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NOTORNIS

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Pest mammal eradication leads to landscape-scale spillover of tūī (*Prosthemadera novaeseelandiae*) from a New Zealand mainland biodiversity sanctuary

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Abstract: Maungatautari is a 3,240 ha pest-fenced ecosanctuary free of virtually all mammalian predators in Waikato, New Zealand. We used triennial 5-minute counts within the ecosanctuary and biennial surveys of residents up to 20 km from the perimeter pest fence to measure spillover of tūī from Maungatautari into the surrounding area over a 9-year period (2006–2014) following pest eradication. Following pest eradication in the ecosanctuary, tūī relative abundance increased there and in the surrounding largely unmanaged area. The mean number of tūī per 5-minute count within the ecosanctuary was 2.23 (se = 0.163) in 2005 and increased following predator eradication in 2006 to 3.33 (se = 0.206) in 2008, 3.76 (se = 0.193) in 2011, and 2.68 (se = 0.279) in 2014. The mean maximum number of tūī ato ne time observed by residents in the largely unmanaged area increased from 4.4 (max = 47, n = 320) in 2006 to 15.6 (max = 300, n = 138) in 2014. Tūī numbers in both the ecosanctuary and the surrounding area were positively correlated with time since pest eradication. In the largely unmanaged area surrounding Maungatautari, tūī numbers were also positively correlated with distance from the ecosanctuary. Wind was negatively correlated with the number of tūī recorded in 5-minute counts at Maungatautari. Our findings show that pest-free ecosanctuaries can facilitate increased abundance of volant birds in surrounding landscapes if habitat is available.

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Keywords: tui, Prosthemadera novaeseelandiae, seasonal movement, dispersal, spillover, ecosanctuary, Maungatautari, pest-fence, sink habitat

INTRODUCTION

Tūī (*Prosthemadera novaeseelandiae*) is an iconic New Zealand honeyeater (Meliphagidae), widespread throughout most of the country but sparse in dry, eastern, deforested parts of the South Island and some highly pastoral areas of the North Island (Higgins *et al.* 2001; Robertson *et al.* 2007). Before 2006, when we began this study, tūī were uncommon in central Waikato compared with many other parts of New Zealand (Robertson *et al.* 2007).

Received 13 May 2019; accepted 23 August 2019 *Correspondence: fitzgeraldn@landcareresearch.co.nz During the breeding season (October–February in Waikato; *unpubl. data*) tūī movement is restricted to a foraging range of approximately 500 m (Bergquist 1985). However, they may forage widely (tens of km) during the non-breeding season, crossing large gaps of non-woody habitat (Craig *et al.* 1981; Stewart & Craig 1985; Higgins *et al.* 2001; Innes *et al.* 2005).

The diet of tūī includes nectar and fruit of a wide variety of native and introduced plants (Higgins *et al.* 2001). This, combined with their ability to move large distances, makes tūī ecologically important pollinators and seed dispersers (Castro & Robertson 1997; Robertson *et al.* 2008; Kelly *et al.* 2010) able to exploit novel environments such as urban and rural residential gardens.

Globally, invasive alien species have been the most important driver of bird extinction over the past 500 years, and mammals are the most important group of invasive alien species causing declines in extant birds, primarily through reduced reproductive success and direct predation (del Hoyo *et al.* 2010). This is particularly true in New Zealand, where introduced mammalian predators are the primary factor limiting endemic forest bird abundance in large forest tracts by predation of eggs, chicks, and incubating adults. Therefore, bird populations frequently recover after pest predator control (Innes et al. 1999; Moorhouse et al. 2003; Smith & Westbrooke 2004; Armstrong et al. 2006; Innes et *al.* 2010). In the absence of effective ship rat (*Rattus rattus*) and brushtail possum (*Trichosurus vulpecula*) management, tūī nesting success in the Waikato is poor (Innes et al. 2005; Innes et al. 2015). When the densities of these key introduced predators are reduced, tūī is one of the most conspicuously responsive species (Saunders 2000; Innes et al. 2004; Fitzgerald & Innes 2014; Miskelly 2018).

Being conspicuous and easily identifiable, with a propensity to range widely and respond rapidly to mammalian predator control, tūī provide an opportunity to investigate native biodiversity 'spillover' – where the benefit from a reserve extends beyond its boundary into nontarget habitat (Brudvig *et al.* 2009). We used 5-minute counts of tūī at Maungatautari – a fenced ecosanctuary (Campbell-Hunt & Campbell-Hunt 2013) – and surveys of residents within 20 km of Maungatautari, over a 9-year period following pest eradication, to determine if tūī numbers increased in the ecosanctuary, and if there was evidence of spillover of tūī into the surrounding, largely unmanaged, non-target area.

METHODS

Study area

Maungatautari (175.574°E, 38.025°S) is an extinct andesite volcano, approximately 30 km SE of Hamilton city in central Waikato, New Zealand, with contiguous native forest cover from 240 to 797 m above sea level. The forest ranges from lowland rimu (*Dacrydium cupressinum*)/tawa (*Beilschmiedia tawa*) forest to montane forest dominated by tāwari (*Ixerba brexioides*), kāmahi (*Weinmannia racemosa*), and tāwheowheo (*Quintinia serrata*) (Clarkson *et al.* 2002). Construction of a 47 km pest-resistant fence encircling 3,240 ha of the forest was completed in August 2006 and eradication of all pest mammals except house mice (*Mus musculus*) commenced in November 2006 (Speedy *et al.* 2007). This created the largest area of virtually pest-free forest on the New Zealand mainland.

Our study area included the pest-fenced Maungatautari ecosanctuary and a near-circular largely unmanaged zone extending 20 km out from the perimeter pest fence (Fig. 1). Land use within this 171,960 ha unmanaged zone is predominantly intensive agriculture (88%; 150,970 ha) with fragments of exotic forest and scrub (5%; 7,870 ha), indigenous woody vegetation (4%; 7,650 ha), and urban and other built-up areas (< 2%; 2,850 ha; Land Cover Database version 4.1). Indigenous vegetation and built-up areas are not distributed uniformly across the study area; 51% of the indigenous vegetation occurs 15–20 km from Maungatautari, and 96% of urban and built-up areas are 10–20 km from Maungatautari (Fig. 1).

Maungatautari is not the only project focusing on mammalian predator control in the region, but it is by far the largest and most comprehensive. The most significant other project in our study area is Waikato Regional Council's 'Hamilton Halo' project, which began in 2007 with the aim of increasing tuī abundance in Hamilton by reducing the abundance of ship rats and possums in surrounding forest. 'Halo' in this instance refers to a conceptual ring of protected habitat surrounding the area of intended benefit (Hamilton), which is different from other definitions of the term (e.g. Birt et al. 1987; Brudvig et al. 2009; Glen et al. 2013). The Hamilton Halo project was guided by research identifying movement and factors limiting numbers of tuī in the greater Hamilton area (Innes et al. 2005; Fitzgerald et al. 2015) and involves periodic ship rat and possum control at three sites totalling 518 ha of native forest, 6.8% of the indigenous woody vegetation within our study area (Te Tapui Scenic Reserve, Maungakawa Scenic Reserve, and Tirohanga Road Reserve; Innes et al. 2013). Pest management techniques varied from site to site and year to year, but typically consisted of poison bait stations on a 75 m grid with brodifacoum, diphacenone, pindone, or cholecalciferol to target both species on 3-years-on and 2-years-off regime that aimed to have both pest species below target levels by the onset of each tuī nesting season (October to January). Target residual pest abundances were assessed by standard indexing techniques, namely <5% residual trap catch (NPCA 2011) for possums and <5% tracking rate (Gillies & Williams 2013) for ship rats. Most (383 ha) of this pest mammal control was >15 km from Maungatautari.

Resident survey method

We surveyed residents within 20 km of Maungatautari biennially about their recollection of tūī presence and abundance at their property.



Figure 1. Study area showing distances from the Maungatautari perimeter pest fence. Urban and other built-up areas are shown in black and indigenous forest in grey. State highways are indicated with narrow parallel lines. Numbers indicate sites of episodic ship rat and possum control undertaken by Waikato Regional Council in the 'Hamilton Halo' project. 1 - Tirohanga Road Reserve, 2 - Maungakawa Scenic Reserve, 3 - Te Tapui Scenic Reserve.

Surveys were conducted in January–March 2007–2015 and referred to the preceding calendar year (2006–2014). To avoid self-selection, the survey questionnaire was delivered to mailboxes of 2,000 residents in January 2007, distributed proportionately by area in 5 km bands from the pest fence (0–5 km, n = 232; 5–10 km, n = 407; 10–15 km, n = 589; 15–20 km, n = 722). In subsequent surveys, questionnaires were delivered by post or email to all respondents who had participated in a previous survey and provided a valid address.

In each survey, participants were asked: 1) What was the maximum number of tūī you saw at one time at your property during the previous year?; 2) In what month(s) did this occur?; 3) Do you think tūī have increased, decreased, or stayed the same since the previous survey?; 4) Are tūī present at your property during summer (December–February, the main breeding season)?; 5) Do tūī nest at your property?, and 6) Do you regularly put out food for tūī?

We used $t\bar{u}\bar{\imath}$ as a focal species because it is a conspicuous iconic species, and one of the native birds most familiar to members of the public. The maximum number of birds seen at one time was chosen as a measure of abundance as non-breeding congregation at preferred food sources is a conspicuous characteristic of $t\bar{u}\bar{\imath}$ behaviour (Higgins *et al.* 2001; Lyver *et al.* 2008). It is also a simple and probably memorable measure that anecdotal reports suggested was often noted by the public without requiring specific instruction from us.

Bird counts

We undertook 5-minute bird counts every third year at Maungatautari from 2002 using methodology based on Dawson & Bull (1975). All 5-minute counts were done by experienced observers at least 1 hour after sunrise and 1 hour before sunset, over a 17-31day period in November-December each survey year. Observers recorded all birds seen or heard during a 5-minute period while stationary at each count station. Observers also recorded estimates of i) cloud cover (0; none-2; rain), ii) rain (0; none-4; heavy), iii) wind (0; calm or leaves move silently–3; strong), and iv) other noise (0; none-2; loud) that could affect bird detection. Counts were not done in rain (scored \geq 3) or strong wind. Count stations were spaced at least 200 m apart along lines following existing tracks, and counts were bounded at 100 m to minimise repeated counting of birds in different counts. The analyses presented are based on a subset of 5-minute bird counts undertaken in 2005, 2008, 2011, and 2014, covering the same period as the surveys of residents in the surrounding landscape. In 2005 and 2008, 35 count stations were used, each separated by approximately 15 min walk (mean 315 m apart), and count stations were visited twice, each time by a different observer on a different day. From 2011, the number of count stations was increased to 50 but visited only once each survey year to provide a larger sample size with similar counting effort as earlier surveys. The count stations used from 2011 were at new locations (mean separation of 208 m) along the same tracks used in previous surveys. The 5-minute counts were undertaken during the tūī breeding season, so reflect changes in birds established there, rather than transient birds from other sources. In total, 231 separate 5-minute counts were used for analysis of the change in tūī relative abundance at Maungatautari.

Analysis

Resident surveys

We used a generalised linear mixed model (GLMM) with a negative binomial error distribution and a log link function to test the effect of time (years since

the first survey), distance from Maungatautari, the interaction between distance and time, and the provision of supplementary food on maximum tūī counts. We initially specified a Poisson distribution for this model but this produced unreliable estimates due to over-dispersion which was resolved by using a negative binomial distribution.

We used a GLMM with a binomial distribution and logit link function to test the effect of time, distance from Maungatautari, and the interaction between time and distance on the occurrence of tur breeding activity. We included a unique identifier for each survey respondent as a random effect in both models fitted to the data from resident surveys to account for non-independent repeated surveys of the same people. Two of the survey questions referred to tuī abundance, and two asked about evidence of breeding. We expected the related questions to give similar results if they were equally reliable. To test this we used Pearson's correlation tests in the base R package to check that changes in the maximum number of tuī (question 1) were consistent with impressions of whether tuī had increased, decreased, or stayed the same (question 3), and whether the presence of tuī during the breeding season (question 4) and observation of breeding (question 5) were correlated. The correlation between questions 1 & 3 was not strong (r = 0.35; 95% CI 0.28-0.42) so we did not use the reported impression of change in tuī abundance in analyses as it is less informative and likely less reliable as it requires respondents to recall two time periods rather than one. Correlation between presence during the breeding season and observed nesting was also low (r = 0.23; 95% CI 0.17–0.29). We consider both the presence of tuī during the breeding season and observation of nesting behaviour to be reliable indicators of breeding activity (but with differing conspicuousness) so we combined these measures to produce a single variable for analysis.

Five-minute counts

We used a GLMM with Poisson error distribution and a log link function to test the effect of time (years), cloud, rain, wind, other noise, and time of day on counts of tūī at Maungatautari between 2005 and 2014. The log of the number of times a station was counted in a year was included as an offset in the model to adjust for the different number of times some stations were counted (Hutchinson & Holtman 2005), and we included a unique identifier for each observer and station as random variables in the model to account for the repeated measures design.

We used the sjstats package (Lüdecke 2019) to calculate variance inflation factors (VIF) to check for multicollinearity between model variables. Maximum VIF did not exceed a conservative threshold of 2 (Zuur *et al.* 2010), so we retained all variables.

We assume that all the effects included in the models are real, whether statistically significant or not, so we estimate parameters from the full models rather than alternative approaches such as backward stepwise regression or information-theoretic tools (Bolker *et al.* 2009).

We used the glmmTMB package (Brooks *et al.* 2017) in the R statistical computing environment (3.5.2; R Core Team 2018) to fit GLMMs to the data using maximum likelihood estimation. We tested all GLMMs for potential misspecification, such as using an inappropriate error distribution, indicated by residual over- and under-dispersion, zero-inflation, and residual outliers using a simulation-based approach with 10,000 iterations using the DHARMa package (Hartig 2019).

RESULTS

The relative abundance of $t\bar{u}\bar{i}$ counted within the ecosanctuary increased significantly with time following predator eradication (Table 1). The mean number of $t\bar{u}\bar{i}$ per 5-minute count was 2.23 (se = 0.154) in 2005, 3.23 (se = 0.219) in 2008, 3.76 (se = 0.193) in 2011, and 2.68 (se = 0.279) in 2014. The effect of wind (mean score 0.94) and other noise (0.08) was negatively correlated with $t\bar{u}\bar{i}$ counts. Cloud cover (mean 0.78), rain (mean 0.07), and time of day were not significantly correlated with differences in $t\bar{u}\bar{i}$ relative abundance.

We received 320 responses to the 2,000 questionnaires delivered in the 2006 survey, and 225, 205, 167, and 138 for the 2008, 2010, 2012, and 2014 surveys respectively. Where respondents gave additional information on the location of their observations, these typically described rural and urban gardens.

Table 1. Generalised linear mixed model log estimates of fixed effects and fit statistics for modelled change in the relative abundance of tūī within Maungatautari ecosanctuary following predator eradication. Estimate values give the log of the expected relative change in the number of tūī per 5-minute count when a fixed effect increases by one and all other fixed effects are held constant

Response	Fixed effect	Estimate	Standard Error	z-value	<i>P</i> -value
Tūī count	Time (yr)	0.114	0.013	8.959	< 0.001
	Cloud	0.029	0.094	0.311	0.756
	Rain	0.073	0.136	0.536	0.592
	Wind	-0.233	0.053	-4.387	< 0.001
	Other noise	-0.327	0.161	-2.023	0.043
	Time of day	0.050	0.028	1.779	0.075



Figure 2. Months in which survey respondents recorded maximum tūī counts as a proportion of all responses each survey year, 2006–2014.

Means (and maxima) of the maximum number of tūī reported at each property within the whole study area in 2006, 2008, 2010, 2012, and 2014 were 4.4 (47), 5.5 (55), 8.6 (60), 11.7 (300), and 15.6 (300) respectively. Tūī aggregations were largest in spring (September–October) and smallest in early autumn (March; Fig. 2). We received six reports of large congregations of ≥100 birds from five residents (2 in 2012 and 4 in 2014).

The maximum number of tūī reported by residents in the study area increased significantly

with time and the provision of artificial food and decreased with distance from Maungatautari (Table 2; Fig. 3). Including an interaction between time and distance in the model resulted in significant deviation between observed and expected residuals, so we did not include the interaction in the full model.

There was some evidence for an increase in $t\bar{u}\bar{\iota}$ breeding occurrence in the largely unmanaged area with time, but distance and the interaction between time and distance were not significant (Table 2)





Figure 3. Maximum counts of tūī (circles; values >50 are not shown) reported by residents up to 20 km from Maungatautari ecosanctuary, and modelled change in maximum counts of tūī over time with distance from the ecosanctuary, with (dashed line) and without (solid line) provision of artificial food. Shaded areas show 95% confidence intervals around the predicted value for each distance.

Response	Fixed effect	Estimate	Standard Error	<i>z</i> -value	<i>P</i> -value
Maximum tūī count	Time (yr)	0.136	0.008	17.886	< 0.001
	Distance (km)	-0.057	0.010	-5.681	< 0.001
	Provision of food	0.256	0.098	2.600	0.009
Breeding	Time (yr)	0.159	0.083	1.919	0.055
	Distance (km)	-0.047	0.034	-1.398	0.162
	Time × Distance	0.005	0.006	0.741	0.459

Table 2. Generalised linear mixed model log estimates of fixed effects and fit statistics for modelled change in maximum counts of tūī and change in breeding occurrence within 20 km of Maungatautari sanctuary following predator eradication within the ecosanctuary. Estimate values give the log of the expected relative change in the response variable when a fixed effect increases by one and all other fixed effects against which it is modelled are held constant

DISCUSSION

Tūī increased at Maungatautari after pest eradication, as well as in the surrounding largely unmanaged area where counts of tūī were larger closer to the ecosanctuary. Together, these changes in tūī relative abundance are evidence of spillover of tūī from Maungatautari into the surrounding landscape, which has important biological and social implications.

Increase in tūī abundance within the ecosanctuary We found that tūī relative abundance within pestfenced Maungatautari increased following the eradication of all mammalian predators except mice from the sanctuary in 2006. This increase is consistent with independent non-temporal measures from Maungatautari (Iles & Kelly 2014; Bombaci *et al.* 2018), and data from other sanctuaries, such as Zealandia, Wellington (Miskelly 2018).

Hartley (2012) suggested that the effect of weather variables and noise on 5-minute counts should be investigated. We avoided counting birds in rain, strong wind, or other noisy conditions, but there was still strong evidence that the moderate wind and other noise during which we undertook some counts had substantial negative effects on the number of birds counted. We suggest that wind and other noise at least be included in analyses of 5-minute counts to control for their potential effects on bird counts and, therefore, on the inferences drawn from them.

Tūī spillover into the surrounding landscape

We found that $t\bar{u}\bar{\imath}$ relative abundance increased at residential properties in the non-target landscape surrounding Maungatautari over the same period in which $t\bar{u}\bar{\imath}$ increased within the ecosanctuary. Brudvig *et al.* (2009) note that spillover is largely a function of within-patch processes and is greatest from patches with greater density of the taxa of interest. This conceptual model implies that temporal increases in within-patch density, as seen with $t\bar{u}\bar{\imath}$ at Maungatautari, will also result in increasing spillover. We found maximum congregations of $t\bar{u}\bar{\imath}$ were larger with proximity to the sanctuary, which is also evidence of spillover of indigenous biodiversity into the wider landscape (Brudvig *et al.* 2009; Tanentzap & Lloyd 2017). The known mobility and life-history of $t\bar{u}\bar{\imath}$, and increases in their relative abundance, together with the scale of the Maungatautari project suggest that significant landscape-scale spillover of $t\bar{u}\bar{\imath}$ is occurring from this mainland biodiversity sanctuary.

The maximum tuī count data from resident surveys are strongly right-skewed, with a small number of very large aggregations of tūī. Congregations of 100 or more tuī were reported 6 times. Such exceptional congregations of tuī have not been previously reported in Waikato. In late-August 2015, we visited the property where the largest number (300) had been reported in both 2012 and 2014. This property was a large (approximately 10 ha) rural garden 6.7 km from Maungatautari. The landowners noted that there were fewer tur present that day than at the peak. Despite this, we estimated from counts and photographs that there were at least 210 tūī present, mostly in approximately 100 mature flowering Taiwan cherry trees (Prunus *campanulata*) from which they were feeding on nectar. This property demonstrates the potential for very large ephemeral congregations of tut at sites with abundant food resources.

Maximum counts of $t\bar{u}\bar{1}$ at rural and urban residences were most often observed in spring, immediately before the breeding season. This is consistent with previous reports of pre-breeding congregation of $t\bar{u}\bar{1}$ at preferred nectar sources (Bergquist 1985; Stewart & Craig 1985; Higgins *et al.* 2001) as well as of Australian Meliphagidae (Pyke 1980; McGoldrick & Mac Nally 1998). In the Waikato, these preferred food sources are typically coastal banksia (*Banksia integrifolia*), followed by kōwhai (*Sophora* spp.), flowering cherry (*Prunus* spp.), rewarewa (*Knightia excelsa*), camellia (*Camellia* spp.), and eucalypts (*Eucalyptus* and *Corymbia* spp.; Innes *et al.* 2005).

Evidence for increased occurrence of nesting in gardens in the landscape surrounding Maungatautari during our study was not as strong as for non-breeding change. This is unsurprising, as tūī are often relatively inconspicuous when breeding, and the natal philopatry shown by Bergquist (1985) suggests that most of the tūī that disperse seasonally from Maungatautari will return there to breed.

Limitations of the study

Pest control involving periodic targeting of ship rats and possums at the Hamilton Halo sites within and beyond our study area is also likely to have contributed to increased tūī abundance. However, this effect is likely to be modest compared with the influence of Maungatautari, where there has been sustained eradication of the full suite of mammalian predators, except mice, over a much larger area.

The survey respondents may not be representative of all residents in the study area, and the locations of the counts they recorded represent a small, non-random subset of the available habitat in the study area. The survey data therefore provide a measure of tūī relative abundance at the survey sites (residents' gardens), not an overall measure of abundance in the study area.

Our study lacks spatial replication, as it is focussed on a single ecosanctuary, so the results apply only to the study area. However, the inferred movement of tūī in this study is entirely consistent with other studies (Craig *et al.* 1981; Bergquist 1985; Stewart & Craig 1985; Higgins *et al.* 2001; Innes *et al.* 2005). The relative isolation of Maungatautari from other mammalian predator-control sites was advantageous for this study, but the large size (3,240 ha) of the reserve precluded replication. Repeating the study elsewhere is needed to determine if the results are more widely applicable.

Biological and social importance of tūī spillover

Scofield *et al.* (2011) suggested that, in many cases, degraded habitat outside pest-fenced ecosanctuaries will never be able to sustain the species found within the ecosanctuaries. The 'habitat' of a species refers to the resources and conditions present in an area that produce occupancy, including survival and reproduction (Hall *et al.* 1997). In situations described by Scofield *et al.* (2011), emigration from a fenced ecosanctuary may create a source-sink dynamic, where species are able to occupy the low quality "degraded" habitat but reproductive success there is less than within-habitat mortality

(Pulliam 1988; Faaborg et al. 2010). Predator abundance is an important attribute of habitat, and the relatively unmanaged area surrounding Maungatautari is likely to be sink habitat for species that are highly vulnerable to mammalian predation (e.g. hihi Notiomystis cincta, kokako Callaeas wilsoni, and tieke Philesturnus rufusater; Innes et al. 2010; Norbury et al. 2015). A sink population relies on immigration to persist, but despite low rates of reproductive success, sink habitat can contribute to larger total population size as offspring from the source can disperse and produce some offspring in sinks (Pulliam & Danielson 1991). It is also possible for sink habitat to have high population density due to immigration, so density can be a misleading discriminator of source and sink habitat (Van Horne 1983; Pulliam 1988; McArthur et al. 2019). It is unknown to what extent tuī that emigrate permanently from Maungatautari can breed successfully outside the sanctuary, and therefore whether it is sink habitat for this species, but the tuī we studied were undertaking winterspring (non-breeding season) movement. Most tūī originating from the ecosanctuary may return there to breed (Bergquist 1985), which is when they are most vulnerable to mammalian predation (Innes et *al.* 2010). The increased presence of tuī in the wider landscape will help restore indigenous dominance in ecosystem processes such as pollination and seed dispersal. Furthermore, public awareness, engagement, and acceptance of pest mammal control are improved when people experience tangible benefits of restoration, such as tūī visiting their properties (Campbell-Hunt 2002).

Connectivity between habitat patches (so-called 'corridors') is a key factor in spillover (Brudvig et al. 2009), and the rescue-effect that can maintain species and genetic diversity in fragmented landscapes (Brown & Kodric-Brown 1977; Piessens *et al.* 2004). Habitat is a species-specific concept, so it is important to frame connectivity and spillover in the context of the taxon of interest. It is also important to clarify which movement processes are of interest, e.g. seasonal movement, breeding dispersal, natal dispersal, or post-translocation dispersal, and to recognize the limitations in the understanding of many of these. Seasonal movement is important for enabling birds to access food resources that may be absent from remaining, often fragmented habitat, and breeding and natal dispersal are key to colonisation of the landscape surrounding sanctuaries, but these processes are poorly known for many New Zealand birds. Posttranslocation dispersal (Richardson *et al.* 2015) may be somewhat better known because monitoring is frequently mandated by the NZ Department of Conservation in translocations, which are very common (Miskelly & Powlesland 2013).

The habitat matrix surrounding Maungatautari, and detailed studies of tūī movement (Bergquist 1985; Stewart & Craig 1985; Innes *et al.* 2005), suggest that tūī readily cross pasture gaps of at least several kilometres, and this has potential for positive social and biodiversity gains over a considerably larger area than the fenced ecosanctuary alone.

Biodiversity spillover is a key to achieving widespread benefit from the long-term goal to make New Zealand predator-free (Russell et al. 2015; Parkes et al. 2017), but few studies have shown empirical evidence of biodiversity spillover from pest-fenced ecosanctuaries in New Zealand (Tanentzap & Lloyd 2017). Overall, our results provide strong evidence that predator exclusion from the Maungatautari ecosanctuary has enhanced tūī visits to the surrounding landscape via spillover. We predict that this will lead to more tur breeding in the surrounding landscape, as in Hamilton City (Innes et al. 2015), and this could be enhanced further by management to reduce the abundance of mammalian predators there during the tur breeding season. Reducing the abundance of predators in the landscape surrounding the ecosanctuary may also provide scope for 'evolutionary rescue' of some species (Urlich 2015). Our results also show that maximum counts of tūī can provide an effective way to engage citizen science to monitor landscapescale population dynamics of conspicuous, iconic species.

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Black-fronted tern (*Chlidonias albostriatus*) colony dynamics in New Zealand braided rivers

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Abstract: Black-fronted terns (*Chlidonias albostriatus*) are globally endangered and are one of six endemic bird species that rely on New Zealand's braided river ecosystems for breeding. Like other marsh tern species, black-fronted terns are predicted to have low breeding-site fidelity due to the instability of their breeding habitat, small colony sizes and high predation rates. We used breeding colony location data collected from nine South Island rivers for 3–12 years (2004–2015) to investigate the breeding-site fidelity in black-fronted terns. The distribution of breeding colony locations from seven of the nine rivers analysed were not significantly different to a simulated random distribution. The tendency of black-fronted terns to form breeding colonies near past breeding site compared to new sites was only significant for two of the nine rivers analysed. Overall, there was low breeding-site fidelity in black-fronted tern colonies from year to year across the rivers analysed.

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INTRODUCTION

The black-fronted tern (*Chlidonias albostriatus*) is one of six endemic bird species that rely on New Zealand's braided river ecosystems for breeding. Black-fronted terns have a small, declining population and are classified as globally endangered (BirdLife International 2012), primarily due to predation. The current black-fronted tern population is estimated to be less than 10,000

mature individuals (Keedwell 2002; O'Donnell & Hoare 2011). The black-fronted tern is one of the approximately 13% of all bird species that breed in colonies (Rolland *et al.* 1998), along with more than 95% of seabirds and all other tern species (Jones & Kress 2012; Palestis 2014). Breeding-site fidelity (also known as philopatry or tenacity) is the tendency of individuals to return to the same colony site, usually in succeeding breeding seasons (Austin 1949). The level of breeding-site fidelity demonstrated by different species can be impacted by many factors including age (Austin 1949; Freer

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1979), past breeding success (Burger 1982; Cuthbert 1988; Thibault 1994; Porneluzi 2003) and habitat stability (McNicholl 1975; Freer 1979; Visser & Peterson 1994; Burger & Gochfeld 2001).

High breeding-site fidelity can have significant adaptive implications for different species. Familiarity with a site generated through high breeding-site fidelity facilitates mate retention and reduces the energy and time expenditure required to locate suitable breeding sites and food resources (McNicholl 1975; Collar 2013). However, environmental changes can render past breeding habitat sub-optimal, dangerous or unusable. Environmental cues contribute to settlement decisions even in species with high breeding-site fidelity, as birds will abandon a historical breeding site if conditions change to the extent that costs of remaining are outweighed by the benefits of abandonment (Burger 1984). High breedingsite fidelity in species with limited behavioural plasticity can be highly detrimental to survival, such as a species naive to predation which may be unable to identify and respond appropriately to novel threats presented by introduced mammalian predators in their environment (Igual *et al.* 2007).

There are substantial differences in the site fidelity exhibited by different tern species. As a general rule, larger colonies in more stable habitat (e.g. rocky islands) tend to have greater site fidelity compared with smaller colonies in less stable habitats (e.g. sand bars) (Palestis 2014). For example, marsh terns (*Chlidonias* spp.) are believed to exhibit site fidelity to a lesser degree than other tern species due to the dynamic nature of their breeding habitats (Palestis 2014). Most of the marsh tern group breed on floating weeds and vegetation in wetlands and marshes, except for black-fronted terns, which breed in gravel braided river beds (Lalas 1977). Braided rivers are highly dynamic systems characterised by high habitat turnover resulting in a dynamic mosaic of channels, bars, islands, and ponds (Tockner et al. 2006; Gray & Harding 2007). Both braided river and marshland breeding habitats appear similarly dynamic and dependent on water levels and flows, potentially making strong site fidelity disadvantageous, or difficult to achieve.

We predict black-fronted terns to have low breeding-site fidelity, similar to those observed in other *Chlidonias* spp., because of their dynamic braided river breeding habitat and small colony sizes. However, the evidence for this is equivocal and there are studies that suggest instances when black-fronted terns exhibit higher breeding-site fidelity than expected. For example, Pierce (1983) noted that in the Cass River (1977–1980) six to eight breeding colonies were present each season, usually in the same localities. Similarly, Keedwell (2002) identified 'main colony sites', in which colonies formed consistently, especially following seasons of successful breeding. In contrast, Robertson *et al.* (1983) suggested that black-fronted tern colony locations changed each year following observations of a region of the Ahuriri River that contained a single black-fronted tern colony in 1975 and four colonies in 1982. O'Donnell & Moore (1983) also referenced the changing of colony locations each year as an adaptation to the dynamic braided river environment.

The locations and sizes of black-fronted tern colonies have been recorded over 12 years (2004– 2015), through braided river bird surveys and other research projects; however, no analysis has yet been conducted on colony dynamics and site fidelity. The aim of this study was to determine whether blackfronted terns show signs of breeding-site fidelity in particular river sections. Analysis of past breeding colony locations will identify whether black-fronted terns exhibit strong breeding-site fidelity, identify particular areas or colony locations that are selected preferentially for black-fronted tern breeding, and inform targeted management approaches for blackfronted terns.

METHODS

Historical data collection

Bird counts have been carried out on braided rivers across the South Island of New Zealand since the 1960s. The majority of bird counts are collected following the standard walk-through survey method described in O'Donnell & Moore (1983). Eighty-four South Island rivers have been surveyed one or more times by volunteers and members of the former New Zealand Wildlife Service, Department of Conservation, the Royal Forest and Bird Protection Society, the Ornithological Society of New Zealand, Braided River Aid, and various river care groups (O'Donnell & Hoare 2011).

Since 2004, GPS coordinates for the colony and breeding locations of black-fronted terns were collected during most braided river surveys. Outside of the formal surveys, GPS colony coordinates have also been collected through research, and opportunistically by people working in and/or frequenting braided river systems.

A total of 598 black-fronted tern GPS breeding locations (≥ 1 pair) were recorded from 34 different South Island rivers and one wetland (the Ruataniwha wetland, Mackenzie Basin). Data were collected from 2004–2015, with a range of 1-12 years surveyed in each river.

Linearising data

River centrelines were used to assign a linear distance (measured from the downstream extent

of the surveyed area) to all GPS breeding locations. The Tasman River was too wide (up to 4 km) to linearize using a single centreline and so a centreline was generated for each half of the river survey area. Each breeding location was allocated a linear distance corresponding to its location along the centreline it was closest to. The two linearised data sets from the Tasman River are, henceforth, referred to as 'Tasman LHS' and 'Tasman RHS'.

Only data from rivers that had been collected consistently and for more than two years were included in the analysis. Therefore, data from nine rivers were included in the analysis (Table 1): Wairau, Waiau (Canterbury), Hurunui, Ashley-Rakahuri, Rakaia, Ashburton, Rangitata, Tasman, and Dart. Of the 26 rivers excluded, 20 contained < 3 years of data and six had inconsistent data collection (differential survey effort or inconsistent river sections surveyed). River areas deemed permanently unsuitable for black-fronted tern breeding (e.g. gorges) were excluded from the analysis of river lengths. For this analysis, each river was treated in isolation; although the reality is that rivers are not fully independent as some birds do move between river systems from one breeding season to the next (Keedwell 2002). The survey data provide a snapshot of tern colony locations at a point in time and there was no way to identify individuals or determine their origin or destination.

Colony distribution

The nature of black-fronted tern colonies, generally small (2–50 pairs) with nests widely distributed (inter-nest distances of 1–100 m), makes them difficult to define (Keedwell 2002; Bell 2013). For the purposes of this study, arbitrary 300 m continuous river sections were used to divide the surveyed area of each river. Using 300 m river sections allowed the

single GPS location recorded for each black-fronted tern colony to be generalised over a more realistic area. We also used the river sections to reduce potential inconsistencies in GPS location recording. There is currently no standard protocol for GPS colony location collection, therefore there is no way to determine what the GPS waypoint represented with respect to the colony's location, e.g. centre, upper, or lower limit.

Three variations of the river sections were generated, one starting at the downstream boundary of the survey area and the other two were offset upstream by 100 m and 200 m respectively. Three variations of river sections were used to counter the arbitrary assignment of the river sections and ensure that all colony locations in different seasons that were less than 300 m apart would be in the same river section in two of the three variations.

Colony locations were assigned to river sections based on their linear distance along the survey area. Three colony distributions were generated for each river, one for each of the three river section variations. For each river section variation, the frequency of black-fronted tern colonies was calculated using the presence/absence of blackfronted tern colonies in each river section, during each breeding season surveyed.

The mean observed frequency distribution of black-fronted tern colony locations (i.e. mean number of years a river section had a breeding colony) for each river was calculated and compared to a mean expected random distribution, generated using 1,000 replicates of random sample distributions matching each rivers specifications (number of sections and data points). The random distribution was generated under the assumption that each colony data point had equal probability of occurring in any particular 300 m river section.

Table 1. Summary data for the nine rivers (listed north to south) surveyed consistently and included in the colony distribution analysis.

River	Survey length (km)	Total number of colonies	Mean colonies/ year	Number of years surveyed	Range of years surveyed
Wairau	96.3	49	9.8	5	2009–2013
Waiau (Canterbury)	88.5	33	11.0	3	2008-2010
Hurunui	69.9	22	4.4	5	2006-2010
Ashley-Rakahuri	19.2	50	4.2	12	2004-2015
Rakaia	65.4	16	5.3	3	2011-2013
Ashburton	52.2	26	4.3	6	2007-2015
Lower Rangitata	45.6	36	8.8	4	2007-2015
Tasman LHS	15.3	54	5.4	10	2004-2015
Tasman RHS	14.7	20	2.9	10	2004-2015
Dart	18.0	14	3.5	4	2007-2010

The observed and expected colony frequency distributions for each river were compared using Pearson's Chi-squared Goodness of Fit test with a simulated P-value. All analysis was conducted in R (3.3.0) via R studio (0.99.903) and using dplyr (0.5.0), RVAideMemoire (0.9-64), and tidyr (0.6.1) packages. Plyr (1.8.4) and ggplot2 (2.2.1) were used to produce the graphs.

Colony clustering

Each 300 m river section in the observed datasets, described above, was assigned an arbitrary value (cluster index) based on the presence or absence of a colony (across all surveyed breeding seasons) within the river section being assessed and both of its adjacent river sections (Table 2). We also explored grouping the data into triplets, in which the presence/absence of colonies in each of the three river sections dictated the arbitrary cluster index value, rather than relating it to the river section being assessed. While this approach yielded similar results, it appeared to contribute less value

Table 2. The protocol for assigning cluster index values to river sections based on the presence (O) or absence (X) of colony locations in both the central and neighbouring river sections.

Neighbouring river section	Central river section	Neighbouring river section	Cluster index
Х	Х	Х	0
Х	Х	О	1
О	Х	Х	1
0	Х	О	2
Х	0	Х	3
О	0	Х	4
Х	О	О	4
0	0	0	5

from a management perspective, as you were unable to distinguish between areas of repeated colony use and those which were separated by river sections which had never had a colony establish. The cluster index values assigned to the first and last river sections on a river were excluded from the analysis. The mean frequency of cluster index values was calculated for each rivers' mean colony distribution. A 2x3 contingency table was used to analyse the mean frequency of clustering of the colony location data for each river. A Chi-square test of independence or Fisher's exact test (if there were less than five data points in the contingency table) was used to test for significant differences (P < 0.05) between the probability of having a colony present in a neighbouring river section based on the presence or absence of a colony in the section being assessed. Analyses were conducted in R using the packages referenced above.

RESULTS Colony distribution

The observed frequency distribution of blackfronted tern colonies was not significantly different to the expected distribution generated through random selection for seven of the nine rivers analysed. The Ashley (χ^2 =68.095, P=0.003) and Tasman (RHS χ^2 =44, P=0.013, LHS χ^2 =66, P=0.016) Rivers were the exceptions, with their distributions significantly from differing the frequency distribution expected from random selection. Although nonsignificant, a further six rivers shared the trend that river sections, in which colonies were not observed, and those in which colonies were most frequently observed, occurred more than expected at random (Fig. 1). Main breeding areas (a river section in which the greatest colony frequency was recorded) were used for breeding in 30–100% (x=57.5 \pm 5.7% SE) of the breeding seasons recorded (Table 3). All rivers contained 1-2 main breeding areas in their surveyed lengths.

Colony clustering

Clustering of black-fronted tern colonies was significant for only two of the nine rivers analysed, the Ashburton (P=0.03) and Rakaia (P=0.02) Rivers. In these two rivers, if a colony in the central river section, it was significantly more likely that a colony would be present in the neighbouring river sections and vice versa. Although nonsignificant, this trend was consistent for the other seven rivers.

DISCUSSION

Black-fronted terns demonstrated low breedingsite fidelity. Only two of nine rivers had a spatial colony distribution significantly different to that expected due to random selection, indicating that black-fronted terns do not demonstrate strong tendencies to return to the same breeding locations from season to season. This is further supported by the lack of significant clustering of breeding locations in seven of the nine. Our *a priori* prediction was that black-fronted terns would exhibit low breeding-site fidelity because of the instability of their braided river breeding habitat (McNicholl 1975; Switzer 1993) and generally poor breeding success (Keedwell 2002, 2003; Anderson et al. 2007). Low breeding-site fidelity indicated by these results is comparable to that found in other marsh terns, i.e. black (Chlidonias niger), whiskered (C. hybridus) and white-winged black terns (C. leucopterus). Low

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Table 3. Black-fronted tern use of main breeding areas (river section in which the greatest frequency of black-fronted tern breeding was recorded) in each river (listed north to south).

River	No. of seasons main breeding areas used	% of seasons main breeding areas used	No. of main breeding areas
Wairau	3	60.0	2
Waiau (Canterbury)	3	100.0	1
Hurunui	3	60.0	2
Ashley-Rakahuri	7	58.3	1
Rakaia	2	66.7	2
Ashburton	3	50.0	1
Lower Rangitata	2	50.0	2
Tasman LHS	5	50.0	1
Tasman RHS	3	30.0	1
Dart	2	50.0	2



Figure 1. Observed (light grey) and expected (black) proportion of river sections containing different colony frequencies (number of colonies per river section).

breeding-site fidelity in other *Chlidonias* terns has been attributed to habitat instability, with yearto-year variability in vegetation, water levels and suitable nest site availability forcing changes in breeding colony locations (Shuford 1999; Ledwoń et al. 2013).

Environmental conditions, predation events and experience may disrupt the connection of the terns to their breeding colony locations causing them to choose new sites. It may be that the terns intend to return to the colony location from a previous year, but changes to river condition render it unsuitable (e.g. covered in vegetation). Past blackfronted tern breeding colony locations could easily become unsuitable from one season to the next due to changes in the river channels, weed invasion or island erosion. Rather than persisting in sub-optimal habitat the terns move to a more suitable location (but often close by the previous colony site). Burger (1984) found this to be the case for least terns. Least terns were observed returning to their previously used colony sites, but would abandon it if it was deemed unsuitable (Burger 1984). Alternatively, black-fronted terns are returning to a region that offer good breeding prospects (e.g. good food supply) and are then randomly locating colonies in any suitable habitat in that zone. For either option, strong breeding-site fidelity without the ability to cue of environmental factors (colony site factors, or wider factors, such as food supply) would likely be highly disadvantageous for black-fronted terns.

The stability of a breeding site is only one of several factors that may contribute to breeding site selection; past breeding success, colony size and predation rates have also been linked to breeding-site fidelity (Burger 1982; Switzer 1993; Keedwell 2002; Lombard *et al.* 2010). However, the increased breeding-site fidelity linked to high chick survival found by Keedwell (2002) is one of very few studies have investigated these factors in relation to potential breeding-site fidelity in black-fronted terns. Further investigation of these factors may contribute substantially to more targeted and effective management of black-fronted terns.

Greater use of colony locations in rivers or river sections that remain stable and suitable for extended time frames is expected. The 'main colony sites' presented by Keedwell (2002) appear to support the reuse of stable sites. She monitored eleven colony sites, of which three were used in all four years of the study and five for three years leading to the suggestion that there were sites where the terns nested more consistently (Keedwell 2002). Bell (2017) also found that black-fronted terns tended to consistently breed in river areas, sometimes on the same islands. These trends were seen in colony distributions in the Ashley and Tasman rivers and were significantly different to a random distribution. These two rivers also had the longest survey records of ten and twelve years, respectively, and had longterm programs of predator control in place. It may take extended periods of surveying to be able to identify these preferred locations over those that may be used for two or three seasons before being abandoned. For example, in the Waiau River, a colony has been recorded on the large and relatively stable gravel beds near the Shark's Tooth for all three surveyed years, and anecdotally is referenced

to have been present at this location most years. However, overall the colony distribution was not different to random and the presence of clustering was not significant. It is possible that the movement of colony locations in other, more dynamic areas of the river may have impacted on the significance of the reuse of the Shark's tooth location.

Tern Island, a 300 m long island in the Upper Ohau River, is another example of the repeated use of stable, suitable colony locations by black-fronted terns. Data from the Tern Island colony were not included in the current analysis as the data were not collected as part of a full survey. Tern Island has had a black-fronted tern breeding colony for more than 10 (and possibly up to 25) successive breeding seasons prior to 2017. The Upper Ohau River is relatively stable because its flow has been artificially stabilised since 1991, reducing natural fluctuations in flow and the frequency and size of flooding events, and this in turn has allowed the continued existence of Tern Island beyond the life of the average braided river island. In addition, Tern Island was the focus of an intensive "best effort" predator control project by Project River Recovery (Anderson & Woolmore 2009). Tern Island appears to be an example of how greater habitat stability and protection from predation can facilitate repeated use of black-fronted tern colony locations. It also demonstrates that this species is capable of high breeding-site fidelity if the environment is stable.

Interpretation of the GPS colony location data may be complicated by the lack of a standard protocol for the collection of GPS colony data, and GPS location inaccuracies may result in some error around the actual location of colonies. Generation of a standard protocol for the collection of colony GPS locations would facilitate a more accurate interpretation of colony dynamics data in the future. In the current study, broad (300 m) river sections were used to generalise the colony GPS locations and reduce the influence any error in the data.

Our ability to interpret the results is limited because we were unable to determine whether the same terns are returning to these clustered colony locations, or whether different groups of terns were attracted to the clustered colony locations each year because of some general environmental factor (e.g. suitable habitat or a food source). However, the dynamic nature of the braided river environment dictates that the location of 'ideal' habitat or a food source will most likely change dramatically from one breeding season to the next. Therefore, factors associated with site fidelity seem more likely to be the reason for the regional clustering of colony locations observed. Further research using individual marking is required to determine the importance of site fidelity in determining blackfronted tern colony dynamics.

Black-fronted terns are confronted with a relatively dynamic and unstable environment that has been linked to low breeding-site fidelity in other tern species (Gummer 2003; Palestis 2014). Analysis of historical black-fronted tern colony locations supports our a priori hypothesis of low breedingsite fidelity. The instability of their braided river habitat likely forces the terns to change colony sites in response to environmental cues. Black-fronted terns may exhibit greater fidelity to breeding colony locations that remain suitable, an unusual occurrence in this ecosystem type, such fidelity is supported by other studies by Keedwell (2002) and Rebergen & Woolmore (2016). Additionally, tools such as social attraction, may be used to facilitate the establishment or re-establishment of black-fronted tern colonies in 'safe' locations (Hamblin 2017). It may be possible to explicitly test the link between an unstable environment and low site fidelity if each section of river can be ranked in terms of stability. From this likelihood models can be developed to predict whether colonies will remain in the same relative position from year to year. Greater consistency in the location of black-fronted tern colonies would substantially increase the efficiency and effectiveness of their management, particularly in determining which sites to invest in managing weeds and predators.

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New Zealand pipit (*Anthus n. novaeseelandiae*) nesting and breeding behaviour in urban Onerahi, Whangarei

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Abstract: Four New Zealand pipit nesting attempts were monitored in an urban wasteland field in Onerahi, Whangarei. A female laid two clutches in dense kikuyu (*Pennisetum clandestinum*) in October and December 2015 and fledged young from both clutches. Pipits were then absent from the site from February until late August 2016. The male reappeared and used the exact same home range, with a new female. This female laid two nests in the more open low gorse (*Ulex europaeus*) and aristea (*Aristea ecklonii*) cover in September and October 2016 but both nests were depredated at 3–5 and seven days after hatching, respectively. All three chicks, the female, and possibly the male were killed during the latter predation event. There were differences in adult behaviour throughout the breeding cycle. The female constructed the nest and undertook all the incubation. During the incubation period the male was only present at the nest site in the early morning and did not roost at the site each evening. The pair was present throughout the day after the chicks hatched. Pipits used more frequent calling rates when there was a perceived threat, and when that threat was near a nest.

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INTRODUCTION

The New Zealand pipit (*Anthus novaeseelandiae*) is considered to be part of a complex which includes Australian and New Guinean birds (Gill *et al.* 2010). New Zealand pipits increased in number as the land was converted to open habitats (Buller 1888; Guthrie-Smith 1927) but pipits have subsequently declined (Robertson *et al.* 2007; Beauchamp 2009) and are now absent from intensively farmed areas as well as some less intensively farmed areas. Pipits were absent from 1994–2004 (AJB *unpubl. data;* Robertson *et al.* 2007) in areas where they were formerly common (Garrick 1981), including the roads into Huiarua Station. This may have occurred because the habitat became too dry (Hamel 1972), or because there was significant and permanent loss

Received 19 May 2019; accepted 12 August 2019 *Correspondence: wekaman@xtra.co.nz of roadside breeding habitats during the 1983–1986 drought (Beauchamp 1997).

Pipit habitat requirements for nesting, nest site use, and the duration of nesting are not well studied in New Zealand. Anecdotal records from Kapiti Island at sea level, indicated that pipits bred over eight months (August-March) and had multiple clutches of 1-4 young (Wilkinson & Wilkinson 1952). Nests were constructed in open sites under or adjacent to tufts of vegetation or beside logs (Guthrie-Smith 1927; Higgins et al. 2006) or within or under dense grass at the end of short tunnels (Wilkinson & Wilkinson 1952; Higgins et al. 2006). In alpine Australia, Norment & Green (2004) found that all nest sites on alpine frost flats were placed below shrubs with entrances aligned away from predominant winds and that the most successful nests were in denser habitat.

Previous authors found that nests laid by

adjacent pairs were on average 78.3 m (range 52–150 m, n = 24) apart (Norment & Green 2004). These authors suspected that their study included a polygamous group of a male and two females, and two clutches were incubated simultaneously by the females *c*. 9 m apart (Norment & Green 2004). The spacing between nests laid by the same pairs during the same season in other studies were 0.15–25 m apart (McEvey 1949, 1952; Higgens *et al.* 2006). The home ranges of pairs of pipits do not necessarily abut in New Zealand (Beauchamp 2013), and on Chatham Island home ranges are often >100 m apart (Beauchamp 2002).

On Kapiti Island incubation lasted about 14 days and the young fledged 14–16 days later (Wilkinson & Wilkinson 1952; Wilkinson 1957; Garrick 1985; Moon 1988). On the Snowy Mountains, Australia, incubation was 13.9 days (SD = 0.6, range 13–14.5), and the duration of nesting and pre-fledging averaged 27.5 days (Norment & Green 2004). The time between loss of a nest and relaying three eggs (which are usually laid a day apart) is as little as six days, and the time between fledging young and relaying was <14 days (Lord 1956; Norment & Green 2004).

Studies of Sprague's pipit (*Anthus spragueii*; Robins & Dale 1999), the American pipit (*A. rubescens*; Verbeek & Hendricks 1994) and the water pipit (*A. spinoletta*, Rauter & Reyer 1997) have found that the female does the nest building and all of the incubation. Where sexing has been possible, the division of labour in the New Zealand pipit is undescribed (Norment & Green 2004; Higgins *et al.* 2006).

Studies in New Zealand and Australia have found that pipits occupy breeding areas temporarily and then flock together in the late summer. These groups sometimes comprise both adults and the still dependent fledged young of the late clutches (Norment & Green 2004; Beauchamp 2009, 2013).

The late nest occupancy and post-fledging periods (weeks 2–4 after hatching) are considered to be the times when pipits are most vulnerable to predators (Guthrie-Smith 1927; Wilkinson & Wilkinson 1952; Beauchamp 2007) as the nestlings are noisy after feeding (Beauchamp 2007), and fledglings fly poorly (Wilkinson & Wilkinson 1952). I previously assessed where these risk periods were for pipits using 20 years of observations, but there was limited information on activities during incubation and nesting behaviour by chicks and parents, and I did not know the exact flight capability of young at fledging (Beauchamp 2009).

In this paper I describe the breeding performance and breeding behaviour during two breeding seasons at an urban site in Onerahi, Whangarei and then discuss how this relates to previous observations, habitat and threats to pipit in the Northland and other rural landscapes.

METHODS

Study area

The study area was a privately-owned fallow field (2.87 ha; Fig. 1) which between 2007-2015 regenerated to rank kikuvu (Pennisetum clandestinum), watsonia (Watsonia bulbillifera), 0.3–3.0 m high gorse (Ulex europaeus), and 3–5 m high aristea (Aristea ecklonii; Fig. 1C). Three paths through the site were improved in 2014 to include mown grass and some bare ground, and a former 620 m² tip site was cleared and mown annually from November 2015 (Fig. 1C). The total field, including the tall gorse, was mown to the ground by a tractor in February 2016, but by the start of September 2016 the kikuvu and watsonia region had recovered to form a dense mat. However, the areas that had formerly been high gorse were 20 cm high gorse regrowth and aristea, or open bare ground.

The pipits' foraging home range included a church with a gravelled car park (305 m²), low-grassed street berms (0.4 ha), and a park (0.5 ha). The nearest open rural grassland was 370 m to the east (Fig. 1B).

Three domestic cats (*Felis catus*) roamed into the field, and a mature harrier (*Circus approximans*) with a light underwing patrolled the field. Three residents ran unleashed dogs (*Canis familiaris*) along the paths. No introduced mammalian predator control occurred in the field region.

Field observations

I observed four pipit nesting events during two breeding seasons on a piece of fallow urban land between 16 October 2015 and 3 November 2016 (Table 1, Figs 1 & 2). Monitoring was biased to the early morning and evening (69%, n = 80, Fig. 3) and confined to short periods to reduce observer impact on pair behaviour. The pipit pairs were visited during the pre-breeding (mean = 21 minutes, *SD* = 12, range 2–60, n = 43); incubation (mean = 18 minutes, *SD* = 11, range 2–22, n = 66); and nestling (mean = 35 mins, *SD* = 19, range 5–98, n = 41) phases of nests 1–4; and the fledgling phase of nests 1 and 2 (mean = 38 mins, *SD* = 23, range 7–108, n = 24).

Pipits were sexed using the male's protective behaviour (Beauchamp 2013), after which the bird's plumage was inspected to ascertain what the differences were between the sexes. The plumage of the first pair was similar, but the male had a lighter and slightly less speckled breast. The plumage of the male in the second pairing was similar to the first, but the female had more limited breast speckling and far lighter lower belly and flank than the female in the previous season. The sex of the second female was confirmed from inspection of the reproductive track of her depredated body at the end of the season. The male used exactly the same parts of the local environment each year

Table 1. Dates of the breeding period phases of the four New Zealand pipit (*Anthus n. novaeseelandiae*) breeding attempts at Onerahi, Whangarei. Phase start and end dates are provided, with the number of days on which data were collected indicated in parentheses.

Phase	Nest 1	Nest 2	Nest 3	Nest 4
Pre-incubation	15 Oct 2015 – 21 Oct 2015 (4)	3 Dec 2015 – 13 Dec 2015 (7)	4 Sep 2016 – 12 Sep 2016 (7)	2 Oct 2016 – 11 Oct 2016 (9)
Incubation	22 Oct 2015 – 6 Nov 2015 (4)	14 Dec 2015 – 27 Dec 2015 (9)	13 Sep 2016 – 26 Sep 2016 (4)	12 Oct 2016 – 26 Oct 2016 (13)
Nestlings	7 Nov 2015 – 20 Nov 2015 (10)	28 Dec 2015 – 12 Jan 2016 (12)	27 Sep 2016 – 1 Oct 2016 (3)	27 Oct 2016 – 3 Nov 2016 (6)
Fledglings	21 Nov 2015 – 2 Dec 2015 (8)	13 Jan 2016 – 23 Jan 2016 (9)	n/a	n/a

despite there being other sites within the region that were flown over but otherwise not used. These differences were interpreted as the same male with a different partner each season.

The pipit pairs were monitored by moving on foot throughout the site, but I never stopped closer than 4 m from the location of any known nest. I recorded the location of birds relative to fixed points, the calls given, the rate of *tjswee* and *tiswit* calls in relation to the proximity of the nest and the fledglings, the direction and location of foraging from the nest sites, and the time that the female spent away from nest 4 during incubation. Food delivery rates were recorded using Redfield 10x42 binoculars from a position 15–25 m from all nests. The activity of adult pipits was scored every 5 seconds for a maximum of 10 minutes, and the distance moved within these periods noted. Adult pipit calling rates were recorded separately when the pipits were within a radius of 10–50 m and 5–9 m of nest 2 to assess whether the rate changed with my proximity to the nest.

I could not access nests 1 and 2 laid in kikuyu without unnecessarily disturbing the nests and thus I only inspected nests 3 and 4 in more open habitat briefly when the pair was absent to establish the exact location of the nest and the number of eggs/ chicks present.

RESULTS

Pair presence at the site

On 15 October 2015, two pipits fed together on one of the paths in a block of fallow land surrounded

by urbanization (3 ha, Fig. 1B & 1C). The pair was subsequently seen on the street verges up to the church car park, but no courtship activity was observed. The first pair disappeared on 23 January 2016, the last day the fledgling of that season was seen (Table 1). A single bird was next seen near the church car park on 28 August 2016, and a pair was seen in the field on 4 September 2016. Pipits disappeared from the site on 3 November 2016 when the second brood of nestlings, the female, and maybe the male, were killed (Table 1; Fig 2). The pairs were only present when nesting and raising young (Fig. 2).

Pre-nesting and nest building

The first pair was found at the site seven days before incubation of nest 1 and eight days before incubation of nest 3. The time between the last sighting of young from nest 1 and the start of incubation at nest 2 was 12 days; and the time between the loss of nest 3 and the start of incubation at nest 4 was 11 days (Table 1).

During the pre-nesting phase the pair predominantly foraged together (Table 2). The movements were generally a slow stop-start walk covering an average of 5.2 m.min⁻¹ (SD = 4.3, n = 6). Pipits preened on the ground or on elevated surfaces at the foraging sites (Table 3). Pipits were generally quieter in the pre-incubation period than in other phases of breeding (Table 3). The only time that the male was heard uttering a territorial song was on 11 December 2015 while he carried out an arched display flight over the former nest site (nest 1, Fig. 1C).

Table 2. Encounter rates of New Zealand pipit (*Anthus n. novaeseelandiae*) pair members in the breeding field at Onerahi during different phases of the breeding period.

Breeding phase	One adult detected	Pair detected	No adults detected	Proportion of visits that the pair was detected at the site(%)	Proportion of the overall visitation effort (%)
Pre-incubation	9	24	13	52.2	25.6
Incubation	41	18	10	26.1	38.3
Nestlings	21	19	1	46.3	22.8
Fledglings	7	12	5	50.0	13.3

Period	Proportion of visits that each call type was detected				Visits when pipits were detected (<i>n</i>)	Visits when any calls were detected (%)
	tjwsit	tjwsee	tzeer	pipit		
Pre-incubation	2.2	11.4	2.2	2.2	44	26.7
Incubation	0.2	39.1	1.1	18.7	64	58.3
Nestlings	38.6	34.0	2.2	23.0	39	67.5
Fledglings	26.0	47.8	0	37.4	23	66.7

Table 3. New Zealand pipit (Anthus n. novaeseelandiae) calls during breeding at Onerahi, Whangarei.



Figure 1. New Zealand pipit (*Anthus n. novaeseelandiae*) nest and foraging locations at Onerahi, Whangarei. A) Study site location in Onerahi. B) Adult foraging areas; hatched lines are the principal foraging areas in the field and surrounding street. C) Field sites in dark margin including • = nest location and number; G = gorse; T = trees; K = kikuyu and watsonia.

The first season's nests were 3.5 m and 3.2 m from the public track system, respectively, were 40 m apart and both were situated in 50–70 cm high dense kikuyu with watsonia (Fig. 1C). Neither nest could be accessed without compromising the protection of the dense habitat or altering the behaviour of the adults and consequently the nests were only investigated after the young had fledged. Nest 1 could not be located and nest 2 comprised a relatively limited grass bowl within the grass mat 200 mm above the ground and topped by kikuyu.

The second season's nests were 6 m and 8 m from formed paths, were 44 m apart, and both were located in open areas of gorse and aristea respectively (Fig. 1C). Nest 3 contained three eggs on 25 September 2016. The only nest building seen was between 0730 h and 1030 h on 9 October 2016, the day of the predicted laying of the first egg of a three-egg clutch in nest 4.

During the pre-incubation phase the first pair used at least six sites for night roosting together (Fig. 1C) and were absent from the site for five nights. The second pair was never detected roosting in the field in the pre-nesting phase and was seen leaving the site at twilight (n = 8 days of observations).

Incubation

At nests 3 and 4 the female did all of the incubation, and all afternoon and evening first encounters with pipits were with the foraging female (n = 11). At nest 4 the female foraged on average 6 (SD = 3.6, n = 13) times an hour and for between 2 and 9 minutes. The duration of these foraging periods increased as incubation progressed (Fig. 5).

During the incubation period the male was only found on-site before 1017 h and after 1700 h (n = 7 visits). The *tjwsee* call (Fig. 4) was given by the male while moving around the site, but not at the nest. The *tzeer* call was given by both sexes more often than during other parts of the breeding cycle, especially during low sweeps over the nest sites. The *tzeer* call was also uttered with the only period of song heard during the study (Table 3; Sonogram J in Higgins *et al.* 2006).

During the incubation period the male was only seen around sunset during three evenings and he only roosted on-site twice (n = 12 days of observation). On the 13th day of incubation of nest 2 the male appeared to be set to roost at the site, but 7 minutes before sunset he flew towards Limestone Island; a site that pipits use to roost (AJB *unpubl. data*).

Nestlings

After the nestlings hatched the male was detected more often at the site (Table 2). The female foraged for food for the young before the first hatched chick was dry and brooded the young until day six, and then intermittently thereafter. Most first encounters were of solitary adults walking and feeding (64%, n = 25; Table 4), and adults moved on average 55 m.min-1 (SD = 6.6, n = 11).

The pipits foraged within the site differently during each nesting attempt (Table 5). The foraging area used by the adults for nest 1 was more limited in size than that used in subsequent nesting attempts (Fig. 1B, Table 5). The foraging area used for nest 2 included the road verges (40% of observations) and

Table 4. New Zealand pipit (Anthus n. novaeseelandiae) behaviour during breeding phases at Onerahi, Whangarei.

Period	No. of five-	No. of days	Behaviour category (%)						
	second units	that data were collected	Dash & jump	Feed	Preen	Stand	Walk	Fly	
Pre-incubation	553	3	2.4	13.7	15.6	20.6	46.1	0.5	
Incubation	229	4	5.2	23.1	3.1	14.0	47.6	2.6	
Nestlings	432	6	2.8	14.4	0.5	13.9	60.6	3.5	
Fledglings	1,057	17	4.4	12.4	0.2	9.8	65.8	3.2	

Table 5. Number of flights to urban berms and car parks and different field sites by New Zealand pipits (*Anthus n. novaeseelandiae*) after food delivery to nestlings at Onerahi, Whangarei.

Location	Nest 1	Nest 2	Nest 3	Nest 4	Total
Urban berms and car parks	3	19	4	7	33
Field sites					
Top clear soil and gorse	21	6	9	17	53
Lower rank grassland	1	8	2	4	15
Middle rank grassland gorse interface	0	13	5	18	36

especially the cracks along the concrete verge of the berms. The same non-field areas were used in both nesting seasons by all of the adult birds.

Food-delivery to the nests averaged 12.2 deliveries per hour (SD = 7.6, n = 9.5 hours of observation) and on-nest time averaged 6 seconds (SD = 4.6, n = 46). Parents delivered food equally to the nest ($\chi^2 = 2.96$, P > 0.05, n = 57), and the male was more cautious during food delivery and when I was within 25 m of the nest. After food delivery, only 24.6% (n = 17) of the flights from the nest were towards their foraging partner, and flights were generally to an area not used during their last food collection period (65%; n = 75; $\chi^2 = 9.72$, df = 1, *P*<0.005). Nestlings first called after food delivery at nests 1, 2 and 4, at eight, eight and seven days old, respectively. At nest 2, on day eight, nestlings called 50% (n = 8) of the time after adults delivered food (n= 46) in groups of calls of 7–9 MHz (Fig. 4). During the two days before I observed young (days 15 and 16), adults delivered food to sites up to 6 m from

the nest, indicating that the young were already dispersed in the kikuyu.

The *tjwsee* (Fig. 4, 3-5 kHz) contact call (Beauchamp 2007) was given by both parents from the time that the eggs hatched, and was either uttered at the nest or within 50 m of the nest (88%, n = 50 deliveries). Parents called on average 18 (*SD* = 5.7, range 9.1–25.7, n = 12) times a minute from the top of the highest vegetation near the nest when intruders were 20–45 m from the nest; and on average 34.6 times (SD = 5.7 range 30–42, n = 3) a minute when intruders were closer than 20 m to the nest (t = 4.667, df = 3, P < 0.018).

In the late nesting period, contact calls were also interspersed with single or groups of repeated *tzree* calls (Fig. 4).

Fledglings

Young pipits only fledged from nests 1 and 2 (Table 1, Fig. 2). Three fledglings from nest 1 were first seen at *c*. 15 days old on 21 November 2015. Their



Figure 2. Detection and breeding of New Zealand pipits (*Anthus n. novaeseelandiae*) in 2015–2016 at Onerahi, Whangarei. light grey = nest building, medium grey = incubation, black = on nest, dark grey = fledged with parents.



Figure 3. Observer arrival times at the New Zealand pipit (*Anthus n. novaeseelandiae*) study site at Onerahi, Whangarei. Open bars: nests 1 & 2 and closed bars: nests 3 & 4.



Figure 4. New Zealand pipit (*Anthus n. novaeseelandiae*) calls at the nest site. A: chick calls after adults leave the nest; B: *tjwsee* calls; C: *tzree* and inter-dispersed *tjwsee* calls



Figure 5. Duration of female New Zealand pipit (*Anthus n. novaeseelandiae*) foraging times when incubating nest 4 at Onerahi, Whangarei.

tails were half-grown and their flights of *c*. 35, *c*. 27 and *c*. 26 m, respectively, were in a straight line and their landings were clumsy when compared with adults. The last fledgling's tail was fully developed on 2 December 2015, when it was last seen with both parents (Fig. 1B). The *tjwsee* and *tjwiit* contact calls given to dependent young ceased on day 25 when at least one fledgling was still present at the site.

At nest 2, two young were seen on day 17 and

three fledglings were seen at the eastern margin within 7 m of each other, and 80 m from the nest site, on day 20. The three young had tails that were half, two-thirds and almost fully developed. On discovery, each bird flew off in a different direction of *c*. 77 m, *c*. 37 m and >123 m, and then they either flew or walked back to the sites of initial detection. There, the fledglings were fed by adults coming in from the north and east outside of the field. On day

23 only one fledgling remained in the field. An adult flew directly to where the fledgling was located and fed it and later, when the fledgling had moved between visits, the adult circled the field calling for it. On day 24, during the hour before sunset, pipits were only seen at 1920 h when an adult and juvenile flew in from the north, landed near nest 2 and then departed 3 minutes later towards Limestone Island.

Predator interactions and pipit mortalities

Nestlings were lost from nest 3 at *c*. 4 days old and before any chick calling was heard. No remains were found on the nest that day and the nest was not damaged.

Cats were seen 15 times and pipits had six encounters with five different domestic cats during the 98 days of observations (mean 1 interaction per 4.5 h, n = 40.7 h), including three at locations where young pipits were fed. All encounters involved both adult pipits. The behaviour exhibited by the adult pipits indicated that they recognized cats as predators but that they did not utter any specific distress calls, like those used when harriers (n = 3)flyovers) were nearby. The pair initially remained motionless 1-2 m apart and 3-7 m from the cat before flying off. During one encounter within shrubland, where dependent young were nearby, the adults moved from the ground to perches above the cat giving *tiwsee* and *tzree* calls at a rate of >0.5 per second and enticed the cat to follow them from the site.

Nestlings were lost from nest 4 at seven days old, just after chick calling started. No remains were found on the nest and the nest was not damaged. The deceased adult female was found 2 m from the nest with a claw or beak puncture wound to the left pectoral muscle, and feathers missing from her abdomen, and tail. It is likely that the nestlings and both adults were lost at the same time as the male was never seen again. The cause of death was unknown. The most likely predator was a cat or a harrier but rats cannot be discounted. Hedgehogs and possums were unknown in the neighbourhood. The male may have just deserted the site as he did at the end of the previous breeding season.

DISCUSSION

Breeding biology differences

This study confirmed previous breeding phenology (Heather & Robertson 2015), that the habitat used by pipits for breeding was not used all year (Beauchamp 2013), and that the duration of the breeding season in New Zealand was similar to the 104 days recorded in alpine Australia (Norment & Green 2004). It also found that the nests constructed by the same pair in the same season were 42 and 40 m apart, which are consistent with the distances found in other studies (Higgins *et al.* 2006).

However, there were some differences as well. Some existing literature indicates that both sexes of the New Zealand pipit incubate (Wilkinson & Wilkinson 1952), but this is not consistent with the incubation behaviour in the genus Anthus, where only the female usually incubates (Tyler 2004). The female of the second pair in this study did the only nest building seen, and in all four nesting attempts females did all of the incubation and contributed an equal part to chick rearing. This study also found that the male was not near the nest or female during incubation after early morning and did not roost near the nest most evenings. The male's role appeared to be defence of the female before nesting, and defence and feeding of the young post-hatching (Beauchamp 2009, 2013). This differs from other studies of New Zealand pipit which suggest that the male is present all the time, and especially when there are threats to occupancy of that site or for the female from other pipits (McEvey 1949; Beauchamp 2002, 2013). These differences in sex-based roles during breeding may explain why one male could apparently defend two concurrent nesting females with nests situated 9 m apart in alpine areas of Australia (Norment & Green 2004). It would be quite easy for a male to defend two nearby nesting females if the females did all of the nest building and incubation and could do most of the chick feeding.

It is very likely that the male of both pairings in this study was the same as the pairs used exactly the same roadside areas despite there being considerably more habitat that could have been used. The sites used by the pairs included areas of the roadside which were outside of the field and not all that obvious as pipit habitat. The male also moved each season to and from sites to the north, the exact location of which could not be established. It is therefore likely that the male roamed over and defended a large area, and that the female only used a portion of that area (the urban field) for breeding.

It is possible that the widening and cutting of the grass tracks and the mowing of a former dump site in mid-2015 made the site more suitable for pipit foraging and nesting. The habitat created at Onerahi was similar to that in nearby grazed farmland, and which in Northland frequently has rank grassed road verges (Beauchamp 2007, 2013).

The field was mowed between the first and second seasons, but the dense kikuyu and watsonia were available in both seasons and low gorse and aristea vegetation replaced tall gorse in the second season. The weather and climate conditions were similar each year and there were no climatic reasons why in one season the nests would have been laid in the long grass and the other in low open gorse. The main difference was the female partner and it appears that in 2015 the first female chose to use dense grassland for her two nests, while in 2016 the second female chose open low gorse habitats for her two nests. The male did not appear to know where nest 4 was situated during the hatching period and this suggests that the nest location and habitat were likely chosen by the female. Unlike water pipits, the male partner did not feed the female while she was incubating (Rauter & Reyer 1997).

Habitat, parent-chick calling and breeding success

At Onerahi the successful nest sites were in denser habitat, and the young pipits remained concealed in a complex habitat for *c*. 16 days. Fledglings were only seen when they could fly. The adults accompanied the young when they moved due to my disturbance; however, when young were disturbed while the adults were absent the young birds returned to their former sites. Consequently, high circular flights over the site to find young were rare, and the chick "*zhep*" calls frequently given by dispersed and half-tail developed pipits at Mangawhai on 31 October 2004 (Beauchamp 2007) was heard only once at Onerahi.

This study found that pairs used differential call rates to indicate the proximity of a threat to the nestlings. I reassessed calling rates from cassette tapes I recorded at Ormiston Road in 2001 to see whether similar call rate differences were evident (Beauchamp 2013). These differences existed, so I searched Ormiston Road on 25 February 2016 and located a nest and group of fledglings using the *tjwsee* calling and call rate as indicators of nest proximity. In hindsight, I concluded that adults were more reluctant to divulge the location of nests with young than I had previously assumed during work on Ormiston Road (Beauchamp 2013), and I needed to be >20 m away from, and out of direct view of the nest site before adults would visit nests.

Nesting success

The call rates at Onerahi, which were verified at Ormiston Road, suggest that adult pipits are capable of communicating warnings to their young at very densely vegetated nest sites, and that nestlings can emerge later and are better developed for flight in these sites. The extra protection offered by dense grassland could potentially lessen the risk of predation after leaving the nest and before leaving the natal area (Beauchamp 2007, 2013). The limited data collected during this study suggests that selection pressure at the nest may be acting against female pipits that build nests in open sites, and favour those nesting in very dense grassland. Consequently, the mainland pipit populations may be more likely to be located in areas where there are dense grassland nest sites including the road verges and forestry margins in places like Northland. During droughts, when the roadsides are grazed, or when roadside areas are mown, safe nesting sites may well be removed. This loss of nesting habitat alone may explain the loss of pipits in areas of the East Cape and the lack of pipits in the Waikato (Robertson *et al.* 2007).

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SHORT NOTE

Long-lived variable oystercatchers (Haematopus unicolor)

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The variable oystercatcher (*Haematopus unicolor*, VOC) is an endemic species found around much of the coastline of New Zealand (Dowding 2014). The population was estimated at about 2,000 birds in the early 1970s (Baker 1973), but has increased rapidly since then, and more recent estimates are in the range 5,000–7,000 individuals (Bell 2010; Dowding 2017). Under the New Zealand Threat Ranking Scheme, the species is currently ranked At Risk (Recovering) (Robertson *et al.* 2017); under IUCN criteria, it is ranked Least Concern (BirdLife International 2019).

Many oystercatcher species are long-lived (Ens & Underhill 2014). We record here a number of VOCs that have exceeded 30 years of age, including one recently seen alive at more than 37 years, and compare this to maximum ages recorded for other oystercatcher taxa.

During his study of the species in the 1970s, Allan Baker banded a number of birds at Waipu Estuary, North Auckland (35.99395°S, 174.48338°E). In the 1990s, some of these were re-captured and re-banded with new colour combinations by JED. Seven birds in this group were of known age, and five of them subsequently reached 31 years or more (Table 1).

Received 26 June 2019; accepted 20 August 2019 *Correspondence: *Emily.Roberts@trc.govt.nz* An individual that is older than any of the birds listed in Table 1 has recently been sighted. On 27 April 2019, ECR read the metal band number (K-7446) from photographs of a VOC foraging on the south side of the Mokau Estuary (38.70130°S, 174.62231°E), on the Waikato-Taranaki boundary. She had seen what was almost certainly the same bird at the same location on 19 November 2017, but the complete band number was not read on that occasion. K-7446 was banded by Ray Benfell as a chick on Somes Island, Wellington Harbour (41.25760°S, 174.86548°E) on 2 January 1982. At the time of the 2019 sighting, the bird was therefore 37 years 4 months of age. The straight-line distance between the banding site and the 2019 sighting is ~285 km.

In 2004, Barry Hartley reported this bird to the Banding Office as "seen since February 1998 at Mokau and the metal band number recorded on 23 January 2004". VOCs typically first breed at about 5 years old (Dowding 2014); as K-7446 was 16 years old in 1998, Mokau may not have been its first breeding site. The 2004 sighting was about 2.4 km north of the 2017 and 2019 sightings.

The bird was not captured in 2019, so it was not possible to examine the band closely, but it appeared from photographs to be in good condition (see <u>https://inaturalist.nz/observations/23328562</u>). The entire inscription was legible, and there was no

Original band	Date banded	Age	New bands	Date re-banded	Last sighting	Age at last sighting
K-3343	15 Jan 1970	Р	K-5286 KOG	25 Nov 1994	Nov 2002	32y 10m
K-3395	12 Apr 1970	J	K-10750 KYB	20 Oct1999	Oct 2004	34y 7m
K-4636	3 Jan 1971	Р	K-10768 WKW	18 Dec 1999	Nov 2004	33y 11m
K-4644	7 Jan 1971	Р	K-10740 YOW	8 Feb 1999	Jan 2003	32y 0m
K-2955	9 Jan 1979	Р	K-5297 YOG	23 Mar 1995	Feb 1996	17y 1m
K-2954	10 Jan 1979	Р	K-5346 GYK	6 Jan 1997	Feb 2002	23y 1m
K-2958	11 Jan 1979	Р	K-5285 GOG	25 Nov 1994	Jan 2010	31y 0m

Table 1. Age at last sighting of variable oystercatchers (*Haematopus unicolor*) of known age banded at Waipu in the 1970s and re-banded in the 1990s. P = pullus, J = juvenile (less than 1 year old).

evidence of callousing or other injury to the bird's foot. It is also evident from the photographs that the bird has a distinctive scattering of white feathers on its head and breast.

Many New Zealand bird species are known to be long-lived (e.g. Wilson 2004), and VOCs appear to be no exception. We believe K-7446 to be the oldest known oystercatcher of any of the three New Zealand species. The oldest South Island pied oystercatchers (H. finschi, SIPO) known were 21 years minimum (P.M. Sagar pers. comm.), but given the annual adult survival value for the species, some SIPO may be expected to live longer (Sagar & Veitch 2014). Two Chatham Island oystercatchers (H. chathamensis) have reached 30 years old; one was banded as an adult and reached 30 years minimum (Moore 2014), and one banded as a chick was last seen at age 30 years 0 months (Department of Conservation CIO database). Colour bands on New Zealand oystercatchers typically last about 12–15 years before wearing through and being lost (JED *pers. obs.*). Birds carrying a metal band only are more likely to be overlooked, so recapture and replacement of colour bands helps to determine maximum ages for these and other species that survive longer than a single set of colour bands.

The most numerous and well-studied oystercatcher globally is the Eurasian oystercatcher (*H. ostralegus*). The oldest known individual of that species reached 43 years 4 months, with the secondoldest 36 years 11 months (Fransson *et al.* 2017). The oldest American oystercatcher (H. palliatus) was at least 23 years 10 months (Lutmerding & Love 2017). In Australia, the oldest known pied oystercatcher (H. longirostris) was 32 years 2.3 months (Department of the Environment 2019a), and the oldest sooty oystercatcher (H. fuliginosus) was 25 years 6.7 months (Department of the Environment 2019b).

Based on the records we have found, K-7446 appears to be the oldest oystercatcher of any of the New Zealand species, and is possibly the second-

oldest oystercatcher of any species globally. It was alive when sighted in April 2019, and appears to have been site-faithful for many years, so it will be interesting to monitor its further survival.

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Keywords: Variable oystercatcher, oystercatchers, longevity, age record

SHORT NOTE

Evidence of late breeding of spotless crakes (*Porzana tabuensis*) at two North Island peat bog lakes

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Knowledge of breeding ecology and behaviours has important management implications for the conservation of any species. In particular, accurate knowledge of the timing and duration of the breeding season for native, threatened species is important as it often defines when and for how long conservation interventions should occur, and what those interventions should be. For example, predator control is often prioritised to occur when a native species is nesting and at its most vulnerable, particularly if that species nests on the ground or fledglings are known to be particularly vulnerable to predators. In contrast, habitat modifications that are often necessary but known to be intrusive (e.g. intensive weed control) should occur when native threatened species are not breeding.

The spotless crake (*Porzana tabuensis*) is a small, secretive, cryptic wetland bird from the Rallidae family. Spotless crakes are widespread from the Philippines to south-west Polynesia, including Australasia. Overall, the species is classed as least concern by the IUCN, but the New Zealand subspecies (pūweto, *Porzana tabuensis tabuensis*) is declining (Robertson *et al.* 2017; BirdLife International 2018). Spotless crakes are distributed erratically throughout the North Island of New Zealand, and rarely found in the South Island (Robertson *et al.* 2017; BirdLife International

2018). Ecological knowledge of the species and its behaviours is limited, with few published reports on the timing of breeding in spotless crakes in New Zealand. Hadden (1970) suggested that egg laying occurs between late-August and late-September, while Buddle (1941) proposed that egg laying occurs from October until early-December. The latter is supported by observations of spotless crake eggs being laid between mid-October and mid-December on Raoul Island (cited by Oliver 1955). Yet, Fraser (1972) reported 'newly hatched young' in early-September, and as late as late-January. The current study provides evidence that spotless crake breeding occurs into February, indicating a long breeding season for the species in New Zealand.

Ten fyke nets and ten box-cage traps were used to catch crakes at Lakes Ruatuna and Rotomanuka (37°55.631'S, 175°18.222'E), Waikato, between 15 February and 4 March 2017. Nets and traps were set on the surface of raupo (Typha orientalis) beds, or in the Carex tussock-lands. Birds that were caught were banded with metal D-bands with an internal diameter of 4.5 mm, then fitted with a BD2 Holohil® transmitter using a standard figure-8 legloop harness adapted for rail species (Rappole & Tipton 1991; Haramis & Kearns 2000). Transmitters weighed less than 3% of a bird's body weight (<1.1 g) and birds were subsequently followed for c. 5 weeks. The purpose of attaching transmitters to birds was to measure home range sizes of spotless crakes to inform wetland restoration efforts and

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allow better interpretation of monitoring data and management practices. The results of this aspect of the study are not the subject of this paper and are presented elsewhere (Williams 2017a; Williams 2017b). However, due to the intrusive nature of the work (i.e. handling and trapping birds), the project was purposefully timed to take place in February and March after the crake breeding season was expected to have finished.

A spotless crake pullus chick and an adult with a brood patch were caught in fyke nets in February. The chick was captured at Lake Rotomanuka on 21 February 2017 and followed until the battery of its radio-tag expired on 12 March 2017. The adult was captured at Lake Ruatuna on 28 February 2017 and had evidence of a brood patch. This crake was followed until the study ended on 31 March 2017, and during this time behavioural evidence suggested the bird may have been sharing brooding duties with its mate during the first eleven days of observations (28 February to 9 March 2017).

The wing feathers of the chick were not fully developed, and still had sheaths and emergent feathers <10 mm in length (Fig. 1a). The pink on the chick's bill only extended just beyond the nares (Fig. 1b) and had not reached the edge of the upper mandible, let alone spread to the lower mandible as would be expected with a chick more than 40 days old. Eye colour was olive-drab, and the head was covered in black down (Fig. 1b). However, the feathers of the crural tract had reached a stage where they were continuous with the ventral tract and were brownish grey in colour (Fig. 1c). This was consistent with Kaufmann (1988)'s description



Figure 1. a) A photo showing the developmental features of a spotless crake chick, caught at Lake Rotomanuka on 21 February 2017. This photo shows that the sheaths and emergent feathers of the wing were <10 mm respectively, indicating that the chick must be <40 days old; b) eye colour was olive-drab; the head was covered in black down; the pink on the bill had extended beyond the nares but still had not reached the edge of the upper mandible; c) and the feathers of the crural tract were brownish grey and appeared to be continuous with the ventral tract. These combined observations were most consistent with Kaufmann (1988)'s description of a 29-day old chick.

of a 29-day old chick. If the bird was older than 29 days, we would have expected the small pink patch on its black bill to have expanded beyond the nares and onto the lower mandible (Kaufmann 1988). Chicks older than 40 days would be expected to have an iris that had progressed beyond olivedrab to brownish-orange, and all feathers should at least have partially emerged, including those on the head and wings (Kaufmann 1988). The sheaths on the primary and secondary wing feathers would be expected to be 15-18 mm long, with emergent feathers 18–26 mm long (Kaufmann 1988). As these milestones were not yet apparent on the crake, but the eye colour and feather development were consistent with Kaufmann (1988)'s observations at 29 days, we estimate the chick to have been from 29–39 days old, most likely closer to the former rather than the latter age. Incubation times are reported to be between 20 and 22 days (Fitzgerald 2013), so extrapolating backwards from when the bird was caught on 21 February 2017, it is likely the clutch the bird came from was laid after 1 January, with hatching taking place in late-January (c. 23^{rd}). This is the second record of spotless crake chicks hatching in late-January (Fraser 1972). Most literature suggests that peak egg laying by spotless crakes occurs during September and November (Oliver 1955; Heather & Robertson 1996), and that laying also occurs between late-August and mid-December. Kaufmann & Lavers (1987) reported an earliest date of 30 August and a latest date of 19 December. The chick caught in the current study is likely to have hatched from an egg laid outside the previously reported range of laying dates.

There was also evidence of late breeding by the adult bird caught on 28 February 2017. In the hand, the bird had a noticeable brood-patch, although this was small with some feather regrowth around the edges. Additionally, for the first 11 days of radio-tracking the bird was stable in its territory and behaviour, spending the majority of monitored time either foraging or stationary in one particular location. For example, the bird spent 75.2% of the monitored time within an area <0.085 ha, and regularly remained stationary within this area for up to two hours at a time. This observation indicated that the bird was likely to have been brooding small chicks. In contrast, the tagged chick was constantly active across the full range of its territory (0.39 ha).

In support of the theory that the tagged adult was brooding, loud, periodic 'begging' calls were often heard while the bird was in the suspected nest area. Similarly, vocal exchanges (mostly soft 'books') were often heard at this location between the tagged adult and a second adult bird. These usually coincided with the arrival of our tagged adult at the suspected nest location or just prior to it leaving to forage. Searches of the suspected nest site during this time revealed three inactive nest platforms, hidden in *Carex* tussocks, fitting the description of a spotless crake brooder nest (Kaufmann & Lavers 1987). After 11 days, the tagged adult no longer visited the suspected nest site and instead began foraging in an area 0.26 ha in size that was 100 m north of its previous territory.

The observations of the chick and the adult caught in February 2017 indicate that spotless crake breeding can occur in February and that the breeding season for the species in New Zealand can extend for seven months from August to February. The stable territory, sounds of chick begging calls, and site-specific vocal patterns of the tagged adult bird suggest the bird was brooding young chicks in late-February. For this to have occurred, egg laying must have taken place at the end of January, a month later than any previous records. Furthermore, the chick caught in this study appeared likely to have hatched in late-January. Considering there have been few studies of spotless crake nests, it is possible that late breeding could be more frequent than previously thought, particularly in the Waikato region.

A long breeding season for spotless crakes is significant for wildlife managers for several reasons. It suggests that spotless crakes have the potential to produce multiple clutches within a single season and hence that crake populations might increase quickly in response to predator control and to habitat management interventions. The management of wetlands where crakes are present should take into account the long breeding season, with water levels and predator control maintained, and weed control avoided from August until the end of February.

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with Department of Conservation radio-tracking protocols (DOCDM-708212).

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Keywords: *Porzana tabuensis,* wetland, early breeding, radio transmitter

SHORT NOTE

Swamp harrier (*Circus approximans*) road-kills, 1962–2018, and the effect of rabbit density

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Brockie *et al.* (2009) review, in detail, road-kill data for mapping the spread of diseases, the impact on animal populations, and planning road sign placements that prevent deer collisions. Recently Collinson *et al.* (2014) proposed an international standardised protocol for comparing road-kill. However, their proposal requires a start at 90 minutes after dawn, making little allowance for methods required to assess different species of interest. For example, in a study of toads (*Bufo bufo*) in Wales, all 178 corpses were removed by scavengers within an hour of dawn (Slater 2002); following the protocol would therefore not identify much toad road-kill.

In New Zealand, road-kills offer a convenient way of mapping geographic ranges, e.g. wallabies around Rotorua and Waimate, and may sometimes be used to estimate relative abundance over time of animals large enough to be easily seen and identified. In this paper the aim was to look for longterm changes in swamp harrier (*Circus approximans*) abundance, and relate the distribution of carcases to that of rabbits (*Oryctolagus cuniculus*), one of their main food items (Baker-Gabb 1981; Seaton *et al.* 2013).

To develop a suitable counting technique many variables had to be considered: i) weather

(hedgehogs [Erinaceus europaeus] are attracted by rain, and common brushtail possums [Trichosurus *Vulpecula*] repelled), ii) traffic speed and intensity (heavy traffic kills more, but carcases do not last as long), iii) season (most populations peak in summer, hedgehogs hibernate in winter), iv) time of day (most birds are hit by day, mammals at night), v) size and colour (weasels [Mustela nivalis] are smaller than rats [*Rattus* spp.] but easier to see being brightly coloured), vi) scavengers (may eat on site, or remove bodies, by day or night), vii) attraction to dead conspecifics, viii) traffic avoidance behaviour (road-wise common starlings [Sturnus vulgaris] are rarely hit), ix) inexperience (most Australian magpies [*Gymnorhina tibicen*] are juveniles); and x) population dispersion (animals living in groups, like rabbits, show more variation in counts than do hares [*Lepus europaeus*], which are evenly spaced).

The best way of avoiding these problems was to accumulate long distance counts. For the mammals I was most interested in counting (i.e. possums, hedgehogs, rabbits, and hares, 4,000 km was chosen because counts over 2,000 km were giving repeatable results; for rarer species like mustelids far longer distances would be required. Comparing ratios (cars do not distinguish rabbits from hares, or stoats [*M. erminea*] from weasels) allows comparisons of relative density without the need to ensure every item of roadkill was identified.

During road-kill counts to measure changes

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in mammal abundance throughout New Zealand, 1962–2018 (Flux *et al.* in prep), birds were occasionally identified. This sub-set of counts is analysed here, hence the gaps 1971–1977 and 2003–2016 for the South Island when counts recorded only "birds" without listing species. Only the three-week count in February 2017 aimed to cover all South Island areas with as little overlap as possible, the 6,893 km total included practically all of the 4,500 km of State highway, and the rest 7% of 34,100 km designated "road" (Fig. 1). Birds were also identified on 2,398 km in 2018. For the North Island, harrier numbers were published by Brockie *et al.* (2009), and Sadleir & Linklater (2016).



Figure 1. Map of 6,893 km of State highways covered in February 2017 (shown in red with black edges), and roads (red). In 2018 only the Alexandra area, and east and west routes there from Picton, were covered (2,398 km). Yellow roads show the rabbit problem area; blue circles are dead harrier locations. Map used by permission of A. Smith, Critchlow Associates.

All counts were by the same observer, at random locations, preferably alone, while driving 150 m behind a slow truck, whenever viewing conditions were suitable, avoiding sun glare, rain, busy motorways and towns. Collinson *et al.* (2014) recommend a maximum speed of 20–50 km/h, but this would impede other traffic. Also, in New Zealand there are far fewer mammals to identify, and this can be done at the legal speed limit of 100 km/h. "Random" here means starting and ending at pre-determined points, not when an interesting

kill was seen or unusually high numbers were encountered. Hence, the only road-kill kiwi (*Apteryx australis*) seen, near National Park at a sign saying "Beware, kiwi crossing", was not included. Where possible the car was stopped to check doubtful identifications – a pile of feathers round a possum might be two harriers, not one (Fig. 2a).



Figure 2. A) Adult harrier flying in to share a possum with a young harrier. They made no attempt to pull it off the road, flying away from approaching cars. B & C) Blackbacked gull pulling rabbit off the road.

For the South Island, Table 1 shows no significant change in the overall number of harriers killed per 100 km since the 1960s (two-tailed Chi square test with Yates correction for each time period against the average, P > 0.0001). This agrees with their status as "no change" between the 1969–79 and 1999–2004 atlas surveys (Robertson *et al.* 2007). Note that road traffic, judged by the number of licensed vehicles, has increased from 0.6 million in 1963 to 4.2 million in 2017 with no apparent effect (Motor Industry Association 2019). The number of rabbits killed on roads has increased ten-fold since the 1980s when Rabbit Boards were disbanded (Flux 1997), which may have contributed to the slightly higher recent harrier totals in Table 1.

Years	Number of harriers	Distance covered (km)	Harriers per 100 km	Significance	Chi square P value
1962–1970	5	1,025	0.49	NS	0.96
1978–1989	24	6,270	0.38	NS	0.28
1990-2002	17	3,192	0.53	NS	0.92
2017-2018	53	9,291	0.58	NS	0.32

Table 1. Stability in numbers of harriers killed per 100 km on South Island roads over four time zones, 1962–2018.

However, significantly (two-tail Chi square test with Yates' correction, P < 0.0001) higher numbers of harriers were killed in the rabbit problem area (Central Otago, and Pukaki to Fairlie) than in the rest of the South Island (Table 2). Curiously, this difference holds for possums (P < 0.0001) despite

the lack of trees. Even hares are more abundant (P = 0.006). Since hares are dominated by rabbits and compete with them for food (Flux 2008), I had expected fewer hares in the rabbit problem area, not more.

Table 2. Road-kills of harriers, rabbits, hares, and common brushtail possums per 100 km in the rabbit problem area (Central Otago, and Pukaki to Fairlie) are significantly higher than in the rest of the South Island, 2017–18, but not in proportion to the 20-fold higher rabbit numbers.

	Distance (km)	Harrier (n)	Rabbit (n)	Possum (n)	Hare (n)
Rabbit area	806	1.86 (15)	95.78 (727)	31.51 (254)	2.23 (18)
Rest of South Island	8,485	0.45 (38)	4.74 (412)	6.65 (565)	1.19 (101)

From the 2007 Atlas (Robertson *et al.* 2007), Central Otago is not a favoured breeding area for harriers, despite the abundant road-kill food available. They appear to be transient or opportunist feeders. As juvenile harriers disperse widely, and would find road-kills easy pickings, there may be proportionately more killed in Central Otago, but unfortunately age ratios were not recorded. Table 3 compares harrier counts in the North Island with those of Brockie *et al.* (2009), and Sadleir & Linklater (2016). They show reasonably similar results within the range 0.18 to 0.27 harriers/100 km, apart from one high of 0.78 in 1994. In this year Brockie *et al.* (2009) record more than three times as many possums killed, and they may have attracted harriers.

Table 3. Comparison of harrier road-kill counts in the North Island with those published by Brockie *et al.* (2009) and Sadleir & Linklater (2016).

	Distance (km)	Number of harriers	Harriers/100 km
Flux (1970–1990)	2,649	7	0.26
Flux (1991–1994)	3,005	8	0.27
Flux (1995–2016)	1,353	3	0.22
Brockie (1984)	1,660	3	0.18
Brockie (1994)	1,660	13	0.78
Brockie (2005)	1,660	3	0.18
Sadleir (2016)	5,814	16	0.25

Harrier deaths on roads raise interesting questions: does the benefit of easily scavenged food outweigh the risk and thus increase the harrier (and native owl) populations; and are scavengers being selected to avoid cars, or to remove road-kills before eating them? Harriers lift animals off the road and eat them in nearby fields, but I have not seen harriers pulling carcases to the verge the way blackbacked gulls (*Larus dominicanus*) do (Fig. 2b,c). This behaviour may be innate, as gulls often pull dead fish ashore, and might explain their low position in the list of birds killed (Table 4) as they are common scavengers far inland (Miskelly 2013). It may seem counter-intuitive but, like cats at present (Flux 2017), road-kill may well promote biodiversity in New Zealand by killing more introduced pests than native species. **Table 4.** Complete list of birds recorded as road-kill for the South Island in 2017–18 (9,291 km).

Species	Number counted
Swamp harrier (Circus approximans)	53
Eurasian blackbird (Turdus merula)	31
Australian magpie (Gymnorhina tibicen)	29
Mallard (Anas platyrhynchos)	26
Pukeko (Porphyrio melanotus)	19
House sparrow (Passer domesticus)	10
Red-bill gull (Larus novaehollandiae)	5
Weka (Gallirallus australis)	5
Song thrush (Turdus philomelos)	5
Common starling (Sturnus vulgaris)	3
Silvereye (Zosterops lateralis)	3
Spur-winged plover (Vanellus miles)	2
Dunnock (Prunella modularis)	2
European goldfinch (Carduelis carduelis)	2
Morepork (Ninox novaeseelandiae)	2
Little owl (Athene noctua)	1
Paradise shelduck (Tadorna variegata)	1
Grey teal (Anas gracilis)	1
Pied stilt (Himantopus himantopus)	1
Welcome swallow (Hirundo neoxina)	1
Chaffinch (Fringilla coelebs)	1
European greenfinch (Carduelis chloris)	1
Yellowhammer (Emberiza citrinella)	1
Black-backed gull (Larus dominicanus)	1
unidentified "sparrow-size"	89
unidentified "blackbird-size"	14
TOTAL	309

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Keywords: harrier, *Circus approximans*, road-kills, rabbit, hare, possum, birds

SHORT NOTE

Earlier laying by little penguins (*Eudyptula minor*): a possible effect of global warming

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There is growing evidence that changes in the marine environment caused by global warming are affecting the timing and success of breeding, and juvenile survival of a range of seabird species (Chambers *et al.* 2011). While most little penguin (Eudyptula minor) populations are likely to be affected in time there are few detailed, long-term biological data sets available at present to show this. An increase in sea surface temperature (SST) is expected to have a positive effect on the little penguins on Phillip Island, SE Australia, with earlier and more productive breeding and greater survival of first year birds (Cullen et al. 2009; Dann & Chambers 2013). That trend is already noticeable in the little penguin (variant 'albosignata', hereafter referred to as white-flippered penguin) population on Banks Peninsula, Canterbury, New Zealand (CNC *pers. obs.*). This note describes the extent and timing of these changes in their breeding season based on an analysis of laying dates recorded during a long-term study.

The breeding biology of the white-flippered penguin has been studied since 1976 in a nest-boxed colony in Harris Bay on the north side of Godley Head (43.58°S, 172.79°E), east of Christchurch City. Initially the colony comprised 30–40 pairs but predators reduced it to a low of 10 pairs in 1988 (Challies 2015) after which it increased again to

around 30 pairs. During the study all nests were checked every 4–7 days and the presence of adults, eggs, and/or chicks recorded. This note is based on the dates the first egg in each clutch was laid. These were estimated from the number of eggs and the sex of the parent present when eggs were first seen in the nest. It is usual for the female to be absent from the nest for 2 days between laying the first and second eggs, while the male remains in the nest and takes the first incubation shift. Supplementary estimates were obtained by back-dating 37 days (the incubation period) from the day the first chick was estimated to have hatched.

The breeding season of white-flippered penguins extends from late-August to early-November with over 90% of clutches being laid in September and October. During the 42 seasons monitored (1976–2017) the laying periods ranged in length from 23 to 71 (mean 50.6) days with median dates between 2 September and 31 October (mean 3 October). Despite the wide seasonal variation, it was apparent from the scatter of median dates that the breeding seasons became progressively earlier over this period. A linear fit to these data supported this observation (days/seasons, b = -0.475; r = -0.456).

To quantify this shift in the timing of breeding the laying dates for groups of seasons were combined and treated as frequency distributions. Those for the first and last 12 seasons (1976–1987 & 2006–2017) were pooled separately to describe the

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extent of the trend. A comparison of the monthly frequencies (Table 1) shows an obvious shift in the main laying period from October to September with an extension of the season into August and a contraction in November. The mean date of laying became earlier by about 13 days during the 30 seasons between the mid-points of the subsets with laying starting up to 16 days earlier (Table 2).

Table 1. Monthly frequencies of the laying dates of white-flippered penguins for the 1976–1987 and 2006–2017 breeding seasons.

	1976-1987		2006-2017
Month	Ν	%	N %
August	1	0.3	19 5.5
September	106	30.2	196 56.6
October	211	60.1	123 35.6
November	33	9.4	8 2.3
Totals	351	100	346 100

Table 2. Means and ranges of the laying dates of white-flippered penguins for the 1976–1987 and 2006–2017 breeding seasons. *rounded to nearest day. **mean \pm standard deviation x 1.96.

		Laying dates*		
Seasons	Ν	Mean	95% range**	
1976–1987	351	9 Oct	9 Sep – 8 Nov (60 days)	
2006–2017	346	26 Sep	24 Aug – 29 Oct (66 days	

These data were further divided into 7 consecutive 6-season subsets to describe the general pattern of this change. A plot of the means (Fig. 1) shows laying became progressively earlier in a near linear fashion from around the early 1990s (b = $\frac{1}{2}$ -0.613; r = -0.936). The mean laying date for seasons 1976–1987, i.e. 9 October (Table 2), was assumed to be the level before the trend started. A later season would not give some adults enough time to rear chicks before moulting in February. Clutches were laid in early- to mid-November during 9 of the 12 seasons 1976–1987; they comprised 9.4% of the total (Table 1). This is effectively the end of the laying season for white-flippered penguins. The regression lines shown in Fig. 1 intersect at 1990, which suggests the shift to earlier laying started about then. Overall, laying became earlier by about 16.5 days between 1990 and 2017 at a linear rate equivalent to 0.6 days / season.



Figure 1. Trend in the timing of laying of white-flippered penguins during the 1976–2017 breeding seasons. Shown are the means with 95% confidence limits and sample sizes of consecutive 6-season subsets of laying dates. The horizontal line represents the mean laying date for the 12 seasons 1976–1987, and the diagonal line is the linear fit to the 4 means spanning the 24 seasons 1994–2017.

Breeding success improved during the shift to earlier laying with increases in both the proportion of pairs fledging 1 or 2 chicks, and in the proportion of these that fledged 2 chicks (CNC *unpubl. data*). This was reflected in the fledging rates for seasons 1976–1987 and 2006–2017 which averaged 1.12 and 1.33 chicks / 2-egg clutch respectively. It was not possible in this study to obtain comparable estimates of juvenile survival.

Without supporting data on the local marine environment and how the penguins use it, any discussion of the reasons for the earlier laying is speculative. The time of laying in non-migratory seabirds such as the white-flippered penguin is strongly influenced by the availability of their prev (Warham 1990). Little penguins feed predominately on small shoaling pelagic fish with the species taken varying seasonally and from year to year (Cullen et al. 1992; Fraser & Lalas 2004). It seems likely that the principal prey species of the penguins have become available to them in greater numbers progressively earlier in spring and that they have responded by breeding earlier. This is consistent with the widely reported poleward shift in the distribution of pelagic fish species commonly linked to global warming (e.g. Last et al 2010; McLeod et al. 2012).

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