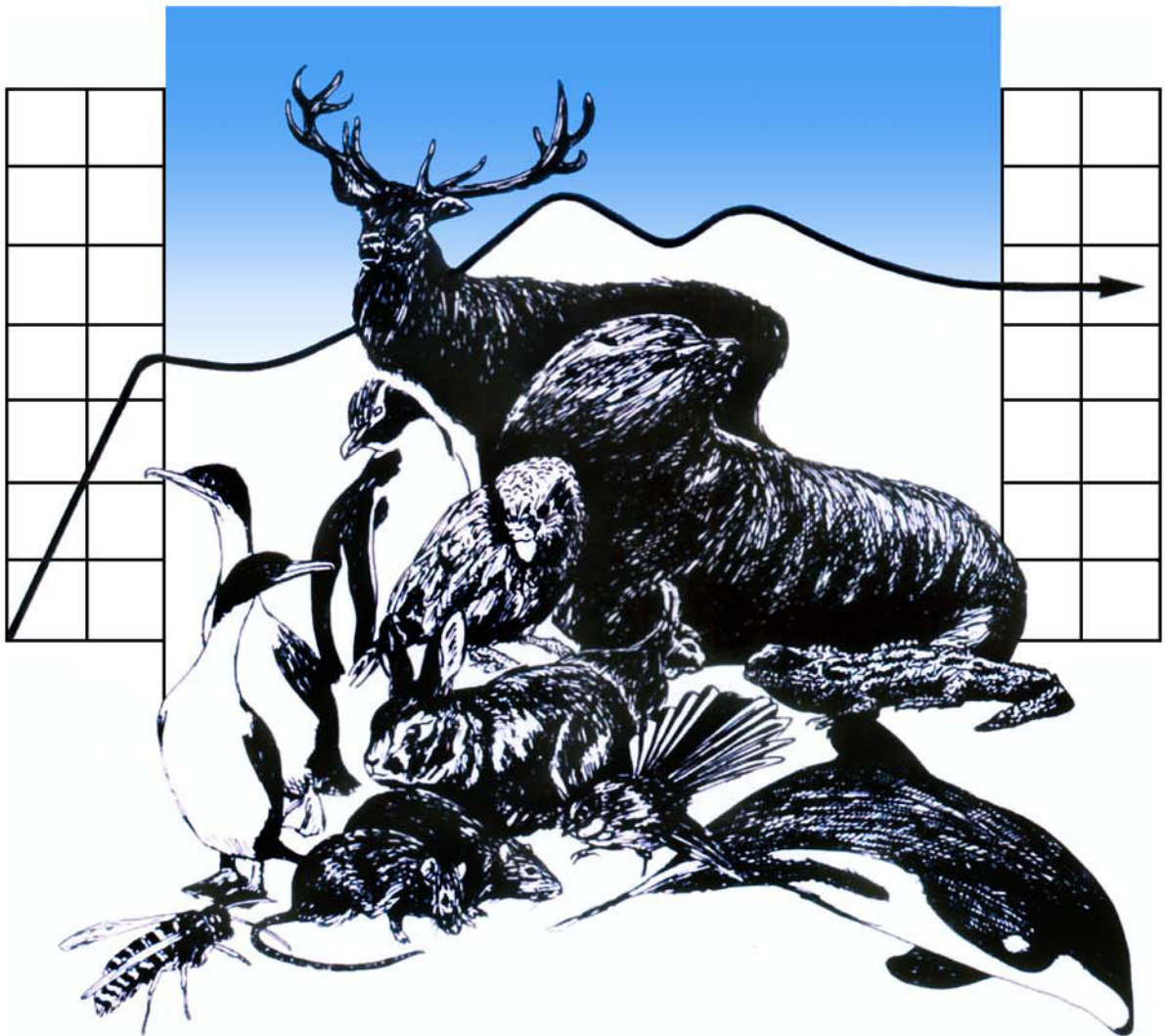




DEPARTMENT OF ZOOLOGY



WILDLIFE MANAGEMENT

**STEP ON IT:
CAN FOOTPRINTS FROM
TRACKING TUNNELS BE
USED TO IDENTIFY LIZARD
SPECIES?**

Scott Jarvie

A report submitted in partial fulfilment of the
Post-graduate Diploma in Wildlife Management

University of Otago

2012

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Abstract

Inventory and monitoring of animal populations is essential to achieve many conservation management objectives. There are few effective or efficient methods for surveying and monitoring cryptic species, which includes a high proportion of herpetofauna. An alternative method recently proposed for lizards is footprint tracking tunnels. In this study the utility of tracking tunnels for detection and monitoring of lizards was tested with species from the South Island, New Zealand. For all skink (*Oligosoma* spp.) tracking cards examined, no footprint measurements could be taken because they were either indistinct or obscure. In contrast, all gecko species' (*Hoplodactylus duvaucelii*, *Woodworthia* spp., *Naultinus* spp., and *Mokopirirarau* 'southern forest') provided footprints that were able to be used; subsequent analysis focused on gecko species. Footprint measurements from tracking cards were found to have a strong correlation with foot morphometric measurements for *Naultinus gemmeus* and *Woodworthia* 'Otago/Southland'. Models based on leave one out cross validation found that species discrimination was possible from tracking card footprints for these two species; the best model correctly assigned species for *N. gemmeus* 96.1% of the time, as opposed to *W.* 'Otago/Southland'. My findings suggest that footprints from tracking tunnels may be able to be used to distinguish among species for surveying and monitoring of lizards. Additional research is needed to assess the ability to further discriminate intra- and inter-genera lizard footprints from tracking tunnels.

Keywords: cross-validation; detection; footprints; New Zealand; monitoring; species discrimination; surveying; tracking tunnel

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Introduction

Inventory and monitoring is a critical component of species conservation management (Hare *et al.* 2007; Riberio-Júnior *et al.* 2008; Lettink *et al.* 2011). The requirement to undertake surveys to determine species' presence (Tocher *et al.* 2000; Hoare *et al.* 2012) and for long-term population monitoring to determine responses to conservation management (Hoare *et al.* 2007; Reardon *et al.* 2012) is essential to many research and management objectives.

However, detection and monitoring of small, visually cryptic species can be difficult. There are currently no efficient and reliable techniques for a high proportion of herpetofauna and invertebrates (Watts *et al.* 2008; Bell 2009). The main reasons for the limited development of techniques for lizards include high ecological impacts of surveying and monitoring (Enge 2001; Towns & Ferreira 2001), inefficient monitoring and surveying techniques (Whitaker 1994; Bell & Patterson 2008), and low detectability and catchability of taxa (Jewell 2007; Knox *et al.* 2012).

In New Zealand, the interplay of a long evolutionary isolation, and recent geological and climatic stresses (Trewick *et al.* 2007; Neall & Trewick 2008) has strongly affected the evolution of the biota (Wilson 2004; Gibbs 2006; Wallis & Trewick 2009), including the lizard fauna where there is evidence for speciation, lineage diversification (Chapple *et al.* 2009; Nielsen *et al.* 2011), and ecological specialisation (Daugherty *et al.* 1994; Jewell 2008). The number of extant lizard species is extraordinary considering New Zealand's relatively small size and cool-temperate climate (Daugherty *et al.* 1994). There are currently 99 species of lizards recognised in New Zealand (including putative species; Hitchmough *et al.* 2010), placed within one genus of skinks (*Oligosoma*; Chapple *et al.* 2009) and seven

genera of geckos (*Hoplodactylus*, *Naultinus*, *Mokopirirakau*, *Pacificus*, *Toropuku*, *Tukutuku*, and *Woodworthia*; Nielsen *et al.* 2011). Lizards can be found in virtually every available habitat, including marine, grassland, wetland, forest, and alpine bluff and rock scree environments (Jewell 2008; Chapple & Hitchmough 2009).

New Zealand lizards are generally visually cryptic and difficult to detect (Knox *et al.* 2012; Hoare *et al.* 2012), thus are a difficult taxonomic grouping to obtain data for distribution and population size (Hitchmough *et al.* 2010). For example, 8% are so rarely encountered that their status cannot be determined with any accuracy ('data deficient' in Hitchmough *et al.* 2010). Lizards have traditionally been surveyed and/or monitored by active searches, e.g. visual encounter surveys, searches of natural retreat sites, and nocturnal spotlight searches (Towns 1991; Tocher & Marshall 2001; Hare & Cree 2005), live trapping, e.g. pitfall traps and G-minnow traps (Whitaker 1982; Newman 1994; Hoare *et al.* 2007; Bell 2009), and artificial retreats (also known as artificial shelters, coverboards, artificial cover objects or foam covers; Lettink & Cree 2007; Wilson *et al.* 2007; Bell 2009). An alternative method recently proposed to survey and monitor lizards is through footprint tracking (Siyam 2006; van Winkel 2008). Non-invasive methods such as footprint tracking are particularly important when studying low-density or cryptic species that are difficult to detect by standard methods (Brown *et al.* 1996; Watts *et al.* 2008)

Footprint tracking tunnels (King & Edgar 1977) are widely used in New Zealand to detect the presence of, and index the density of, small-introduced mammals (e.g. Brown *et al.* 1996; Blackwell *et al.* 2002). Tracking tunnels currently rely on ink and card/paper to record target species' tracks (Blackwell *et al.* 2002). Many tracking tunnels also record the prints of other

taxa that walk through them, including invertebrates and herpetofauna (Russell *et al.* 2010; Watts *et al.* 2011a). Recently, tracking tunnels – set to monitor for rodent incursions on a pest-free island – confirmed the presence of a small remnant population of common geckos *Woodworthia maculata* which had gone unnoticed for many years (van Winkel 2008). Tracking tunnels have also been shown to be useful for detection and monitoring of invertebrates (Watts *et al.* 2008; Watts *et al.* 2011a; Watts *et al.* 2011b). Based on mammal and invertebrate studies, tracking tunnels are likely to be an effective and efficient method of obtaining data for distribution and inventory, and may be useful for generating indices of abundance to examine population trends and site occupancy of lizards.

Footprint tracking card analysis for lizards has traditionally been carried out in a manual identification procedure by experienced biologists who can distinguish tracks of some different species based on visual characteristics, such as shape, lamellae counts (if clear) and imprint other than foot (e.g., tail drag or ventral scale pattern; Siyam 2006; van Winkel 2008). However, the identification among taxa with similar morphology is either extremely difficult or even impossible (Siyam 2006). Consequently, uncommon species may be overlooked and classified as a more common, but similar, species, leading to negatively biased estimates of species presence or richness (e.g. Siyam 2006). The recent development of automated methods of differentiating tracks of small mammals (Russell *et al.* 2009) shows that measurements of footprints, i.e. various aspects of prints, can be used to identify morphology similar species.

The objective of this study was to test the utility of footprint measurements from tracking tunnels to accurately identify terrestrial skinks (*Oligosoma* spp.) and geckos (*Hoplodactylus*

duvaucelii and *Woodworthia* spp.), and arboreal geckos (*Naultinus* spp. and *Mokopirikirarau* ‘southern forest’) from the South Island, New Zealand. Specifically, the aim was to address four questions: (1) to determine whether tracking card measurements reflect morphological measurements for lizards; (2) to evaluate whether footprint measurements reflect morphological measurements for lizards; (3) to test if there is sexual size dimorphism for any lizard species, and if so, are footprint measurements useful indicators; and (4) to evaluate whether footprint measurements can be used to discriminate among lizard species.

Methods

Study species

The lizard fauna used in this study of South Island species (Table 1) includes four species of diurnal skink (common skink *Oligosoma polychroma*, grand skink *O. grande*, green skink *O. chloronton*, and Otago skink *O. otagense*), four species of diurnal gecko (jewelled gecko *Naultinus gemmeus*, Marlborough green gecko *N. manukanus*, Nelson green gecko *N. stellatus*, and rough gecko *N. rudis*) and four species of primarily nocturnal gecko (common gecko *Woodworthia* ‘Otago/Southland’, Dauvaucel’s gecko *Hoplodactylus duvaucelii*, Canterbury gecko *W. brunneus*, southern forest gecko *Mokopirikirarau* ‘southern forest’). The species range in size from small-to-large (maximum snout-vent length (SVL) range from 72 mm in *N. rudis* to 161 mm in *H. duvaucelii*; Jewell 2008; Chapple *et al.* 2009; Nielsen *et al.* 2011). All species are dietary generalists, consuming a wide range of arthropod prey and/or smaller lizards, as well as fruit and nectar from native plants (e.g. Barwick 1982; Whitaker 1987; Jewell 2008).

Tracking tunnels

'Black Trakka' tunnels (500 × 100 × 100 mm; Gotcha Traps, Warkworth, NZ) were used in this study. These tracking tunnels were set with a pre-inked tracking card inserted within the run-through. The ink cards come with specially formulated ink (Gotcha Traps) that improves the definition of footprints for a range of species (Siyam 2006; Watts *et al.* 2011*b*). Tracking tunnels work by an animal walking over the ink and leaving a track on the non-inked outer portions of the card on exiting.

Distinguishing lizard species by their footprints

Lizards were captured and held for < 1 h in captivity while their footprints were recorded on tracking cards. The size (measured to the nearest 0.1 mm using a Crafright Digital Calliper) and arrangement of footprints (e.g. length and width of 4th toe, and length of palm and sole on front and rear feet, respectively) were measured after they had walked over the tracking cards. This was repeated at least twice for each lizard and average print lengths were obtained. For each lizard I recorded the age (adult, sub-adult or juvenile), sex of mature individuals (assessed by examining the cloacal region and/or everting the hemipenes), reproductive condition of mature females (gravid or not gravid; usually obvious from their distended abdomens and/or palpation), mass (measured to the nearest 0.1 g using either a Pesola spring balance or a Mettler Toledo PR2003 Delta Range balance), snout-to-vent length, vent-tail length (VTL) and tail regeneration (if present; measured to the nearest 1 mm using a clear plastic ruler), length of 4th toe of all feet, and the length of palm and sole of front and rear feet, respectively (measured to the nearest 0.1 mm using a Crafright Digital Calliper). All lizards were released within 1 m of where they were caught.

Statistical methodology

Prior to analysis, tracking card footprint measurements were obtained from the average of all clear prints for individuals. Tests were then done to determine whether tracking card footprint measurements reflected foot morphological measurements. The analysis was performed in three stages. Initially, species-specific analysis was conducted, in which I examined the relationship between the tracking card footprint measurements and morphological measurements to test for linear relationships. Tracking card measurements were specified as the response variable and morphological measurements as the predictor variable. This was followed by analysis to evaluate whether there was sexual size dimorphism for two lizard species (*N. gemmeus* and *W. 'Otago/Southland'*). The model used was based on leave one out cross validation (Stone 1975; Geisser 1975). Finally, leave one out cross validation was used to evaluate whether footprint measurements can discriminate among lizard species. For sexual dimorphism and species discrimination analyses, the factors used were combinations of length and width of 4th toe of the geckos' front and rear feet, ratios of length of 4th toe to 4th toe width for front and rear feet, and the length of palm and sole of front and rear feet, respectively.

The leave one out cross validation model uses all of the data but can also provide unbiased error estimates, even at small sample sizes (Olden & Jackson 2000). With leave one out cross validation, the model uses a single observation from the original sample as the validation (test) set, and the remaining observations as the training set. This is repeated such that each observation in the sample is used once as the validation data (Stone 1975; Wenger & Olden 2012). All analyses were conducted in the statistical programme R (version 2.15.0; R Development Core Team 2012).

Table 1. Morphometric and ecological information for lizard species studied from the South Island, New Zealand. SVL stands for snout-vent length.

Species	Maximum SVL (mm)	Activity phase	Habitat preference	Status
<i>Hoplodactylus duvaucelii</i>	161 ^a	Nocturnal, but sun basks ^a	Generalist ^{ab}	Relict ^{cd}
<i>Mokopirirarau</i> ‘southern forest’	88 ^e	Nocturnal, but sun basks ^a	Arboreal ^{ae}	At Risk – Declining ^d
<i>Naultinus gemmeus</i>	80 ^a	Diurnal ^a	Arboreal ^{af}	At Risk – Declining ^d
<i>N. manukanus</i>	68 ^a	Diurnal ^a	Arboreal ^{ag}	At Risk – Declining ^d
<i>N. rudis</i>	72 ^a	Diurnal ^a	Arboreal ^a	At Risk – Declining ^d
<i>N. stellatus</i>	80 ^a	Diurnal ^a	Arboreal ^a	At Risk – Declining ^d
<i>Oligosoma chloronoton</i>	125 ^a	Diurnal ^a	Terrestrial ^{ah}	At Risk – Declining ^d
<i>O. grande</i>	115 ^a	Diurnal ^a	Terrestrial ^{ai}	Nationally Critical ^d
<i>O. otagense</i>	130 ^a	Diurnal ^a	Terrestrial ^{ai}	Nationally Critical ^d
<i>O. polychroma</i>	79 ^a	Diurnal ^a	Terrestrial ^{aj}	Not Threatened ^d
<i>Woodworthia brunneus</i>	80 ^a	Nocturnal, but sun basks ^a	Generalist ^a	At Risk – Declining ^d
<i>W.</i> ‘Otago/ Southland’	89 ^a	Nocturnal, but sun basks ^a	Generalist ^a	At Risk – Declining ^d

Information from: ^aJewell 2008, ^bThompson *et al.* 1992, ^cWorthy 1998, ^dHitchmough *et al.* 2010, ^eHoare *et al. In press*, ^fKnox *et al.* 2012, ^gHare *et al.* 2007, ^hTowns *et al.* 2002, ⁱReardon *et al.* 2012, ^jWhitaker *et al.* 2002.

Results

Footprint tracking card data

For footprint tracking cards, I obtained data for 71 skinks (*Oligosoma* spp.) and 44 geckos (*Hoplodactylus duvaucelii*, *Naultinus* spp., and *Mokopirikarau* ‘southern forest’, *Woodworthia* spp.) (Table 2). All skink tracking cards footprints were indistinct (Figure 1a), thus no measurements were able to be taken. Whereas all gecko tracking cards provided footprints that could be used (Figure 1b and Figure 1c). Consequently, statistical analysis focused on geckos. Analysis was prioritised for *N. gemmeus* and *W.* ‘Otago/Southland’ due to larger sample sizes.

Table 2. Morphometric measurements for all lizards tracked in the study. SVL stands for snout-vent length.

Species	Number tracked	SVL (mm)	Mass (g)
		mean (\pm SE)	mean (\pm SE)
<i>Hoplodactylus duvaucelii</i>	2	100.5 (\pm 0.5)	45 (\pm 4.0)
<i>Mokopirikarau</i> ‘southern forest’	1	55.0	5.7
<i>Naultinus gemmeus</i>	27	69.2 (\pm 0.8)	12.2 (\pm 0.5)
<i>N. manukanus</i>	1	65.0	10.8
<i>N. rudis</i>	2	70.0 (\pm 5.0)	13.4 (\pm 2.4)
<i>N. stellatus</i>	2	79.0 (\pm 3.0)	13.0 (\pm 1.8)
<i>Oligosoma chloronoton</i>	1	85.0	18.0
<i>O. grande</i>	8	78.9 (\pm 4.1)	11.2 (\pm 1.8)
<i>O. otagense</i>	13	104.84 (\pm 2.9)	25.9 (\pm 2.3)
<i>O. polychroma</i>	46	56.1 (\pm 1.2)	3.3 (\pm 0.2)
<i>Woodworthia brunneus</i>	1	70.0	11.0
<i>W.</i> ‘Otago/Southland’	13	75.8 (\pm 1.0)	13.9 (\pm 0.7)

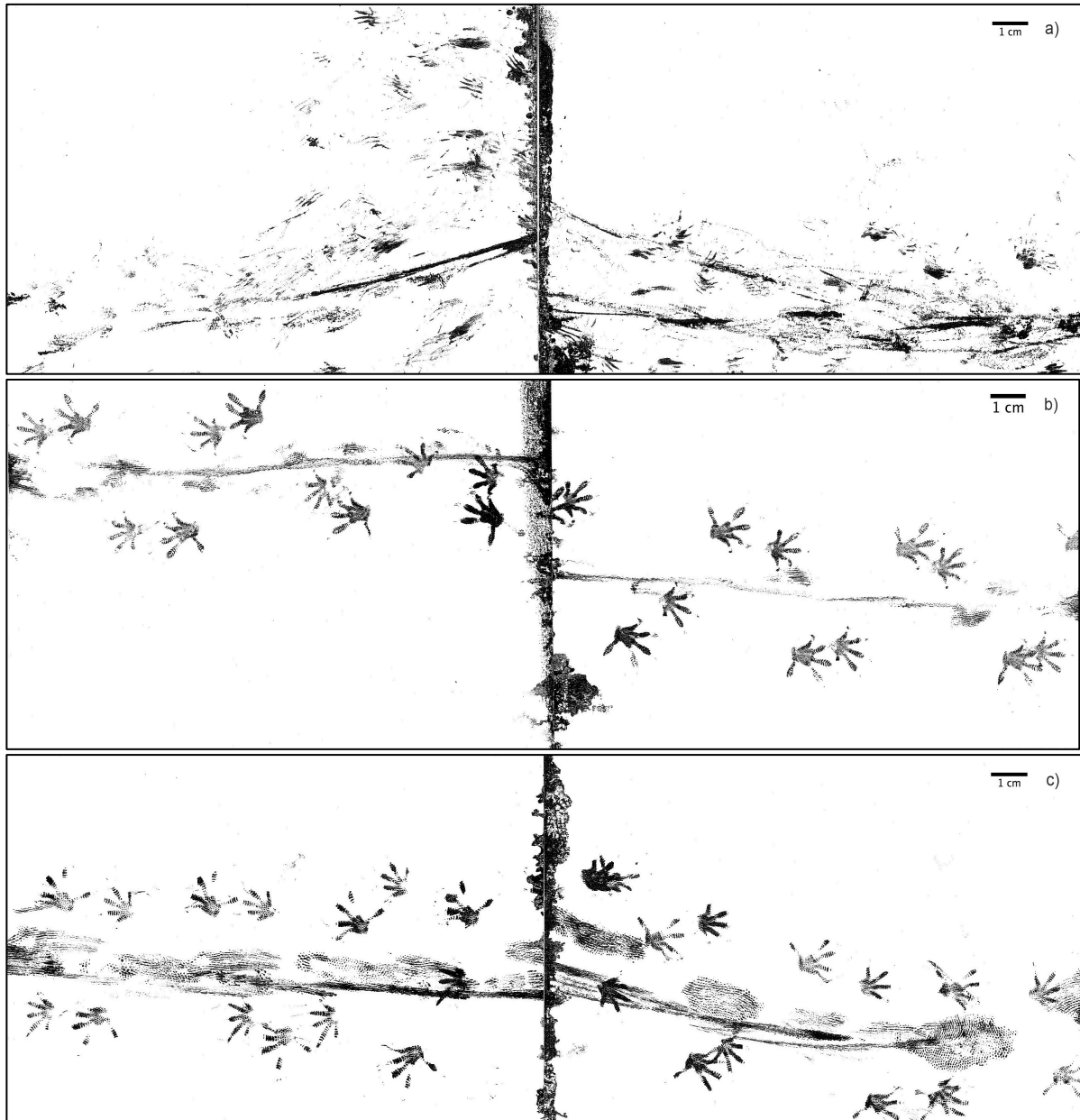


Figure 1. Lizard footprints from tracking cards used in this study. Footprints of (a) grand skink *Oligosoma grande*, (b) common gecko *Woodworthia* ‘Otago/Southland’, and (c) jewelled gecko *Naultinus gemmeus*. The ink section is not shown but was in the middle of the tracking cards.

Footprint tracking card data versus morphometric measurements

The relationship between footprint tracking card data and foot morphometric measurements for both *W.* ‘Otago/Southland’ ($\beta = 2.1125$, $SE = 0.8384$, $df = 11$, $t\text{-value} = 2.520$, $P < 0.01$)

and *N. gemmeus* ($\beta = 1.52$, $SE = 0.38$, $df = 25$, $t\text{-value} = 2.247$, $P < 0.001$) were significant (Figure 2). Although there was no correlation found between foot morphology measurements and standard morphometric measurements, e.g. rear sole vs. rear 4th toe, there were trends for species, i.e. species with larger SVL had larger footprints tracking card measurement, or *vice versa* (Figure 3). I was unable to examine interactions between factors due to having insufficient data.

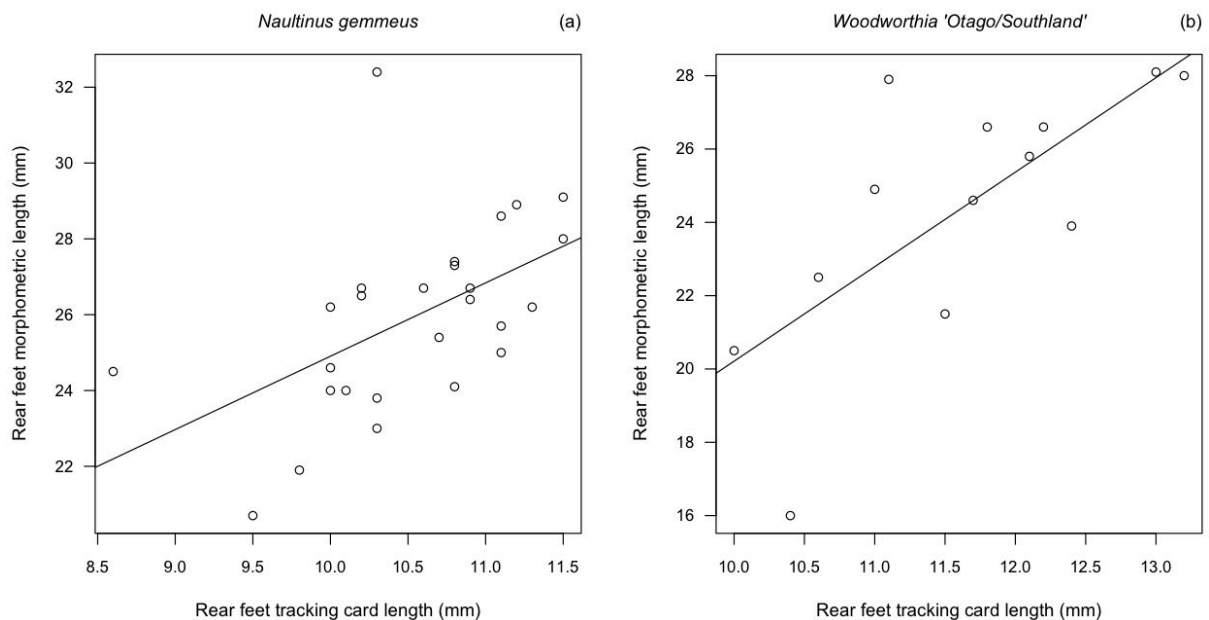


Figure 2. Correlations between rear feet morphometric length and rear feet print length for: (a) jewelled gecko *Naultinus gemmeus* ($\beta = 2.1125$, $SE = 0.8384$, $df = 11$, $t\text{-value} = 2.520$, $P < 0.01$), and (b) common gecko *Woodworthia* 'Otago/Southland' ($\beta = 1.52$, $SE = 0.38$, $df = 25$, $t\text{-value} = 2.247$, $P < 0.001$).

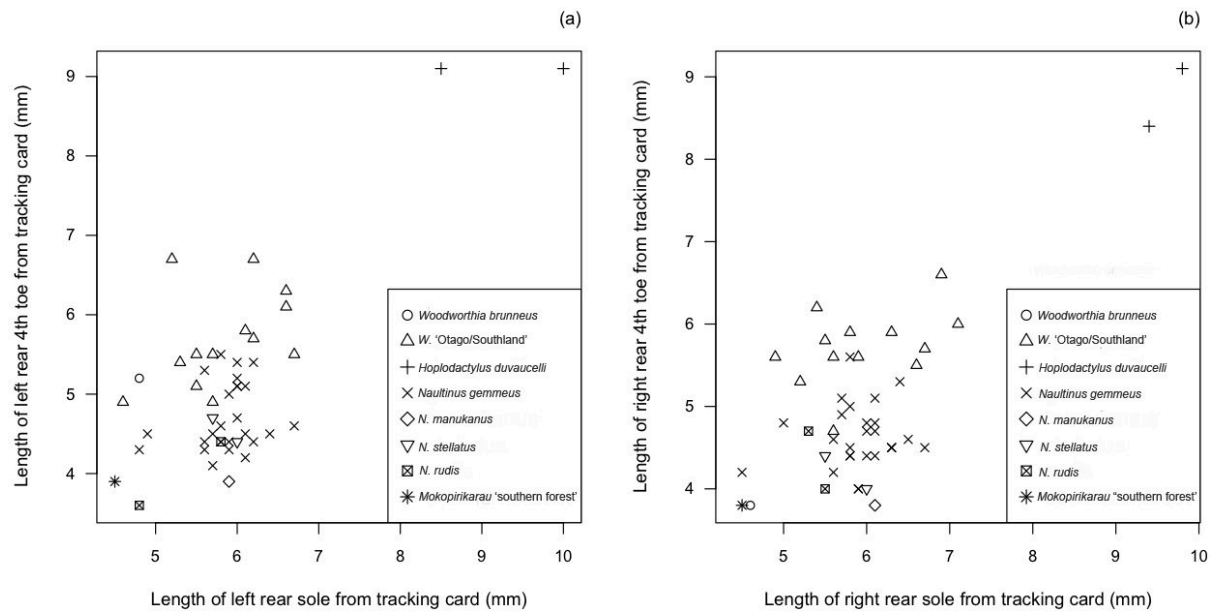


Figure 3. All species prints vs. prints for: (a) left rear 4th toe width vs. left rear sole length, and (b) right rear 4th toe width vs. right rear sole length.

Discrimination from tracking card footprint measurements

While there was no sexual size dimorphism for either *W.* 'Otago/Southland' or *N. gemmeus* (Figure 4), there was species discrimination between the two species (Figure 5). The best model for discriminating among species correctly assigned *N. gemmeus* (as opposed to *W.* 'Otago/ Southland') 96.1% of the time when the factors included rear foot width and rear ratio, i.e. the ratio of 4th toe length to 4th toe width for rear feet (Table 3). Furthermore, it should be noted that candidate models that included footprint width measurements were better at discriminating between the two species than models that did not include width measurements. For example, the four models that did not include footprint width measurements correctly assigned species for *N. gemmeus* compared to *W.* 'Otago/ Southland' 77.0-87.8% of the time. In contrast, all models that included width measurements correctly assigned species >90% of the time.

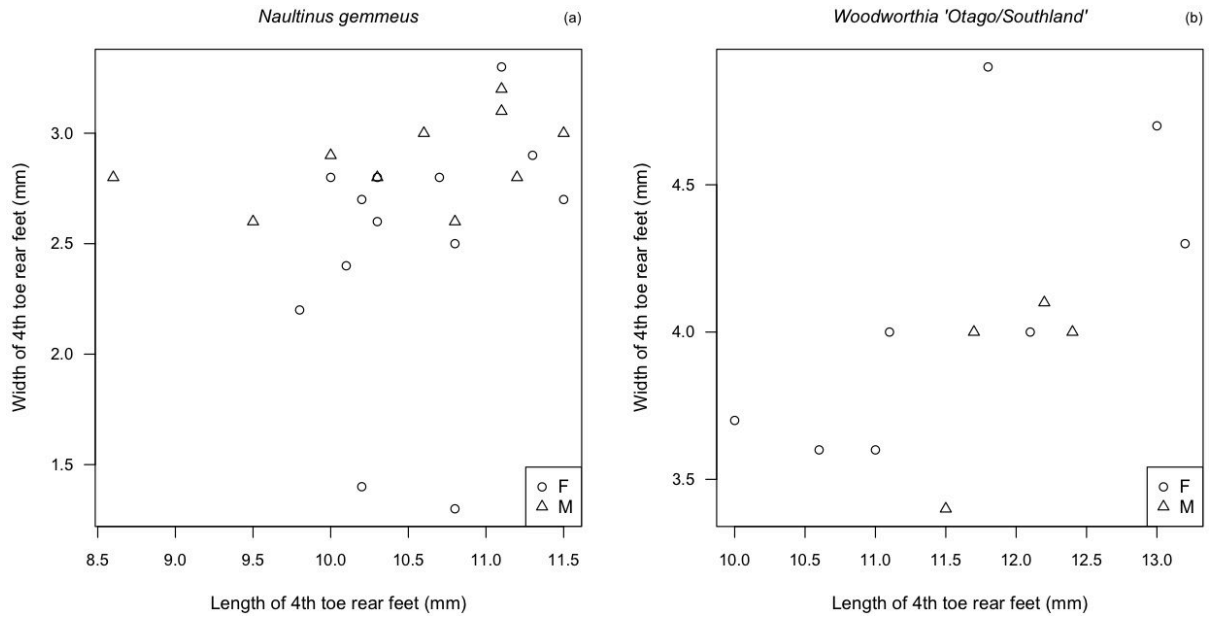


Figure 4. Sex discrimination for: (a) *Naultinus gemmeus*, and (b) *Woodworthia* 'Otago/Southland'. F = Female, M = Male.

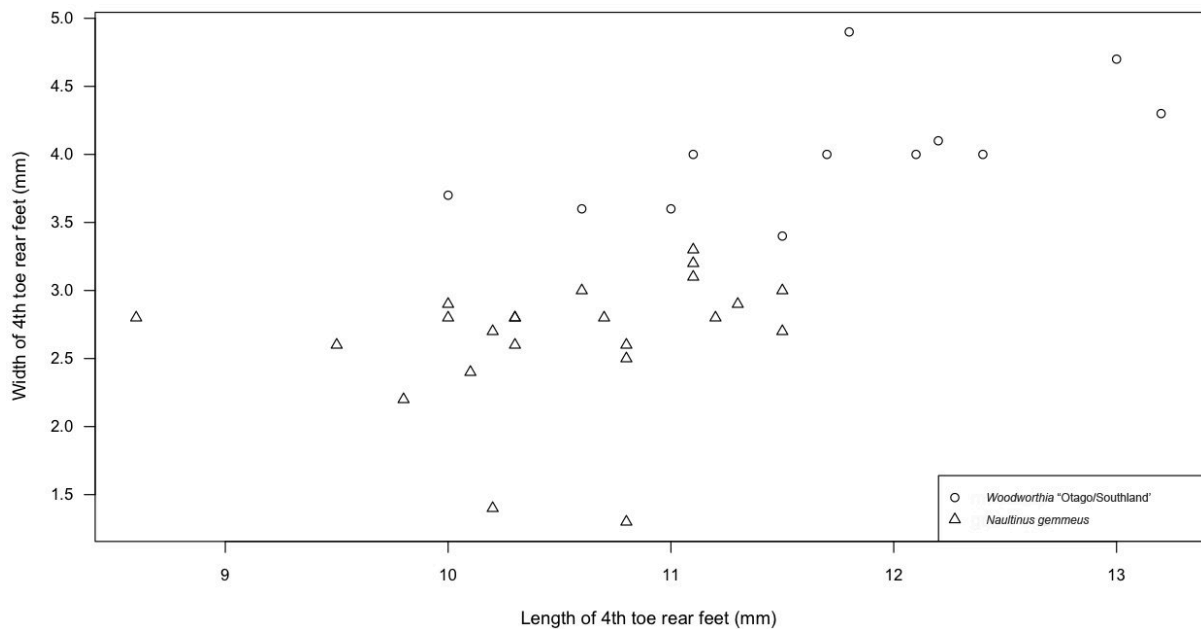


Figure 5. Species discrimination for *Naultinus gemmeus* and *Woodworthia* 'Otago/Southland'.

Table 3. Candidate models for species discrimination from footprint tracking tunnels for *Naultinus gemmeus* as opposed to *Woodworthia* ‘Otago/Southland’ from the South Island, New Zealand. FL = Front length, FW = Front width, FR = Front ratio, RL = Rear length, RW = Rear width, RR = Rear ratio, FRR = Front rear ratio. All effects are additive, as indicated by the ‘+’ symbol. The model which assigned the species correctly the most is indicated in bold.

Model	Species Discrimination (%)
<i>FL + FW + FR + RL + RW + RR + FRR</i>	90.1
<i>FL + FW + FR + RL + RW + RR</i>	94.3
<i>FL + FW + FR + RL + RW + FRR</i>	92.6
<i>FL + FW + RL + RW + RR + FRR</i>	91.3
<i>FL + FW + RL + RW + FRR</i>	93.5
<i>FL + FW + RL + RW</i>	95.2
<i>FL + FW + FR</i>	94.8
<i>FL + FW</i>	95.2
<i>FL + FR</i>	77.0
<i>FR + RR</i>	80.9
<i>FR + RR + FRR</i>	80.0
<i>RL + RW</i>	95.6
<i>RL + RR</i>	87.8
<i>RW + RR</i>	96.1
<i>RL + RW + RR</i>	95.2

Discussion

Evaluating the effectiveness of species management relies upon efficient surveying and monitoring techniques; however, for many cryptic species such techniques are poorly developed (Watt *et al.* 2008; Riberio-Júnior *et al.* 2008; Bell 2009). Footprint tracking

tunnels provide an alternative method to detect and monitor lizards (Siyam 2006; van Winkel 2008). In this study I was only able to examine relationships between morphological measurements and tracking card data for gecko species due to indistinct footprints being obtained from all skink species. The reasons that can broadly be used to explain differences in footprints from the tracking tunnels between gecko and skink species include habitat use, locomotion and morphology (Reilly *et al.* 2007; Jewell 2008; McElroy *et al.* 2008). A combination of these elements makes some taxonomic groupings footprints tracking card data more distinguishable than others. For example, geckos generally have broad toes with many lamellae, a prehensile tail and a less sprawling locomotion that make tracking card footprints more discernable. In comparison, skink species have mostly narrow toes with few lamellae and a more sprawling locomotion that may obscure tracks, thus they often leave less discernable footprints (Jewell 2008; Chapple *et al.* 2009; Nielsen *et al.* 2011).

Discrimination

While sexual size dimorphism has been recorded in New Zealand lizards (contrasting patterns have been reported: either females are larger than males (Sheehan 2003, unpubl. BSc (Hons) thesis, University of Otago; Spencer *et al.* 1998; Yeong 2003, unpubl. BSc (Hons) thesis, University of Otago; Hare *et al.* 2007; Penniket 2012), or males are larger than females (Todd 2003; but see Parrish & Gill 2003 for no sexual size dimorphism)), there were no significant differences found in this study. The subtle differences that were detected in the standard morphological measurements were largely swamped by intraspecific variability. Furthermore, the most distinctive features in which morphological measurements differed were difficult or impossible to identify when footprint measurements were used as indicators.

There were clear trends between the length of footprints and standard morphometric measurements, such as SVL, for all gecko species. While this finding is not unsurprising, as you would expect that larger individuals would leave larger footprints or *vice versa*, it provides further evidence that: (1) footprint length might be able to be used as a proxy for the size of tracked individuals (Siyam 2006), and (2) footprint length could be used as diagnostic tool to identify a individual's life history stage where species can be identified from the footprint (van Winkel 2008). For example, tracking tunnels have been found to be effective at detecting juvenile geckos (van Winkel 2008), a notoriously difficult group to detect using other methods (Pike *et al.* 2008).

Species discrimination

Although it can be difficult to distinguish between the footprints of some lizard species (Siyam 2006), this study has shown that discrimination between gecko species is possible. The leave one out cross validation model(s) used to discriminate between *N. gemmeus* and *W.* 'Otago/ Southland' could reliably identify the two species based on footprint measurements alone; in fact, the top five models identified the two species >95% of the time (Table 3). The ability to discriminate among species from footprint measurements improves the efficacy of tracking tunnels for geckos (Siyam 2006; van Winkel 2008), thus it should enable more accurate and efficient data to be obtained on species' biology and habitat use (Watts *et al.* 2008; Watts *et al.* 2011b). The addition of factors other than measurements from tracking cards, such as lamellae counts (if clear; Siyam 2006; Jewell 2008) and/or imprint other than foot (e.g., tail drag or ventral scale pattern; Siyam 2006), may also be informative in discriminating among species.

While species discrimination can be reliably attained from footprints for *N. gemmeus* and *W.* ‘Otago/ Southland’, it should be noted that these species belong to two separate genera of the seven genera found in New Zealand. Additional research is therefore needed to assess the ability to further discriminate intra- and inter-genera footprints. The priority for testing should be for species from different genera than have already been tested (e.g. *Mokopirirakau* and *Toropuku*), especially sympatric genera (e.g. *Woodworthia* and *Hoplodactylus*); this is because for most gecko genera, species occur in separate non-overlapping geographical areas (Jewell 2008).

Conclusion

Lizards can be extremely cryptic and difficult to survey and monitor; however there is an increasing awareness of the requirement to undertake surveys to determine species’ presence, and for long-term population monitoring to determine responses to conservation management. While findings from this study show that footprints generated from tracking tunnels can be used to reliably discriminate between two sympatric gecko species, a challenging taxonomic group to survey and monitor, they were unable to distinguish footprints from skink species. The use of tracking tunnels to survey and/or monitor lizard species should therefore depend on the taxonomic groups involved, and the type of data required.

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Appendices

Appendix 1.

Foot morphology and print measurements for geckos used in this study. Measurements were obtained from clear prints only.

Animal	Mean foot morphology (mm)		Mean print measurements (mm)			
	Front foot length	Rear foot length	Front foot print length	Rear foot print length	Width of front 4 th toe print	Width of rear 4 th toe print
<i>Hoplodactylus duvaucelii</i> 1	35.3	44.9	13.6	17.7	5.6	6.2
<i>H. duvaucelii</i> 2	37.2	40.3	13.9	19.0	5.1	5.8
<i>Mokopirikirau granulatus</i> 'southern forest'	15.1	19.8	6.7	8.4	1.6	2.0
<i>Naultinus gemmeus</i> 1	20.8	27.4	8.3	10.8	2.4	1.3
<i>N. gemmeus</i> 2	22.3	26.4	8.8	10.9	2.6	1.5
<i>N. gemmeus</i> 3	19.6	23.8	8.9	10.3	2.4	2.8
<i>N. gemmeus</i> 4	21.8	26.2	8.7	11.3	2.4	2.9
<i>N. gemmeus</i> 5	20.6	25.0	8.6	11.1	3.0	3.3
<i>N. gemmeus</i> 6	21.1	24.5	8.6	8.6	2.5	2.8
<i>N. gemmeus</i> 7	22.9	28.0	9.6	11.5	2.5	3.0
<i>N. gemmeus</i> 8	22.0	26.7	8.6	10.2	2.2	2.7
<i>N. gemmeus</i> 9	22.8	24.0	7.8	10.0	2.4	2.9
<i>N. gemmeus</i> 10	20.8	26.7		10.9	2.6	3.1
<i>N. gemmeus</i> 11	20.9	26.2	7.7	10.0	2.0	
<i>N. gemmeus</i> 12	20.3	26.7	7.5		2.2	1.4
<i>N. gemmeus</i> 13	21.4	27.3	9.0	10.8	2.3	2.6
<i>N. gemmeus</i> 14	24.9	32.4	10.1	10.3	2.4	2.8
<i>N. gemmeus</i> 15	21.6	29.1	10.0	11.5	2.4	2.7
<i>N. gemmeus</i> 16	18.2	24.0	8.9	10.1	2.0	2.4
<i>N. gemmeus</i> 17	16.9	21.9	7.5	9.8	2.0	2.2
<i>N. gemmeus</i> 18	19.3	24.1	9.0	10.8	2.1	2.5
<i>N. gemmeus</i> 19	18.7	25.4	8.8	10.7	2.4	2.8

Animal	Mean foot morphology (mm)		Mean print measurements (mm)			
	Front foot length	Rear foot length	Front foot print length	Rear foot print length	Width of front 4 th toe print	Width of Rear 4 th toe print
<i>N. gemmeus</i> 20	17.3	23.0	6.5	10.3	2.0	2.6
<i>N. gemmeus</i> 21	21.3	24.6	8.7	10.0	2.4	2.8
<i>N. gemmeus</i> 22	19.6	26.5	8.8	10.2	2.1	1.4
<i>N. gemmeus</i> 23	19.7	26.7	9.0	10.6	2.5	3.0
<i>N. gemmeus</i> 24	22.4	28.9	9.4	11.2	2.4	2.8
<i>N. gemmeus</i> 25	22.0	25.7	8.4	11.1	2.5	3.1
<i>N. gemmeus</i> 26	16.1	20.7	7.4	9.5	2.2	2.6
<i>N. gemmeus</i> 27	18.3	28.4	7.5		1.9	
<i>N. gemmeus</i> 28	21.7	28.6	8.9	11.1	2.7	3.2
<i>N. manukanus</i>	19.8	21.6	8.4	9.9	2.0	2.4
<i>N. stellatus</i> 1	24.1	27.3	8.0	10.2	2.2	2.8
<i>N. stellatus</i> 2	20.0	25.1	7.6	9.9	1.8	2.2
<i>N. rudis</i> 1	19.9	23.2	6.9	8.9	1.8	2.4
<i>N. rudis</i> 2	21.2	20.0	7.5	10.1	2.2	2.8
<i>Woodworthia brunneus</i>	15.3	18.6		9.2	2.8	3.6
<i>W. maculata</i> 1	25.0	28.1	10.7	13.0	3.6	4.7
<i>W. maculata</i> 2	19.4	24.6	8.9	11.7	3.3	4.0
<i>W. maculata</i> 3	22.4	26.6	9.4	11.8	4.0	4.9
<i>W. maculata</i> 4	22.5	25.8	9.9	12.1	3.4	4.0
<i>W. maculata</i> 5	19.2	23.9	9.8	12.4	3.3	4.0
<i>W. maculata</i> 6	17.0	20.5	8.8	10.0	3.0	3.7
<i>W. maculata</i> 7	15.9	22.5	8.6	10.6	2.9	3.6
<i>W. maculata</i> 8	20.7	26.6	9.4	12.2	3.2	4.1
<i>W. maculata</i> 9	22.6	27.9	8.5	11.1	3.2	4.0
<i>W. maculata</i> 10	19.9	24.9	9.3	11.0	3.2	3.6
<i>W. maculata</i> 11	21.8	28.0	8.9	13.2	3.5	4.3
<i>W. maculata</i> 12	20.3	21.5	9.9	11.5	3.0	3.4