Obtaining meaningful comparisons of nest success: data from New Zealand robin (*Petroica australis*) populations

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Abstract: Nest success, the proportion of clutches resulting in one or more fledglings, is a key indicator for assessing the effect of management on bird populations. However, the figures reported for New Zealand populations are usually "apparent nest success", the number of successful nests divided by the total number found. Apparent nest success invariably overestimates the true success rate, and the degree of bias depends on the population and monitoring regime. Consequently, apparent nest success rates cannot be reliably compared. We used Stanley's (2000) method for estimating stage-specific daily survival probabilities for New Zealand robin (*Petroica australis*) nests at Tiritiri Matangi, Paengaroa, Boundary Stream and Pureora. We show how Stanley's method can be used to eliminate biases, to calculate point estimates and confidence intervals for nest success, and to model the factors affecting nest success. At Pureora, where monitoring was extremely intensive, the apparent overall nest success (39%) was close to that estimated from daily survival probabilities (37%). Apparent nest success rates were extremely biased for the other populations due to less intensive monitoring, with the bias exacerbated by changes in survival probabilities with season and/or stage of the nesting cycle. Modelling the data showed that failure rates were: (1) higher early in the breeding season for at least some mainland populations, (2) different for incubation and nestling stages, with the pattern depending on the season (early or late) and type of predator, and (3) substantially lowered by predator control at Pureora, with the impact varying between sites and stages. Taking these factors into account, the estimated nest success (and 95% confidence limits) was 60% (44-74) at Pureora after predator control, 47% (23-73) at Boundary Stream, 37% (26-49) at Tiritiri Matangi, 25% (11-48) at Paengaroa, and 25% (17-35) at Pureora without predator control.

Introduction

Nest success is defined as the proportion of clutches laid that result in one or more offspring fledged. Estimates of nest success have been used extensively in avian population biology, and are becoming increasingly important in New Zealand for assessing effects of conservation management, particularly predator control (Clout *et al.*, 1995; Innes *et al.*, 1999). Estimates of the number of fledglings produced per female are more useful for studying population dynamics. However, birds (especially altricial species) can repeatedly re-nest after failures, so large differences in nest success rates may not be reflected in numbers of fledglings produced. Estimates of nest success therefore provide a more sensitive indicator of the effectiveness of management, and also a more sensitive indicator of differences among habitats.

Despite the importance of nest success, most New Zealand workers are not using reliable methods to estimate it. The nest success rates listed in reports are usually "apparent success", the number of successful nests divided by the total number found. This invariably overestimates nest success because nests that fail shortly

after laying are underrepresented in the sample, a problem that has been recognised since the 1950s (e.g. Snow, 1955; Hammond and Forward, 1956). As well as being inaccurate, apparent nest success cannot be reliably compared because the degree of bias will vary for different species, habitats, and monitoring regimes. Green (1989) provided a simple equation that can potentially be used to transform apparent nest success rates into true nest success rates. However, Green's (1989) equation assumes that the number of nests available to be found at any time is independent of how many have been found already. This is clearly not the case for intensively monitored populations, and Green's (1989) equation would overcompensate for the bias in such situations, resulting in underestimation of nest success. The standard method of avoiding bias is to calculate daily survival probabilities for nests (Mayfield, 1961, 1975).

Obtaining a Mayfield estimate involves tallying the number of exposure days for each nest. This is the interval between the date on which the nest was discovered and the date it failed, succeeded (one or more young fledged), or was last visited. The estimated daily survival probability, $\hat{p}$, is 1 – (number of nest failures)/(number of exposure days). The nest success rate is $\hat{p}^{\,t}$, where t is the number of days from egg laying to fledging. The exact number of exposure days before failure is often unknown, so Mayfield (1975) assumed that failure occurred midway between the last two checks. Miller and Johnson (1978) noted that this midpoint assumption leads to bias if intervals are long and/or survival probabilities are low. They suggested assuming the number of exposure days was 40% of the interval between checks rather than 50%. Johnson (1979) showed that the Mayfield estimate was a maximum likelihood estimator of nest success and derived its standard error. He also developed a maximum likelihood estimator for the number of exposure days for failed nests, avoiding the need for the 50% or 40% rule.

The key assumption of Mayfield's (and Johnson's) method is that the daily survival probability is constant. One source of violation is that the survival probability may change over the nesting period. It is possible to address this by calculating survival probabilities separately for the incubation and nestling stages (Mayfield, 1975). However, unless nests are checked daily, it is often unclear how many exposure days to assign to each stage and whether nests failed before or after hatching. Stanley (2000) recently developed an iterative method for obtaining joint estimates of stage-specific daily survival probabilities even if the exact time of transition from one stage to the next is unknown. Stanley's method therefore extends the methods of Mayfield and Johnson so that it is possible to estimate daily survival probabilities for the incubation and nestling stages separately, and to do so without any *ad hoc* assumptions about transition time or time of failure.

In this paper, we use Stanley's method to model and estimate daily survival probabilities using recent data collected for New Zealand robins (*Petroica australis*). Robins are now being used as an indicator species in New Zealand (Powlesland, 1997). This involves (1) obtaining data from mainland populations with and without management (Powlesland *et al.*, 1999; Speed and Burns, 1999), and (2) obtaining data from robins reintroduced to mainland locations (Armstrong, 2000; Howard and Christensen, 2001; Raeburn, 2001). Nest success rates are a key measure in these studies. Nest success rates have now been reported from a range of robin populations (Wiles, 2000), but in all cases the figures given are apparent nest success. We therefore calculated daily survival probabilities from a sample of populations in order to obtain estimates of nest success that could be reliably compared. We analysed data from recently reintroduced populations at three locations: Tiritiri Matangi (an offshore island), Paengaroa (a small mainland restoration area), and Boundary Stream (a larger mainland restoration area). We also analysed data from two sites in Pureora Forest Park, comparing times when predator control was and was not in place. For each location, we first constructed alternative models to assess what factors affected daily survival probabilities, and then estimated the nest success from those probabilities using the best model.

Methods

Species and populations

Tiritiri Matangi (36°36'S, 174°53'E) is a 220 ha island in the Hauraki Gulf, 3.5 km east of Whangaparaoa peninsula and 28 km north of Auckland, New Zealand. Farming ceased on Tiritiri Matangi in 1971, at which time the island had about 15 ha of remnant broadleaf forest in gullies and coastal areas (Mitchell, 1985). Most of the remainder of the island was planted with native trees from 1983-1995. The only mammals on Tiritiri Matangi were kiore (*Rattus exulans*), which were eradicated in 1993. Robins were reintroduced in 1992, 44 birds being translocated from the Mamaku Plateau in April (Armstrong, 1995). A further 14 were translocated from the Mamaku Plateau in June 1993. The population at the start of the breeding season expanded from 33 birds in 1992-1993 to 65 birds in 1996-1997, and subsequently seemed to be constrained at that level by the available habitat (Armstrong and Ewen, 2002).

Paengaroa Scenic Reserve (39°39'S, 175°43'E) is a 101 ha forest block 8 km southwest of Taihape. It

consists of a river terrace and south-facing slope running from 520 to 706 m, all covered by podocarp and broadleaf forest. The reserve is fenced to exclude ungulates, and bait stations filled with brodifacoum cereal pellets have been used since 1992 to control possums. There is a line of bait stations near the perimeter, plus two additional lines running through the reserve. The stations are approximately 100 m apart on all lines, giving 97 in total and an average of 0.96 per ha. Robins were reintroduced in 1999, 40 being translocated from Waimarino forest in March and April. The population at the start of the breeding season declined from 19 in 1999-2000 to 14 in 2000-2001.

Boundary Stream Scenic Reserve (39°06'S, 176°48'E) is an 800 ha forest block 45 km north of Napier. It is largely covered by broadleaf and podocarp forest, and since 1996 has had an intensive pest management programme targetting both predators and herbivores. There are possum bait stations throughout the reserve at approximately 150 m intervals (0.44 per ha). Brodifacoum baits have been used for most of the project, but pindone is now being used. Live and kill traps are used to control cats and mustelids. Robins were reintroduced in 1998, 28 birds being translocated from the Tarawera Conservation Area from March to May (Howard, 1998). The population at the start of the breeding season expanded from 26 birds in 1998-1999 to about 60 in 2000-2001.

The Pureora data for this study came from the Tahae (38°24'S, 175°38'E) and Waimanoa (38°33'S, 175°42'E) study sites, both of which are podocarp broadleaf forest. The Tahae study site (and surrounding area totalling 16 587 ha) received an aerial drop of 1080 carrot baits in September 1996, and the Waimanoa site (and surrounding area totalling 8577 ha) received an aerial poison drop of 1080 carrot baits in August 1997. These poison drops were to control possums, but rat populations were decimated as well. Robins had persisted at both sites in the absence of predator control, but their abundance appears to have been limited by predation. Powlesland *et al*. (1999) have already compared the apparent nest success at these sites in the presence and absence of predator control. In this paper we re-analyse their data to obtain estimates of nest success from daily survival probabilities.

Monitoring

At Tiritiri Matangi all robin pairs were monitored over the first five years, except for a few pairs missed in 1995-1996 and 1996-1997. The number of pairs monitored increased from 7 in 1992-1993 to 23 in 1996-1997. At Paengaroa, all pairs were monitored in 1999-2000 (9) and 2000-2001 (6). At Boundary Stream, all pairs were monitored in 1998-1999 (6) and 1999-

2000 (8). At Tahae, 8 pairs were monitored in 1996-1997 (1080 drop) and 23 pairs in 1997-1998 (no 1080 drop). At Waimanoa, 14 pairs were monitored in 1996-1997 (no 1080 drop) and 11 pairs in 1997-1998 (1080 drop).

The monitoring procedure varied among locations. On Tiritiri Matangi, monitoring was designed to measure the number of fledglings produced by each pair. We therefore attempted to ensure that all nests were detected before fledging, but not necessarily at an early stage. Nests were checked regularly (weekly or more frequently) when young were due to fledge, but often less frequently during the incubation and early brooding stages. At Paengaroa and Boundary Stream, all pairs were checked on a weekly basis throughout the breeding season, and their nests checked weekly once detected. At Pureora, pairs were checked at least once a week, and nests were checked at least every 3 days once detected.

We usually found nests by feeding mealworms to the male, who would normally call the female off the nest to feed her. (Males sometimes eat the worms themselves, particularly if fed more than 50 m from the nest, and occasionally feed females on the nest.) We then watched the female until we found the nest, repeating the feeding procedure if necessary. If a female was observed continuously for about 30 minutes and did not have a brood patch, we concluded that she did not have a nest. The contents of low nests could be checked by direct observation, whereas the status of high nests (eggs, chicks, or failed) was determined by observing the parents.

Collation of data

Stanley's model codes each interval between checks according to the outcome (coded 1 0 for survived or 0 1 for failed), the duration between checks (number of days), and stage(s) of the nesting cycle. Intervals between checks can be divided into 5 types [called "nest types" by Stanley (2000)] according to the stage(s) of the nest when checked: Type A (both checks during egg laying), Type B (first check during egg laying, second check during incubation), Type C (both checks during incubation), Type D (first check during incubation, second check after hatching), and Type E (both checks after hatching). Types A and B are most relevant to species that lay a large clutch over many days. Robin clutches are only 2-3 eggs, and we found few clutches during egg laying. Consequently, we only considered interval types C-E, and treated the few checks that occurred during egg laying as being during incubation. A nest might contribute several intervals to the data set. For example, a nest might be found during incubation, still be at the incubation stage 8 days later, have hatched when checked 5 days later, still have live chicks 3 days

later, and have failed 7 days later. This nest would be coded 1 0 8 C 1 0 5 D 1 0 3 E 0 1 7 E. The chicks in another nest might have already hatched when the nest was first found, and fledge 6 days later. This nest would be coded 1 0 6 E.

For successful nests, the number of days in the last interval should only include those up to the time of fledging. It is therefore necessary to estimate fledging dates. We estimated fledging dates from the feather development of chicks when last checked in the nest, on the behaviour of the chicks when checked after fledging, and from the date of hatching if known, assuming 21 days in the nest (Powlesland, 1997). For failed nests, it is necessary to estimate the stage expected at the last check. That is, if a nest was checked during incubation, and found to have subsequently failed, it is necessary to categorise the interval as Type C or D. We considered the interval to be Type D if the last check was 19 or more days after eggs were first discovered, 19 days being a typical incubation period for robins (Powlesland, 1997). We considered the interval to be Type C if less than 19 days had elapsed since the earliest possible laying date, i.e., the date when the female was last observed not to have a nest. In some cases neither criterion applied, and it remained ambiguous as to whether the interval should be Type C or D. In these cases we assumed that eggs were laid at the midpoint of the possible range of dates, and assumed that hatching would have taken place 19 days later.

Model selection and parameter estimation

Once the nest checks have been converted into alpha-numeric code as shown above, these data can be pasted into the Stanley's program, replacing the sample data included. The program can be downloaded from Ecological Archives at http://www.esapubs.org/archive/ecol/E081/021/default.htm. The program uses the NLIN procedure in SAS, and therefore can be run by pasting the code (including the data) into the SAS editor. We used SAS Version 8.

The output generated includes estimates of the daily survival probability, $\hat{p}$, for each stage, the associated standard error, $se(\hat{p})$, and the estimated correlation, r, between survival rates at different stages. The iteration routine in the program occasionally converges on an incorrect $\hat{p}$ value, producing a value greater than 1 or producing a value of 1 when this is incorrect. It is easy to check whether a $\hat{p}$ value of 1 is correct. For example, if $\hat{p} = 1$ for the incubation stage, then there should be no failures for Type C intervals. We found that convergence problems could be fixed easily by changing the starting $\hat{p}$ values used in the iteration from 0.90, as used in Stanley's code, to 0.99. Analysis of simulated data has shown that the $\hat{p}$ values estimated by the program are otherwise close to the true

values (Stanley, 2000).

The confidence intervals given with the SAS output are based on a t-distribution, which is not sensible for survival rates, and should not be used (Stanley, 2000). A sensible confidence interval can be obtained using a log-odds transformation on $\hat{p}$, and assuming the transformed variable is normally distributed (Burnham *et al.*, 1987: p. 214). Using this method, the approximate 95% confidence interval is given by

$$\hat{p}_L = \frac{\hat{p}}{\hat{p} + (1-\hat{p})C}$$

and

$$\hat{p}_U = \frac{\hat{p}}{\hat{p} + (1-\hat{p})/C}$$

where

$$C = \exp\left[\frac{2se(\hat{p})}{\hat{p}(1-\hat{p})}\right]$$

Because we did not have Type A or Type B intervals, we removed the lines of the program attempting to calculate a survival rate for the egg-laying stage. We therefore obtained daily survival rates for only the incubation stage ($\hat{p}_1$) and the nestling stage ($\hat{p}_2$). If the durations of the incubation stage (t_1) and nestling stage (t_2) are known, the estimated probability of a nest surviving from egg laying to fledging is

$$\hat{p}_1^{\,t_1} \hat{p}_2^{\,t_2}$$

To obtain a confidence interval for this estimate the standard error is also needed. Using the delta method (Seber, 1982: pp. 7-8), the approximate standard error is

$$\sqrt{\left(se(\hat{p}_1)\frac{\partial\left(\hat{p}_1^{\,t_1}\hat{p}_2^{\,t_2}\right)}{\partial\hat{p}_1}\right)^2 + \left(se(\hat{p}_2)\frac{\partial\left(\hat{p}_1^{\,t_1}\hat{p}_2^{\,t_2}\right)}{\partial\hat{p}_2}\right)^2 + 2\mathrm{cov}\left[\hat{p}_1\hat{p}_2\left(\frac{\partial\left(\hat{p}_1^{\,t_1}\hat{p}_2^{\,t_2}\right)}{\partial\hat{p}_1}\right)\left(\frac{\partial\left(\hat{p}_1^{\,t_1}\hat{p}_2^{\,t_2}\right)}{\partial\hat{p}_2}\right)\right]}$$

where

$$\frac{\partial\left(\hat{p}_1^{\,t_1}\hat{p}_2^{\,t_2}\right)}{\partial\hat{p}_1} = t_1\hat{p}_1^{\,t_1-1}\hat{p}_2^{\,t_2}$$

and

$$\frac{\partial\left(\hat{p}_1^{\,t_1}\hat{p}_2^{\,t_2}\right)}{\partial\hat{p}_2} = t_2\hat{p}_2^{\,t_2-1}\hat{p}_1^{\,t_1}$$

and

$$\mathrm{cov}\left[\hat{p}_1\hat{p}_2\right] = r.se(\hat{p}_1).se(\hat{p}_2)$$

Table 1. Analysis assessing factors likely to cause year-to-year variation in stage-specific daily survival probabilities of New Zealand robin nests on Tiritiri Matangi Island from 1992-1993 to 1996-1997.

Model[1]	K[2]	AIC[3]	Δ_i[4]	W_i[5]
year*stage	10	261.40	2.75	0.15
kiore*stage	4	262.26	3.61	0.10
trans*stage	**4**	**258.65**	**0.00**	**0.60**
stage	2	261.96	3.31	0.11
year	5	269.57	10.92	0.00
kiore	2	266.63	7.98	0.01
trans	2	265.45	6.80	0.02
constant	1	267.13	8.48	0.01

[1]Candidate models for factors affecting daily nest survival probabilities, with best model shown in bold (see text for explanation of models).
[2]Number of parameters in model.
[3]Akaike's Information Criterion.
[4]Difference in AIC value from that of the best model.
[5]Akaike weights, indicating the relative support for the models ($W_i = e^{-\Delta_i/2} / \sum e^{-\Delta_i/2}$).

Once the standard error is calculated, a 95% confidence interval can be obtained using the log-odds transformation as shown above. We used this method to obtain confidence intervals for the probability of robin nests successfully fledging young, assuming an incubation period of 19 days and a nestling period of 21 days.

Before estimating survival probabilities and associated confidence intervals, it is important to determine the best model for survival rates. In particular, if the daily survival rate is similar during incubation and nestling stages, it will be better to use a combined daily survival rate rather than separate stage-specific survival rates. It is simple to create a model with a combined survival rate using Stanley's (2000) program. It is just a matter of re-labelling intervals so they are all Type C or Type E (it does not matter which). The output from the two models (combined survival rate and stage-specific survival rates) can then be compared to determine which is the best model based on Akaike's Information Criterion, or AIC (Burnham and Anderson, 1998). The SAS output from Stanley's (2000) program includes the "Weighted Loss" or "Objective", which is equivalent to the negative of the log-likelihood of the model, or $-\log_e(L)$. $AIC = -2 \log_e(L) + 2k$, where k is the number of estimable parameters. In our scenario, k = 2 for a model with separate survival rates for incubation and nestling stages and no other factors, and k = 1 for a model with a combined survival rate.

The best model is that with the lowest AIC, which indicates the best compromise between fit to the data (always higher in a more complex model) and simplicity (fewer parameters). In addition to specifying the best model, AIC values can be used to assess the relative support for different models and therefore the ambiguity in model selection. The relative support for the models, based on likelihood theory, is indicated by their Akaike weights (Burnham and Anderson, 1998). These are calculated from the differences in AIC values in comparison to the best model (see Table 1 for calculation).

As well as simplifying the model by collapsing stages, we increased the complexity of the model by calculating separate survival rates for different years, seasons, and habitats, for recently-translocated females versus other females, and for poisoned and unpoisoned sites. This involved modifying the data sets to create additional interval types, and adding additional terms to Stanley's (2000) program to calculate separate survival rates for each situation.

Table 2. Estimated stage-specific daily survival probabilities and success rates of New Zealand robin nests on Tiritiri Matangi Island.

	n[1]	$\hat{p}_1$[2]	$\hat{p}_2$[3]	$\hat{p}_1^{t_1} \hat{p}_2^{t_2}$[4]
All females[5]	123	0.963 (0.943-0.975)	0.987 (0.978-0.992)	0.37 (0.26-0.49)
Recently-translocated[6]	17	0.964 (0.909-0.986)	0.960 (0.909-0.986)	0.21 (0.07-0.48)
Other[6]	106	0.959 (0.950-0.967)	0.992 (0.983-0.996)	0.38 (0.27-0.50)

[1]Number of nests.
[2]Estimated daily survival probability (and 95% Confidence Limits) during incubation stage.
[3]Estimated daily survival probability during nestling stage.
[4]Estimated probability of survival from egg laying to fledging (and 95% Confidence Limits), assuming a 19 day incubation stage and 21 day nestling period.
[5]From model {stage} (Table 1).
[6]From model {trans*stage} (Table 1).

Table 3. Analysis assessing effects of season and habitat on stage-specific daily survival probabilities of New Zealand robin nests on Tiritiri Matangi, using data for all years combined except for recently-translocated females. Symbols as for Table 1.

Model	K	AIC	Δ_i	W_i
habitat*season*stage	12	186.14	3.41	0.13
habitat*stage	**6**	**182.73**	**0.00**	**0.76**
season*stage	4	188.09	5.36	0.05
stage	2	188.55	5.82	0.04
habitat*season	6	195.51	12.78	0.00
habitat	3	191.04	8.31	0.01
season	2	198.11	15.38	0.00
constant	1	197.24	14.51	0.00

Table 5. Analysis assessing effects of year and season on stage-specific daily survival probabilities of New Zealand robin nests at Paengaroa from 1999-2000 to 2000-2001. Symbols as for Table 1.

Model	K	AIC	Δ_i	W_i
year*season*stage	8	97.73	2.42	0.21
year*season	4	103.81	8.50	0.01
year*stage	4	108.01	12.70	0.00
season*stage	**4**	**95.31**	**0.00**	**0.72**
year	2	105.36	10.05	0.00
season	2	100.90	5.59	0.04
stage	2	105.19	9.88	0.01
constant	1	103.78	8.47	0.01

Models considered for each location

For Tiritiri Matangi, we initially assessed factors likely to cause year-to-year variation in nest survival rate, ignoring potential effects of habitat and season (Tables 1 and 2). Under the most complex model {year*stage}, a separate survival rate was calculated for each year for each stage. We considered a simpler model {kiore*stage} where survival rates were different only for the first year after reintroduction, before kiore were eradicated. Kiore are known nest predators, and signs at some nests in the first year indicated kiore predation. It therefore made sense to suggest that the first year was atypical. We also considered a model {trans*stage} where survival rates were calculated separately for females in their first year after translocation in comparison to other females. Recently-translocated

females included all females in the first year, but also included 7 of the 12 females breeding in the second year. We created a model {stage} where survival was constant between years and females. We also simplified each of these models by removing stage-specific survival rates, e.g., model {year*stage} was simplified to {year}.

After the first model selection procedure, we did further modelling to assess the effect of season (early or late) and habitat using years that could be combined (Table 3 and 4). We considered nests to be early if laid before 15 October, the median date, or late otherwise. We calculated the laying date based on the approximate hatching date (assuming 19 days incubation) or fledging date (assuming 40 days total), and used the midpoint of possible laying dates for clutches that did not hatch. We divided nests into three categories according to habitat: those in Bush 1 (2.5 ha), those in Bush 22

Table 4. Estimated stage-specific daily survival probabilities and success rates of New Zealand robin nests in different habitats on Tiritiri Matangi Island, excluding recently-translocated females. Symbols as for Table 2.

	n	$\hat{p}_1$	$\hat{p}_2$	$\hat{p}_1^{t_1} \hat{p}_2^{t_2}$
Bush 1[1]	31	0.958 (0.913-0.980)	0.969 (0.943-0.983)	0.23 (0.11-0.41)
Bush 22[1]	33	0.956 (0.907-0.980)	1.000 (1.000-1.000)	0.43 (0.19-0.70)
Other patches[1]	42	0.972 (0.937-0.987)	0.993 (0.976-0.998)	0.50 (0.30-0.70)

[1]From model {habitat*stage} (Table 3).

Table 6. Estimated stage-specific daily survival probabilities and success rates for early (initiated before 15 October) and late New Zealand robin nests at Paengaroa. Symbols as for Table 2.

	n	$\hat{p}_1$	$\hat{p}_2$	$\hat{p}_1^{t_1} \hat{p}_2^{t_2}$
early[1]	13	0.902 (0.807-0.953)	0.979 (0.902-0.996)	0.09 (0.02-0.37)
late[1]	22	1.000 (1.000-1.000)	0.962 (0.928-0.981)	0.45 (0.21-0.67)
overall[2]	35			0.25 (0.09-0.52)

[1]From model {season*stage} (Table 5).
[2]Weighted average based on estimated number of early and late nests (see text).

(3.8 ha), and those in smaller patches (0.3-1.0 ha). We created models that considered these factors both together and in isolation. As above, we considered these factors in combination with stage-specific survival rates, but also with stage-specific survival removed.

Once we found the best model describing the data, we used parameter estimates from that model to obtain point estimates and 95% confidence intervals for nest success. We also calculated nest success using the model {constant}, which assumes a constant survival probability, and using a Mayfield estimate. We used a "Mayfield 40-50" method whereby we used the 50% rule for intervals of 10 days or less and the 40% rule for longer intervals.

For Paengaroa and Boundary Stream, we used a similar approach to that used for Tiritiri Matangi but only considered the effects of year, season, and stage (Tables 5-8). There were two years and two seasons in both cases, and we calculated the median laying date separately for each population. Nesting at Paengaroa was monitored continuously throughout the first breeding season, but did not start until later in the second breeding season. We therefore used the median laying date from the first year, 16 October. Nesting at Boundary Stream was monitored continuously throughout both breeding seasons so we used the median date for the combined data set, 1 November. For the Pureora data, we assessed the effects of poison (1080 dropped that year) and site (Tahae or Waimanoa), assuming no difference between years (Tables 9-10). We could not assess the effects of both site and year because these are confounded.

Results

Tiritiri Matangi

On Tiritiri Matangi 123 nests were found over the 5 breeding seasons, of which 71 fledged one or more young. The apparent nest success is therefore 58%. Under the Mayfield 40-50 method there were 2281 exposure days. The daily survival rate is therefore 0.977 (1-52/2281), and the standard error using Johnson's (1979: p. 653) estimator is 0.0031. Stanley's method produces similar estimates if a constant survival probability is assumed. The daily survival rate is estimated to be 0.978 with a standard error of 0.0031, which yields a confidence interval (using the log-odds transformation) of 0.971-0.984. When extrapolated to a 40-day period (19 days incubation plus 21 days nestling), this gives an estimated nest success rate of 41% with a 95% confidence interval of 31-51%.

Modelling the data with Stanley's program shows, however, that the daily survival rate is unlikely to be constant between stages (Table 1). Adding stages to the model substantially lowers the AIC, indicating that survival rates should be calculated separately for incubation and nestling stages. The model {stage}, which assumes that stage-specific survival rates are constant, gives daily survival probabilities of 0.963 and 0.987 for the incubation and nestling stages respectively (Table 2). With intervals of 19 and 21 days, this means that a nest has only a 48% chance of surviving from egg laying to hatching, but has a 76% chance of surviving from hatching to fledging. This gives a 37% nest success rate, in comparison to the 41% rate estimated when stages are combined. The combined model slightly overestimates nest success because monitoring was biased toward the stage when the daily survival rate is higher. Monitoring was biased toward the nestling stage because nests were often undetected for all or part of the incubation period but were monitored through to fledging once detected.

Of the models that considered year-to-year variation in survival rates, the best model was {trans*stage}, where daily survival rates were different for nests of recently-translocated females, and differed between stages, but were otherwise constant (Table 1). The estimated nest success rate was only 21% for recently-

Table 7. Analysis assessing effects of year and season on stage-specific daily survival probabilities of New Zealand robin nests at Boundary Stream from 1998-1999 to 1999-2000. Symbols as for Table 1.

Model	K	AIC	Δ_i	W_i
year*season*stage	8	73.18	9.36	0.00
year*season	4	66.94	3.13	0.06
year*stage	4	68.39	4.57	0.03
season*stage	4	66.44	2.62	0.07
year	2	64.90	1.09	0.16
season	**2**	**63.82**	**0.00**	**0.28**
stage	2	64.97	1.15	0.16
constant	1	64.07	0.25	0.24

Table 8. Estimated daily survival probabilities and success rates for early (initiated before 1 November) and late New Zealand robin nests at Boundary Stream. Symbols as for Table 2.

	n	$\hat{p}$	$\hat{p}^{t_1+t_2}$
early[1]	15	0.974 (0.947-0.987)	0.35 (0.11-0.59)
late[1]	15	0.989 (0.971-0.996)	0.65 (0.31-0.85)
overall[2]	30		0.47 (0.26-0.69)

[1]From model {season} (Table 7).
[2]Weighted average based on estimated number of early and late nests (see text).

translocated females in comparison to 38% for other females. The difference is at the nestling stage, with nests of recently-translocated females having a daily survival rate of 0.960 in comparison to 0.992 for other females (Table 2).

For the data set excluding recently-translocated females, the best model was {habitat*stage}, where stage-specific survival rates were calculated separately for the two largest patches (Bush 1 and Bush 22) and for the smaller patches combined (Table 3). Season (early versus late nesters) did not have a significant effect. The difference between habitats is due to the low survival rate during the nestling stage in Bush 1 (0.969) in comparison to that in Bush 22 (1.000) or the other patches (0.993) (Table 4). The daily survival probabilities during incubation were 0.958, 0.956 and 0.972 for Bush 1, Bush 22, and the other patches respectively. These figures indicate that most nest failures occur during the incubation stage, except in Bush 1.

Paengaroa

At Paengaroa 35 nests were found over the 2 breeding seasons, of which 15 fledged one or more young. The apparent nest success is therefore 43%. Stanley's method estimates the daily survival probability to be 0.969 if a constant probability is assumed, giving 29% nest success rate over a 40-day period. However, model selection showed {season*stage} to be the best model, indicating that the daily survival probability changed over the course of the breeding season and between stages (Table 5). Season was the most important variable, early nests having an estimated success rate of only 9% in comparison to 45% for later nests (Table 6). For early nests, the daily survival probability was much lower during the incubation stage (0.902) than the nestling stage (0.979). In contrast, late nests had a 100% daily survival probability during incubation in comparison to 0.963 for the nestling period. Because monitoring started late in 2000-2001, only 4 of the 16 nests found that year were initiated before 15 October. We therefore cannot confirm from these data that early nests suffered similarly poor success in 2000-2001 as in 1999-2000. However, any young that had fledged from early nests would have been detected by the subsequent monitoring unless they died immediately after fledging. No such fledglings were found, strongly suggesting that nest success was zero or negligible for early nests in 2000-2001, similar to 1999-2000.

The seasonal change in nest success introduces another source of bias when calculating overall nest success rates, regardless of whether monitoring is consistent throughout the breeding season. A higher proportion of nests will be detected when the success rate is high, biasing the sample toward those periods

and causing nest success to be overestimated. An unbiased estimate of overall nest success can be obtained by weighting the early and late nest success rates according to the estimated number of nests. This can be expressed as

$$\hat{p} = \frac{\hat{n}_e \hat{p}_e + \hat{n}_l \hat{p}_l}{\hat{n}_e + \hat{n}_l}$$

where $\hat{n}_e$ and $\hat{n}_l$ are the estimated number of early and late nests, and $\hat{p}_e$ and $\hat{p}_l$ are the nest success rates during those periods. We are confident that we knew the number of successful nests, as it is extremely unlikely that a nest could have been undetected right through to fledging. The number of early and late nests can therefore be estimated by dividing the number of successful nests by the estimated success rate, i.e. $\hat{n}_e = s_e / \hat{p}_e$ and $\hat{n}_l = s_l / \hat{p}_l$ where s_e and s_l are the number of successful nests in the early and late periods. Substituting this into the above equation gives

$$\hat{p} = \frac{\hat{p}_e \hat{p}_l (s_e + s_l)}{s_e \hat{p}_l + s_l \hat{p}_e}$$

The approximate standard error for this estimate can be obtained using the delta method, giving

$$\sqrt{\left(\frac{se(\hat{p}_e) \hat{p}_l^2 s_e (s_e + s_l)}{(s_e \hat{p}_l + s_l \hat{p}_e)^2} \right)^2 + \left(\frac{se(\hat{p}_l) \hat{p}_e^2 s_l (s_e + s_l)}{(s_e \hat{p}_l + s_l \hat{p}_e)^2} \right)^2}$$

At Paengaroa there were 3 successful early nests (s_e) and 12 successful late nests (s_l). The values of $\hat{p}_e$, $se(\hat{p}_e)$, $\hat{p}_l$ and $se(\hat{p}_l)$ were 0.09, 0.07, 0.45 and 0.12 respectively. Plugging these values into the above equations gives an overall nest success of 25%, with a 95% confidence interval (based on the log odds transformation) of 9-52% (Table 6).

Boundary Stream

At Boundary Stream 30 nests were found over the two breeding seasons, of which 18 (60%) fledged one or more young. Stanley's method estimates the daily survival probability to be 0.983 if a constant probability is assumed, giving a 51% nest success rate over a 40-day period. Model selection produced ambiguous results for this data set (Table 7). The model {season} had the lowest AIC, but {constant}, {year} and {stage} also had reasonable support ($\Delta_i < 2$). Models with more than one factor all had less support, but this probably means there were too few data to model all the important factors rather than meaning that only one factor is important. Under {season}, the daily survival rate is

Table 9. Analysis assessing effects of poison (aerial 1080 operation) and site on stage-specific daily survival probabilities for New Zealand robin nests at two sites in Pureora Forest Park (Waimanoa and Tahae) in 1996-1997 and 1997-1998. Symbols as for Table 1.

Model	K	AIC	Δ_i	W_i
poison*site*stage	**8**	**592.70**	**0.00**	**0.53**
poison*site	4	597.02	4.32	0.06
poison*stage	4	593.65	0.95	0.34
site*stage	4	610.06	17.36	0.00
poison	2	597.04	4.34	0.06
site	2	611.16	18.46	0.00
stage	2	606.68	13.98	0.00
constant	1	609.30	16.60	0.00

estimated to be 0.974 for nests initiated before 1 November and 0.989 for later nests (Table 8). This gives nest success rates of 35% and 65% for early and late nests respectively. Using the same calculations as for Paengaroa, the estimated number of early and late nests is 23 (8/0.35) and 15 (10/0.65), giving an overall nest success of 47% with 95% confidence limits of 26-69%.

Pureora

At Pureora a total of 147 nests were found. At Tahae, 13 of 19 nests found in 1996-97 (with 1080 drop) fledged young, giving an apparent success rate of 68%, and 20 of 62 nests found in 1997-98 (no 1080 drop) fledged young, giving an apparent success rate of 32%. At Waimanoa, 20 of 32 nests found in 1997-98 (with 1080 drop) fledged young, giving an apparent success rate of 63%, and 5 of 34 nests found in 1996-97 (no 1080 drop) fledged young, giving an apparent success rate of 15%.

Modelling of daily survival rates shows that the poison drops were the critical factor affecting nest success, the overall estimated nest success rate being 60% with predator control and 25% without. The best model, however, is {poison*site*stage}, implying that there were also differences between the two sites and between stages of breeding (Table 9). In the absence of predator control, the daily survival rate at both sites was lower during the nestling stage than the incubation stage (Table 10). Combining the two sites, the daily survival rates without predator control were 0.977 during incubation, corresponding to 64% survival over a 19-day period, and 0.956 during the nestling stage, corresponding to 39% survival over a 21-day period. At Waimanoa, survival during both stages was substantially higher with predator control (Table 10). However, at Tahae this improvement was only apparent at the nestling stage. Combining data for both years and sites, the overall daily survival rate was estimated to be 0.981 and 0.979 during the incubation and nestling stages respectively, giving an overall nest success rate of 37%. This is close to the overall apparent success rate of 39% (58/147), and the estimated success rate was close to the apparent rate for most sites and years (Table 10).

Discussion

Modelling daily survival rates allowed us to assess the degree of bias associated with apparent nest success, to assess the uncertainty of our estimates, and to understand some of the factors affecting nest success.

The degree of bias clearly varies with monitoring intensity. With the intensive monitoring at Pureora (pairs checked at least weekly and nests checked at least every 3 days), the apparent nest success (39% overall) was only slightly higher than that estimated from daily survival probabilities (37% overall). The difference was much greater for the other populations: 58% *vs* 37% for Tiritiri Matangi, 43% *vs* 25% for Paengaroa, and 60% *vs* 47% for Boundary Stream.

Table 10. Estimated stage-specific daily survival probabilities and success rates of New Zealand robin nests at two sites in Pureora Forest Park, during the year of a 1080 operation and during the previous or following year when there was no operation. Symbols as for Table 2.

Site	1080	n	$\hat{p}_1$	$\hat{p}_2$	$\hat{p}_1^{t_1} \hat{p}_2^{t_2}$
Tahae[1]	yes	19	0.978 (0.936-0.993)	0.993 (0.969-0.998)	0.56 (0.29-0.81)
	no	62	0.981 (0.968-0.989)	0.964 (0.944-0.977)	0.32 (0.21-0.46)
Waimanoa[1]	yes	32	0.995 (0.979-0.999)	0.981 (0.962-0.990)	0.60 (0.41-0.76)
	no	34	0.969 (0.943-0.984)	0.935 (0.886-0.964)	0.13 (0.05-0.30)
combined[2]	yes	51	0.990 (0.977-0.996)	0.985 (0.972-0.992)	0.60 (0.44-0.74)
	no	96	0.977 (0.966-0.984)	0.956 (0.938-0.969)	0.25 (0.17-0.35)

[1]From model {poison*site*stage} (Table 9).
[2]From model {poison*stage} (Table 9).

This mainly reflects less intensive monitoring, and most of the bias could be was eliminated even if a constant daily survival probability was assumed. However, models assuming constant survival were also slightly biased due to changes in survival probability with season and/or stage of the nesting cycle. The effect of stage-specific survival will depend on the direction of the change and on the monitoring regime. Monitoring is usually biased toward the nestling stage because nests are often undetected until at least part way through the incubation stage, then monitored through to fledging once detected. This causes a positive bias in estimated nest success if the failure rate is higher during the incubation stage than during the nestling stage, as was the case on Tiritiri Matangi. Seasonal changes will always cause a positive bias in estimated success rates because a higher proportion of nests are detected (and therefore monitored) during periods with higher nest success.

While apparent nest success rates can be reasonably accurate with intensive monitoring, such monitoring is often impractical and may even affect the nest success rates being measured. With care, Stanley's method can be used to obtain accurate estimates of nest success with much less intensive monitoring. Analysis of the Tiritiri Matangi data showed that the Mayfield 40-50 method (assuming failures occur at the 40% mark between checks if greater than 10 days and at the 50% mark otherwise) gave very similar estimates to those of Stanley's method if daily survival probability was assumed to be constant. However, Stanley's method allowed us to eliminate the additional bias caused by stage-specific survival probabilities. In addition, the likelihood values calculated by Stanley's program allowed easy comparison of alternative models so that we could select an appropriate model for each population.

Powlesland (1997) provided protocols for monitoring robins. To these we can add some protocols for obtaining reliable estimates of nest success rates, which apply to all forest birds. First, we recommend the use of Stanley's program, which is easy to use and has advantages over both apparent nest success rates and the traditional Mayfield method. There are other methods for modelling age-specific survival and/or variation in survival rates (e.g. Heisey and Nordheim, 1995; Natarajan and McCulloch, 1999), but these are complex and require large data sets. Second, ensure that nests are checked close to fledging time to accurately determine if and when young fledge. This ensures that nests are classified accurately as successful or failed, and ensures that the number of exposure days during the nestling period (Type E interval) is accurate. Third, also concentrate checks around the likely hatching time to determine if and when young hatch. This is necessary to accurately assign intervals as Type C or Type D. It

is possible to predict hatching dates by candling (Weller, 1956) or floating (Westerkov, 1950) eggs although this may not be desirable. Fourth, ensure that there is a reasonable sample of monitoring during both the incubation and nestling periods, given that daily survival rates can be quite different during these periods. Fifth, monitor throughout the breeding season, given that survival rates may change over time.

To get accurate estimates of nest success, it is also necessary to have accurate data on incubation and nestling periods. It is therefore useful to find a sample of nests at the time of egg laying, to check these intensively around the likely hatching date and again around the likely fledging date. Daily survival rates can still be estimated without knowing incubation and nestling periods, however, and these are the best statistics for comparing predation pressure. Converting daily survival rates to nest success rates mainly serves to provide numbers that are easy to understand. The results from Pureora give us confidence that the 19- and 21-day periods used for robins gave good estimates of nest success. The apparent success rates from intensive monitoring were slightly higher than those calculated from daily survival probabilities, which is expected if the periods are accurate.

There are currently some limitations to the analyses we performed which readers should be aware of. First, AIC values become biased when sample sizes are low (Burnham and Anderson, 1998). This problem is usually overcome by calculating the corrected AIC

$$AIC_c = AIC + \frac{2k(k+1)}{n-k-1}$$

where k is the number of parameters and n is the sample size. It is unclear, however, what constitutes the sample size when calculating daily nest survival rates. It might be reasonable to use the number of nests as the sample size. In our analyses we simply reported the raw AIC, which would have been subject to some bias, particularly for the Paengaroa and Boundary Stream data sets. This bias can result in the selection of overly complex models. A second limitation is that there is currently no provision for modelling parallel effects of two variables without including the interaction between them. For example, survival might be higher in the second half of the breeding season with a similar proportional effect during incubation and nestling stages. The model {season+stage} would be superior to {season*stage} in this case, but there is no simple way of fitting the former model using Stanley's program. Finally, as with all analyses it is necessary to understand the underlying assumptions. The key assumption underlying our analysis is that survival rates are constant for all intervals in any category. This may be violated if there are changes over time, spatial variation, or

differences among pairs that are not accounted for. For survival analysis using mark-recapture data, goodness-of-fit procedures are available to assess whether these assumptions are likely to be valid (White and Burnham, 1999). Such procedures are not currently available for daily nest survival, so it is up to the biologist to assess whether the assumptions are reasonable based on his/her knowledge of the system. It is well recognised that the assumption of constant survival is unlikely to hold for colonial seabirds where mortality tends to occur catastrophically (Johnson and Shaffer, 1990). However, this assumption is probably reasonable for New Zealand forest birds as long as we consider factors that may cause spatial or temporal variation. A big advantage of Stanley's program, in comparison to the traditional Mayfield method, is that effects of season, habitat and management on nest survival can be taken into account.

There is no simple rule as to the number of nests that need to be sampled to estimate nest success, and the sample needed depends on the precision of estimate required. The wide confidence intervals obtained for Boundary Stream (23-73%) and Paengaroa (11-48%) with 30 and 35 nests respectively suggest that the total number of nests should be greater than this number. The sample size needed also depends on the number of factors that need to be considered. The analyses for Boundary Stream and Paengaroa show that the best model explaining data from a sample of 30-35 nests is unlikely to have more than 2 parameters.

Data for both Paengaroa and Boundary Stream suggest that nests were most vulnerable in the first half of the breeding season. This suggests that the impact of predators in those areas (probably rats, possums and mustelids) are greatest in spring rather than summer. This is confounded to some extent by changes in pest control regimes. Bait stations were not re-filled during the 1999 winter at Boundary Stream, and were not re-filled at the end of the 1999-2000 breeding season (December-February) at Paengaroa. In both cases, this could have allowed rat and possum numbers to increase prior to the second breeding season, potentially accounting for poor success of early nests. However, early nests had equally poor success in the first breeding seasons, when there had been no discontinuation of predator control. For Boundary Stream, the evidence for variation in nest success between years was almost as strong as the evidence for variation in nest success between seasons. The estimated nest success was lower in the second year (42%) than the first year (63%), which could be explained by the break in predator control in the 1999 winter. However, if this were the case we would expect to see the difference mainly at the beginning of the breeding season. Instead, the estimated nest success was similar for early nests (39% in 1999-2000, 33% in 2000-2001), but much lower for late nests in 2000-2001 (54%) than in 1999-2000 (80%).

Data for Tiritiri Matangi, Paengaroa, and Boundary Stream show that the vulnerability of robin nests may change between incubation and nestling stages, but that this may depend on the season and type of predator. Survival on Tiritiri Matangi was much lower during incubation, with few failures after hatching except in Bush 1. We suspect that ruru (morepork, *Ninox novaeseelandiae*) account for the higher nestling mortality in Bush 1 as they have consistently roosted in that bush, and that Indian mynas (*Acridotheres tristis*) are the main cause of failure during the incubation stage. In the absence of predator control, robin nests at Pureora had lower survival during the nestling period suggesting that mammalian predators had greatest impact at that stage. Late nests at Paengaroa had lower survival during the nestling stage than the egg stage, consistent with Pureora. However, early nests had much lower survival at the incubation stage than the nestling stage.

Taking all these factors into account, the estimated nest success rates were highest at Pureora with predator control (60%) and Boundary Stream (47%), and lowest at Pureora without predator control (25%) and at Paengaroa (25%). The Pureora analysis confirmed that predator control results in a substantial increase in nest success in the mainland areas, but also showed that the impact of predator control may vary between stages of the nesting cycle, and between sites. It is interesting that nest success on Tiritiri Matangi was intermediate to the other values (37%), and lower than that achieved with predator control at Pureora and Boundary Stream. One explanation is that avian predation pressure could be higher on Tiritiri Matangi than on the mainland (Armstrong *et al.*, 2000). Despite the small sample sizes for Paengaroa and Boundary Stream, there appears to be a strong contrast in nest success rates for these mainland restoration areas. Similar bait stations are used at the two locations, and there are actually more stations per ha at Paengaroa. One possible reason for the lower nest success at Paengaroa is that bait stations are not placed in a regular grid and there are gaps of up to 500 m between lines. The main reason may be that the smaller size of Paengaroa (about 1 km x 1 km in comparison to 4 km x 2 km for the main reserve at Boundary Stream) allows more rapid reinvasion by predators. Similarly, the effectiveness of the 1080 drops at Pureora may reflect the scale (16 587 ha and 8577 ha) of those operations.

Acknowledgements

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