for an optimal model. The number of variables assessed were markedly less than can typically be tested using logistic regression based model selection, and there are many more sources of environmental data available. There is potential to greatly improve the model by factoring in many more empirical or derived geospatial terrain descriptors. Of particular importance is to factor vegetation land cover into the model at sufficient accuracy. The New Zealand Landcover Database (LCDB2) was not considered useful for this analysis as described above. However, for a site the size of Tongariro Forest it would not be prohibitive to digitise a geospatial data layer that accurately quantifies the extent of vegetation type across the forest using existing high resolution aerial imagery or satellite multi-spectral imagery to determine land cover. Modern laser based terrain imaging such as 'light detection and ranging' (LIDAR) is now detailed enough to quantify the height of vegetation on the ground as well terrain form accurate to up to 0.15m resolution (Brock 2009, Rosette *et al.* 2010). A remote sensing approach using high resolution Light Detection and Ranging (Lidar) combined with aerial colour and satellite multispectral imagery would enable powerful terrain and landcover modelling.

Key recommendations for pest management that arise from our findings are that:

- summer and autumn are marginally better times of year than spring to intercept stoats with monitoring or control devices;
- spring is a marginally more accurate time of year for annual population monitoring as abundance indices are least confounded by the activity of individuals;

- trapping operations would benefit from servicing lines with minimal disturbance during early morning and late afternoon, especially during autumn, to avoid human disturbance at these highly active times of day;
- high variability in the activity of individual stoats means one particular trap layout and service regime will not necessary be optimal for all stoats;
- Stoats are potentially most trappable at sites denoted according to figures 3 and 4 in Chapter 4;
- Areas within Tongariro Forest that are high likelihood for stoat visitation are potentially places of high vulnerability for threatened species. Interventional management of kiwi, where chicks are released following nest manipulation of after captive rearing of eggs, might benefit from releasing individuals at low-likelihood sites for stoat visitation.

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