Fat chance? Endangered penguin rehabilitation has mixed conservation outcomes

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Abstract
Rehabilitation of sick or injured wildlife supports wild populations of threatened species by improving the health of individuals. Post-release assessment of the efficacy of rehabilitation relies on re-sighting and identification of both rehabilitated and comparable wild individuals. For species or age classes with naturally low survival rates and re-sighting probabilities, evaluating the long-term success of rehabilitation is challenging. We use a rehabilitation database in conjunction with a long-term monitoring database to determine rehabilitation outcomes for yellow-eyed penguin (Megadyptes antipodes) chicks across 10 breeding seasons. Although rehabilitated chicks fledged at a higher mass, their post-fledging survival probability was lower (0.23 ± 0.10—0.47 95% CI) than that of healthy (>5 kg) wild-fledging conspecifics (0.38 ± 0.26—0.51 95% CI), or even of underweight (<5 kg) chicks fledging naturally (0.28 ± 0.11—0.53 95% CI). Removing underweight chicks for rehabilitation did not improve parent survival to the following season nor did it influence future breeding propensity; c. 100% of parents subsequently attempted to breed regardless of previous breeding outcome or interventions. Most wildlife rehabilitation programmes assume that efforts are improving the conservation status of the species, but longer-term implications must be tested to ensure that scarce resources are expended on the best possible conservation outcomes.

KEYWORDS
fledgling mass, penguin, rehabilitation, survival

1 INTRODUCTION

Seabirds are indicators of the health of marine ecosystems (Croxall et al., 2012), but seabird populations are declining faster than those of any other group of birds (Croxall et al., 2012; Paleczny, Hammill, Karpouzi, & Pauly, 2015). Rehabilitation of sick or injured individuals in threatened populations is commonly undertaken to support wild populations, as survival of individuals post-rehabilitation might be more effective in reinforcing wild populations than rearing animals in captivity for release. Post-rehabilitation survival can be comparable to that of non-rehabilitated animals (e.g., African penguins Spheniscus demersus, Sherley et al., 2014). However, Pyke
and Szabo (2018) reported that most programmes involving rescue, rehabilitation, and release of threatened species fail to assess conservation outcomes or to demonstrate that the interventions have resulted in any benefits to wild populations. Rescue databases have been rarely used and contribute little to conservation (Pyke & Szabo, 2018). The actual benefits of different forms of intensive management must be evaluated to ensure that conservation goals are being met and resources are being used wisely (Margalida et al., 2017; McCarthy & Possingham, 2007). Here we use a rehabilitation database in conjunction with a long-term monitoring database for the endangered yellow-eyed penguin (Megadyptes antipodes) to illustrate how conservation outcomes of wildlife rehabilitation can be assessed.

Penguins represent the second-most threatened seabird taxa, with most species facing similar threats, including habitat degradation, marine pollution, climate change, and the impacts of fisheries (Ropert-Coudert et al., 2019; Trathan et al., 2015). In New Zealand, the endangered yellow-eyed penguin or hoiho/takaraha is affected by these and additional threats, including predation from introduced mammals (Seddon, Ellenberg, & van Heezik, 2013), and unregulated ecotourism (Boersma et al., 2020; Ellenberg, Setiawan, Cree, Houston, & Seddon, 2007). Due to the endangered conservation status of yellow-eyed penguins, rehabilitation has been used as an ad-hoc population management strategy and has involved veterinary assessment and temporary captive management of sick, injured, orphaned, or underweight penguins, for treatment before release back into the wild. Since 2012, rehabilitation has become an integral tool to prevent local population declines (DOC, 2020).

In recent years, most of the yellow-eyed penguins admitted to rehabilitation have been fully-grown fledglings in poor body condition, which are assumed will starve if left in the wild (M.J. Young, C.R. Pullar, Department of Conservation, New Zealand, unpublished data). Removing fledglings from the wild for rehabilitation has been justified by conservation managers as a means to prevent mortality from starvation, but also to relieve breeding adults of parental responsibilities leading up to their annual moult, which occurs shortly after the fledging period and requires a period of “fattening up” to ensure sufficient mass gain to endure the period of fasting associated with moulting. Fledging weight is an important predictor of juvenile survival (Magrath, 1991; Naef-Daenzer, Widmer, & Number, 2001), particularly for seabirds (Coulson & Porter, 1985; Sagar & Horning, 1998). In yellow-eyed penguins, there is a positive relationship between chick fledgling weight and juvenile survival, with heavier chicks being more likely to survive (McClung, Seddon, Massaro, & Setiawan, 2004).

While rehabilitation to improve fledging weights of starving chicks appears valid, it is less clear that rehabilitated chicks will survive in the longer term and contribute to the viability of wild populations. The concept of removing or reducing the number of chicks raised in the wild to increase adult survival is also questionable, given that investment into reproduction in long-lived seabirds is a trade-off between current reproductive success and investment in offspring, and survival and future productivity (Sæther, Andersen, & Pedersen, 1993). The removal of young from the wild in order to “take the pressure off” adult breeders and relieve them of chick rearing duties before the annual moult, was experimentally tested in yellow-eyed penguins in the 1990s (Efford & Edge, 1998), following a controversial widespread clutch reduction programme in 1990/91 (Darby & Paterson, 1991). There was no evidence for improved adult survival (Edge, Jamieson, & Darby, 1999). However, this research was undertaken during a period of favorable environmental conditions and productivity which led to rapid population growth, and thus requires re-evaluation in light of current negative population trends and long-term climatic change (Mattern et al., 2017).

Poor reproductive performance in any given year is a natural consequence of marine stochasticity, and rehabilitation of poorly nourished or abandoned young risks release of these individuals back into the same marine conditions that caused starvation in the first place. Rehabilitated chicks might be released from facilities in good condition, however if they do not subsequently survive then rehabilitation efforts might serve only to improve individual animal welfare outcomes but contribute little to species conservation. If intervention and rehabilitation have no measurable benefit when undertaken during poor breeding seasons, for example, by increasing juvenile or adult survival, or adult breeding propensity, then conservation resources allocated to chick rehabilitation might be better spent on other population recovery activities.

The objectives of this study were to: (a) demonstrate the value of using a rehabilitation database in conjunction with a long-term monitoring database; (b) assess success in terms of survival of rehabilitated underweight yellow-eyed penguin chicks taken from the wild for supplementary feeding, in relation to their admission mass, and describe reasons for admission and time spent in temporary captivity; (c) compare the probability of survival post-fledging of rehabilitated chicks to that of wild-fledged chicks; and (d) determine if the removal of underweight chicks was associated with improved survival or breeding propensity of adults in the following breeding season. Measuring the longer-term success of rehabilitation of underweight chicks has been difficult.
due to low juvenile survival (20.5%; Stein, Young, Darby, Seddon, & van Heezik, 2017) and low re-sighting probability of immatures until they recruit into the breeding populations (Maness & Anderson, 2013). By using data collected over 13 years and stored in a long-term monitoring database we were able to evaluate the survival of wild-fledging and rehabilitated individuals, and their respective parents, post-intervention.

2 | METHODS

2.1 | Study area

Penguins admitted for rehabilitation originated from breeding areas along the coastal Otago region of the South Island of New Zealand, including the Otago Peninsula and the Catlins coast (Figure 1). We considered only yellow-eyed penguin chicks rehabilitated at Penguin Place Conservation Reserve (hereafter, Penguin Place) on Otago Peninsula, which takes in wild, free-living birds for rehabilitation from breeding locations on the Otago Peninsula and Catlins coastlines. Release of rehabilitated birds occurred at Pīpīkāretu, Otago Peninsula (Figure 1).

2.2 | Data collation

We acquired nesting and re-sighting data from the Yellow-eyed Penguin Database (YEPDB), which is hosted by the Department of Conservation (DOC), New Zealand, and includes decades of monitoring data across multiple locations. Access and use of the data in this project is granted in accordance with a Memorandum of Understanding with DOC. Within the YEPDB, we used data from the “Nest” and “Captive” tables, supplemented by data obtained through searches using a primary key to retrieve information on individual birds from the “Band,” “Nest,” “Recover,” “Captive,” and “Autopsy” tables. In addition, Penguin Place provided us with raw data tables from their rehabilitation database to cross-check YEPDB records as well as data on admission mass, reason for admission, and time spent in captivity.

2.3 | Assessment of rehabilitation success and chick condition

Pre-fledging chicks were admitted to Penguin Place once they reached their asymptotic dimensions (from c. 70 days, van Heezik, 1990) during the austral years of 2007/08 to 2016/17. They were fed twice daily to bring their weight to >5.0 kg. Once assessed as healthy, the chicks were individually marked with either a stainless-steel flipper band, or with a subcutaneous transponder inserted in the nape of their neck. Chicks were transported a short distance to the north end of Pīpīkāretu, Otago Peninsula, where they were either hard-released on the beach or rocky foreshore (2007/08–2013/14), or held in a soft-release pen above the beach for a minimum of one night before being released (2014/15–2016/17). If the chicks remained at the pen after the soft release, they were fed once daily until fledging. On the rare occasion a chick lost weight before fledging, it was readmitted to rehabilitation for additional feeding before another soft-release attempt.

Previous modeling of juvenile yellow-eyed penguin survival probability indicates an apparent survival rate >0.25 for chicks >5.0 kg at pre-fledge (McClung et al., 2004). In the current study we considered chicks to be underweight if they were <5.0 kg at pre-fledging, and any chicks >5.0 kg with no other complications were considered healthy. We calculated summary statistics, including: the total number of chicks that were assessed at their natal location, the proportion of these chicks that were underweight, and the proportions that were rehabilitated by region, annually; the rate of successful rehabilitation (from uplift to release back into the wild); and the total proportion of chicks that were rehabilitated from wild populations.
2.4 Apparent survival of wild vs. rehabilitated chicks

Age-at-first-breeding is highly variable for yellow-eyed penguins (2–12 years, Stein et al., 2017), but c. 90% of known-age birds that survive the immature period (post-fledging to pre-recruitment) commence breeding by age five (M.J. Young and A.M. Stein, University of Otago, unpublished data). We therefore considered the apparent survival rates of wild-fledged and rehabilitated chicks for each cohort from fledging up to the age of five. We gathered information for each bird from re-sighting, nest, and mortality data from the YEPDB to track all chicks fledged from cohorts 2007/08 to 2014/15 (eight seasons), up until the end of the 2019/20 season. Any birds not re-sighted within 5 years of fledging were assumed to have died. Because monitoring of all yellow-eyed penguin breeding sites takes place along the coast every year, it is very unlikely that a live individual would not be sighted over the five-year period. We considered pre-fledging mass as a predictor of survival: wild-fledging chicks are weighed in the month prior to fledging once fully grown, and rehabilitated chicks are weighed in the week prior to their release.

2.5 Survival and breeding propensity of adult penguins

Using the monitoring database (YEPDB) we determined the survival and breeding propensity of all adult breeding birds in the following year, after attempting breeding that year, to establish if any breeding outcomes (e.g., removing chicks) were associated with reduced adult survival or breeding propensity in the following year. Because not all adult yellow-eyed penguins were individually marked throughout their range, we limited this analysis to a subset of the breeding sites where both adults were uniquely marked with either a flipper band or transponder, and that bred in the seasons 2007/08 to 2013/14 (seven seasons). Where the identity of one of a pair of adult birds was not recorded in a breeding season, and because yellow-eyed penguins are monogamous across seasons (Setiawan, Darby, & Lambert, 2004), we assigned the missing identity information based on breeding relationships in the years prior and after the missing observation.

We determined the apparent survival and breeding propensity of adults from re-sighting, nesting, and mortality data, from the YEPDB up to 3 years following a breeding event (i.e., for birds that bred in the 2013/14 season, we considered breeding, re-sighting or mortality information up to the end of the 2016/17 season). If an adult bird bred in year $n$, but was not re-sighted in year $n+1$, $n+2$ or $n+3$, it was assumed to have died (after Stein et al., 2017). If a bird bred in year $n$, was not re-sighted in year $n+1$, but was re-sighted in year $n+2$ and/or year $n+3$, it was classed as alive and not breeding in year $n+1$. We included only breeding adults that survived from year $n$ to year $n+1$ in the model of breeding propensity.

We modeled the relationships between the explanatory variables and the two response variables (adult survival and adult breeding propensity in year $n+1$, following breeding in year $n$) in two separate models. Adults were sexed based on morphometrics after Setiawan et al. (2004), inferred from a measured mate or by comparing relative sizes of mates. If it was not possible to determine the sex of an adult penguin it was removed from the data set.

2.6 Statistical methods

All statistical analyses were executed in R (R version 3.6.3, www.R-project.org, accessed: August 5, 2020). We used binomial generalized linear mixed models (GLMM) fitted using the glmer function in the lme4 package (Bates, Mächler, Bolker, & Walker, 2015), as response data had a binomial distribution and the model structure allowed for the inclusion of random factors (Bolker et al., 2009). All predictors included in the models were categorical, with the exception of fledging mass, which was centered and scaled using the z-transformation following Grueber, Nakagawa, Laws, and Jamieson (2011).

In the juvenile survival model, we included “Treatment” (three levels: fledged from the wild over 5 kg, fledged from the wild under 5 kg, and fledged after rehabilitation), “Cohort” and “Region” (Otago Peninsula, Catlins) as predictors of survival post-fledging. “Nest ID” was included as a random factor to account for the pseudoreplication associated with siblings from the same nest (see Supporting Information S1 for the model structure).

We included the following input variables for both adult survival and breeding propensity model sets: parental load, based on the number of chicks that hatched in year $n$ (0, 1 or 2); adult sex (M or F); breeding experience in year $n$ (0, 1); breeding site; breeding outcome in year $n$ (Five levels: 1. Failed breeding—incubation stage; 2. Failed breeding—chick stage; 3. Succeeded breeding—fledged chick < 5.0 kg; 4. Succeeded breeding—fledged chick > 5.0 kg; 5. Succeeded breeding—chick rehabilitated); austral year in year $n$. Nest ID was included as a random factor to account for the pseudoreplication introduced by birds of the same breeding pair being included in the models (see Supporting Information S2).

For each model set, the full model was fitted with all plausible explanatory variables for analysis, and full model fit was assessed (GLMM: marginal and conditional...
Table 1  Numbers of Otago Peninsula and Catlins yellow-eyed penguin chicks weighed at c. 90 days, numbers that were considered underweight, and proportions of those <5.0 kg chicks uplifted for rehabilitation at Penguin Place Conservation Reserve, from 2007/08 to 2016/17

| Region          | Number of wild chicks weighed | Number of wild chicks < 5.0 kg | Proportion wild chicks < 5.0 kg | Number taken into rehabilitation | Proportion < 5.0 kg rehabilitated |
|-----------------|-------------------------------|-------------------------------|--------------------------------|----------------------------------|----------------------------------|
| Catlins         | 1,580                         | 752                           | 47.6%                          | 167                              | 22.2%                            |
| Otago Peninsula | 1,090                         | 317                           | 29.1%                          | 109                              | 34.4%                            |
| Total           | 2,670                         | 1,069                         | 40.0%                          | 276                              | 25.8%                            |

$R^2_{GLMM}$ following Nakagawa & Schielzeth, 2013). We used the `dredge` function from the package `MuMIn` to test all plausible derivatives of the full models. We used the adjusted Akaike Information Criterion (AICc) to select the most plausible models, and the top models (2ΔAICc) were model-averaged (following Burnham & Anderson, 1998). Parameters were considered statistically and biologically significant if zero was not contained in the 95% confidence interval derived from the model-averaged estimates. We calculated the probability of survival of wild-fledged and rehabilitated chicks post-fledging, the probability of adult survival in year $n + 1$, and adult participation in breeding in year $n + 1$, by back-transforming model-derived parameter estimates and their 95% confidence intervals from the logit scale to provide biologically relevant interpretation of these results (after Grueber et al., 2011). Apparent survival rates, based on recovery rates, were also calculated.

3 | RESULTS

Over ten breeding seasons from 2007/08 to 2016/17, a total of 2,670 chicks were weighed and measured at breeding sites on the Otago Peninsula and Catlins coasts when they reached c. 90 days, and of these 1,069 were considered underweight (<5.0 kg; 40.0%; Table 1; for more information, see Table S3). Of those deemed underweight, 167 (22.2%) of Catlins chicks and 109 (34.4%) of Otago Peninsula chicks were brought into temporary captivity for rehabilitation. Eighteen chicks, all from the Otago Peninsula coast, were ≥5.0 kg when admitted for rehabilitation, usually because one or both of their parents died or were in captivity due to injury before their chicks had fledged.

3.1 | Assessment of rehabilitation success and chick condition

The mean admission mass recorded across all 10 years was 3.63 ± 0.88 kg ($n = 282$). Lowest mean admission masses were seen in 2007 (mean ± sd = 2.45 kg ± 0.35, $n = 2$) and 2013 (3.15 kg ± 0.58, $n = 63$); in all other years they ranged between 3.41 ± 0.59 and 4.12 ± 0.84 kg.

Twenty-eight chicks died or were euthanized by a veterinarian (9.5%), and 266 chicks were released at Pipikāretu. Chicks that died in captivity generally had a lower admission mass (mean = 3.3 ± 1.0 kg) than chicks that survived to be released (mean = 3.6 ± 0.9 kg; Figure S1), but this difference was not significant (Welch two sample t-test, $t = -1.59, df = 30.1, p = .122$).

The length of time spent in rehabilitation was negatively correlated with chick admission mass (mean ± sd = 38.0 ± 16.4 days; Pearson’s product-moment correlation, $R^2 = –0.378$; Figure S1). There was no relationship between chick admission mass and the duration of the stay in temporary captivity for chicks that died or were euthanized (mean ± sd = 27.7 ± 29.1 days, Pearson’s product-moment correlation, $R^2 = 0.053$; Figure S1).

Starvation was the primary reason for chick rehabilitation ($n = 278, 94.6%$; see Table S4). Parent mortality, or assumed mortality, and parent injury accounted for high numbers ($n = 70$) of starvation-related admissions. For 64 underweight chicks (all <5.0 kg), no further information was provided at the time they were admitted to rehabilitation. Other admission reasons, including sibling disparity, where a sibling was unusually larger (≥1.0 kg) (4.8%, $n = 14$), or when a chick was injured (0.7%, $n = 2$), were uncommon (Table S4).

In all years, the mean release mass of rehabilitated yellow-eyed penguin chicks (mean ± sd = 5.44 ± 0.4 kg) was higher than that of wild-fledging underweight (<5 kg) chicks (4.59 ± 0.34 kg), and healthy (>5 kg), wild-fledging chicks (5.39 ± 0.32 kg), with wild-fledging chicks having greater mass variance than rehabilitated chicks (Figure 2).

3.2 | Apparent survival of wild vs. rehabilitated chicks

Just 17.5% of the variation associated with chick post-fledging survival was explained by the model ($R^2$M), with
both fixed and random factors explaining 22.0% of the variation overall \( (n = 1,516 \text{ fledging events}) \). **Cohort** and **Treatment** had the highest relative importance in the model-averaged model, and all model terms were significant at their means, with chicks that received rehabilitation having significantly lower modeled survival than wild-fledging chicks, regardless of their fledging mass (Table 2).

**TABLE 2** Post-fledging survival probabilities of chicks, calculated by model-averaging the top generalized linear mixed models (GLMM) (\( 2\Delta \text{Aikaike Information Criterion} \) corrected for small sample size \( \text{AICc} \); \( n = 1,516 \text{ fledging events} \)) for marked yellow-eyed penguin chicks that fledged from rehabilitation at Penguin Place Conservation Reserve and wild locations on the Otago Peninsula and Catlins coasts from 2007/08 to 2014/15, and that were resighted up to 5 years after fledging. Cohort is presented as a weighted mean across all years.

| Parameter | Coefficient estimate | Standard error | 95% confidence interval | Relative importance |
|-----------|----------------------|---------------|------------------------|---------------------|
| (Intercept) | -0.49 | 0.28 | (-1.03, 0.05) | — |
| Weighted mean (Cohort) \( ^a,^{**} \) | -1.20 | 0.56 | (-2.29, 0.11) | 1.00 |
| Natal region (Otago Peninsula) \( ^b,^{**} \) | -0.47 | 0.18 | (-0.83, -0.11) | 1.00 |
| Treatment (rehabilitation) \( ^c,^{**} \) | -0.69 | 0.26 | (-1.21, -0.18) | 1.00 |
| Treatment (wild <5 kg) | -0.48 | 0.27 | (-1.01, 0.06) | 1.00 |
| \( z \) (mass at fledging) | 0.09 | 0.12 | (-0.05, 0.39) | 0.55 |

\(^a\)Cohort (2007) is the reference category.

\(^b\)Natal region (Catlins) is the reference category.

\(^c\)Treatment (Wild >5 kg) is the reference category.

\(^{**}\)Significant result based on the 95% confidence interval not containing zero.

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**FIGURE 2** (a) Fledging mass (±sd) of yellow-eyed penguin chicks by cohort for the period 2007/08 to 2016/17. Chicks that were supplementary fed in temporary captivity (white) were weighed in their final week of rehabilitation at Penguin Place Conservation Reserve. Wild-fledging chicks (dark grey) were weighed once they reached their asymptotic dimensions in the month prior to fledging. (b) Fledging mass (±sd) of wild-fledging underweight (<5 kg) chicks (light grey), versus uplift mass of underweight (<5 kg) chicks (dotted) that were contemporaneously taken into rehabilitation for supplementary feeding.
When all other predictors were at their means, model-predicted survival probabilities were higher for wild-fledging chicks over 5 kg ($Pr\text{[survival post-fledging, wild >5 kg]} = 0.38$, binomial 95% confidence interval: 0.26–0.51), than for wild-fledging chicks under 5 kg ($Pr\text{[survival post-fledging, wild <5 kg]} = 0.28$, binomial 95% confidence interval 0.11–0.53), or for chicks that fledged following rehabilitation ($Pr\text{[survival post-fledging, rehabilitated]} = 0.23$, binomial 95% confidence interval: 0.10–0.47). Regardless of intervention, overall model-predicted survival post-fledging (when all other modeled parameters were at their means) was 23.1% for cohorts fledged
from 2007/08 to 2014/15. Combined model-predicted post-fledging survival probabilities were lowest in 2008 ($\Pr = 0.18$), 2010 (0.11), and 2014 (0.06), and for all other cohorts, survival probability was above 23.2%, with survival probability being highest in 2007 (0.37), 2009 (0.37), 2011 (0.36) and 2012 (0.34) when all other predictors were at their means.

A total of 279 marked chicks were seen post-fledging, which resulted in a recovery rate from re-sightings of 18.4% from the 1,516 individuals marked before fledging from the wild or from rehabilitation. This apparent post-fledging survival was significantly higher for wild-fledged chicks than for rehabilitated chicks in 2007, 2009, and 2012, with rehabilitated chicks having a higher survival probability only in 2013 (Figure 3).

3.3 | Survival and breeding propensity of adult penguins

3.3.1 | Adult survival from year $n$ to year $n + 1$

The full model had a marginal ($R^2M$) value of 0.28 and a conditional ($R^2C$) of 0.62. This means 28% of the variation in adult survival was explained by the fixed effects, while 62% was due to both fixed and random factors ($n = 1,160$ observations). Three models were selected from a set of plausible models at $\Delta AICc$, where the explanatory variables Year and Breeding outcome were selected for all three models, with Sex and Parental Experience also appearing in two of the top models. In the model-averaged model, Breeding outcome and Year had the largest relative importance (Table 3).

Across all years of the study, the mean adult survival probability was 83.5% in year $n + 1$ (95% binomial confidence interval: 33.5–98.0%), regardless of breeding outcome in year $n$. Model-predicted adult survival was low in 2008/09 (72.1%), 2009/10 (72.3%), 2012/13 (73.9%) and 2013/14 (46.0%), whereas in 2007/08, 2010/11 and 2011/12, adult survival probability was above 92.0%.

Of all breeding outcomes in year $n$ associated with adult survival in year $n + 1$, only those adults whose chicks were removed for rehabilitation in year $n$ were associated with significantly lower adult survival in year $n + 1$ (mean = 78.2%, 95% binomial confidence interval: 28.2–97.0%; Figure 4; Table 3). For all other adults that attempted breeding in year $n$, their model-predicted survival probabilities were over 92.5% in year $n + 1$.

3.3.2 | Adult breeding propensity from year $n$ to year $n + 1$

Overall, model fit for the full model was poor; the marginal and conditional $R^2$ values indicated that the fixed effects alone accounted for only 5% of the variation in the data, while the random factor (Nest ID) and all fixed
effects explained 91% of the variation in participation in breeding in year $n + 1$ ($n = 901$ observations). In the full model, the Year was a significant predictor.

Year had the highest relative importance and was contained in all three models, while Sex and Parental Experience were in one model each (Table 4). Breeding outcome, the parameter of interest, was not included in any of the top models at $2\Delta AIC_c$. Regardless of whether a chick was removed for rehabilitation or not in year $n$, the probability of an adult breeding in the following year was close to 100% for all years, with the most variation occurring in 2008 and 2013 (Figure S2).

### 4 | DISCUSSION

By using data from the rehabilitation database, in combination with data from long-term monitoring of wild populations, we were able to reveal some unexpected trends that provide a more nuanced view of the conservation outcomes of rehabilitation efforts for yellow-eyed penguins. While our results show that starvation is the primary reason that yellow-eyed penguin chicks were uplifted from their natal locations, rehabilitation to a body mass higher than that of wild fledglings did not result in higher survival of rehabilitated chicks, nor did it improve the subsequent survival or breeding propensity of their parents; in fact, chicks of lower body mass that are left in the wild had higher survival than chicks uplifted for rehabilitation and released at a higher body mass. The long-held management belief that removing chicks would improve adult survival appears to be unfounded; it is quite possible that underweight chicks were starving because their parents were already incapacitated or dead. To this end, the focus on monitoring nesting outcomes (i.e., survival of eggs and chicks) rather than individual adult condition and survival, has resulted in long-term misdirected effort to rehabilitate underweight chicks, a symptom of poor adult survival. Once adults are no longer detected at nests during daytime visits because both are at sea foraging, returning only in the evenings to feed chicks, the current monitoring framework fails to effectively monitor and support adults, the most critical age class for population stability.

Chicks that were removed for rehabilitation were assumed to probably otherwise have died of starvation given their emaciated state, but survived rehabilitation and fledged (~91%), indicating that intervention does play an important role in increasing the numbers of chicks fledged during years of poor food supply. This rate is comparable to that of African penguins *Spheniscus demersus* (c. 84%, Sherley et al., 2014), and higher than those reported for other seabird species (e.g., Hartlaub's gulls, *Larus hartlaubii*, 65%, Cape cormorants, *Phalacrocorax capensis*, 40%, Cape gannets, *Morus capensis*, 64%, kelp gulls, *L. dominicanus*, 48%, Parsons & Underhill, 2005; 87%, Montesdeoca, Calabuig, Corbera, & Oros, 2017), although these lower rates may reflect the severity of admission conditions, such as oiling and disease.

Unsurprisingly, the time spent in rehabilitation was inversely proportional to admission weight, with chicks remaining in rehabilitation for an average of 38.0 ± 16.4 days, similar to the average of 45 ± 19 days for African penguins (Sherley et al., 2014). Earlier intervention, that is, before chicks get very thin, could reduce the duration of captivity and associated resources required.

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**Table 4** Breeding propensity in year $n + 1$ (binomial) for adult yellow-eyed penguins, determined by model-averaging the top generalized linear mixed models (GLMM) ($2\Delta$ Akaike Information Criterion corrected for small sample size [AICc]), from a subset of marked individuals on the Otago coast, New Zealand ($n = 901$), that bred in year $n$, from 2007/08 to 2013/14.

| Parameter             | Coefficient estimate | Standard error | 95% confidence interval | Relative importance |
|-----------------------|----------------------|----------------|-------------------------|---------------------|
| (Intercept)           | 12.51                | 1.56           | (9.45, 15.58)           | —                   |
| Year (2008)$^a$**     | −3.25                | 0.87           | (−4.96, −1.55)          | 1.00                |
| Year (2009)$^b$       | 1.49                 | 0.97           | (−0.42, 3.39)           | 1.00                |
| Year (2010)$^b$       | 1.72                 | 1.03           | (−0.30, 3.74)           | 1.00                |
| Year (2011)$^a$**     | 2.39                 | 1.14           | (0.16, 4.63)            | 1.00                |
| Year (2012)$^b$       | 1.59                 | 1.01           | (−0.39, 3.57)           | 1.00                |
| Year (2013)$^a$**     | −3.67                | 1.03           | (−5.69, −1.66)          | 1.00                |
| Sex (male)$^b$        | 0.05                 | 0.22           | (−0.61, 1.06)           | 0.23                |
| Parental experience   | −0.10                | 0.49           | (−2.33, 1.43)           | 0.22                |

$^a$Year (2007) is the reference category.

$^b$Sex (Female) is the reference category.

**$^*$Significant result based on the 95% confidence interval not containing zero.**
for a successful release. Evaluating chick body mass as they approach their asymptotic size at c. 70d (van Heezik, 1990) would allow early intervention before body condition has deteriorated to the point of emaciation (van Heezik, 1990), as was observed with most chicks that were removed for rehabilitation.

Post-fledging survival probability was 23.1% for all marked chicks that fledged, regardless of intervention, from 2007/08 to 2014/15, which is comparable to previously reported post-fledging recovery rates from re-sightings (20.5%, Stein et al., 2017; 20.8%, Efford, Darby, & Spencer, 1996). Heavier, wild-fledging yellow-eyed penguin chicks had the highest probability of survival (0.38), whereas rehabilitated chicks had a significantly lower post-fledging survival probability, despite being consistently heavier at fledging than wild-fledged chicks. Moreover, underweight (<5 kg) chicks that fledged from wild locations had a slightly higher probability of post-fledging survival (0.28) than rehabilitated chicks (0.23). Emaciated seabird chicks are more likely to develop growth issues, including bony deformities (e.g., Buckle & Alley, 2011), and higher corticosterone levels (e.g., Kitaysky, Kitaiskaia, Piatt, & Wingfield, 2006) which might explain the lower survival probabilities for rehabilitated yellow-eyed penguin chicks. However, given that the expected outcome for these emaciated chicks was starvation if no intervention had taken place, even a reduced post-fledging survival is assumed to be of conservation benefit if this translates into recruitment, and if greater gains would not be achieved by expending resources elsewhere.

Uplifting chicks did not influence subsequent propensity to breed in parent birds, with participation in the year following a breeding event being close to 100% in all years. Removing underweight yellow-eyed penguin chicks to prevent their starvation does not affect the future breeding propensity of their parents, as long as their parents are alive. Long-lived seabird species have many years to produce sufficient offspring to replace themselves, and so do not take excessive breeding risks (Goodman, 1974) and are unlikely to invest in offspring at the expense of their own survival and future breeding success (Erikstad, Fauchald, Tveraa, & Steen, 1998; Weimerskirch, Zimmermann, & Prince, 2001). However, for long-lived seabirds, mate retention is related to breeding success (Ismar, Daniel, Stephenson, & Hauber, 2010) with divorce rates being higher when breeding has been unsuccessful (Bradley, Wooller, Skira, & Serventy, 1990; Dubois & Cézilly, 2002). Removing underweight chicks from nests for rehabilitation could conceivably be perceived by breeding seabirds as a failed breeding event if both chicks are removed during the chick-rearing period, and therefore has the potential to increase divorce rates and their associated fitness costs to adults (Ismar et al., 2010). We did not evaluate the association between chick intervention and the relationship status of their parents in the following season.

4.1 | Conclusions and management implications

Evidence-based decision-making requires robust data to evaluate the outcomes of management actions. Our results provide no support for the current strategy, which was based on no empirical data, of “relieving” breeding yellow-eyed penguins of chick-rearing responsibilities when chicks were observed to be underweight, so that adults might better prepare themselves to moult. Our use of both the rehabilitation and the sightings databases enabled robust evaluation of the success of rehabilitation to extend beyond the moment of release, since we were able to assess how rehabilitated individuals fared back in their natural environment by comparing the post-release survival of rehabilitated individuals with that of wild-reared individuals. While rehabilitation of adult yellow-eyed penguins has increased the mean annual survival of adult females, and consequently has increased the total number of nests and chicks fledged by 10% over 10 years (Ratz & Lallas, 2010), chicks left in the wild had higher survival than those uplifted for rehabilitation and released at a higher body mass. Prolonged captivity and hand-rearing can have lasting effects on wildlife, and loss of adaptive behaviors can lead to reduced fitness (Griffin, Blumstein, & Evans, 2000).

Rehabilitation efforts are often high-profile and high publicity, and can even be emotionally rewarding, but they are also resource-intensive management interventions. In order to achieve positive conservation outcomes in yellow-eyed penguins, our results indicate that determination of an appropriate level of monitoring of yellow-eyed penguin populations is essential to future evidence-based decision-making, focusing on individual birds rather than solely on the outcomes of nesting attempts. This requires marking all wild-fledging and rehabilitated birds and their parents and making the effort to re-sight these birds at critical times during the annual cycle (e.g., pre-moult, moult). The development of a protocol for monitoring and intervention that is endorsed and implemented by all groups managing this species, focusing on detecting all age classes at appropriate times of the day (e.g., when adults return to the shore in the evening to feed their chicks), and during the year, should ensure that all yellow-eyed penguins requiring rehabilitation will receive attention. However, if resources are limited the rehabilitation focus should be on adults.

Evaluating the survival of rehabilitated yellow-eyed penguins should continue in order to determine whether the implementation of improved practices yields better
post-release survival rates in comparison to naturally fledging penguins across the same time period, and whether these result in benefits at the population level. The use of rehabilitation to reduce chick starvation, but also to increase adult and juvenile survival, is likely to become a more common practice in the new species management framework (DOC, 2020), providing opportunities for ongoing research, evaluation, and redirection of conservation effort where necessary. Given the widespread threats many seabird species face, the use of rehabilitation in an attempt to enhance survival and achieve desired conservation outcomes is becoming more prevalent. Managers should endeavor to interrogate both rehabilitation and field databases to evaluate whether successful rehabilitation outcomes translate to measurable conservation gains in free-ranging populations.

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CONFLICT OF INTEREST
The authors declare no potential conflict of interest.

AUTHOR CONTRIBUTIONS
Melanie J. Young and Bryony Alden conceptualized the study; Bryony Alden, Melanie J. Young, and Julia Reid collected data; Melanie J. Young and Bryony Alden analyzed the data and wrote the first draft; Yolanda van Heezik and Philip J. Seddon supervised the project, provided feedback and edited subsequent drafts with Julia Reid.

ETHICS STATEMENT
Monitoring and interventions were undertaken as part of the Department of Conservation’s (DOC) yellow-eyed penguin monitoring programme overseen by DOC’s Coastal Otago and Murihiku District Offices. All birds were marked according to New Zealand National Bird Banding Scheme (NZNBBS) best practice by approved banders or transponder best practice guidelines approved by DOC’s Animal Ethics Committee. Rehabilitation was undertaken by staff at Penguin Place Conservation Reserve under a Wildlife Act 1953 permit issued by DOC (38615-FAU).

DATA AVAILABILITY STATEMENT
Application for access to data from the Yellow-eyed Penguin Database can be made to d.houston@doc.govt.nz (D. Houston, Department of Conservation) and to info@penguinplace.co.nz for access to the rehabilitation database.

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