

The first recorded interaction between two species separated for centuries suggests they were ecological competitors

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Abstract: Human-induced reductions in species' ranges have resulted in the geographic separation of some previously sympatric species that interacted historically. Some previously co-occurring species are now being reconnected via translocation. However, interactions between these species can be difficult to predict, particularly in extreme instances where all populations of previously co-occurring species have become completely separated from each other. Here, we present video footage that, for the first time, captures an interaction between two species separated for centuries due to human disturbance, but that are now being reconnected via translocations; little spotted kiwi (LSK) (*Apteryx owenii*) and tuatara (*Sphenodon punctatus*). The video shows an aggressive interaction, apparently caused by competition for a burrow being used by the LSK for nesting. This footage suggests we have much to learn about how these species may have co-existed prior to human arrival in New Zealand.

Keywords: burrows, little spotted kiwi, nests, translocation, tuatara

Introduction

Ecosystem fragmentation can disrupt trophic interactions (Martinson & Fagan 2014) and cause geographic separation of species that used to co-occur. In such cases, unintended consequences due to competition or predation may occur when species are reintroduced as part of ecological restoration efforts (e.g. Elbroch et al. 2017). New Zealand is home to numerous species that previously co-occurred, but are now completely separated due to restriction to just one or two refugia sites following human arrival (e.g. stitchbird/hihi, Brekke et al. 2011; kākāpō and takahē, Clout & Craig 1995; black stilt/kakī, Pierce 1984). Current conservation actions are restoring sympatry, leading to secondary contact between native species that were separated by human activity. Two of New Zealand's iconic, endemic species, the little spotted kiwi/kiwi pukupuku (*Apteryx owenii*) (LSK) and the tuatara (*Sphenodon punctatus*) are excellent examples of species that were each once widespread across both main islands of New Zealand, occupying similar niches, but were restricted to a handful of isolated sites following European colonisation (Newman 1878; Buller 1894; Holzapfel et al. 2008).

Subfossil records confirm that LSK and tuatara were found throughout the North and South Island of New Zealand prior to human arrival (Fig. 1A; Cree & Butler 1993; Worthy & Holdaway 2002; Wood 2009). However, tuatara are believed to have been extirpated from mainland New Zealand by the 1700s (Newman 1878; Buller 1894), and LSK were reduced

to just one site on Kapiti Island by the 1980s (Holzapfel et al. 2008). Thus, these two species have been separated for around 300 years – around 7.5 and 12 generations for tuatara and LSK respectively (Fig. 1B; Mitchell et al. 2010; Ramstad et al. 2013). Today, as a result of translocations, tuatara exist on 41 offshore islands and in five mainland sanctuary locations, and LSK on seven offshore islands and in four mainland sanctuaries. LSK and tuatara currently co-occur in six sites (Fig. 1C; Cree 2014; Jarvie et al. 2017; Germano et al. 2018).

Little spotted kiwi and tuatara are both primarily nocturnal and insectivorous, and both use burrows (Cree 2014; Heather & Robertson 2015). Given their similar use of similar habitats and previously overlapping ranges, LSK and tuatara would likely have encountered one another historically. Their interactions have not been observed and remain unknown to science. However, tuatara frequently invade the burrows of another burrowing bird, the fairy prion/tītī wainui (*Pachyptila turtur*), on Stephens Island/Takapourewa rather than digging their own burrows. The tuatara seemingly benefit from the association via not having to spend energy digging a burrow and via kleptothermy (heat stealing) (Corkery et al. 2014), but there is little advantage to this symbiosis for the prions. The two species compete for space when in single chamber burrows (Walls 1978), tuatara regularly prey upon prion eggs and chicks while sharing burrows (Newman 1987), and prions have been shown to enter burrows later and spend less time in them with their chick when tuatara are present (Corkery et al. 2015). Whether similarly competitive interactions

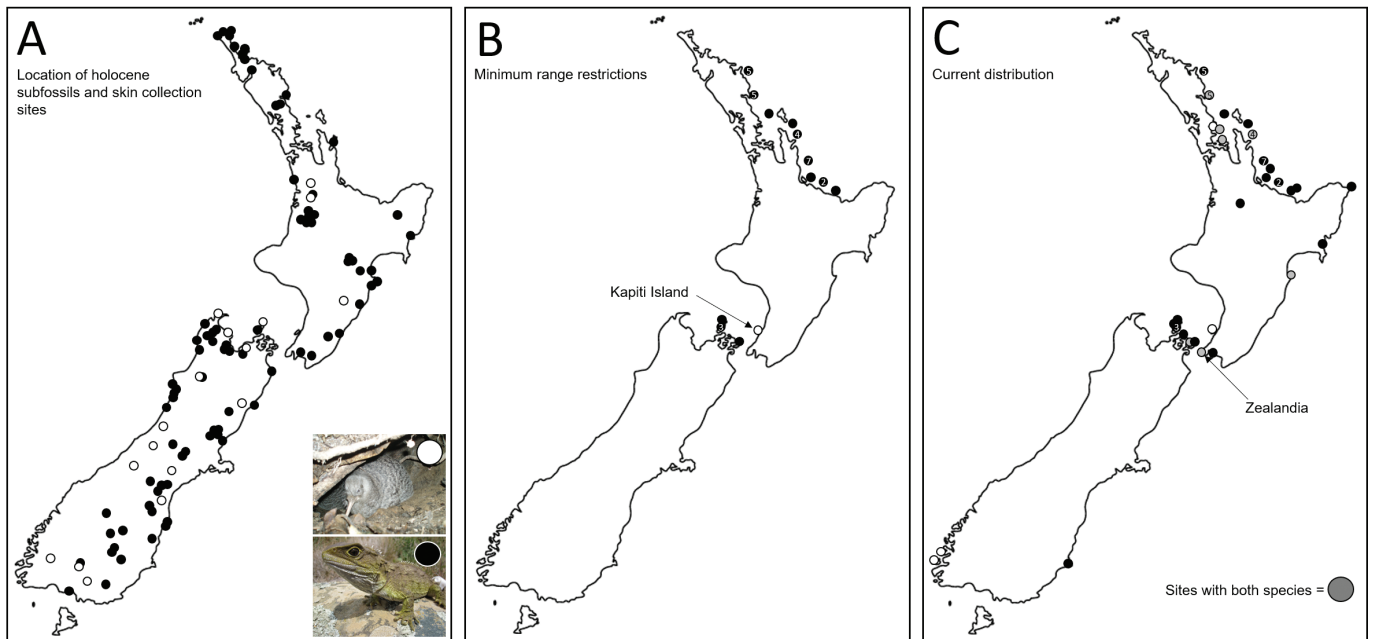


Figure 1. Map of New Zealand illustrating changes in distribution of LSK (open circles) and tuatara (filled circles) over time. (A) Locations where holocene subfossil remains have been found or museum skins were collected. (B) Minimum range restrictions for each species. The restriction of LSK to one site (labelled on map Kapiti Island) occurred in the 1980s. The tuatara distribution shown is from the 1990s. However, as tuatara had been reduced to offshore islands that were not home to LSK by the 1700s, the two species had been separated for >300 years prior to being reunited via conservation translocations in the 21st century. (C) Current distribution of both species with sites where both species occur shown as grey circles and study site, Zealandia, labelled. In (B) and (C), numbers in circles indicate island groups where tuatara occur on the specified number of islands. Where numbers appear in grey circles in (C), LSK occur on just one of the islands in that group in each case. Maps modified from (Cree 2014; Shepherd & Lambert 2008; Ramstad et al. 2013; Jarvie et al. 2017). Tuatara image courtesy of Anna Carter, LSK image taken by HRT.

between burrow-nesting LSK and tuatara are part of these species' natural history is not known. Using footage captured on a camera trap as part of a larger study on LSK, we report on a seemingly competitive interaction between these long-separated species for the first time.

Methods

Throughout the 2011/12 and 2012/13 LSK breeding seasons (August–March), we monitored 16 LSK nests in Zealandia Sanctuary, Wellington, New Zealand, using camera traps as part of a larger study into inbreeding and hatching success in LSK (Taylor et al. 2017). Zealandia houses the first mainland population of both LSK and tuatara to have been established since their respective mainland extirpations. Forty LSK were introduced to Zealandia from Kapiti Island between 2000 and 2001, and the census population size at the time of this study was 120 birds (H. Robertson, DOC, pers. comm., June 2012). Tuatara were first introduced to Zealandia in 2005 when 70 individuals were translocated from Stephens Island/Takapourewa, and another 130 released in 2007 (McKenzie 2007). The population at the time of this study was estimated to be 200 (NJN, unpubl. data).

We recorded LSK nests using Bushnell Trophy Cam – Model 11-9436c trail cameras (Bushnell, Kansas City, USA) – positioned between 1 and 3 m from nest entrances and set to record when triggered by motion in front of the sensor. These cameras have infrared for recording at night without disturbing wildlife and record both video and sound. We set the

cameras to record one minute of footage each time they were triggered. The interaction described below was captured across 13 separate one-minute video segments between 21:20 on 7 February 2012 and 04:24 on 8 February 2012, each of which was analysed in detail with all relevant action and sound noted.

Results

The footage described below came from a camera stationed outside the nest burrow of a male LSK (band number O-31659) that had been monitored by radio tag (Taylor et al. 2014) for the entire 2011/12 breeding season and by camera from 10 November 2011 to 23 April 2012. The LSK nest burrow was inside a hole that had already been marked as a known tuatara burrow by staff at Zealandia Sanctuary. A male tuatara had been recorded outside the nest burrow on 22 November 2011, 15 days after the male LSK began incubating (see Table S1 in Supplementary Material), but had not been recorded since that time. At the time the interaction described below was recorded, the nest was known to contain the male LSK's chick, which was estimated to be 8 days old (Digby 2013; HRT unpubl. data).

A detailed account of the subsequent footage can be seen in Table 1. In brief, between 04:06 and 04:24 on 8 February 2012, the camera trap recorded 11 one-minute videos, capturing a series of interactions between the adult male LSK, a male tuatara that was in the nest when the male LSK returned for the evening, and the LSK chick inside the nest. The full sequence of videos can be viewed at <https://youtu.be/gVEvA92BOfE>.

When the male LSK first returns to the nest, it attempts to

Table 1. Details of all action captured by camera trap outside an LSK nest on the evening of 7 February and the morning of 8 February 2012, including interactions between an adult male LSK, its chick, and a male tuatara. As discussed in the text, there are clearly pieces of action missing here where the camera's motion sensor did not trigger filming (such as the return of the LSK chick and the initial entry of the tuatara into the nest burrow), hence the gaps in the timeline.

Time camera triggered	Video content
7 February 2012	
21:20	LSK chick emerges from the nest burrow and moves away from the nest.
21:38	Adult male LSK emerges from the nest burrow and moves away from the nest.
8 February 2012	
04:06	Male LSK returns to the nest and pokes its head and the front half of its body into the nest burrow through the entrance, but seems unable to fully enter the nest and so withdraws. It attempts to enter the nest a second time, but again withdraws.
04:07	Male LSK again attempts to enter the nest, is seemingly able to get in further, but again withdraws and then moves away from the entrance out of shot.
04:09	Male LSK returns to outside the nest and makes two more unsuccessful attempts at entering.
04:10	Male LSK backs out of the nest entrance, and probes around it a little with its bill. The male LSK attempts to enter the nest again and this time jumps back suddenly as if startled.
04:11	Repeat of behaviour seen at 04:10, followed by male LSK spending some time probing around the nest entrance with its bill. Male LSK then stands still looking directly into the entrance and makes a single bill snap.
04:15	Male LSK is out of shot, but a male tuatara can clearly be seen with its head poking clear out of the nest burrow entrance.
04:16	Male LSK has returned to the nest entrance and the tuatara is still sitting with its head out of the nest burrow. Male LSK probes around the tuatara's head. Tuatara flicks its head to one side quickly away from the male's bill and male LSK jumps back. Male LSK moves closer to the nest entrance, tuatara moves a little, flicking its head back inside the burrow, and male LSK appears to flinch backwards. Tuatara then moves forward quickly so its entire head and neck are clear of the entrance, and male LSK jumps backwards.
04:18	Male LSK and tuatara both reasonably still for a full minute, with the tuatara back into the nest burrow more fully.
04:20	Male LSK begins probing tuatara's face with its bill for around 10 seconds before tuatara lunges forward so that it is half out of the burrow, causing male LSK to jump backwards. Tuatara then lunges again, past the male LSK, so it is completely clear of the nest burrow and mainly out of the camera frame, with its tail remaining in shot. Male LSK quickly moves towards tuatara and steps hard onto its tail and (out of shot) body.
04:22	Tuatara has returned inside the nest burrow, this time with its tail protruding. Male LSK is still present and probes around the entrance a little, flinching as tuatara moves fully inside the nest. Male LSK attempts to follow tuatara into the nest, but then takes its head out again.
04:24	Male LSK is not present and tuatara cannot be seen. LSK chick can clearly be heard calling from inside the nest. After around 40 seconds, tuatara re-emerges from inside the nest, with LSK chick clearly visible moving around inside the nest behind tuatara.

re-enter several times, but appears to be prevented from doing so. The male LSK spends a few minutes probing around the nest entrance with its bill, putting its head into the nest entrance, and flinching back from time to time, at one point making a bill snap noise towards the entrance. When the camera triggers at 04:15, the cause of the male LSK's apparent distress is revealed to be a male tuatara, which has now partly emerged from the nest and remains sitting in the entrance.

Over the course of the next few minutes, the male LSK probes around the tuatara's head (Fig. 2A), jumping backwards as the tuatara flicks its head and then again when the tuatara lunges forward out of the entrance (Fig. 2B). When the tuatara emerges fully from the nest, the male LSK moves quickly towards it and stamps on its tail (Fig. 2C). The male LSK then disappears from shot and the tuatara is seen to have returned inside the nest burrow, with its tail protruding.

Two minutes later, the tuatara can no longer be seen, but the LSK chick can be heard calling from inside the nest. The

tuatara then partly emerges from the nest burrow and the LSK chick can clearly be seen moving around in the nest behind the tuatara (Fig. 2D).

We continued monitoring this nest with the trail camera until 23 April 2012. The LSK chick and male were recorded on several subsequent nights, before seemingly leaving the nest burrow for good on 1 March 2012 (chick) and 2 March 2012 (male). The tuatara was not recorded at the nest again during the time the male LSK and chick were resident, but what appeared to be the same tuatara (according to size, spines and skin pattern) was captured on the camera 29 times over 10 different days after the kiwi vacated the nest burrow (Table S1). The nest was inspected in the days following the LSK male and chick vacating it and at the end of the season and was found to be empty.

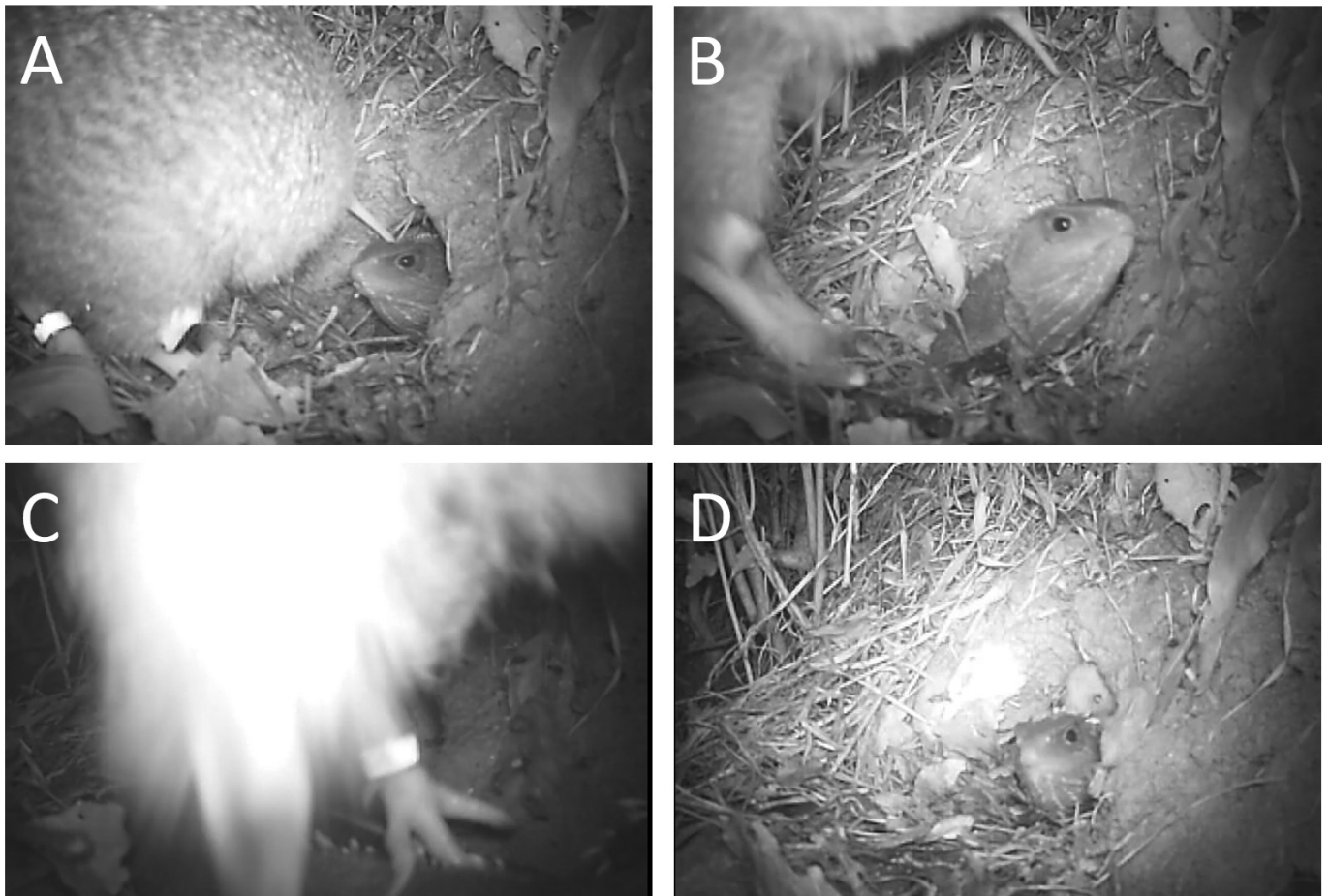


Figure 2. Selected stills from the video footage recorded between 04:06 and 04:25 on 8 February 2012 showing an interaction between a male adult LSK and a male tuatara in Zealandia Sanctuary, Wellington, New Zealand. (A) Example of male LSK probing around tuatara while tuatara is sitting inside LSK nest burrow. (B) Tuatara lunges forward out of the nest entrance and male LSK jumps backwards. (C) Tuatara emerges completely from nest burrow and male LSK stamps on the tuatara's tail. (D) Tuatara partly emerges from nest while LSK chick can be seen in the nest behind the tuatara. To view full video, please visit <https://youtu.be/gVEvA92BOfE>.

Discussion

The interaction captured here suggests a potentially antagonistic relationship between two species that previously co-occurred, but rarely encounter each other in modern day New Zealand. Although care is required when interpreting any animal behaviour, the male LSK in this video footage shows several signs of aggression, including bill snapping and stamping (HRT, pers. obs.). Likewise, the tuatara makes typically territorial lunges towards the male LSK and appears engorged in the gular (throat) region and head crest – another sign of aggression (Gillingham et al. 1995). The male LSK is seemingly perturbed by the presence of the tuatara, visibly flinching at its movements and refusing to leave the nest burrow – repeatedly trying to enter for around 20 minutes. This behaviour is seemingly similar to the reluctance of fairy prions/tīti wainui to enter nest burrows when tuatara are present (Corkery et al. 2015). Meanwhile, the LSK chick's calls are typical of 'deterministic chaos', random, non-linear vocalisations hypothesised to be used by animals in situations where it is important not to be ignored (Digby 2013) and thus could be a distress call. In light of the above, it is difficult to interpret the sequence of events described here as anything other than antagonistic.

Of the 16 LSK nests filmed during our wider study, this recording was the only series of interactions between LSK and tuatara captured on video. It is possible that there were other interactions that went unrecorded. It is also possible that other interactions could have occurred inside nests or at a short distance from the entrance, outside of the frame of the camera. Since this video was captured, only one other video of an interaction between an LSK and tuatara has been reported; a seemingly neutral encounter on Motuihe Island where an LSK probes a tuatara's head, with no reaction from the tuatara and neither animal in a burrow (Newshub 2018). Little spotted kiwi and tuatara were first reintroduced to the same site (Zealandia) in 2005. Given the isolated nature of the interaction recorded here in the time since, it seems that interactions between LSK and tuatara in Zealandia remain rare and, at least in this case, did not result in predation of the chick that was in this nest (deduced from absence of chick remains when nest was inspected). However, we would be interested to know how many observational studies of tuatara and LSK in different sites have taken place, as the lack of recorded interactions could also be due to a lack of research effort in this space.

Even if rare, it would not be surprising if there were other

instances of tuatara entering LSK nests or LSK choosing existing tuatara burrows to nest in, as both species take advantage of existing cavities where possible rather than digging a whole new burrow (HRT and NJN, pers. obs.). Tuatara will have a network of other burrows they can use if one is occupied by a nesting LSK (Newman 1987), but this will be constrained by social interactions with other tuatara and so their ability to use alternative burrows will be linked to population density. The LSK cannot move its nest once established. As population densities of both species increase, competition for burrows could intensify.

We have no footage of the tuatara attempting to use the burrow while the LSK was incubating (aside from the one occasion 15 days after the male LSK began incubating reported above). This lack of recorded interactions suggests the tuatara avoided using the burrow while the LSK was nesting, presumably preferring to use other burrows within its territory. Following vacation of the nest by the LSK, the tuatara was recorded outside the nest repeatedly (on 10 out of 51 days; Table S1). It is possible that, given the relatively low density of tuatara in Zealandia, the tuatara had other burrows it could use most nights to avoid competition with an adult LSK. However, on the occasion in question, the tuatara seems to have found the burrow occupied solely by the chick – a far less threatening prospect and a potential prey item – making the tuatara's occupancy of the burrow less risky.

Clearly, more observational studies from sites where kiwi and tuatara are both present are needed to better understand the relationship between these two species. Camera traps combined with radio tagging of both species offer one possible way to further investigate the frequency and nature of interactions between kiwi and tuatara, while minimising disturbance to natural behaviour. These two taxa now co-occur in 11 sites (see Table S2 in Supplementary Material). Of these, six are home to LSK and five to other, larger kiwi species; predominantly North Island brown kiwi (*A. mantelli*) (Table S2). Burrow sharing between tuatara and other kiwi species may be possible (again, ranges overlapped historically), but predation of chicks as seen in fairy prions seems less likely to be a concern in these cases for all but the largest tuatara, given the large size of these chicks (~420 g at hatching in North Island brown kiwi vs ~161 g within 7 days of hatching for LSK; Prior et al. 2013; HRT unpubl. data). However, tuatara are known to eat seabird eggs as well as chicks (Moller 1985) and egg predation by tuatara could be a risk for all five kiwi species, along with nest desertion due to aggressive interactions.

Interactions between LSK and tuatara are not the only potential sources of conflict between protected, native species in New Zealand. Weka (*Gallirallus australis*) are known to predate LSK eggs (Jolly 1989) and tend to be proactively excluded from sites that are home to LSK, despite weka themselves being listed as at greater danger of extinction than LSK (IUCN 2012a, b). Presumably, when both species were plentiful, weka predation of LSK eggs did not have a major impact on numbers as it now has the potential to do.

We are not suggesting that tuatara currently represent a significant threat to LSK eggs or chicks (or those of any other kiwi species). Tuatara are ectotherms and their food intake is on a much smaller scale than the mammalian predators that represent the main threat to kiwi. What we have recorded here may not be representative of the wider picture for either species. However, it does seem likely that competition for burrows would increase where densities of each species are higher and our observations do suggest the potential for such

interactions. Our findings highlight the importance of gathering more data to ascertain whether this interaction was an isolated incident to assist management planning for both species in the future. Traditional ecological knowledge of Māori has been found to be a valuable source of information on pre- and post-colonisation tuatara ecology (Ramstad et al. 2007) and so could also be informative here.

It is impossible to go back in time and observe how species like LSK and tuatara interacted prior to human disturbance. Recordings such as the one presented here offer tantalising hints of what pre-human relations between LSK and tuatara may have been and suggest a need to delve deeper into the relationship between these iconic and ancient species to aid conservation and restoration efforts.

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Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

Table S1. Record of all instances where the male tuatara was captured by the camera trap outside or in the LSK nest burrow.

Table S2. Locations where tuatara and kiwi currently co-occur in New Zealand.

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