



Research

## A demographic model to support customary management of a culturally important waterfowl species

Mark R. Herse<sup>1</sup> , Phil O'B. Lyver<sup>2</sup>, Andrew M. Gormley<sup>2</sup>, Nigel J. Scott<sup>3</sup>, Angus R. McIntosh<sup>1</sup> , David Fletcher<sup>4</sup> and Jason Tylianakis<sup>1</sup> 

**ABSTRACT.** Scientific support invited by Indigenous peoples and local communities (IPLC) to assist with customary environmental management can improve conservation and community livelihoods. For example, demographic models can help to understand how alternative wildlife management strategies affect population dynamics and harvest sustainability. We developed a demographic model to assist Ngāi Tahu, the southern-most Māori tribe in Aotearoa/New Zealand, in customary management of a culturally important population of Black Swans (*kaki anau*, *Cygnus atratus*). We used recent demographic data, including results of an experimental egg harvest study, to inform *tangata tiaki* (Ngāi Tahu environmental guardians) about how customary egg harvest and background pressure from sport hunting of swans aged  $\geq 1$  year differentially affect population growth. We also assessed how sport hunting of swans affects the sustainability of customary egg harvest. Estimated population growth (1.018 or presently growing 1.8% annually; 95% CI: 0.808–1.241) was most sensitive to changes in adult and subadult survival, followed by juvenile (first-year) survival, breeding propensity, and nest hatching success. Uncertainty in population growth was almost entirely attributable to uncertainty in swan survival rates after hatching. Sustainable population-level rates of egg harvest varied from none to more than half of all eggs, depending on small changes in adult and subadult survival. Population sensitivity to adult and subadult survival suggests that limiting and monitoring their mortality are crucial to population and egg harvest sustainability, whereas contemporary government-mandated species management, through Fish and Game New Zealand, allows adult and subadult mortality from sport hunting, with little record of offtake. Recognizing the rights and interests of Ngāi Tahu, and monitoring swan mortality more closely, could improve Ngāi Tahu abilities to practice customary harvest, enhance population and environmental monitoring, and, when appropriate, control swan numbers in a culturally appropriate and less wasteful way. The model we present could aid decision making and communication between Ngāi Tahu and New Zealand's Crown government within a potential future co-management arrangement. Demographic models can be useful tools for supporting customary environmental management, but developing, maintaining, and implementing these tools requires support for adaptive policies and management arrangements that recognize IPLC rights to the environment and decision making.

**Key Words:** *adaptive management; biocultural conservation; equity; gamebird management; Indigenous peoples; kaitiakitanga; mahinga kai; tikanga; waterfowl; wetlands*

### INTRODUCTION

Contemporary environmental management systems are struggling to curb global declines in biodiversity and ecosystem health (Díaz et al. 2019, IPBES 2019a). One limiting factor for management is the ability to continually monitor biodiversity and ecosystems at fine resolutions across large areas, and to implement adaptive conservation measures locally (Cumming et al. 2006, Guerrero et al. 2013). To help overcome this limitation, and to reclaim rights and responsibilities for the environment more generally, many 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 2019b) are vocal and active in empowering their customary environmental management systems (Ens et al. 2012, Witter et al. 2015, Lyver and Tylianakis 2017). Within many customary management systems, IPLC continually engage with and monitor their environments, while over time accumulating long-term experiential knowledge of biodiversity and ecosystems at fine resolutions (Gadgil et al. 1993, Moller et al. 2004, Berkes 2009). Customary resource use and engagement with the environment underpin many aspects of well-being for IPLC, including

livelihoods, cultural identities, and community kinship, and these relationships can motivate sustainable practices and enforcement of local conservation (Cinner and Aswani 2007, Lyver et al. 2008, Halim et al. 2012, Sheil et al. 2015, Caillon et al. 2017). Thus, supporting IPLC in the customary management of their lands and resources could be both a practical and just way to enhance environmental monitoring and protection (Sobrevila 2008, Artelle et al. 2019, Herse et al. 2020, Dawson et al. 2021, Reyes-García et al. 2022).

In many places, the legal authority of IPLC to decide whether resource use can occur, what uses and strategies are appropriate, and who should be allowed access to use, are either missing or neglected (Kinan and Dalzell 2005, Goldman 2011, Ruru et al. 2017, Snook et al. 2020). In such cases, management decisions by non-IPLC authorities are often biased toward competing interests of recreational or commercial harvest (Ban et al. 2017), alternative land uses, e.g., mining (Parlee et al. 2018), or preservationist strategies, e.g., protected areas, that prioritize separation between IPLC and their environment (Brockington and Igoe 2006, Solomon 2014) and do not value customary harvests (Hunn et al. 2003, Tyrrell 2008, Lyver et al. 2019a). Environmental scientists have increasingly used demographic models of animal

<sup>1</sup>School of Biological Sciences, University of Canterbury, Christchurch, New Zealand, <sup>2</sup>Manaaki Whenua Landcare Research, Lincoln, New Zealand, <sup>3</sup>Strategy and Influence, Te Rūnanga o Ngāi Tahu, Christchurch, New Zealand, <sup>4</sup>David Fletcher Consulting Limited, Karitane, New Zealand

populations to inform decision making about customary resource use and management (Brook et al. 2006, Zador et al. 2006, Bradshaw and Brook 2007, Chaloupka and Balazs 2007, Jones et al. 2015, McKechnie et al. 2020). For example, Chaloupka and Balazs (2007) used a demographic model to inform public policy debates in Hawai'i, USA, about the sustainability of re-initiating customary harvests of green sea turtles (*Chelonia mydas*), which were prohibited following overexploitation by commercial harvest and subsequent listing of the green sea turtle as an "endangered species." In Australia, Bradshaw and Brook (2007) used demographic models to assess strategies for balancing customary use of exotic, endangered banteng (*Bos javanicus*) by Aboriginal communities, and offtake of recreational and commercial harvest. However, IPLC voices and interpretations of scientific evidence are largely absent from such studies if they are not initiated by IPLC or do not include IPLC representation. Likewise, when IPLC wish to engage in customary management and welcome scientific support, collecting, interpreting, and disseminating data in partnership with IPLC is important to ensure that their rights, values, and priorities are fully recognized (Ens et al. 2012, Rayne et al. 2020, Dawson et al. 2021).

Here we present a demographic model developed in partnership with Ngāi Tahu, the southern-most tribe of Māori in Aotearoa/New Zealand, to support customary management of Black Swans (*kakī anau*, *Cygnus atratus*) at a 200-km<sup>2</sup> coastal lagoon and key Black Swan breeding area, Te Waihora/Lake Ellesmere (Fig. 1). Harvests of Black Swans and their eggs have been important components of customary management and food gathering at Te Waihora for generations, but restricted since New Zealand's colonial government seized control of local species management in the early 20th century CE (Lamb 1964, Pauling and Arnold 2008, Herse et al. 2021). Current law in New Zealand classifies Black Swans as "gamebirds" that can be hunted for sport by gamebird license holders (New Zealand Government 1953), yet prohibits customary harvest without special permission (Herse et al. 2020, 2021). Contemporary government-mandated gamebird managers use daily bag limits (quotas), set annually, to maintain swan numbers in the recreational interests of sport hunters (New Zealand Government 1987), and in the past have permitted culls by local farmers (European New Zealanders) to limit grazing of pasture and potential economic loss (Williams 1979). The extent of pressure from sport hunting and past culling is poorly known because the contemporary gamebird management body, Fish and Game New Zealand (FGNZ), does not require licensed sport hunters or landowners to report their offtake, and periodic regional phone surveys by FGNZ of offtake trends are not site specific (Herse et al. 2020).

Ngāi Tahu is interested in managing the swan population at least partly through self-authorized customary egg harvests, without oversight or special permission (Herse et al. 2020, 2021). The right of Ngāi Tahu to self-authorize harvest and management of swans is guaranteed within New Zealand's founding document between *tangata whenua* (original people of the land) and the Crown government, the Treaty of Waitangi 1840, whereby "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" (Kawharu 1989:321). Similarly, Ngāi Tahu rights to "determine and develop priorities and strategies for the development or use

of their lands or territories and other resources" are protected under the United Nations Declaration on the Rights of Indigenous Peoples (United Nations General Assembly 2007:23). However, these rights have not been realized or enacted under current gamebird management regulations. In addition to FGNZ-permitted sport hunting and culling, damage to aquatic plants by a massive storm in 1968 (the "Wahine" storm), coupled with extensive agricultural runoff over the past half century, has degraded Te Waihora, depleted swans' macrophyte food supply (Lineham 1983, Gerbeaux 1989, Hearnshaw and Hughey 2010), and reduced swan numbers by approximately 90% (Williams 1979, Ford et al. 2017). Thus, it is unclear whether the current swan population can sustain potential customary egg harvest or any of the ongoing sport hunting, and how such pressures on swan fertility (hatching success) and survivorship, respectively, affect the population.

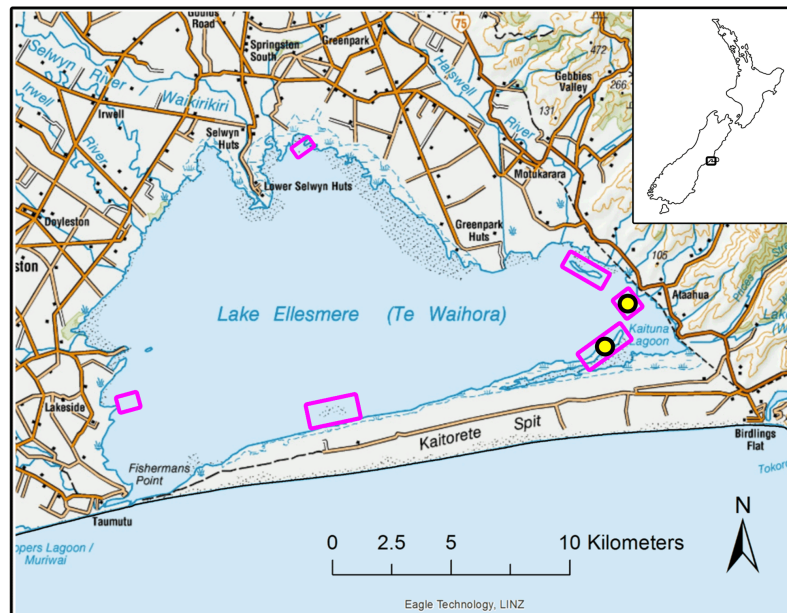
Our goal was to provide Ngāi Tahu with up-to-date information on the Te Waihora swan population with which to enter discussions with FGNZ and New Zealand's Crown government, about potential strategies for re-initiating customary egg harvests. To that end, we started by using recent demographic data and an age-classified matrix population model to (a) estimate the current annual population growth rate or change in population size ( $\lambda$ ; Caswell 2001). We then used the model to assess (b) how changes in swan fertility and age-specific survivorship differentially affected  $\lambda$ , and (c) how current levels of uncertainty in these demographic rates differentially contributed to uncertainty in  $\lambda$ . To understand the egg-harvest equivalence of sport hunting, we estimated (d) the expected lifelong output of both freshly laid eggs and hatched eggs (i.e., measures of reproductive value; Caswell 2001) by individual swans aged  $\geq 1$  year, which are collectively most susceptible to being shot (Williams 1977). Finally, we used results of a recent experimental egg harvest study (Herse et al. 2021) to (e) assess how offtake from sport hunting affects the sustainability of potential customary egg harvest by Ngāi Tahu. Based on the model results, we explore potential pathways for incorporating customary egg harvest into local species management. We end by outlining potential ways of improving support for customary management, which could enhance environmental monitoring and protection (Ens et al. 2016, Herse et al. 2020, Dawson et al. 2021, Lyver et al. 2021).

## METHODS

### Study species and population

The modern Black Swan (*C. atratus*) originates from Australia and is congeneric with the endemic New Zealand Black Swan (*poūwa*, *C. sumnerensis*), which became extinct on New Zealand's mainland around the 15th century, after Māori arrival and prior to European arrival (Rawlence et al. 2017). Europeans reported *C. atratus* as absent in New Zealand during the 19th century and introduced several pairs from Australia in the 1860s (Lamb 1964). However, rapid population growth following the introductions, and recent DNA evidence, suggest that waves of *C. atratus* dispersal from Australia before and during the 19th century, and/or genetic rescue of an extant population through admixing with introduced individuals, may have occurred (Rawlence et al. 2017, Montano et al. 2018a). Consequently, scientists have debated whether modern Black Swans are native to New Zealand (Montano et al. 2018b, Rawlence et al. 2018). Some Ngāi Tahu

**Fig. 1.** Map of our study area at Te Waihora/Lake Ellesmere, home to the largest population of Black Swans (*Cygnus atratus*) on the South Island of Aotearoa/New Zealand. Purple boxes outline swan breeding areas where we used orthophotography to census nests. Black and yellow circles indicate the current locations of the largest two swan breeding colonies at Te Waihora, where the data on nest fertility and egg harvest that we used in models originate. The map is a modified version of the NZ Topographic Basemap available on ArcGIS 10.5 (Environmental Systems Research Institute, Redlands, CA, USA; ©Eagle Technology Group Ltd.).



tribal members consider Black Swans native to New Zealand (Bataille 2020), and the species is recognized as such within the Te Waihora Joint Management Plan between Ngāi Tahu and the Minister of Conservation (Te Rūnanga o Ngāi Tahu and Department of Conservation 2005). More importantly, Black Swans are highly valued by some Ngāi Tahu people as key elements of cultural practices such as *kaitiakitanga* (environmental guardianship) and *mahinga kai* (“customary gathering of food and natural materials and the places where those resources are gathered”; New Zealand Government 1998:102, Bataille 2020, Bataille et al. 2021), which are important to Māori cultural integrity (Kawharu 2000), knowledge production (Lyster et al. 2019b), and conservation (Wehi and Lord 2017). The species is also valued by some gamebird license holders and other members of the public, whereas some farmers consider swans to be pests because they sometimes graze on pasture (Bataille et al. 2020, 2021).

Black Swans (hereafter “swans”) mostly breed in colonies at shallow lakes, lagoons, and estuaries (Williams 1981, 2013a). Te Waihora contains the largest population of swans on New Zealand’s South Island, with estimates of population size varying from ~5000 to 10,000 individuals during the past two decades (Ford et al. 2017, Herse et al. 2020). Similar to other swan species globally, most Black Swans at Te Waihora live for fewer than 10 years, and less than half of adults attempt nesting each year (Williams 1979, 1981, 2013, Bart et al. 1991). Black Swans are typically monogamous and breeding at Te Waihora is generally synchronous, beginning in August to September as winter water levels decline, and decreasing in October after most nests hatch (Williams 1981, 2013a, Herse et al. 2021). Mean clutch size is 5–

6 eggs (Williams 2013a, Herse et al. 2021). A second bout of breeding, which comprises up to approximately one-third of all nesting during a given breeding season, sometimes occurs during October–December (Donald Brown, Ngāi Tahu, Christchurch, New Zealand, 19 June 2018, *personal communication*; Herse et al. 2021). In a previous experimental egg harvest study, Herse et al. (2021) found that following the complete removal of first clutches of eggs, swans tended to replace a portion of those eggs, such that the average nest-level hatching success among harvested nests was 2.61 cygnets (cf. 5.68 cygnets per unharvested nest). Although Herse et al. (2021) could not determine whether re-nesting following clutch failure was by original nest occupants versus other swans using newly available nests, individual pairs have been documented re-nesting following clutch failure (Williams 1979), indicating that at least some of the second bout of breeding is due to re-nesting. Pressures on nest hatching success in our study area include nest depredation, flooding, and infertility, but hatching success is nevertheless generally high at the largest nesting colonies (Adams 1971, Meis 1988, Herse et al. 2021). Juvenile swans (cygnets) reach independence ~3–5 months after hatching and sexual maturity at 2–4 years of age (Williams 2013a).

In addition to food availability, current pressures on swan survivorship include sport hunting (Williams 1979, Herse et al. 2020). Gamebird managers set bag limits based on trends in swan numbers and offtake rates estimated from periodic aerial surveys and phone surveys, respectively, and aggregated at scales of hunting regions or subregions over which individual bag limits apply (Herse et al. 2020). During recent years, gamebird license holders within the ~2,500-km<sup>2</sup> hunting subregion containing Te Waihora have each been allowed to shoot 5 swans per day during



most of May–July, and 20 swans per day during most of August–September (Herse et al. 2020). However, current rates of gamebird shooting and their impacts on the swan population at Te Waihora are poorly understood for several reasons. New Zealand law requires private landowners to adhere to local gamebird bag limits but does not require landowners to obtain licenses to shoot swans on their property (New Zealand Government 1953), or to report their offtake. Similarly, FGNZ does not require gamebird license holders to report their offtake. In addition, regional surveys of offtake are not site specific and include areas outside of the Te Waihora subregion (Herse et al. 2020).

### Matrix population model

We developed an age-classified matrix population model (Leslie 1945, Caswell 2001) to describe swan population dynamics. The model is defined by

$$\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t \quad (1)$$

where  $\mathbf{A}$  is a projection matrix including age-specific, per-capita estimates of swan fertility and survival rates, and  $\mathbf{n}_t$  is a vector of numbers of individuals per age class during time  $t$  (Caswell 2001). Time units span one year beginning when eggs hatch and ending immediately prior to hatching during the following nesting season (“post-breeding census”; Caswell 2001). We assumed the population was closed to immigration and emigration because swan dispersal among waterbodies within the region is infrequent (Williams 1977; Herse, Lyver, Scott, Tylianakis, and Ngāi Tahu, unpublished data), and local species management cannot control movements of the population’s small proportion of dispersive individuals.

Considering age at first reproduction is 2–4 years (Williams 2013a), it would be reasonable to develop a stage-classified model based on hatchling, sexually immature subadult, and adult stage classes. However, because we could not distinguish subadults from non-breeding adults during population censuses, we could not estimate the proportion of adults attempting breeding per year; we could only estimate this proportion for subadults and adults combined. In addition, we lacked data on the current age distribution of swans at Te Waihora, and did not know if or how ongoing mortality from sport hunting varied across annual age classes. Thus, we based the model on a simplified life cycle with hatch-year (HY, age < 1 year since hatching) and after-hatch-year (AHY, age ≥ 1 year since hatching) age classes (Fig. 2). The fertility term in this model includes the proportion of AHY swans, i.e., subadults plus adults, that attempt breeding each year, which we could estimate. Demographic rates of finer resolution age or stage classes could be parameterized later with additional data if they become available.

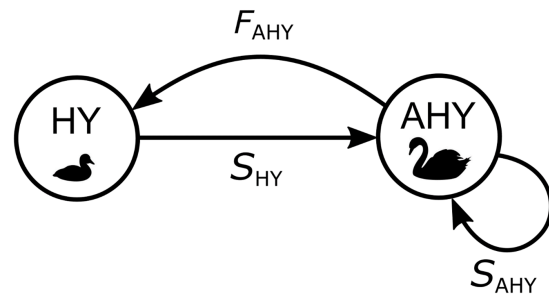
The model can be written in matrix form as

$$\begin{pmatrix} N_{HY} \\ N_{AHY} \end{pmatrix}_{t+1} = \begin{pmatrix} 0 & F_{AHY} \\ S_{HY} & S_{AHY} \end{pmatrix} \begin{pmatrix} N_{HY} \\ N_{AHY} \end{pmatrix}_t \quad (2)$$

where  $N_{HY,t}$  and  $N_{AHY,t}$  are the number of HY and AHY swans, respectively, during time (year)  $t$ ;  $F_{AHY}$  is annual fertility or number of eggs hatched per AHY swan;  $S_{HY}$  is the probability of a swan surviving the first year after hatching (i.e., the “hatch year”); and  $S_{AHY}$  is annual survival probability for AHY swans. Fertility of HY swans (top left element of matrix in Equation 2)

is 0 because HY swans do not breed (Williams 2013). Modeled demographic transition rates (matrix elements) are time-invariant, but could be updated annually with new data.

**Fig. 2.** Life-cycle diagram of the age-classified matrix model we used to describe Black Swan (*Cygnus atratus*) population dynamics at Te Waihora/Lake Ellesmere, Aotearoa/New Zealand. Circles represent age classes (HY = hatch year, age < 1 year since hatching; AHY = after hatch year, age ≥ 1 year since hatching), whereas arrows represent annual per-capita demographic transition rates ( $F_{AHY}$  = annual fertility or number of eggs hatched per AHY swan;  $S_{HY}$  = probability of surviving the first year after hatching;  $S_{AHY}$  = annual survival probability for AHY swans).



Factors that affect annual fertility of AHY swans include propensity to attempt breeding, nest hatching success, and mortality of AHY swans (Williams 1979, 1981, Herse et al. 2021). Hatching success differs between unharvested and harvested nests because, in recent years, swans tend to replace only a subset of harvested eggs (Herse et al. 2021). Thus, we estimated  $F_{AHY}$  using the expression:

$$F_{AHY} = 0.5(f_0(1-h) + f_a h) b S_{AHY} \quad (3)$$

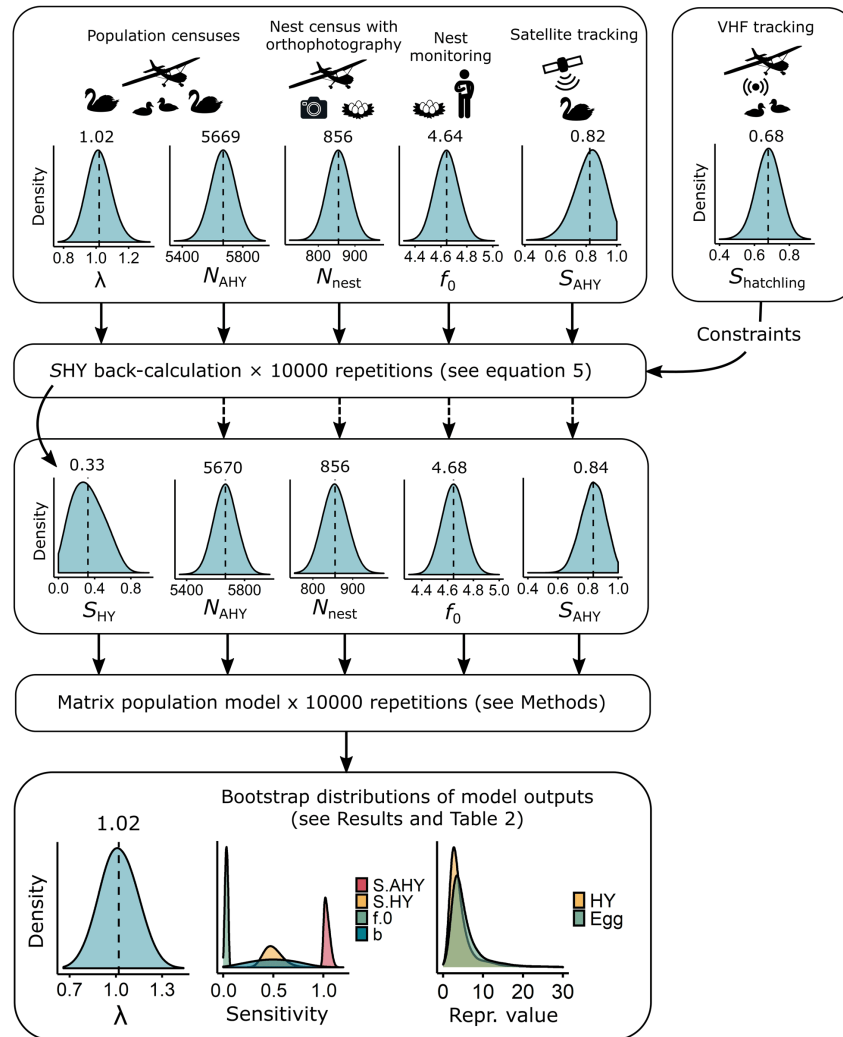
where  $f_0$  is fertility per unharvested nest,  $f_a$  is fertility per harvested nest,  $h$  is the proportion of total nests harvested, and  $b$  is the proportion of AHY swans that attempt breeding, as noted above. Multiplying fertility per nest by 0.5 gives fertility per breeding swan, because breeding is typically monogamous (Williams 2013a). The model assumes that during fixed-output egg harvests, harvesters remove entire clutches of eggs from harvested nests (as opposed to removing fewer eggs per nest from a larger number of nests), because this was the strategy found to have the least impact on population-level hatching success during a recent harvest experiment (Herse et al. 2021). The  $S_{AHY}$  term in Equation 3 accounts for some swans not surviving the current year to attempt breeding in year  $t + 1$ .

The limited availability of macrophyte food at Te Waihora could prevent the swan population from increasing above a certain size, regardless of pressure from sport hunting or customary harvest (Williams 1979, Herse et al. 2021). However, we did not include density dependence in the model because we lacked information to define a swan population carrying capacity for Te Waihora.

### Estimation of demographic parameters

We estimated demographic parameters and associated variances in three steps using a parametric bootstrap approach that included empirical data and indirect methods (Fig. 3). First, we used recent

**Fig. 3.** Flow diagram illustrating the steps we followed to develop the matrix model and estimate demographic parameters for the Black Swan (*Cygnus atratus*) population at Te Waihora/Lake Ellesmere, Aotearoa/New Zealand. First, we used empirical data to define initial bootstrap sampling distributions for population growth ( $\lambda$ ), underlying parameters of annual fertility per after-hatch-year (AHY) swan (FAHY), and annual survival probability for AHY swans (SAHY). Second, we used random sampling from initial distributions to back-calculate, and hence generate a bootstrap distribution for, survival probability of swans over their first (hatch) year (SHY). Back-calculations of SHY incorporated information on survival of swan hatchlings (Shatchling), and adjusted the distributions for SAHY and underlying parameters of FAHY. Last, we used random sampling from the resulting bootstrap distributions to parameterize the matrix model and generate bootstrap distributions for a suite of demographic parameters for the focal population.



demographic data to define initial bootstrap sampling distributions for estimates of  $\lambda$ ,  $S_{AHY}$ , and underlying parameters of  $F_{AHY}$  (Equation 3, Table 1, Fig. 3). Second, we used random sampling from the initial distributions to back-calculate, and hence generate a bootstrap distribution for, estimates of  $S_{HY}$ , which we lacked data to confidently estimate directly (Table 1, Fig. 3). Back-calculations of  $S_{HY}$  incorporated information on survival of swan hatchlings and resulted in adjusted bootstrap distributions for  $S_{AHY}$  and underlying parameters of  $F_{AHY}$  (Table 1, Fig. 3). Finally, we used random sampling from the resulting bootstrap distributions to parameterize the matrix model and

generate bootstrap distributions for a suite of demographic parameters for the Te Waihora population (Table 2, Fig. 3). All bootstrap distributions were based on  $n = 10,000$  samples. We provide more detail on each of these steps below and in Appendix 1.

To define initial sampling distributions used for back-calculating  $S_{HY}$ , we estimated  $N_{HY}$  and  $N_{AHY}$  based on mean counts of swans made by two independent observers during a post-breeding aerial census in December, 2018 (Fig. 3, see Appendix 1). We estimated  $f_0$  and  $f_a$  using data from observations of unharvested and harvested nests, respectively, during an experimental egg harvest

at Te Waihora during the peak nesting period (August–September) in 2018 (Fig. 3, Fig. A1.1, see Appendix 1; Herse et al. 2021). Thus, the model assumes that all breeding during a given year occurs during peak nesting season, which we visually estimated to include ~88% of all nests at Te Waihora in 2018 (see Appendix 1). However, the model accounts for contributions of late-season nesting to estimated population growth rate,  $\hat{\lambda}$ , indirectly through back-calculations of  $S_{HY}$  (detailed below), which incorporated information on  $N_{HY}$  and total population size, including cygnets hatched from late season nests. We estimated  $b$  as the proportion of AHY swans that attempted breeding during the peak nesting period at Te Waihora in 2018, as determined by aerial censuses of nests (assuming each nest represented two breeding swans; Williams 2013a) and AHY swans (Fig. 3, Fig. A1.2, see Appendix 1). The estimate of  $b$  in 2018 (0.30) was similar to estimates from previous studies (0.16–0.34; Williams 1981). We estimated  $S_{AHY}$  based on known fates of 17 GPS-marked AHY swans we monitored at Te Waihora during 2019–2020 (Fig. 3, see Appendix 1), which had an estimated mean survival rate similar to those estimated from previous long-term band-recovery studies (Fig. 3, Fig. A1.3; Williams 1979, Barker and Buchanan 1993).

**Table 1.** Means and associated 95% confidence limits (in parentheses) of bootstrap distributions of demographic rates used to model Black Swan (*Cygnus atratus*) population dynamics at Te Waihora/Lake Ellesmere, Aotearoa/New Zealand. Demographic rates include population growth rate ( $\lambda$ ), fertility (number of eggs hatched) per unharvested ( $f_0$ ) and harvested ( $f_a$ ) nest, total number of nests ( $N_{nest}$ ), total number of after-hatch-year or AHY swans ( $N_{AHY}$ ), survival probability of swan hatchlings over their first 40 days of life (Shatchling), survival probability over the first (hatch) year (SHY), and annual survival probability for AHY swans (SAHY). Distributions marked with subscript “a” were used to back-calculate SHY, and adjusted based on constraints related to Shatchling (see main text). Distributions marked with subscript “b” were used to parameterize the matrix model, whereas distributions marked with an asterisk were adjusted but not used in the matrix model.

Demographic rate	Initial bootstrap distribution	New or adjusted bootstrap distribution
$\lambda$	1.020 (0.890, 1.170) <sup>a</sup>	1.017 (0.898, 1.150) <sup>*</sup>
$f_0$	4.64 (3.55, 5.83) <sup>a</sup>	4.68 (3.60, 5.88) <sup>b</sup>
$f_a$	2.67 (1.64, 3.83) <sup>b</sup>	-
$N_{nest}$	856 (800, 913) <sup>a</sup>	856 (799, 912) <sup>b</sup>
$N_{AHY}$	5669 (5521, 5815) <sup>a</sup>	5670 (5520, 5815) <sup>b</sup>
$S_{shatchling}$	0.68 (0.54, 0.80) <sup>a</sup>	0.68 (0.54, 0.80) <sup>*</sup>
$S_{SHY}$	-	0.33 (0.06, 0.66) <sup>b</sup>
$S_{SAHY}$	0.82 (0.65, 1.0) <sup>a</sup>	0.84 (0.71, 0.94) <sup>b</sup>

**Table 2.** Means and associated 95% confidence limits (in parentheses) of bootstrap distributions for different parameters corresponding with demographic rates ( $f_0$  is fertility or number of eggs hatched per unharvested nest;  $b$  is annual breeding propensity; SHY is the probability of surviving the first or hatch year; SAHY is annual survival probability for AHY swans) that determined estimated Black Swan (*Cygnus atratus*) population

growth ( $\lambda$ ) at Te Waihora/Lake Ellesmere, Aotearoa/New Zealand. ‘Sensitivity’ and ‘elasticity’ are measures of the effects of absolute and proportional changes, respectively, in a given demographic rate on  $\lambda$ . To assess sources of uncertainty in  $\lambda$ , we quantified the ‘contribution’ of variance in each demographic rate to total variance in  $\lambda$ . ‘Reproductive value’ refers to estimates of the expected total number of fresh eggs and hatched eggs (i.e., HY swans) produced by an individual AHY swan during its lifetime, on average. All estimates are based on a model that assumes no egg harvest pressure ( $h = 0$ ); this special case of the model leads to the elasticities for  $f_0$ ,  $b$ , and SHY being identical.

Demographic rate	Sensitivity of $\lambda$	Elasticity of $\lambda$	Contribution to uncertainty in $\lambda$
$f_0$	0.032 (0.008, 0.056)	0.145 (0.041, 0.229)	0.027
$b$	0.502 (0.120, 0.886)	0.145 (0.041, 0.229)	0.001
$S_{SHY}$	0.499 (0.361, 0.694)	0.145 (0.041, 0.229)	0.530
$S_{SAHY}$	1.037 (1.002, 1.097)	0.855 (0.771, 0.959)	0.442

We used random samples from the initial bootstrap distributions described above to back-calculate  $S_{HY}$ . Because population growth rate,  $\lambda$ , the dominant eigenvalue of matrix  $\mathbf{A}$ , can be solved by the characteristic equation:

$$\det(\mathbf{A} - \lambda \mathbf{I}) = \det \begin{pmatrix} -\lambda & F_{AHY} \\ S_{HY} & S_{AHY} - \lambda \end{pmatrix} = \quad (4)$$

$$(-\lambda)(S_{AHY} - \lambda) - (S_{HY})(F_{AHY}) = 0$$

where  $\mathbf{I}$  is a  $2 \times 2$  identity matrix (Caswell 2001), we rearranged Equation 4 and estimated  $S_{HY}$  using the expression:

$$S_{HY} = \frac{\lambda^2 - \lambda S_{AHY}}{F_{AHY}} \quad (5)$$

where  $\lambda$  was estimated based on the annual trend in swan population size at Te Waihora during 2017–2019, as determined by aerial censuses (see Appendix 1). Specifically, we estimated  $\lambda$  in Equation 5 as the exponent of the slope of the linear regression line relating log population size to year (Fig. 3, Fig. A1.4; see Appendix 1; Peery et al. 2006). We applied several constraints to Equation 5 to ensure that  $\hat{S}_{HY}$  was  $> 0$  and less than the estimated survival rate of  $n = 50$  marked swan hatchlings over their first 40 days of life at Te Waihora in 2018 (Fig. 3; see Appendix 1). If constraints were not met during a draw of samples, we discarded samples of all parameters in that draw and sampled again. The mean of the resulting bootstrap distribution for  $S_{HY}$  (Table 1, Fig. 3) was congruent with estimates extrapolated from a survival analysis of the swan hatchling data and estimates from previous studies (Fig. A1.5, see Appendix 1; Williams 1979, Meis 1988). The application of constraints to back-calculations of  $S_{HY}$  resulted in adjusted bootstrap distributions of parameters used in back-calculations (Table 2, Fig. 3).

We used random samples from bootstrap distributions described above to parameterize the matrix model (Table 1, Fig. 3). We used functions available in the R “popbio” package (Stubben et al.

2020, R Core Team 2021) to estimate a suite of demographic parameters for the swan population, assuming no egg harvest pressure ( $h = 0$ ). We estimated annual  $\lambda$  as the dominant eigenvalue of the matrix  $\mathbf{A}$  (Fig. 3), as described above (Caswell 2001). To determine how changes in  $S_{\text{HY}}$  and  $S_{\text{AHY}}$ , and lower-level rates of  $F_{\text{AHY}}$  ( $f_0$  and  $b$ ), differentially affected  $\lambda$ , we calculated sensitivity ( $s_x$ ) and elasticity ( $e_x$ ) of  $\hat{\lambda}$  to absolute and proportional changes, respectively, in each underlying demographic rate  $x$  (see Appendix 1; Caswell 2001). Elasticity can be interpreted as a measure of the relative importance of a given demographic rate for determining  $\lambda$  (Caswell 2001). Both sensitivity and elasticity are useful and simply measure effects of changes in demographic rates at different scales (i.e., absolute versus proportional); measuring both ensured that we would not overlook an effect that is apparent on only one scale (Caswell 2001). To assess how current levels of uncertainty in demographic rates differentially contributed to uncertainty in  $\lambda$ , we used variances of bootstrap distributions of  $s_x$  and  $e_x$  to calculate the proportional contribution of each demographic rate to the total variance in  $\lambda$  (see Appendix 1; Caswell 2001). To determine the egg-harvest equivalence of removing one AHY swan from the population, we estimated the life expectancy and reproductive value (i.e., expected per-capita lifelong reproductive output,  $r_{\text{HY}}$ , or number of HY swans produced; Caswell 2001) of AHY swans, and then estimated the expected per-capita lifelong number of fresh eggs laid as

$$\frac{r_{\text{HY}}}{S_{\text{egg}}} \quad (6)$$

where  $S_{\text{egg}}$  is the estimated mean survival (hatching) probability of an individual egg from an unharvested nest (Herse et al. 2021).

#### Sustainability of mixed management

To assess how offtake from sport hunting of AHY swans affects the sustainability of potential customary egg harvests, we used the matrix model to estimate  $\lambda$  based on varying rates of  $S_{\text{AHY}}$  and  $h$  individually and in combination. Te Waihora-specific information on sport hunting of swans does not exist, as described above (Herse et al. 2020), and our estimate of  $S_{\text{AHY}}$  accounts for risk from this pressure. Thus, we considered a range of  $S_{\text{AHY}}$  covering the model estimated mean  $S_{\text{AHY}} \pm 0.1$  (in increments of 0.02), which was a wide enough range to detect both positive and negative  $\hat{\lambda}$  across all possible rates of  $h$ . We considered the full range of potential  $h$  (0–1, in increments of 0.1) because the swan population used to sustain high rates of egg removal during the early and mid-20th century (Lamb 1964, Williams 1979). For each combination of  $S_{\text{AHY}}$  and  $h$ , we held both of these rates constant and used  $n = 10,000$  random samples from each of the bootstrap distributions of the other parameters described above to estimate  $\lambda$ . This approach allowed us to assess uncertainty in  $\hat{\lambda}$  for each combination of  $S_{\text{AHY}}$  and  $h$ .

#### RESULTS

The demographic data we used for modeling swan population dynamics were congruent with data from previous studies (Table 1; see Appendix 1), and the model provided ecologically plausible estimates of demographic parameters (Figs. 3, 4, Table 2).

#### Differential effects of demographic rates on population growth

The mean of the bootstrap distribution of  $\lambda$  was 1.018 (1.8% annual growth) (95% CI 0.808–1.241). Both sensitivity and elasticity analyses showed that  $\lambda$  was affected most strongly by changes in  $S_{\text{AHY}}$ , followed by changes in  $S_{\text{HY}}$ ,  $b$ , and, least of all,  $f_0$  (Table 2, Fig. 3). Based on the means of the bootstrap distributions of  $s_x$  and  $e_x$ , the effect of an absolute change in  $S_{\text{AHY}}$  on  $\lambda$  was about 30 times greater than that of  $f_0$ , whereas the effect of a proportional change in  $S_{\text{AHY}}$  on  $\lambda$  was almost six times greater than that of  $f_0$  (Table 2). Uncertainty in  $\lambda$  was almost entirely due to uncertainty in  $S_{\text{HY}}$  and  $S_{\text{AHY}}$  (Table 2).

#### Life expectancy and reproductive value of after-hatch-year swans

The model estimated that life expectancy of AHY swans was 5.7 years (95% CI: 3.4–17.0; see Appendix 1), and the mean number of fresh eggs and hatched eggs each AHY swan would produce in its lifetime, assuming no egg harvest pressure, were 5.9 (95% CI: 2.1–20.2) and 4.5 (95% CI: 1.7–15.3), respectively (Fig. 3).

#### Sustainability of mixed management

Assuming the mean of the bootstrap distribution of  $S_{\text{AHY}}$ , the model estimated that the proportion of all swan nests at Te Waihora that could have all eggs from first clutches harvested sustainably was  $\sim 0.3$  (Fig. 4). However, the level of egg harvest that the population could sustain depended strongly on  $S_{\text{AHY}}$  (Fig. 4). For instance, the estimated proportion of all swan nests that could have first-clutch eggs harvested sustainably decreased to zero if  $S_{\text{AHY}}$  decreased by only 0.02, and approximately doubled to  $\sim 0.6$  if  $S_{\text{AHY}}$  increased by 0.02 (Fig. 4). If  $S_{\text{AHY}}$  increased by 0.04, the model estimated that harvesting almost all eggs from first clutches at Te Waihora would be sustainable (Fig. 4).

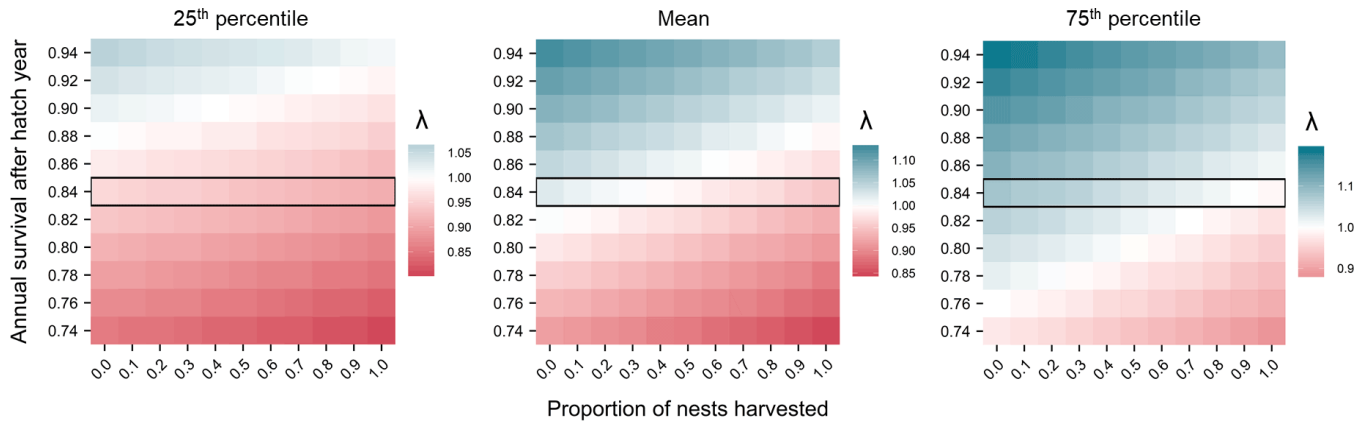
#### DISCUSSION

Sustainable species management requires understanding how populations respond to different demographic pressures and iteratively adapting management to population and environmental fluctuations (Moller et al. 2004, Weinbaum et al. 2013). The Te Waihora swan population was more sensitive to changes in survival of subadults and adults (AHY individuals) than to changes in fertility, consistent with other long-lived waterfowl species (Cooch et al. 2014, Koons et al. 2014, Wood et al. 2019). Moreover, population sensitivity to fertility was mostly due to underlying sensitivity to breeding propensity rather than nest hatching success. In addition, uncertainty in the current swan population growth rate was almost entirely attributable to uncertainty in swan survival rates after hatching (Table 2). These results could be particularly useful for informing potential efforts to enhance population monitoring and harvest management.

The limitations of our model reflect some of the challenges associated with collecting demographic data on animal populations. Specifically, indirect estimates of HY swan survival, and small sample size for estimates of AHY swan survival, resulted in large uncertainty in model estimates. More robust estimates of survival in long-lived species have been based on data from long-term monitoring (e.g., mark-recapture) programs that include hundreds or thousands of observations (Sandercock 2006). Such monitoring programs are costly to develop and maintain and have not been undertaken for swans in New Zealand in decades (Williams 1977, 1979, Barker and Buchanan 1993). Nevertheless, our estimates of swan survival were congruent with



**Fig. 4.** Heatmaps showing how changes in annual survival probability for after-hatch-year Black Swans (SAHY, *Cygnus atratus*), and nest harvest pressure ( $h$ ), influence population growth rate ( $\lambda$ ) at Te Waihora/Lake Ellesmere, Aotearoa/New Zealand. Warm colors indicate a declining population ( $\lambda < 1$ ), cool colors indicate a growing population ( $\lambda > 1$ ), and neutral white indicates a stable population ( $\lambda = 1$ ). The middle plot shows the mean of a bootstrap distribution of  $\lambda$  for each combination of SAHY and  $h$ , whereas the left and right plots show the 25th and 75th percentile, respectively, for each combination.



previous estimates for swans in New Zealand based on long-term mark-recapture datasets (Figs A1.3, Fig A1.5; Williams 1977, 1979, Barker and Buchanan 1993), and with estimates for other swan species globally (Bart et al. 1991), indicating that they are at least realistic. However, the lack of information on density dependence to incorporate into our model could have resulted in unrealistically high estimates of population growth under some modeled management scenarios (Fig. 4). For example, AHY survival and population growth are likely regulated at least partially by availability of macrophyte food, which is scarce at Te Waihora (Lineham 1983, Gerbeaux 1989, Ford et al. 2017) and could prevent AHY survival from increasing to some of the levels we considered, regardless of potential reductions in sport hunting. More robust data (e.g., from a long-term monitoring program) could improve the precision and reduce potential bias of our estimates and allow the inclusion of additional demographic parameters such as density dependence. In addition, data on finer-resolution age or stage classes could help to account for potential transient population dynamics (Koons et al. 2005, Ezard et al. 2010), which we found to be minor (Fig. A1.6). Despite these data limitations, our model was useful for assessing differential effects of age-specific demographic rates on population growth, and how offtake from sport hunting affects the sustainability of potential customary egg harvests by Ngāi Tahu.

#### Management implications

Our results raise immediate concerns about contemporary species management by FGNZ, which has implications for customary management by Ngāi Tahu. The Te Waihora swan population is highly sensitive to mortality of AHY swans, yet FGNZ manages swan numbers through permitted sport hunting of (mostly) AHY swans, regulated through fixed quotas. Even a slight over-estimation of the population's capacity to sustain sport hunting, if not compensated for by increased survival and/or reproduction of remaining individuals, could lead to population declines (Pöysä et al. 2004, Sandercock et al. 2011) and preclude sustainable customary egg harvests. The risk of such an over-estimation is

elevated because the swan hunting season (May–September) overlaps with the breeding season (peak nesting in August–September), and groups of hunters on farms surrounding Te Waihora sometimes shoot large numbers of swans (> 100) as they stage for nesting (Donald Brown, Ngāi Tahu, Christchurch, New Zealand, 9 February 2021, *personal communication*). This activity could have a disproportionately large impact on the population by reducing not only annual adult survival but also the proportion of surviving adults that attempt breeding, particularly if shooting during the pre-nesting period disrupts social cues that facilitate synchronous colonial breeding (Burger 1988, Reed and Dobson 1993, Wilhelm and Storey 2002). *Tangata tiaki* and customary egg harvesters have reported that the abundance of breeding swans at Te Waihora's largest swan nesting colony has declined, which could be at least partly due to swans being killed immediately prior to, or during, nesting (Donald Brown and Craig Pauling, Ngāi Tahu, Christchurch, New Zealand, 9 February 2021, *personal communication*). Essentially, landowners are using the FGNZ gamebird regulations to control swan numbers in their area to limit potential swan impacts on new grass and crops. In addition, FGNZ does not monitor baseline mortality rates of swans or require landowners or gamebird license holders to report their offtake, as described above. Considering this study and related studies (Herse et al. 2020, 2021), and concerns expressed by local *tangata tiaki*, regional FGNZ managers recently indicated that they plan to adjust local gamebird regulations to reduce sport hunting pressure on swans at Te Waihora. However, lack of monitoring and resulting uncertainty in FGNZ management limit the utility of our demographic model, and the ability of *tangata tiaki* to assess sustainable rates of egg harvest within the current reporting environment. Thus, the need to monitor baseline rates of swan survival and effects of hunting more closely, to ensure that gamebird regulations are sustainable and do not preclude sustainable customary harvest, is a key recommendation to emerge from this study.

Fully recognizing the rights and interests of Ngāi Tahu, and empowering *tangata tiaki* authority in local species management,



could lead to win-win outcomes that improve population and environmental monitoring (Herse et al. 2020) and, if/when appropriate, control swan numbers without wasting resources or killing swans unnecessarily (Bataille 2020, Bataille et al. 2021, Herse et al. 2021). *Tangata tiaki* and customary egg harvesters could enhance monitoring of swans and Te Waihora by continually generating information on breeding activity (e.g., locations and sizes of nesting colonies, hatching success) and environmental pressures (e.g., water pollution, flooding, nest depredation), which is currently lacking in local species management by FGNZ (Herse et al. 2020, 2021). Customary harvest could also be a practical, culturally appropriate, and less wasteful alternative to non-consumptive culling for controlling swan numbers to limit grazing of pasture in problem areas (Bataille 2020, Bataille et al. 2021, Herse et al. 2021). *Tangata tiaki* have rights to decide what level of swan numbers is appropriate to maintain (United Nations General Assembly 2007, Orange 2011), whereas current decision making is biased toward the interests of sport hunters and farmers (New Zealand Government 1987, Bataille 2020, Bataille et al. 2021). Although most landowners around Te Waihora value wetland health, active farmers generally prioritize economic gains, which motivates some to shoot swans to limit potential grazing impacts (Bataille 2020, Bataille et al. 2021). Ironically, grazing of pasture by swans can be partly attributed to macrophyte scarcity caused by pollution from farming (Lineham 1983, Gerbeaux 1989, Hearnshaw and Hughey 2010, Williams 2013a). Thus, efforts to reduce swan grazing impacts for farmers should prioritize curbing pollution that degrades Te Waihora and leads swans to feed on pasture (Williams 1979, 2013a), before resorting to local swan population control. However, if *tangata whenua* and the Crown make an equitable decision to control swan numbers, customary egg harvest could provide a fine-tune dial for managing population size, such that a potential over-harvest would pose less of a threat to the population when compared to an excess of sport hunting (or culling under the guise of gamebird regulations; Fig. 4). Harvesting from early life stages (eggs or juveniles) is a commonly used strategy by IPLC to fine-tune or reduce impacts of customary harvest (Gudmundsson 1979, Hunter et al. 2000, Lyver et al. 2008).

#### **Caveats to the implementation and potential benefits of customary management**

Supporting efforts by IPLC to engage with their environments, generate and maintain ecological knowledge, and practice customary management can improve local conservation and community livelihoods (Popp et al. 2019, Freitas et al. 2020). However, achieving the potential benefits of customary management requires addressing several related caveats. Here we focus on three caveats that are relevant to customary management by Ngāi Tahu and other IPLC elsewhere.

First, improving IPLC access to information about proposed or ongoing environmental management by non-IPLC groups could allow customary managers to make informed decisions, which are key to sustainability (Armitage 2005, Akins et al. 2019). For instance, in this study, the lack of available information on FGNZ-permitted sport hunting of swans creates uncertainty for *tangata tiaki* who wish to harvest eggs sustainably. Regional gamebird management (currently through FGNZ) could alleviate this uncertainty by monitoring baseline rates of swan survival and

permitted mortality more closely, e.g., by establishing a band-recovery program (Williams 1979, Sandercock 2006), and sharing their findings with *tangata tiaki*. The model we developed could aid communication within a potential future co-management arrangement between *tangata tiaki* and representatives of New Zealand's Crown government, within which participants could share information about the swan population and different ecological pressures. Such collaboration and sharing of knowledge among IPLC and non-IPLC groups can improve collective understanding of social-ecological systems, and sustainability in environmental management (Folke et al. 2005, Armitage et al. 2009, Popp et al. 2019, Wehi et al. 2019). Importantly, effective collaborations in environmental management require government support for adaptive policies that recognize IPLC rights to resources and decision making, monitoring efforts (e.g., band-recovery programs), and time to establish trust among different groups (Folke et al. 2005, Akins et al. 2019). Collaborations between IPLC and scientists (IPLC and non-IPLC) can also provide a pathway to partially fund the generation of new knowledge, e.g., using demographic models (Jones et al. 2015, McKechnie et al. 2020) and support customary management (Ens et al. 2016, Popp et al. 2019, Freitas et al. 2020).

Second, curbing human-driven environmental degradation is important to supporting customary management (Tang and Gavin 2016, Lyver et al. 2019b). For instance, agricultural pollution at Te Waihora over the past half-century has prevented growth of swans' primary food source, macrophytes (Lineham 1983, Gerbeaux 1989), and apparently reduced swans' propensity to lay replacement eggs following harvest (Williams 1979, Herse et al. 2021). Thus, regardless of pressure from sport hunting of swans, pollution at Te Waihora limits local Ngāi Tahu abilities to engage in sustainable egg harvests, through swans' reduced resilience to egg harvest, and some egg harvesters' fears of consuming eggs containing pollutants (Bataille 2020, Bataille et al. 2021). Over time, declines in *tangata tiaki* and customary harvester engagement with Te Waihora could lead to a loss of local knowledge about swans and their responses to egg harvest and other pressures. Because customary harvests and sharing of resources are central to the well-being of many IPLC (Tyrrell 2008, Caillon et al. 2017, Freitas et al. 2020), including Māori (Kawharu 2000, Bataille 2020, Bataille et al. 2021), reduced engagement in customary management can have cascading effects on cultural health and diversity (Lyver et al. 2019b, Fernández-Llamazares et al. 2021, Yletyinen et al. 2022). Thus, to alleviate these threats, we urge governments to adopt place-based environmental management policies that recognize links between environmental and cultural well-being (Gavin et al. 2015, Caillon et al. 2017, Akins et al. 2019, Lyver et al. 2019a).

Finally, improving social equity in environmental governance is imperative to achieving the potential benefits of customary management (Brondizio and Tourneau 2016, Ruru et al. 2017). Restrictive policies that neglect IPLC rights and values limit engagement and the continual generation and updating of knowledge (Stephenson et al. 2014, Parlee et al. 2018). Such policies can lead to inappropriate conservation approaches that are biased toward dominant cultures and against IPLC (Moller 1996, Tyrrell 2008, Eichler and Baumeister 2018, Parlee et al. 2018, Guibrinet et al. 2021). For example, New Zealand law fully

protects most native bird species from offtake of any kind, regardless of their conservation status or value for Māori, yet classifies other species valued by sport hunters as gamebirds, including one with a conservation status of “nationally vulnerable” (*pārerā* or Grey Duck, *Anas superciliosa*; New Zealand Government 1953, Williams 2013b, Wehi and Lord 2017, Lyver et al. 2019a). Even in the case of the Black Swan, a species commonly shot by sport hunters and farmers, *tangata tiaki* cannot authorize customary egg harvests without special permission from the Minister of Conservation or regional FGNZ managers, which is inconsistent with the Treaty, as described above, and creates a barrier for Ngāi Tahu engagement (Bataille 2020, Bataille et al. 2021). Putting aside the hypocrisy of restrictions on customary egg harvest (government-mandated gamebird managers destroyed and collected and sold swan eggs for decades during the 20th century while prohibiting customary harvest by Ngāi Tahu; Lamb 1964, Williams 1979, Pauling and Arnold 2008), the results of this study suggest that the long-term scrutiny of customary egg harvest is unfounded, considering the Te Waihora population is far more sensitive to AHY swan mortality than to changes in nest hatching success. Thus, implementing customary management requires confronting cultural biases and power asymmetries against IPLC, and adopting equitable policies that empower IPLC to engage with and protect their lands and resources in culturally appropriate ways (Pinkerton et al. 2014, Ruru et al. 2017, Wehi and Lord 2017).

In conclusion, we emphasize that engaging different cultures and perspectives in environmental management can improve knowledge production, adaptability, and sustainability within social-ecological systems, especially if individuals and groups share power, build trust, and find common grounds to work from, e.g., mutual interests in environmental stewardship (Folke et al. 2005, Armitage et al. 2009, Tengö et al. 2014, Bataille et al. 2021). However, differences in perspectives, priorities, abilities, expectations, and authority among individuals and groups can spur conflicts that sow division and mistrust and constrain management (Moller 1996, 1998, Coombes and Hill 2005, Brondizio et al. 2021). Averting such dilemmas is important to cooperation and sustainability and therefore requires steps to resolve and mediate conflicts (Coombes and Hill 2005, Brondizio et al. 2021), including recognition of the rights and aspirations of IPLC (United Nations General Assembly 2007, McGregor et al. 2020, Reyes-García et al. 2022), and establishment of collaborative cross-cultural learning and capacity-building initiatives (Whyte 2013, Tengö et al. 2014, Tipa et al. 2016). Reversing human-driven declines in biodiversity and ecosystem health will clearly not be easy, so we urge governments and environmental managers to pursue adaptive solutions that are both effective and socially equitable.

*Responses to this article can be read online at:*  
<https://www.ecologyandsociety.org/issues/responses.php/13410>

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#### Author Contributions:

*All authors contributed to the design of the study and the writing of the manuscript. M.R.H. led the data collection, modeling, and*

*writing of the manuscript. N.J.S. and P.O.L. secured the primary funding for the study.*

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#### Data Availability:

*The data and R code that support the findings of this study are jointly held by Te Rūnanga o Ngāi Tahu and Manaaki Whenua Landcare Research. The data are archived at MWLR (<https://doi.org/10.34721/HPRD-HY85>).*

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#### LITERATURE CITED

- Adams, J. S. 1971. Black swans at Lake Ellesmere. *Wildlife-Review* 3:23-25.
- Akins, A., P. O'B. Lyver, H. F. Alrøe, and H. Moller. 2019. The universal precautionary principle: new pillars and pathways for environmental, sociocultural, and economic resilience. *Sustainability* 11(8):2357. <https://doi.org/10.3390/su11082357>
- Armitage, D. 2005. Adaptive capacity and community-based natural resource management. *Environmental Management* 35(6):703-715. <https://doi.org/10.1007/s00267-004-0076-z>
- Armitage, D. R., R. Plummer, F. Berkes, R. I. Arthur, A. T. Charles, I. J. Davidson-Hunt, A. P. Diduck, N. C. Doubleday, D. S. Johnson, M. Marschke, P. McConney, E. W. Pinkerton, and E. K. Wollenberg. 2009. Adaptive co-management for social-ecological complexity. *Frontiers in Ecology and the Environment* 7(2):95-102. <https://doi.org/10.1890/070089>
- Artelle, K. A., M. Zurba, J. Bhattacharyya, D. E. Chan, K. Brown, J. Housty, and F. Moola. 2019. Supporting resurgent Indigenous governance: a nascent mechanism for just and effective conservation. *Biological Conservation* 240:108284. <https://doi.org/10.1016/j.biocon.2019.108284>
- Ban, N. C., L. Eckert, M. McGreer, and A. Frid. 2017. Indigenous knowledge as data for modern fishery management: a case study of Dungeness crab in Pacific Canada. *Ecosystem Health and Sustainability* 3(8):1379887. <https://doi.org/10.1080/20964129.2017.1379887>
- Barker, R. J., and I. M. Buchanan. 1993. Estimating adult survival rates of New Zealand Black Swans banded as immatures. *Journal of Wildlife Management* 57(3):549-555. <https://doi.org/10.2307/3809281>

- Bart, J., S. Earnst, and P. J. Bacon. 1991. Comparative demography of the swans: a review. Pages 15-21 in J. Sears and P. J. Bacon, editors. Proceedings of the Third International Swan Symposium. Wildfowl Supplement No. 1. International Waterfowl and Wetlands Research, Slimbridge, UK.
- Bataille, C. Y. 2020. Cross-cultural interest groups' values and desired states inform biocultural management of wetlands in Aotearoa New Zealand. Dissertation. University of Canterbury, Christchurch, New Zealand.
- Bataille, C. Y., S. K. Malinen, J. Yletyinen, N. Scott, and P. O'B. Lyver. 2021. Relational values provide common ground and expose multi-level constraints to cross-cultural wetland management. *People and Nature* 3(4):941-960. <https://doi.org/10.1002/pan3.10244>
- Berkes, F. 2009. Indigenous ways of knowing and the study of environmental change. *Journal of the Royal Society of New Zealand* 39(4):151-156. <https://doi.org/10.1080/03014220909510568>
- Bradshaw, C. J. A., and B. W. Brook. 2007. Ecological-economic models of sustainable harvest for an endangered but exotic megaherbivore in Northern Australia. *Natural Resource Modeling* 20(1):129-156. <https://doi.org/10.1111/j.1939-7445.2007.tb00203.x>
- Brockington, D., and J. Igoe. 2006. Eviction for conservation: a global overview. *Conservation & Society* 4(3):424-470.
- Brondizio, E. S., K. Andersson, F. de Castro, C. Fudemma, C. Salk, M. Tengö, M. Londres, D. C. Tourne, T. S. Gonzalez, A. Molina-Garzón, G. Russo Lopes, and S. M. Siani. 2021. Making place-based sustainability initiatives visible in the Brazilian Amazon. *Current Opinion in Environmental Sustainability* 49:66-78. <https://doi.org/10.1016/j.cosust.2021.03.007>
- Brondizio, E. S., and F.-M. L. Tourneau. 2016. Environmental governance for all. *Science* 352(6291):1272-1273. <https://doi.org/10.1126/science.aaf5122>
- Brook, B. W., D. M. J. S. Bowman, C. J. A. Bradshaw, B. M. Campbell, and P. J. Whitehead. 2006. Managing an endangered Asian bovid in an Australian national park: the role and limitations of ecological-economic models in decision-making. *Environmental Management* 38(3):463-469. <https://doi.org/10.1007/s00267-005-0157-7>
- Burger, J. 1988. Social attraction in nesting least tern: effects of numbers, spacing, and pair bonds. *Condor* 90(3):575-582. <https://doi.org/10.2307/1368345>
- Caillon, S., G. Cullman, B. Verschuuren, and E. J. Sterling. 2017. Moving beyond the human-nature dichotomy through biocultural approaches: including ecological well-being in resilience indicators. *Ecology and Society* 22(4):27. <https://doi.org/10.5751/ES-09746-220427>
- Caswell, H. 2001. Matrix population models: construction, analysis and interpretation. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.
- Chaloupka, M., and G. Balazs. 2007. Using Bayesian state-space modelling to assess the recovery and harvest potential of the Hawaiian green sea turtle stock. *Ecological Modelling* 205 (1-2):93-109. <https://doi.org/10.1016/j.ecolmodel.2007.02.010>
- Cinner, J. E., and S. Aswani. 2007. Integrating customary management into marine conservation. *Biological Conservation* 140(3-4):201-216. <https://doi.org/10.1016/j.biocon.2007.08.008>
- Cooch, E. G., M. Guillemain, G. S. Boomer, J.-D. Lebreton, and J. D. Nichols. 2014. The effects of harvest on waterfowl populations. *Wildfowl Special Issue* 4:220-227.
- Coombes, B. L., and S. Hill. 2005. "Na whenua, na Tuhoe. Ko D. o.C. te partner"—Prospects for Comanagement of Te Urewera National Park. *Society & Natural Resources* 18(2):135-152. <https://doi.org/10.1080/08941920590894516>
- Cumming, G. S., D. H. M. Cumming, and C. L. Redman. 2006. Scale mismatches in social-ecological systems: causes, consequences, and solutions. *Ecology and Society* 11(1):14. <https://doi.org/10.5751/ES-01569-110114>
- Dawson, N. M., B. Coolsaet, E. J. Sterling, R. Loveridge, N. D. Gross-Camp, S. Wongbusarakum, K. K. Sangha, L. M. Scherl, H. Phuong Phan, N. Zafra-Calvo, W. G. Lavey, P. Byakagaba, C. J. Idrobo, A. Chenet, N. J. Bennett, S. Mansourian, and F. J. Rosado-May. 2021. The role of Indigenous peoples and local communities in effective and equitable conservation. *Ecology and Society* 26(3):19. <https://doi.org/10.5751/ES-12625-260319>
- Diaz, S., J. Settele, E. S. Brondizio, H. T. Ngo, J. Agard, A. Arneth, P. Balvanera, K. A. Brauman, S. H. M. Butchart, K. M. A. Chan, L. A. Garibaldi, K. Ichii, J. Liu, S. M. Subramanian, G. F. Midgley, P. Miloslavich, Z. Molnár, D. Obura, A. Pfaff, S. Polasky, A. Purvis, J. Razzaque, B. Reyers, R. R. Chowdhury, Y.-J. Shin, I. Visseren-Hamakers, K. J. Willis, and C. N. Zayas. 2019. Pervasive human-driven decline of life on Earth points to the need for transformative change. *Science* 366(6471):eaax3100. <https://doi.org/10.1126/science.aax3100>
- Eichler, L., and D. Baumeister. 2018. Hunting for justice: an Indigenous critique of the North American model of wildlife conservation. *Environment and Society* 9:75-90. <https://doi.org/10.3167/ares.2018.090106>
- Ens, E., M. L. Scott, Yugul Mangi Rangers, C. Moritz, and R. Pirzl. 2016. Putting indigenous conservation policy into practice delivers biodiversity and cultural benefits. *Biodiversity and Conservation* 25(14):2889-2906. <https://doi.org/10.1007/s10531-016-1207-6>
- Ens, E., G. M. Towler, C. Daniels, Yugul Mangi Rangers, Manqurrk Rangers. 2012. Looking back to move forward: collaborative ecological monitoring in remote Arnhem Land. *Ecological Management & Restoration* 13(1):26-35. <https://doi.org/10.1111/j.1442-8903.2011.00627.x>
- Ezard, T. H. G., J. M. Bullock, H. J. Dalglish, A. Millon, F. Pelletier, A. Ozgul, and D. N. Koons. 2010. Matrix models for a changeable world: the importance of transient dynamics in population management. *Journal of Applied Ecology* 47 (3):515-523. <https://doi.org/10.1111/j.1365-2664.2010.01801.x>
- Fernández-Llamazares, Á., D. Lepofsky, K. Lertzman, C. G. Armstrong, E. S. Brondizio, M. C. Gavin, P. O'B. Lyver, G. P. Nicholas, P. Pascua, N. J. Reo, V. Reyes-García, N. J. Turner, J. Yletyinen, E. N. Anderson, W. Balée, J. Cariño, D. M. David-Chavez, C. P. Dunn, S. C. Garnett, S. Greening (La'goot), S. Jackson (Niniwum Selapem), H. Kuhnlein, Z. Molnár, G. Odonne, G.-B. Retter, W. J. Ripple, L. Sáfián, A. S. Bahraman,



- M. Torrents-Ticó, and M. B. Vaughan. 2021. Scientists' warning to humanity on threats to Indigenous and local knowledge systems. *Journal of Ethnobiology* 41(2):144-169. <https://doi.org/10.2993/0278-0771-41.2.144>
- Folke, C., T. Hahn, P. Olsson, and J. Norberg. 2005. Adaptive governance of social-ecological systems. *Annual Review of Environment and Resources* 30:441-473. <https://doi.org/10.1146/annurev.energy.30.050504.144511>
- Ford, D. E., F. D. Hughey, and K. Taylor. 2017. Te Waihora/Lake Ellesmere: state of the lake 2017. Report No. 3. Waihora Ellesmere Trust Technical, Christchurch, New Zealand.
- Freitas, C. T., P. F. Macedo Lopes, J. V. Campos-Silva, M. M. Noble, R. Dyball, and C. A. Peres. 2020. Co-management of culturally important species: a tool to promote biodiversity conservation and human well-being. *People and Nature* 2 (1):61-81. <https://doi.org/10.1002/pan3.10064>
- Gadgil, M., F. Berkes, and C. Folke. 1993. Indigenous knowledge for biodiversity conservation. *Ambio* 22(2-3):151-156.
- Gavin, M. C., J. McCarter, A. Mead, F. Berkes, J. R. Stepp, D. Peterson, and R. Tang. 2015. Defining biocultural approaches to conservation. *Trends in Ecology & Evolution* 30(3):140-145. <https://doi.org/10.1016/j.tree.2014.12.005>
- Gerbeaux, P. J. 1989. Aquatic plant decline in Lake Ellesmere: a case for macrophyte management in a shallow New Zealand lake. Dissertation. Lincoln College, Lincoln, New Zealand.
- Goldman, M. J. 2011. Strangers in their own land: Maasai and wildlife conservation in Northern Tanzania. *Conservation & Society* 9(1):64-79.
- Gudmundsson, F. 1979. The past status and exploitation of the Mývatn waterfowl populations. *Oikos* 32(1-2):232-249. <https://doi.org/10.2307/3544230>
- Guerrero, A. M., R. R. J. McAllister, J. Corcoran, and K. A. Wilson. 2013. Scale mismatches, conservation planning, and the value of social-network analyses. *Conservation Biology* 27 (1):35-44. <https://doi.org/10.1111/j.1523-1739.2012.01964.x>
- Guibrunet, L., P. R. W. Gerritsen, J. A. Sierra-Huelsz, A. C. Flores-Díaz, E. García-Frapolli, E. García-Serrano, U. Pascual, and P. Balvanera. 2021. Beyond participation: how to achieve the recognition of local communities' value-systems in conservation? Some insights from Mexico. *People and Nature* 3(3):528-541. <https://doi.org/10.1002/pan3.10203>
- Halim, A. A., N. Othman, S. R. Ismail, J. A. Javan, and N. N. Ibrahim. 2012. Indigenous knowledge and biodiversity conservation in Sabah, Malaysia. *International Journal of Social Science and Humanity* 2(2):159-163. <https://doi.org/10.7763/IJSSH.2012.V2.88>
- Hearnshaw, E. J. S., and K. F. D. Hughey. 2010. A tolerance range approach for the investigation of values provided by Te Waihora/Lake Ellesmere. Land Environment and People Research Report No. 17. Lincoln University, Lincoln, New Zealand.
- Herse, M. R., P. O'B. Lyver, N. J. Scott, A. R. McIntosh, S. C. Coats, A. M. Gormley, and J. M. Tylianakis. 2020. Engaging Indigenous peoples and local communities could alleviate scale mismatches in social-ecological systems. *BioScience* 70 (8):699-707. <https://doi.org/10.1093/biosci/biaa066>
- Herse, M. R., J. M. Tylianakis, N. J. Scott, D. Brown, I. Cranwell, J. Henry, C. Pauling, A. R. McIntosh, and P. O'B. Lyver. 2021. Effects of customary egg harvest regimes on hatching success of culturally important waterfowl species. *People and Nature* 3 (2):499-512. <https://doi.org/10.1002/pan3.10196>
- Hunn, E., D. Johnson, P. Russell, and T. Thornton. 2003. Huna Tlingit traditional environmental knowledge, conservation, and the management of a "wilderness" park. *Current Anthropology* 44(Supplement):79-103. <https://doi.org/10.1086/377666>
- Hunter, C., H. Moller, and J. Kitson. 2000. Muttonbird selectivity of Sooty Shearwater (titi) chicks harvested in New Zealand. *New Zealand Journal of Zoology* 27(4):395-414. <https://doi.org/10.1080/03014223.2000.9518249>
- Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES). 2019a. Summary for policymakers of the global assessment report on biodiversity and ecosystem services. S. Diaz, J. Settele, E. S. Brondízio, H. T. Ngo, M. Guèze, J. Agard, A. Arneth, P. Balvanera, K. A. Brauman, S. H. M. Butchart, K. M. A. Chan, L. A. Garibaldi, K. Ichii, J. Liu, S. M. Subramanian, G. F. Midgley, P. Miloslavich, Z. Molnár, D. Obura, A. Pfaff, S. Polasky, A. Purvis, J. Razzaque, B. Reyers, R. Roy Chowdhury, Y. J. Shin, I. J. Visseren-Hamakers, K. J. Willis, and C. N. Zayas, editors. IPBES secretariat, Bonn, Germany. <https://doi.org/10.5281/zenodo.3553579>
- Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES). 2019b. Indigenous peoples and local communities. IPBES secretariat, Bonn, Germany. <https://ipbes.net/glossary/indigenous-peoples-local-communities>
- Jones, C. J., P. O'B. Lyver, J. Davis, B. Hughes, A. Anderson, and J. Hohapata-Oke. 2015. Reinstatement of customary seabird harvests after a 50-year moratorium. *Journal of Wildlife Management* 79(1):31-38. <https://doi.org/10.1002/jwmg.815>
- Kawharu, I. H. 1989. Translation of the Treaty of Waitangi. Page 321 in I. H. Kawharu, editor. *Maori and Pakeha perspectives of the Treaty of Waitangi*. Oxford University Press, Auckland, New Zealand.
- Kawharu, M. 2000. Kaitiakitanga: a Maori anthropological perspective of the Maori socio-environmental ethic of resource management. *Journal of the Polynesian Society* 109(4):349-370.
- Kinan, I., and P. Dalzell. 2005. Sea turtles as a flagship species: different perspectives create conflicts in the Pacific Islands. *Maritime Studies* 3(2):195-212.
- Koons, D. N., J. B. Grand, B. Zinner, and R. F. Rockwell. 2005. Transient population dynamics: relations to life history and initial population state. *Ecological Modelling* 185(2-4):283-297. <https://doi.org/10.1016/j.ecolmodel.2004.12.011>
- Koons, D. N., G. Gunnarsson, J. A. Schmutz, and J. J. Rotella. 2014. Drivers of waterfowl population dynamics: from teal to swans. *Wildfowl Special Issue* 4:169-191.
- Lamb, R. C. 1964. *Birds, beasts & fishes: the first hundred years of the North Canterbury Acclimatisation Society*. North Canterbury Acclimatisation Society, Christchurch, New Zealand.



- Leslie, P. H. 1945. On the use of matrices in certain population mathematics. *Biometrika* 33(3):183-212. <https://doi.org/10.1093/biomet/33.3.183>
- Lineham, I. 1983. Eutrophication of Lake Ellesmere: a study of phytoplankton. Dissertation. University of Canterbury, Christchurch, New Zealand.
- Lyver, P. O'B., J. Davis, L. Ngamane, L. Anderson, and P. Clarkin. 2008. Hauraki Maori Matauranga for the conservation and harvest of Titi, *Pterodroma macroptera gouldi*. *Papers and Proceedings of the Royal Society of Tasmania* 142(1):149-159. <https://doi.org/10.26749/rstpp.142.1.149>
- Lyver, P. O'B., J. Ruru, N. J. Scott, J. M. Tylianakis, J. Arnold, S. K. Malinen, C. Y. Bataille, M. R. Herse, C. J. Jones, A. M. Gormley, D. A. Peltzer, Y. Taura, P. Timoti, C. Stone, M. Wilcox, and H. Moller. 2019a. Building biocultural approaches into Aotearoa - New Zealand's conservation future. *Journal of the Royal Society of New Zealand* 49(3):394-411. <https://doi.org/10.1080/03036758.2018.1539405>
- Lyver, P. O'B., P. Timoti, T. Davis, and J. M. Tylianakis. 2019b. Biocultural hysteresis inhibits adaptation to environmental change. *Trends in Ecology & Evolution* 34(9):771-780. <https://doi.org/10.1016/j.tree.2019.04.002>
- Lyver, P. O'B., P. Timoti, S. J. Richardson, and A. M. Gormley. 2021. Alignment of ordinal and quantitative species abundance and size indices for the detection of shifting baseline syndrome. *Ecological Applications* 31(4):e02301. <https://doi.org/10.1002/eap.2301>
- Lyver, P. O'B., and J. M. Tylianakis. 2017. Indigenous peoples: conservation paradox. *Science* 357(6347):142-143. <https://doi.org/10.1126/science.aao0780>
- McGregor, D., S. Whitaker, and M. Sritharan. 2020. Indigenous environmental justice and sustainability. *Current Opinion in Environmental Sustainability* 43:35-40. <https://doi.org/10.1016/j.cosust.2020.01.007>
- McKechnie, S., D. Fletcher, J. Newman, C. Bragg, P. W. Dillingham, R. Clucas, D. Scott, S. Uhlmann, P. O'B. Lyver, A. M. Gormley, Rakiura Titi Islands Administering Body, and H. Moller. 2020. Separating the effects of climate, bycatch, predation and harvesting on tītī (*Ardenna grisea*) population dynamics in New Zealand: a model-based assessment. *PLoS ONE* 15(12): e0243794. <https://doi.org/10.1371/journal.pone.0243794>
- Meis, T. 1988. Waterfowl management in North Canterbury. Thesis. University of Canterbury, Christchurch, New Zealand.
- Moller, H. 1996. Customary use of indigenous wildlife - towards a bicultural approach to conserving New Zealand's biodiversity. Pages 89-125 in B. McFagen and P. Simpson, editors. *Biodiversity: papers from a seminar series on biodiversity*. Science and Research Division, Department of Conservation, Wellington, New Zealand.
- Moller, H. 1998. From mutual mistrust to co-management. *Fish and Game New Zealand Newsletter* 6:17-24.
- Moller, H., F. Berkes, P. O'B. Lyver, and M. Kislalioglu. 2004. Combining science and traditional ecological knowledge: monitoring populations for co-management. *Ecology and Society* 9(3):2. <https://doi.org/10.5751/ES-00675-090302>
- Montano, V., W. F. D. van Dongen, M. A. Weston, R. A. Mulder, R. W. Robinson, M. Cowling, and P.-J. Guay. 2018a. A genetic assessment of the human-facilitated colonization history of Black Swans in Australia and New Zealand. *Evolutionary Applications* 11(3):364-375. <https://doi.org/10.1111/eva.12535>
- Montano, V., W. F. D. van Dongen, M. A. Weston, R. A. Mulder, R. W. Robinson, M. Cowling, and P.-J. Guay. 2018b. Response to Rawlence et al. (2017): Native or not? Extinct and extant DNA of New Zealand Black Swans. *Evolutionary Applications* 11(3):378-379. <https://doi.org/10.1111/eva.12587>
- New Zealand Government. 1953. *Wildlife Act 1953. Public Act 1953 No 31*. New Zealand Government, Wellington, New Zealand.
- New Zealand Government. 1987. *Conservation Act 1987. Public Act 1987 No 65*. New Zealand Government, Wellington, New Zealand. <https://www.legislation.govt.nz/act/public/1987/0065/latest/DLM103610.html>
- New Zealand Government. 1998. *Ngāi Tahu Claims Settlement Act 1998. Public Act 1998 No 97*. New Zealand Government, Wellington, New Zealand. <https://www.legislation.govt.nz/act/public/1998/0097/latest/whole.html>
- Orange, C. 2011. *The Treaty of Waitangi*. Second edition. Bridget Williams Books, Wellington, New Zealand. <https://doi.org/10.7810/9781877242489>
- Parlee, B. L., J. Sandlos, and D. C. Natcher. 2018. Undermining subsistence: barren-ground caribou in a "tragedy of open access." *Science Advances* 4(2):e1701611. <https://doi.org/10.1126/sciadv.1701611>
- Pauling, C., and J. Arnold. 2008. Cultural health of the lake. Pages 77-83 in K. Hughey and K. Taylor, editors. *Te Waihora/Lake Ellesmere: state of the lake and future management*. Lincoln University, Lincoln, New Zealand.
- Peery, M. Z., B. H. Becker, and S. R. Beissinger. 2006. Combining demographic and count-based approaches to identify source-sink dynamics of a threatened seabird. *Ecological Applications* 16(4):1516-1528. [https://doi.org/10.1890/1051-0761\(2006\)016\[1516:CDACAT\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[1516:CDACAT]2.0.CO;2)
- Pinkerton, E., E. Angel, N. Ladell, P. Williams, M. Nicolson, J. Thorkelson, and H. Clifton. 2014. Local and regional strategies for rebuilding fisheries management institutions in coastal British Columbia: what components of comanagement are most critical? *Ecology and Society* 19(2):72. <https://doi.org/10.5751/ES-06489-190272>
- Popp, J. N., P. Priadka, and C. Kozmik. 2019. The rise of moose co-management and integration of Indigenous knowledge. *Human Dimensions of Wildlife* 24(2):159-167. <https://doi.org/10.1080/10871209.2019.1545953>
- Pöysä, H., J. Elmberg, P. Nummi, and K. Sjöberg. 2004. Ecological basis of sustainable harvesting: Is the prevailing paradigm of compensatory mortality still valid? *Oikos* 104(3):612-615. <https://doi.org/10.1111/j.0030-1299.2004.12788.x>
- R Core Team. 2021. *R: A language environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

- Rawlence, N. J., A. Kardamaki, L. J. Easton, A. J. D. Tennyson, R. P. Scofield, and J. M. Waters. 2017. Ancient DNA and morphometric analysis reveal extinction and replacement of New Zealand's unique Black Swans. *Proceedings of the Royal Society B: Biological Sciences* 284(1859):20170876. <https://doi.org/10.1098/rspb.2017.0876>
- Rawlence, N. J., A. Kardamaki, L. J. Easton, A. J. D. Tennyson, R. P. Scofield, and J. M. Waters. 2018. Native or not? Ancient DNA rejects persistence of New Zealand's endemic Black Swan: a reply to Montano et al. *Evolutionary Applications* 11(3):376-377. <https://doi.org/10.1111/eva.12577>
- Rayne, A., G. Byrnes, L. Collier-Robinson, J. Hollows, A. McIntosh, M. Ramsden, M. Rupene, P. Tamati-Elliffe, C. Thoms, and T. E. Steeves. 2020. Centring Indigenous knowledge systems to re-imagine conservation translocations. *People and Nature* 2(3):512-526. <https://doi.org/10.1002/pan3.10126>
- Reed, J. M., and A. P. Dobson. 1993. Behavioural constraints and conservation biology: conspecific attraction and recruitment. *Trends in Ecology & Evolution* 8(7):253-256. [https://doi.org/10.1016/0169-5347\(93\)90201-Y](https://doi.org/10.1016/0169-5347(93)90201-Y)
- Reyes-García, V., Á. Fernández-Llamazares, Y. Aumeeruddy-Thomas, P. Benyei, R. W. Bussmann, S. K. Diamond, D. García-del-Amo, S. Guadilla-Sáez, N. Hanazaki, N. Kosoy, M. Lavides, A. C. Luz, P. McElwee, V. J. Meretsky, T. Newberry, Z. Molnár, I. Ruiz-Mallén, M. Salpeteur, F. S. Wyndham, F. Zorondo-Rodriguez, and E. S. Brondizio. 2022. Recognizing Indigenous peoples' and local communities' rights and agency in the post-2020 Biodiversity Agenda. *Ambio* 51:84-92. <https://doi.org/10.1007/s13280-021-01561-7>
- Ruru, J., P. O'B. Lyver, N. J. Scott, and D. Edmunds. 2017. Reversing the decline in New Zealand's biodiversity: empowering Māori within reformed conservation law. *Policy Quarterly* 13(2):65-71. <https://doi.org/10.26686/pq.v13i2.4657>
- Sandercock, B. K. 2006. Estimation of demographic parameters from live-encounter data: a summary review. *Journal of Wildlife Management* 70(6):1504-1520. [https://doi.org/10.2193/0022-541X\(2006\)70\[1504:EODPFL\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2006)70[1504:EODPFL]2.0.CO;2)
- Sandercock, B. K., E. B. Nilsen, H. Brøseth, and H. C. Pedersen. 2011. Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of Willow Ptarmigan. *Journal of Animal Ecology* 80(1):244-258. <https://doi.org/10.1111/j.1365-2656.2010.01769.x>
- Sheil, D., M. Boissière, and G. Beaudoin. 2015. Unseen sentinels: local monitoring and control in conservation's blind spots. *Ecology and Society* 20(2):39. <https://doi.org/10.5751/ES-07625-200239>
- Snook, J., A. Cunsolo, D. Borish, C. Furgal, J. D. Ford, I. Shiwak, C. T. R. Flowers, and S. L. Harper. 2020. "We're made criminals just to eat off the land": colonial wildlife management and repercussions on Inuit well-being. *Sustainability* 12(19):8177. <https://doi.org/10.3390/su12198177>
- Sobrevila, C. 2008. The role of Indigenous peoples in biodiversity conservation: the natural but often forgotten partners. World Bank Group Report No. 44300. World Bank Group, Washington, D.C., USA.
- Solomon, M. 2014. Locked out of national parks: a call to action from Kaiwhakahaere Tā Mark Solomon. *Te Karaka* 63:14-17. [https://ngaitahu.iwi.nz/our\\_stories/locked-national-parks/](https://ngaitahu.iwi.nz/our_stories/locked-national-parks/)
- Stephenson, J., F. Berkes, N. J. Turner, and J. Dick. 2014. Biocultural conservation of marine ecosystems: examples from New Zealand and Canada. *Indian Journal of Traditional Knowledge* 13(2):257-265.
- Stubben, C., B. Milligan, and P. Nantel. 2020. popbio: Construction and analysis of matrix population models, version 2.7. <https://cran.r-project.org/web/packages/popbio/index.html>
- Tang, R., and M. C. Gavin. 2016. A classification of threats to traditional ecological knowledge and conservation responses. *Conservation and Society* 14(1):57-70.
- Te Rūnanga o Ngāi Tahu, and Department of Conservation. 2005. Te Waihora Joint Management Plan: Mahere Tukutahi o Te Waihora. Te Rūnanga o Ngāi Tahu, and Department of Conservation, Christchurch, New Zealand. <https://api.ecan.govt.nz/TrimPublicAPI/documents/download/2738434>
- Tengö, M., E. S. Brondizio, T. Elmqvist, P. Malmer, and M. Spiereburg. 2014. Connecting diverse knowledge systems for enhanced ecosystem governance: the multiple evidence base approach. *Ambio* 43(5):579-591. <https://doi.org/10.1007/s13280-014-0501-3>
- Tipa, G., G. R. Harmsworth, E. Williams, and J. C. Kitson. 2016. Integrating mātauranga Māori into freshwater management, planning and decision-making. Pages 613-637 in P. G. Jellyman, T. Davie, C. P. Pearson, and J. S. Harding, editors. *Advances in New Zealand freshwater science*. New Zealand Hydrological Society, Wellington, New Zealand.
- Tyrrell, M. 2008. Nunavik Inuit perspectives on beluga whale management in the Canadian Arctic. *Human Organization* 67(3):322-334. <https://doi.org/10.17730/humo.67.3.47826252k0623352>
- United Nations General Assembly. 2007. United Nations Declaration on the Rights of Indigenous Peoples (No. A/RES/61/295). United Nations General Assembly, New York, New York, USA.
- Wehi, P. M., J. R. Beggs, and T. G. McAllister. 2019. Ka mua, ka muri: the inclusion of mātauranga Māori in New Zealand ecology. *New Zealand Journal of Ecology* 43(3):3379.
- Wehi, P. M., and J. M. Lord. 2017. Importance of including cultural practices in ecological restoration. *Conservation Biology* 31(5):1109-1118. <https://doi.org/10.1111/cobi.12915>
- Weinbaum, K. Z., J. S. Brashares, C. D. Golden, and W. M. Getz. 2013. Searching for sustainability: are assessments of wildlife harvests behind the times? *Ecology Letters* 16(1):99-111. <https://doi.org/10.1111/ele.12008>
- Whyte, K. P. 2013. On the role of traditional ecological knowledge as a collaborative concept: a philosophical study. *Ecological Processes* 2:7. <https://doi.org/10.1186/2192-1709-2-7>
- Wilhelm, S. I., and A. E. Storey. 2002. Influence of cyclic pre-lay attendance on synchronous breeding in Common Murres. *Waterbirds* 25(2):156-163. [https://doi.org/10.1675/1524-4695\(2002\)025\[0156:IOCPAO\]2.0.CO;2](https://doi.org/10.1675/1524-4695(2002)025[0156:IOCPAO]2.0.CO;2)

Williams, M. 1977. Locations of recoveries of Black Swans, *Cygnus atratus* Latham, Banded at Lake Whangape and Lake Ellesmere, New Zealand. *Australian Wildlife Research* 4:289-299. <https://doi.org/10.1071/WR9770289>

Williams, M. 1979. Status and management of Black Swans *Cygnus atratus*, Latham at Lake Ellesmere since the “Wahine” Storm, April 1968. *New Zealand Journal of Ecology* 2:34-41.

Williams, M. 1981. The demography of New Zealand's *Cygnus atratus* population. Pages 147-160 in G. V. T. Matthews and M. Smart, editors. *Proceedings of the Second International Swan Symposium*. International Waterfowl and Wetlands Bureau, Slimbridge, UK.

Williams, M. 2013a. Black Swan | Kakiānau. In C. M. Miskelly, editor. *New Zealand Birds Online*. <https://nzbirdsonline.org.nz/species/black-swan>

Williams, M. 2013b [updated 2022]. Grey Duck | Pārerā. In C. M. Miskelly, editor. *New Zealand Birds Online*. <https://nzbirdsonline.org.nz/species/grey-duck>

Witter, R., K. R. M. Suisseea, R. L. Gruby, S. Hitchner, E. M. Maclin, M. Bourque, and J. P. Brosius. 2015. Moments of influence in global environmental governance. *Environmental Politics* 24(6):894-912. <https://dx.doi.org/10.1080/09644016.2015.1060036>

Wood, K. A., L. Cao, P. Clausen, C. R. Ely, L. Luigujõe, E. C. Rees, J. Snyder, D. V. Solovyeva, and R. Włodarczyk. 2019. Current trends and future directions in swan research: insights from the 6th International Swan Symposium. *Wildfowl Special Issue* 5:1-34.

Yletyinen, J., J. M. Tylianakis, C. Stone, and P. O'B. Lyver. 2022. Potential for cascading impacts of environmental change and policy on indigenous culture. *Ambio* 51:1110-1122. <https://doi.org/10.1007/s13280-021-01670-3>

Zador, S. G., J. F. Piatt, and A. E. Punt. 2006. Balancing predation and egg harvest in a colonial seabird: a simulation model. *Ecological Modelling* 195(3-4):318-326. <https://doi.org/10.1016/j.ecolmodel.2005.11.002>

**Appendix 1.** Supporting information for research article titled ‘A demographic model to support customary management of a culturally important waterfowl species.’

## **Estimation of demographic parameters and associated variances**

### *Age-specific numbers of swans*

We estimated the number of hatch-year (HY) and after-hatch-year (AHY) swans at Te Waihora/Lake Ellesmere each year during 2017–2019 based on post-breeding aerial censuses. We conducted censuses on 9 December in 2017 and 2019, and 16 December in 2018. Observers aimed to record birds individually (i.e., in 1s), but if they encountered large groups of swans, they counted in 10s. If swan densities were low, each observer counted HY and AHY swans simultaneously, but if they encountered large concentrations of swans, they counted HY and AHY swans separately during successive flight loops or passes. If counts of either HY or AHY swans within a given pre-determined section of Te Waihora differed between observers by > 20% of their combined mean, both observers repeated the census of that section, resulting in two counts of both HY and AHY swans per observer (for more details, see Herse et al. 2020).

The mean of each observer’s total counts of HY swans at Te Waihora differed by < 10% of their combined mean for each year. The mean of each observer’s total counts of AHY swans differed by < 20% of their combined mean for each year. We used these means of total counts for generating bootstrap distributions of several demographic rates described below.

### *Annual per-capita fertility for after-hatch-year swans*

We estimated annual per-capita fertility (number of eggs hatched) for AHY swans ( $F_{\text{AHY}}$ ) using information on annual fertility per unharvested nest ( $f_0$ ) and per harvested nest ( $f_a$ ; assumes all first-clutch eggs were removed from harvested nests), and the proportion of AHY swans that attempt breeding ( $b$ ) (see main text, equation 3).

We estimated  $f_0$  based on observations of  $n = 22$  unharvested nests at the three largest nesting colonies at Te Waihora in 2018 (Herse et al. 2021). This sample of nests excluded nests for which we could not confidently determine fates of any eggs, and nests which had cameras present or different egg removal treatments as part of a separate study (because camera presence reduced rates of egg laying and hatching success; Herse et al. 2021). We used the ‘rpois’ function in R to generate a Poisson-based bootstrap distribution of colony-size-weighted  $f_0$ , with uncertainty weighted by the colony-specific sample size of nests. Specifically, for each of the three nesting colonies where we collected data, we first generated a bootstrap distribution of  $f_0$  as `weight*rpois(n = 10000, lambda = fertility*sample)`, where `weight` is a weight assigned to the colony based on its size (abundance of nests in 2018, as determined by aerial censuses, described below), `n` is the number of generated observations (samples), `lambda` is the estimate of mean fertility or number of eggs hatched per unharvested nest in 2018, and `sample` is the colony-specific sample size of nests in 2018. We then defined the bootstrap distribution of  $f_0$  as the sum of the three colony-size-weighted distributions described previously. Although demographic rates can change through time, the resulting distribution of  $f_0$  encompassed estimates from previous studies at Te Waihora, indicating that they were at least realistic (Fig. A1.1).

An experimental customary harvest of swan eggs at Te Waihora in 2018 revealed that during fixed-output harvests, removing entire clutches of eggs had the least impact on population-level hatching success (Herse et al. 2021). Thus, we estimated  $f_a$  based on observations of  $n = 13$  nests completely harvested as part of the experimental egg harvest (Herse et al. 2021). This sample of nests excluded completely-harvested nests which flooded and/or had cameras present as part of a separate study (because camera presence reduced post-harvest rates of egg laying and hatching success; Herse et al. 2021). These data are from the two largest swan nesting colonies at Te Waihora, which have historically contained a majority



of all nests at Te Waihora (Miers and Williams 1969, Williams 1979, Meis 1988), and been the focal areas for customary egg harvest (Herse et al. 2021). Thus, the model assumes that egg harvest occurs at these colonies. We generated a Poisson-based bootstrap distribution of  $f_a$  using the same approach described above for  $f_0$ .

We estimated  $b$  using information on abundance of nests ( $N_{\text{nest}}$ ) and AHY swans ( $N_{\text{AHY}}$ ) at Te Waihora in 2018. We censused nests using a combination of orthophotography of high-density nesting areas, and visual censuses of low-density nesting areas, during the peak-incubation period of the 2018 breeding season (Fig. 1, Fig. A1.2). We used a 50-megapixel Canon digital single-reflex lens (DSLR) camera equipped with a 50-mm focal length lens, mounted on vibration-isolating Sorbothane® mounts and programmed using Avitrix Flight Management System, to photograph high-density nesting areas (Fig. A1.2). Photos were then stitched together into mosaics by SKYVUW Ltd. (Taradale, New Zealand). We counted and marked locations of nests in ArcGIS 10.5 (Environmental Systems Research Institute, Redlands, California) (Fig. A1.2). We estimated  $N_{\text{nest}}$  based on the mean of a conservative count of nests for which we were confident in classifying as active at the time of the census ( $n = 840$ ), and a total count that included an additional 31 nests for which we were less confident ( $n = 871$ ). We used the ‘rpois’ function in R to generate Poisson-based bootstrap distributions of  $N_{\text{nest}}$  and  $N_{\text{AHY}}$ . Thus, we defined both bootstrap distributions as `rpois(n = 10000, lambda = abundance)`, where `n` is the number of simulated observations, and `lambda` is the mean count of nests (for  $N_{\text{nest}}$ ) or AHY swans (for  $N_{\text{AHY}}$ ). For each back-calculation of estimated survival probability over the first year after hatching ( $S_{\text{HY}}$ , described below; Fig. 2) and run of the matrix model (see main text, Fig. 3), we estimated  $b$  as

$$\frac{2N_{\text{nest}}}{N_{\text{AHY}}} \tag{Eqn A1.1}$$

Multiplying  $N_{\text{nest}}$  by 2 gives the estimated number of nesting swans at Te Waihora because breeding is generally monogamous (Williams 2013).

#### *Annual survival probability for after-hatch-year swans*

We estimated annual survival probability for AHY swans ( $S_{\text{AHY}}$ ) using GPS-tracking data collected as part of a separate study (Herse M.R., Lyver P.O’B., Scott N.J., Tyliaakis J.M., Ngāi Tahu, unpublished data). We based estimates on known fates of  $n = 17$  GPS-marked swans captured at Te Waihora in January 2019 (of  $n = 24$  total swans captured and marked) and monitored for one year. We captured molting swans from a boat using a landing net and fit each bird with a PinPoint GPS Iridium® neck collar we co-designed with Lotek UK (Wareham, United Kingdom) and Lotek NZ (Havelock North, New Zealand). Collars weighed 70 g, which was  $< 2\%$  of AHY swan body weight (Williams 2013). Of these 17 swans, 14 (82%) survived and 3 (18%) died during the 1-year monitoring period. Causes of mortalities appeared to be unrelated to GPS collars (because swans were alive and active for several months after collars were deployed) or sport hunting (although at least one swan was shot following the 1-year monitoring period). Because annual survival of swans has only two possible outcomes (survived or died), we used the ‘rbinom()’ function in R to generate a binomial-based bootstrap distribution of  $\hat{S}_{\text{AHY}}$  based on the parameters from our data. Specifically, we generated the distribution as `rbinom(n = 10000, size = 17, prob = 14/17) / 17` where `n` is the number of simulated observations (i.e., deployments of GPS-collars), `size` is the number of trials per observation (in this case, the number of collars deployed in 2019), and `prob` is the probability of ‘success’ (i.e., survival probability in 2019). We divided the resulting number of trial successes per observation by the number of trials per

observation to give the probability of success per trial. The resulting bootstrap distribution of  $S_{\text{AHY}}$  was centred on estimates from long-term studies of band-recovery data in the 1950s–1980s, and we therefore consider our estimates to be ecologically plausible (Fig. A1.3; Williams 1979, Barker and Buchanan 1993).

#### *Survival probability for hatch-year swans*

For back-calculations of  $S_{\text{HY}}$  (see main text, equations 4 and 5), we estimated population growth rate ( $\lambda$ ) based on the annual trend in swan population size at Te Waihora during 2017–2019, as determined by aerial censuses. An analysis of a larger census dataset collected at > 100 waterbodies, including Te Waihora, in 2017 found that observer bias was negligible (Herse et al. 2020). Thus, we modelled the population size trend based on the annual mean of the two observers' counts. Specifically, we estimated  $\lambda$  in equation 5 as the exponent of the slope of the linear regression line relating log population size to year (Fig. 3, Fig. A1.4) (Peery et al. 2006). The slope of the linear regression was congruent with that of data collected as part of a community-science annual bird survey led by Waihora Ellesmere Trust (WET; Ford et al. 2017, 2018) (Fig. A1.4). Thus, we assumed that the logarithm of the population growth rate follows a normal distribution and defined a bootstrap distribution of  $\lambda$  as  $\exp(\text{rnorm}(n = 10000, \text{mean} = \text{slope}, \text{sd} = \text{se}))$  where  $\exp$  is the exponent function,  $n$  is the number of generated observations,  $\text{mean}$  is the slope of the linear regression, and  $\text{sd}$  (standard deviation) is the standard error of  $\text{slope}$  ( $\text{se}$ ).

We applied constraints to back-calculations of  $S_{\text{HY}}$  to make them conform with estimated survival rates of swan hatchlings at Te Waihora. In 2018, we fit  $n = 50$  hatchling cygnets at Te Waihora with very-high-frequency (VHF) radio transmitters (Model: PipLL ag393, weight: 2.3g, Lotek NZ and Lotek UK) during September–October while cygnets were still in nests. Radio transmitters weighed < 2% of cygnet body weight at the time of tagging. We located marked cygnets approximately weekly using a combination of aerial- and ground-based radio telemetry until VHF transmitter batteries died in December. We coded encounters as 'seen,' 'heard only,' 'not detected,' or 'dead.' We used this censored data to develop a Kaplan-Meier (KM) estimator of the probability of surviving from hatching to 40 days ( $S_{\text{hatchling}}$ ; Fig. A1.5), which is the period over which we detected cygnet mortalities prior to all remaining individuals being censored. We generated a binomial-based bootstrap distribution of  $S_{\text{hatchling}}$  as  $\text{rbinom}(n = 10000, \text{size} = 50, \text{prob} = 0.679)/50$  where  $n$  is the number of simulated observations (i.e., deployments of VHF transmitters),  $\text{size}$  is the number of trials per observation (in this case, the number of VHF transmitters deployed in 2018), and  $\text{prob}$  is the probability of 'success' (i.e., survival probability in 2018 based on the KM estimator). We divided the resulting number of trial successes per observation by the number of trials per observation to give the probability of success per trial. For each back-calculation of  $S_{\text{HY}}$ , we sampled from distributions of  $S_{\text{HY}}$  and  $S_{\text{hatchling}}$  and required that  $S_{\text{HY}}$  be <  $S_{\text{hatchling}}$ . We also required that daily survival probability based on  $S_{\text{HY}}$  be < daily survival based on  $S_{\text{hatchling}}$ . To assess the plausibility of the resulting bootstrap distribution of  $S_{\text{HY}}$  back-calculations, we used functions available in the 'survival' R package (Therneau et al. 2021) to fit survival regressions to the KM curve and extrapolated those regressions to one year after hatching (Fig. A1.5). We fitted regression models using a suite of alternative probability distributions (exponential, Gaussian, logistic, log-logistic, log-normal, and Weibull; Therneau et al. 2021; Fig. A1.5). The bootstrap distribution of  $S_{\text{HY}}$  was centred near estimates of cygnet survival probability over the first year based on the most parsimonious survival regression models (Burnham and Anderson 2002), and we therefore consider estimates from the bootstrap distribution to be ecologically plausible (Fig. A1.5).

#### **Modelling of demographic parameters**

We estimated  $\lambda$  as the dominant eigenvalue of the matrix  $\mathbf{A}$  (Fig. 3), as described above (Caswell 2001). We used partial derivatives ( $\partial$ ) to calculate sensitivity ( $s_x$ ) of  $\lambda$  to an absolute change in each demographic rate  $x$  as

$$s_x = \frac{\partial \lambda}{\partial x} = \sum_{i,j} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x} \quad \text{Eqn A1.2}$$

where  $a_{ij}$  is the element of  $\mathbf{A}$  for row  $i$  and column  $j$  and  $\frac{\partial a_{ij}}{\partial x}$  is the partial derivative of  $a_{ij}$  corresponding with  $x$  (Caswell 2001). We calculated elasticity ( $e_x$ ) for each demographic rate  $x$  as

$$e_x = \frac{x}{\lambda} s_x \quad \text{Eqn A1.3}$$

(Caswell 2001). This approach allowed us to compare sensitivity and elasticity of  $S_{\text{HY}}$ ,  $S_{\text{AHY}}$ , and lower-level demographic rates comprising  $F_{\text{AHY}}$  ( $f_0$  and  $b$ ) (Caswell 2001).

To assess sources of uncertainty in  $\lambda$ , we used variances ( $var$ ) of bootstrap distributions of  $s_x$  to calculate the proportional contribution ( $c_x$ ) of each demographic rate  $x$  to the total variance in  $\lambda$  as

$$c_x = \frac{s_x^2 var(s_x)}{\sum_x s_x^2 var(s_x)}, \quad \text{Eqn A1.4}$$

as described by Caswell (2001).

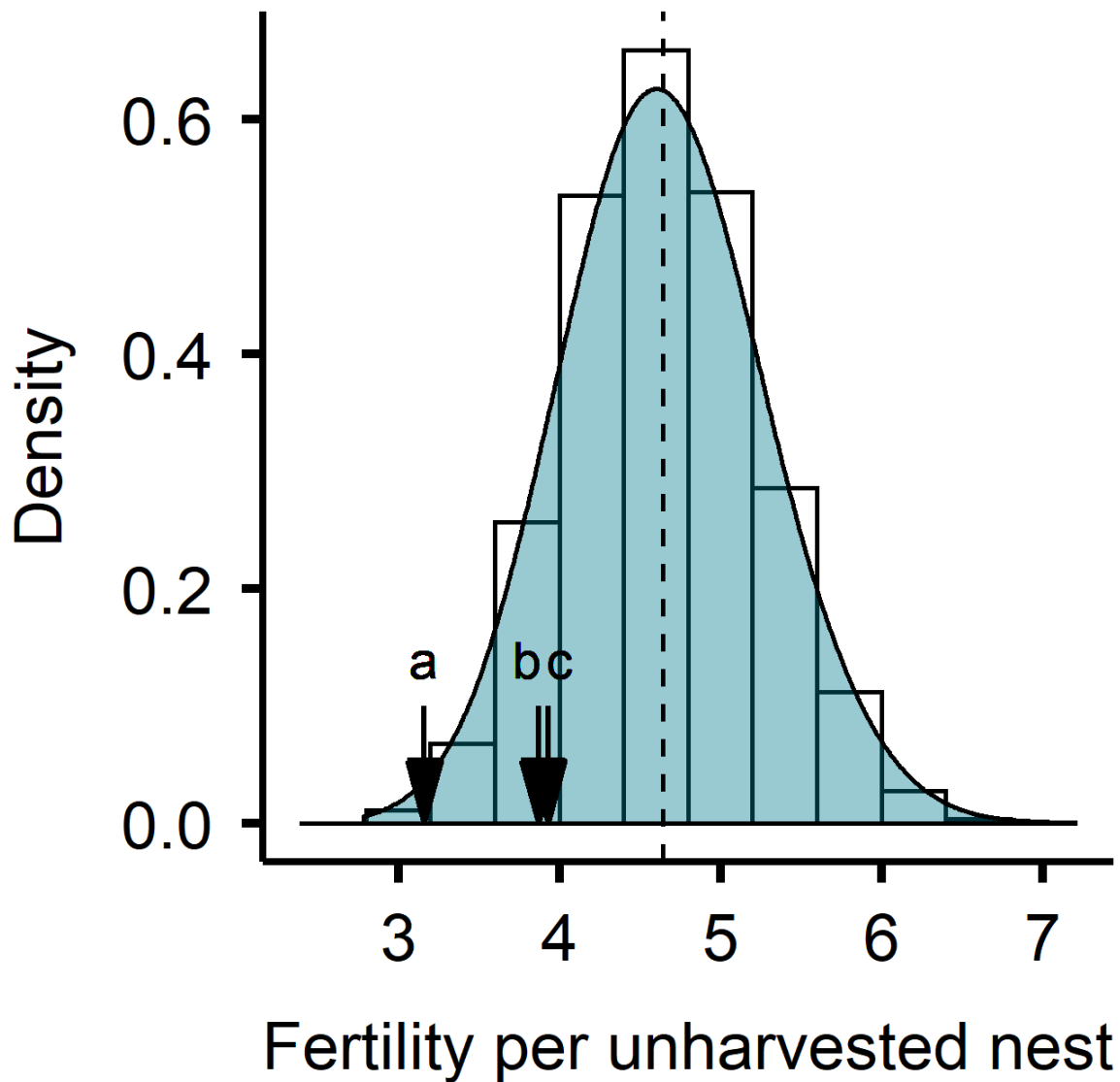
We estimated reproductive value of individual AHY swans (i.e., the lifelong total number of offspring produced, measured as number of fresh eggs laid and number of eggs hatched) following the methods described by Caswell (2001), which incorporate information on age-specific reproduction and life expectancy, and the methods described in the main text (see equation 6). Estimates of life expectancy were skewed due to rare but extremely large values of  $\hat{S}_{\text{AHY}}$  (close to 1; see Fig. A1.3) being drawn during random sampling. Thus, the estimate of life expectancy for AHY swans that we report in the main text corresponds with the median of the bootstrap distribution of life expectancy.

## Literature Cited

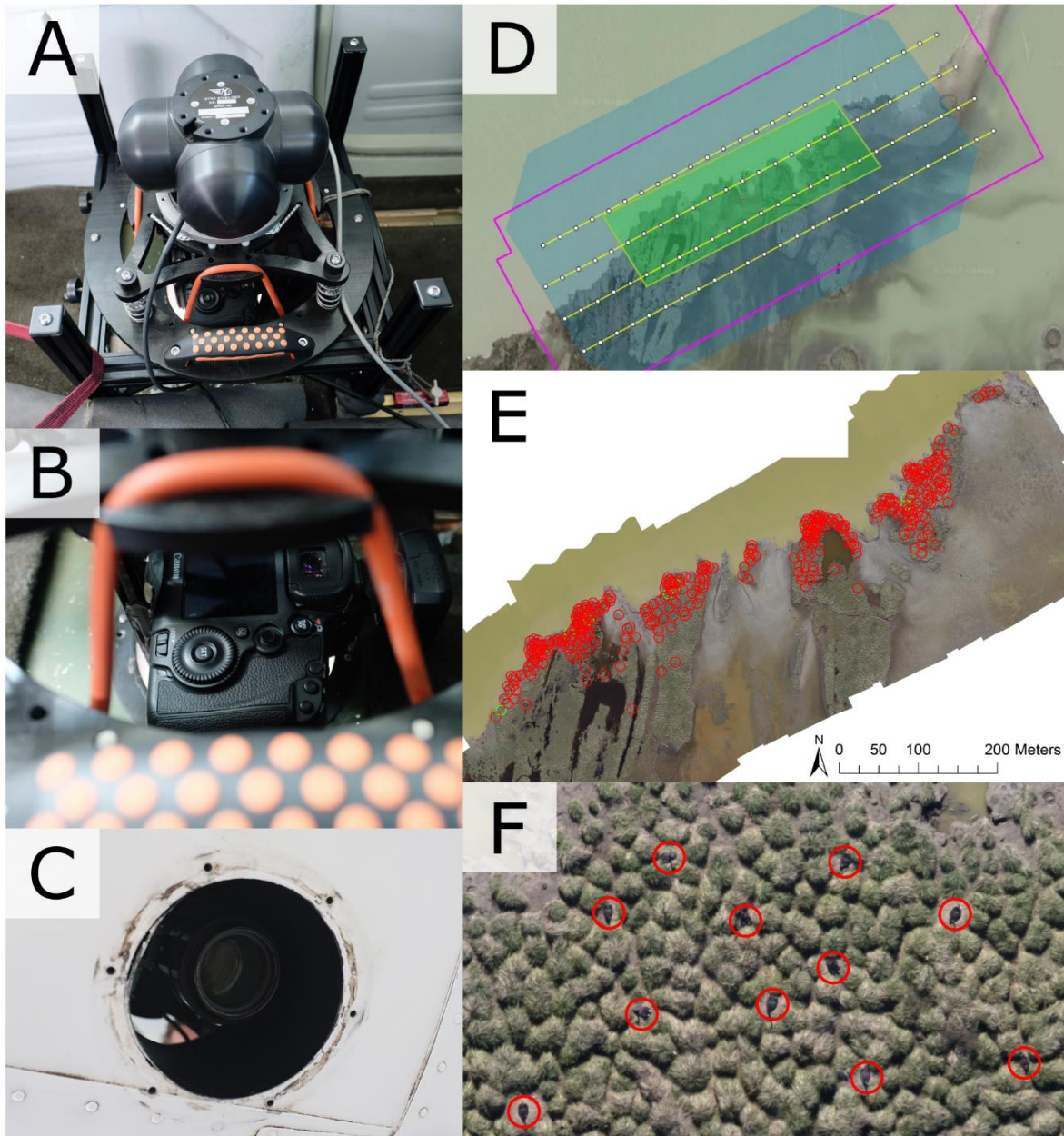
- Adams, J. S. 1971. Black swans at Lake Ellesmere. *Wildlife-a Review* 3:23-25.
- Barker, R. J., and I. M. Buchanan. 1993. Estimating adult survival rates of New Zealand Black Swans banded as immatures. *Journal of Wildlife Management* 57(3):549-555.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed). Springer, New York.
- Caswell, H. 2001. *Matrix Population Models: Construction, Analysis and Interpretation* (2nd ed.). Sinauer Associates, Sunderland, Massachusetts.
- Ford, D. E., F. D. Hughey, and K. Taylor. 2017. *Te Waihora/Lake Ellesmere: State of the Lake 2017*. Waihora Ellesmere Trust Technical Report No. 3.
- Ford, D. E. 2018. Annual census of wetland birds on Te Waihora/Lake Ellesmere. *Lincoln Planning Review* 9(1-2):44-45.
- Herse, M. R., P. O'B. Lyver, N. J. Scott, A. R. McIntosh, S. C. Coats, A. M. Gormley, and J. M. Tylianakis. 2020. Engaging Indigenous Peoples and Local Communities Could Alleviate Scale Mismatches in Social-Ecological Systems. *BioScience* 70(8):699-707.

- Herse, M. R., J. M. Tylanakis, N. J. Scott, D. Brown, I. Cranwell, J. Henry, C. Pauling, A. R. McIntosh, and P. O'B. Lyver. 2021. Effects of customary egg harvest regimes on hatching success of culturally important waterfowl species. *People and Nature* 3(2):499-512.
- Meis, T. 1988. Waterfowl Management in North Canterbury. MSc Thesis, University of Canterbury, Christchurch, New Zealand.
- Miers, K. H., and M. Williams. 1969. Nesting of the Black Swan at Lake Ellesmere, New Zealand. *Wildfowl* 20:23-32.
- Peery, M. Z., B. H. Becker, and S. R. Beissinger. 2006. Combining demographic and count-based approaches to identify source-sink dynamics of a threatened seabird. *Ecological Applications* 16(4):1516-1528.
- Therneau, T. M., T. Lumley, E. Atkinson, and C. Crowson. 2021. survival: Survival Analysis version 3.2-10. <https://cran.r-project.org/web/packages/survival/index.html>
- Williams, M. 1979. Status and management of black swans *Cygnus atratus*, Latham at Lake Ellesmere since the "Wahine" Storm, April 1968. *New Zealand Journal of Ecology* 2:34-41.
- Williams, M. 2013. Black swan. In Miskelly, C. M., editor. *New Zealand Birds Online*. [www.nzbirdsonline.org.nz](http://www.nzbirdsonline.org.nz)

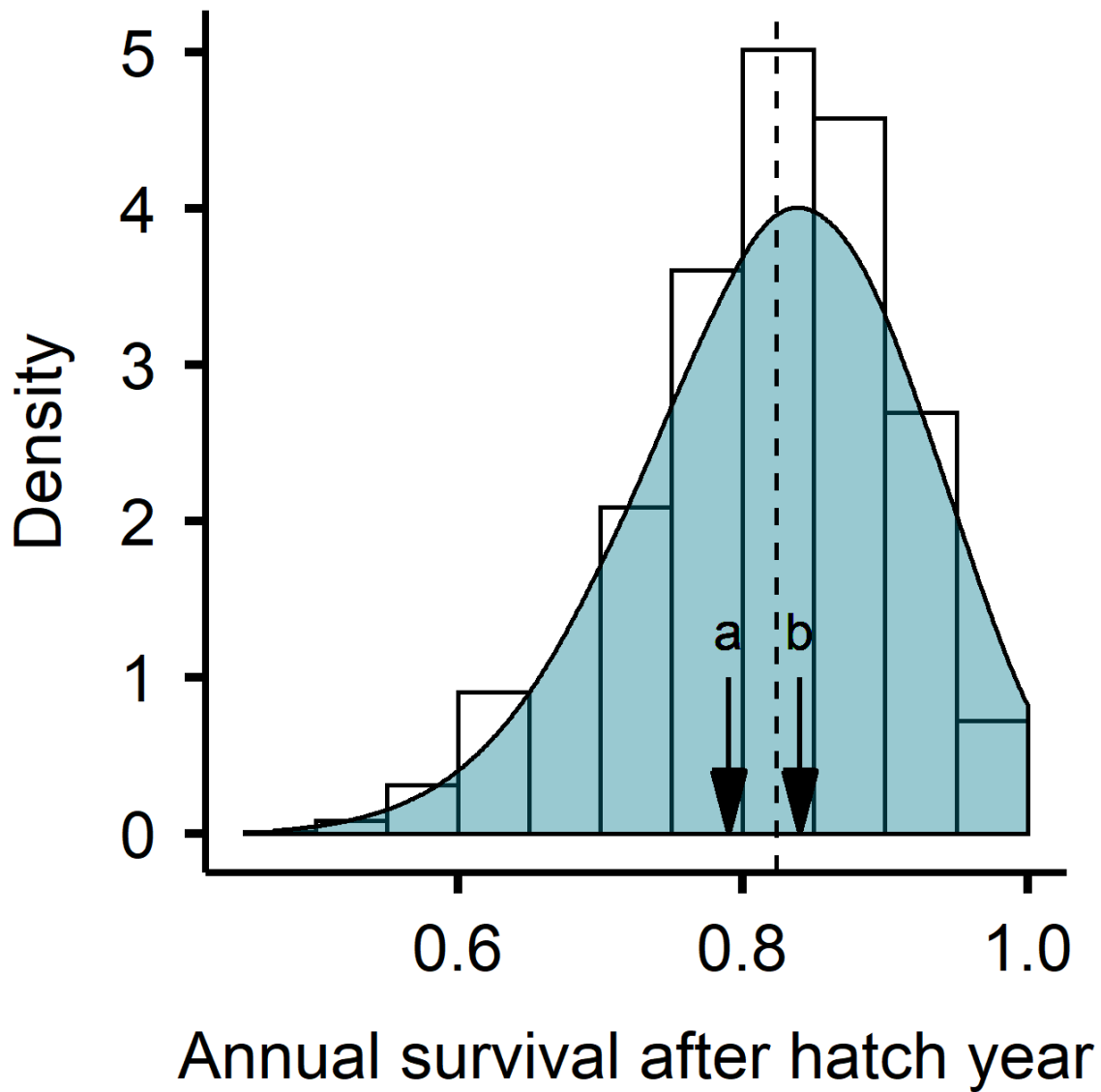




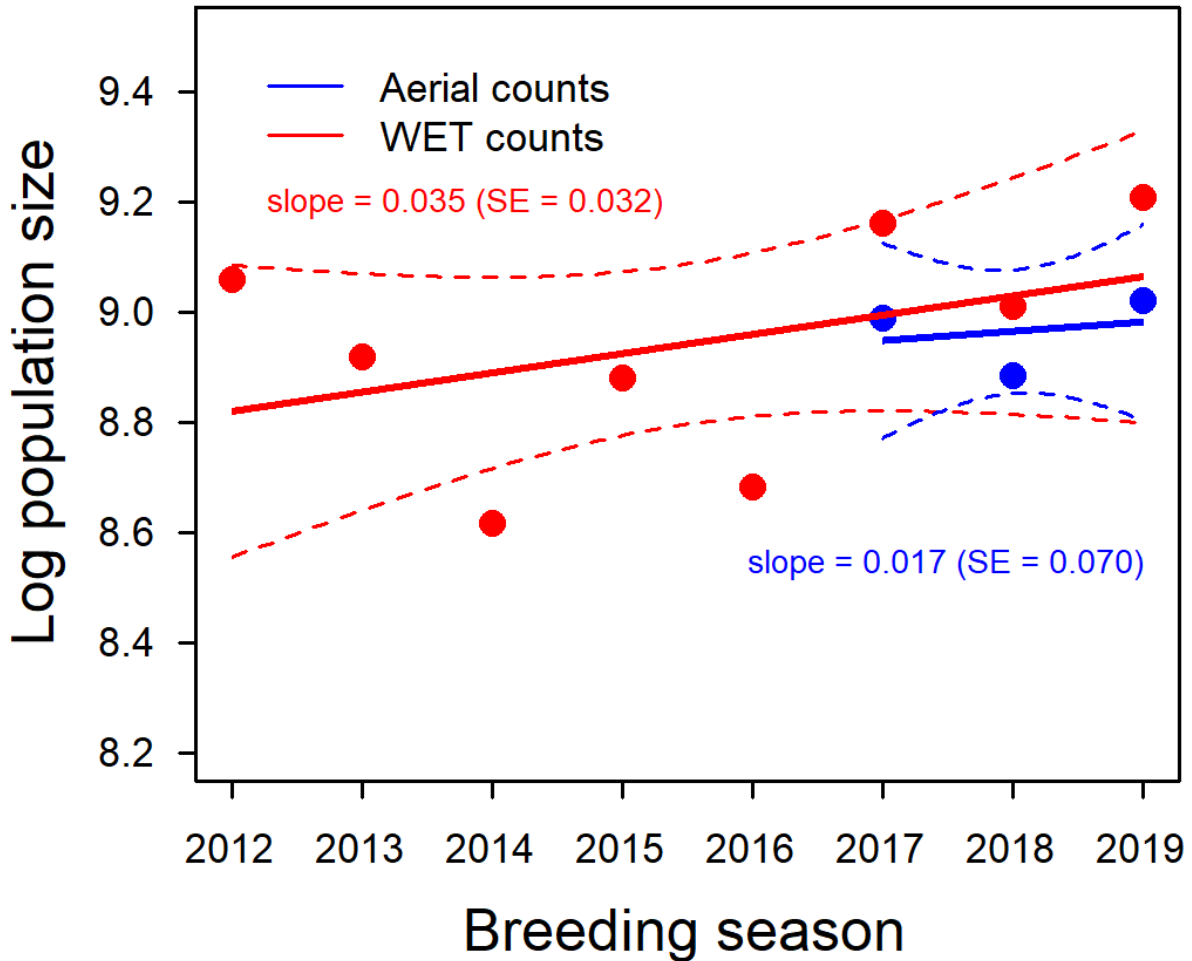
**Figure A1.1.** Density plot and histogram of the initial Poisson-based bootstrap distribution of estimated black swan fertility (number of eggs hatched) per unharvested nest ( $f_0$ ) at Te Waihora/Lake Ellesmere, Aotearoa/New Zealand, in 2018. The vertical dashed line indicates the mean of the bootstrap distribution. Arrows **a** and **b** are estimates of  $f_0$  in 1960 and 1961, respectively, at Te Waihora (Miers & Williams, 1969), whereas arrow **c** is an estimate of  $f_0$  in 1971 at Te Waihora (Adams, 1971).



**Figure A1.2.** Images and maps showing how we assessed the total number of nests ( $N_{\text{nest}}$ ), and the proportion of after-hatch-year black swans attempting to breed ( $b$ ), at Te Waihora/Lake Ellesmere, Aotearoa/New Zealand, in 2018. Photos A–C show a Canon digital single-reflex lens (DSLR) camera mounted on vibration-isolating Sorbothane® mounts, which we used to photograph nesting colonies through the bottom of a Cessna 185 Skywagon fixed-wing aircraft. Photo D shows an example of the flight transects and image locations for photographing nesting colonies. Photo E shows all the swan nests (red circles) identified at the largest nesting colony, whereas photo F shows a closer view of the nesting colony.

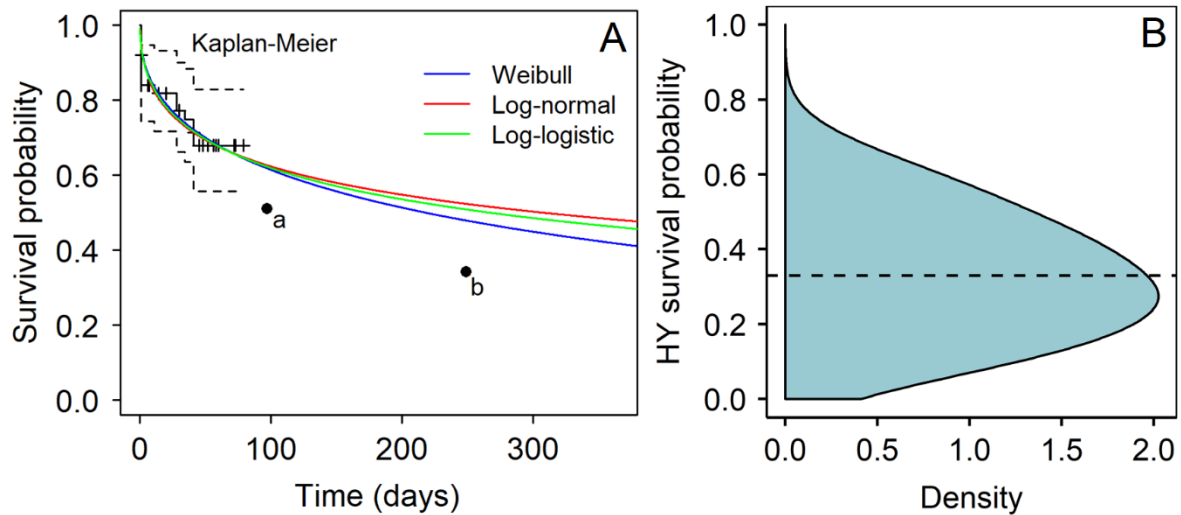


**Figure A1.3.** Density plot and histogram of the initial binomial-based bootstrap distribution of estimated annual survival probability for after-hatch-year (AHY) black swans at Te Waihora/Lake Ellesmere, Aotearoa/New Zealand, during 2019–2020. The vertical dashed line indicates the mean of the bootstrap distribution. Arrow **a** indicates an age-distribution-weighted estimate of mean annual survival probability for AHY swans at Te Waihora during 1956–1974 (Williams, 1979), whereas arrow **b** indicates an estimate of mean annual survival probability for AHY swans at Lake Wairarapa, Aotearoa/New Zealand, during 1974–1989.

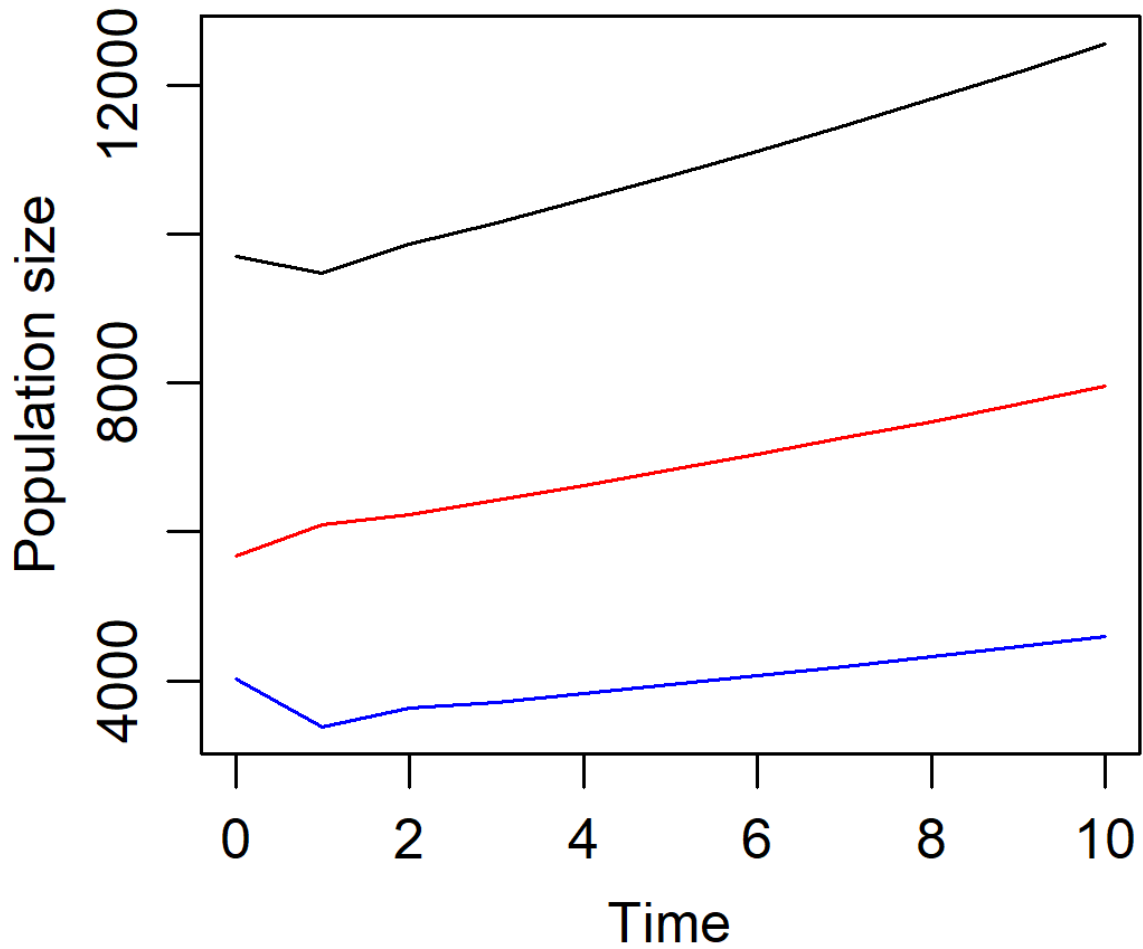


**Figure A1.4.** Raw data (points) and linear regressions (lines) of log black swan population size at Te Waihora/Lake Ellesmere, Aotearoa/New Zealand, related to breeding year. The blue line corresponds with our aerial census data, whereas the red line corresponds with community-science data collected by Waihora Ellesmere Trust (WET; Ford et al., 2017). We assigned each datum to breeding year based on the timing of corresponding nesting season. For example, we assigned both our aerial data collected in December of 2017, and WET data collected in February of 2018, to the year 2017, which is when nesting during the 2017–2018 breeding season occurred. The dashed lines indicate 95% confidence limits.





**Figure A1.5.** Plot A shows estimates of the probability of surviving to a given age (days since hatching) for juvenile black swans at Te Waihora/Lake Ellesmere, Aotearoa/New Zealand in 2018, which we used to assess whether a bootstrap distribution of estimated survival probability over the first (hatch) year ( $S_{HY}$ ) was ecologically plausible. In plot A, the solid black line indicates a Kaplan-Meier (KM) estimator of survival for  $n = 50$  radio-marked hatchlings at Te Waihora in 2018, whereas vertical hatch marks indicate the timing of data censoring, and dashed lines indicate 95% confidence limits. Coloured lines show alternative survival regression models (only the top-ranked models with parsimonious  $\Delta AICc$  values  $< 2$  are shown). Point **a** indicates an estimate of cygnet survival probability from hatching to leg-banding age ( $\sim 3$  months) at Te Waihora in 1986 (Meis, 1988). Point **b** indicates an estimate of cygnet survival probability from hatching to the end of the first band-recovery period (hunting season) at Te Waihora (Meis, 1988; Williams, 1979). Plot B shows the density plot and histogram (flipped along the x axis to aid comparison with plot A) for the back-calculated bootstrap distribution of estimated survival for hatch-year (HY) swans over their first year of life at Te Waihora in 2018. In plot B, the horizontal dashed line indicates the mean of the bootstrap distribution.



**Figure A1.6.** Plot showing model estimates of number of hatch-year (blue line) and after-hatch-year (red line) black swans, and total population size (i.e., hatch-year plus after-hatch-year swans; black line), at Te Waihora/Lake Ellesmere, Aotearoa/New Zealand, projected across future time (years), beginning in 2018 (i.e., Time = 0). Transient population dynamics die off after about two years, as indicated by the disappearance of oscillations in the trends.