RESEARCH ARTICLE

Effects of customary egg harvest regimes on hatching success of a culturally important waterfowl species

Mark R. Herse1 | Jason M. Tylianakis1 | Nigel J. Scott2,3 | Donald Brown4 | Iaean Cranwell5,6,7 | John Henry8 | Craig Pauling3,4,9 | Angus R. McIntosh110 | Andrew M. Gormley10 | Phil O’B. Lyver10

1 School of Biological Sciences, University of Canterbury, Christchurch, New Zealand; 2 Te Ao Tūroa, Te Rūnanga o Ngāi Tahu, Christchurch, New Zealand; 3 Ngāi Tūāhuriri, Te Ngāi Tūāhuriri Rūnanga, Tuahiwi, New Zealand; 4 Ngāi Te Ruahikihiki, Te Taumutu Rūnanga, Leeston, New Zealand; 5 Kāti Irakehu, Wairewa Rūnanga, Little River, New Zealand; 6 Kāti Kuri, Wairewa Rūnanga, Little River, New Zealand; 7 Kāti Makō, Wairewa Rūnanga, Little River, New Zealand; 8 Kāti Huirapa o Arowhenua, Temuku, New Zealand; 9 Ngāi Te Rakihakaputa, Te Taumutu Rūnanga, Leeston, New Zealand and 10 Manaaki Whenua Landcare Research, Lincoln, New Zealand

Abstract

1. Customary harvests of wildlife underpin the livelihoods, cultural identities, well-being and ecological knowledge of many Indigenous peoples and local communities (IPLC), whereas government restrictions on harvests can erode these relationships. Supporting IPLC in place-based resource management, including sustainable customary harvests, can aid wildlife, their habitat and the cultures that value them.

2. Using an experiment jointly initiated by the Māori tribe Ngāi Tahu and researchers (Māori and non-Māori) in Aotearoa/New Zealand, we identified low-impact strategies for harvesting black swan (kakī anau, Cygnus atratus) eggs at an important coastal lagoon, Te Waihora/Lake Ellesmere. The experiment tested whether nest-level hatching success (number of eggs hatched) depended on nest-level harvest pressure; whether this effect was additive; and the extent to which harvest influenced post-harvest egg laying and hatching probability, relative to several control variables.

3. Nest-level harvest pressure determined nest-level hatching success and had a non-additive effect on population-level hatching success. Specifically, harvesting one-third or two-thirds of a clutch caused a loss of approximately one hatching per egg removed, because swans tended to replace few of those harvested eggs and hatching probability of unharvested eggs was generally high (but lower in nests with two-thirds of eggs removed). Conversely, harvesting an entire clutch caused a loss of approximately one hatching for every two eggs removed, because swans often subsequently re-laid new, albeit smaller, clutches.

4. During fixed-output harvests, removing entire clutches early during nesting could induce re-laying and prevent abandonment of unharvested eggs. Moreover, harvesting from areas of nesting colonies with low nest density, where hatching probability of unharvested eggs was lowest, could limit disturbance. Finally, restoring
Harvests of wildlife have sustained and shaped many cultures over centuries (McGovern et al., 2006; Moss & Bowers, 2007; Tyrrell, 2008). For instance, wild birds and their eggs can be vital sources of nutrition and income for Indigenous peoples and local communities (IPLC, or ‘ethnic groups who are descended from and identify with the original inhabitants of a given region, in contrast to groups that have settled, occupied or colonized the area more recently’; IPBES, 2019a) (Corre & Bemanaja, 2009; González, 1999; Gudmundsson, 1979; Lyver & Moller, 1999; Natcher et al., 2012; Sheil et al., 2015). Customary strategies for protecting wild bird populations have been implemented by many IPLC over generations to reduce harvest impacts. For example, Hauraki Māori in Aotearoa/New Zealand (NZ) have used a combination of habitat protection, harvest restrictions and other rules (e.g. harvesting specific life stages) for centuries to protect breeding populations of sooty shearwater (tītī, Ardenna grisea; Lyver et al., 2008). Similarly, Huna Tlingit in Alaska, USA, have established intergenerational rules around customary egg harvests (e.g. removal of specific proportions of eggs per harvested nest) to protect breeding populations of glaucous-winged gulls Larus glaucescens (Hunn et al., 2003). The diachronic nature of customary resource management means that harvests are often rooted in local tradition and central to the cultural identities, worldviews, well-being and ecological knowledge of IPLC (Hunn et al., 2003; Lyver et al., 2008, 2009; Natcher et al., 2012; Pauling & Arnold, 2008; Rayne et al., 2020; Thomson, 1939). However, unsustainable exploitation, habitat loss and degradation, and other environmental changes that diminish wildlife populations threaten their nutritional, economic, cultural and biological values for IPLC (Gudmundsson, 1979; Haynes, 1987; Jones et al., 2015; Natcher et al., 2012; Parlee et al., 2018; Sheil et al., 2015).

Modern environmental laws within western and colonial countries that favour Eurocentric, protectionist conservation strategies often allow sport hunting of adults from some bird species (‘game birds’), yet criminalize the customary harvest of eggs, chicks and adults from the same species and/or other non-threatened species, regardless of their significance for IPLC (Herse et al., 2020; Hunn et al., 2003; Lyver, Ruru, et al., 2019; Merkel & Barry, 2008). Re-initiating sustainable customary harvests against this legal background is therefore challenging, especially if local knowledge of traditionally harvested populations and management practices have declined, or if IPLC find themselves managing resources in novel social-ecological contexts (Lyver, Timoti, et al., 2019; Natcher et al., 2012; Tyrrell, 2008). In such cases, empirical estimates of demographic rates and harvest impacts can contribute to re-generating and adapting low-impact harvest strategies. For example, when IPLC want to re-initiate customary egg harvests, nest monitoring and experimental harvests can provide data to estimate current rates of nesting (e.g. clutch size, egg hatching probability) and effects of egg harvest and other limiting factors (Dexter & Bayliss, 1991; Lewis et al., 2017; Schaefer et al., 2019; Zador et al., 2006). However, IPLC abilities to re-initiate customary egg harvests depend largely on who generates and interprets the data and has the power to decide whether harvests can occur and at what level (Tyrrell, 2008; Wright et al., 1995). In western and colonial countries where IPLC have limited authority in resource management, data interpretation and decision-making tend to be biased towards majority cultures and conservation strategies that do not value customary harvests of wildlife (Hunn et al., 2003; Lyver, Ruru, et al., 2019; Tyrrell, 2008; Wright et al., 1995). Thus, in addition to recognizing IPLC rights ‘to determine and develop priorities and strategies for the development or use of their lands or territories and other resources’ (United Nations General Assembly, 2007), supporting IPLC in place-based resource management requires generating and interpreting data within appropriate cultural contexts that recognize their values (Akins et al., 2019; Freitas et al., 2020; Lyver, Ruru, et al., 2019).

Here we present results from a field experiment jointly initiated by Ngāi Tahu, the southern-most tribe of Māori in NZ, and researchers (both Māori and non-Māori) to understand how customary egg harvest impacts black swan (kakī anau, Cygnus atratus) nesting at a foraging habitat in degraded wetlands surrounding nutrient-overloaded waterbodies could offset eutrophication effects by providing plant resources that swans require to lay eggs indeterminately.

5. In addition to improving IPLC well-being, implementing strategies such as these could enhance place-based resource management by supporting IPLC engagement with nature, which increases the number and detection resolution of ecological feedbacks (e.g. population numbers, habitat conditions) and resilience to environmental change. Moreover, customary harvest could be a practical, culturally appropriate and less wasteful alternative to non-consumptive culling for mitigating human–wildlife conflict (e.g. waterfowl grazing on pasture).

**KEYWORDS**
biocultural conservation, kaitiakitanga, mahinga kai, mātauranga Māori, native species, taonga, traditional egg harvest, wetlands

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1 | **INTRODUCTION**

Harvests of wildlife have sustained and shaped many cultures over centuries (McGovern et al., 2006; Moss & Bowers, 2007; Tyrrell, 2008). For instance, wild birds and their eggs can be vital sources of nutrition and income for Indigenous peoples and local communities (IPLC, or ‘ethnic groups who are descended from and identify with the original inhabitants of a given region, in contrast to groups that have settled, occupied or colonized the area more recently’; IPBES, 2019a) (Corre & Bemanaja, 2009; González, 1999; Gudmundsson, 1979; Lyver & Moller, 1999; Natcher et al., 2012; Sheil et al., 2015). Customary strategies for protecting wild bird populations have been implemented by many IPLC over generations to reduce harvest impacts. For example, Hauraki Māori in Aotearoa/New Zealand (NZ) have used a combination of habitat protection, harvest restrictions and other rules (e.g. harvesting specific life stages) for centuries to protect breeding populations of sooty shearwater (tītī, Ardenna grisea; Lyver et al., 2008). Similarly, Huna Tlingit in Alaska, USA, have established intergenerational rules around customary egg harvests (e.g. removal of specific proportions of eggs per harvested nest) to protect breeding populations of glaucous-winged gulls Larus glaucescens (Hunn et al., 2003). The diachronic nature of customary resource management means that harvests are often rooted in local tradition and central to the cultural identities, worldviews, well-being and ecological knowledge of IPLC (Hunn et al., 2003; Lyver et al., 2008, 2009; Natcher et al., 2012; Pauling & Arnold, 2008; Rayne et al., 2020; Thomson, 1939). However, unsustainable exploitation, habitat loss and degradation, and other environmental changes that diminish wildlife populations threaten their nutritional, economic, cultural and biological values for IPLC (Gudmundsson, 1979; Haynes, 1987; Jones et al., 2015; Natcher et al., 2012; Parlee et al., 2018; Sheil et al., 2015).

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200-km² coastal lagoon and key breeding area, Te Waihora/Lake Ellesmere (Figure 1). Current law in NZ declares black swans (hereafter ‘swans’) as non-threatened game birds (Wildlife Act 1953; Williams, 2013), yet prohibits Ngāi Tahu from harvesting their eggs without special permission (Herse et al., 2020). Swans can replace their eggs in unattended nests of other females (Williams, 2013). Larger clutches can result from females laying their eggs in unattended nests of other females (Williams, 2013). Breeding generally monogamous, but some promiscuity occurs in colonies (Williams, 2013). Females and, periodically, males incubate eggs for ~36 days until precocial young (cygnets) hatch (Williams, 2013).

2.2 History of local harvest management

Swan eggs, cygnets, adults and their habitat are highly valued as customary food sources and key elements of mahinga kai (i.e. ‘the customary gathering of food and natural materials and the places where those resources are gathered’; Ngāi Tahu Claims Settlement Act 1998) for some tribal members within Ngāi Tahu (Lyver, Ruru, et al., 2019; Pauling & Arnold, 2008). Ngāi Tahu harvested swans and their eggs customarily at Te Waihora until the early 20th century when the Canterbury Acclimatization Society (CAS), established by European
settlers in the previous century to manage fish and wildlife declared ‘game’ (including swans), was granted statutory authority to collect swan eggs (Lamb, 1964; McDowall, 1994). Swan eggs provided an important source of revenue for the CAS and were sold to local manufacturers of Ovaltine® (a nutrient-rich drink) and race-horse food (Lamb, 1964; Williams, 1979). The CAS erected guard towers in nesting colonies to deter Ngāi Tahu harvesters (Pauling & Arnold, 2008), who sometimes harvested eggs inconspicuously at night. The swan population increased to ~80,000 breeding and non-breeding adults in the 1960s and the CAS limited population growth and grazing and fouling of surrounding pastures each year by collecting tens of thousands of eggs, destroying nests, extending sport hunting seasons, eliminating hunting limits and culling hundreds to thousands of swans (Lamb, 1964; Miers & Williams, 1969; Williams, 1979). During those years, breeding pairs readily replaced clutches collected by the CAS, with reports of some females laying >15 eggs within nesting seasons (Williams, 1979). The swan population declined dramatically in 1968 when a massive storm (the ‘Wahine’ storm) killed tens of thousands of swans and destroyed all the macrophyte beds in Te Waihora (Williams, 1979). The CAS stopped collecting eggs and reinstated hunting limits in the 1970s to ensure sport hunting could continue (Williams, 1979). The swan population declined further to ~5,000–10,000 adults by the end of the century (Ford et al., 2017) as swan nesting habitat was increasingly converted to pasture, and eutrophication due to agricultural runoff, coupled with turbidity, prevented macrophyte recovery (Gerbeaux, 1989; Williams, 1979, 2013).

According to NZ’s founding document, Treaty of Waitangi 1840, ‘the Queen of England agrees to protect the chiefs, the subtribes and all the people of New Zealand in the unqualified exercise of their chieftainship over their lands, villages and all their treasures’ (Orange, 2011). However, harvesting swan eggs currently remains illegal without special permission from the Minister of Conservation or the successor to NZ’s acclimatization societies, Fish and Game NZ (FGNZ). Fish and Game NZ is a quasi-government organization funded by sales of fishing and hunting licenses but mandated by the Crown under the Conservation Act 1987 to ‘manage, maintain, and enhance the sports fish and game resource in the recreational interests of anglers and hunters’. Regional FGNZ managers regulate swan population mortality from sport hunting through bag limits (quotas), which are based on annual, regional-scale trends in swan adult abundance or hunting rates estimated from surveys (Herse et al., 2020). Ngāi Tahu are interested in re-initiating self-authorized harvests of swan eggs without special permission or oversight from FGNZ or the Minister of Conservation. Understanding how egg removal impacts swan nesting within Te Waihora’s current environment was the motivation for this study and first step towards instituting low-impact customary egg harvests.

## 2.3 Egg harvest experiment

Customary harvesters determine egg freshness and the stage of embryo development based on eggshell colour and texture, and generally select eggs with shells that are white (rather than greenish-blue or brown) and rough (rather than smooth) to touch, which indicate that they were recently laid and are fresh (see Appendix S1). Thus, the number of eggs removed from a harvested nest depends at least partly on how many eggs are fresh, which can range from none to all eggs. To better understand how nest-level harvest pressure (removal of one-third vs. two-thirds vs. all eggs from a clutch) influences nesting (see aims a–d above), we conducted an egg harvest experiment at Te Waihora during the breeding season of 2018 (Figure 1).

We conducted the harvest experiment at Te Waihora’s three largest swan nesting colonies, which collectively produced ~75% of all swan nests at the lagoon in 2018, as determined by aerial censuses (M. Herse, P. Lyver, N. Scott, J. Tylianakis & Ngāi Tahu, unpublished data). Prior to conducting the experiment, we obtained all necessary research permits (Department of Conservation Research Collection Permit no. 59892-FAU) and approval from an animal ethics committee at Manaaki Whenua Landcare Research (approval code no. 17/06/01). The largest colony (~400 breeding pairs) nested in a ~6-ha strip of ungrazed exotic pasture grasses (e.g. Festuca arundinacea) on Kaitorete Spit and neighboured the second largest colony (~150 breeding pairs), which nested 2 km away on a 1-ha island of similar habitat near the village of Ataahua (Figure 1). The third largest colony (~130 breeding pairs), at the Yarrs Flat wetland, nested ~15 km from the larger colonies on a 2-ha island of ungrazed exotic pasture grasses and sea rush Juncus kraussii interspersed by shrubby saltmarsh ribbonwood Plagianthus divaricatus (Figure 1).

We included 40 nests per colony (120 total nests) in the experiment. This sample size balanced statistical power to model harvest effects with minimizing time spent in nesting colonies and potential disturbance during data collection. We assigned 10 nests per colony to each of three harvest treatment groups (30 total nests per harvest treatment group): removal of two eggs, four eggs and all five to seven eggs from a clutch. We monitored the remaining 10 unharvested nests per colony (30 total unharvested nests) to determine baseline nesting rates. Marking and monitoring protocols (described below) were the same for harvested and non-harvested control nests, which allowed us to distinguish the effects of harvest from potential disturbance due to nest marking and monitoring. A preliminary assessment in 2017 revealed that mean clutch size during incubation at the largest colony was 6.0 eggs (standard deviation 1.0, range 4–10 eggs, n = 100 nests). Limiting harvest to clutches of six eggs would have allowed us to consistently harvest exactly one-third and two-thirds of eggs from clutches in the partial-harvest treatment groups. However, we aimed to conduct the harvest during as few visits to colonies as possible at the onset of nesting, and limiting harvest to only clutches containing six eggs would likely have delayed the experiment and limited the ability of harvesters to gather experimentally removed eggs that were fresh and deemed edible. Thus, we included nests containing ≤5 eggs and implemented harvest treatments of two eggs, four eggs and all eggs regardless of clutch size. Because mean pre-harvest clutch size (including unharvested nests) in 2018 was 5.6 (standard deviation 0.7, range 5–7, n = 120 nests)
and did not vary significantly among harvest treatment and non-harvest control groups (ANOVA, $F_{3,116} = 1.365, p = 0.26$) or nesting colonies (ANOVA, $F_{2,117} = 2.243, p = 0.11$), partial harvests of two eggs versus four eggs amounted to harvesting approximately one-third versus two-thirds of a clutch, respectively, on average.

We established the experiment and harvested eggs during four weekly visits to nesting colonies from 15 August to 6 September as swans began nesting. During the first two visits, each colony contained <40 nests (the intended nest sample size at each colony) with ≥5 eggs each, so we searched each colony site exhaustively and included every nest with ≥5 eggs. We uniquely marked each nest with a wooden stake placed 1 m from the nest and recorded the number of eggs present. Harvesters then either left nests intact (for controls) or harvested the pre-determined number of eggs, rotating among the harvest treatment and non-harvest control groups with each nest found. Most harvested eggs were fresh and had not yet been incubated, whereas a small proportion had been incubated for less than 1 week but were still considered by harvesters to be palatable. Thus, all experimentally harvested eggs were consumed by harvesters and their extended families. We uniquely marked each unharvested egg using a felt-tipped marker. We measured nest height (cm) and the distances (m) from the focal nest to the nearest shoreline of open water and to the nearest neighbouring nest (marked or unmarked) that was clearly used during the current season (with or without eggs). During subsequent visits, colonies contained more nests than we intended to include in the experiment, so we selected nests by iteratively walking to a random point (generated using ArcGIS 10.4, Environmental Systems Research Institute) within the colony and selecting the nest nearest to the point with ≥5 eggs. We installed motion sensing cameras to monitor a subset of nests at each colony as part of a separate study (see Figure S1). Swans typically moved off their nests as we arrived and returned to nests within a few hours of researchers leaving, with no apparent difference in behaviours between control and harvested nests, as determined by nest cameras.

We visited all marked nests weekly from the time they were marked until all marked nests were inactive in early December. During each visit, we uniquely marked each newly laid egg, swapped memory cards on cameras, and recorded presences and absences of previously marked eggs, number of cygnets present, and evidence of eggs hatching (e.g. cygnets present, embryo sacs in nest) or failing (e.g. cold or punctured eggs, flooding). We measured the distance to the nearest neighbouring nest again when we determined all eggs or the last remaining egg in a clutch had hatched or failed. We considered new eggs laid in an active nest (containing fresh or warm eggs) to be part of a continuation of the ‘first’ nesting attempt by the same female. Similarly, for a given nest that we harvested completely, we considered new eggs laid between the harvest and subsequent visit one week later to be part of a continuation of the first nesting attempt by the same female, because we had not observed the nest inactive. We considered new eggs laid in a previously inactive nest to be part of a ‘second’ nesting attempt at the nest, which could have been laid by a different female (Miers & Williams, 1969). Among first nesting attempts, we found newly laid eggs during seven weekly trips to colonies from 15 August to 27 September, with 97% (262 of 270) found during weeks 2–6.

During peak nesting in early September, a southerly wind-driven flood destroyed approximately half of the nests at the northern colony at Yarrs Flat (Figure 1) but had little effect on the other colonies (see Supporting Information). Preliminary analyses revealed that during this single-day event, nest flooding probability was determined by the colony’s exposed location, not variation among nests in nest height or distance to water (see Table S1; Figure S2). Even in the absence of flooding, post-harvest egg hatching probability at this colony was remarkably low (Figure S3). Moreover, in contrast to the other colonies, hatching probability at Yarrs exhibited negative density dependence (Figure S4), possibly due to the shrubby, subdivided nesting habitat that was unique to this site and could increase aggressive encounters between swans and lead to nest abandonment (Miers & Williams, 1969). Considering data at the flooded colony were limited, and the habitat at the two larger colony sites better reflected most other breeding areas at Te Waihora, we limited our inferences on harvest to data collected from the two larger colonies (combined $N = 80$ nests) and refer only to those colonies below.

### 2.4 Statistical analyses

We developed a set of models to assess the effects of nest-level harvest pressure on swan hatching success in three steps. First, we modelled effects of nest-level harvest pressure (a categorical predictor with four levels: no eggs, two eggs, four eggs and all five to seven eggs) on (a) swan propensity to lay replacement eggs and (b) hatching probability for individual unharvested eggs. Second, we modelled (c) the net effect of harvest on hatching success (number of eggs hatched) per nest. Last, we (d) used model predictions of hatching success to assess the population-level impacts of hypothetical fixed-output harvests that varied in nest-level harvest pressure.

To isolate the effects of harvest, we statistically controlled for six other factors which we hypothesized a priori to be potential drivers of hatching success or underlying demographic rates (a and b above). This study was not designed to identify the least-impactful time to harvest eggs during the months-long nesting season: customary harvest practice at Te Waihora involves visiting breeding colonies at the onset of nesting when large numbers of fresh eggs are available, so we conducted the experimental harvest during this period. Thus, time of egg laying and harvest are confounded. Nevertheless, we included (1) time (week) of the nesting season when harvest took place (for models of a and c) or when an unharvested egg was laid (for models of b), because the experimental harvest took place over several weeks and earlier harvest has been associated with higher propensity to lay replacement eggs in other waterbird species (e.g. Zador et al., 2006). Including time of egg laying (an egg-level explanatory variable) in models of egg hatching probability (an egg-level response variable) accounted for within-clutch variation in time of egg laying, which would have been obscured otherwise. We included (2) distance to nearest neighbouring nest (an assumed index of nest
density; Williams, 1979) at the time an egg (for models of b) or nest (for models of a and c) was first found, because nest density could influence hatching success negatively (e.g. aggressive encounters, competition for nesting resources) and/or positively (e.g. safety from predators; Jones, 2003; Koons et al., 2014; Miers & Williams, 1969). We also included (3) distance to open water, which could reflect parental quality and propensity to abandon nests if nesting space is limited and swans favour nesting sites that are near water and increase cygnet fledging success. Conversely, some swans may avoid nesting directly beside water to avoid flood risk (Miers & Williams, 1969).

We included (4) nest height because it could reflect parental investment in breeding (Soler et al., 1998) and/or influence flood risk. We included (5) camera presence when harvest took place (for models of a and c) or when an individual egg was present in a nest (for models of b), which could attract or deter nest predators (Richardson et al., 2009; Winder et al., 2016), and/or agitate swans and cause nest abandonment. Last, we included (6) the number of eggs present before the harvest or nest monitoring began because smaller clutches may have been incomplete, and because pre-harvest clutch size could have influenced post-harvest egg laying and/or hatching success.

We classified fates of eggs as either hatched or failed based on visual observations during visits (e.g. egg remains, cygnets in the nest), the duration for which an egg or clutch was present, and/or observations from cameras. We excluded data from four nests affected by flooding because we were interested in assessing effects of harvest on nesting in the absence of chance events like flooding. We also excluded data from second nesting attempts due to insufficient sample size (N = 10 nests) and because we were not confident that clutches within these nests were laid by the same females that first used them. We summarize data from second nesting attempts in the Supporting Information. Of the 289 eggs which were not affected by flooding or part of second nesting attempts, we omitted 19 (6.5%), for which we could not confidently determine fates, from models of egg hatching probability. In models of hatching success, we excluded one nest for which the fate of the entire clutch (five eggs) was unknown; in the remaining cases, where the fate of only a portion of eggs in a clutch were unknown (14 total eggs), we were conservative and assumed that they did not hatch.

We modelled egg laying and hatching success (nest-level responses) using Poisson generalized linear mixed models (GLMMs; Bolker et al., 2009) and egg hatching probability (an egg-level response) using binomial GLMMs. We included a random effect of nesting colony in all models to account for spatial non-independence among nests. We also included a random effect of nest (nested within colony) in models of egg hatching probability to account for non-independence among eggs that shared a nest, and in models of egg laying and hatching success to account for over-dispersion in the data (Bolker et al., 2009). For each response, we first considered a model which included additive effects of all the hypothesized explanatory variables described above and two-way interactions among harvest pressure, distance to neighbour and either time of harvest or time an unharvested egg was laid (see above). These models included the most complex combination of control variables which we considered to be ecologically relevant for assessing harvest effects on nesting (Burnham & Anderson, 2002). Explanatory variables used together in models were not strongly correlated (r ≤ 0.53). We used linear effects because nonlinear effects did not improve model fits during preliminary analyses. We developed models in r using the ‘lme4’ package (Bates et al., 2015; R Core Team, 2019).

After fitting each full model, we found that some hypothesized explanatory variables were not important for estimating nesting responses. To prevent overfitting and resulting increases in model variance, we assessed whether simpler versions of the hypothesized full model were more parsimonious in estimating responses (Burnham & Anderson, 2002). Specifically, we compared each full model with all possible nested subsets of fixed effects (which were all ecologically plausible) using the r package ‘MuMln’ (Bartoń, 2019) and corrected Akaike’s information criterion (AICc) to balance model fit against complexity (Burnham & Anderson, 2002). After identifying the most parsimonious model for each response, we confirmed that residuals were not spatially autocorrelated (Figure S5) and variances were not over-dispersed (see Supporting Information; Nakagawa et al., 2017). Here we present results from the most parsimonious models.

To assess how variation in nest-level harvest pressure during fixed-output harvests would impact population-level hatching success, we used the most parsimonious model of hatching success to predict outcomes of alternative harvest regimes. Specifically, we compared cumulative hatching successes among three hypothetical, alternative strategies for harvesting 12 eggs from six nests containing six eggs each. These strategies included (a) harvesting two eggs from each nest; (b) harvesting four eggs from each of three nests and leaving three nests intact; and (c) harvesting all six eggs from each of two nests and leaving four nests intact. Model predictions assumed that nest cameras were absent and other important explanatory variables (except harvest) were at their respective mean values.

3 | RESULTS

Model results are based on data from 76 nests and 421 eggs, or a subset of those nests and eggs (described below). Immediately prior to harvest and monitoring, the mean clutch size of these 76 nests was 5.5 (standard deviation 0.6) and did not vary significantly among harvest treatment and non-harvest control groups (ANOVA, $F_{3,72} = 0.975$, $p = 0.41$) or nesting colonies (ANOVA, $F_{1,74} = 0.566$, $p = 0.45$). We harvested 213 eggs from 57 nests (two eggs from 20 nests, four eggs from 19 nests, and all five to seven eggs from 18 nests) and did not harvest from 19 control nests.
### 3.1 Egg laying

Following harvest and the onset of monitoring, swans laid a total of 71 new eggs in 23 of 57 (40%) harvested nests and a total of 10 new eggs in 6 of 19 (32%) unharvested nests. Post-harvest egg laying was not related to pre-harvest clutch size (Table 1), which suggests that most clutches within marked nests were complete when we harvested eggs and began monitoring. Mean clutch size

#### TABLE 1 Results of model selection evaluating the effects of harvest, temporal effects, camera presence and nest attributes on (a) the number of eggs laid per nest following harvest, (b) hatching probability for individual unharvested eggs and (c) hatching success (number of eggs hatched per nest). Temporal effects include harvest timing (week) in models of a and c (nest-level response variables), and time (week) an egg was laid in models of b (an egg-level response variable). All models include nesting colony as a random factor, and models of b also include nest as a random factor (nested within nesting colony). Model intercepts are not shown. The multiplication sign ‘×’ indicates two main effects and their interaction. Column ‘np’ is number of parameters (including the intercept and random effects), ‘logLik’ is log-likelihood, ‘AICc’ is corrected Akaike’s information criterion and ‘wi’ is Akaike’s weight. For each response variable, the top ten models are shown. In (a), 95% confidence limits for all fixed effect coefficients except those of camera presence, harvest and pre-harvest clutch size overlapped zero in all models. In (b), 95% confidence limits for all fixed effects except that of distance to neighbouring nest overlapped zero in all models. In (c), 95% confidence limits for all fixed effect coefficients except those of camera presence, harvest and pre-harvest clutch size overlapped zero in all models.

| Model (fixed effects only)                  | np  | logLik  | AICc | ΔAICc | wi   |
|--------------------------------------------|-----|---------|------|-------|------|
| (a) Egg laying                             |     |         |      |       |      |
| Camera + Harvest × Harvest time            | 11  | −89.24  | 204.60 | 0    | 0.08 |
| Camera + Harvest                           | 7   | −94.66  | 204.97 | 0.36 | 0.07 |
| Harvest                                    | 6   | −96.09  | 205.40 | 0.79 | 0.05 |
| Camera + Harvest + Distance to water       | 8   | −93.93  | 206.01 | 1.41 | 0.04 |
| Harvest + Distance to water                | 7   | −95.20  | 206.04 | 1.44 | 0.04 |
| Camera + Harvest + Harvest time            | 8   | −94.23  | 206.61 | 2.01 | 0.03 |
| Camera + Harvest + Distance to neighbour   | 8   | −94.25  | 206.64 | 2.04 | 0.03 |
| Camera + Harvest × Harvest time + Distance to water | 12  | −88.95  | 206.86 | 2.26 | 0.03 |
| Camera + Harvest × Harvest time + Distance to neighbour | 12  | −89.04  | 207.04 | 2.43 | 0.02 |
| Camera + Harvest × Harvest time + Pre-harvest clutch size | 12  | −89.14  | 207.23 | 2.63 | 0.02 |
| (b) Egg hatching probability               |     |         |      |       |      |
| Distance to neighbour × Time laid          | 6   | −109.51 | 231.34 | 0.00 | 0.05 |
| Distance to water + Distance to neighbour × Time laid | 7   | −109.00 | 232.44 | 1.10 | 0.03 |
| Harvest + Distance to neighbour × Time laid| 9   | −106.90 | 232.49 | 1.15 | 0.03 |
| Nest height + Distance to neighbour × Time laid | 7   | −109.16 | 232.74 | 1.40 | 0.03 |
| Camera + Distance to neighbour × Time laid | 7   | −109.20 | 232.82 | 1.48 | 0.02 |
| Distance to neighbour + Time laid          | 5   | −111.31 | 232.84 | 1.50 | 0.02 |
| Harvest + Distance to water + Distance to neighbour × Time laid | 10  | −106.24 | 233.34 | 2.00 | 0.02 |
| Harvest + Distance to neighbour + Time laid| 8   | −108.40 | 233.35 | 2.01 | 0.02 |
| Pre-harvest clutch size + Distance to neighbour × Time laid | 7   | −109.51 | 233.45 | 2.11 | 0.02 |
| Camera + Distance to water + Distance to neighbour × Time laid | 8   | −108.45 | 233.45 | 2.11 | 0.02 |
| (c) Hatching success                       |     |         |      |       |      |
| Camera + Harvest + Pre-harvest clutch size | 8   | −141.19 | 300.57 | 0.00 | 0.07 |
| Camera + Harvest + Pre-harvest clutch size + Nest height | 9   | −140.08 | 300.94 | 0.37 | 0.06 |
| Camera + Harvest + Harvest time + Pre-harvest clutch size + Distance to neighbour | 10  | −138.79 | 301.03 | 0.46 | 0.06 |
| Camera + Harvest + Harvest time + Pre-harvest clutch size | 9   | −140.16 | 301.09 | 0.52 | 0.06 |
| Camera + Harvest × Distance to neighbour + Pre-harvest clutch size | 12  | −136.03 | 301.10 | 0.53 | 0.05 |
| Camera + Harvest + Pre-harvest clutch size + Distance to neighbour | 9   | −140.28 | 301.32 | 0.76 | 0.05 |
| Camera + Harvest + Harvest time + Pre-harvest clutch size + Nest height | 10  | −139.08 | 301.59 | 1.03 | 0.04 |
| Camera + Harvest + Harvest time + Pre-harvest clutch size + Nest height + Distance to neighbour | 11  | −137.71 | 301.61 | 1.04 | 0.04 |
| Camera + Harvest + Pre-harvest clutch size + Nest height + Distance to neighbour | 10  | −139.16 | 301.76 | 1.19 | 0.04 |
| Camera + Harvest + Distance to water + Pre-harvest clutch size | 9   | −140.82 | 302.40 | 1.83 | 0.03 |
in unharvested nests at the time swans finished laying eggs was 6.2 (standard deviation 1.1). Post-harvest egg laying depended on the number of eggs harvested (Figure S6; Table 1), with swans tending to lay 2–4 new eggs on average following a complete harvest of all five to seven eggs, and fewer new eggs, if any, following a partial harvest of two or four eggs (Figure 2a). Thus, swans tended to lay fewer new eggs than were harvested (Figure 2a). The effect of harvest on post-harvest egg laying was moderated by harvest timing (Figure 2a; Figure S6; Table 1). This interactive effect of harvest and harvest timing on post-harvest egg laying was driven by swans tending to lay more new eggs following harvest of two eggs if the harvest occurred earlier during the nesting season (Figure S6). Of the 18 nests harvested completely, swans continued using 11 (61%) within the first week following harvest. Camera presence at nests at the start of the experiment negatively affected egg laying (Figure S6; Table 1). Collectively, these fixed effects explained more than half (0.56) of the variance in egg laying, whereas the random effect of nesting colony explained less (0.19). Nest height, distance to neighbour and distance to water were not significant predictors of post-harvest egg laying (Table 1).

3.2 | Egg hatching probability

Models of post-harvest egg hatching probability were based on known fates of 270 eggs from 68 nests. The eight excluded nests (cf. models of post-harvest egg laying described above) comprised seven nests which were harvested completely and remained empty for ≥1 week following harvest, and one nest for which we could not confidently determine the fates of any eggs. Hatching probability decreased with distance to neighbour (Figure 3; Figure S7; Table 1). Moreover, positive density dependence of hatching probability was moderated, albeit marginally, by the time of the nesting season when an egg was laid, such that density dependence strengthened over the season (Figure 3; Figure S7; Table 1). Harvest did not significantly affect hatching probability of unharvested eggs and was not retained in the most parsimonious

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**FIGURE 2** Plots showing the effects of nest-level harvest pressure (number of eggs harvested per nest) on (a) the number of eggs laid per nest after harvest, (b) egg hatching probability for individual eggs that were not harvested, and (c) hatching success (number of eggs hatched) per nest, in the absence of flooding. In (b), estimates for nests which had all eggs harvested correspond with new eggs that were laid within one week of the harvest, which we considered to be part of the same, first nesting attempt. For each response variable, estimates are based on the most parsimonious model that included an effect of harvest, and held the other variable(s) in the model constant by fixing pre-harvest clutch size, distance to neighbour and time (week of harvest in plots a and c; week an unharvested egg was laid in plot b), and the nest camera level at ‘absent’.

**FIGURE 3** Plot showing the interactive effect of distance to nearest neighbouring nest (an index of nest density) and time (week) of harvest when an unharvested egg was laid on egg hatching probability during first nesting attempts in the absence of flooding. To show how time of harvest mediated the effect of distance to neighbour on egg hatching probability, we plotted relationships between hatching probability and distance to neighbour for eggs laid during the second week of nest monitoring in late August versus the sixth week in late September, because most (97%) newly laid eggs were found during or between these weeks. Dashed lines are 95% confidence limits. Estimates are based on the most parsimonious model.
model (Figure 2b; Figure S7; Table 1). However, mean hatching probability of unharvested eggs was lowest in nests which had four eggs harvested (Figure 2b; Figure S7). Consequently, the effect of harvest was retained in an alternative, competitive model of hatching probability (Figure 2b; Table 1). The random effect of nest explained nearly two-thirds (0.64) of the variance in hatching probability, whereas the most important fixed effects of distance to neighbour and week an egg was laid explained much less (0.15). The random effect of nest colony explained no variance in hatching probability. Nest height, distance to water and camera presence were not significant predictors of hatching probability (Table 1).

In the absence of flooding, distinguishing between different causes of egg failures proved difficult. Of the 70 eggs which failed, 10 (14%) did not show signs of disturbance and were thus either abandoned and/or infertile, whereas 60 (86%) were consumed either by predators while nests were still active, or by scavengers following nest abandonment. Using nest cameras (see Supporting Information), we identified predators or scavengers at seven nests during time intervals when ≥1 egg went missing. Of those seven nests, we identified Australasian swamphen (pūkeko, Porphyrio melanotus) at six nests, southern black-backed gull (karoro, Larus dominicanus) at three nests, and swamp harrier (kāhu, Circus approximans) and rat (Rattus sp.) at one nest each.

### 3.3 Hatching success

Models of hatching success were based on data from 75 nests. The single excluded nest (cf. models of post-harvest egg laying described above) contained no eggs for which we could confidently determine fates. Harvest pressure was the most important determinant of hatching success (Figure 2c; Figure S8; Table 1). Hatching success was highest in unharvested nests and lowest in nests which had four eggs harvested (Figure 2c; Figure S8). Although pre-harvest clutch size did not differ significantly among harvest treatment and non-harvest control groups, hatching success increased slightly with pre-harvest clutch size (Figure S8; Table 1). Camera presence at the start of the experiment reduced hatching success due to negative effects of camera presence on post-harvest egg laying, as described above (Figure S8; Table 1). These fixed effects accounted for approximately half (0.46) of the variance in nesting success, whereas the random effect of nesting colony explained very little (<0.01). Nest height, distance to neighbour and distance to water were not significant predictors of hatching success (Table 1).

Model predictions estimated that during hypothetical harvests of 12 eggs from six nests, harvesting two eggs from each nest resulted in the lowest cumulative hatching success, and approximately doubled the negative impact of harvesting all eggs from each of two nests and leaving four nests intact (Figure 4).

**FIGURE 4** Illustration showing how three alternative strategies for harvesting 12 eggs from six nests would affect overall hatching success according to the most parsimonious model of hatching success. Model predictions shown here assume a pre-harvest clutch size of six eggs, absence of cameras at nests, and no flooding. Harvested eggs are above each nest, whereas cygnets from unharvested eggs and newly laid eggs (not shown) are below each nest. The top row of nests (a) shows baseline hatching success of unharvested nests, which each hatch 5.68 ± 0.69 (standard error) cygnets. In (b), two eggs are harvested from each nest, and each nest hatches 3.39 ± 0.52 cygnets. In (c), four eggs are harvested from each of three nests, which each hatch 1.52 ± 0.32 cygnets. In (d), all six eggs are harvested from each of two nests, which each hatch 2.61 ± 0.49 cygnets.
4 | DISCUSSION

Understanding how wildlife harvests influence demographic rates is critical to species management and conservation outcomes (Mills, 2013). In this study, the effects of egg harvest on swan hatching success depended on nest-level harvest pressure and occurred primarily via direct removal of eggs and indirect, harvest-pressure-dependent impacts on post-harvest egg laying and clutch size. Specifically, harvesting one-third or two-thirds of a clutch of eggs resulted in the loss of approximately one hatching for each egg removed, because swans tended to replace few or none of those harvested eggs, and egg hatching probability was generally high in areas unaffected by flooding (Figures 2 and 4). In contrast, harvesting an entire clutch resulted in the loss of approximately one hatching for every two eggs removed, as swans often quickly reused empty nests to re-lay new, albeit smaller, clutches (Figures 2 and 4). Harvesting two-thirds of a clutch also impacted hatching success by reducing the probability of hatching for unharvested eggs (Figure 2b). Confidence limits around estimates for eggs within such nests were large, likely due to small sample size coupled with high variability in egg hatching probability among nests. However, the reduced hatching probability of eggs within nests that had two-thirds of eggs removed reflects the tendency of some swans to abandon nests following the removal of most, but not all, eggs. Taken together, these results clearly indicate that nest-level harvest impacts are not additive, and there is potential to adapt egg harvests to limit population-level impacts.

4.1 | Potential strategies for low-impact egg harvests

A common concern of governments, conservationists and the public is that customary harvests of wildlife by IPLC are not sustainable (Cuming, 1994; Hunn et al., 2003; Tyrrell, 2008). Nevertheless, western sport hunting and methods of food production (e.g. intensive, large-scale farming and cattle and poultry production) are legal yet frequently unsustainable (IPBES, 2019b; Weinbaum et al., 2013). We argue that conservation costs should be distributed fairly across demographics and cultures (Akins et al., 2019; Artelle et al., 2019; Gavin et al., 2015; Lyver, Ruru, et al., 2019). To that end, this study revealed three potential strategies for limiting the population-level impacts of future customary harvests of swan eggs.

First, during fixed-output harvests, removing entire clutches of eggs could minimize impacts on population-level hatching success. Although harvesting a small proportion of eggs from a clutch had a smaller nest-level impact than harvesting all eggs, the cumulative effect of harvesting few eggs from many nests resulted in nearly double the impact on population-level hatching success compared to harvesting the same total number of eggs from as few nests as possible (Figure 4), for the reasons described above. Thus, harvesting entire clutches early during the nesting season, when eggs are fresh and swans are mostly likely to re-use nests, may be the harvest strategy with the least impact (Zador et al., 2006). Determining a sustainable proportion of eggs to harvest from a population will require population-level models that account for demographic rates of all life stages (Mills, 2013). Another question is whether variation in brood size caused by different egg harvest regimes could influence parental investment, brood survival and recruitment into the breeding population. However, several studies of these demographic parameters in other waterbird species have found hatch date to be a more important driver than brood size (Krapu et al., 2000; Spear & Nur, 1994). Moreover, black swans at Te Waihora commonly form creches of mixed-family units during brood-rearing, with reports of two-thirds of all cygnets at the lagoon joining creches each summer (Williams, 1981). Likewise, the colonial nature of swan breeding ecology at Te Waihora may offset effects of individual brood size on juvenile survival and recruitment.

Second, the impacts of egg harvest could be reduced by harvesting from areas of breeding colonies with low nest density, where egg hatching probability was lower relative to areas with higher nest density. Density dependence is common in colonial-nesting birds and can influence breeding in positive and negative ways (Koons et al., 2014). For example, competition for resources (e.g. food, space and foliage for nesting and brood-rearing) can limit breeding in areas with high nest density (Koons et al., 2014). Conversely, high nest density can facilitate functional responses to predation risk (e.g. ‘safety in numbers’) that increase hatching success (Jones, 2003; Koons et al., 2014). Swans may have exhibited both positive and negative density dependence in the mid-20th century, when the abundance and density of nests at Te Waihora was much higher and swans frequently nested <2 m apart with reduced hatching success (Miers & Williams, 1969). However, we seldom observed swans nesting <2 m apart and found only positive density dependence at the two largest colonies. Harvesting from areas with low density of nests is a potential option for reducing harvest of eggs which are most likely to hatch, which could be coupled with the first strategy, as it helps to identify nests, rather than the number of eggs within them, to harvest. Harvesting from low density areas, which are often near the periphery of colonies, could also reduce potential disturbance (e.g. facilitation of nest predation) of unharvested nests caused by harvester presence within the colony (Zador et al., 2006).

Third, restoring foraging and nesting habitat within degraded wetlands bordering the lagoon could lessen the impacts of egg harvests by providing the plant food resources that swans require to lay eggs indeterminately (Williams, 1979). Bird clutch size can be limited by food and nutrient availability (Alisauskus & Ankney, 1994; Bolton et al., 1992; Braithwaite, 1977). Likewise, waterfowl hatching success can be limited by abundance of macrophytes, which are often the primary food source (Broyer & Curtet, 2010; Squires et al., 1992). The mean clutch size of black swans at Te Waihora decreased following the sudden loss of macrophyte beds in the 1968 ‘Wahine’ storm (Williams, 1979, 1981), and has since returned to levels observed before then (Cutten, 1966), possibly owing to a shift towards supplemental foraging on pasture (Williams, 2013). However, the results of this study show clearly that swans no longer lay eggs indeterminately,
as indicated by females replacing only a subset of harvested eggs (Figure 2). This pattern is almost certainly due to the previous loss of macrophytes and ongoing suppression of their growth and recovery due to agricultural runoff. Co-management efforts by Ngāi Tahu and the regional government aim to restore the ecological and cultural health of Te Waihora (Ford et al., 2017; Pauling & Arnold, 2008). Achieving those goals requires re-establishing swan foraging habitat, and protecting and restoring nesting habitat, to support swans and facilitate sustainable customary harvests of their eggs.

### 4.2 Potential benefits of customary harvests

We see several important benefits of supporting sustainable customary harvests by IPLC. Obviously, customary harvests for subsistence provide critical sources of nutrition for millions of people globally, including many IPLC (Milner-Gulland & Bennett, 2003). In addition, customary harvests are often central to IPLC cultural identity and well-being (Hunn et al., 2003; Lyver et al., 2009; Wilson, 2003). Many IPLC, including Māori, consider themselves to be intrinsically linked to nature through their genealogy (Lyver, Ruru, et al., 2019; Richardson, 2008). Customary harvest can be an important way for resource users to connect with their traditional lands, ancestors, cultural identity and family and community members through sharing of resources (Lemelin et al., 2010; Lyver et al., 2009; Wilson, 2003). Maintaining those connections for future generations to use is a key motivation among IPLC for conserving wildlife and their habitat (Lyver, Ruru, et al., 2019). Likewise, restrictions on customary harvest can undermine IPLC motivation to take part in conservation (Lyver & Tylianakis, 2017; Tyrrell, 2008).

Engaging more people in place-based resource management, such as customary harvests, also increases the number and detection resolution (both spatially and temporally) of ecological feedbacks (e.g. wildlife population numbers, habitat conditions), which can inform adaptive responses to environmental change (Berkes, 2009; Cumming et al., 2017; Herse et al., 2020; Thompson et al., 2020). For instance, current management of swans by FGNZ is based on annual, regional-scale trends in adult abundance and/or harvest rates, which could obscure local ecological drivers of populations (Herse et al., 2020; Weinbaum et al., 2013). Importantly, Māori who regularly engage with swans and their habitat through sustainable customary egg harvests could continuously monitor local variability in swan numbers, nesting productivity, habitat conditions and non-harvest pressures (e.g. nest predation, flooding). Coupling the regional- and local-scale data-gathering abilities of FGNZ and tangata tiaki, respectively, could facilitate adaptive harvest management (Herse et al., 2020). More generally, the regular interaction of IPLC with their environment, and culturally important species especially, can allow IPLC to adapt their knowledge to novel social and environmental contexts, leading to sustainable strategies that protect wildlife (Freitas et al., 2020; Lyver & Tylianakis, 2017; Tyrrell, 2008). Such regular engagement with the environment can improve sustainability within society by promoting collective action towards ecosystem conservation (Akins et al., 2019; Amel et al., 2017; Johannes, 2002). In contrast, environmental laws that aim to protect wildlife by prohibiting customary harvests can exacerbate threats by separating resource users from their environment, which can erode long-term ecological knowledge, community kinship, management practices and skills needed to adapt to environmental change and live sustainably (Lyver, Timoti, et al., 2019; Lyver & Tylianakis, 2017; Tyrrell, 2008).

Customary harvests could also be used to mitigate human-wildlife conflict. In most places, some species impose costs upon people’s livelihoods (e.g. depredation of crops, livestock or wild food sources) or safety (e.g. bird collisions with aircraft, attacks on humans; Dickman, 2010; Madden, 2004). Numerous techniques have been proposed by ecologists and implemented to mitigate conflict, such as physical separation (e.g. using fencing or other buffers), provisioning of alternative food sources for the ‘pest’ species, and lethal control through culling (Dickman, 2010; Williams, 1979). We argue that customary harvest could be a practical alternative in some cases. For instance, some farmers and Māori tribes worry about swan grazing impacts on pasture and macrophytes, respectively. Farmers have been permitted to cull swans around Te Waihora for decades to limit grazing and fouling of pasture, with little or no documentation of mortality rates (Williams, 1979). In addition, authorities at the nearby Christchurch Airport worry about potential risk of swans colliding with commercial jets and have proposed, without evidence, that culling swans would reduce the risk. Robust information on pasture damage and risk towards aircraft are needed to justify lethal control. However, if lethal control is warranted, harvesting swan eggs could provide an alternative means to control populations in problem areas without wasting resources, while also recognizing Māori rights to manage resources in culturally appropriate ways (Lynch & Blumstein, 2020; Sekar & Shiller, 2020). In these cases, using the low-impact strategies outlined above may be counter-productive, and more intensive strategies (e.g. harvesting throughout nesting colonies over the entire nesting season) could be appropriate. Thus, customary egg harvest strategies can be adapted to serve the management needs of a given area.

In conclusion, we contend that supporting IPLC in place-based resource management, including customary harvests, could be a practical and socially equitable way to manage wildlife, their habitat, and the cultures that value them (Akins et al., 2019; Artelle et al., 2019; Freitas et al., 2020; Gavin et al., 2015; Lyver, Ruru, et al., 2019; Lyver, Timoti, et al., 2019; Rayne et al., 2020). However, achieving those goals will require policies and flexible government arrangements that support the continual, long-term engagement of IPLC with resources, so IPLC can adapt to changes in their social and biophysical environment (Armitage et al., 2009; Lyver, Ruru, et al., 2019; Lyver, Timoti, et al., 2019).

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CONFLICT OF INTEREST
The authors do not have any conflicts of interest to report.

AUTHORS’ CONTRIBUTIONS
All authors contributed substantially to the conception and design of the experimental egg harvest and paper during a series of meetings and biannual huis (customary gatherings). All authors approved of the original and revised manuscript. In addition, M.R.H. led the design of the experiment, data analyses and writing of the paper. J.M.T., P.O’B.L., N.J.S., A.R.M. and A.M.G. contributed to the experimental design, data analyses and/or provided detailed comments on the writing of the manuscript. N.J.S. secured the primary funding for the study. C.P. assisted with fieldwork and the egg harvest.

DATA AVAILABILITY STATEMENT
The data from this study are jointly held by Tairawhiti Taskua o Ngāi Tahu and Manaaki Whenua Landcare Research (MWLR). The data are archived at MWLR (https://doi.org/10.7931/gj1a-f647).

ORCID
Mark R. Herse https://orcid.org/0000-0002-4387-0378
Jason M. Tylianakis https://orcid.org/0000-0001-7402-5620
Angus R. McIntosh https://orcid.org/0000-0003-2696-8813

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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