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RESEARCH

Determinants of hatching and recruitment success for captively reared kakī (*Himantopus novaezelandiae*)

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Abstract: Captive-rearing of wildlife for release has been used with variable success in the conservation management of a range of species. These programmes protect individuals through a vulnerable life stage with the aim of releasing them to re-enforce wild populations once threats are minimised. To maximise the effectiveness of captive-rearing, species' managers must understand how management decisions and procedures affect individual outcomes during both the rearing phase and post-release. We used management records for 1177 kakī (*Himantopus novaezelandiae*; black stilt) eggs and 846 released individuals collected from 2013 to 2020 to investigate: (1) effects of parentage, clutch characteristics, and embryo age on hatchability; and (2) impacts of release variables, captive-rearing conditions, supplementary feeding, and individual health on post-release survival. Multivariate generalised additive models were created to explore these relationships. Top models showed that, in general, highest hatchability was associated with eggs that were heavier, from intermediate-sized clutches, with longer parental incubation, and that were laid by dams 12 to 18 years of age. We show that intensive egg pulling from nests does not have a negative impact on the hatchability of subsequent clutches (up to three). While it is important to maximise hatchability outcomes where possible, hatchability rates for the period are high and comparatively larger gains for the species can be made addressing low survival of released individuals. Trends in survivability show that individuals released as sub-adults, that used supplementary food more often, and that were less inbred, had the best survival outcomes. Having had (but recovered from) encephalitis and/or pododermatitis in captivity reduced an individual's probability to survive once released. These trends can be used to inform best practice species management and provide rationale for further study of kakī hatchability and survivability.

Keywords: captive-rearing, conservation research, hatchability, *Himantopus*, kaki, management, recruitment, species recovery, survivability

Introduction

The goal of conservation management for endangered species is commonly to restore wild populations to a self-sustainable threshold. This often requires reintroducing species to parts of their indigenous distribution where they have been extirpated. To be successful, release areas should be free from the threats that caused initial species' decline (IUCN/SSC 2013). However, while threat reduction *in situ* is ideal, the available resources, social license, technology, and timeframes are often insufficient to accomplish such reduction. In cases where threat reduction is insufficient, or to augment the rate of species recovery, captive-rearing for release can be used (Powell & Cuthbert 1993; Kleiman et al. 2010). Captive-rearing programs can circumvent periods of high mortality in a species' life history by temporarily removing individuals from their natural environments and associated threats, such as predation (Powell et al. 1997; Kuehler et al. 2000; Maloney & Murray 2000; Brightsmith et al. 2005; Jarvie et al. 2015), loss of habitat or prey (Biggins et al. 1998; Kreger et al. 2005), or disease (Rogers et al. 2016).

Impacts from human activities have led to a large number of captive-rearing programmes globally (Seddon et al. 2007). Such programmes are expensive when compared with other *in situ* management and require dedicated staff and facilities, so are often implemented only as a last resort (Snyder et al. 1996; Drechsler et al. 2011). Even when resources are sufficient, programmes can fail due to lack of specific husbandry knowledge and/or poor reintroduction outcomes (Beck et al. 1994; Snyder et al. 1996). Despite these limitations, successful captive rearing programmes provide high value to populations of endangered species, many of which would not persist otherwise (Ellis et al. 1992; Powell et al. 1997; Crone et al. 2007).

Kakī (*Himantopus novaezelandiae*; black stilt) are a critically endangered wading bird species found in braided river and wetland ecosystems in New Zealand (NZ; Robertson et al. 2017). Once widespread, the population has undergone large

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declines due to invasive predators (Pierce 1986; Pierce 1996), habitat loss/modification (Pierce 1996), and human disturbance (Reed et al. 1993). The wild population troughed at 23 adults, which triggered the implementation of active population management in 1981 (van Heezik et al. 2005). Management has since focused on pest control, deterrence of hybridisation with pied stilt/poaka (*Himantopus leucocephalus*), and the implementation of a captive-rearing programme (Maloney & Murray 2002).

Purpose-built captive-rearing facilities for kakī were established in 1986. Located in Twizel, Canterbury, the kakī breeding unit consists of incubation facilities, brooder rooms with attached outdoor aviaries, and three large open flight aviaries, and is staffed year-round by NZ Department of Conservation (DOC) staff. The captive-rearing programme collects eggs from both wild and captive breeding pairs to alleviate nest losses due to predation by introduced mammals (van Heezik et al. 2005) which persist in the release area despite long-term intensive trapping. Egg removal also stimulates multi-clutching; the most productive pairs can produce up to four clutches a season (van Heezik et al. 2005). This intensive management style maximises the productivity of active breeders and the number of individuals raised and released by the programme. Following incubation, hatched chicks are reared until they reach the less vulnerable sub-adult stage and are released into the wild at approximately 250 days old. Though the vast majority of birds are released at the sub-adult stage, both juvenile (< 200 days old) and adult (> 2 years old) birds are also released when they are unable to be housed in rearing facilities (i.e. when facilities reach capacity) or when they become surplus to captive breeding requirements (e.g. pairing fails, captive breeding aviaries are full). Kakī are considered sexually mature before the end of their second year and can be reproductively active into their early twenties. Throughout incubation, rearing, and also post release, records of management conditions, health parameters, and survival are kept for each individual. The captive-rearing programme has successfully reduced the immediate extinction threat for kakī through the annual releases of sub-adult birds (Cruz et al. 2013). Most recently, 154 individuals were released to the wild in 2021. However, despite the high number of annually released individuals, the current wild population of kakī is estimated at only c. 140 adults (Department of Conservation 2021). The disparity between the high input of individuals and a low resulting adult population highlights the low survival of released individuals. This, coupled with current low rates of adult survival, results in a population that would be unlikely to persist if captive-rearing inputs were removed (Pierce 1996; Cruz et al. 2013).

To accelerate species recovery, captive rearing aims to produce the highest number of individuals possible while ensuring that released individuals have the greatest chance to recruit into the wild population. To achieve this, it is important to understand which factors drive the hatchability of collected eggs and the survival of released kakī. Therefore, using captive management records from 2013 to 2020, we built multivariate generalised additive models to investigate: (1) the effect of parentage, clutch characteristics, and embryo age on hatchability of eggs collected from the wild, and (2) the impact of release variables, captive-rearing conditions, supplementary feeding and, health on success of the individuals once released into the wild. This information can be used to inform best practice species management and provide rationale for further study of kakī hatchability and survivability.

Methods

Data collection & analysis

Information on kakī parentage, captive management, and release conditions has been collected by the Department of Conservation since the captive rearing facilities were established. Data from 2013 to 2020 were considered most appropriate for the proposed multivariate analyses due to high levels of completeness. All analyses were done in open access R studio (version 1.4.1106), using statistical software R (version 4.1.1; R Core Team 2022).

Generalised Additive Models

We used generalised additive models (GAMs) to investigate the relationships between management variables and the hatchability of kakī eggs and the survival of released individuals. GAMs were produced using a logit link function using the mgcv R package (Wood 2004) with binomial hatched/did not hatch, and survived/did not survive, response variables for separate models. Thin plate regression splines were used to smooth continuous predictor variables. GAMs were chosen as they are able to describe non-linear relationships between predictors and response variables, common in ecological data.

Response variables

The response variable for hatching models was whether or not fertile kakī eggs hatched. Individuals that died during the hatching process, were recorded as unhatched. Those that hatched but died or were euthanised soon after, were recorded as hatched. Fertility was assessed using candling, which occurred upon the eggs' arrival at the captive rearing facility and at two to four day intervals subsequently. Eggs that showed any sign of embryonic development were classified as fertile. To assess hatchability, eggs with no evidence of embryonic development including infertile, addled, and eggs of unknown fertility were excluded from analysis. This study does not attempt to differentiate between infertile eggs and those that died early in the incubation period.

The response variable for survival models was whether released kakī survived one year in the wild. This measure relies on the resighting of an individual's band combination in the wild, and therefore likely underestimates the survival of non-breeding individuals. This measure of survival was chosen as individuals that survive one year in the wild will be sexually mature (if released as sub-adults). Additionally, one year following release coincides with the highest annual resighting effort focused around the breeding season and egg collection.

Predictor variables

Predictor variables in the hatchability models included the following: dam age (Croxall et al. 2008), sire age (Preston et al. 2015), the clutch number that the egg belonged to (Nager et al. 2000), the number of eggs in the clutch (Reid et al. 2000), approximate embryo age and egg weight at time of collection (Smith et al. 2011), date collected, whether the egg was damaged, inbreeding coefficient (Bensch et al. 1994; Heber & Briskie 2010), and the field location from which the egg was collected. Clutch size, date collected, and location were recorded by the attending DOC ranger at the time of egg collection. Date collected was converted to the Julian date format, with the zero set to the first of July. This allowed comparisons to be made between early and late season clutches.

Location of nest was recorded as a categorical variable to assess the impact of location specific factors affecting birds/nests in distinct areas. Egg damage was assessed as a binomial categorical variable (damaged, not damaged), not including any measure of the magnitude of damage. Egg weights were measured upon the egg's arrival at the captive-rearing facility. Embryo age at collection was estimated using a combination of candling and backdating from hatch dates. Backdating was based on a 25-day incubation period, standard for kakī (Reed et al. 1993). Where eggs did not hatch, the known age of hatched clutch mates was used in combination with candling. Parent age, clutch number, and kinship were generated when the parents of an egg were known, and pedigree data was sufficient. Inbreeding coefficients were generated in PMx (Lacy et al. 2012), using a measure of mean kinship between parents.

For the survival model, predictors included: age at release, release location (Efrat et al. 2020), weight at release, year released, captive behaviour (Biro & Stamps 2008), the frequency that an individual used supplementary food in the period after release, management type (parent or hand reared; Ellis et al. 2000; Efrat et al. 2020), the presence/absence of ulcerative pododermatitis (Bumblefoot; Reissig et al. 2011), congenital deformities (e.g. splayed legs, twisted spine, clubbed feet), injury, illness and, specifically, encephalitis while in captivity. Release variables were collected on the day of release by captive-rearing staff, including an assessment of a bird's general health. Individuals that failed to recover from any captive conditions or were deemed unfit for release were held back until recovered or were euthanised. Release location was analysed as a categorical variable, assessing any difference between the Tasman and Mt Gerald release sites. Behavioural and medical conditions were recorded throughout individual's internment at the captive-rearing facility. Behaviour of individual birds was categorised into either, aggressive, submissive, or no notable behaviours. The injury predictor specifically assesses the presence/absence of traumatic injury (e.g. severe bill damage, broken leg). The illness predictor assesses the presence/absence of significance illness apart from encephalitis and pododermatitis (e.g. pneumonia, air sacculitis). Supplementary feeding was provided for c. 40 days post release at a single location near the release site. Supplementary food was available in excess for the first 10 days, followed by a 30-day weaning period (Cottam et al. 2001). Bird's use of supplementary food was recorded daily by an attending DOC ranger and summed for the period. Individuals identified by band combination were recorded to have used supplementary food when seen eating from a food plate.

Model selection

Categorical predictors were checked for dependencies using variable inflation factor (VIF), and nested categorical predictors were avoided to reduce dependent variable relationships. Continuous predictor variables were checked for concurvity, a function that described non-linear dependencies between predictor variables (Amodio et al. 2014). Variables with estimated pairwise concurvity greater than 0.3 (He et al. 2006) were ranked using univariate deviance explained and the worst performing variable was removed from the model. Full models were created using all independent predictor variables with no interaction terms. Once created, backward stepwise model selection was used to remove predictor variables. The Akaike's Information Criterion (AIC; Akaike 1998) value derived using the MuMin package (Barton 2018) was used to rank models. Variables with the highest p-value were removed and models retested until the model with the lowest AIC was reached. Models with ΔAIC < 2 were also considered plausible and have been presented to explore relationships not captured in the top model. Akaike weights were calculated to assess the relative importance of each model (Wagenmakers & Farrell 2004).

Model validation

Model validation was performed using the *gam.check* function from the mgcv package. This function returns both k-index values and p-values for each predictor. K-index represents an estimate of residual variance; the further below one, the more likely there is a pattern in the residuals. The p-value is computed by simulation, where residuals are reshuffled randomly to obtain the null distribution of the differing variance estimator. Often low p-values suggest that the basis dimension, k, has been set too low or that the data are under-fitted. In this case, values for the hatchability model were low for four of five variables and did not improve upon altering basis dimension, additionally clear patterns in the residual plots were noted. The output from gam.check is heuristic and this result likely indicates problems with data such as low deviance explained, lack of explanatory covariates, and unmodelled spatial or temporal structure of the data (Wood 2017). Care should therefore be taken when interpreting the results of these analysis. In contrast, k-index values for survivability models were c. 1 and p-values high for all variables, indicating better model fit for these data.

To evaluate the predictive performance of the final hatchability and survivability models, we calculated AUC, the Area Under the Receiver Operating Curve (ROC) for each, using the pROC package in R (Robin et al. 2011). AUC provides a measure of the predictive capability of a model, with values ranging from 0.5 (no predictive power) to 1 (perfect predictive power).

Results

Hatchability model

During the period from 2013 to 2019, a total of 1177 kakī eggs with known parentage were assessed by the Department of Conservation for hatching failure or success. Of this cohort, 223 eggs did not hatch (19.2%), with a further 92 eggs classed as either infertile or of unknown fertility. To assess hatchability, eggs that were infertile, of unknown fertility, or which had incomplete data were removed from the analysis. The remaining study cohort had 999 eggs, with overall hatchability of 88.6%.

The top-ranked model for hatching success included the predictor variables of embryo age at egg collection, clutch size, dam age, sire age, egg weight, collection location, and the year the egg was laid (Table 1). The only other model with ΔAIC < 2 also included clutch number. Approximate embryo age at egg collection ($p < 0.01$), clutch size ($p = 0.01$), dam age ($p < 0.01$), and egg weight ($p < 0.01$) were all significant predictors of hatchability. Deviance explained for the top model was 21.8% with an AUC value of 0.83 (95% CI: 0.78–0.87).

Top-ranked models indicated that eggs were more likely to hatch from pairs which had already laid several clutches that season, and from clutches that were four to three eggs in size (Fig. 1). Eggs laid by dams c. 13 to 18 years of age had the highest probability of hatching, whereas older dams and sires had poorer hatching outcomes (Fig. 1). Eggs that were heavier and had older embryos at the time of collection

Table 1. Rank and statistics of logistic regression models explaining the hatch fate of kakī (*Himantopus novaezelandiae*) eggs laid from 2013–2019. Models are ranked by Akaike Information Criterion (AIC). Models presented include those with ΔAIC < 2. Predictor variables included the number of eggs in the clutch (Clutch.size), age of the dam (Dam.age), age of the sire (Sire.age), weight of egg upon collection (Egg.weight), the approximate age of the embryo at collection (Embryo.age), where the egg was found (Location.found), the year the egg was laid (Egg.yr), and the pair's seasonal clutch number (Clutch.no). Displayed are the degrees of freedom (df), AIC value, difference in AIC compared to the top model (ΔAIC), Akaike weights, percentage deviance explained (de), and adjusted R^2 (R^2 adj.).

Rank	Model predictors	df	AIC	ΔAIC	Akaike weight	de (%)	R^2 adj.
1	Clutch.size + Dam.age + Sire.age Egg.weight + Embryo.age + Location.found + Egg.yr	25	605.4	0	0.30	21.8	0.182
2	Clutch.size + Dam.age + Sire.age Egg.weight + Embryo.age + Location.found + Egg.yr + Clutch.number	26	605.6	0.2	0.26	22.1	0.182

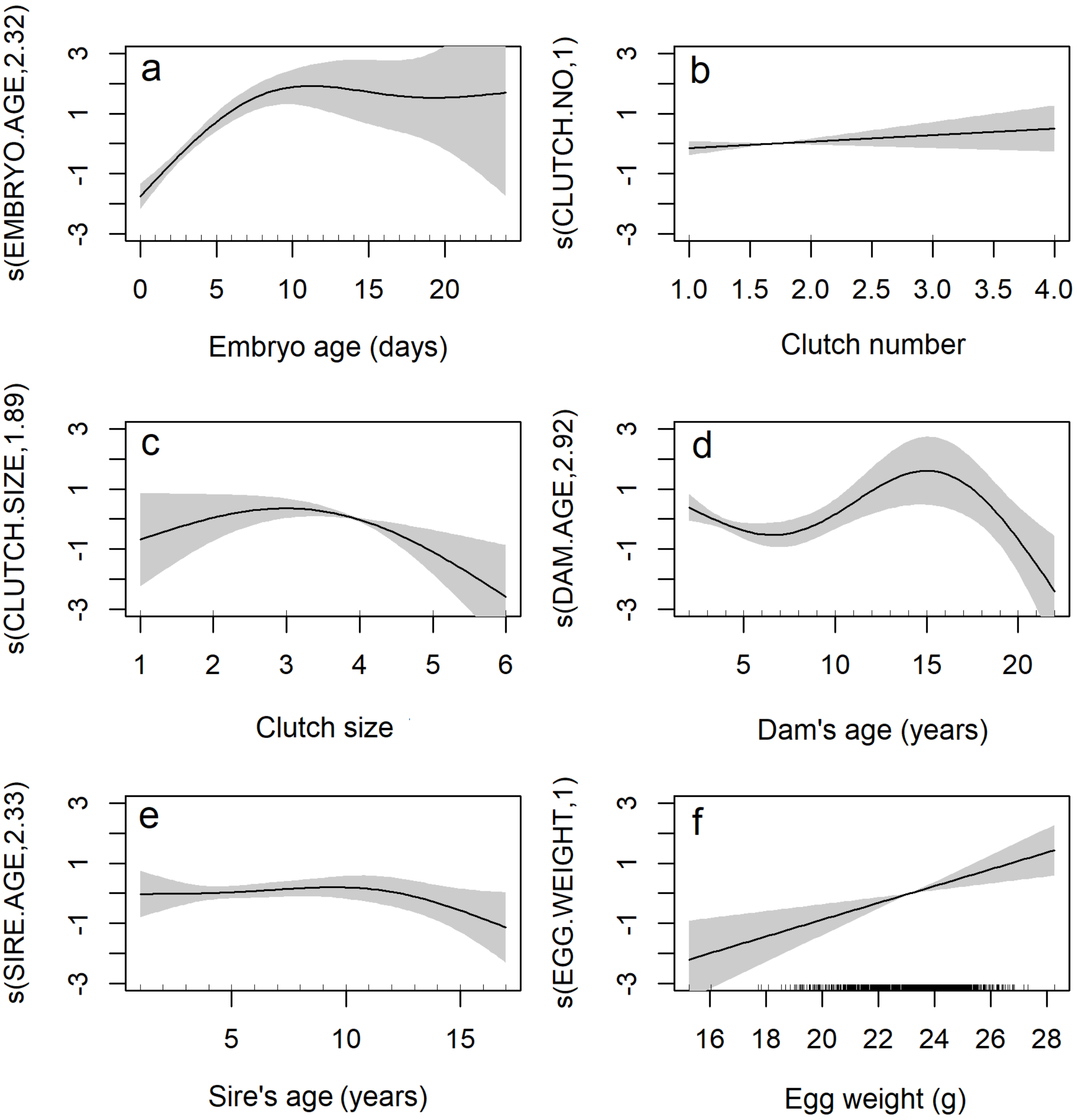

Figure 1. Effect of continuous explanatory variables for logistic regression models with ΔAIC < 2 (Akaike's Information Criterion) for the hatch fate of kakī (*Himantopus novaezelandiae*) eggs laid from 2013-2019. The 95% confidence interval of the response is represented by the shaded area. The y-axes display the smoothed and centred function of each variable representing the partial effect of the predictor variable on the hatch fate of kakī eggs. Predictor variables include: (a) the estimated age of the embryo upon collection (days), (b) pair's seasonal clutch number, (c) the number of eggs in the clutch, (d) age of dam (years), (e) age of sire (years), and (f) the egg weight upon collection. Each data point is represented by a rug plot along the x-axis.

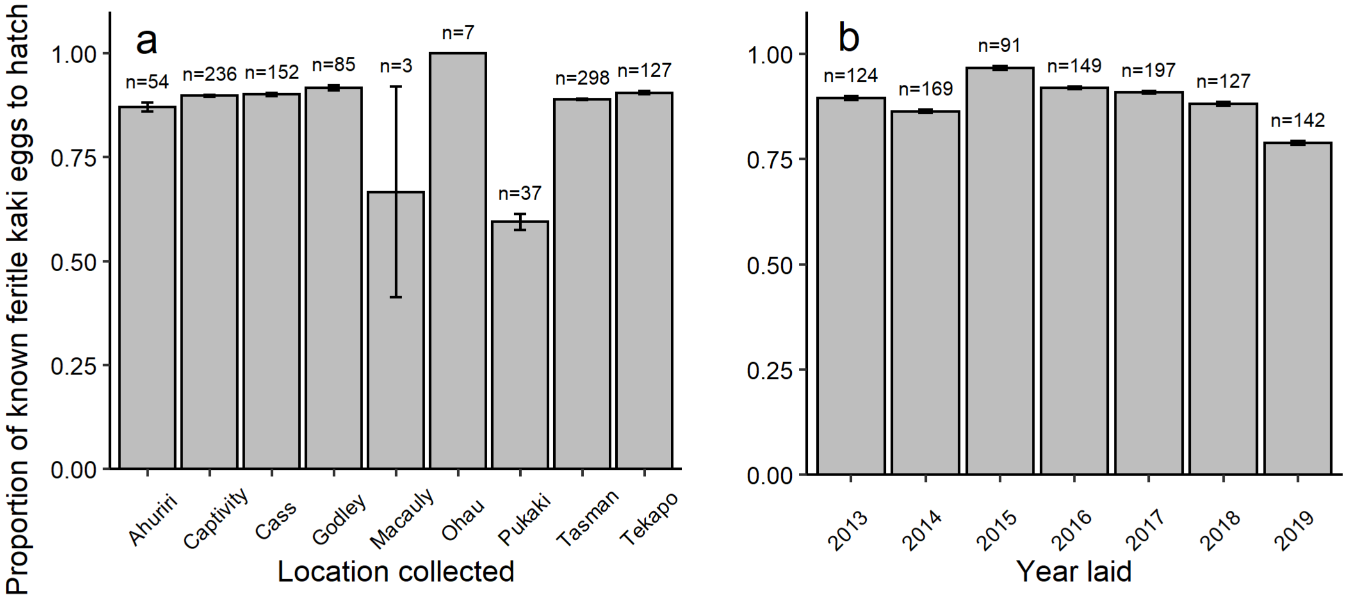

Figure 2. Effect of categorical explanatory variables for logistic regression models with ΔAIC < 2 (Akiake's Information Criterion) for the hatch fate of kakī (*Himantopus novaezelandiae*) eggs laid from 2013–2019. Predictor variables include: (a) the location eggs were collected from and (b) the year eggs were laid. Sample sizes (*n*) for each category are provided above the associated bar.

Table 2. Rank and statistics of logistic regression models explaining the survival of kakī (*Himantopus novaezelandiae*) individuals released from 2017–2020. Models are ranked by Akaike Information Criterion (AIC). Models presented include those with ΔAIC < 2. Predictor variables included the individuals age at release (Release.age), what year the individual was released (Release.year), how often an individual used supplementary food (Sup.feeding), individuals' inbreeding coefficient (F.value), where the individual was released (Release.location), and whether the bird was injured (Injury), had pododermatitis (Bumblefoot), or had encephalitis while in captivity (Symptoms). Displayed are the degrees of freedom (df), AIC value, difference in AIC compared to the top model (ΔAIC), Akaike weights, percentage deviance explained (de), and adjusted R^2 (R^2 adj.).

Rank	Model predictors	df	AIC	ΔAIC	Akaike weight	de (%)	R^2 adj.
1	Release.age + Release.year Sup.feeding + F.value	9	489.13	0.0	0.21	13.2	0.130
2	Release.age + Release.year Sup.feeding + F.value + Symptoms	10	489.17	0.04	0.21	13.5	0.132
3	Release.age + Release.year Sup.feeding + F.value + Symptoms + Release.location	11	489.33	0.20	0.20	13.9	0.131
4	Release.age + Release.year Sup.feeding + F.value + Symptoms + Release.location + Injury	12	489.60	0.47	0.17	14.2	0.132
5	Release.age + Release.year Sup.feeding + F.value + Symptoms + Release.location + Injury + Bumblefoot	13	490.41	1.27	0.12	14.5	0.133

were more likely to hatch than eggs that were lighter and had younger embryos (Fig. 1). Hatchability of eggs varied with year and location found, though some locations had low samples sizes (Fig. 2).

Survival model

During the period 2014 to 2020, a total of 846 kakī were released to the wild by the Department of Conservation. Of that cohort, 262 individuals were known to have subsequently survived a year in the wild. Of the 846 birds released, 404 had missing or incomplete data for at least one predictor variable and were removed from analysis. Of the remaining 442 individual kakī, 133 were confirmed to have survived a year in the wild (30.0%). This proportion was similar to survival rates of the full cohort (31.0%).

The top-ranked model for kakī survival included the predictor variables of release age, year of release, inbreeding coefficient, how often an individual used supplementary food, and whether the individual was injured while in captivity (Table 2). Models with ΔAIC < 2 also included whether the individual had pododermatitis and/or encephalitis and the location where the individual was released (Table 2). Release age ($p = 0.01$), use of supplementary feeding ($p = 0.01$), and inbreeding coefficient ($p = 0.02$) were all significant predictors of survival. Deviance explained for the top model was 13.2% with an AUC of 0.74 (95% CI: 0.69–0.78).

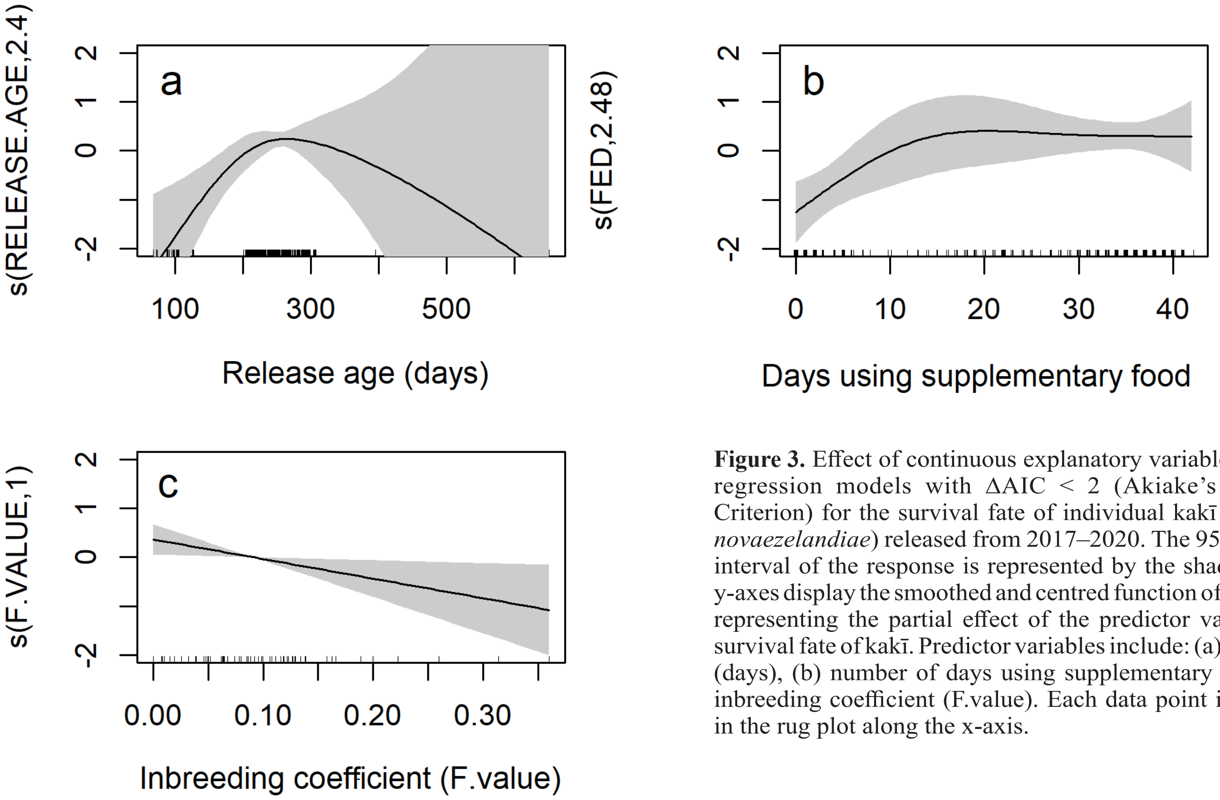

Figure 3. Effect of continuous explanatory variables for logistic regression models with ΔAIC < 2 (Akiake's Information Criterion) for the survival fate of individual kakī (*Himantopus novaezelandiae*) released from 2017–2020. The 95% confidence interval of the response is represented by the shaded area. The y-axes display the smoothed and centred function of each variable representing the partial effect of the predictor variable on the survival fate of kakī. Predictor variables include: (a) age at release (days), (b) number of days using supplementary food, and (c) inbreeding coefficient (F.value). Each data point is represented in the rug plot along the x-axis.

Top-ranked models indicated that birds that were released at the Mt. Gerald release site, used supplementary food more, and had lower inbreeding coefficients were more likely to survive in the wild (Fig. 3). Kakī that were released as sub-adults had the greatest chance of surviving, compared with juvenile and adult releases, although confidence intervals were extremely wide owing to the small number of adult releases (Fig. 3). Kakī that had pododermatitis or encephalitis had lower chance of surviving than counterparts. The survival of released kakī varied by the year they were released (Fig. 4).

Discussion

In this investigation we aimed to better understand factors that drive both the hatchability and survivability of kakī eggs and individuals. Such information can be used to maximise outputs from captive rearing and to accelerate species recovery. Top models showed that in general, eggs that were heavier and had older embryos at the time of collection, that belonged to intermediate sized clutches and that were laid by dams 12 to 18 years of age had the highest hatchability. We show that intensive egg pulling from wild nests does not have a negative impact on the hatchability of subsequent clutches (up to three). Trends in survivability show that individuals released as sub-adults, that used supplementary food more often, and that were less inbred had the best survival outcomes. Having encephalitis and/or pododermatitis in captivity reduced an individual's probability to survive once released into the wild.

Hatchability models

Among the predictor variables included in the top hatchability models, approximate embryo age at collection, clutch number, and clutch size all have direct implications for management decisions. Hatchability of eggs increased in a linear fashion with age at egg collection, until eight days after laying. This trend is consistent with husbandry guidelines suggesting that hatchability is increased in eggs that experience natural incubation for the first third of the incubation period (Burnham 1983; Ellis et al. 2000). Although ideal in terms of hatchability, delaying the collection of wild kakī eggs exposes them to increased predation risks. Management changes regarding the timing of egg collection should be delayed until density of avian and mammalian predators can be reduced sufficiently around kakī nesting areas.

For kakī, eggs in clutches of three to four had the greatest hatchability. Clutches with greater than four and less than two eggs are abnormal for waders; such clutches were rare in these data (5.0%; MacLean 1972; Wallander & Andersson 2002). Atypical clutch sizes can result from egg dumping (Overbeek et al. 2017), predation events, or other nest disturbance (e.g. weather, anthropogenic; Keedwell et al. 2002). Such factors can cause nest abandonment or disruption of incubation. Collection of eggs from nests with clutches comprising three to four eggs should be prioritised to maximise efficiency of captive rearing efforts. Additionally, any reduction in the density of invasive pest species, native predators (e.g. black backed gulls, swamp harriers), or egg dumping might decrease the frequency of abnormal nests.

Management of productive kakī pairs is intensive, with active egg pulling from wild nests stimulating multi-clutching. Here we show that multi-clutching has no negative impact on the hatchability of kakī eggs. This finding is consistent with data from other species which show that replacement eggs and clutches generally have similar hatchability to that of first clutches, although examples of triple and quadruple clutching in

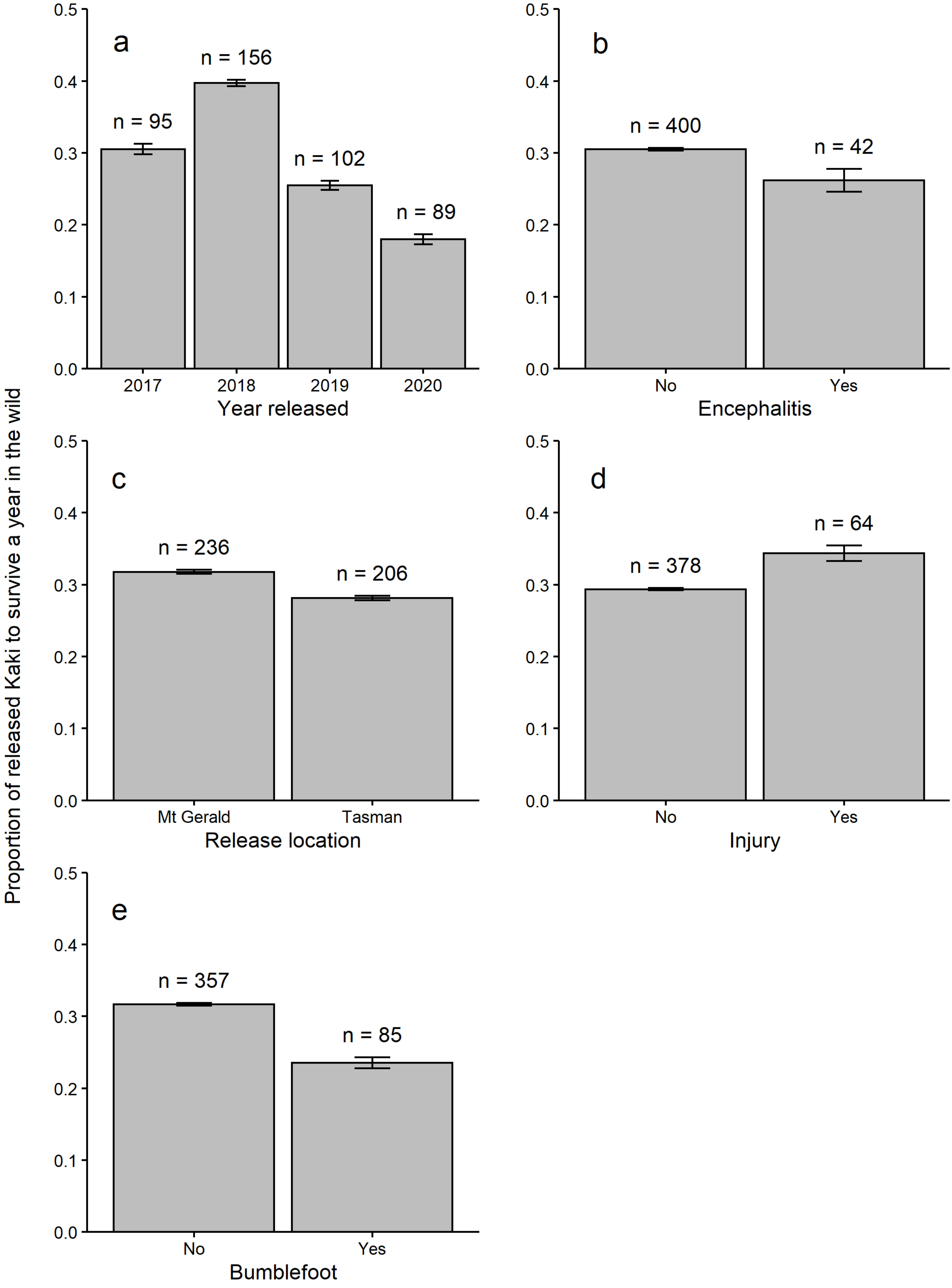

Figure 4. Effect of categorical explanatory variables for logistic regression models with ΔAIC < 2 (Akiake's Information Criterion) for the survival fate of individual kakī (*Himantopus novaezelandiae*) released from 2017–2020. Predictor variables include: (a) the year of release, (b) whether an individual had encephalitis in captivity, (c) the location of release, (d) whether the individual sustained any injuries in captivity, and (e) whether an individual had pododermatitis in captivity. Sample sizes (*n*) for each category are provided above the associated bar.

other species are rare (Bird & Laguë 1982; Harvey et al. 2004).

It is usual for DOC to collect all wild kakī eggs able to be located; however, when captive-rearing facilities approach capacity, decisions on which eggs to prioritise are required. We present trends that will assist species managers in making such decisions. Eggs laid by dams that were 12 to 18 years old had the greatest hatchability, whereas eggs parented by dams and sires towards the upper extreme of age (22 and 17 years old, respectively) had a marked decrease in hatchability. Due to the small number of adult kakī that reach old ages, it is difficult to determine whether declines in hatchability are due to natural senescence or an artefact due to individual variation in a small sample size. Species managers can target pairs of ideal ages for multi-clutching and allow unsuitable pairings to keep their original clutches.

Heavier eggs or heavier clutches could also be prioritised for collection. However, selecting eggs by weight presents several challenges for rangers in the field. Collecting only the heaviest eggs could result in the formation of atypical clutches and create problems with subsequent brood size. Additionally, egg weight is intrinsically linked with the age of the embryo (Narushin & Romanov 2002). Kakī eggs lose weight throughout incubation so eggs collected later in an incubation cycle will be lighter, and vice versa. This means that field rangers would need to make *in situ* measurements of both egg weight and approximate embryo age to make an informed decision, which is an impracticality in the field. Although we did not find a strong correlation between these predictor variables, it is a commonly described relationship that should not be disregarded (Narushin & Romanov 2002).

While it is important to maximise hatchability outcomes where possible, hatchability rates for the period are high and comparatively larger gains for the species can be made addressing low survival of released individuals. It is also important to note that this study does not assess the impact of predictor variables on the hen, egg fertility or post-hatching survival, and caution should be used when using only hatchability trends to justify changes to management regimes.

Survivability models

Survivability models highlighted key relationships between kakī survival and manageable variables including release age, inbreeding coefficient, use of supplementary feeding, and release location. Kakī released as sub-adults had the highest survivability, whereas outcomes for individuals released as juveniles and adults were poorer. Juveniles are unlikely to have well-developed foraging strategies, social behaviour, or anti-predator responses to be successful in the wild. Conversely, adults have a longer time to acclimatise to captivity and might find the transition to a wild regime more difficult than do younger birds (Champagnon et al. 2012). The sample size for individuals released as adults was low (< 10 individuals) and any trends might not accurately reflect adult survival in the wild. These results support current practice of prioritising sub-adult releases where possible, while highlighting the poor outcomes from juvenile releases.

We report a negative effect of inbreeding on released individuals' ability to survive in the wild. The increased expression of deleterious alleles in inbred individuals has negative impacts on fitness (Lynch & Walsh 1998; Keller & Waller 2002). However, decreased fitness can often be masked in captive conditions where necessities are provided (Crnokrak & Roff 1999; Joron & Brakefield 2003). Our result provides a rationale to prioritise egg collection from pairs with the lowest relatedness, where possible. Additionally, more intensive *in situ* management to reduce the number of highly related pairs in the population could be considered (Robledo-Ruiz et al. 2022). Such an effort would likely involve increasing the number of captive breeding pairs, rather than breaking up unsuitable wild pairs, as population stability is currently prioritised over pair quality.

Supplementary feeding has been provided to a number of threatened species with the hope of improving wild outcomes; the success of such programmes has varied (Hoodless et al. 1999; Piper et al. 1999; Oro et al. 2008; Fenn et al. 2020). The rationale behind supplementary feeding is to provide additional calories as released individuals acclimate to wild conditions and learn to forage naturally. Here we report that use of supplementary feeding had a positive relationship with the survival of kakī in the wild, supporting the continuation of current practice. However, it is difficult to disentangle the confounding effect of birds that die without ranger knowledge within the supplementary feeding period. Such birds were recorded as not using supplementary feeding despite having already failed to survive one year, artificially worsening outcomes for birds with low use of supplementary food. A dedicated study on the impact of supplementary feeding should be undertaken to determine optimal duration, and efficacy of current feeding practices.

Individuals released at the Mt. Gerald site were more likely to survive than those released at the Tasman site. This suggests that the Mt. Gerald release site or surrounding dispersal habitat might enhance kakī survival, potentially driven by greater food availability and/or lower predator density. Managers could prioritise releasing kakī at Mt. Gerald in order to maximise recruitment of the captively-reared birds. However, releasing individuals in multiple locations can safeguard the species from localised increases in threats.

Kakī health while in captivity might be indicative of their probability of post-release survival. We show that individuals affected by pododermatitis (bumblefoot) and/or encephalitis were less likely to survive once released. All individuals undergo a health assessment prior to release and must be fully recovered from any prior conditions before being released. Despite this, our results show that both encephalitis and pododermatitis likely had sub-clinical impacts on recovered individuals. Impacts could take the form of long-term brain-function and motor-control limitations for encephalitis infection (LB, unpubl. data), and problems with walking/standing, bone degradation, and osteomyelitis for bumblefoot (Reissig et al. 2011). Such pathologies are likely masked in captivity where resources are provided in excess, but impacts may be more pronounced once affected individuals are released.

Contrary to expectation, we found that kakī that were injured in captivity had better survival probability than their uninjured counterparts. Similar to encephalitis and bumblefoot infections, individuals with significant injuries can suffer from long-term impacts, negatively affecting their ability to survive in the wild (Fajardo et al. 2000; Monadjem et al. 2014). This aberrant trend highlights problems with using categorical or subset data with lower sample sizes, e.g. injured birds (n = 64), bird with encephalitis (n = 42), to define relationships with low effect sizes and can function as a general warning against overinterpretation of presented results.

Top models for both hatchability and survival had low deviance explained values of c. 22% and c. 13% respectively. This result suggests that important drivers of both response variables were missing from our analysis. Survival models in particular could likely be improved with the inclusion of variables detailing predator density/interaction at high use areas (Cruz et al. 2013), food availability (Oro & Furness 2002; Davis et al. 2005), and weather conditions (Yasué et al. 2003; Salewski et al. 2013). In other species, variables such as specific parentage, position in laying order (Sockman 2008), dam condition (Cucco et al. 2012), and egg size and shape (Perrins 1996; Cucco et al. 2012) have been shown to impact hatchability. Despite the low deviance explained values, trends presented in this analysis may be used by species managers to justify both changes to, and conservation of, current management practices as they relate to the collection of wild kakī eggs from the wild and release of captive-reared individuals.

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Data and code availability

There are no publicly available data or code associated with this article.

Author contributions

SB and LB conceptualised the project and undertook the investigation and data curation. SB undertook the analysis and wrote the original draft of this manuscript with support from all authors. The authors declare no conflicts of interest.

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Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. Statistics for the predictor variables used in logistic regression models for the hatching fate of kakī eggs laid from 2013–2019.

Appendix S2. Statistics for the predictor variables used in logistic regression models for the survival fate of individual kakī released from 2017–2020.

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