

Using long-term data for a reintroduced population to empirically estimate future consequences of inbreeding

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Abstract: Inbreeding depression is an important long-term threat to reintroduced populations. However, the strength of inbreeding depression is difficult to estimate in wild populations, both because pedigree data are inevitably incomplete and because good data are needed on survival and reproduction. Predicting future population consequences is especially difficult because this also requires projecting future inbreeding levels and their impacts on long-term population dynamics which are subject to many uncertainties. We illustrate how such projections can be derived through Bayesian state-space modeling methods, using a 26-year dataset for North Island robins (*Petroica longipes*) reintroduced to Tiritiri Matangi Island in 1992. We used pedigree data to model increases in the average inbreeding level (\bar{F}) over time based on kinship of possible breeding pairs, and empirically estimate N_e/N (effective/census population size). We used multiple imputation to model the unknown components of inbreeding coefficients, allowing us to estimate effects of inbreeding on survival for all 1458 birds in the dataset while simultaneously modeling density dependence and environmental stochasticity. This modeling indicated that inbreeding reduced juvenile survival (1.83 ± 0.81 lethal equivalents) and may have reduced subsequent adult survival (0.44 ± 0.81 lethal equivalents) but had no apparent effect on numbers of fledglings produced. \bar{F} increased to $0.10 (\pm 0.001)$ as the population grew from $33 (\pm 0.3)$ to $160 (\pm 6)$ individuals over the 25 years, giving a N_e/N ratio of $0.56 (\pm 0.01)$. Based on a model that also incorporates habitat regeneration, the population is projected to reach a maximum of 331–1144 birds (median 726) in 2130, then begin slowly declining. Without inbreeding, the population would be expected stabilize at 887–1465 birds (median 1131). Such analysis therefore makes it possible to empirically derive the information needed for rational decisions about inbreeding management while accounting for multiple sources of uncertainty.

Introduction

Inbreeding is an important threat to the long-term viability of small populations, along with demographic stochasticity, environmental stochasticity and Allee effects (Shaffer 1981). It is particularly relevant to populations established by translocation, both because they often have relatively few founders (Jamieson & Lacy 2012) and because they are often constrained to small habitat areas so are subject to the loss of genetic diversity characteristic of all small or fragmented populations (Keller et al. 2012; Frankham et al. 2019). These considerations affect decisions about suitability of potential reintroduction sites, numbers of individuals translocated, and potential ongoing management to facilitate gene flow (Groombridge et al. 2012; Weeks et al. 2015). The best choices depend on the objectives, the management alternatives, and the predicted consequences of those alternatives.

A key objective in translocation programs is maximize the persistence of translocated populations. Although the consequences of inbreeding depression are generally well understood for captive populations, resulting in established guidelines for management (Ballou et al. 2010), they are less well understood for wild populations. In the face of uncertainty managers may simply assume all small populations will suffer from severe inbreeding depression unless intensively managed (Frankham et al. 2019). However, this approach may not be optimal in terms of the multiple objectives likely to be involved. In particular, it may result in expensive unnecessary interventions, compromising conservation budgets, or may result in all small sites being rejected, compromising our ability to increase numbers of populations or return species to sites for restoration purposes.

The long-term consequences of inbreeding in wild populations are particularly difficult to predict because: (1) the strength of inbreeding depression is highly variable and unpredictable (e.g. Lacy et al. 1996); (2) estimating inbreeding depression in a given population requires good data on vital rates in relation to inbreeding coefficients, taking confounding factors into account (Nietlisbach et al. 2019); (3) inbreeding coefficients require pedigree data, which are always patchy for wild

populations or require genetic methods which are both expensive and complex to interpret (Nietlisbach et al. 2019); (4) predicted increases in inbreeding levels depend on the population's effective population size (N_e) rather than census population size (N), making it is necessary to estimate N_e/N which may subject to high uncertainty (Engen et al. 2010); (5) predicted increases in inbreeding depend both on the population's initial growth and its long-term regulation, meaning density dependence in population parameters needs to be estimated while simultaneously accounting for inbreeding depression and annual variation; (6) in many habitats density dependence is not expected to remain constant over time as carrying capacity will change with habitat regeneration or degradation.

Meeting these challenges will be impossible in most translocation programs, particularly in the early years when data are sparse. In these cases, managers can only make the best possible inferences based on published information (e.g. Frankham et al. 2019) but should attempt to use decision processes that fully account for the uncertainty involved (Canessa et al. 2016). However, where intensive long-term monitoring is feasible, it is possible to address the challenges above to enable the future consequences of inbreeding to be estimated empirically, providing a strong basis for future genetic management. This is facilitated by advances in Bayesian hierarchical modeling (Kéry & Schaub 2012), which allow the unknown components of pedigrees to be modeled through multiple imputation and also allow the effects of age, inbreeding, density dependence and random annual variation on demographic rates to be modeled simultaneously, meaning biases are minimized and uncertainties are propagated into long-term projections. We illustrate how this approach was used to analyze 26 years of data on pedigrees, vital rates, and population growth for a toutouwai (North Island robin *Petroica longipes*) population reintroduced to a small (220 ha) island in 1992, and project dynamics for the next 150 years. We compare the projections to those under a hypothetical scenario where there is no inbreeding depression in order to estimate the future consequences of inbreeding and therefore the need for management.

Methods

Species and site

The toutouwai is a small (26-32 g) territorial insectivorous forest passerine endemic to the North Island of New Zealand and surrounding islands. Toutouwai breed in their first year and form monogamous pairs, with pairings random in relation to inbreeding coefficients (Jamieson et al. 2009). Paired females have not been recorded to have extra-pair copulation or extra-pair paternity (Ardern et al. 1997). Unpaired females receive copulations from neighboring males, so can fledge young but at a lower rate than paired females (Parlato & Armstrong 2012). The species was extirpated from ca. 90% of its original range by forest clearance and exotic mammalian predators (Parlato et al. 2015) but has been reintroduced to > 30 sites following revegetation and/or predator control (Miskelly & Powlesland 2013; unpublished data).

Toutouwai were reintroduced to 220-ha Tiritiri Matangi Island (36.6° S, 174.9°) via translocations of 44 birds in April 1992 and 14 birds in June 1993. This island has largely remained free of exotic predatory mammals, with the only mammal species (Pacific rat, *Rattus exulans*) eradicated via an aerial poison drop in September 1993. However, it was farmed until 1971, and in 1992 had ca. 13 ha of toutouwai habitat consisting of 15 forest remnants (Armstrong & Ewen 2002). Due to restoration planting from 1983–1995 and natural regeneration, it is expected to ultimately have ca. 150 ha of mature forest (Mitchell 1985). Research from 1992–2003 indicated that the toutouwai population reached an initial carrying capacity of ca. 70 birds, with its growth regulated by density dependence in juvenile survival, and that the population had a high probability of persistence if initial demographic rates persisted (Armstrong & Ewen 2002; Dimond & Armstrong 2007). However, there was tentative evidence of inbreeding depression in juvenile survival (Jamieson et al. 2007), meaning juvenile survival may decline with future increases in inbreeding, which would depend on the population's rate of increase. Toutouwai began occupying planted areas in 2000/2001, and there was subsequent gradual expansion into the maturing planted forest which

had expanded to 33 ha by 2017. The population has been harvested five times for reintroductions to other sites in the region, providing further information on its density-dependent regulation (Dimond & Armstrong 2007).

Monitoring

We conducted regular surveys from April 1992 to January 2018 to obtain data on survival and population size, and conducted breeding monitoring up to the 2011/2012 breeding season to determine numbers of young fledged, individually color-band those young, and determine pedigrees. We initially collected blood samples from all chicks for minisatellite DNA profiling, but after confirming that genetic parents matched putative parents for all chicks produced in the first three years (Ardern et al. 1997) we assumed this to also be the case for subsequent years.

Surveys involved walking through forested areas playing territorial calls to attract toutouwai and recording color combinations of birds found. We always conducted surveys in September (start of breeding season) and January, but conducted additional surveys after translocations (to account for post-release effects), after an aerial poison drop (to account for bykill of toutouwai), at harvests (to facilitate censoring of birds removed), and additional occasions over winter (to model changes in juvenile survival with age). Banded fledglings were considered to enter the population at the January survey. Breeding monitoring involved checking pairs regularly from September to February (Armstrong & Ewen 2002 for details). We color-banded most chicks in the nest 9–14 days after hatching, but if nests were inaccessible we caught and banded fledglings after they left the nest. This intensive monitoring resulted in both putative parents being known for 94% of the 1257 recruits into the breeding population up to 2012/2013, with the remainder banded as adults. From 2013 onward we continued to band adult recruits at the start of the breeding season and banded a sample of nestlings to obtain further data on juvenile survival. We always counted the number of unbanded (including newly-banded) birds in the September survey to allow estimation of breeding population

size, with unbanded individuals being readily distinguished from one another due to having distinct territories and most birds being banded.

Modeling

The analysis consisted of four steps: (1) estimating abundance each year from 1992–2017; (2) modeling inbreeding data from 1992–2012; (3) modeling survival and reproduction data from those years in relation to inbreeding, population density, age, and random annual variation; and (4) projecting future population dynamics with a stochastic simulation model based on steps 2-3, with and without inbreeding depression. We did all steps using OpenBUGS 3.2.3 (Lunn et al. 2014), as its MCMC (Markov chain Monte Carlo) fitting allowed the flexibility needed. We did the four steps in sequence as it was prohibitively slow to fully integrate all procedures but used state-space formulations to propagate estimation error from one step to the next. We used uninformative priors for all parameters estimated, and standard MCMC diagnostics including checking convergence of three chains (Kéry & Schaub 2012). All code and data are provided in Appendices S1–S6.

1. *Abundance*

Abundance was known quite precisely in most years due to the intensive nature of the monitoring and high detection probabilities (see Results). Nevertheless, to avoid potential biases due to imperfect detection, we obtained probability distributions for numbers of males and females at the start of each breeding season by simultaneously analyzing encounter histories of banded birds and counts of unbanded birds found in September surveys (Appendix S7). The model fitted to the encounter histories was similar to that used for analyzing survival (Step 3) except that variation in survival over time was modelled solely as random effects.

2. Inbreeding

We analyzed the pedigree data both to understand how the inbreeding level of the population changed over time and to understand how inbreeding affected survival and reproduction rates. By directly modelling observed changes in inbreeding, we avoid many of the complexities involved with predicted changes in effective population size (N_e) from demographic data alone (e.g. Mills & Smouse 1994). We used PMx 1.0 (Ballou et al. 2011) to calculate kinship coefficients for all possible male-female pairings each year where the individuals' grandparents were known and their pedigree could be traced to at least one founder, assuming those founders were unrelated. Kinship coefficients of pairs are equivalent to the inbreeding coefficients of their offspring, hence we use F to refer to both.

The average inbreeding level (\bar{F}) of a population under random mating is expected to increase in proportion to twice the effective population size each generation (Crow & Kimura 1970, p. 101). The increase from one year to the next is therefore expected to be

$$\bar{F}_{y+1} = 1 - (1 - \bar{F}_y) \left(1 - \frac{1}{2N_{e_y}}\right)^{1/GT}, \quad (1)$$

where N_{e_y} is the effective population size in year y and GT is the generation time (which was set to 3.1 years as this was consistently the average age of breeding adults). Re-calculating the effective population size annually allows for population growth or decline, which may partially reflect changes in vital rates through inbreeding depression. N_{e_y} is in turn given by $N_y * Ne/N$, where N_y is the estimated population size and Ne/N is a parameter that we assume to be constant. We fitted this model (Appendix S1) to the data on kinships for all possible male-female pairings each breeding season (Appendix S2), allowing us to empirically estimate Ne/N . N_y values were obtained in Step 1, with estimation error incorporated by sampling from normally-distributed state spaces defined by the estimates and standard errors.

We simultaneously modeled the relationship between the mean and variance of kinships, as the variance in kinships will affect the degree to which the population inbreeding level changes at

random due to the pairings made. The changes in variance over time were predicted well by the model

$$V(F_y) = \bar{F}_y(1 - \bar{F}_y)c, \quad (2)$$

where $V(F_y)$ is the variance in kinship among the possible male-female pairings each year and c is a constant estimated by fitting the model to the data.

To model the effects of inbreeding on survival and reproduction of the whole population, we needed to model inbreeding coefficients of all individuals regardless of how well their pedigree was known. PMx calculates inbreeding coefficients from the known part of the pedigree, but also calculates the proportion of the pedigree that is known. Therefore, to account for pedigree uncertainty we modelled inbreeding coefficients as

$$F_i = FK_i * \text{known}_i + FU_i * (1 - \text{known}_i), \quad (4)$$

where FK_i is the inbreeding coefficient for the known portion of the pedigree, known_i is the proportion known, and FU_i is a random number sampled from a beta distribution with mean and variance calculated from the possible male-female pairings in individual i 's year of birth (these beta distributions gave a good fit to the data). The same calculation applied to kinships of breeding pairs, i.e. kinships of a pair in any year were modeled the same way as the F_i values of their offspring that year.

3. Survival and reproduction

We analyzed survival using a state-space formulation of the Cormack-Jolly-Seber (CJS) model (Appendix S3), with detection probability modeled the same way as for estimating abundance. The probability of an individual surviving an interval depended on the time spent in each of three stages: fledgling (up to March in year of fledging), older juvenile (March-September), and adults (September onward). The stage-specific survival probabilities were given by

$$\log(\phi_{i,j}) = a. \phi + b. \text{sex. } \phi * \text{sex}_i + b. \text{F. } \phi * F_i + b. \text{rel. } \phi * \text{rel. } \phi_{i,j} + b. \text{pois} * \text{pois}_j, \quad (5)$$

$$\log(\phi_{i,j}) = a. \phi + b. \text{juv. } \phi + b. D. \phi * D_y + b. F. \phi. \text{juv} * F_i + \text{re. } y. \phi. \text{juv}_y, \quad (6)$$

and

$$\log(\phi_{i,j}) = \log(\phi_{i,j}) + b. \text{fl} + b. \text{band. fl} * \text{band. fl}_i, \quad (7)$$

where $a. \phi$ is the intercept, $b. \text{juv. } \phi$ is the effect of being a juvenile, $b. \text{fl}$ is the additional effect of being a fledgling, $b. \text{band. fl}$ accounts for the higher survival to March in birds banded as fledglings ($\text{band. fl}_i = 1$) rather than in the nest ($\text{band. fl}_i = 0$), $b. \text{sex. } \phi$ is the effect of sex on adult survival, $b. \text{rel. } \phi$ is the post-release effect on survival (see Supporting Information), $b. \text{pois}$ is the poison effect ($\text{pois}_j = 1$ for interval immediately after the poison drop, 0 otherwise), $b. F. \phi. \text{ad}$ and $b. F. \phi. \text{juv}$ are effects on inbreeding on adult and juvenile survival, and $b. D. \phi$ is the effect of current density, and $\text{re. } y. \phi. \text{juv}_y$ is the annual random effect on juvenile survival. Density was defined as the number of females in September divided by the current habitat area, as this had previously been found to be a better predictor of juvenile survival than other density measures (Dimond & Armstrong 2007).

The use of log link functions here means that $b. F. \phi. \text{juv}$ and $b. F. \phi. \text{ad}$ give the numbers of haploid lethal equivalents (B) at juvenile and adult stages respectively (Nietlisbach et al. 2019). We initially included an annual random effect on adult as well as juvenile survival but removed it because there no indication of annual variation in adult survival and the model had poor convergence when this random effect was included in conjunction with $b. F. \phi. \text{ad}$. We also initially divided the juvenile period into four stages rather than two, but simplified this age structure after finding no indication that monthly juvenile survival probability changed from March-September.

The number of females each year was sampled from normally-distributed state-spaces with means and standard deviations as obtained in Step 1. Based on the changes in forest cover, we assumed the habitat area remained 13 ha through the 1999/2000 breeding season then increased by 1.1 ha per year (Fig. 1).

We analyzed the reproduction data using a generalized linear mixed model with Poisson error term (Appendix S4). The expected number of young fledged by female i in year y was initially calculated as

$$\log(\mu_{i,y}) = a.f + b.age * age_{i,y} + b.rel.f * rel.f_{i,y} + b.unp * unp_{i,y} + b.D.f * D_y + b.F.f * F_{i,y} + re.y.f_y, \quad (8)$$

where $a.f$ is the intercept, $b.age$ is the effect of female age ($age_{i,y} = 0$ if first-year, 1 otherwise), $b.rel.f$ is the post-release effect on reproduction ($rel.f_{i,y} = 1$ if female translocated that year, 0 otherwise), $b.unp$ indicates the effect of being unpaired ($unp_{i,y} = 1$ if female unpaired that year, 0 otherwise), $b.D.f$ is the effect of population density, $b.F.f$ is the effect of inbreeding on reproduction ($F_{i,y}$ is the inbreeding coefficient of her potential offspring that year), and $re.y.f_y$ is the annual random effect on reproduction.

4. Population projections

Based on the results of Step 3, we projected population dynamics from 2017–2167 using a model including all factors found to have clear or tentative effects on survival or reproduction (Table 1). We did this using an integrated approach whereby the reduced survival and reproduction models were re-run using the raw data (Appendix S5), and the population projections done simultaneously as part of the same code (Appendix S6). The advantage of this approach is that the set of parameter values sampled in each MCMC iteration is used in a corresponding run of the population model, meaning covariances among parameters are propagated into projections.

The projection component of the model began by selecting the initial (2017) numbers of males ($N.M_y$), first-year females ($N.F0_y$) and older females ($N.F1_y$) from normally-distributed state spaces (Table 2) and rounding to the nearest integers. Initial values were also assigned for expected mean and variance in inbreeding coefficients (Table 2). The steps below were then repeated for each of the 150 years.

The number of young fledged ($N.f_y$) was sampled from a Poisson distribution with mean

$$N.f.\mu_y = a.f * N.F0.par_y + (a.f + b.unp) * N.F0.unp_y + (a.f + b.age) * N.F1_y, \quad (9)$$

where $N.F0.par_y$ and $N.F0.unp_y$ are the numbers of first-year females that are paired and unpaired respectively (we assume any unpaired females were first-years, hence $N.F0.unp_y = N.F_y - N.M_y$ if females outnumber males, 0 otherwise). The number surviving to be first-year adults next year ($N.O_{y+1}$) was sampled from a binomial distribution with probability

$$\emptyset.fj_y = \emptyset.fl_y^{0.167} * \emptyset.juv_y^{0.5}, \quad (10)$$

where 0.167 and 0.5 are the number of years spent at the fledgling and older juvenile stages (see Supporting Information) and the stage-specific survival probabilities are

$$\log(\emptyset.juv_y) = a.\emptyset + b.juv.\emptyset + b.D.\emptyset * D_y + b.F.\emptyset.juv * F.ave_y + re.y.\emptyset.juv_y, \quad (11)$$

and

$$\log(\emptyset.fl_y) = \log(\emptyset.juv_y) + b.fl. \quad (12)$$

Equations 11 and 12 are identical to equations 6 and 7 respectively, but with the average inbreeding coefficient for the cohort ($F.ave_y$) substituted for the inbreeding coefficient of an individual bird. To allow random variation in these average inbreeding coefficients from the expected values, each $F.ave_y$ value was sampled from a normal distribution with mean \bar{F}_y and variance $V(F_y)/N.f_y$. The density (D_y) was calculated as above, assuming habitat area would continue to increase by 1.1 ha per year until it reached 150 ha.

The number of first-year females ($N.F0_{y+1}$) was then sampled from a binomial distribution with probability $1-\theta$, where θ was the probability of a recruit being male (estimated as part of the survival modelling), hence the number of first-year males was $N.M0_{y+1} = N.O_{y+1} - N.F0_{y+1}$.

The numbers of adult males and females surviving from last breeding season ($N.M1_{y+1}, N.F1_{y+1}$) were sampled from binomial distributions with probabilities given by

$$\log(\emptyset.ad.F_y) = a.\emptyset + b.F.\emptyset.ad * F.ave_y, \quad (13)$$

and

$$\log(M) = a. \emptyset + b. \text{sex} + b. F. \emptyset. \text{ad} * F. \text{ave}_y. \quad (14)$$

These were added to the numbers of first-year adults to get the numbers of adult males ($N. M_{y+1} = N. M0_{y+1} + N. M1_{y+1}$) and females ($N. F_{y+1} = N. F0_{y+1} + N. F1_{y+1}$) next breeding season.

The expected mean and variance for the next cohort's inbreeding coefficients were then calculated using equations 1 and 2, and all steps repeated.

Results

The reintroduced toutouwai population on Tiritiri Matangi grew from 33 ± 0.3 (SE) to 160 ± 6 individuals from 1992–2017, including recoveries following the harvests (Fig. 1). The population sex ratio was generally close to 50:50 due to the similarity of male and female survival rates and even sex ratio of recruits (Table 1). The average kinship of possible breeding pairs increased to 0.10 by 2012 (Fig. 2), assuming founders were unrelated. The model fitted to the kinship data also gave an expected average inbreeding coefficient (\bar{F}) of 0.10 ± 0.001 in 2017, with 95% prediction intervals for individual inbreeding coefficients ranging from 0.00–0.36. The N_e/N ratio was estimated to be 0.56 ± 0.01 .

Mean reproduction rates were 1.81 ± 0.12 fledglings per year for first-year females and 2.35 ± 0.11 for older females, excluding unpaired females which produced few fledglings (Table 1), and also excluding females in their first breeding seasons translocation who also produced fewer fledglings (Appendix S8). There was no indication that reproduction rates changed with inbreeding (Fig. 3), density, or random temporal variation hence these effects were excluded from the population model (Table 1; Appendix S8).

Annual adult survival probability was 0.77 ± 0.01 for males and 0.74 ± 0.02 for females, excluding post-release periods (Appendix S8). Juvenile survival was initially similar to adult survival (Fig. 3) but declined with density and also showed substantial random annual variation (Table 1), hence these effects were included in the population model. The effects of inbreeding were included

on both rates, as inbreeding significantly reduced juvenile survival (b. F. ϕ . juv = 1.83 ± 0.81) and tentatively reduced adult survival (b. F. ϕ . ad = 0.44 ± 0.35) (Table 1, Fig. 3). We obtained similar, but less precise estimates, if we just used data for birds with known inbreeding coefficients (b. F. ϕ . juv = 1.12 ± 0.87 , b. F. ϕ . ad = 0.30 ± 0.65).

Based on the population model incorporating these parameters (Table 1–2) the population is projected to reach a median of 726 birds (95% prediction interval 331–1144) in 2130, and to then begin slowly declining due to the gradual increase in inbreeding (Fig. 4). In contrast, if there were no inbreeding from 2017 onward (b. F. ϕ . juv and b. F. ϕ . ad set to 0) the population would be expected to stabilize at 1131 birds (95% prediction interval 887–1465) (Fig. 4).

Discussion

The potential importance of inbreeding to reintroduced populations is well recognized (Jamieson & Lacy 2012; Keller et al. 2012; Weeks et al. 2015; Frankham et al. 2019). However, to our knowledge this is the only study of a reintroduced population where future consequences of inbreeding are derived from a realistic population model fitted to vital rate data for that population. Jamieson and Lacy (2012) presented a preliminary analysis of part of our data to illustrate potential population consequences of inbreeding. However, at that stage the estimated number of lethal equivalents was quite imprecise (95% CI for B ranging from -0.36 to 8.65), and was based on a simple analysis where confounding effects of density dependence and other temporal variation were ignored and the unknown portions of pedigrees assumed to be unrelated to the rest of the pedigree (Jamieson et al. 2007). In addition, Jamieson and Lacy's (2012) projections were based on a hypothetical scenario where the population had a long-term carrying capacity of 40 pairs. In contrast, the projections presented here incorporate a realistic model of population dynamics based on 25 years of data and accounting for multiple sources of uncertainty.

Although the absence of data-based projections that incorporate effects on inbreeding in reintroduced populations seems surprising, it probably reflects the challenges involved. Bozzuto et al. (2019) quantified the effects of inbreeding on reintroduced Alpine ibex (*Capra ibex ibex*) populations by fitting state-space models to long-term count data for 26 populations where inbreeding levels were quantified by genotyping. However, such opportunities are rare. To make inferences from a single population, it is essential to have data on inbreeding coefficients and vital rates of individuals. However, pedigrees for wild populations are usually incomplete and collected over few generations, causing biases in pedigree-based inbreeding coefficients (Nietlisbach et al. 2019). Genomic metrics of inbreeding help address these issues but are costly and also subject to error, so are unlikely to render pedigree data obsolete (Andrews et al. 2016). VanRaden (1992) developed a kinship-based method for inferring inbreeding coefficients (F_i) with incomplete pedigrees, whereby the inbreeding coefficients of individuals with unknown parents are assumed equal to the average F_i value for individuals in the same cohort whose parents are known. The calculations can be done iteratively with the software PEDIG (Boichard 2002) or INBUPGF90 (Misztal et al. 2002). However, the values produced are point estimates, meaning the unknown component of F_i is treated as a fixed value with no associated uncertainty. To account for this uncertainty, we instead used a multiple imputation process whereby the unknown component for each individual is sampled in each MCMC iteration from a broad distribution reflecting the variance in inbreeding coefficients likely to be found in that cohort (Fig. 2). This approach allowed uncertainty in F_i values to be reflected in estimation of lethal equivalents and subsequently propagated into population projections along with other sources of parametric uncertainty.

There are several possible extensions to the methods we present. While the approach described above accounts for uncertainty in inbreeding coefficients by sampling the unknown components from distributions, those distributions are assumed to be similar for all members of a cohort. The distributions could potentially be made individual-specific by incorporating a variant of

VanRaden's (1992) method where the unknown inbreeding components assigned to individuals are passed to their descendants. However, it would probably be extremely challenging to incorporate the iterative algorithms used in such calculations into an MCMC framework, and we anticipate this modification would have negligible impact due to the high variance in inbreeding coefficients in relation to the means (Fig. 2). It would also be ideal to do all four steps presented here in an integrated framework. However, this will require more efficient MCMC samplers or faster processors to overcome the computational challenges inherent in modelling large complex data sets in state-space frameworks. We strongly recommend that population projection is integrated with parameter estimation (Steps 3-4), as we found that this integration greatly improved the precision of the projections due to covariances being accounted for.

Population projections could also be modified to incorporate additional theoretical complexities. Purging of deleterious recessives over time (Hedrick & García-Dorado 2016; Grossen et al. 2020) would result in lower impacts of inbreeding than those predicted through our modeling (Fig. 5). Even if it is impossible to quantify purging from the pedigree data (López-Cortegano et al. 2018), the model could potentially be modified to assess sensitivity to hypothetical purging levels. However, we found the calculation of weighted inbreeding levels (García-Dorado 2012) to be incompatible with the MCMC model-fitting approach we employed (Appendix S9) hence technical challenges need to be overcome to allow this extension. It is also possible that the relative effects of inbreeding will decrease with density as a result of soft selection (Saccheri & Hanski 2006). Such interactions will be difficult to detect from field data, and our model failed to converge when we tried adding an inbreeding*density interaction to equation 6. Our projections for Tiritiri Matangi toutouwai are likely to be robust to soft selection given that the population reached maximum density within 5 years due to the small amount of habitat initially available (Fig. 1), and is expected to remain at relatively constant density in the future as the population increases through habitat regeneration (Fig. 4). However, this will not be the case for many reintroduced populations. Given that

the necessary interactions terms are likely to be inestimable, informative priors for these terms could be used to model potential effects of soft selection, hence this additional source of uncertainty could be accounted for in management decisions.

The obvious management action for reducing inbreeding depression in wild populations is gene flow augmentation through translocation, i.e. genetic rescue. Genetic rescue is clearly a valuable management tool (Bell et al. 2019; Frankham et al. 2019; Miller et al. 2019), but its effects are complex and difficult to predict (Hedrick & García-Dorado 2016). Decisions about genetic rescue require considering a suite of potential actions involving different numbers, timings and source populations. In addition, such decisions need to be framed to consider a suite of objectives, including the need to minimize costs, risks of disease transfer, impacts to source populations, and deaths of translocated animals unable to establish in existing populations. It is invaluable to managers to be able to anticipate the future consequences of inbreeding depression when initiating such decision processes. In our population the effects of inbreeding are predicted to be relatively minor, at least for the next 150 years, but there is considerable uncertainty about those effects. Therefore, a key issue will be stakeholders' attitudes to that uncertainty, i.e. whether they wish to consider management actions that will potentially reduce the level of risk.

Predicting how such management can influence demographic outcomes is crucial to improve the decision-making capabilities of managers. Many small populations are at increased risk of extinction because genetic considerations have not been well integrated into conservation management (Ralls et al. 2018). However, while minimizing loss of genetic diversity may be viewed as an objective in its own right, stakeholders may be more concerned about the impacts of genetic diversity loss on future population size and persistence. Our approach not only provides an understanding of how inbreeding levels in a population are expected to change over time, but also enables population projections to be empirically derived both with and without inbreeding depression. It further allows the effects of age, density dependence, and random temporal variation

on demographic rates to be accounted for, as well as estimation error, allowing robust management decisions to be made based on the type of data likely to be available in many conservation programs.

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Table 1. Estimates, standard deviations, and 95% credible intervals for parameters used to project the dynamics of the reintroduced toutouwai population on Tiritiri Matangi Island from 2017–2167. Parameters b.F.ad and b.F.juv indicate numbers of lethal equivalents at adult and juvenile stages respectively. Values for all parameters estimated from the data, including those removed from the model, are shown in Appendix S8.

Parameter	Meaning	mean	sd	2.5 %	median	97.5 %
a.f	reproduction intercept (log of mean fledglings per 1st-year female)	0.63	0.05	0.52	0.63	0.74
b.age.f	effect of being per older female on log reproduction rate	0.29	0.06	0.16	0.29	0.41
b.unp.f	effect of being unpaired female on log reproduction rate	-	-	-	-	-
a.∅	survival intercept (log of annual adult female survival probability)	0.29	0.02	0.33	-0.29	0.24
b.sex.∅	effect of sex (being male) on log adult survival	0.04	0.03	0.01	0.04	0.09
b.F.∅.ad	effect of inbreeding coefficient on log adult survival	0.44	0.35	1.13	-0.43	0.22

b.juv.ø	effect of being juvenile on log survival	0.52	0.37	0.18	0.51	1.29
	additional effect of being fledgling (up to March) on	-		-		-
b.fl	log survival	3.08	0.32	3.73	-3.08	2.46
	effect of population density (females/area) on log	-		-		-
b.D.ø	juvenile survival	0.51	0.18	0.88	-0.50	0.17
b.F.ø.ju	effect of inbreeding coefficient on log juvenile	-		-		-
v	survival	1.83	0.81	3.45	-1.83	0.27
	random annual variation (standard deviation) in log					
s.y.ø.juv	juvenile survival	0.31	0.10	0.15	0.30	0.53
θ	probability of recruit being male	0.48	0.02	0.44	0.48	0.53
	ratio of effective population size to census population					
N_e/N	size	0.56	0.01	0.54	0.56	0.58
	constant used for modeling variance in inbreeding	0.11	0.00	0.10		0.11
c	coefficients	1	2	7	0.111	6

Table 2. Estimates, standard deviations, and 95% credible intervals for variables characterizing the reintroduced toutouwai population on Tiritiri Matangi Island in September 2017.

Variable	Meaning	mean	sd	2.5%	median	97.5%
$N.M_y$	number of males	81.3	2.9	77	81	88
$N.F0_y$	number of first-year females	47.6	4.3	41	47	58
$N.F1_y$	number of older females	31.5	1.2	30	31	34
\bar{F}_y	average inbreeding coefficient	0.0961	0.0014	0.0934	0.0960	0.0988
$V(F_y)$	variance in inbreeding coefficients	0.0097	0.0001	0.0094	0.0097	0.0099

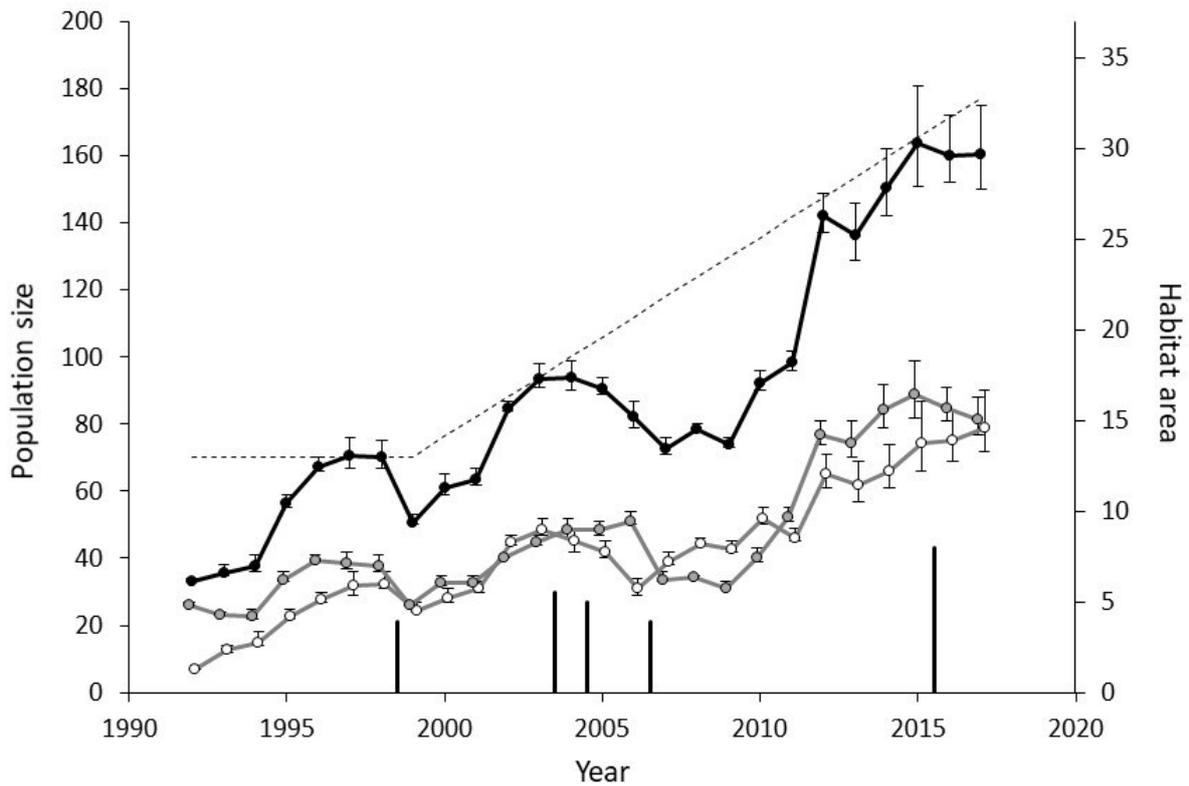


Fig. 1. Growth of the toutouwai population reintroduced to Tiritiri Matangi Island in 1992. Dots show estimated numbers of males (gray), females (white) and both sexes combined (black) at the start of each breeding season, with error bars around points showing 95% credible intervals. The dotted line shows the increase in habitat area through regeneration of planted forest. The vertical bars at the bottom of the graph show the numbers of individuals harvested for translocations to other sites.

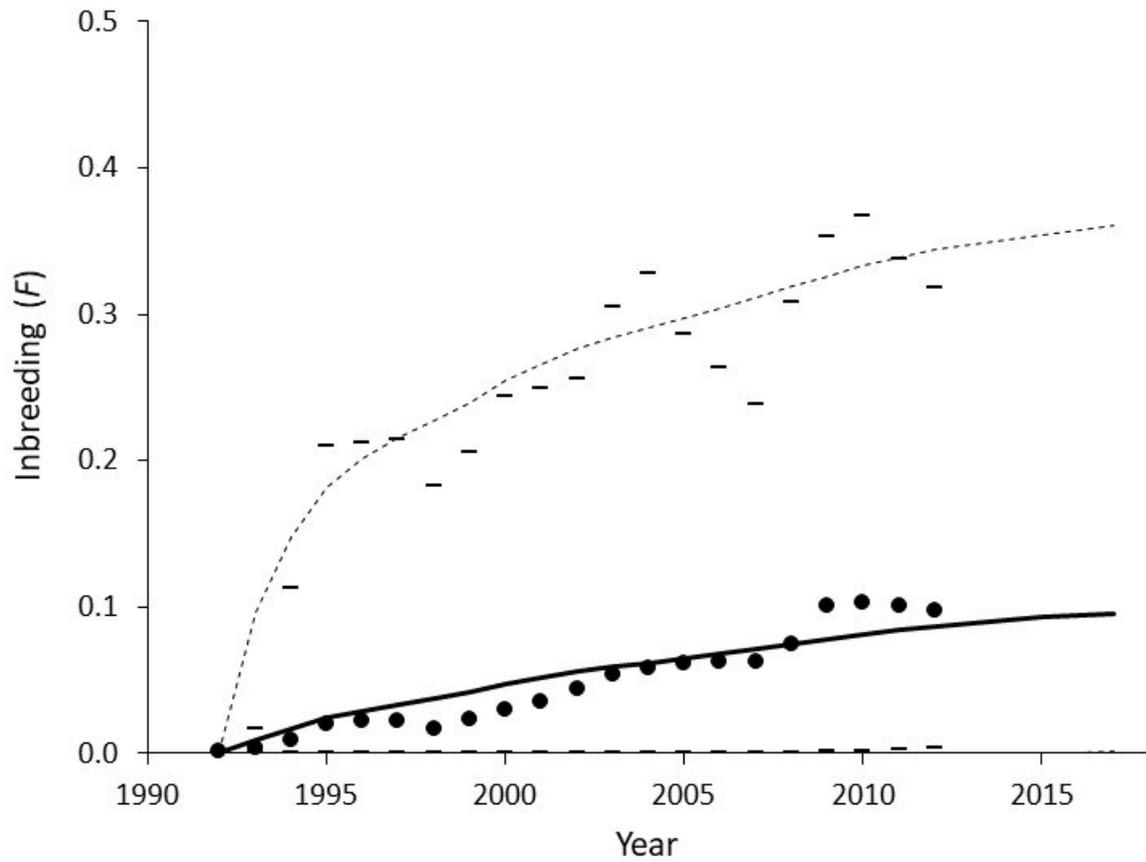


Fig. 2. Increased inbreeding over time in the toutouwai population reintroduced to Tiritiri Matangi Island in 1992, assuming the founding birds were unrelated. Dots show the average level of kinship among the possible male-female pairings in the first 21 breeding seasons, and dashes show 95% percentiles for those kinships based on beta distributions. The solid line shows the average inbreeding coefficient (\bar{F}) expected based on a model fitted to the raw kinship data (equations 1–2), with dotted lines showing 95% prediction intervals for inbreeding coefficients of individual birds.

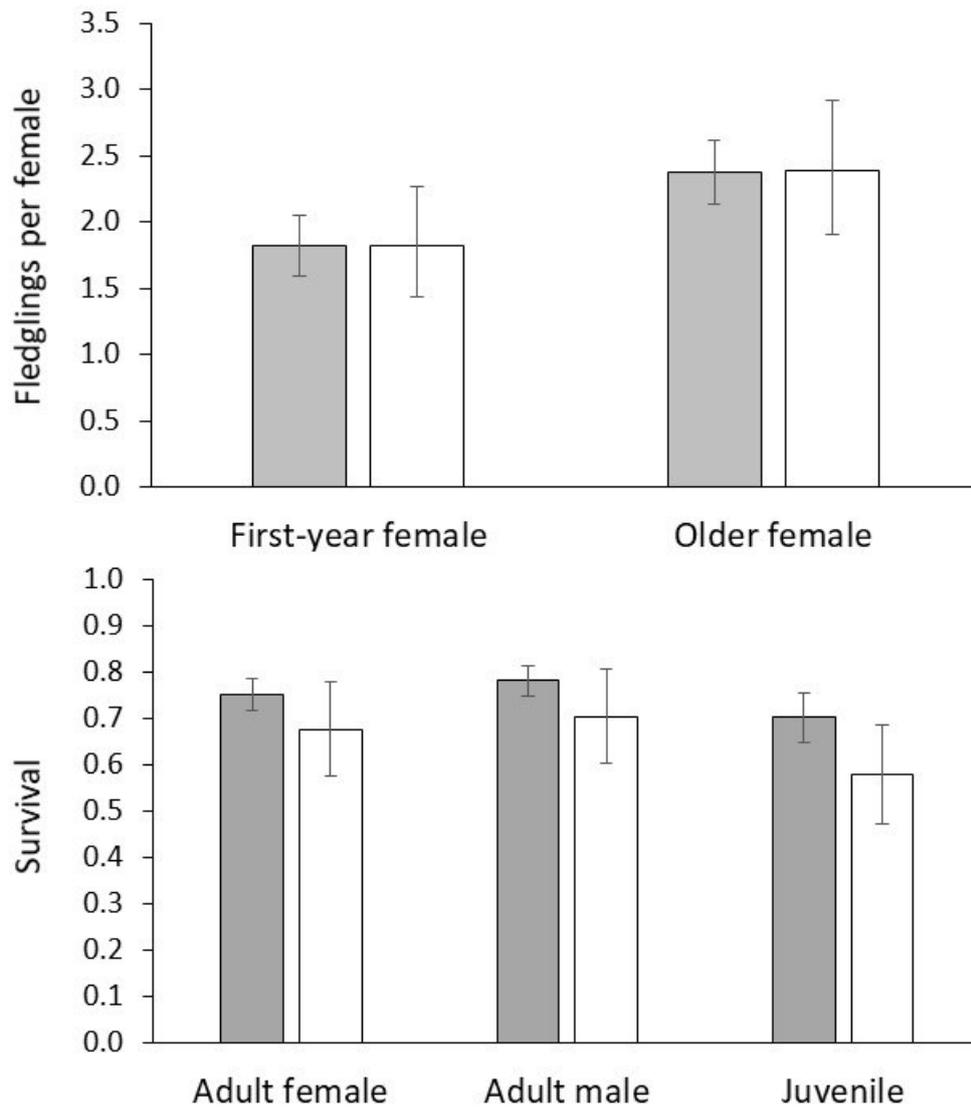


Fig. 3. Estimated effects of inbreeding on reproduction and survival rates of toutouwai reintroduced to Tiritiri Matangi Island. Grey bars show estimated rates for outbred birds ($F=0$), white bars show estimated rates for highly-inbred birds ($F=0.25$), and error bars show 95% credible intervals. Values for juveniles are rates expected near zero population density. All rates shown exclude post-release effects and unpaired females.

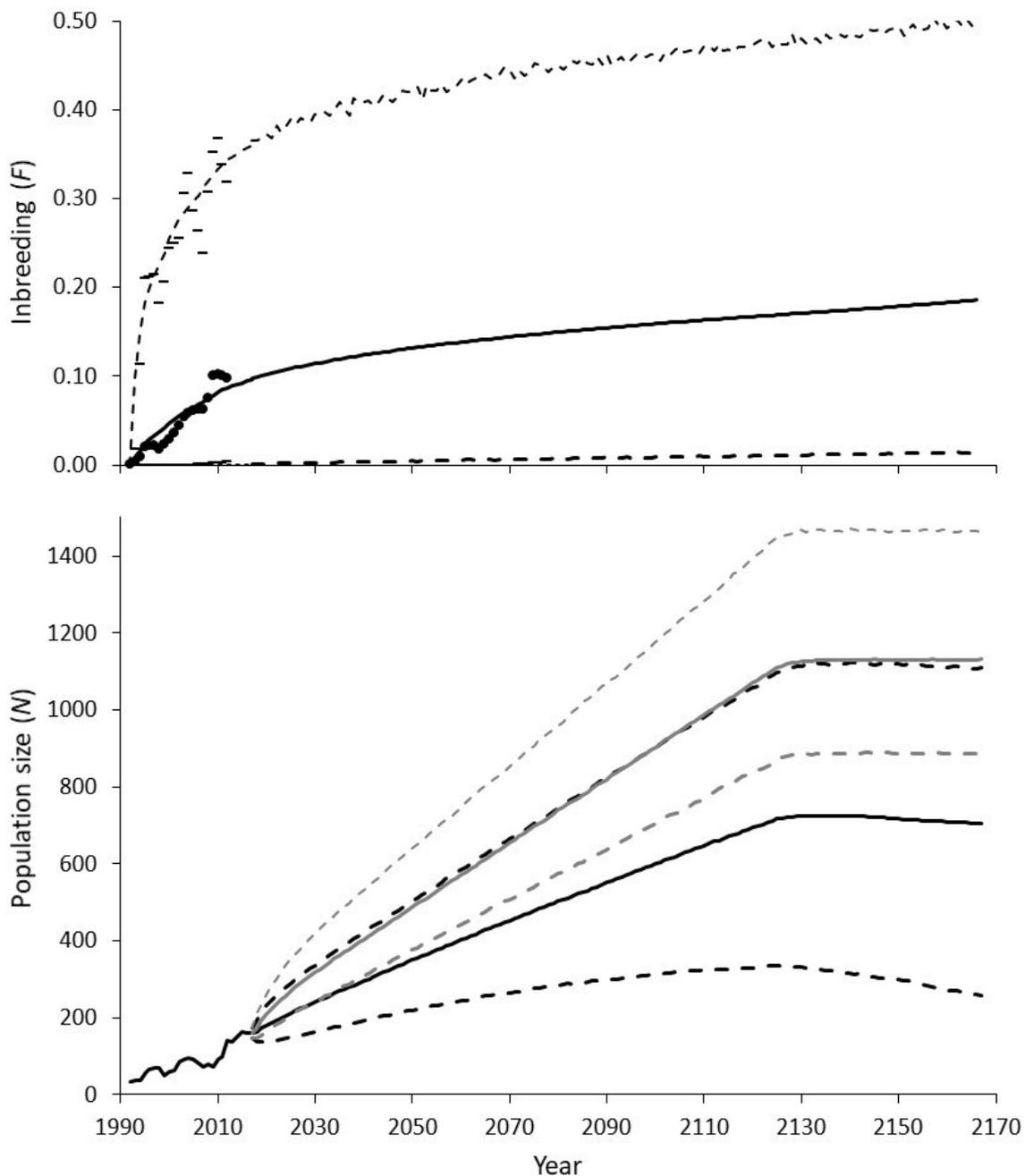


Fig. 4. Projected consequences of inbreeding on future growth of the reintroduced toutouwai population on Tiritiri Matangi Island. The solid line in the top panel shows the projected increase in the average inbreeding coefficient (\bar{F}), with dotted lines showing 95% prediction intervals for inbreeding coefficients of individual birds. The solid lines in the lower panel show the median projected increase in the toutouwai population (black) in comparison to a hypothetical scenario where there is no inbreeding depression from 2017 onwards (gray), with dotted lines showing 95% prediction intervals. The projections simultaneously model increasing habitat area and density dependence in juvenile survival. There is assumed to be a linear increase in habitat area until it reaches 150 ha, and this accounts for the linear median increases in the toutouwai population under both scenarios.

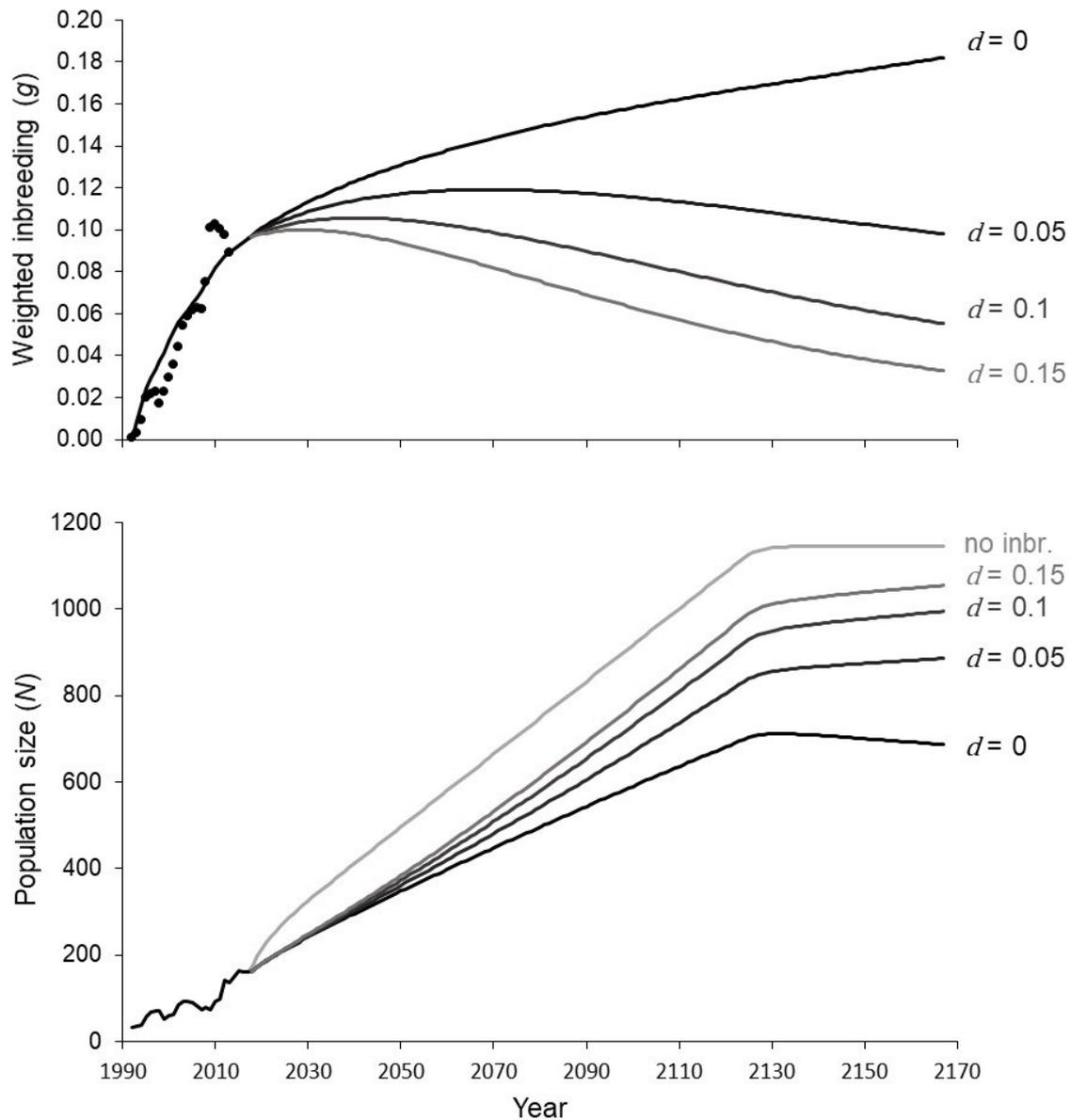


Fig. 5. Potential effects of purging on the long-term impact on inbreeding for the Tiritiri Matangi toutouwai population based on a deterministic model (Appendix S9). The lines labelled $d=0.05$, $d=0.10$ and $d=0.15$ show expected trends under hypothetical purging levels (d is the magnitude of the deleterious effect exposed by inbreeding) in relation to the scenarios modelled in this study where there was either no purging ($d=0$) or no inbreeding depression.