Original article

Factors affecting abundance of different stages of the endophilic tick *Ixodes anatis* in brown kiwi (*Apteryx mantelli*) shelters

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ABSTRACT

Ixodes anatis is a species of endophilic (nidicolous) tick species parasitizing brown kiwi (*Apteryx mantelli*). Even though they are endemic to New Zealand like their host, very little is known about these ticks or their population dynamics and relationships with their hosts. We conducted a study from May 2013 to June 2014 to evaluate the effect of shelter location (one of three gullies), habitat (forest, scrub and pasture) and type (tree, soil and surface) on the abundance of the different life stages of *I. anatis*. In total, 12,172 ticks were collected from 63 shelters, which were sampled monthly for 11 months over the 14 month period. Un-engorged larvae predominated over other stages accounting for 87.2% of the samples collected. We found that location, habitat in which the shelters were located, and the type of shelter were significant predictors of *I. anatis* abundance. Tree shelters in forests had significantly higher tick abundance than those in scrub and pasture. Tree and soil shelters in general had significantly more ticks than surface shelters. Shelters located in Kauri Bush a drier site, had higher abundances than those in wetter sites. While some of these changes can be explained with the movement of the host, we believe more research needs to be done on the effect of shelters' microclimate on *I. anatis'* life cycle.

1. Introduction

Ticks of the genus *Ixodes* are common parasites of animals with over 200 species described to date (Guglielmone et al., 2014) infecting a wide range of host species. *Ixodes* ticks have season-dependent population dynamics with temperature, humidity, and tick stage known to affect stage-to-stage development and host-seeking activity (or questing) (Randolph, 2004). As a general rule, tick densities increase in warmer temperatures (Lindgren et al., 2000; Padgett and Lane, 2001) until a critical temperature is reached that stops development and leads to desiccation (Padgett and Lane, 2001). However, there is much variation in the relative abundances of the various life stages (Dantas-Torres and Otranto, 2013; Estrada-Peña, 2001). Humidity also influences different stages of the development and questing of ticks. For example, when not feeding, ticks have been found to be highly susceptible to desiccation and require a relative humidity of more than 85% to thrive (Obsomer et al., 2013; Oorebeek and Kleindorfer, 2008; Tack et al., 2013). At high humidity, ticks quest for longer periods thus

improving their chances of finding a host (Obsomer et al., 2013). Before conditions become unfavourable, ticks, especially larval and nymphal stages, may enter diapause (Oorebeek and Kleindorfer, 2008). In temperate regions, for example, temperatures in winter are too low to allow moulting and questing activity (Tack et al., 2013) and ticks go into morphogenetic diapause (Fourie et al., 1993; Lindgren and Gustafson, 2001; Oorebeek and Kleindorfer, 2008).

Ticks have evolved two host feeding strategies, they can either be (1) exophilic (non-nidicolous), actively questing or seeking their host, or (2) endophilic (nidicolous), remaining in or near nests and burrows of hosts (Sobrino et al., 2012). While exophilic ticks may be highly exposed to environmental conditions and dependent on host accessibility, endophilic ticks are generally better protected from fluctuating environments and have more accessible hosts (Ruiz-Fons and Gilbert, 2010; Wilson et al., 1990). There are numerous studies focussing on the biology and ecology of exophilic ticks (Dantas-Torres and Otranto, 2013; Fourie et al., 1993; Padgett and Lane, 2001; Ruiz-Fons and Gilbert, 1990; Wilson et al., 1990), due to their impact on livestock and

human health. However, studies looking into endophilic ticks, especially in wildlife, are few (Frenot et al., 2001; Sobrino et al., 2012; Van Oosten et al., 2014).

Apteryx spp. (five species) are nocturnal, ground dwelling, insectivorous birds endemic to New Zealand (Weir et al., 2016). The brown kiwi (*Apteryx mantelli*) is the most common kiwi species and was the focus of this study. Brown kiwi use burrows dug in the soil, tree cavities and thickets of vegetation, for shelter during the day (Dixon, 2015; Jamieson et al., 2016). They breed from June to February between mid-winter to mid-spring (Potter and Cockrem, 1992; Ziesemann et al., 2011). Eggs are incubated for 74–84 days (Calder et al., 1978) with first clutches hatching in October and second clutches in February.

Ixodes anatis is a host-specific endophilic tick found on two species of kiwi, *A. mantelli* (brown kiwi) and *A. australis* (southern brown kiwi or Tokoeka) (Dumbleton, 1953; Heath, 2010). Little is known about their relationship with the host, their abundance, life cycle and the factors controlling it. In the only population where research on these ticks has taken place, on Ponui Island (Swift et al., 2015), hosts are heavily parasitized with individual birds carrying up to hundreds of ticks (Castro, 2006; Heath, 2010). In a previous study, Swift et al. (2015) found that brown kiwi shelter use was a significant predictor of mean intensity and prevalence of *I. anatis*, and that ticks were more abundant in shelters that were holes in the ground and under trees. Since *Apteryx* spp. use shelters for nesting and roosting (Jamieson et al., 2016; Dixon, 2015), and kiwi move between and share roosts, each *I. anatis* life stage may feed on the same or different bird (Heath, 2010). The aim of this study was to investigate the effect of brown kiwi shelter type, overall habitat type at shelter location, and gully location on the abundance of the various stages of *I. anatis* throughout the year to start to understand the life cycle of this enigmatic tick.

2. Materials and methods

2.1. Study site

Ponui Island (36°55'S, 175°11'E) is located approximately 16 km South East of Auckland in the Inner Hauraki Gulf of New Zealand's North Island (Fig. 1). The brown kiwi population originated from 13 birds from two different source populations, translocated onto the island in 1964 (Miles and Castro, 2000). Old records suggest brown kiwi historic densities in New Zealand of 40–100 birds/km^2 (Buller and Keulemans, 1888) however, current densities of most mainland populations rarely exceed four adult birds/km^2 (McLennan and Potter, 1992). In our study site, the density is very high at about 100 kiwi birds/km^2 (Cunningham et al., 2007). We have conducted a long-term study of 35–50 tagged birds since 2004 on the island, allowing us to know where shelters are located and whether they are actively visited by birds. Ponui Island displays a collage of different habitats of which two thirds is pasture and the remaining third is a combination of scrub (consisting mainly of *Coprosma* spp.*, Leptospermum ericoides* and *Pseudopanax* spp.), swamp (largely *Typha orientalis*) and broadleaf-podocarp forests (Shapiro, 2005).

The study site, on the southern half of the island, covers approximately 200 ha and is spread over three main gullies (Fig. 1, Kauri Bush, Red Stoney Hill Gully (RSHG) and Pipe Gully). Ponui Island lies on a North/South axis and therefore RSHG and Pipe Gully are located on the Western side while Kauri Bush lies on the Eastern side of the central ridgeline. This northern North Island region receives south-westerly winds. The maximum summer temperatures range from 22 to 26 °C whilst in winter the maximum temperature drops to an average of 10–12 °C. Over winter, there is usually more rainfall, especially during the months of June, July and August (NIWA, 2014).

2.2. Brown kiwi distribution

Brown kiwi on Ponui Island use all types of habitat in all the three

gullies on a regular basis (Cunningham and Castro, 2011). Generally, brown kiwi use soil and tree shelters in the forest more often than other shelter types (Dixon, 2015; Jamieson et al., 2016). However, shelter use is seasonal, with birds using forest habitats relatively more often in winter and spring, and scrub, swamp, and pasture in summer and autumn (Dixon, 2015). Besides season, age and pairing status also affect shelter use, with younger and unpaired birds more likely to use a variety of habitats when compared to mated birds (Dixon, 2015). They do not necessarily use the same shelter on consecutive nights, but often share them with their partners (Ziesemann et al., 2011). Some shelters and tree cavities are used for both nesting and roosting (Dixon, 2015; Jamieson et al., 2016). The study birds have non-breeding home ranges averaging 5.32 ± 1.7 ha for males and 6.19 ± 2.48 ha for females with great overlap between all the study birds (Ziesemann, 2011) and this leads to many birds using the same shelters (pers. obs.). All the gullies have areas of forest and scrub vegetation, but pasture is only present in Kauri Bush and RSHG (Fig. 1).

2.3. Experimental protocol

We checked 63 shelters for ticks at monthly intervals from May to November 2013, in January 2014, and from April to June 2014. However, not all shelters were sampled each month. The main reason for this is that during the main part of the breeding season (June to December), known nests and shelters with birds in them were avoided to prevent disturbing possible nesting birds. In addition, by the end of the project, two of the surface shelters had collapsed and were not sampled.

Shelters were clustered into three main types: *soil shelters*, comprising dug or naturally occurring burrows (for example as a result of tree roots decomposing and leaving a hole); *tree shelters* (including any hole in a tree, fallen branch or living root); and *surface shelters* (including shelters under sparse vegetation or in the open) (Figs. 2 and 3). Only shelters used by birds in the last five years were used in this study.

2.4. Field work

We used a non-destructive sampling technique first described in Swift et al. (2015) with the following improvements: instead of large bottles, we used mini rubber hot water bottles (21 × 12 cm, 500 ml) because the larger bottles were too big to go through most of the shelter entrances even after folding them. These larger bottles rubbed against the sides of the shelters damaging them, as well as losing ticks when they were pulled out. The water bottles were placed inside a black polar fleece sleeve, instead of a white one, which made it easier to spot the different tick stages since most of the stages are light coloured. Thermos flasks were used to carry boiling water to the chosen shelter sites and the hot water bottles were filled immediately before being placed into the shelter as far as the hand could reach. The reason for this was to avoid loss of temperature before the hot water bottles were in place. Prior to the main study, we investigated the temperature loss of the water bottles, under the protocol described above, to determine how long the bottles held temperatures useful for collecting ticks (body temperature). We placed water bottles in 15 shelters, measured the surface temperature of the bottles and counted the number of ticks visible on the polar-fleece cover hourly for five hours. The water bottles were then left in the shelters to obtain a final measurement 24 h after the start of the experiment (as in Swift et al., 2015). We found that water temperature at the time of placement ranged from 45 to 50 °C but had fallen to 30–35 °C after the first two hours (close to kiwi body temperature of 38 °C). We also found that the majority of the ticks on the fleece were collected in the first two hours after placement, with tick numbers decreasing after this time. Our final protocol was to leave the hot water bottles in the shelters for one and a half hours to better coincide with the 38 °C body temperature, collect the most ticks, and allow sampling the large number of shelters spread over a 200 ha study
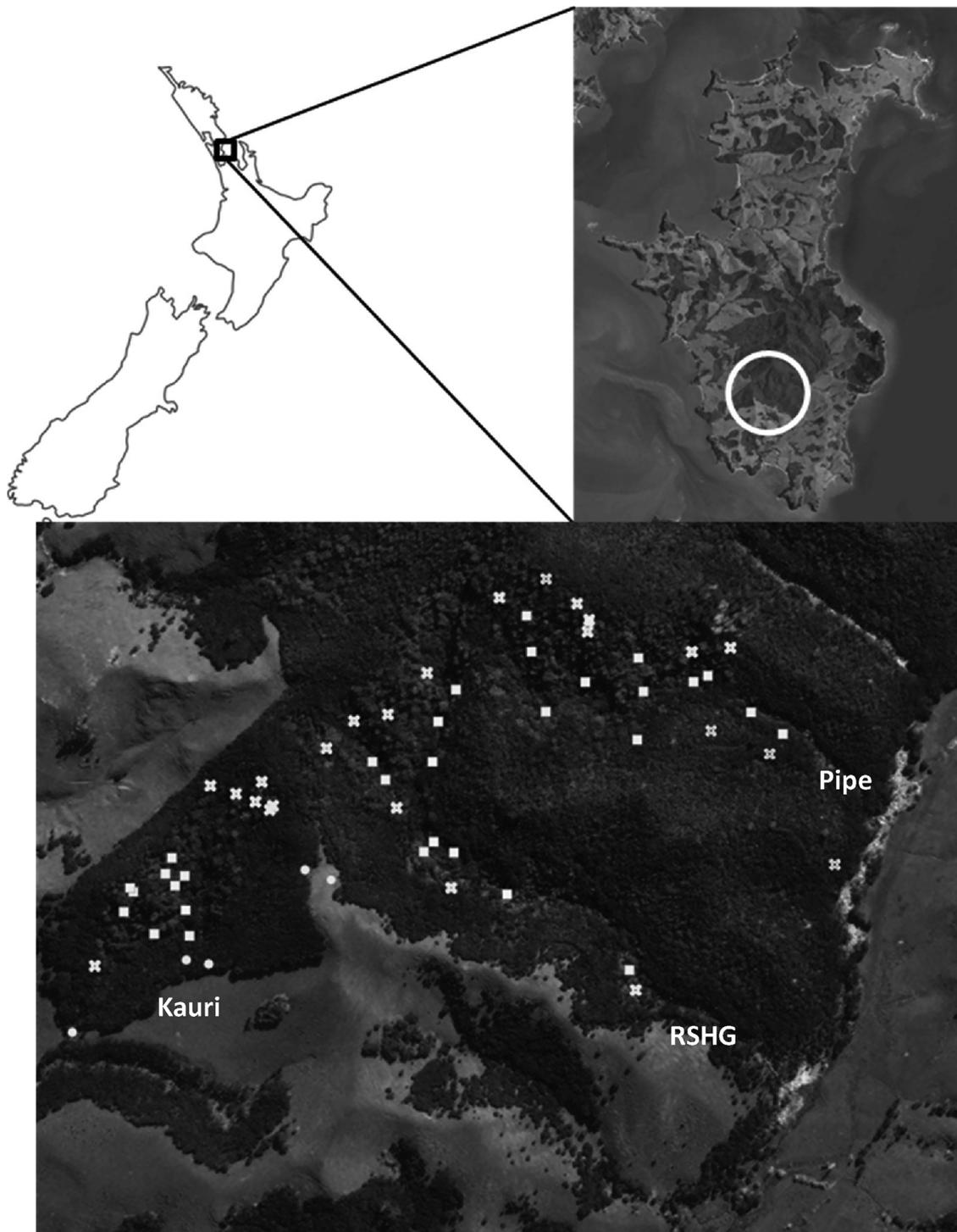
Fig. 1. Map of the study area on Ponui Island (36.8622°S, 175.1842°E), marked by the white circle on the top right image and expanded underneath. The expanded map shows the distribution of the shelters by habitat with the squares representing forest shelters, 'x' representing shelters in scrub and circles (n = 5) representing pasture shelters.

site. On arrival to each site, we recorded the state of the shelter, presence/absence of spider webs or birds in shelters, fresh digging marks and any other relevant observations that could indicate a bird was inside or had used the burrow recently. After the allocated time, the sleeve-covered bottle was removed from the shelter and put into a resealable plastic bag. However, if the fleece appeared clean, it was removed and it alone went into the Ziploc bag. During placement and removal, presence of ticks on clothes and hands of the person carrying out the experiment was noted. On return to the field station, the plastic

bags containing the sleeves were stored at 4 °C for at least one hour to slow down the activity of the ticks before counting them.

Each sleeve was inspected for ticks using a stereo microscope (Olympus VMZ) and hand held magnifying lenses. Numbers of individual ticks of each life cycle stage (larvae, nymphs or adults) as well as sex, where possible, were recorded. Each tick was carefully removed with entomology tweezers after counting, and placed into separate smaller plastic bags labelled for each shelter and containing some leaf litter. The ticks were identified using the guide from Dumbleton (1953),
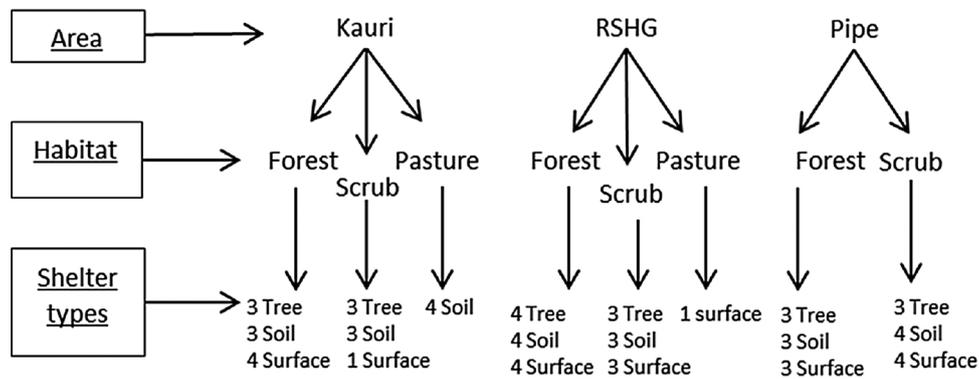
Fig. 2. Experimental design: The number of shelters separated by location, habitat and type.

where the location of the anal groove was used to differentiate between *I. anatis* (anterior groove) and *H. longicornis* (posterior groove) also present in the study site. After counting and classifying ticks, they were returned to their respective shelters within 24 h.

2.5. Statistical analysis

Due to the non-Gaussian distribution of our aggregated count data, Generalised Estimating Equations (GEE) were used to model the effect of location (RSHG, Kauri and Pipe), habitat (forest, scrub and pasture) and shelter type (soil, tree and surface) on the abundance of ticks collected. GEE also accounted for repeated measure sampling of the same shelters every month. We used a negative binomial distribution model with the log link function as our data was over-dispersed (variance greater than mean) count data. Pairwise comparisons were carried out at 95% confidence intervals with Sidak corrections to account for multiple comparisons. Results were considered significant when $p < 0.05$. Analyses were undertaken for counts of all stages combined

because there were too few adults to make meaningful comparisons. All tests were carried out using IBM SPSS Statistics 22.

3. Results

We counted a total of 12,172 ticks from the 63 shelters over the 14-month period; 87.2% (n = 10,612) were larvae, 10.2% (n = 1244) were nymphs and 2.6% (n = 316) were adults. All stages of ticks were present throughout the year but their abundance in shelters varied over time. The larvae numbers were high between January to June with three observed peaks in May 2014, August 2014 and April 2015 (Fig. 4). The nymph numbers showed corresponding peaks from June onwards and were relatively high. Adult ticks increased as time progressed, however most of the adults were collected when a bird was present in the shelter or had been in there recently. In general the numbers of each successive tick stage declined over time.

Birds were present in 14 of the 63 shelters through the study period and the prevalence of ticks in these shelters varied dramatically
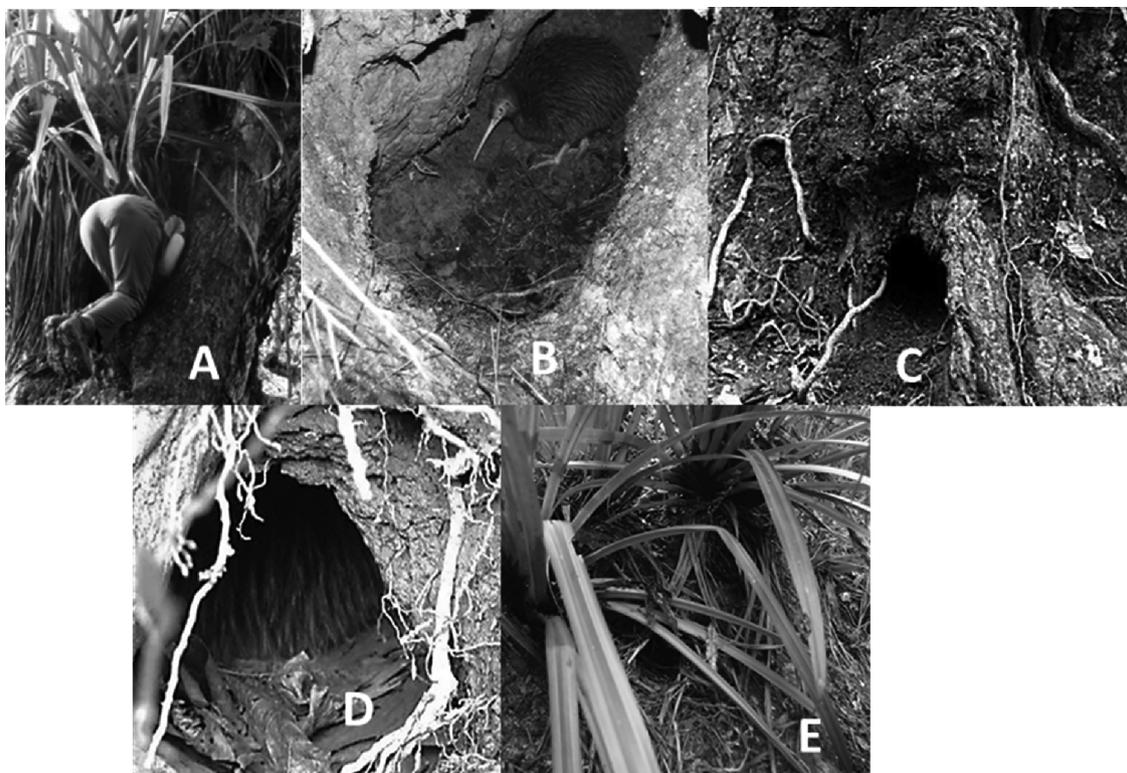

Fig. 3. Different shelter types that the Brown kiwi use which were used for this experiment. A shows a person looking into a tree shelter, B is a kiwi inside a huge tree and C is another type of tree shelter in the roots of a tree. D represents dug out soil shelters (the kiwi back can be seen). E represents surface shelters, in this case just under a fallen clump of *Astelia* sp. (Photos by the authors).
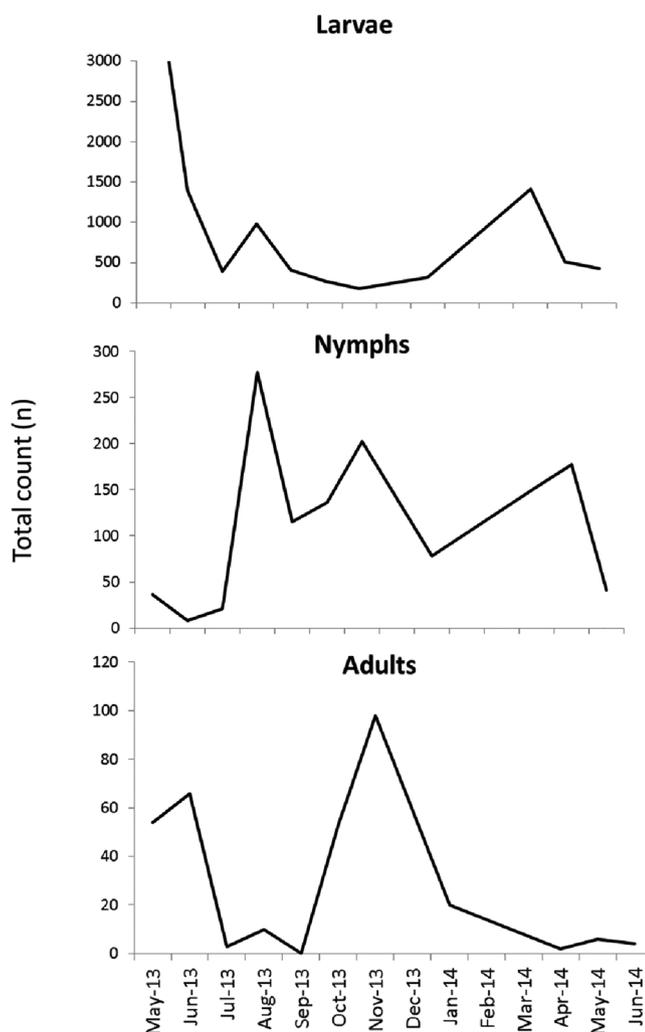
Fig. 4. Total Numbers of different stages of I. anatis found over 14 month sampling of 63 brown kiwi (*A. mantelli*) shelters on Ponui Island, New Zealand. Three types of shelters (soil, tree and surface) located in three different habitat types (forest, scrub and pasture) from three different adjacent locations (Kauri, RSHG and Pipe) were sampled.

between 100%, in a shelter where a bird was found twice, to 27.27%, in a shelter where a bird was found once, indicating that the presence of birds was not a predictor of tick prevalence. The distribution of ticks in the shelters was not uniform, with 39.68% of shelters having ticks more than 50% of the sampling times and only three shelters recorded with no ticks throughout the study.

Location, habitat and shelter type all had a significant effects on tick numbers (GEE model; Table 1). Kauri and RSHG had similar tick counts (n = 5124 and 4791 respectively) when compared to Pipe (n = 2257);

Table 1
The GEE model showing the various factors and interactions used with Chi-square values and significance levels.

Predictor Variables	Wald Chi-Square	df	Sig.
(Intercept)	194.157	1	< 0.0001
Location	19.260	2	< 0.0001
Habitat	23.951	2	< 0.0001
S.type	83.896	2	< 0.0001
Location*Habitat	3.674	2	0.159
Location*S.type	35.085	4	< 0.0001
Habitat*S.type	19.446	2	< 0.0001
Location*Habitat*S.type	6.844	4	0.144

Table 2
Pairwise tests between the different fixed effect variables with means, significance levels and 95% confidence intervals. Values in bold denote significant differences.

Variable		Mean	Pairwise test	Sidak Sig. (p value)	95% Wald Confidence Interval for Difference	
					Lower	Upper
Location	Kauri	5.95	Pipe	00.426	−2.01	7.47
	RSHG	5.05	Kauri	0.932	−3.08	4.87
	Pipe	3.22	RSHG	0.759	−6.8	3.13
Habitat	Forest	11.11	Pasture	**0.007**	1.98	16.11
	Scrub	3.63	Forest	**0.002**	2.32	12.65
	Pasture	2.07	Scrub	0.779	−5.93	2.82
Shelter type	Tree	6.29	Surface	0.068	−0.25	9.78
	Soil	11.50	Soil	0.396	−13.94	3.53
	Surface	1.53	Tree	**0.008**	−17.87	−2.08

however this difference was not significant (Wald chi-square = 1.892, df = 2, p-value = 0.388). There was a significant interaction between location and shelter type, where tree shelters in Kauri Bush had the highest tick abundance. There was also a significant interaction between habitat and shelter type with tree and soil shelters located in the forest having higher tick abundance as compared to those in scrub and pasture (Table 2). In general, tree shelters had higher tick abundance than the other types (Table 2). Pasture shelters had the lowest tick abundance with only 165 ticks retrieved from the five pasture shelters sampled.

4. Discussion

We found that location, habitat in which the shelters were located, and the type of shelter were significant predictors of *I. anatis* abundance and that there were interactions between location and habitat of the shelters and tick abundance.

4.1. Seasonal stage variations

Larval abundance peaked at the start of the study in May and August 2013 and again in April 2014 with numbers declining towards winter. It is not uncommon for larvae to show peaks when conditions are favourable (Oorebeek and Kleindorfer, 2008) as this provides the opportunity for eggs to develop and hatch.

The larval trends are followed closely by peak in nymph numbers with the first two peaks observed in the winter and spring months of August and November of 2013. This was 2–3 months after the larval peak indicating that larvae had moulted during winter and spring. The next peak occurred in May 2014 immediately after the April 2014 larval peak. In 2014, May and April had an average temperature of 16.8 °C and average relative humidity of 95.3% (NIWA, 2014). This combination of mild temperature and high humidity may have been ideal for quick moulting of larval stages of *I. anatis* (Bansal, et al. In prep.). Adult ticks were present in small numbers throughout the study, but peaked in November 2013 and were mostly present in shelters where birds were present for the experiment or shelters which had been recently used. This association of adult ticks and the presence of kiwi or recent burrow use suggest that they may have come off the birds themselves, which corresponds to similar findings by Swift et al., 2015, or could be freshly moulted questing adults.

Generally, *Ixodes* spp. follow a seasonality that depends on host densities and their breeding cycles because this ensures that the ticks can complete their own life cycle (Frenot et al., 2001; Oorebeek and Kleindorfer, 2008). Where density of host populations is naturally high throughout the year, as records indicate for brown kiwi shortly after human arrival in New Zealand (Buller and Keulemans, 1888), and as was the case for our study site, a parasite may not need to have a life

cycle that synchronises with its host's. Therefore, we believe that the seasonality we observe in this study has more to do with variations in the microclimate of the shelters rather than host breeding cycles.

4.2. Effect of location, habitat and shelter type

Tree shelters had a higher tick prevalence compared to soil shelters even though brown kiwi in our study area use almost the same number of soil and tree shelters (Dixon, 2015; Jamieson, 2015). Enclosed shelters have been known to provide more of a stable microclimate less prone to fluctuations (Kerr and Bull, 2006). Surface shelters, on the other hand, ranging from an open spot on the ground to areas under a few fallen tree branches or decaying vegetation, had significantly low prevalence of all stages of ticks as they are more prone to the effect of climatic fluctuations. The interaction between shelter location and type was interesting. We expected that ticks would be more abundant in the wetter areas of RSHG and Pipe Gully probably providing higher relative humidity. However, tree shelters in Kauri Bush, located in the leeward side of the island, had higher tick numbers. This intriguing finding deserves further research, for example studying the effect of temperature and humidity on *I. anatis* life cycle.

The microclimate within bird shelters has been shown to be influenced by the nature of the vegetation and habitat (Pringle et al., 2003). Furthermore, vegetation may also affect the abundance and distribution of host species. We found a significantly higher number of ticks in shelters located within the forest, corresponding with brown kiwi roosting behaviour (Dixon, 2015). This build-up of parasite numbers is probably a result of frequent use of these shelters by the birds thus providing continuous host availability and robust tick transmission. Pasture shelters only had larval stages whose numbers significantly decreased with monthly sampling. This decline in larvae numbers could be related to the movement of brown kiwi from pasture to scrub and forest shelters with the approach of the breeding season (Dixon, 2015). However, the number of pasture shelters limited us since we could only find five.

While we did find significant interaction between various factors that might explain *I. anatis* abundance in kiwi shelters, future research needs to focus on finding what microclimates are available within shelters and how these fluctuate with season, habitat and location. A longer study perhaps including laboratory studies are needed to piece together the life cycle of *I. anatis*.

Declaration of interest

The authors report no conflicts of interest.

Author contributions

Pilot and preliminary experiments: IC and DI. Experimental design: IC and NB. Fieldwork: NB, AK, IC, and DI. Writing: NB, IC, with comments from WP, DI and AK. Analysis: NB, IC.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ttbdis.2019.03.008.

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