# NOTORNIS

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## NOTORNIS

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## Post-translocation movements and ranging behaviour of roroa (great spotted kiwi, *Apteryx maxima*)

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**Abstract:** Translocations are increasingly used in kiwi (*Apteryx* spp.) conservation management, and their outcome is largely influenced by post-release dispersal and survival. A translocation of roroa (great spotted kiwi, *A. maxima*) to the Nina Valley, near Lake Summer Forest Park, is the first reintroduction of the Arthur's Pass roroa population. In 2015, eight wild-caught adults were translocated from Arthur's Pass National Park, following the release of ten captive-hatched subadults during 2011–13. We monitored the translocated kiwi by radio telemetry during 2015–17. Dispersal was highly variable among the released wild birds. The straight-line distance from the release site to the last recorded location ranged 0.5–10.3 km. Seven of the wild birds remained in the Nina Valley and covered an area up to 1,700 ha (95% utilisation distribution). Releasing the wild birds had no measurable impact on the ranging behaviour of previously released subadults. The current population founder group comprises a maximum of 13 unrelated individuals, and therefore further releases are necessary for a genetically viable population. Additionally, expansion of the pest-controlled area is crucial for the long-term persistence of the reintroduced population in the Nina Valley.

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Keywords: reintroduction, conservation translocation, translocation outcome, post-release effects, home range, dispersal, *Apteryx maxima*, *Apteryx haastii* 

#### INTRODUCTION

Kiwi (*Apteryx* spp.) are flightless ground-dwelling birds endemic to the three main islands of New Zealand, and most of them are threatened with extinction (Robertson *et al.* 2021). Roroa (great

spotted kiwi, *A. maxima*, previously known as *A. haastii*, Shepherd *et al.* 2021) is native to the north-western part of the South Island, New Zealand, with a range currently separated into four known subpopulations: i) Arthur's Pass, ii) Paparoa Range, iii) Westport, and iv) the north-west Nelson region. Roroa population size is estimated to have decreased from approximately 16,000 to 14,000

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individuals during 2008–2018, and is likely still declining (Holzapfel *et al.* 2008; Germano *et al.* 2018). Until recently, much of the extant roroa population received little or no regular management for invasive predators, which are considered the primary driver of population decline (Innes *et al.* 2015). Consequently, roroa conservation status is 'Nationally Vulnerable' (Robertson *et al.* 2021).

Several management actions have been adopted to address the ongoing kiwi population decline and reduce the threat of extinction. Kiwi conservation management focuses mostly on either suppression or elimination of invasive predators, i.e. mustelids (Mustelidae), common brushtail possum (Trichosurus vulvecula), and feral cats (Felis catus), mainly through trapping and poisoning using aerial 1080 (sodium fluoroacetate); and advocacy and avoidance training to mitigate predation by dogs (Canis familiaris) (Robertson et al. 2011). Another management regime involves head-starting chicks under the Operation Nest Egg (ONE) programme. This approach consists of removing eggs from the wild, hatching them in captive facilities, and keeping the young kiwi in a predator-free environment until they reach a size at which they can fend off stoats (Mustela erminea), their main predator, before they are released back to the wild (Colbourne et al. 2005; Gillies & McClellan 2013). Subadults from the ONE programme are either returned to their source population or released elsewhere to establish or reinforce an existing kiwi population.

Kiwitranslocations have become an increasingly popular tool in the conservation management of all kiwi species (Miskelly & Powlesland 2013; Jahn et al. 2022a). To date, translocations have played a relatively minor role in roroa management compared to the other kiwi species. Roroa transfers involve mainly wild-caught birds, whereas releases of ONE subadults dominate in North Island brown kiwi (A. mantelli), rowi (A. rowi), and tokoeka (A. australis) management (Jahn et al. 2022a). The first documented translocation of roroa was a 1915 release of 19 birds onto Te Hauturuo-Toi/Little Barrier Island, but despite initial population establishment, this introduction failed, likely within 15 years post-release (Oliver 1955; Colbourne 2005). There were no other attempts to establish new populations until the 21<sup>st</sup> century. Wild-caught roroa from the north-west Nelson and Westport populations were reintroduced in 2004 to Lake Rotoiti, Nelson Lakes National Park, and in 2010 to the Flora Valley, Kahurangi National Park (Gasson 2005; Toy & Toy 2020). Following these initial efforts, ONE subadults from the Arthur's Pass population were reintroduced in 2011 to the Nina Valley. The Nina Valley is part in Lake Sumner Forest Park, Conservation Area Nina Doubtful Rivers, and Lewis Pass Scenic Reserve.

The Nina Valley reintroduction project was similar to the Rotoiti and Flora translocations focusing on ecosystem restoration and being driven by attempts to restore the former species distribution (Holzapfel et al. 2008; Hulsman et al. 2010; Morrison & Yong 2014). The project was initiated by the Hurunui College Nina Valley Restoration Group in co-operation with the Department of Conservation (DOC). During 2011–13, ten ONE subadults initially sourced as eggs taken from the Hawdon Valley, Arthur's Pass National Park, were released to the Nina Valley to re-establish a roroa population. Subsequently, eight wild-caught adults from the Hawdon Valley were translocated to the Nina Valley in April 2015 to expand the initial founder group. The birds were released at several sites in the central part of the Nina Valley, within the 1,600 ha trapped area that stretches alongside the Nina River.

The Nina translocation was the first – and to-date only - roroa reintroduction within the Arthur's Pass population. Therefore, it was vital to monitor the birds' post-release behaviour, to inform the planning of future releases, and provide information for potential management interventions. Lessons on post-release dispersal and territory establishment were available from Lake Rotoiti (Gasson 2005) and intensive monitoring was underway in the Flora Valley (Toy & Toy 2020), but it was not clear if the same behaviours would occur in the genetically distinct Arthur's Pass population (Taylor et al. 2021). We intensively monitored the translocated population in the Nina Valley to understand the released birds' dispersal pattern and identify where and when they established home ranges. Based on these data, and monitoring data from the source population in the Hawdon Valley prior to this translocation, we were able to address the following research questions: i) What were the dispersal paths and distances moved of wildcaught adult roroa following the translocation? ii) What were the changes in the home range size of adults before-and-after the translocation? iii) Were there any changes to the ranging behaviour of the previously translocated ONE subadults following the release of wild-caught adults into the same general area?

#### METHODS

#### Study areas

The translocation of roroa was carried out from the Hawdon Valley (42°57′S, 171°45′E), Arthur's Pass National Park, to the Nina Valley (42°28′S, 172°19′E) near Lake Sumner Forest Park. Both valleys are within the historical range of roroa (Taylor *et al.* 2021). They are 70 km apart, east of the main divide near Arthur's Pass and Lewis Pass, respectively, indicating similar climate characteristics. The floor

of the Hawdon Valley lies at 570–780 m a.s.l. and is surrounded by mountain peaks 1,400–1,930 m a.s.l. The floor of the Nina Valley lies at 610–860 m a.s.l. and is surrounded by mountains 1,500–1,780 m a.s.l. River terraces and steep slopes in both valleys are covered by native montane beech forest until the bush line at about 1,300 m. The dominant tree species are mountain beech (*Fuscospora cliffortioides*), silver beech (*Lophozonia menziesii*), with red beech (*F. fusca*) at lower altitudes (Read & O'Donnell 1987; Blakely *et al.* 2008).

#### Translocation and monitoring

Eight wild-caught birds, four male and four female, were translocated to the Nina Valley in April 2015. These birds were part of a roroa monitoring programme in the Hawdon Valley for up to five years before the translocation. All were of unknown age but were confirmed to be breeding pairs by radio telemetry monitoring. The birds were tracked, captured, and transported to the Nina Valley according to best practice guidance (Morrison & Yong 2014). The pairs were placed in pre-determined release burrows 800-900 m apart (closer only if separated by the Nina River), outside of known roroa territories, to mimic natural territorial structure. One pair was placed together in one large burrow while three other pairs had males and females placed in separate nearby burrows to allow paired individuals to stay in close contact. Burrow entrances were blocked for the rest of the day to encourage birds to remain sheltered and calm. The entrances were unblocked one hour after sunset, and the birds were allowed to move freely. A similar approach had been previously adopted for the release of ten unpaired subadult ONE birds during 2011–13. The average age of these roroa at release was 1.1 years (range 0.9–1.3 years). They were released in January 2011 (2), February 2011 (3), February 2012 (3), and January 2013 (2). In these instances, the 2–3 subadults were placed together in one large release burrow.

After the 2015 translocation, we monitored all eight translocated wild-caught birds and four kiwi previously released as ONE subadults using ground-based radio telemetry. The remaining ONE birds were not monitored because they had either dropped their transmitters before 2015 (4), died soon after the release – likely drowned (1), or occupied remote areas of the Nina Valley (1), which prevented regular monitoring. However, we included location data for one unmonitored ONE bird that was incidentally captured and paired with a monitored ONE bird. All the monitored birds were fitted with leg-mount diagnostic transmitters designed for roroa (Sirtrack V2.0 GSK, <2% of the body weight, 142-174 MHz) before the 2015 translocation transfer, and then for up to two years following the release. The transmitters allowed us to locate each bird for health checks and transmitter changes, or to remotely triangulate bird locations (Neill & Jansen 2014). To triangulate the birds, we recorded the bearing of the signal multiple times from several (>3) points to achieve at least a 90° overall angle between the bearings (Kenward 2001). Subsequently, we estimated the locations of monitored kiwi from a series of intercepting bearings using triangulation software Locate 3.34 (Pacer Computing).

Monitoring intensity differed throughout the monitoring period. In the first week after the release of the wild-caught adults, we aimed to triangulate all the birds every day. In the following month, we attempted to triangulate the birds at least once a week, and subsequently, the frequency of checks decreased to once every two weeks. After five months post-release, we attempted to triangulate the birds at least once every 2–3 weeks and after 18 months every 4–6 weeks. Locations of the roroa in the Hawdon Valley were triangulated fortnightly during the three months before the translocation. Locations of the four ONE birds in the Nina Valley were also triangulated for three months before the introduction of additional birds. As site visits were generally multi-day trips, we attempted to triangulate the birds on each day, when practicable. Both triangulation and close approach (homing) took place during the day to locate nocturnal kiwi at their daytime shelters. Daytime triangulation provided ample time for a single surveyor to obtain multiple bearings while a kiwi is stationary at its daytime shelter. This approach generally reduced large location error when attempting to triangulate a moving animal, compared to more accurate GPS tracking (Guthrie et al. 2011). To measure triangulation accuracy, we estimated the location error from a beacon test carried out by placing a transmitter underground at a known location in the birds habitat and then triangulating it multiple times (Millspaugh & Marzluff 2001). We estimated the location error of triangulated location fixes at 42.0 m ( $\pm$ 7.1 SE, n = 8) with the mean distance between the observer's location and the beacon 201 m (26.4 SD).

#### Data analysis

The home range and dispersal path estimations were based on the analysis of daytime location fixes, similarly to other roroa studies (Jahn *et al.* 2013; Toy & Toy 2020). Most of the location fixes used in the analysis (76%) were obtained through triangulation. Additionally, we supplemented the triangulation data with locations from kiwi recaptures and transmitter retrievals, done by DOC staff or contractors.

To estimate the dispersal path of the

translocated birds, we constructed a smoothed line between the release site and the last known location for each bird by calculating a rolling average of up to nine consecutive location fixes. We chose to use nine fixes because this was the overall number of location fixes for the bird with the shortest duration of post-release monitoring. Additionally, we calculated the straight-line distance between the release site and the last known location for each bird to supplement the information on the dispersal path length. To identify the area most likely crossed by each bird during post-release dispersal, we analysed their utilisation distribution (UD) based on the movement path using R 4.0.3 (R Core Team 2020) and the package 'move' 4.0.6 (Kranstauber et al. 2020). To construct the UD, we used the dynamic Brownian bridge movement model suited for irregular sampling because it incorporates the Brownian motion variance, location fixes timestamps, and the location error (Kranstauber et al. 2012). We used the data collected after the 2015 translocation to estimate the dispersal path and the UD for all the translocated wild-caught adults and four ONE birds that were released during 2011–12 (none of the birds released in 2013 were actively monitored). Lastly, we tested whether the UD size of the translocated adults was larger than that of the resident ONE birds. We used a Mann-Whitney *U* test, and we repeated this method in the following tests.

To identify possible changes in the home range size resulting from the translocation, we compared the home ranges of the adults in the Hawdon Valley before the translocation and after the translocation in the Nina Valley. Given that several birds moved substantially in the first six months post-release, we excluded this period from the home range estimation. We used location (homing) data obtained from DOC from up to five years before the translocation (3.1 years on average) to supplement the triangulation data collected during the three months immediately before the transfer. The longer monitoring period before the translocation compensated for infrequent location fixes and was not expected to substantially increase home range estimates due to a high population density and stable territorial structure of roroa in the Hawdon Valley. Because the data had substantial time gaps, we did not use the dynamic Brownian bridge movement model due to a large uncertainty of the movement paths between the consecutive location fixes. Therefore, we constructed minimum convex polygons (MCP) to estimate home range sizes, similar to other roroa studies (Keye et al. 2011; Jahn et al. 2013; Toy & Toy 2020). We used the R package 'splancs' 2.1.42 (Rowlingson & Diggle 2021) to calculate the size of MCP based on all location fixes and 'ggmap' 3.0.0 (Kahle & Wickham 2013) to map both MCP and UD. To inspect if the home range of translocated birds had become stable or kept shifting, we carried out an incremental area analysis with the R package 'adehabitatHR' 0.4.19 (Calenge 2006). Subsequently, we tested whether the MCP home range size of the wild adults increased due to the translocation.

To assess possible impacts of the wild birds' translocation on the ranging behaviour of the previously released ONE birds, we examined their home ranges in the two years before-andafter the release of the wild adults. Three of the four ONE birds were released to the Nina Valley in 2011, the fourth individual in 2012, so the two vear pre-release period started after the birds had been in the Nina for 26 and 14 months respectively. We assumed that this was sufficient time for the ONE birds to settle and establish stable home ranges, despite their transitioning from subadult to adult life stages during the monitoring period (Colbourne *et al.* 2020). To investigate if the home ranges of the ONE birds shifted following the release of the wild adults, we carried out an overlap analysis of their MCPs using the R package 'splancs' 2.1.42 (Rowlingson & Diggle 2021). We included ONE bird location fixes from two years pre- and 0.5–2 years post-translocation of the wild adults, including location data (homing) obtained from DOC. We excluded the six months period after the wild bird's translocation from the MCP comparison to focus on the long-term effects of the wild bird's introduction as the immediate effects were captured in the previous UD analysis. Additionally, we tested whether there was a difference in the MCP home range sizes between the two periods.

#### RESULTS

#### Dispersal path and utilisation distribution

All but one of the eight released wild adults stayed in the Nina Valley during the post-translocation monitoring (Fig. 1). The only bird known to have left the valley (male 'wild 3') was still within approximately one kilometre of the release site two weeks post-release but could not be detected afterwards. Eight weeks later, it was found dead, hit by a car, more than 10 km from the previous last known location in the Nina Valley. Another bird (male 'wild 2') was not detected from 11 months post-release after being reliably found in a defined area for eight months. We could not detect the transmitter's signal despite repeated searches over several months within and outside the Nina Valley, including an aircraft telemetry search of the nearby valleys. However, we assumed that the bird likely survived and stayed, but its transmitter failed. This was based on repeated male calls recorded in its presumed territory 17–20 months post-release and nightly activity pattern indicating possible incubation by its mate, female 'wild 2' (PJ & LM *unpubl. data*). Attempts were made to recapture male 'wild 2' during transmitter checks of female 'wild 2', but no male roroa was found.

We aimed to monitor all the wild-caught adults for at least two years post-release but we achieved this with only three birds translocated in 2015 (Table 1). Two birds dropped their transmitters at approximately one year post-release and could not be found for transmitter re-attachment. The DOC staff and contractors could not recapture another bird for a transmitter change despite several attempts one year after the translocation, so we monitored it until the transmitter battery died 1.5 years post-release. The remaining two birds either dispersed and died or were not able to be detected



**Figure 1.** Utilisation distributions (UD) and dispersal paths of (a) wild-caught roroa (great spotted kiwi, *A. maxima*) translocated in 2015 and (b) roroa from the Operation Nest Egg (ONE) released during 2011–13 in the Nina Valley. The maps display release sites (grey circles) of the birds translocated on 16 April 2015 (pairs 'wild 2–4') and 23 April 2015 (pair 'wild 1'). The coloured dots show the location fixes of the birds following the 2015 translocation until May 2017. Solid lines connect each bird's first and last point during this monitoring period and represent the rolling average of up to nine consecutive location fixes. The coloured polygons display 95% UD for each bird except for male 'ONE 1', which was not actively monitored, so we did not have a sufficient number of location fixes for the UD calculation. The last location of male 'wild 3' is not shown as it left the Nina Valley after at least two weeks and dispersed within ten weeks post-release 10.3 km north-west from the release site.

Table 1. Estimated dispersal path, distance, and size of utilisation distribution (UD) of the translocated wild-caught
roroa (great spotted kiwi, A. maxima) and previously released Operation Nest Egg (ONE) roroa in the Nina Valley.
The number of location fixes and monitoring length include only the period following the 2015 translocation of the
wild-caught birds. Mean dispersal speed is based on the estimated dispersal path. The 75% and 95% UD represent an
area where the individual would be located with the specified probability during the monitoring period.

pair	sex	dispersal path (m)	straight distance (m)	# location fixes	monitoring length (days)	dispersal speed (m/day)	75% UD (ha)	95% UD (ha)
	М	2,844	463	35	728	4	71	213
wild I	F	2,985	1,079	39	746	4	91	204
wild 2	М	4,999	2,968	31	325	15	519	1,692
	F	7,046	1,660	44	736	10	433	1,459
wild 3	М	10,929	10,304	9	71	154	55	125
	F	5,824	5,552	20	346	17	141	420
wild 4	М	4,857	1,888	28	362	13	279	645
	F	3,614	1,514	33	554	7	555	1,653
ONE 1	F	629	62	15	718	1	9	36
ONE 2	М	2,951	475	40	749	4	56	172
	F	2,550	274	35	749	3	62	183
ONE 3	М	2,533	514	21	749	3	101	240

due to likely transmitter failure, as mentioned above. In contrast, we managed to monitor all four ONE birds for the two years following the 2015 translocation.

Although the seven surviving wild birds appeared to settle within the project area, only two (pair 'wild 1') settled in the proximity of their release site and stayed during the monitoring period. The length of their dispersal path was similar to the path length of three previously released ONE birds, that had been in the valley for more than four years at the time of the wild adults' release (Table 1). The remaining five birds moved widely around the valley without any clear pattern. In most cases, the dispersal path changed direction several times before home ranges started to stabilise after approximately six months. Three of the four translocated pairs separated during the first four months. However, two reunited within the six months post-release in new areas, after being in different parts of the valley (>2 km apart) between approximately 1–3.5 months and crossing the Nina River repeatedly. The last pair ('wild 3') parted within two weeks post-release, headed in nearly opposite directions (Fig. 1), and the male later died outside the Nina Valley.

During the post-translocation monitoring period, the mean dispersal speed and the size of the utilisation distribution (UD) were highly variable among the released wild-caught birds (Table 1; Fig. 1). Both the core 75% UD and broader 95% UD were significantly larger among the newly released wild-caught birds compared to the resident ONE birds (P = 0.036, Mann-Whitney U test). The larger UD of the wild birds was consistent with their longer dispersal paths and straight-line distance between the first and last known locations, despite a 35% shorter average monitoring period compared to the ONE birds.

#### Home range size before and after translocation

After six months post-release, the translocated wild birds appeared to be restricted to more defined areas, indicating stabilisation of their home ranges. The home range area (100% MCP, Fig. 2) kept incrementally increasing and appeared to reach an asymptote only in the three translocated wild birds that were monitored for the entire two years postrelease. They had >22 location fixes per bird in the period 0.5–2 years post-release. The home range of the four surviving wild birds was still increasing at the end of their monitoring periods, which lasted 0.9–1.5 years, resulting in a lower number of location fixes (<15). Similar to the three wild birds, home ranges of three of four resident ONE birds reached an asymptote within the two year monitoring period. In contrast, the home range of the last bird (male 'ONE 3') continued to gradually increase even after two years.

The MCP home range size varied substantially among the monitored individuals (Fig. 3). The mean home range size of the translocated wild adults was 76.34 ha ( $\pm$ 11.16 *SE*), significantly larger



**Figure 2.** Minimum convex polygons (100% MCP) and location fixes of the monitored ONE and wild-caught roroa (great spotted kiwi, *A. maxima*) in the Nina Valley after six months from the 2015 translocation (mid-October 2015 – May 2017). This monitoring period ranged among individual birds between 5–19 months. An MCP was not possible to construct for an unmonitored ONE male with a single recorded location.

(P = 0.036, Mann–Whitney U test) than the home range size of the resident ONE birds at 37.31 ha (±13.93 *SE*). The mean home range size of the wild adults increased from that in the Hawdon Valley (54.39 ha ± 5.13 *SE*), but this increase was not significant (P = 0.055, paired Mann–Whitney U test).

## Home range stability of the previously released ONE birds

The ONE birds that were released 3–4 years before the 2015 translocation did not show any clear signs of changing their ranging behaviour following the release of wild adults. This was despite several translocated individuals moving through the ONE birds' territories (Fig. 1). Particularly, the ONE birds in known pairs ('ONE 1' and 'ONE 2') showed generally lower UD and MCP home ranges (Table 1; Fig. 3), indicating higher site fidelity. There was no major shift in the MCP home ranges of the resident ONE birds following the wild birds' translocation. Between the two monitoring periods, their MCPs had a mean overlap of 39.7% ( $\pm 6.8$  SE). Also, there was no significant difference in the MCP home range size of the ONE birds before-and-after the release of the wild adults, excluding the 6-months

post-release period (P = 0.625, paired Mann–Whitney *U* test).

#### DISCUSSION

#### Post-translocation dispersal

Dispersal of released animals plays a critical role in translocation outcomes (Richardson *et al.* 2015) and is often reported as one of the main issues encountered by various translocation projects (Brichieri-Colombi & Moehrenschlager 2016; Berger-Tal *et al.* 2019). Kiwi translocations to unfenced mainland sites also contend with dispersal outside the project area, particularly from small reserves under 3,000 ha, although this issue occurs in reserves of any area size (Jahn *et al.* 2022a). Indeed, post-release dispersal appeared to be one of the main factors contributing to the failure of several previously reintroduced kiwi populations (MacMillan 1990; Colbourne & Robertson 2000).

In the Nina Valley, only one released bird was observed to disperse outside the project area, and travelled more than 10 km from its release site within ten weeks of translocation. It is unknown if the bird was settling in this remote area or was continuing to disperse because no information was available on its dispersal path between the Nina Valley and the location where it was eventually struck by a car. The remaining seven translocated wild-caught adults stayed within the valley. However, three were monitored for just under one year due to either dropped transmitters or probable transmitter failure, so longer-term



**Figure 3.** Comparison of 100% minimum convex polygon sizes representing home ranges of the monitored roroa (great spotted kiwi, *A. maxima*) before-and-after the 2015 translocation from the Hawdon Valley to the Nina Valley. The post-translocation period excludes the first six months post-release, in which the birds showed increased movements. The birds are grouped into pairs based on their origin – the Operation Nest Egg (ONE) birds released in the Nina Valley during 2011–13 and wild-caught birds translocated in 2015.

movements remain uncertain. Post-translocation monitoring of the ten previously released ONE subadults did not indicate dispersal outside the Nina Valley either (S Yong, DOC, *unpubl. data*). Our monitoring and bird recaptures in the Nina Valley confirmed the survival of two ONE birds for 4.2 years, one for 5.2 years, and three birds for at least 6.2 years post-release.

The absence of a clear dispersal pattern among translocated birds post-release is similar to other roroa reintroduction projects. Translocated roroa both at Lake Rotoiti (Gasson 2005) and in the Flora Valley project areas (Toy & Toy 2020) displayed high variability in overall dispersal distance and dispersal period before settling to stable home ranges. Interestingly, both projects observed shorter dispersal periods and distance in established translocated pairs that stayed together than those individuals who either re-paired or were translocated without a mate. Such behaviour is consistent with the observed dispersal in the Nina Valley, where the only pair that did not separate ('wild 1') showed the shortest dispersal path, distance, and lowest dispersal speed and UD, a pattern of behaviour similar to the resident ONE birds with established territories (Table 1). In contrast, pairs that separated, temporarily or permanently, moved around substantially more before settling down. Pair 'wild 1' was the only pair in the Nina placed in the release burrow together, while individuals from the other pairs were placed approximately 20 m apart, but this factor did not seem to play a role for pair bond survival at Lake Rotoiti or the Flora Valley.

The straight-line dispersal distance was the highest in the pair that separated soon after release ('wild 3') and the individuals headed in near-opposite directions (Fig. 1; Table 1). Only one, the female dispersing over 5.5 km upstream, likely remained in the valley, at least during the monitoring period. Pairs 'wild 2' and 'wild 4' also had long dispersal paths, but repeatedly changed direction resulting in larger UDs, although still within the Nina Valley. Large dispersal distances up to 10 km from the release site were also observed in some roroa translocated to the Flora Valley, resulting in at least 14% of the birds (6 of 44) settling outside the project area (Toy & Toy 2020). Similarly, one individual had a dispersal path >11 km within a year post-release at Lake Rotoiti. However, the project area at Lake Rotoiti is delineated by natural barriers, the lakeshore on one side and a high mountain range on another, which likely limited the dispersal to within the project area boundaries (Gasson 2005).

#### Home range establishment

The post-translocation monitoring of two years

for the released wild-caught adults only produced observable stable home ranges for three birds. Due to the noted transmitter difficulties, the remaining four birds were only monitored for 0.9-1.5 years post-release, resulting in a home range estimation based on 0.4–1 year of data points. During this shorter monitoring period, these birds still had increasing home range areas, so it was likely the home ranges were not fully realised yet. In the Flora Valley project area, roroa have been observed to disperse for up to 2.5 years before establishing stable home ranges, based on monitoring data of up to eight years post-release (Toy & Toy 2020). Therefore, it is possible that the home ranges of the four birds with shorter monitoring duration could have kept expanding or shifting before eventually stabilising.

The estimated home range size (MCP) of the translocated wild-caught birds in the Nina, at 76.34 ha (±11.16 SE), was similar to the mean annual home range size (annual period July–June) in the Flora Valley, 73.26 ha ( $\pm 4.82$  SE), based on an average 3.8 years post-release monitoring duration for each bird (Toy & Toy 2020). In contrast, the mean home range size of translocated roroa at Lake Rotoiti 6-8 years post-release was 34.42 ha (±9.40 SE); however, the monitoring took place during only the winter season (Jahn et al. 2013) and therefore is not directly comparable. The mean home range size of translocated birds in the Nina Valley was larger than their pre-translocation mean home range in the Hawdon Valley, which was 54.39 ha (±5.13) *SE*). Although the difference was not statistically significant, given the truncated monitoring of four of the birds post-release, it is likely that the difference would be significant if monitoring for all birds could have been achieved for the full twoyear period. The significantly larger home range estimates of translocated wild adults compared to the resident ONE birds in the Nina Valley was likely caused by an ongoing range shift/expansion. In other naturally established populations, the home ranges of adult roroa appear substantially smaller, such as in the North Branch Hurunui, Lake Sumner Forest Park (32.64 ha ±2.15 SE, summer-mid-autumn only), or in Gouland Downs, Kahurangi National Park (pair territory size 23 ha, range 9.9–42 ha) (McLennan & McCann 1991; Keye *et al.* 2011).

#### Translocation impacts on resident birds

The release of the wild-caught adults into the Nina Valley did not appear to substantially impact the ranging behaviour of the previously released ONE birds, likely due to a very low population density and little competition for resources. Apart from a minimal temporary home range shift of unpaired male 'ONE 3' and an insignificant increase in the

ONE birds' nightly activity immediately after the release of wild adults, there were no other obvious behavioural changes among the ONE birds (Mander 2016). The ONE birds' home ranges (MCP) before-and-after the 2015 translocation were not identical but had a substantial overlap, which is consistent with a naturally occurring range shift over time (Toy & Toy 2020). Additionally, we found no significant change in the home range size of the resident ONE birds following the release of the wild adults suggesting that the ONE birds were successful in maintaining/defending their territories after the release of the wild-caught birds. The monitoring periods were not the same duration, as we compared home ranges 24 months before and 6-24 months after the release of wild adults. The pre-translocation period was longer due to data points being collected less frequently than after the translocation, but we did not expect it to affect the results.

The comparison of ONE birds' home ranges should, however, consider the transitioning between age class of the monitored birds. While the ONE birds were already adults by the time of the 2015 translocation, they were only recruited to the adult population during the 2-year pretranslocation monitoring period. The ONE birds were 2.4–3.4 years old at the start of the monitoring period, and they would be considered adults at four years or whenever they start breeding (Colbourne et al. 2020). Subadult roroa (generally 0.5-4 years old) have been shown to frequently share the territory and even the nesting burrow with their parents (Jahn et al. 2013; Toy & Toy 2021b), unlike subadult North Island brown kiwi that usually disperse and establish their own territories (Basse & McLennan 2003). Given that all of the monitored ONE birds appeared settled within 2 km from their original release sites and there was no need to disperse from natal territories, we assumed their ranging behaviour was similar to those of adults throughout the pre- and post-translocation monitoring periods.

#### Future of the Nina population

Since 2011, 18 roroa have been released in the Nina Valley, ten ONE and eight wild-caught birds. Of these, two birds (one ONE and one wild) are known to have died. The 2015 translocation proposal planned for subsequent releases to establish a self-sustaining and genetically viable population founded by at least 40 unrelated individuals by 2020 (Morrison & Yong 2014), but this target has not yet been met. All of the released birds were sourced from the lower Hawdon Valley. The ten ONE birds were produced by seven different pairs and an offspring of one of these pairs died. Assuming that all birds last recorded alive in the Nina Valley

survive and breed, the current founder group is 13 unrelated individuals: seven wild-caught adults and ONE offspring of six different pairs in the Hawdon Valley. However, most of these birds came from adjacent territories in the Hawdon Valley, and despite not knowing their pedigree, a degree of some relatedness is likely (Taylor *et al.* 2021).

possibility The of supplementing the reintroduced Nina population by natural immigration is very low. Prior to the reintroduction project, roroa in the Nina and surrounding valleys had likely been functionally extinct, with only occasional calls reported (Hulsman et al. 2010). None of the translocated birds is known to have paired with any original birds that may have survived in the Nina Valley. During a 2012 acoustic survey, only 14 roroa calls from possibly four individuals were recorded, which were likely then recently released ONE birds (Morrison & Yong 2014; Jahn et al. 2022b). Based on an acoustic survey in 2017-18 (Jahn et al. 2022b), it appears that the roroa population in the Nina Valley is growing due to successful breeding by translocated birds. Therefore, roroa releases to the Nina should resume as soon as possible to avoid genetic overrepresentation among the progeny of the current founder group and potential inbreeding. Failure to establish the population with a sufficiently genetically diverse founder group may lead to inbreeding depression or genetic drift, which may compromise the longterm population sustainability and ultimately lead to local extinction (Groombridge et al. 2012; Jamieson & Lacy 2012; Weeks et al. 2015).

The current species management plan marks completion of the Nina reintroduction project as high priority and identifies an issue of insufficient pest control in the project area (Roroa Practitioner Group 2021). Only approximately 1,600 ha of the valley is trapped for stoats, mainly alongside the Nina River. Such an area could theoretically cover approximately 25 roroa territories, based on the observed average home range size. However, existing home ranges appear to be spread on the valley slopes, and therefore only a limited portion of each territory is managed for predators along the valley floor. Currently proposed translocation guidelines recommend that translocation project areas should provide habitat for at least 100 pairs to allow sufficient retention of genetic diversity (Department of Conservation 2018). That will require the entire Nina River catchment to be under a sustained pest control regime ideally with a buffer zone covering surrounding valleys to provide safe space for post-release or natal dispersal from the Nina Valley.

#### Implications for kiwi translocations

The post-translocation behaviour of roroa in

the Nina Valley underscores large habitat size requirements for kiwi reintroduction projects in unfenced mainland areas. Large UDs and long dispersal paths show the need for intensive and sufficiently long post-release monitoring. This monitoring has a potential to inform management interventions such as retrieval of dispersed birds, as demonstrated in the Flora Valley (Toy & Toy 2020), or in other large flightless birds, e.g. takahē (Porphyrio hochstetteri; Department of Conservation 2020). Radio telemetry is a commonly used method for monitoring translocated kiwi populations, but the monitoring period and effort are highly variable, and usually, a sample of released birds is monitored for only a part of the dispersal period (Jahn et al. 2022a). Extended monitoring duration and increased numbers of monitored birds enable better adaptive management, detection of likely population founders based on territory establishment and breeding, and selection of future release sites based on gaps between territories. However, such approach can be more expensive, labour-intensive, and intrusive to radio-tagged birds (Toy & Toy 2021a). Subsequent periodic acoustic surveys, coupled with occupancy analysis (Jahn et al. 2022b) and potential identification of individuals by their calls (Digby et al. 2014; Dent & Molles 2016), can facilitate non-intrusive and cost-effective population monitoring. Additionally, regular genomic assessments can provide a tool to identify and manage possible inbreeding depression or genetic drift (Ramstad & Dunning 2021), and therefore maximise the probability of a long-term positive translocation outcome.

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## Habitat loss drives population decline and reduced mass of Rakiura tokoeka (*Apteryx australis australis*, Stewart Island brown kiwi,) at Mason Bay, Stewart Island/Rakiura

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**Abstract:** Between 1993 and 2018, the number of Rakiura tokoeka (*Apteryx australis australis*, Stewart Island brown kiwi) territories in 125 ha of retired farmland near Island Hill Homestead, Mason Bay, declined from 17 to 12 at a mean rate of 1.43% per year, and the minimum number of adults declined by 1.39% per year. These rates triggered a New Zealand conservation status of 'Nationally Endangered' for the subspecies assuming that they were typical of the whole of Stewart Island/Rakiura. Feeding habitat for tokoeka has been lost as the study site reverts from rough pasture to flax (*Phormium tenax*) and scrub; the mean mass of adult birds has decreased by 7.5% over 30 years despite a 30% decline in population density. Key predators of adult kiwi are absent, and predation of Rakiura tokoeka by feral cats (*Felis catus*) is known but is likely to be insignificant. With a conservation status of fakiura tokoeka is more appropriately classified as 'At Risk – Naturally Uncommon'. This research highlights the risks of extrapolating results from a single study, in this case with a limited geographical extent rather than a limited duration.

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Keywords: kiwi, population dynamics, predation, habitat loss, mass, conservation status

#### INTRODUCTION

Conservation biology has historically placed a strong emphasis on measuring changes in the populations of threatened species and determining the causes for both negative and positive changes. The quantitative measures and rates of change underpin threat classification systems such as the IUCN Red List (IUCN 2012) and the New Zealand Threat Classification System (Townsend *et al.* 2008) and, in turn, these are used by conservation

*Received 20 April 2020; accepted 16 March 2022* \*Correspondence: *hrobertson@doc.govt.nz*  planners and managers to determine priorities for the investment of conservation funds.

Predation by introduced mammals, including humans, has been the primary agent of decline and current limitation of New Zealand native forest birds (Innes *et al.* 2010). Because New Zealand's avifauna evolved with avian rather than mammalian predators, the extinction of 54 bird species since human settlement in New Zealand *c.* 800 years ago (Robertson *et al.* 2021) was driven primarily by predation by introduced mammals, but habitat loss was undoubtedly a contributing factor driving population decline and extinction risk to New Zealand birds (Holdaway 1989; Innes *et al.* 2010). Globally, habitat loss is regarded as the main driver of population decline and extinction in birds (Collar *et al.* 1994; BirdLife International 2018), especially for those species that are habitat specialists and/or have small body sizes (Owens & Bennett 2000).

The Stewart Island brown kiwi (hereafter called Rakiura tokoeka) Apteryx australis australis (Scofield et al. 2021, Checklist Committee (OSNZ) 2022), is widespread and common throughout Stewart Island/Rakiura (Harper 2009), and they are also present on adjacent Ulva and Pearl islands. Rakiura tokoeka often live in family groups, with multiple juveniles, subadults, and adults sharing a burrow, hollow log, tree stump or clump of dense foliage, and fiercely defending their territory (Guthrie-Smith 1914; Colbourne 1991). Up to seven adults have been recorded in a single territory (Robertson et al. 2019b). Subadult and adult helpers assist the 'alpha' pair to incubate the one-egg clutch and to brood recently hatched chicks. Adults and helpers of both sexes develop well-defined brood patches (Colbourne 1991, 2002). Unlike other kiwi taxa, Rakiura tokoeka are renowned for feeding and occasionally calling in daylight (Colbourne & Powlesland 1988), especially females that have incubated all night, and males soon after their eggs have hatched (Colbourne 1991).

The Rakiura tokoeka was long regarded as the least threatened of all kiwi taxa because it had a large population of c. 20,000 birds on Stewart Island/Rakiura (Heather & Robertson 2005). The island is still largely cloaked in forest and natural shrubland communities, and the tokoeka there are not exposed to any predation by mustelids (stoat [*Mustela erminea*], ferret [*M. furo*], or weasel [M. nivalis]), and the few dogs (Canis familiaris) present are confined to a small area in and around the only settlement at Oban on the north-eastern side of the island. Apart from common brushtail possums (*Trichosurus vulpecula*), which occasionally compete for burrows (Morrin 1989), disturb nests and eat kiwi eggs (McLennan et al. 1996), and very rarely kill adult kiwi (Robertson et al. 2011), the only mammalian predators present are feral cats (*Felis catus*). They are known to prey on kiwi chicks (<50 days old), juveniles (50 days to 6 months old), subadults (6 months to 4 years old), and very rarely adult kiwi (McLennan et al. 1996; Robertson et al. 2011; Isabel Castro, pers. comm.). Without the other mammalian predators of kiwi on Stewart Island, the impact of predation was considered likely to be relatively minor and the population was expected to be stable.

Despite kiwi feathers having a distinctively simple structure, with a single rachis and unlinked barbs (Heather & Robertson 2015), Karl & Best (1982) did not detect any tokoeka feathers in the 44% of 229 feral cat scats that contained bird remains, collected mainly from southern Stewart Island/Rakiura, in areas where Rakiura tokoeka were present (e.g. Colbourne & Powlesland 1988). Although Harper (2005) did not always attempt to distinguish the species of bird from feathers found in 27% of 219 feral cat scats from central Stewart Island/Rakiura, small native and introduced passerines were most commonly found, and remains of tokoeka were not identified. Evidence of consumption of tokoeka by feral cats on Stewart Island/Rakiura has been found in the form of tokoeka DNA in feral cat scats collected at Mason Bay (Danielle Middleton, Manaaki Whenua Landcare Research, pers. comm.), but whether the tokoeka was killed by the cat or eaten as carrion is unknown.

Our preliminary data on the decline of the study population at Mason Bay (46°55'S, 167°48'E) between 1993 and 2008 were influential in Miskelly et al. (2008) classifying Rakiura tokoeka as 'Nationally Vulnerable' according to the New Zealand Threat Classification System criteria (Townsend et al. 2008). This assessment was accompanied by the qualifier 'Recruitment Failure' because of concerns that predation by cats could have been a driver of the observed decline in the number of adult birds and territories. In 2008, we proposed that the population decline at Mason Bay may have been driven by habitat loss as rough farmland reverted to communities of New Zealand flax/harakeke (Phormium tenax), red tussock (Chionochloa rubra), and mānuka (Leptospermum scoparium)-dominated scrub, following the removal of sheep in the mid-1980s (RMC & HAR unpubl. data). These observed, but unquantified, habitat changes have provided good cover and daytime shelters for tokoeka, but have reduced feeding opportunities, particularly in areas dominated by dense swards of flax that build up an impenetrable mass of tough dead leaves at ground level. Like other kiwi species, Rakiura tokoeka feed by walking about and probing their long bill into the soil or leaf litter layer to catch a wide variety of invertebrates, including earthworms, beetles (Coleoptera) and their larvae, spiders, wētā (Orthoptera), Lepidoptera larvae, centipedes, and cicada (Hemiptera) nymphs (Colbourne & Powlesland 1988).

To assess whether the decline was localised to Mason Bay or was more widespread, a second population monitoring site was established in 115 ha of mature forest habitat at Port Adventure (47°03'S, 168°11'E) on the eastern coast of Stewart Island/Rakiura where feral cats are also present. In January 2011, our initial monitoring, including searches with trained kiwi conservation dogs, found only one recently hatched chick but no juvenile or subadult tokoeka among the 21 birds caught. This suggested that poor recruitment due to cat predation may have been skewing the age structure heavily in favour of adults (Robertson *et al.* 2019b).

The expert panels assessing the conservation status of New Zealand birds in 2012 (Robertson et al. 2013) and 2016 (Robertson et al. 2017) designated the conservation status of Rakiura tokoeka as 'Nationally Endangered'. The observed decline up to 2008, and then through to 2013 at Mason Bay, together with low numbers of young kiwi detected at Port Adventure in 2011, suggested that the population may be declining at >70% in three generations, which would trigger 'Nationally Critical'. Because there was uncertainty whether the decline at Mason Bay was typical of the whole population, and because the Port Adventure data were based on a single visit, a lower threat category was designated, pending the collection of further data. The designation was accompanied by the qualifiers 'Data Poor', 'One Location', and 'Recruitment Failure' (2012 assessment only). These qualifiers indicated the lack of knowledge about the cause and extent of the population decline of this essentially single-island endemic subspecies, and the belief in 2012 that recruitment failure was a likely significant driver of the population decline at Mason Bay and the reason for the lack of young tokoeka caught at Port Adventure in 2011.

Habitat loss is one of the key threats to birdlife globally (Collar et al. 1994). It can lead to individuals moving to alternative feeding and breeding sites, or have an impact on the individual fitness (survival, body condition, or fecundity) of those that remain (Goss-Custard et al. 1995; Burton et al. 2006), and ultimately lead to a new lower population limit or carrying capacity at a site (Newton 1998). In this paper, we assess whether the decline in the population size of Rakiura tokoeka at Mason Bay was driven by predation by cats and/or by habitat loss as the study area reverts from rough farmland. A measure of mass change of the adult birds could distinguish between these hypotheses; bird mass would be stable or higher with decreasing population density if the decline is driven by predation, but stable or lower with decreasing population density if habitat loss has reduced the carrying capacity of the site.

#### METHODS

#### Study area

Stewart Island/Rakiura is the smallest (174,600 ha) and least modified of the three main islands of New Zealand. Mason Bay, on the western coast of Stewart Island/Rakiura, lies in the path of the prevailing westerly winds which bring frequent rainfall, cool temperatures in winter, and generally

mild conditions in summer. From approximately 2.5 km inland from the beach, an attempt was made to farm sheep on the stable ancient linear sand dunes and the flats between them. The 2,000ha Island Hill Run was established in 1884 and the drier land was burned and converted to rough pasture, some swamps were drained in an effort to make more land suitable for grazing, and in the 1970s an airstrip was cleared and used by aircraft to bring superphosphate fertilizer to spread on the better pasture, and to fly out possum skins and live deer (Cervidae). Commercial farming ceased in 1985 and the farm was finally destocked in 1987 (Peat 2010), allowing the rough pasture to revert naturally to New Zealand flax/harakeke, red tussock, and scrub dominated by mānuka.

We mapped the territories of Rakiura tokoeka in a 125-ha area to the north and east of the Island Hill Homestead (Fig. 1), approximately centred on the western end of the old airstrip (46°55′S, 167°48′E).



**Figure 1.** Map of Stewart Island/Rakiura, New Zealand, showing the location of the Mason Bay and Port Adventure study areas.

#### Catching and handling birds

Rakiura tokoeka were caught using a variety of methods described in the Kiwi Best Practice manual (Robertson & Colbourne 2017). Most were caught by hand or in hand nets when we found them feeding at night, often when a trained and muzzled conservation dog indicated their presence nearby. We also used conservation dogs to indicate their presence in a burrow or under dense vegetation by day, and caught birds by hand when they shared a daytime shelter with a radio-tagged family member. We occasionally used playback to attract adults at night. Each bird captured or re-captured was measured, sexed, aged, mass determined, and body condition scored, according to the methods described by Robertson & Colbourne (2017), except that we discovered during this study that Rakiura tokoeka were still growing, and hence still classified as subadults, up to about 6 years old (see results). Every bird handled was permanently marked with a uniquely numbered fish fingerling tag inserted in the patagium of the wing, or banded with a uniquely numbered metal band which had a combination of colours of reflective tape added to allow individual identification at night. Radio-transmitters (Sirtrack<sup>™</sup> two-stage, 25 g or, more recently, 11 g) were temporarily strapped to the tarsus with a single soft plastic hospital identification bracelet according to the method described by Miles & McLennan (1998).

#### **Territory mapping**

Long-term monitoring of Rakiura tokoeka started in November 1993, to take advantage of the many birds living in 11 territories that had been banded during an ecological and behavioural study conducted in 1988–1991 (Colbourne 1991, 2002). In 1993, the original study area was expanded from 80 ha to 125 ha by including six additional territories largely to the north and east of the original scientific study area. The monitoring surveys were done approximately every five years; the first two surveys were done in November and the last four surveys (from 2003) in February; the entire study spanned 24.25 years from November 1993 to February 2018.

Based on records of captures, daily checks of the location of radio-tagged birds, occasional sightings of birds with and without coloured reflector bands, and projected locations of transmitter signals and calls at night, we mapped the approximate boundaries of each territory. Rakiura tokoeka were strongly territorial with very little apparent overlap of neighbouring territories. Territory boundaries were often streams or swamps, although some territories spanned these features on some visits. Many adults remained faithful to a particular territory for decades. We used the 'fieldworker's estimate' (Macdonald et al. 1980) by starting with a maximum convex polygon of locations, and then modified the shape to exclude overlap of territories and include adjacent suitable habitat bounded by the same geographical features (i.e. major streams), with the assumption that these sites would have been used if we had more daily location data.

Because each territory of Rakiura tokoeka can be occupied by multiple adults and subadults, the daily checks usually involved sighting the radiotagged bird to determine if any extra birds were with it, even after a pair of adults had been caught and radio-tagged in a territory.

**Table 1.** The number of Rakiura tokoeka (*Apteryx australis australis*) captured during six approximately 5-yearly surveys at Mason Bay, Stewart Island/Rakiura. The minimum number of birds and minimum number of adult birds known to be alive is based on captures, sightings, projected calls, and recaptures of birds in subsequent surveys, with the assumption that birds did not leave and then re-enter the study area between surveys. The number of territories was calculated using the 'field worker's estimate' method by mapping all the above records and observing that territories are not overlapping and assuming that small spaces between known locations of birds are not occupied by additional birds.

	Year						
	1993	1997	2003	2008	2013	2018	
Adult female	9	14	13	12	9	9	
Adult male	12	18	10	18	12	11	
Chick (in nest)	1	0	0	0	0	0	
Juvenile (<6 months)	0	0	0	1	1	1	
Subadult (>6 months)	2	2	5	2	3	6	
Total captures	24	34	28	33	25	27	
Percentage young	13	6	18	9	16	26	
Minimum # birds alive	42	45	38	36	35	38	
Minimum # adult birds	39	43	33	33	30	30	
# Territories	17	16	14	13	11	12	
Min # adults/territory	2.29	2.69	2.36	2.54	2.73	2.50	

Over the six surveys at Mason Bay from 1993 to 2018, we caught 79 different Rakiura tokoeka a total of 171 times. At first capture, 26 were adult females, 30 were adult males, one was a chick in a nest, three were juveniles (<1 kg and therefore assumed to be < 6 months old), and 19 were subadults (Table 1). The chick was not seen again. One of the two juveniles that were caught before 2018 (and hence capable of being recaptured on a subsequent survey) was recaptured on the two subsequent surveys (once as a subadult, and then as an adult) still in its natal territory. Six (43%) of 14 subadults caught before 2018 were recaptured as adults within the study area during subsequent 5-yearly surveys.

In November 1993, there were 17 occupied territories containing a minimum of 42 birds, of which 39 were adults. Over the 24.25 years to February 2018, the estimated number of adults in the 125-ha study area declined at an average rate of 1.39% per year (Figure 2) while the actual number of territories declined from 17 to 12 at an average rate of 1.43% per year (Figure 2, Figure 3). If the mean generation time (the average age of female parents) of Rakiura tokoeka is assumed to be 20–25 years, then over three generations (60–75 years), this would result in a 57–65% decline in

the number of adults and a 58–66% decline in the number of territories.

The mean territory size has increased 42% from 7.4 ha in 1993 to 10.4 ha in 2018, and the density of adults has declined 30% from one adult per 3.2 ha to one adult per 4.2 ha. The number of adults per territory has varied over the six surveys (Table 1), with a weak linear increase over the 25-year period (r = 0.62, P = 0.19), but the actual increase may be greater because our experience from 5-yearly visits to Mason Bay is that we usually underestimate the number of extra adults alive in a few territories.

We detected simple pairs in territories 58% of the time, but the other territories were occupied by up to five adults (three males and two females). In the 31 instances where three adults were present in a territory, there were significantly more trios with two males (23) than with two females (8) (Binomial test, z = 2.69, P = 0.007), but in the three territories with four adults there were two of each sex in one territory and one male and three females in the other two territories. At least some of the additional adults in territories were offspring from that territory; e.g. a 680 g juvenile female that was wing-tagged in Territory 4 in February 2008 was still in the same territory 10 years later, along with her putative parents.



**Figure 2.** Exponential decline in the minimum number of adult Rakiura tokoeka (*Apteryx australis australis*) (triangles and dotted line) in 125 ha at Mason Bay, Stewart Island/Rakiura between November 1993 and February 2018 ( $y = 40.46e^{-0.014x}$ , r = -0.885, P = 0.019). The number of territories (circles and solid line), which was known exactly, declined from 17 to 12 over the same period.



**Figure 3.** Maps showing the approximate boundaries of territories of Rakiura tokoeka (*Apteryx australis australis*) in the 125-ha study area at Mason Bay, Stewart Island/Rakiura (see Fig. 1), at approximately 5-year intervals from 1993 to 2018. Territory boundaries are shown as bold lines, the former boundaries at the previous assessment are shown as faint lines.

#### **Morphometrics**

Including unpublished data from the 1988–1991 scientific study, the averaged measurements of 74 adult Rakiura tokoeka caught at Mason Bay are given in Table 2. At this site, tokoeka have had their mass determined during only a limited part of the year, from 12 October to 21 February, mainly in late January or early February, and so the annual mean mass is likely to be higher than those we recorded because kiwi gain mass as their condition improves through autumn and winter in the lead-up to the breeding season (e.g. McLennan 1988).

In February 2008, a *c*. 3-month-old juvenile female (bill length 57.2 mm, mass 680 g) was captured, wing-tagged and released. It was recaptured in the same territory five years later (bill length 147.8 mm, mass 2,890 g), but when again recaptured in the same territory in February 2018, its bill length had grown a further 5.4 mm to 153.2 mm, and its mass had increased to 3,120 g. This female probably did not stop growing until it was about six years old, at the upper end of the usual 5–6 year growth period of kiwi (Beale 1991; Bourdon *et al.* 2009).

Table 2. Measurements of Rakiura tokoeka (Apteryx australis australis) at Mason Bay, Stewart Island/Rakiura taken using
the methods described by Robertson & Colbourne (2017). Up to nine repeated measurements of each individual taken
between 1988 and 2018 were averaged and then these were used to calculate the overall mean, standard deviation (SD)
and extremes of all averaged measurements, except for mass, where the actual extreme measurements are presented.

Female	Mean	SD	n	Minimum	Maximum
Bill length (mm)	142.7	5.8	35	133.4	156.4
Tarsus width (mm)	13.9	0.7	32	12.0	15.8
Tarsus depth (mm)	19.6	1.1	32	17.9	22.2
Tarsus length (mm)	96.5	3.6	32	88.3	104.5
Mass (g)	3,264	269	35	2,780	4,120
Male	Mean	SD	n	Minimum	Maximum
Bill length (mm)	105.1	4.1	38	97.5	118.0
Tarsus width (mm)	13.2	0.7	36	11.5	14.5
Tarsus depth (mm)	18.4	0.8	36	16.9	20.0
Tarsus length (mm)	91.5	3.5	36	84.4	98.3
Mass (g)	2,657	192	38	2,200	3,170

The mass of adults recorded in late January or in February during research work in 1988 and 1990 (RMC *unpubl. data*), and during territory mapping from 2003 to 2018, showed some variation from year to year; however, both adult females and adult males had a similar and highly significant linear decrease in mass over the 30 years (r = -0.33, P =

0.017 and r = -0.34, P = 0.005, respectively, Figure 4). Adult female body mass decreased by a mean of 8.5 g per year, and adult males were on average 7.1 g lighter per year. Over the 30 years, these equated to losses of 255 g or 7.5 % of mean body mass for females, and 213 g or 7.5% of mean body mass for adult males.



**Figure 4.** Mass of adult Rakiura tokoeka (*Apteryx australis australis*) at Mason Bay, Stewart Island/Rakiura recorded between 26 January and 20 February in 1988, 1990, 2003, 2008, 2013, and 2018. The mean decrease in mass of 8.5 g per year for females (a) was significant (r = -0.33, n = 53, P = 0.017), as was the mean decrease of 7.1 g per year for males (b) (r = -0.34, n = 65, P = 0.005).

#### DISCUSSION

Two possible mechanisms were suggested for the serious decline in the number of territories of Rakiura tokoeka at Mason Bay: recruitment failure through predation of young tokoeka by feral cats, or habitat loss following the retirement of farmland reducing the carrying capacity of the study site.

The dominant year-round prey of feral cats on Stewart Island/Rakiura is rats (Karl & Best 1982; Harper 2005) and although feral cats ate more birds as rat abundance declined, they did not prey-switch to specialise on birds when rat abundance was low (Harper 2005). Given the lack of kiwi feathers detected in a total of 448 feral cat scats from Stewart Island/Rakiura (Karl & Best 1982; Harper 2005), it seems likely that predation of Rakiura tokoeka by feral cats is infrequent and insignificant. Predation rates may vary from year to year, and from site to site; for example, in contrast to catching or detecting only one chick at Port Adventure in 2011, during the next visit to the site in February 2017, one chick and four juveniles hatched in the 2016/17 breeding season and three subadults hatched in earlier years were caught or seen (Robertson *et al.* 2019b). The following year, we caught three subadults at Mason Bay (mass of 1,425-1,875 g) that likely hatched in the 2016/17 breeding season. This suggests that 2016/17 was a particularly productive year for Rakiura tokoeka and/or that feral cat predation on young Rakiura tokoeka was low at both sites that particular year. Compared with kiwi species, such as North Island brown kiwi (Apteryx mantelli), that have young that become independent from <2 months old (Heather & Robertson 2015), the social system of Rakiura tokoeka may afford better protection of chicks and juveniles from predation by feral cats because chicks are not left unattended in the nest, and juveniles often share daytime dens with subadults or adults.

Habitat loss often refers to situations where natural communities are destroyed or become fragmented when forests are logged, shrubland communities are cleared, wetlands are drained or filled, or cities expand. Habitat loss resulting from slow habitat change during seral succession clearly affects bird communities as shown, for example, by changes in the abundance of bird species in different habitat guilds during vegetation restoration programmes (e.g. Munro *et al.* 2011; Graham *et al.* 2013), but the mechanisms underlying population declines during seral succession or vegetation restoration have received little attention compared with species that have benefitted from such processes.

Carrying capacity, the maximum population of a species that a site can sustain, is an often-quoted concept but is very difficult to estimate or measure accurately because resource limits vary in both space and time, and such variations can be temporary in nature, such as during a severe drought (Robertson et al. 2019a). The carrying capacity of a site is often estimated from observed population densities in apparently stable populations in similar habitat elsewhere (e.g. Colbourne & Robertson 1997), but changes in physiology (e.g. mass, levels of stress hormones), feeding behaviour, breeding productivity, immigration/emigration, and survival can provide greater insights into the mechanisms underlying demographic changes in populations close to or beyond carrying capacity. The direction of changes in these parameters are generally predictable; for example, as the carrying capacity of a site is approached or exceeded, time spent foraging increases and reproductive effort decreases (Morris & Mukherjee 2007).

If habitat loss has been the primary driver of the observed population decline at Mason Bay, then predation by feral cats would have been insignificant because any Rakiura tokoeka killed would have been part of the 'doomed surplus'.

Our data indicate that reduced food availability, likely caused by a loss of short grassland habitat which is easy for birds to forage in, has been the main driver of the observed population decline at Mason Bay. The mean mass of adult birds decreased by 7.5% over a 30-year period of habitat change, despite a 30% decrease in the density of adults over the last 25 years of that period. If predation had been the main driver of population decline, we would have expected the body mass of adults to have been stable or to have increased as the population density declined.

We note that even with a 42% increase in the mean territory size at Mason Bay from 7.4 ha to 10.4 ha, they are still smaller than the mean territory size (14.4 ha) recorded in 115 ha of mature forest at Port Adventure (Robertson et al. 2019b). The density of one adult per 4.2 ha at Mason Bay is also higher than the one per 5.0 ha recorded at Port Adventure despite more adults per territory (mean 2.88) at Port Adventure in 2017 (Robertson et al. 2019b). The number of adults per territory at Mason Bay showed a non-significant increase over the last 25 years but, because some additional adults in territories are usually missed during our surveys, it is likely that over time an increasing number of young tokoeka delay leaving their natal territory and remain as helpers well into adulthood. An example of delayed dispersal was the 10.25-yearold female that was found in her natal territory with her putative parents in 2018, some 6 years after most other kiwi species start breeding (Robertson & de Monchy 2012). We expect that there will have been other behavioural changes over the same period that have led to mortality and/or emigration

exceeding recruitment and/or immigration, but we have not been able to measure these during our few brief but regular visits.

It may seem counterintuitive that densities of the endemic Rakiura tokoeka at Mason Bay have declined as the habitat reverts from rough farmland dominated by exotic grass and legume species to more natural communities dominated by native species. We do not know the quantity of fertilizer that was applied to the pasture in the study area before our research, but this may have led to artificially high soil fertility and density of soil invertebrates at the start of our studies.

We believe that the main habitat change affecting tokoeka since the cessation of farming has been a considerable increase in the ground surface covered by New Zealand flax/harakeke, red tussock, mānuka scrub and, in places by bracken fern (Pteridium esculentum), umbrella fern (Sticherus cunninghamii), and rank exotic grasses. Although historical aerial photographs with sufficient resolution to quantify habitat changes are lacking from this remote site, the main loss of feeding habitat appears to have been caused by the rapid spread of flax, which now forms dense monocultural stands of 0.5 ha or more (Fig. 5). Flax is a tall perennial monocotyledonous tussock-herb that has fan-like tufts of fibrous, stiff and swordlike leaves that fall to the base of the plant when they die (Wehi & Clarkson 2007). It is native to Stewart Island/Rakiura, but some plants almost certainly represent introductions of high-quality races (Wilson 2009) because of their economic importance for weaving, ropemaking, and to act as windbreaks. Flax provides very good cover and daytime shelters for tokoeka, but the dense accumulated mass of tough dead leaves at ground level makes foraging slow and difficult for tokoeka.



**Figure 5.** Dense swards of flax (*Phormium tenax*) have replaced large areas of open grassland at Mason Bay, Stewart Island/Rakiura. Photograph: Sabine Bernert.

Interestingly, between our surveys in 2013 and 2018, there was a major die-off of flax from an unknown disease with characteristics akin to 'yellow-leaf disease'. This disease of northern New Zealand is caused by a phytoplasma bacterium and it led to the widespread die-off of flax and the closure of the flax fibre industry in New Zealand (Beever *et al.* 1996). Isolated flax bushes and those on the periphery of stands seemed to be the most affected in 2018. If the outbreak of this unknown disease continues, it may provide a natural test of our thesis that the decline of Rakiura tokoeka at Mason Bay has been driven primarily by the rapid spread of flax and loss of body mass of the tokoeka.

Based on densities we have encountered on Stewart Island/Rakiura, we conservatively estimate the population to be 15,000-20,000 adults. Given that the decline appears to be driven by habitat changes localised to Mason Bay, it appears likely that the overall population is close to stable (i.e.  $\pm 10\%$  in three generations), and so the conservation status of Rakiura tokoeka should be classified as 'At Risk - Naturally Uncommon'. Using data from a draft of this paper, the bird assessment panel accepted that Rakiura tokoeka should be re-classified as 'At Risk - Naturally Uncommon' pending an assessment of whether the total population is above or below 20,000 mature birds (Robertson et al. 2021). This new classification carries the qualifier 'Conservation Dependent' in recognition of the need for ongoing biosecurity measures to keep Stewart Island/Rakiura free of mustelids. If the population is stable and actually greater than 20,000 adult birds, then this subspecies would be classified as 'Not Threatened', which is a far cry from the 'Nationally Critical' classification that our Mason Bay data initially pointed to. This research highlights the risks associated with extrapolating results from a single study, in this case with a limited geographical extent rather than duration, because valuable conservation funds could have been spent addressing what is likely to be only a localised problem.

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## A basic statistical approach to determining adult sex ratios of moa (Aves: Dinornithiformes) from sample series, with potential regional and depositional biases

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Abstract: Adult sex ratio is a basic component of breeding systems. Estimates of sex ratios of moa (Aves: Dinornithiformes) have ranged from near balanced to significantly female-biased. However, ratios have usually been estimated by simple ratios of females to males identified by some level of sexual size dimorphism or, at most, tested against a balanced ratio by  $\chi^2$  test. Application of binomial tests confirmed a great heterogeneity, and high levels of uncertainty in estimates of moa sex ratios from different areas and from different kinds of fossil deposits. Large samples gave more constrained estimates than small, but even for some of the larger, binomial analysis often revealed a range of possible ratios, including one with a bias to males. Some causes of extreme values for swamp and lake bed deposits, including sexual differences in territorial behaviour, have been suggested before. However, a new issue – significant and sometimes abrupt changes in female and perhaps male body size through time – was identified here from series of genetically identified and radiocarbon dated moa from North Canterbury, New Zealand. The size changes compromise allocation of individuals to sex by morphometrics of limb bones, especially in undated samples. Intensive radiocarbon dating of series of genetically sexed moa of different taxa from a range of areas will be required to identify potential regional and temporal differences in their sex ratios before any interpretation of the evolution of size dimorphism and breeding systems based on moa sex ratios will be possible.

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Keywords: sex ratio, moa, statistics, Dinornithiformes, depositional bias, identification bias

#### INTRODUCTION

Adult sex ratio is fundamental to a species' breeding system (West *et al.* 2002; Liker *et al.* 2013; Székely *et al.* 2014). Ratios are not always straightforward to measure or identify even in living taxa which complicates interpretation of the role of sex ratio in breeding systems and of drivers of variation in sex ratios (West & Sheldon 2002; Postma *et al.* 2011; Bell *et al.* 2014). Sex ratios are especially difficult to measure in extinct taxa. Many assumptions have

Received 23 February 2022; accepted 18 July 2022 \*Correspondence: turnagra@gmail.com to be made in assigning a sex to an individual.

Of the 65% of bird species whose published sex ratios suggest male or female bias, most are biased towards males (Donald 2007). As noted by Allentoft *et al.* (2010), the three families of extinct moa (Dinornithiformes) may be an exception. Based on the generally employed methods of estimating moa sex ratios from raw numbers of birds sexed by size (or, for some, by genetic analysis), and by  $\chi^2$  Goodness of Fit tests against a balanced ratio as in Bunce *et al.* (2003), Allentoft *et al.* (2010) suggested that sex ratios in giant moa populations rarely deviated from the balanced.

Table 1. Sex ratios for moa published in and after 2003. Abbreviations: DINO, Dinornis novaezealandiae; DIRC	), D.
robustus; EUCU, Euryapteryx curtus sensu lato; PAEL, Pachyornis elephantopus; PAGE, P. geranoides. Different values	s for
each taxon within a reference are for different areas or sites, as in Figure 6.	

Reference	Т	axon – Sex rat	tio (♀/♂)				
	DINO	DIRO	EMCR	EUCU	PAEL	PAGE	
Bunce <i>et al.</i> (2003)	1.2:1	1:1.2					
	1.6:1	1.6:1					
	1:1.6	1.2:1					
	2.2:1	1:1					
		1.6:1					
		1:1					
		1.4:1					
Huynen et al. (2003)						6.25:1	
						1.67:1	
Allentoft et al. (2010)		19:1	7.2:1	2.5:1	2.5:1		
[adults only]		1:1.5	5.5:1				
Allentoft et al. (2014)	"No differential reproductive success between the sexes"						
Holdaway (2022)				3.29:1			
				3:1			
				2.33:1			
				1.23:1			
	1.05						
				1.16			

In support, they cited values of 1:1 to (female-biased) 1.6:1 (reported in error as 1:6.1) for the different sites and areas reported in Bunce *et al.* (2003). Huynen *et al.* (2003) offered 1.7:1 based on genetic sex determinations of all moa taxa examined. Previous estimates of sex ratio are summarised in Table 1. Allentoft *et al.* (2010) echoed Bunce *et al.* (2003) in suggesting that the ratios in any one site (especially swamps and lake beds) could differ from that in the source population because of sexual differences in spacing and other behaviours. Wide variation in moa species compositions in five North Canterbury sites (Allentoft *et al.* 2012) supports a site-specific explanation.

While Huynen *et al.* (2003), Allentoft *et al.* (2010), and Bunce *et al.* (2003) all based at least some of their ratios on genetics, most moa sex ratios have been estimated from the morphometrics of the sexual size dimorphism first mooted by Cracraft (1976a, 1976b, 1976c). The presence of an egg with the skeleton of a large individual of *Emeus crassus* from Pyramid Valley (Holdaway & Worthy 1997; Worthy & Holdaway 2002) suggested that the females were the larger sex. Females were confirmed to be larger by ancient DNA analyses (Bunce *et al.* 2003; Huynen *et al.* 2003; Allentoft *et al.* 2010; Rawlence *et al.* 2012; Allentoft *et al.* 2014, 2015).

Samples from many sites and areas supported a balanced sex ratio for giant moa (Dinornithidae). Others – including many for moa in the Family Emeidae, especially *Euryapteryx* – suggested female-biased ratios. Within *Euryapteryx*, however, evidence was equivocal. One sample (from dunes at Tokerau Beach in the far north of the North Island) had a balanced sex ratio (Worthy 1987), whereas others had ratios of 2–2.59/1đ (Worthy 1987; Holdaway 2022).

Among the factors associated with avian reproductive systems, if there is sexual size dimorphism in birds it is usually biased, as with sex ratio, towards larger males. Females are, however, larger than males in raptors (Falconidae; Accipitridae) and owls (Strigidae) (Krüger 2005), in shorebirds (Calidriformes) (Lindenfors et al. 2003), including skua (Stercorarius) (Catry et al. 1999), and in button quail (Turnicidae) (Leitner et al. 2021), and tinamous (Tinamidae) (Tubaro & Bertelli 2003). Most if not all moa taxa have extreme sexual size dimorphism biased towards larger females (Worthy 1987; Huynen et al. 2003; Bunce et al. 2003; Olson & Turvey 2013; Holdaway 2022): the size differences are assumed to be constant. Slight overlap between the smallest females and largest males introduces only negligible error in the allocation of individuals to sex. However, temporal stability in body size of one or both sexes in moa has been a working hypothesis. If female or male body size changed through time, it could lead to more errors in allocating sex within (particularly undated) samples. Fortunately, the hypothesis can be tested using the long series of high precision radiocarbon ages available for



**Figure 1.** Sex ratios of the species now known as *Dinornis novaezealandiae* (North Island) and *D. robustus* (South Island) based on identifications of morphometric species of *Dinornis* now recognised as females (*D. giganteus; D. novaezealandiae*) and males (*D. struthoides*), for sites and regions from identifications by T. H. Worthy (references in text). Circle, Tokerau Beach; triangle, Tangatupura

four species in a small area in the late Holocene (Holdaway *et al.* 2014; Allentoft *et al.* 2014).

The adult sex ratio has to be known with reasonable certainty before the breeding system in any species of moa can be understood. To better resolve the sex ratios in dinornithid and some emeid moa, we revisited the data sets of Worthy (1987) and Bunce *et al.* (2003), applying  $\chi^2$  Goodness of Fit tests against other possible integer sex ratios, and then extended the analysis to new data sets for giant moa and *Euryapteryx* in the South Island (Fig. 1 and Holdaway [2022]). We then generated binomial probability distributions for each sample for a range of potential sex ratios to better define the ranges of possible values for the sex ratios represented by the samples.

#### MATERIALS AND METHODS Data sources

Samples were gathered from lists in Worthy (1989, 1997, 1998c, 1998b, 2000), Holdaway & Worthy (1997), Worthy & Holdaway (1993, 1994, 1995,



**Figure 2.** Body size in (A) *Pachyornis elephantopus*, (B) *Euryapteryx curtus*, and (C) *Emeus crassus*, all Emeidae (Dinornithiformes), as indicated by length of the tibiotarsus, for genetically sexed, morphologically adult birds. Filled circles, females, with trends indicated by 0.35 Smoothing Factor Local Regression (LOESS, heavy line, with 2.5 and 97.5 percentiles) for the adult females. Filled triangles, males. Median calibrated dates adjusted for 2% old carbon contamination.

1996, 2000, 2002), Bunce *et al.* (2003), Huynen *et al.* (2003), Allentoft *et al.* (2010), and Allentoft *et al.* (2014). Sex ratios for giant moa were assigned as in Bunce *et al.* (2003) from the three formerly recognised morphometrically-based species (sensu Worthy [1994]), with *D. struthoides* becoming the males, and *D. novaezealandiae* and *D. giganteus* 

together, the females, of *D. robustus* (in the South Island) and *D. novaezealandiae* (in the North Island). Site and regional totals for adult giant moa were assembled from Worthy (1997, 1998c, 1998b), and Worthy & Holdaway (1993, 1994, 1995, 1996, 2000). Samples for *Euryapteryx* and *Pachyornis geranoides* were assembled from lists in Worthy (1987) and Holdaway (2022).

#### Moa body size

Lengths of moa tibiotarsi were measured by MEA for genetically identified and sexed individuals (Allentoft *et al.* 2010; Holdaway *et al.* 2014; Allentoft *et al.* 2014). Body size series for the genetically sexed and radiocarbon dated – using median calibrated dates according to the SHCal20 curve (Hogg *et al.* 2020), applied in the OxCal 4.4 software (Bronk Ramsey 2009) – were smoothed using the LOESS (Local Regression) option in PAST© (Hammer *et al.* 2001). A smoothing factor of 0.35 was chosen as giving the best compromise between detail and excessive smoothing: 2.5 and 97.5 percentiles were plotted to compare potential ranges of body sizes at different times.

#### Statistical analyses of sex ratios

Only the *Euryapteryx* samples from Tokerau Beach (Fig. 1) and Tangatupura (Fig. 1) (Worthy 1987) and the giant moa data presented here were subjected to  $\chi^2$  Goodness of Fit analysis. Binomial Distribution analyses were conducted on all samples.

#### $\chi^2$ Goodness of Fit

 $\chi^2$  Goodness of Fit probabilities were calculated against assumed ratios of 1, 2, and 39/18 for data on giant moa (Bunce *et al.* 2003) and those accumulated for this study (Fig. 1), North and South Island *Euryapteryx* (Worthy 1987; Holdaway 2022) and *Pachyornis geranoides* (Worthy 1987).

#### Binomial probabilities

We assumed that the probability for each moa being incorporated in a fossil deposit reflected the sex ratio in the local population, at geographic scales down to the area around a site. For each "interment" from a population with a balanced ratio, the binomial probability for the "interment" being of a female was 0.5. Similarly, for a 29/16 ratio, P(9) = 0.667, for 39/16, P(9) = 0.75, and so on. Ratios of 1.19/16 and 1.49/16 were included to cover the range favoured by earlier studies. The probability of X females in a deposit containing Y members of the species is therefore the binomial probability for X on Y for a given postulated sex ratio. Binomial Distribution analyses were performed in R (R-Core-Team 2017), using the scripts in Appendix 1.



**Figure 3.**  $\chi^2$  Goodness of Fit probabilities for samples of femora (circles), tibiotarsi (triangles) and tarsometatarsi (squares) in relation to three hypotheses of sex ratio (assuming females larger) for (**A**), two North Island populations of *Euryapteryx*. Filled symbols, dotted lines, Tokerau Beach dunes Holocene; blue symbols, solid lines, late glacial Tangatupura swamp, and (**B**) samples of *Dinornis* spp. from areas and sites shown in Fig. 1. Data from Worthy (1987). Blue line: critical  $\alpha = 0.05$ .

#### RESULTS

#### Body size fluctuations in moa

Tibiotarsus length, and hence body size, of genetically-sexed individuals (Allentoft *et al.* 2010; Allentoft *et al.* 2014) changed at different times in the three emeids during the late Holocene of North Canterbury (Fig. 2). Females of *P. elephantopus* and *E. crassus* were largest at slightly different times in the first millennium CE (Fig. 2A, C), whereas female *E. curtus* were suddenly smaller *c.* 1000 CE.

There were too few adult males in the samples to identify any potential trends in size (Fig. 2), but the only male *P. elephantopus* was within the 2.5 percentile range for females about 2,000 years ago (Fig. 2A). The smallest female *E. curtus* was indistinguishable from the largest males just after *c.* 1000 CE (Fig. 2B). At times, the sexes of *E. crassus* were the same size (Fig. 2C).



Figure 4. Binomial distributions for sex ratios of Euryapteryx curtus and Pachyornis geranoides from Tangatupura Swamp, numbers of leg elements bv assigned by Worthy (1987) to sex by length. A, E. curtus femora; B-D, P. geranoides (B) femora; (C) tibiotarsi; (D) tarsometatarsi. Black, 19/18; light blue 1.19/18; light blue dashed 1.49/18; blue, 29/18; green, 39/18; orange, with symbols, 49/18. Vertical blue dotted line, number of females in sample; horizontal blue dotted line, critical value  $\alpha = 0.05$ .

#### $\chi^{\rm 2}$ Goodness of Fit

Euryapteryx curtus *at Tokerau and Tangatupura* 

The Tokerau Beach (dune deposit) samples of all three major leg bones yielded best fits to a balanced ratio (Fig. 3A). The femora from Tangatupura (swamp deposit) suggested a sex ratio of 29/13, but the proportions were also consistent, at very low significance, with a 19/13 ratio too. Numbers of large and small tibiotarsi and tarsometatarsi fit best to a 29/13 ratio (Fig. 3A), and the numbers of tibiotarsi could also represent a 39/13 ratio. Only the tarsometatarsi yielded an unequivocal 29/13 ratio (Fig. 3A).

Dinornis novaezealandiae *and* D. robustus *from sites and areas in Fig. 1.* Two thirds of the sex ratios derived by attribution by previous species identifications had best fits near a ratio of 19/16 (Fig. 3B). Only those from Upokongaro (lower Whanganui River), Pyramid Valley (North Canterbury), and South Canterbury had non-significant fits at 19/16. The South Canterbury and Upokongaro samples had best fits at 39/16 (Fig. 3B), whereas at Pyramid Valley the best fit was "off the scale" at *c*. 199/16. The two lowland, southwestern North Island swamp sites best represented a 29/16 ratio, but neither 19/16 nor 39/16 could be rejected on the small samples (Fig. 3B).

#### **Binomial distributions**

*Tokerau and Tangatupura* - Euryapteryx *and* Pachyornis Although  $\chi^2$  analysis supported balanced sex ratios Figure 5. Binomial distributions for sex ratios of *Euryapteryx curtus* in (A, B) the South Island, and (C, D) the Takaka area, according size distributions to of (A, C) femora, and (B, D) tarsometatarsi, in relation to number of females posited in samples. Conventions as in Fig. 4. Data from Holdaway (2022).



the three major leg bones of *E. curtus* from Tokerau Beach, binomial distributions gave less consistent results, with ratios  $>19/1\sigma$  being better supported for the femora and tarsometatarsi (Fig. 4A, *C*). If only tibiotarsi had been available, however, a balanced ratio would be solidly supported, with no likelihood of ratios of  $1.49/1\sigma$  or above (Fig. 4B).

Binomial analysis of the *Euryapteryx* femora from Tangatupura supported the  $2^{\circ}/1^{\circ}$  ratio favoured in the  $\chi^2$  results (Fig. 4D). In the same site, numbers of large and small sizes of all three major leg bones of *P. geranoides* (formerly *P. mappini*) all fit with a range of ratios of  $1.4-2^{\circ}/1$ . The tarsometatarsus sample was closest to an unequivocal  $2^{\circ}/1^{\circ}$  (Fig. 4E–G).

#### South Island - Euryapteryx

Femora and tarsometatarsi of *Euryapteryx* from the South Island (except North Canterbury), and from the "pit-trapped" sample from the Takaka area, all sexed by size (Holdaway 2022), yielded different sex ratios (Fig. 5). There were too few complete, measurable, tibiotarsi for analysis (Holdaway 2022). A 1.42/16 ratio was favoured for the South Island apart from Takaka and North Canterbury, but ratios between 1 and 22/16 were also possible (Fig. 5A). However, in the general South Island sample of tarsometatarsi, a 32/16 ratio had a highest probability, but any ratio between 22/16 and 42/16 in the living population was also possible (Fig. 5B).

Counts of femora and tarsometatarsi in the relatively small samples from the Takaka caves were consistent with female-biased ratios. These were centred on 39/16 for the femora, but again ratios of 2–49/16 were possible. There was only a marginal probability for 1.49/16 and none for any ratio closer to equality (Fig. 5C). Although the

highest probability for the sex ratio represented by the 10 tarsometatarsi was 29/13, the other ratios tested all had some level of support (Fig. 5D).

#### Dinornis spp.

Sex ratios in the samples of *Dinornis* presented by Bunce *et al.* (2003), varied in relation to the kind of sites (e.g. arrays of caves or of swamps) (Fig. 6). The large sample (87) from the Waitomo karst caves suggested a population ratio of 1.1–1.29/1ð (Fig. 6A), with low but still significant probabilities for the range 1–1.49/1ð. In the eastern hills of the North Island, the sex ratio was somewhere between 1.4 and 29/1ð (Fig. 6B), but there was a surplus of males from lowland North Island sites (Fig. 6C).

Swamps in the rain forest of the western North Island, yielded samples with sex ratios of >22/1 (Fig. 6D). In contrast, the number of females in the very large (316) sample from swamps in the dry eastern South Island suggested a ratio between 1.42/1 and 22/1, but neither was significant (P > 0.05). Only the unrecorded ratios of 32/1 and 42/1 were significantly supported (Fig. 6E).

Sex ratios in samples from caves on Takaka Hill (Fig. 6F), in Takaka Valley (Fig. 6G), in northwest Nelson (Fig. 6H), and in the Punakaiki karst (Fig. 6I) closer to equality (1–<1.4\P1\dit{0}, 1.4–2\P1\dit{0}, 1.1–1.4\P1\dit{0}, 1–1.1\P1\dit{0}, respectively). The small Takaka Valley sample could have come from a population whose sex ratio was anywhere between 1 and 4 females to 1 male (Fig. 6G).

Anomalously, perhaps, for a wetland site, the sex ratio in the sample of 18 from Bell Hill Vineyard was near balanced (Fig. 6J). Bell Hill Vineyard is <6 km from Pyramid Valley where females far outnumbered males (Fig. 1).



**Figure 6.** Binomial distributions for sex ratios of *Dinornis* spp. in areas and sites (**A**–**D**) the North Island (*D. novaezealandiae*), and (**E**–**J**) the South Island (*D. robustus*), according to sex allocations from "morphometric species", in relation to number of females posited in samples. Conventions as in Fig. 4. Data from Bunce *et al.* (2003).

#### Dinornis - Present samples

Of the sites and areas in Fig. 1, only a few – Waitomo karst, Takaka (Hill and Valley combined), West Coast, and Bell Hill Vineyard – were more or less directly comparable in location and extent to those in Bunce *et al.* (2003).

#### North Island (Fig. 7)

The much larger sample (126 cf. 87) for the caves in the dense Holocene rain forest in the Waitomo karst yielded a sex ratio in the range 1-1.12/13; ratios at or above 1.42/13 were excluded (Fig. 7A). The samples from Upokongaro (Makirikiri in **Figure 7.** Binomial probability distributions for sex ratios of *Dinornis novaezealandiae* in North Island areas and sites as shown in Fig. 1, in relation to the number of females posited in the samples.



Worthy [1989]), Riverlands, and Takapau Road (Fig.7 B, C, D, respectively) had ratios of >19/1ð. At Upokongaro, the spring bog upstream from the mouth of the Whanganui River, which was within rain forest until the 19<sup>th</sup> century, the sex ratio in the large (63) sample was 49/1đ (Fig. 7B). The sex ratio in the tiny (6) sample from Riverlands, nearer the river mouth, was centred on 29/1đ but again could have represented a population with ratios in the range 1–49/1đ (Fig. 7C). The population sex ratio reflected in the larger (40) sample from Takapau Road (Fig. 7D) was almost as ambiguous: all tested ratios between 19/1đ and 39/1đ were possible around an apparently favoured value of 1.4–1.59/1.

The small samples (12, 12, and 5) from the hill country and a lowland lake bed in the south-eastern North Island (Fig. 7E–G) also yielded contradictory results. Sex ratios in the (mostly) rock shelter sites in inland Hawke's Bay were biased toward males. Equality was barely supported (Fig. 7E). To the south, lowland Lake Poukawa had a balanced ratio on raw numbers (6:6), but ratios of 1.1-1.4?/1 $\sigma$  were well supported and 2?/1 $\sigma$  was possible. Only ratios of  $\geq$ 3?/1 $\sigma$  were excluded (Fig. 7F). The tiny (5) sample from Martinborough #1 pitfall cave had a similar pattern.

#### South Island (Fig. 8)

The relatively large (39, 51, respectively) samples from caves in the Takaka and West Coast karst yielded sex ratios very close to 19/1d. Ratios as high as 1.59/1d were possible, but very unlikely (Fig. 8A, B). East of the Main Divide, the pothole samples from the Annandale plateau (Worthy & Holdaway 1995) may represent a 29/1d ratio in the resident



**Figure 8.** Binomial probability distributions for sex ratios of *Dinornis robustus* in South Island areas (A) and sites (S) as shown in Fig. 1, in relation to the number of females posited in the samples. Conventions as in Fig. 4, plus dark green for 9:1 and wide black for 9.5:1 ratios, and dashed grey (in H) for 1:1.22 male-dominated ratio.

population, but the sample of only 17 meant that ratios of 1-49/13 were also possible (Fig. 8C).

The classic (Eyles 1955; Gregg 1972; Burrows 1989; Holdaway & Worthy 1997; Allentoft *et al.* 2009; Allentoft *et al.* 2010; Johnston 2014; Allentoft *et al.* 2014; Holdaway 2015, 2021a, 2021b; Johnston *et al.* 2022) lake bed site of Pyramid Valley had the most extreme raw sex ratio – 199/10 – for *Dinornis* of any site or area, (Fig. 8D). Less than 6 km away, the ratio in the small (10) sample from the stream bed/lake shore deposit at Bell Hill Vineyard was near 19/10 and ratios above 1.49/10 were not supported (Fig. 8E).

The ratio for the 17 individuals from sites (including caves and a swamp, (Worthy 1997) in South Canterbury was centred on 39/1*d*. The sample

size was too small to exclude ratios of anywhere between 2 and 49:1 $\sigma$  (Fig. 8F). The large (82) sample from a range of site types in Otago (Worthy 1998c) represented a population sex ratio of 1–1.1q/1 $\sigma$ (Fig. 8G). Immediately to the south, the sample from dunes, swamps, and caves in Southland (Worthy 1998b) may represent a balanced sex ratio, but there was a significant surplus of males in both  $\chi^2$  and binomial analyses (1q/1.21 $\sigma$ ,  $\chi^2 = 0.0144$ , P =0.904) (Fig. 8H).

The ranges of possible sex ratios represented by the samples of *Euryapteryx* from the South Island, Tangatupura, and Tokerau Beach, of *Pachyornis geranoides* from Tangatupura, and of *Dinornis* species in both islands are summarised graphically in Figure 9.
Figure 9. Summary of approximate probability density distributions for binomial probabilities of sex ratios in dinornithid and emeid moa from different areas and sites, summarised from Fig. 4, 5, 7, 8. Darkest, ratios with highest probability. Dinornis spp., D. novaezealandiae (North Island), D. robustus (South Island): Euryapteryx curtus both sensu lato, islands; Pachyornis geranoides, North Island. Green, swamp; blue, lake bed; yellow outline, dunes; black, caves or mixture of sites in sample. Sample sizes on bars. Pyramid V, Pyramid Valley; Bell Hill Vine, Bell Hill Vineyard; S Canterbury, South Canterbury; Tok, Tokerau Beach; Tanga, Tangatupura; Fem, femora; Tbt, tibiotarsus; Tmt, tarsometatarsus.



#### DISCUSSION General

RNH suggested recently (Holdaway 2022) that "A female-biased sex ratio in giant moa (*Dinornis* spp.) was confirmed by early ancient genetics studies (Bunce et al. 2003; Huynen et al. 2003)." The basic statistical analyses reported here suggest that that confidence was misplaced. Indeed, unfortunately, it is probably true to say that at present we do not have a good understanding of moa sex ratios. The vagaries of deposition and preservation, potentially different social organisations in moa (taxonomic) families and species, and uncertainty in non-genetic sexing of individuals combine to generate wide variation in estimates of sex ratio. While some of the variation results from the nature of the deposition and preservation of the samples, a substantial proportion is, as Bunce et al. (2003) and Allentoft et al. (2010) proposed, a potential source of information on moa biology.

That social and ecological spacing could drive the (sometimes extremely) biased sex ratios of birds preserved in swamps and lake beds, is supported, at least for Pyramid Valley, by the presence of four sets (dyads) of closely related, perhaps dominant, adult females (Allentoft *et al.* 2015). The birds were all adults and members of each dyad died at about the same time, which suggests that the lake may have been within the territory of "dynasties" of dominant females. Males may have been excluded, except for brief periods for mating.

#### Potential sources of bias of sex ratio in samples

Low sample size was responsible for by far the greatest uncertainty in the estimation of population ratios from the raw proportions of sexes. After that came issues of allocation of individuals to sex in non-genetic studies, and biological spacing effects on availability of each sex for incorporation in a fossil site.

## Adult body size and sex determination by size dimorphism

Trends in body size and episodes of sudden,

reversible, size change have not been reported in moa before. This study shows that body size in female moa could change. Male body size may also have changed but the samples are too small at present. Dwarfing of females and the presence of an occasional unusually large male (e.g. in *Emeus*) provide a source for the apparent overlap in sizes in many populations (Worthy 1987, 1994). The occasional overlap in size in undated samples raises the possibility of substantial error in the morphometric allocation of individuals to sex, in the absence of genetic data.

Genetically-sexed, time-stamped samples (Fig. 2), confirmed the extreme sexual size dimorphism proposed for *Euryapteryx* (Holdaway 2022), and in P. elephantopus and E. crassus, in North Canterbury. The lack of continuous series of genetically sexed males from the deposits probably reflects behavioural or ecological factors that rarely brought the males to the sites (Allentoft et al. 2010). The paucity of males precludes estimates of sex ratios from these genetically identified series, except perhaps for adult Euryapteryx in the 500 years after 250 BCE (Fig. 2). The samples from that period suggest a balanced sex ratio, in contrast to the significantly female-biased ratio in Bell Hill Vinevard. The juvenile sex ratio at Bell Hill Vineyard was apparently balanced (Allentoft et al. 2010) but the sample is too small to exclude other ratios. The effects of different combinations of males and females added to the juvenile sample from the site are shown in Appendix 2.

#### Differential miring from sexual differences in size

Worthy in Worthy & Holdaway (2002) asserted that the apparently balanced sex ratio in *Pachyornis geranoides* (then *P. mappini*) in Tangatupura resulted from a higher likelihood of the heavier females being mired in the swamp deposit. He concluded that the sex ratios of both species at the site were "about equal" Worthy, in Worthy & Holdaway (2002: 175).

"In the dunes at Tokerau Beach, where entrapment is not relevant, the smaller and larger sexes of *Euryapteryx curtus* are roughly in equal proportions, whereas in the swamp miring site of Tangatupura, the larger sex is more numerous (Fig. 5.24). In the same deposit, the proportions of *Pachyornis mappini* seem to be about equal. Assuming the lighter sex of *E. curtus* was less likely to be mired, we can infer that in both these species, the sex ratios were about equal."

The contention that larger moa (females) were more likely than smaller (males) to be included in swamps or lake beds is not supported by, for example, the presence of almost equal numbers of the smallest emeid (*Emeus crassus*) – which were smaller than male *D. robustus* – among the adult female *D. robustus* in Pyramid Valley (Allentoft *et al.* 2010).

The main factor in moa deposition in Pyramid Valley was probably predation by Haast's eagle (Hieraeetus moorei) (Holdaway 2015). The eagle was never present in the North Island (Holdaway 1992; Worthy & Holdaway 2002), but the neargolden eagle-sized extinct North Island harrier (Circus teauteensis) may have been a previouslyunrecognised predator on smaller moa there. The harrier was present in the eastern North Island in the Holocene (Worthy & Holdaway 2000) and probably during the late glacial period at Tangatupura swamp as well. Evidence of raptor predation is, unfortunately, unlikely to be present as the moa material consisted largely of leg bones. Raptor predation is revealed by damage to pelves and crania (Holdaway 2015).

#### "Ideal" sampling in 'pitfall' caves

An ideal sampling regime would permit deposition such that  $P(\text{each sex in deposit}) \cong$ *P*(each sex in local population). For large, flightless moa, pitfall trapping in caves is unlikely to have favoured either sex. An ideal arrangement would be sufficient numbers of traps spaced at intervals likely to include several home ranges and operating over time periods well above the individual life span. Cave systems, especially 'pitfall' sinkholes, in extensive areas of karst such as around Punakaiki, Takaka, and Waitomo are likely to have been closest to ideal. Many entrances were open for centuries, if not millennia (Worthy & Holdaway 1994). Preservation conditions within the caves ensured the survival of remains of most individuals up to the present. Similar sex ratios for giant moa were recorded in areas dominated by or exclusively involving cave deposits (Fig. 9). All these areas were covered in dense lowland rain forest during the Holocene.

#### Ecological and breeding system differences

The often-substantial differences between sex ratios of giant moa in wet and dry landscapes may indicate that something more than occupation of fixed home ranges by females (Allentoft *et al.* 2010) may be responsible for female dominance in deposits in drier areas. If breeding territory quality was important for moa, as suggested by the presence of related adult females in the same site (Allentoft *et al.* 2015), higher quality territories might have favoured deposition of females regardless of the adult sex ratio of the population. If there was a real bias towards females in North Canterbury, for example, the equal reproductive output of the sexes (Allentoft *et al.* 2010) would have required competition for males. If the apparent bias to females was an artefact of the territorial behaviour of giant moa in a population with a balanced sex ratio, then the equal reproductive output would follow.

Moore (2007) reported studies that showed that both sexes of the southern cassowary (*Casuarius casuarius johnsonii*), a living forest large ratite, defended permanent home ranges, but that home ranges could vary in size and shape seasonally and between years. Males bonded with two or more females simultaneously in a season. Some females bred simultaneously or sequentially with several males. There was a male-dominated sex ratio of 1:1.47 in a sample of 47 adults (Fig. 10) (Moore 2007), a ratio approached by giant moa in Southland (Fig. 8H). The cassowary is a clear warning that even a well-established adult sex ratio can conceal significant heterogeneity within a species' reproductive system.

In modern birds, territory quality (in the sense of food supply for the young) can influence the effect of the quality of the parent on any sex ratio bias in the offspring (Bell et al. 2014). If that effect existed in moa, territory quality could have been a major driver of sexual size dimorphism in moa and potentially also in determining the natal sex ratio. Only one moa juvenile sex ratio is available, the apparently balanced ratio in *Euryapteryx* at Bell Hill Vineyard (Allentoft et al. 2010), but see Appendix 2. This contrasted with an adult sex ratio biased to females. If either sex "sought" to bias the sex ratio of its offspring, the effort ultimately failed. However, holding the "best" territories - with the best food resources – and preferentially producing female offspring would have contributed to any female bias in sex ratio as well as size dimorphism.

Habitat quality could affect growth rates and body size in giant moa, resulting in the smaller "wet forest" female individuals formerly recognised as a separate species. The best territories may well have been in drier, high productivity areas, but near swamps or lakes, where there was rarely a water deficit. It is in such sites, even in wet climates, that the female bias in sample sex ratio is greatest. Habitat quality may also have driven differences in the adult sex ratio, but any effect may be obscured by deposition biases.

Effects of habitat on sex ratio could be explored by following the sex ratio of resident populations of moa taxa with broad ecological requirements, such as the South Island giant (Worthy 1990a; Worthy & Holdaway 2002), through time. Changes in the sex ratio of such resident populations as climate and vegetation/habitat changed around them after



**Figure 10.** Sex ratios of (**A**) 19:1.47*c*, southern cassowary (*Casuarius casuarius johnsonii*), from data in Moore (2007); (**B**) balanced juvenile *Euryapteryx curtus* in the Bell Hill Vineyard deposit.

the glaciation may show whether their sex ratio depended on habitat quality.

Samples of *D. robustus* are available from throughout the South Island (Fig. 2). The sex ratios could be followed by genetic sexing of radiocarbondated individuals. The advance of rain forest could be tracked by dating the southwards spread of the rain forest specialist moa *Anomalopteryx didiformis* (Worthy 1990b; Worthy & Holdaway 2002). *Anomalopteryx didiformis* was not present on Stewart Island (Worthy 1998a) so could not have reached Southland before Foveaux Strait was flooded 10,000 years ago. The giant moa was certainly resident in Southland before then as it did reach the island (Worthy 1998a).

A southward spread of *A. didiformis* would have had to circumvent the *Sophora microphylla* forest whose post-glacial expansion resulted in an extensive dry forest which dominated the central Otago landscape (Pole 2022). *Anomalopteryx didiformis* may have reached Southland well after rain forest developed there, but knowing when it arrived would provide a minimum date for changes in giant moa habitat.

#### Conclusions

The ambiguities in estimates of moa sex ratios identified here, and the possibility that sex ratios of some species may have differed between areas, suggest that attempts to model moa breeding systems and interpret evolution of sexual size dimorphism, e.g. Olson & Turvey (2013) are premature. Progress in understanding the reproductive biology of moa will be possible only when variables such as temporal variation in body size that affected sexual size dimorphism are better known. Genetic sexing of series of radiocarbondated individuals from a range of species through time and space is probably the only way forward.

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**APPENDIX 1:** R scripts used in the statistical analyses

#### A $\chi^2$ Goodness of Fit

#Chi-square Goodness of Fit for sex ratios of 1: 1.26, 1:1, 2:1, 3:1, 4:1, 5:1 #Small sample sizes may give error messages for some unlikely ratios observed <- c(31, 39) #Less than 1:1 expected <- c(.45, .55) #must add up to 1 chisq.test(x=observed, p=expected) # 1:1 expected <- c(.5, .5)#must add up to 1 chisq.test(x=observed, p=expected) # 2:1 expected <- c(.667, .333) #must add up to 1 chisq.test(x=observed, p=expected) #3:1 expected <- c(.75, .25) #must add up to 1 chisq.test(x=observed, p=expected) #4.1expected <- c(.8, .2)#must add up to 1 chisq.test(x=observed, p=expected)

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#### **B** Binomial probability distributions

#Binomial probabilities for sex ratios (female to male) in moa given sample size and number of females # Sample size n <- 40 #Range of number of samples, e.g., from 10 to 45 as here  $k \le seq(10, 45, by = 1)$ par(mar=c(5.1,6.1,4.1,2.1)) <sup>#</sup>Plot for ratios of 1:1, 1.1:1, 1.4:1, 2:1, 3:1, 4:1 and optional 19:1 #First 1:1 plot (k, dbinom(k, n, 0.5), type = "1", lwd = 8,xlim=c(10,45),xlab="",ylim=c(0,0.3),ylab="",col. lab="black", , cex.axis = 3.5,cex.lab=3,axes=F) #Then 1.1:1 lines (k, dbinom(k, n, 0.5238), type = "l", lwd = 10, col="light blue") #Then 1.4:1 lines (k, dbinom(k, n, 0.5833), type ="1", lty=6, lwd = 10, col="light blue") # 2:1 lines (k, dbinom(k, n, 0.667), type = "1", 1wd = 8, col="blue") #3:1 lines (k, dbinom(k, n, 0.75), type = "1", 1wd = 8, col="green") #4:1 lines (k, dbinom(k,n,0.8, log=FALSE),type = "b", col="orange", lwd = 8) lines (k, dbinom(k,n,0.9, log=FALSE),type = "1", col="dark green", lwd = 8) #Optional 19:1 ratio lines (k, dbinom(k,n,0.95, log=FALSE),type = "1", col="black", lwd = 12) #Plot number of females in sample = v abline(v=38, col="blue", lty=2, lwd=4) #Plot critical value = 0.05 abline(h=0.05, col="blue", lty=3, lwd=4) axis(side = 1, lwd = 4, las=0, cex.axis=3, mgp=c(3, 2, 0))axis(side = 2, lwd = 4, las=2, cex.axis=3)

This will generate a multi-curve plot. For the figures included here, "Export" was selected, then "Save as image" and "Height" reset to 750 pixels.

**APPENDIX 2. Part1.** Effects on binomial probabilities of minor changes in sample size and sex of individuals additional to those in the present Bell Hill Vineyard sample of juvenile *Eurypteryx curtus*.

**APPENDIX 2. Part 2.** Effects of increasing sample sizes with balanced sex ratios in the raw data on binomial probabilities of other sex ratios represented by the data.



### SHORT NOTE

## First record of a Baird's sandpiper (*Calidris bairdii*) in Eastern Polynesia

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Baird's sandpiper (Calidris bairdii; Family Scolopacidae) breeds from NE Siberia to Alaska, Arctic Canada, and NW Greenland (Birdlife International 2022). It migrates through North and Central America to spend the non-breeding season in South America (Jehl 1979), mostly in Argentina and Chile, where it is abundant in high deserts of the Chilean Andes (Moskoff & Montgomerie 2020). It is very rare in the Pacific regions, where only a few individuals have been reported. It was recorded as a vagrant in Hawaii (Donaldson 1991), New Zealand (six accepted records, Colin Miskelly pers. comm.), Australia (Milledge 1968; Smith & Swindley 1975; Curry 1979; Smith 1987; McKean 1984; Higgins & Davies 1996) and as far West as Papua New Guinea (Finch 1986) and Western New Guinea (Redman 2011). In contrast, this species has never been reported in Eastern Polynesia. On 10 November 2021, early afternoon, we observed an individual on the islet Tahuna Iti in the atoll of Tetiaroa, French Polynesia (Fig. 1).

Tetiaroa (17°00'S, 149°34'Ŵ) is situated 42 km North from Tahiti in French Polynesia (Fig. 1), and includes 12 islets (motu). A luxury hotel and up to 250 hotel crew members are present on one of the motu. The other 11 motu are uninhabited. A total of 10 seabird species breed in Tetiaroa, and Tahuna Iti hosts the only colonies of greater crested tern (Thalasseus bergii), sooty tern (Onychoprion fuscatus), and grey-backed tern (Onychoprion lunatus) on the atoll, with brown noddy (Anous stolidus), white tern (Gygis alba), red-footed booby (Sula sula), and brown booby (Sula leucogaster) also breeding on this motu. Great and lesser frigatebirds (Fregata minor and F. ariel), black noddies (Anous minutus), Pacific reef egrets (*Egretta sacra*), and invasive red-vented bulbul (Pycnonotus cafer) breed elsewhere on the atoll. Finally, five migratory (non-breeding) species are regularly observed on Tetiaroa: long-tailed cuckoo (Eudynamis tahitiensis), wandering tattler (Tringa incana), Pacific golden plover (Pluvialis fulva), bristle-thighed curlew (Numenius tahitiensis), and sanderling (Calidris alba). The seabirds of Tetiaroa are a tourist attraction, with up to 70 tourists arriving via charter boats from Tahiti several times a week to walk around Tahuna Iti (walking on the island is not permitted) to observe the seabird colonies (tour operators refer to the motu as "bird island"). In July 2021 we began conducting monthly surveys along the coastlines of the entire

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**Figure 1**. Society Islands in French Polynesia depicting the position of Tetiaroa. The position of Tahuna Iti, the islet where a Baird's sandpiper (*Calidris bairdii*) was observed in November 2021 (aka "Bird Island"), is indicated on the inset satellite image of Tetiaroa atoll. Note that the outer ring of coral reef that contains the lagoon and 12 islets is used here to define the perimeter of Tetiaroa. The position of the Society Islands in the Pacific is indicated on the inset map on the bottom left. (Satellite imagery of Tetiaroa: Google Earth).

atoll, during which we count both shorebirds and seabirds. We detected the Baird's sandpiper at 1323 h as we conducted the November survey around Tahuna Iti. A Pacific golden plover was also in the vicinity (sometimes <1 m from the sandpiper), allowing direct size comparisons. The Baird's sandpiper was actively foraging in the wrack line in a sandy area next to the greater crested tern colony. We observed the sandpiper for 17 minutes from a distance of 10–20 m, and the bird was still present and actively foraging as we left the area at 1340 h.

The sandpiper was clearly different from any other waders we have observed in French Polynesia. Differences in size, plumage, and behaviour were obvious, and we took several photos and one video which we then used for identification with the help of books and websites (including Sibley 2014; Billerman et al. 2021). The sandpiper was slightly smaller than a sanderling (C. alba), and had short black legs, an all-black bill and buffy-grey head and upperparts. It had a buffy breast and its dark eye did not contrast strongly with the surrounding feathers (contrarily to the eye of a sanderling in winter plumage). Its wings extended beyond the tail tip, and photos of the bird in flight revealed a dark stripe crossing the rump (Fig. 2). The latter characteristics together with the unmarked flanks allowed us to dismiss the white-rumped sandpiper (*Calidris fuscicollis*), the only other *Calidris* species that also has long wings extending beyond the

tail tip. During our observation, the bird was continuously and actively searching for food, alternatively pecking under the wrack or in the sand, then quickly walking a few steps, before pecking again. It seemed to ignore our presence. It always remained in the same wrack line five to ten meters from the water, although at some point, it took off for no obvious reason to land 5 m further in the same wrack line. The only Calidris species that regularly occurs in the Society Islands is the sanderling (C. alba), which shares the black legs and bill of the Baird's sandpiper, but is otherwise very different (we observed four sanderlings in Tetiaroa two weeks later). Other waders observed during our November count in Tetiaroa included wandering tattlers, Pacific golden plovers and bristle-thighed curlews, though only tattlers and plovers were observed on Tahuna Iti.

The Baird's sandpiper was still present on 15 November at 1135 h, about 200 m from the first observation site, resting on the sand about 20cm from the water. Therefore, we had the opportunity to validate our identification in the field, and as the bird took off to land 20 m further, we could also confirm the dark rump. The Baird's sandpiper was not detected again during our next monthly visits of the atoll, including on Tahuna Iti (we visited Tahuna Iti on 26 December 2021, and again in January, February and April 2022). It was not detected during a previous visit of the islet on 18 October 2021, either. Therefore, the bird stayed in



**Figure 2**. Baird's sandpiper (*Calidris bairdii*) observed in Tetiaroa, French Polynesia, in November 2021. Criteria that allowed identifying the species are shown with black or white arrows, and include the buffy breast (a), wings that are longer than the tail (b,c,d,f), the unmarked flanks (c,d) and the dark rump (e,h). Images g and j allow for size comparison with greater crested terns (*Thalasseus bergii*) and Pacific golden plover (right: *Pluvialis fulva*). A video of the Baird's sandpiper is available here: https://www.flickr.com/photos/188007943@N06/51981192063/in/dateposted/ (Photograph: Simon Ducatez).

Tetiaroa for at least six days, and at most 70 days (unless it was present but not detected).

To the best of our knowledge this is not only the first record of this species for French Polynesia, but also for all of Eastern Polynesia. This species is not mentioned in Thibault & Cibois (2017), and we could not find any mention of Baird's sandpiper for the region. In other areas of Oceania, both adults and juveniles have been reported, although they have a similar appearance in the non-breeding season (Cramp & Perrins 1977), making them difficult to distinguish. The grey tone and the whitish scaling of the upperparts and wing cover feathers of the bird observed in Tetiaroa tend to support the hypothesis of a first-year individual (Cramp & Perrins 1977). According to Jehl (1979), wing moult occurs in October to January in adults, so an adult bird would be expected to be in active moult in November. Therefore, the lack of growing primaries or secondaries on photos of the Tetiaroa bird in flight provides additional support to the bird being a juvenile. Juveniles and adults tend to follow different migratory routes, with adults believed to use a much narrower migration corridor in the centre of North America, suggesting that juveniles might be more likely to get lost in the Pacific (Moskoff & Montgomerie 2020). However, the migratory behaviour of this species is still poorly known, and more studies are required to better determine its migratory routes (e.g. by equipping individuals with transmitters) and its behaviour in the non-breeding range, which remains mostly unknown.

Although Eastern Polynesia covers a vast area and is less often visited by birdwatchers than most regions of the world, Baird's sandpipers are very rarely reported even in more intensively surveyed regions of the Pacific (e.g. Hawaii, Australia or New Zealand) so the presence of this species in Eastern Polynesia is highly unusual. During its regular migration, the Baird's sandpiper covers >8,000 km; >11,000 km for individuals wintering in Tierra del Fuego. Tetiaroa is >7,000 km from the regular wintering area of the Baird's sandpiper in South America, and >8,500 km from its closest breeding grounds in Alaska, distances that are therefore within those covered by this species during its migrations. Flying over the Pacific Ocean instead of land, however, means no or very limited options for stopovers, making this observation particularly remarkable for this species.

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## SHORT NOTE

## The importance of a wastewater treatment wetland to the changing status of New Zealand scaup (*Aythya novaeseelandiae*) in the Nelson/Tasman region

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The status of the endemic New Zealand scaup (*Aythya novaeseelandiae*) has recently been reviewed by Greene (2021) who concluded that the total population was probably about 11,000 birds and that the population was apparently declining, at least in part, as a result of increasing eutrophication of lakes. Here we report changes in the status of New Zealand scaup over recent decades in the Nelson/Tasman region. Our results, which demonstrate a considerable increase in the local New Zealand scaup population, contrast markedly with those of Greene (2021).

New Zealand scaup (hereafter scaup) was recorded by Moncrieff (1938) as occurring in Nelson Province, but without any further details. Walker

(1987) reported it as being 'found mainly on inland lakes and ponds with some cover round the edges. Commonly seen on the main lakes of Nelson Lakes National Park and north-west Nelson'. Owen & Sell (1985) recorded it as a 'rare visitor to the coastal areas of the Nelson region', and noted one shot in 'The Traverse' between Rabbit and Rough Islands as the first record for Waimea Inlet. Butler et al. (1990) recorded 'small populations of scaup may be found at several lakes in the region, particularly Lake Rotoroa in Nelson Lakes National Park, Lake Matiri near Murchison, Druggans Dam in Golden Bay, and Kaihoka Lakes near Whanganui Inlet. Some birds breed, but many are transient so that it is hard to be sure of seeing them at any one location'. These descriptions reflect the mapped distribution of the species in the first New Zealand Atlas 1969–1979 (Bull et al. 1985).

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**Figure 1.** Distribution of New Zealand scaup (*Aythya novaeseelandiae*) in the Nelson/Tasman region (eBird records to October 2021), and location of Nelson North Wastewater Treatment Plant (NNWWTP) and associated wetlands.

The mapping of scaup distribution in 1999–2004 revealed birds near Nelson city for the first time but there were no breeding records (Robertson *et al.* 2007). Records from the online sightings database eBird show that scaup is now widely distributed around Nelson, with many small ponds supporting up to a few tens of birds (eBird 2021a) (Fig. 1). Up to October 2021, scaup have been recorded from 23 out of a total of 115 Atlas grid squares in the Nelson/Tasman region, including all sites where they were recorded in the 1960s and 70s (eBird 2021b).

One site in particular has shown a very dramatic increase in scaup numbers; the Nelson North Wastewater Treatment Plant (NNWWTP). The NNWWTP oxidation ponds at Wakapuaka (41.2049°S, 173.3291°E), covering 26 ha, were constructed in 1979. The pond layout, but not total area, was subsequently modified in 1996. The wastewater treatment plant had a significant upgrade in 2009, when two ~7 ha wetland areas were established. The first planting of the wetlands occurred in June 2009, but was largely unsuccessful, due in part to plants being uprooted by black swan (*Cygnus atratus*) and pūkeko (*Porphyrio melanotus*). Further planting was undertaken in January and

February 2010. The original design had vegetation throughout much of the wetlands and initial planting comprised *Schoenoplectus tabernamontani*, *Eleocharis sphacelata*, and *Baumea articulata*, while along the pond margins plantings included *Cyperus* and *Carex*. Currently the ponds only have riparian vegetation, with substantial areas of flax (*Phormium tenax*) on the banks. The ponds are approximately 1.5 m deep with an earth bottom sealed with bentonite; treated wastewater circulates through them before being discharged to Tasman Bay.

Regular observations of waterfowl at the NNWWTP since January 2008 show the population of scaup growing from zero to over one thousand birds in 2021 (Fig. 2). The first record was of three birds on the oxidation ponds on 14 October 2008. In 2010 there were six records of up to three birds, all on the oxidation ponds. The first scaup recorded in the wetlands were in mid-May 2011 when 50 were reported (John Campbell *pers. comm.* to PF), and on 20 June 2011, 24 were present. Since January 2012, scaup have been recorded consistently in the wetlands, with generally smaller numbers in the oxidation ponds.

Breeding by scaup was first recorded on 28



**Figure 2.** Maximum number of New Zealand scaup (*Aythya novaeseelandiae*) recorded each year at Nelson North Wastewater Treatment Plant and wetlands, 2007–2021.

December 2012 when a female with four nearly fully grown young were seen in the wetlands. Breeding has been recorded every year since, with at least 22 broods seen on 16 November 2020; one in the oxidation ponds, the others in the adjacent wetlands. A total of 162 broods have been recorded between 2013 and 2021, 97.5% of which were in the wetlands, with the remainder in the oxidation ponds. Scaup favour nesting in dense cover near water (Williams 2005), and Guthrie-Smith (1927) noted them nesting among the base of flax plants, thus the spreading and maturing of those planted at the wetlands is likely to provide increasingly favourable conditions.

No studies have been made of the aquatic invertebrate communities in the Wakapuaka oxidation ponds and wetlands. On 17 September 2021, we collected five core samples from within 5 m of the edge of the wetland ponds. These were washed over a 1 mm mesh sieve and all living organisms retained. We recovered small oligochaete worms, and chironomid larvae ('blood worms') of two species: *Chironomus zealandicus* (64.2% of individual larvae counted) and the currently undescribed '*Chironomus* sp. A' (35.8%). The density of chironomid larvae averaged 3,310 per m<sup>2</sup> (range 1,655–4,329 per m<sup>2</sup>), and oligochaetes averaged 815 per m<sup>2</sup>. *Chironomus zealandicus* is the commonest midge occurring at wastewater treatment plants (WWTPs) in New Zealand (Garton & Bickers 2016; Macdonald *et al.* 2017) and can occur at very high densities; for example, Robb (1966) recorded densities of third and fourth instar larvae of up to 16,380 per m<sup>2</sup> at the Bromley WWTP ponds, Christchurch.

Little is known of the diet of scaup, but Wakelin (2004), who examined gizzard samples of 19 birds, found that food taken varied between sites but was similar within sites - main items included snails, chironomid larvae, and Trichoptera larvae. Williams (2005) also recorded scaup taking the tips of aquatic vegetation and also suggested that they may eat zooplankton, which are present in WWTPs. Chironomids may comprise an important part of the diet of Aythya ducks elsewhere (Bengtson 1971; Nilsson 1972; Laughlin 1973; Gardasson & Einarsson 2004). Giles (1990), in a laboratory situation, found that ducklings of the tufted duck (Aythya *fuligula*) aged 14–25 days could fulfil their daily food requirements by 36 minutes of underwater foraging at a density of chironomid larvae of 16,000 per m<sup>2</sup>. Full grown tufted ducks average c. 17% heavier than New Zealand scaup (Robinson 2005) and so food requirements of scaup ducklings may be less than recorded for tufted duck. Day-old New Zealand scaup ducklings can dive to about 2

m (Oliver 1955) so most, if not all, of the wetland floor would be available for foraging. We therefore suggest that the population of chironomids in the Wakapuaka wetlands is contributing to the large, and increasing, population of scaup at this site.

Observations at NNWWTP are similar to those by Crossland (2013) who reported very high numbers of scaup at the Bromley oxidation ponds, Christchurch, which also have associated extensive wetlands. The current population in Nelson and the numbers reported in Christchurch by Crossland (2013) account for about half of the global population estimated by Greene (2021). Robertson & Makan (2022) have questioned this figure, and suggested that the population estimate of 20,000 birds given by Heather & Robertson (2015) may be conservative. Whatever the actual number, it is apparent that the number of scaup at the Nelson and Bromley WWTPs account for a significant proportion of the global population. Both sites are of international importance, meeting Criterion 6 [supporting 1% or more of a population of one species] of the Ramsar Convention on Wetlands of International Importance Especially as Waterfowl Habitat (Ramsar Secretariat 2010).

Greene (2021) suggested that eutrophication and worsening water quality in lakes may be adversely affecting scaup numbers. In contrast, it would appear that the high nutrient conditions in wetlands associated with WWTPs are favouring scaup. Pond-based WWTPs are designed to remove nutrients through assimilation in plants and microbial activity in sediments and depend upon a balancing of algal production and phytoplankton grazers (principally cladocerans and rotifers) for optimal operation. Climate change, in particular increase in temperature, is expected to affect the biological operation of WWTPs (Hughes *et al.* 2021); if chironomid populations decline this could potentially impact scaup.

Most WWTPs in New Zealand are pond-based (Ministry for the Environment 2020), with over 200 waste stabilisation pond (oxidation pond) water treatment plants across the country (Archer 2015). Differences in design and operating practices probably account for what appear to be highly variable numbers of scaup occurring at WWTPs. It is notable that scaup are only rarely recorded from the Bell Island WWTP (41.2924°S, 173.1720°E) located *c*. 16 km from Wakapuaka WWTP (a record of 152 on 13 November 2021 was exceptional). Both of these facilities have stabilisation ponds with clay bottoms and embankments that are concrete-faced for wave protection, but the Bell Island site has no associated wetland area.

Wetlands have been incorporated into a number of treatment plants across the country (Archer & Mara 2003). There would be value in undertaking a national assessment of scaup occurring at WWTPs and associated wetlands across New Zealand.

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- **Keywords:** New Zealand scaup, *Aythya novaeseelandiae*, population estimate, wastewater treatment plant, eutrophication

### SHORT NOTE

## How many New Zealand scaup (*Aythya novaeseelandiae*) are there?

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From an analysis of many published and unpublished counts of New Zealand scaup (pāpango, Aythya novaeseelandiae), Greene (2021) concluded that there are about 11,000 birds nationally and stated that the "...estimate [of] 5,000-10,000 birds (Marchant & Higgins 1990; IUCN 2016) is more accurate than the estimate of 20,000 birds (Heather & Robertson 2015)". The population size of a species is important because it is one of the factors used to determine the national and international conservation status of species (Townsend 2008; IUCN 2016) and hence management priorities. For waterbirds, a threshold of 1% of the population is used to help determine if a wetland is of international significance under the Ramsar Convention (Wetlands International 2012). To meet this 1% threshold, a wetland would have to regularly support c. 75, 110, or 200 New Zealand scaup, depending on which of the three population estimates for the species is accepted.

Greene's estimate of 11,000 birds appears to be derived by simply adding the approximate numbers of birds at four principal strongholds where birds had been counted systematically over recent decades: *c*. 5,000 birds on the Rotorua Lakes (1984–2018), up to 965 birds (1987–1998) on the Bromley Sewage Ponds in Christchurch, *c*. 2,000 birds on the Ashburton lakes (1984–2018) and *c*. 3,000 birds combined on Lakes Alexandrina, McGregor, and Grasmere in the Canterbury high country (1987–1993).

The counts from the Rotorua Lakes complex shown in Figure 7 (p.120) of Greene (2021), not in Figure 5 (p.115) as stated in the text, appear to be incorrect. The total number of New Zealand scaup counted systematically on the 18 lakes between 1985 and 2018 has varied between 3,061 and 7,413 birds (Sachtleben *et al.* 2014; Department of Conservation, *unpubl. data*). The overall rate of increase has been 1.8% per annum, but the numbers showed moderate stability at *c.* 4,000 birds from 1985 to 2006, followed by a big step up to counts of *c.* 7,000 birds in 2011 and 2018 (Fig. 1).

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**Figure 1.** Changes in the numbers of New Zealand scaup (*Aythya novaeseelandiae*) recorded on 18 lakes in the Rotorua Lakes complex, 1985–2018. The average increase was 1.84% per annum between 1985 and 2018 (r = 0.68, P = 0.09, n = 7).

We also note that the 965 birds at Bromley Sewage Ponds from 1987–1998 now appears to be an underestimate. After the first pair bred there in 1991, the breeding population on islands in the ponds had built up to over 200 pairs by 2002 (Crossland 2005). Systematic monthly counts between August 2009 and July 2010 recorded a mean of 4,051 New Zealand scaup (range, 2,594– 5,739) in and around the ponds (Crossland 2013).

Given that Greene (2021) collated data from 12,145 site visits spread across New Zealand, the approach to derive a national estimate from a very limited part of the species' range is surprising because it ignores all the New Zealand scaup living away from these four principal strongholds. This would be akin to estimating the number of bartailed godwits (*Limosa lapponoica*) in New Zealand by adding up the mean numbers seen at the top four sites (Kaipara Harbour, Manukau Harbour, Farewell Spit, and the Firth of Thames) in the summers of 2005–2019. This would have given a national population estimate of 42,307 birds rather than the mean of 77,796 birds from all sites counted (Riegen & Sagar 2020).

The current New Zealand Bird Atlas, organised by Birds New Zealand, and displayed on the eBird website (https://ebird.org/atlasnz/map/ nezsca1), provides an up-to-date picture of the distribution and numbers of New Zealand scaup nationally. Perhaps an atlas scheme such as this prompts ornithologists to visit more sites than usual, including visits at a range of seasons and, especially, to record the numbers of all bird species seen. Many of the eBird records with New Zealand scaup are, however, spot counts or travelling counts that do not purport to systematically cover the entire wetland. We expect that counts at most sewage ponds and at small lakes with clear margins are likely to be complete counts, but many of the counts from lakes with complex shorelines and overhanging trees are likely to be underestimates.

Many New Zealand scaup are found outside of the four strongholds identified by Greene (2021). In the North Island, an analysis of all NZ Bird Atlas eBird records from 1 June 2019 to 30 November 2021 reveals that ≥100 New Zealand scaup have been recorded at 11 sites (Table 1) away from the Rotorua Lakes complex that was used by Greene (2021) to estimate the national population. At one of the 11 sites, Lake Taupo, counts of ≥100 New Zealand scaup were recorded at each of eight different locations around the lake at various dates, with a maximum single estimate of 620 birds at Tokaanu Wharf (38°57'S, 175°46'E) in November 2021. This suggests that the population has grown since 136 adult and 35 subadult New Zealand scaup were counted in a lake-wide survey in January 1986 (John Innes *pers. comm.*). The highest count away from the Rotorua Lakes complex was of 770 birds at Lake Horowhenua, Levin, in May 2020, followed by another count of 560 birds less than a week later. Twenty-one other North Island sites each had maximum counts of 50-99 New Zealand scaup between June 2019 and November 2021 (Table 1).

<b>Table 1.</b> North Island sites, excluding the Rotorua lakes complex, with maximum counts of $\geq$ 50 New Z	Lealand scaup in
NZ Bird Atlas eBird records between June 2019 and November 2021. The province, site, maximum co	unt, and date of
the maximum count is given. SP = Sewage Ponds	

Region	Site	Max count	Date
Northland	Kai Iwi Lakes	114	23 June 21
Auckland	Western Springs	66	8 January 20
South Auckland	Mangere SP	62	8 August 21
Bay of Plenty	Golden Cross Mine	64	15 May 21
	McLaren Falls Park	125	25 October 20
	Tauranga SP	76	28 June 20
	Kawerau SP	51	26 July 20
	Lake Aniwhenua	94	24 October 20
Waikato	Lake Taharoa	160	18 July 19
	Whakamaru Dam	51	5 January 20
	Aratiatia Dam	90	23 June 19
Volcanic Plateau	Waikato River exit, Lake Taupo	145	7 November 20
	Taupo Waterfront, Lake Taupo	204	10 September 20
	2/3 Mile Bays, Lake Taupo	128	21 June 20 & 24 November 20
	Motuoapa, Lake Taupo	150	1 May 20
	Tokaanu Wharf, Lake Taupo	620	2 November 21
	Kinloch, Lake Taupo	125	4 March 21
	Whahaipo Bay, Lake Taupo	135	27 June 21
	Acacia Bay, Lake Taupo	126	27 March 21
Gisborne	Tuai Power Station	55	8 July 20
Hawkes Bay	Lake Lopez	65	13 July 19
Wairarapa	Henley Lake, Masterton	124	29 May 20
	Kourarau Dam	112	17 June 19
	Pounui Lagoon	150	2 May 20
Taranaki	Lake Managamahoe	112	29 April 20
	Leperton SP	57	2 June 20
	Stratford SP	110	13 October 20
	Eltham SP	50	21 April 21
	Lake Rotokare	80	31 May 21
	Lake Opunake	64	22 July 21
	Patea SP	60	3 & 17 April 21
Whanganui	Standalone Pond	53	2 July 19
	Donovan's Wetland	72	10 December 19
Manawatu	Lake Omanu, Foxton	52	23 July 20
	Palmer Rd Ponds, Foxton	131	1 May 21
	Lake Horowhenua	770	14 May 20
	Waikawa Ponds	64	25 May 21
Wellington	Otaki SP	88	18 April 21
	Waikanae SP	89	11 February 21

In the South Island, New Zealand scaup have been recorded in large numbers at many sites outside of the three strongholds used by Greene (2021) to calculate the national population. At 31 different sites,  $\geq 100$  New Zealand scaup have been counted, and at a further 27 lakes or ponds  $\geq$ 50 birds have been recorded between June 2019 and November 2021 (Table 2). Most notable, given that the sites were not mentioned by Greene (2021), were the sewage ponds serving Nelson, Blenheim, and Invercargill, each of which have had maxima of 600 birds or more. At the Nelson Sewage Ponds, over 450 New Zealand scaup have been recorded in NZ Bird Atlas eBird records in every season, and a maximum of 1,262 birds was estimated to be present in June 2021 (Field et al. 2022). Up to 600 New Zealand scaup were seen at the Blenheim Sewage Ponds in February 2021; and 605 were seen at the Invercargill Sewage Ponds, also in February 2021. Another important South Island site not mentioned by Greene (2021) was the Te Nohoaka o Tukiauau/ Sinclair Wetlands, south of Dunedin; New Zealand scaup were the most common waterfowl species there, with a maximum of 617 birds counted in winter 2015 (Thompson & McKinlay 2021).

Greene (2021) claims that populations of two other diving birds that share similar habitats, Australasian crested grebe (*Podiceps cristatus*) and dabchick (Poliocephalus rufopectus), have declined nationally, and suggests that the New Zealand scaup population is also likely to be in decline due to a deterioration in water quality nationally. Although we agree that the quality of many freshwater wetlands has declined because of land management practices in their catchments, the populations of all three species have increased over recent decades. The Australasian crested grebe population increased in the South Island from a low of c. 250 birds in 1980 to c. 350 in 2004 (Jensen & Snovink 2005) and to c. 600 birds by 2012 (Heather & Robertson 2015), and they have recently re-established in Marlborough (NZ Bird Atlas). Dabchicks have increased in the North Island to the point where their national conservation status was downgraded from 'Nationally Vulnerable' in 2012 (Robertson et al. 2013) to 'At Risk - Increasing' in 2016 (Robertson et al. 2017), and they have started to re-colonise the northern South Island (Heather & Robertson 2015). Part of the increase in the numbers of dabchicks, at least in the southern North Island, has been attributed to the construction of sewage oxidation ponds that provide conditions that favour wintering birds (Stidolph & Heather 1988). Dabchick numbers on the Rotorua Lakes complex have doubled from 364 birds in 1985 to 757 birds in 2018 (Sachtleben et al. 2014; Department of Conservation unpubl. *data*). It is perhaps no coincidence that many of the sites favoured by dabchicks and New Zealand scaup are sewage oxidation ponds where the water quality, as perceived by humans, is exceedingly low. Attributing a decline in New Zealand scaup numbers to a lowering of water quality nationally is not supported by data showing an overall population decline, and nor does it fit with the observation that many of the strongholds used by the species today are sites with exceptionally poor water quality rather than pristine lakes.

Because there have been only five band recoveries of wild New Zealand scaup (unpublished data in the FALCON database of the NZ National Bird Banding Scheme), little is known about the seasonal movements of New Zealand scaup. Four recoveries were within 25 km of the banding site and one (S-51627) was 194 km away but, because the bird had been banded at a captive-rearing facility at Pukaha Mt Bruce, the bird may have been released closer to the recovery site in Taranaki. Given the magnitude of fluctuations in counts at particular sites that are easy to census (e.g. Otaki Sewage Ponds, HAR pers. obs.), we expect that there will be at least local movement between nearby sites such as between the Bromley Sewage Ponds and the Pegasus lakes, Kaiapoi lakes, and Northbrook near Rangiora, all within 25 km of one another. There may be much longer seasonal movements judging by the exceptional influx of up to 770 New Zealand scaup to Lake Horowhenua in May 2020, where very few New Zealand scaup are normally present (HAR pers. obs.).

Regardless of movements within or between regions, it seems very likely that the 11,000 birds estimated by Greene (2021) is an underestimate of the true national population, and the estimates of 5,000–10,000 birds by Marchant & Higgins (1990) and Wetlands International (2012) are likely to be serious underestimates. Heather & Robertson (2015) repeated their earlier estimate of 20,000 birds from the 1990s (Heather & Robertson 1996) but noted that the population was increasing. They attributed this to the construction of hydroelectric dams, irrigation dams and oxidation ponds which all provided valuable new habitat, and through new populations being established from a captive-breeding programme run by Ducks Unlimited. A nationwide increase in predator control in and around wetland habitats is also likely to have contributed to an increase in New Zealand scaup.

The national distribution of New Zealand scaup appears to have increased substantially between the 1969–1979 NZ Bird Distribution Atlas (Bull *et al.* 1985) and the 1999–2004 NZ Bird Distribution Atlas (Robertson *et al.* 2007), and then again to the current distribution shown on the NZ Bird Atlas eBird website. **Table 2.** South Island sites, excluding the three strongholds identified by Greene (2021) at Bromley SP, Ashburton Lakes, and Lakes Alexandrina, McGregor and Clearwater combined, with maximum counts of  $\geq 50$  New Zealand scaup in NZ Bird Atlas eBird records between June 2019 and November 2021. The region, site, maximum count and date of the maximum count is presented SP = Sewage Ponds

Nelson West Coast	Site	Max count	Date
West Coast	Nelson SP	1,000	26 June 20
West Coast	Bell Island SP	152	13 November 21
West Coast	Best Island SP	87	10 September 19
	Lake Brunner	66	26 November 20
	Hokitika SP	122	8 November 20
Marlborough	Grovetown Lagoon	65	8 March 21
	Opaoa River/ Blenheim SP	600	2 February 21
	Taylor Dam	80	6 October 19
	Delta Lake	54	18 September 21
	Lake Elterwater	220	18 August 21
Lowland Canterbury	St Anne's Lagoon	200	9 June 19
	Cheviot SP	50	2 July 20
	Pegasus Wetlands	271	15 July 20
	Tutaepatu Lagoon	77	10 September 19
	Northbrook, Rangiora	115	17 June 19
	Kaiapoi lakes	169	22 March 20
	Travis Wetland	50	13 June 21
	Westlake Reserve, Halswell	71	22 March 21
	Lincoln Wetlands	88	27 July 21
	Lake Crichton, Dunsandel	70	1 August 21
	Lake Forsyth	365	21 September 21
	Lake Ellesmere	501	29 July 20
	Cooper Lagoon	50	24 April 20
	Lake Hood, Ashburton	360	22 March 20
	Otipua Wetland, Timaru	51	28 May 20
	Lake Wainono	144	23 November 19
	Bell's Pond, Glenavy	60	21 July 21

Table 2. continued			
Region	Site	Max count	Date
Inland Canterbury	Lake Pearson	180	15 August 20
	Lake Sarah	105	14 February 21
	Lake Evelyn	152	7 February 21
	Lake Selfe	69	9 August 20
McKenzie Basin	Lake Pukaki head	100	2 April 21
	Wairepo Arm, Lake Ruataniwha	270	24 November 21
	Lake Middleton, Lake Ohau	200	11 August 21
	Lake Benmore	319	28 July 19
	Birchwood Ponds, Upper Ahuriri	66	17 October 21
Southern Lakes	Wanaka Waterfront	80	23 December 20
	Lowburn Inlet, Lake Dunstan	170	20 December 20
	Lake Hayes	89	5 October 20
	Queenstown SP	170	13 February 21
	Queenstown Waterfront	69	23 July 19
	Glenorchy Lagoon	83	2 July 20
	Te Anau Downs	345	6 March 20
	Te Anau SP – Upukerora River	83	22 September 21
	Te Anau Marina & Waterfront	141	4 July 20
	Supply Bay, Lake Manapouri	80	17 April 21
Lowland Otago	Tomahawk Lagoons, Dunedin	128	28 July 21
	Lake Waihola	307	30 May 20
	Lake Tuakitoto	65	11 April 21
	Clutha Lagoons, Balclutha	373	23 May 20
	Greenall Road Pond, Balclutha	79	5 July 20
Southland	Waituna Lagoon	100	23 May 21
	Invercargill SP	605	9 February 21
	Tip Lagoon, Invercargill	452	12 May 21
	Oreti Estuary	78	1 May 20
	Riverton SP	06	2 June 20
	Te Waewae Lagoon	72	6 November 21
	Redcliff/Lake Rakatu	425	9 August 20

In the first atlas to 1979, New Zealand scaup were recorded from just ten 10,000-yard grid squares in the North Island south of a line from about New Plymouth to Napier, and in 13 squares in the lowland eastern and southern South Island between about Blenheim to Riverton, to the west of Invercargill. By the time the second atlas was completed in 2004, there were records of New Zealand scaup from 78 10-km grid squares in the southern North Island and 90 squares in the lowland eastern South Island. Estimates of local occupancy probability increased significantly (more than doubled) in both the North Island and the South Island between the first two atlases (Walker & Monks 2018). Even though the current atlas had run for only 27 months to 30 November 2021, there had already been records from 86 southern North Island squares and >170 squares in the lowland eastern and southern South Island, suggesting an ongoing range expansion of the species.

The population in the Rotorua Lakes complex appears to be increasing (Fig. 1), as does the Ashburton Lakes population (see Fig. 7 of Greene [2021]), and there was a 30-fold increase in New Zealand scaup numbers in and around Christchurch, from c. 200 birds in the 1980s to almost 6,000 in the early 2000s, with the Bromley Sewage Ponds being an important breeding site (Crossland 2005). Together with the numerous eBird records of many New Zealand scaup at sites away from these strongholds, the 20,000 birds estimated by Heather & Robertson (2015) may be conservative. In the New Zealand Threat Classification System (Townsend et al. 2008), New Zealand scaup has long been assessed by expert panels as being 'Not Threatened' (Miskelly et al. 2008; Robertson et al. 2013; Robertson et al. 2017; Robertson et al. 2021) and, with their numbers and range apparently increasing, we see no reason to change that classification.

A good estimate of the national population of New Zealand scaup could be obtained by Birds New Zealand working with organisations such as Fish & Game New Zealand, Ducks Unlimited, and the Department of Conservation, to undertake a coordinated and systematic national count. This should be done over as short a period as possible at as many sites as possible, but especially including the four strongholds identified by Greene (2021) and the 90 sites nationwide with maxima of  $\geq$ 50 New Zealand scaup identified in this paper. Large sites, such as Lake Taupo, and sites within 25 km of one another, should be counted within the space of a few hours to reduce double-counting or undercounting. At the same time, it would be useful to count both Australasian crested grebes and dabchicks, which often share the same habitats, to better estimate their current national populations.

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- **Keywords:** New Zealand scaup, pāpango, *Aythya novaeseelandiae*, population, distribution, threat status

### SHORT NOTE

## An observation of a juvenile feeding an injured adult in pūkeko (*Porphyrio melanotus melanotus*)

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Altruism is defined as a behaviour which increases the fitness of recipients while decreasing that of the performer (Hamilton 1964). Inclusive fitness theory states that such behaviours are likely to have evolved primarily between closely related kin (Hamilton 1964; Trivers 1971; Gardner *et al.* 2011), or individuals with shared reproductive interest (Dyble *et al.* 2018). Altruistic behaviours are generally poorly understood, with the sole exception of humans (Warneken & Tomasello 2009). Indeed, there is considerable debate about the evolution of altruism in nonhuman species; however, there is growing evidence that this mechanism is phylogenetically ancient (see de Waal 2008).

Cooperatively breeding species display some of the most conspicuous examples of altruism (Koenig & Dickinson 2016). In some of these species, "helpers" appear to discriminate kin from non-kin and adjust the amount of help in response

to the degree of relatedness. Avian examples of this include long-tailed tits (Aegithalos caudatus; Leedale et al. 2018), chestnut-crowned babblers (Pomatostomus ruficeps; Browning et al. 2012), and bell miners (Manorina melanophrys; Wright et al. 2010). However, there are also reports of altruistic behaviours in cooperatively breeding species (both avian and non-avian), where the helper does not appear to discriminate between recipients based on degree of relatedness; i.e. they are indiscriminate altruists, and will assist conspecifics regardless of relatedness (Wright et al. 1999; Legge 2000; Canestrari et al. 2005; Vitikainen et al. 2017; Duncan et al. 2019). However, in most of these studies (6 of 7) the altruistic behaviours are directed towards the care of young, not adult group members. If an individual spontaneously helps another individual in distress by responding to its begging or distress signals this is interpreted as potential "directed altruism" (de Waal, 2008). Furthermore, if this behaviour is directed towards an individual regardless of their relation to the performer then it is considered "indiscriminate altruism" (Duncan et al. 2019).

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Pūkeko (Porphyrio melanotus melanotus) often live in cooperatively breeding and polygynandrous groups and defend a shared territory (Craig 1980a). If there are multiple breeding females present in a pūkeko group they may all lay in a single nest, a phenomenon known as joint-laying (Craig 1980; Vehrencamp & Quinn 2004; Sweeney et al. 2022), or closely adjacent "satellite" nests. Adults form mixed-sex dominance hierarchies (Craig 1980). Males are typically dominant over females; breeding males are highest ranked, breeding females and non-breeding males are of comparable rank, and non-breeding females typically rank lowest (Jamieson & Craig 1987; Dey et al. 2014). North Island populations are large, sedentary, comprised of related members, and defend territories yearround (Craig & Jamieson 1988; Craig & Jamieson 1990; Lambert et al. 1994; Jamieson 1997).

From September 2017 - October 2020 we monitored a pūkeko population at Watercare Walkway, Māngere, New Coastal Zealand (36.95052°S, 174.76543°E). Captured birds were individually banded with unique colour combinations on both legs. During experimental trials, double-sided, step-activated Chooketeria feeders (Chooketeria Ltd, NZ) were placed in territories and behaviour was recorded using Bushnell HD aggressor trail cameras with 0.2-second trigger speed, 0.5s recovery rate, and an extended nighttime photo range (Bushnell Corporation, USA). One side of the feeder was empty, while the other contained a food incentive of cracked and whole maize (Zea mays). Groups

were trained to use the feeders (Fig. 1). While visually distinguishing sex was not possible due to low sexual dimorphism, it was possible to distinguish adults (>1 year old) from the current year's juveniles. Juvenile beaks and frontal shields gradually turn from black to red over the span of approximately nine months (Craig & Jamieson 1990).

In January 2018, when the observations presented below were made, the focal group consisted of five banded adults, three unbanded adults, and one juvenile, all of unknown sexes. In early January 2018, the beta male, Bird A (Table 1), became tangled in what appeared to be fishing line on its right foot. The second and third digits became tied closely together. When first observed, Bird A walked with only a slight limp. We made several unsuccessful attempts to recapture the individual to remove the line. Over the following couple of weeks, Bird A developed a more pronounced limp and appeared to become weaker (less dominant/ aggressive behaviours were observed, APS pers. obs.). On 16 January 2018 a series of video clips were captured at one of the feeders showing another subordinate male from the group (Bird B) repeatedly feeding Bird A.

In the video recording, Bird A initially approached the feeder alone and went to the left (empty) side. It used its uninjured foot to activate the step, open the lid and peer in for ~10 seconds. It moved ~15 cm away from the feeder, stood for several minutes with the injured right foot held up, then sat down and remained sitting for nine



**Figure 1.** Photo series illustrating potential directed altruism in pūkeko (Porphyrio melanotus melanotus), note datetime stamp for sequence of events. Panels: (a) Bird A approaches feeder holding one foot up (the digits were wrapped in twine; b,) Bird A resting to the left of the Chooketeria feeder (this side of the feeder was empty), while Bird B opens the right-hand side of the feeder (full of maize) with its foot, c) Bird B carries a piece of maize to Bird A; d) Bird A accepts the maize, e) Bird B passes another piece of maize to Bird C (a juvenile); f) Bird C attempts to feed Bird A with the maize while Bird B retrieves another piece.

minutes. Bird B then approached the opposite (full) side of the feeder, opened the lid, retrieved a piece of corn, carried it ~1 metre to the other side of the feeder to where Bird A was sitting and fed Bird A (Fig. 1). There was no clear beak movement observed, and no sound recordings were taken, so it was not possible to establish if Bird A was vocalising (e.g. begging). However, Bird A appeared to be resting and uninterested in what Bird B was doing. Soft

communication calls have been recorded between adult pūkeko at nests during the wider study (APS *pers. obs.*), so it is plausible that Bird A was communicating without it being detectable in the footage (i.e. no clear beak movement).

Bird B repeated this process (opened feeder on opposite side, retrieved piece of corn, carried and fed it to Bird A) six more times before pausing to feed an unbanded juvenile (Bird C) that appeared. Bird

**Table 1.** Demographics of individual pūkeko (*Porphyrio melanotus melanotus*) involved in potential altruistic behaviour including adult males and single juvenile from a single social group. The juvenile was never successfully caught and remains the only unbanded individual in the group. Bird A was the recipient of feeding behaviours from Bird B & C.

ID	Age	Sex	Rank	Mass (g)*	Shield Length (mm)*	Shield Width (mm)* †
А	Adult	Male	Beta	1,050	70.2	26.8
В	Adult	Male	Subordinate	1,310	71.5	26.8
С	Juvenile	Unknown	Unknown	Unknown	Unknown	Unknown
D	Adult	Male	Alpha	1,210	77.1	28.8
Е	Adult	Male	Subordinate	1,320	74.3	28.3

\* = measurements taken 12 weeks before footage of all birds except Bird E which was 6 six months later.

 $\dagger$  = previous studies have shown shield width is highly correlated with dominance rank and therefore considered the most accurate indicator.

C was the only juvenile raised by this group in the months preceding this event and therefore easily identifiable due to its behaviour and darkened beak colour. Bird B fed Bird A four more times, before twice passing a piece of corn to the juvenile, which then offered it to Bird A, in a feeding chain. The juvenile offered food twice (Bird A refused both times; Fig. 1). Bird B then attempted to feed Bird A again. During one of these attempts Bird B spent ~25 seconds breaking up the maize to offer smaller pieces, while Bird A refused the food. In total, Bird B opened the feeder and brought corn to Bird A 19 times over a period of 10 minutes. A final (20<sup>th</sup>) successful food offer was captured 40 minutes after the initial attempt. Bird A accepted the food offering 17 times, it rejected food three times.

In pūkeko, the red frontal shield is correlated with dominance and used as a status signal (Dey *et al.* 2014; Dey & Quinn 2014). In addition, shield width is highly correlated with the overall area of the shield (Dey *et al.* 2017). As part of a broader study, we measured the shields of captured pūkeko from the longest point from the tip of the beak to the highest point of the shield, as well as the widest point across the shield. Upon initial capture in October 2017, 12 weeks before the footage was taken, Bird A had a shield width of 26.8 mm and

Bird B also had a shield width of 26.8 mm (Table 1). A third male, Bird D, had a shield width of 28.8 mm and was regarded as the alpha male (APS *pers. obs.*). A fourth adult male (Bird E) was not captured and measured until 6 months after this footage; however, it was assumed to be a subordinate male at the time of these observations. Even though Bird A and Bird B had equal shield widths (and Bird B had a higher mass; Table 1), Bird A was considered the beta male in the group based on observations of received aggressive behaviours from Bird D, and the aggressive behaviours displayed towards Bird B.

Birds were sexed almost three years after these observations were made and we were surprised to learn that both birds involved in this dynamic were adult males. It was originally assumed by the authors that the observed pair interactions were between the beta male and a dominant female, based on behavioural observations due to the level of interaction observed between them, here and at other times; however, it was between two lower (than alpha) ranking males. The degree of relatedness between the birds is unknown, but given the low dispersal and high site fidelity of North Island pūkeko (Craig & Jamieson 1988), it is likely that they are at least distantly related. Becuase Bird A is a beta male (i.e. contributes to the maintenance of the group territory), its survival is beneficial for the entire group. However, this is the first known instance of a lower ranking male assisting a higher-ranking male within the same social group. If Bird A were to succumb to its injuries, Bird B would have been the likely successor.

In contrast to the reproductive success of dominant females, neither dominance nor copulations appear to be predictors of male reproductive success in pūkeko (Lambert et al. 1994). Territory size and quality are related to the number of breeding males present in a group (Craig & Jamieson 1990). Therefore, the cost of losing a male (from a territory defence perspective), as well as no apparent direct reproductive costs (in terms of access to females), may have been key driver in motivating Bird B to assist Bird A. Furthermore, indiscriminate altruism may be a product of high relatedness in a group (Duncan *et* al. 2019), as occurs when dispersal levels are low. Pūkeko differ from most avian species as both sexes can be highly philopatric and North Island populations in particular have very low dispersal (Craig & Jamieson 1988).

In addition, as noted above, it is plausible that Bird A was emitting begging calls. This possibility, coupled with how low it was to the ground, may have stimulated an innate response in Bird B. This seems unlikely, however, given that pukeko are territorial and can vocally distinguish between kin, neighbours, and strangers (Clapperton & Jenkins 1984; Clapperton 1987). It is more likely that Bird B recognised Bird A, as well as its dominance rank, even if Bird A was emitting begging calls. It was also unusual for a juvenile to attempt to feed an adult. While many other occurrences of adult-adult feeding were observed during this study (although all other instances involved both adult birds feeding at the open feeder and passing maize between them), none involved juvenile-adult feeding or juvenile-juvenile feeding. It is difficult to speculate on what elicited this behaviour. To the best of our knowledge, this is the first example of potential altruistic behaviour between adult birds in a rail species. While this was an anecdotal observation, it indicates the potential for future altruism/reciprocity studies to consider this highly flexible and successful species as a model.

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## SHORT NOTE

# Observations of satellite nesting and nocturnal incubation behaviours in pūkeko (*Porphyrio melanotus melanotus*)

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Pūkeko (Porphyrio melanotus melanotus) range throughout Aotearoa New Zealand, and although their breeding systems can vary greatly, they in polygynandrous generally live groups, especially in the northern portions of their distribution (Jamieson 1997, 1999). These groups are comprised of highly philopatric kin which form mixed-sex dominance hierarchies (Craig 1980b). North Island populations consist of large, sedentary, closely related groups which defend territories year-round. There is also low adult mortality, limited juvenile dispersal, and high female reproductive skew (Craig & Jamieson 1988, 1990; Lambert et al. 1994; Jamieson 1997). Pūkeko are typically cooperative breeders, which occurs in only ~3-4% of avian species (Arnold & Owens 1999; Jetz & Rubenstein 2011). When there is more than one reproductive male and female in a group, chicks are always of mixed parentage (Lambert *et* al. 1994). While other life-history attributes vary widely, cooperatively breeding birds all share one important feature; males make a large contribution to incubation and care of the young (Vehrencamp & Ouinn 2004).

In many cooperative breeders, there is a single breeding pair or female. However, in pūkeko there are sometimes multiple breeding females present. When this occurs, all females generally lay in a single nest, a phenomenon known as jointlaying (Craig 1980b; Vehrencamp & Quinn 2004). Conspecifics in Australia have not been reported to exhibit joint-laying, which suggests that jointlaying may have developed relatively recently in New Zealand populations (Dey & O'Connor 2010). The dominant female's fitness is reduced when joint-nesting occurs due to egg breakage and low hatch rates (Craig & Jamieson 1990; Vehrencamp 2000). Despite this, currently there is no evidence of intentional egg breakage or rejection in pūkeko (Jamieson 1997; Quinn et al. 2012). Current thought is that because males invest heavily in incubation, and renesting can occur rapidly, there is a risk that males will abandon nests that have reduced egg numbers due to egg-breaking or rejection. Thus, the heavy male investment may suppress female-female competition and allow joint-laying to occur, despite the fact that dominant female breeders experience a reproductive cost when a subordinate female also breeds (Quinn et al. 2012; Dev et al. 2014b).

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**Figure 1.** Photographs illustrating observations from text. **A)** Females have consistent and unique colouring/patterns on eggs. The image shows seven eggs from two different females within the same joint nest. **B)** Example of a main nest and "satellite" nest; this satellite nest included a well-formed bowl using collected materials; some satellite nests used little or no collected material. **C)** Screenshot from footage captured on a trail camera. In this image six eggs are visible in the main nest (on the left) and three in the satellite nest (on the right). In later footage from the same day there were five eggs in the main nest and four in the satellite nest. The bird in the image is moving the eggs around in the satellite nest. Unfortunately, footage of the egg being moved between nests was not captured. **D)** Screenshot from trail camera footage demonstrating simultaneous incubation of satellite nest. **E)** Trail camera footage from nocturnal incubation changeover. The departing bird's bands are visible.

Male pūkeko increase fitness by having a male cobreeder present (regardless of breeding female numbers) because they can defend higher quality territories and breeding success is largely dependent on territory quality (Craig 1980b; Vehrencamp 2000). A breeding female benefits from more than one breeding male present in the group due to access to higher quality territories, and likewise males benefit from more than one breeding female present as it increases their potential reproductive success (Quinn et al. 2012). Subordinate females benefit by being able to breed on a high-quality territory. Therefore, there is a conflict of interest between the dominant female and subordinate females and males. This conflict appears to resolve in favour of the males and subordinate females (Vehrencamp & Quinn 2004). Dominant females lay more eggs than subordinate females, especially in the first clutch of the season, and also achieve more copulations (Craig 1974; Craig & Jamieson 1990). This appears to result in the production of more offspring for the dominant females. However,

in contrast, neither dominance nor copulations are predictors of male reproductive success in pūkeko (Lambert *et al.* 1994).

Pūkeko nests are built in tufts of vegetation, with species such as Juncus, Carex or Typha grasses typically favoured (Dey et al. 2014a). Typically, longer foliage is beaten down and intertwined to form the base of the nest and surrounding vegetation may also be incorporated, sometimes as a loose canopy (Haselmayer 2000). The pūkeko rely on the low vegetation to camouflage nests and precocial chicks. Females produce eggs with colouring and patterns that are unique to the individual bird and consistent over time (Craig 1974; 1980a). The morphological features of eggs are distinct enough to allow for accurate visual interpretation of maternity within a joint-nest (Haselmayer 2000; Quinn et al. 2012; Dey et al. 2014; Fig. 1A). Despite this clear individuality, pūkeko appear to lack egg recognition; females do not respond to their eggs being experimentally removed, or even the presence of a heterospecific

egg in a nest (Dev & O'Connor 2010; Quinn et al. 2012). Non-breeding "helpers" of both sexes, never partake in courting or copulations but do assist in rearing chicks (Jamieson *et al.* 1994). On the North Island, laving can occur in any month, with a peak during August-November (Dey & Jamieson 2013). Clutch size is typically 4–6 eggs per female. As such, when multiple females contribute to a single nest the total clutch size can be as high as 18 eggs (Dev & Jamieson 2013). In the North Island, all individual pūkeko that copulate subsequently assist in incubating the eggs (Craig & Jamieson 1990). Hatching is asynchronous and chicks are precocial and capable of leaving the nest within hours; however, they generally remain on the nest for a day or two while other eggs hatch (Craig & Jamieson 1990). Mortality is high during this initial period; reproductive success is ~20%, despite egg loss being low (Craig 1974).

For over three years (September 2017 – October 2020) we monitored a pūkeko population as part of a larger project in Auckland, New Zealand (36.95052°S, 174.76543°E). During experimental trials, Bushnell HD aggressor trail cameras (Bushnell Corporation, USA) were placed in territories of chosen groups and behaviour was recorded. Breeding behaviour was observed in the main study population over three breeding seasons. Nests were located, marked with a GPS point and a flagging stake (50 cm from nest), and were monitored until either, 1) abandonment/ predation/destruction, or 2) hatching completion. Eggs were labelled using a marker pen with numbers to indicate their laying order, as well as either "A" (main) or "B" (satellite, see below) to indicate the nest in which they were laid. Many of the monitored groups contained individuals that were banded with unique colour bands for accurate identification. Regular census counts and ad libitum observations occurred throughout the study period. Here we report on some observations of breeding behaviour from this population of North Island pūkeko.

#### Satellite nests

While describing how pūkeko often build "trial" nests prior to the onset of laying, Craig (1980b) stated that eggs were observed laid in two nests 3 m apart in a pair's territory (but only one nest was incubated). Further, Craig (1980b) describes how all nests within and surrounding the study area were single-bowled but noted "multiplebowled nests, each containing eggs and incubated simultaneously, were found in other habitats". It is unclear how close these multiple-bowled nests were to each other, but the pair's territory nests 3 m apart were not described as multiple-bowled, so it is likely less than 3 m. The observation of pūkeko laying in separate nests was a regular occurrence at our study site. For example, in the breeding season 2018/2019 (the season when nests were mostly intensely monitored), of the 31 nests monitored in the area, over a quarter (n = 8) were double nests, or "satellite" nests (Fig. 1B, C), which are likely the same as Craig's (1980b) multiple-bowl nests. These satellite nests had several factors in common; they ranged approximately 20–80 cm apart from the main nest, the main (original) nest always contained more eggs than the satellite nest, the satellite nest was formed several days after the main nest, eggs were almost always (seven out of eight nests) moved between the nests during the incubation period, and nests were not exclusive to a laying female (i.e. there was always a mix of multiple female eggs in both nests). Nests were frequently observed being incubated simultaneously (Fig. 1D), but this was not always the case; often only one nest was incubated at a time. We suggest that one driver for the formation of a satellite nest might be the expulsion of an egg from a nest, either during incubation changeover or during egg rearrangement by the incubating bird. While pūkeko will typically roll a displaced egg back into the main nest (APS pers. obs.), sometimes, because of vegetation and/or elevation, this was not possible. In these instances, often the egg is abandoned or predated within days. However, for reasons unclear, a new nest may sometimes be formed around the displaced egg by a member of the group. This visual signal of a nest structure may then elicit incubating behaviour in more adults. Further, if the main nest is occupied when a female is ready to lay, the presence of a satellite nest may trigger the female to lay there instead, and this in turn may induce further satellite nest egg laying. On two occasions we potentially witnessed this sequence of events. On each occasion, we noted a singular displaced egg approximately 30 cm from a nest (it was confirmed to be from the original nest and not a newly laid egg because of its label). On examination of the nest 24–48 hours later, a loose nest structure had been formed around the displaced egg. A further 24–48 hours later, a second (newly laid/unlabelled) egg appeared in the satellite nest. One of the described nests is shown three days after the initial expulsion of an egg from the main nest (Fig. 1B) after a newly laid egg appeared next to it.

#### Movement of eggs and nests

When well-hidden in vegetation, nests were marked with metal stakes (1 m tall, 1 cm diameter) to make monitoring easier. Stakes were inserted into the ground close to the outer edge of the nest and they never appeared to affect the birds or influence nest abandonment. On one occasion in mid-August 2018 a nest was constructed in a large tuft of cow parsley (Anthriscus sylvestris). The nest site was marked with a stake and noted to be orientated on the northern side of the main stalk of the cow parsley. However, several days later on the 14 August 2018, the nest and labelled eggs within it (n = 8) had moved to the southern side of the cow parsley approximately 50 cm from the original site and flagging stake. There was little evidence of the original nest (all materials had been moved to the new location). It is unclear what stimulated this behaviour. It occurred immediately after the presence of the marking stake, but this pūkeko group had previous nests that had also been marked with a stake and were not moved. Furthermore, three days later (17 August 2018) a satellite nest was created next to the main nest and the eight eggs were found in each of the two nests (five in the main nest and three in the satellite). The satellite eggs were relabelled to indicate they were now in a second nest. A further eight days later (25 August 2018) only a single nest and six eggs remained; three from the main nest and three from the satellite nest were found together. The nest eventually failed with no successful hatching. This was the only observed instance of an entire nest and eggs being moved to a new location, before being turned into satellite nests and then finally reverting to a single nest again.

What was far more frequently observed in this study was the movement of individual eggs between nests. Frequently, eggs labelled in one nest were noted in a different nest on a subsequent day, and often back in their original nest again on later visit. Of the 13 satellites nests monitored, 12 had eggs moved between nests at least once. The thirteenth satellite nest had only one egg in the nest and neither that egg nor eggs from original nest moved between the two nests. The other 12 nests all had multiple eggs in both nests. Total clutch size (i.e. both nests combined) ranged 5–15 eggs. The number of eggs moved at each nest check ranged between 1–5 (in both directions- as in sometimes 1 egg was moved from nest A to B, but also 2 from B to A).

We hypothesise that a driver for this behaviour is that while the satellite nests were often incubated simultaneously by two members of the group, there were also many instances when only one nest was incubated. A female ready to lay may interpret a satellite nest as a suitable location. However, a bird returning to the nest to incubate may conclude that satellite eggs are displaced eggs. Given that the individual incubating one nest would have a clear view of the second nest (if it was unattended) this may initiate an attempt to move the eggs back into the nest it is currently incubating (see Fig. 1C where

a single bird is incubating the satellite nest and appears to move an egg from the main nest). Why this behaviour would not lead to all eggs being moved back into a single nest remains unclear. Perhaps it is too difficult to move multiple eggs in a row, or perhaps a second bird would arrive and commence incubation of the second nest, hence only one or two eggs would ever be moved at a time. Unfortunately, no footage of the movement of eggs between nests was ever captured. Only one satellite nest was suitable for a trail camera because the sudden die back of vegetation exposed the nest pair. Despite roughly nine days of trail camera monitoring (motion triggered 10 second video recording with a 10 second delay between activation), resulting in over 13 hours of footage of this satellite nest, and evidence of eggs being moved between the nests, no instance of moving eggs was filmed.

#### Nocturnal incubation

Craig (1980b) reported that incubation is shared by breeding males and females, and that it is exclusively done by males at night. This was confirmed by an automatic camera set at night; "in all territories, males sat at dusk and were relieved immediately before dawn by a female" (Craig 1980b). Day shifts of incubation were reported as being approximately three hours in length (Craig 1980b). However, in this study, birds were observed changing incubation shifts 1–10 times during the night, via trail camera (4 of 6 nests monitored).

We were able to monitor one single-bowl nest by motion-activated camera for a period of 37 days (30 August – 6 October 2019). Some nights contained no footage (e.g. batteries depleted). However, on nights when footage was captured (n = 25), nocturnal incubation changeovers were recorded 100% of the time. After 37 days, we terminated the monitoring; hatching typically occurs 23–27 days after incubation commences (Craig 1980b) and the nest was assumed failed.

A typical changeover sequence involved the following series of events: 1) The replacement incubator approaches the nest and interacts with the sitting bird; 2) low vocalisations were detected during these interactions (acoustic recording was used on a small portion of video recordings); 3) After ~10–20 seconds of vocalising, the incubating bird leaves the nest and the replacement begins incubating, competing the exchange. In one specific sequence, two birds were observed joint-incubating (both sitting on the nest) for 3.5 hours (0226 h – 0554 h) until one finally moved away. In another sequence, over the course of a night (8 September 2019) there were ten nocturnal incubation changeovers, including five changes in

just over one hour (0336 h – 0449 h). At least three different birds contributed to these night shifts; one banded and two unbanded individuals (Fig 1E). This indicates that, 1) nocturnal incubation is not solely the dominant male's role in this population, and, 2) no individual bird completes an entire nocturnal incubation shift, instead there were regular changeovers in every observed nest.

There is considerable intra-population behavioural variation and plasticity in reproductive systems and breeding behaviours in pūkeko. For example, they show considerable interpopulation variability in mating systems including monogamous, polyandrous, and polygynous (Jamieson 1997, 1999). Craig's (1980b) study was carried out near Palmerston North on the North Island and this geographical variation (and the potential difference in group structure it infers) may be an explanation why changeovers were not documented in either of the study populations monitored. However, the extent to which variation in mating systems may impact the nocturnal incubating behaviour in pūkeko remains unclear. It is also unclear what distance the rest of the group are from the nest during nocturnal periods. As the camera is set up close to the nest (~1 m), birds are only visible when on or immediately behind the nest. Whether these regular nocturnal changeovers have any impact of hatching success – and just how widespread the behaviour is within the species – would be a direction for future study.

A final possibility is that such night-time variation in behaviours is common among bird species more generally. If so, we may be missing a fair amount of variability in behaviour by assuming nothing changes overnight. Craig (1980b) used an automatic camera, which has limitations relative to continuous filming and infrared recording. He observed no nocturnal incubation changeover sequences and concluded that one bird incubates throughout the night. It is possible that Craig's technology meant a limited ability to detect changeovers. However, he still observed the same bird on the nest at dusk and dawn (all birds were banded/marked), which we rarely observed. This implies at least some intra-population behavioural variation and flexibility in this species' incubation behaviour. Pūkeko are generally considered to be diurnal birds; however, using our cameras set up on feeders, we frequently observed pūkeko foraging and moving throughout the night even away from nests. Though this field site is within the Auckland region, it is relatively dark (McNaughton *et al.* 2022), thus it is unclear whether this activity is due to artificial light at night or natural behaviour variation. These findings add to accumulating evidence that many species are more active at night than previously assumed and engaged in activities we are oblivious to without research (Gaston 2019). How many other behaviours might we be missing by assuming all activities occurs in the daylight hours for diurnal species?

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