

## A MODELLING APPROACH TO DETERMINE A TRANSLOCATION SCENARIO FOR THE ENDANGERED NEW ZEALAND FROG *LEIOPELMA HAMILTONI*

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A stage-structured population model was developed to predict which of nine hypothetical translocation scenarios was likely to produce the best outcome for the rare Hamilton's frog (*Leiopelma hamiltoni* McCulloch). Model outcome was measured in terms of population growth rate and probability of extinction. Only females were modelled. The model predicted that moving at least 20 female adult frogs was the best strategy, and moving subadult frogs alone, or no frogs at all was the worst in terms of mean growth rate of both populations combined. When the new population was considered separately, introducing subadults alone was the worst strategy in terms of mean growth rate and extinction probability. Extinction of the donor population was most likely when 40 adult females were removed, and the extinction risk was reduced when only 20 were removed. We consider the most reasonable management strategy - confirmed by the modelling and supporting qualitative data - is the translocation of 20 adult and 20 subadult female frogs (with the concurrent translocation of 40 males). This scenario provides a balance between risk of extinction in the donor population and probability of success in the translocated population.

*Key words:* amphibian conservation, population viability analysis, relocation

### INTRODUCTION

Hamilton's frogs (*Leiopelma hamiltoni*) are likely to have once been relatively widespread in New Zealand (Worthy, 1987), but are now present only on one small island in the Cook Strait at the top of New Zealand's South Island (Stephens Island: but see Bell *et al.*, 1998; Holyoake *et al.*, 2001). The estimated population size of *L. hamiltoni* on Stephens Island at the time of writing was approximately 300 individuals, almost entirely living in a rock-tumble fragment of total area less than 300 m<sup>2</sup> (Newman, 1990; Brown, 1994; Thomson, 1996; this paper). Three adult frogs are known to reside in a second fragment on Stephens Island, less than 70 m from the main rock tumble (Brown, 1994; Tocher & Brown, 2004).

Clearing of vegetation in the early 20th century destroyed most of the forest cover on Stephens Island, and generally improved conditions for the tuatara (*Sphenodon punctatus*). *L. hamiltoni* is now confined to the rock-tumble fragment (frog bank) by high numbers of predatory tuatara and severe weather conditions that are pronounced in the absence of forest. Recent data suggest the population could be increasing, and may be reaching carrying capacity. Density has apparently quadrupled from the 58 per 100 m<sup>2</sup> reported in the 1970s (Newman, 1990), to 220 per 100 m<sup>2</sup> (this paper).

Management options for *L. hamiltoni* include enhancement of habitat on Stephens Island, captive breeding, and

translocation of a specific cohort to a nearby predator-free island. Translocation to a nearby island with similar habitat is a priority management action for *L. hamiltoni* (Newman, 1996). Managers are faced with deciding how many frogs (and from which age groups) to remove from the only existing population in New Zealand in order to attempt the establishment of another. In particular, a combination of subadult and adult frogs ( $n=10$  in total) collected at random from the donor population (frog bank) each year for three years was being considered as a translocation strategy prior to the modelling exercise carried out here (Mike Aviss, Department of Conservation, *pers. comm.* 2002).

Three translocations have been previously carried out with *Leiopelma* spp. In 1992, twelve *L. hamiltoni* were transferred from the frog bank on Stephens Island to a man-made habitat 70 m away (Brown, 1994). Although several frogs returned to their original site (Tocher & Brown, 2004), a new population founded by three frogs that remained at the release site, seems to be establishing. One hundred *L. pakeka* were translocated to a forest remnant (Boat Bay) on Maud Island in 1984-85 (Bell *et al.*, 2004). *L. pakeka* was subject to a second translocation in 1997 when 300 individuals were translocated to Motuara Island from Maud Island (Tocher and Pledger, unpublished data).

Two main conservation lessons have emerged from these translocations. Firstly, individual growth rates of *L. pakeka* were remarkably high following translocations to both Boat Bay (Ben Bell, Victoria University of Wellington, *pers. comm.* 2001) and

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Motuara Island (unpublished data), presumably lowering age to first reproduction. Secondly, there is evidence that subadults are more likely to remain in the vicinity of the release site, following a translocation, than adults. Adult *L. hamiltoni* have homed over 70 m from the release site to their original capture site (Tocher & Brown, 2004).

Intensive monitoring of *L. hamiltoni* on Stephens Island began in July 1997 to gather data on population demographics and in particular to determine the stability of the *L. hamiltoni* population over a six-year study. Data on *L. hamiltoni* juvenile survival rates in the wild are sparse, and indicate high mortality between hatching and one year of age. Juveniles are thought to have specialized habitat requirements, are more prone to desiccation and may prefer moister locations compared to older animals (Bell, 1978; Newman, 1990; Thomson, 1996). As such, juveniles are not under consideration for translocation.

Appropriate conservation management decisions can only be addressed by combining our knowledge of the life history and current status of *L. hamiltoni* populations with predictions from population modelling. A tailor-made model constructed to simulate the *L. hamiltoni* population at the frog bank is used to compare various hypothetical translocation scenarios, and to identify important assumptions and parameters relating to *L. hamiltoni*. This will ultimately guide managers and future fieldwork. In particular, we constructed a population model representing two *L. hamiltoni* populations: a donor population and a new population formed by translocation. We modelled both populations simultaneously to determine which of nine hypothetical translocation scenarios was likely to produce the best outcome for *L. hamiltoni* in terms of both population growth and extinction probability.

## METHODS

### MODEL STRUCTURE

A density-dependent, stage-structured model (Burgman *et al.*, 1993; Caswell, 2001) was created using all available life history data for *L. hamiltoni* at the frog

bank. As is usual for populations in which the sex ratio is close to 1:1, only females were modelled. Two populations were considered simultaneously: a donor population (population 'D'; frog bank) from which frogs were removed to create a new population (population 'T'). The structure of the model was the same for the two populations, but the values for age at first reproduction (AFR) were allowed to be lower in population T.

We programmed the model in an Excel spreadsheet. There were three stages in the model: juveniles, subadults and adults. Time spent as a juvenile before becoming a subadult was estimated conservatively as 12 months, based on capture-recapture data collected from the frog bank. We used a "pre-breeding-census" model structure, which meant that the juvenile class contained those individuals that had survived their first year. The reason for this choice was to allow the annual fertility rate to be the product of the annual reproductive rate and first-year survival, thereby eliminating the need to specify these two parameters separately (Caswell, 2001). Time spent as a subadult before entering the adult stage was determined by the estimated mean and standard deviation of the age at first reproduction, using the 'variable stage duration' approach described in Caswell (2001).

Projections were made over a 30-year period, the known natural minimum life span of *L. hamiltoni* (unpublished data). For each run of the model we noted for both populations the annual growth rate, as well as whether the population went extinct during the projection period.

Age at first reproduction (AFR), and three vital rates were used as input parameters: the survival rate for subadults and adults, and the fertility rate (the product of reproductive rate and juvenile survival; Caswell, 2001). All three vital rate parameters were subject to some degree of uncertainty, which we incorporated into our runs of the model. In particular, data for fertility and AFR were of low quality. We used a range of values for each parameter (low, medium and high) that we hoped spanned realistic bounds, and allowed the results to be considered in the context of the full range of uncertainties.

TABLE 1. Range of values used to represent uncertainty in the parameters of the population model.

Current estimate of vital rate	Low	Medium	High
Fertility (reproductive rate x juvenile survival)	0.4	1.2	2.0
Subadult survival	0.57	0.73	0.85
Adult survival	0.80	0.88	0.93
CV for Environmental Stochasticity (ES)	0.0	0.1	0.2
Density at which minimum reached (N)	500	2000	5000
Range of vital rate values (R)	0.01	0.25	0.50
AFR for population D (years)	5	6	7
Reduction in AFR for population T (years)	0	1	2

All vital rates were set to be negatively density-dependent (i.e. to decrease with increasing density); for this purpose, density was defined as the total number of adults and subadults. The equation used to specify density-dependence is given in Appendix 1. The strength of the density-dependence was specified by four parameters (see Table 1): A, the vital rate value at the current population density; B, the range of values the vital rate can take (R; expressed as a single value representing the difference between the maximum and minimum value for that vital rate, relative to and centred on the current vital rate value); C, an arbitrarily large density at which the vital rate reaches its minimum value (N); D, an arbitrary amount of environmental stochasticity, representing year-to-year variation in the rate over and above that determined by changes in density (ES, expressed as a coefficient of variation).

Demographic stochasticity was incorporated by using a Poisson distribution to model the number of juveniles recruiting to the population, and a binomial distribution to model the number of subadults and adults surviving from one year to the next (Caswell, 2001).

The following steps were carried out for each 30-year run of the model: (1) We selected the values of the input parameters for a single 30-year run of the model. For each parameter, we selected this at random from one of three values (low, medium and high) that represented our uncertainty (i.e. one value from each line in Table 1). Using these we ran a deterministic version of the model for the donor population in order to obtain its stable stage distribution. This was then used as the initial stage distribution for that population. The current population was estimated to contain approximately 250 subadults and adults. The initial population was therefore chosen to have 125 females (subadults and adults). For some choices of parameter values, the stable stage distribution leads to there being insufficient subadults and/or adults for some of the translocation scenarios. When this occurred, we reselected the parameter values. (2) With the stable stage distribution entered into year 0, we then selected parameter values for each of the following 30 years. For year 1 and for each vital rate we used the value selected in Step 1, and those selected at random for ES, N and R (the density-dependent relationship) to determine the value for the vital rate at the current density; an example is shown in Fig. 1. For year 1 the density is that in year 0 (i.e. 125 females); for year 2 it is the density in year 1, and so on. (3) We then performed a translocation of a specified number of subadults and adults from population D to population T. Nine hypothetical translocation scenarios were modelled; Table 2.

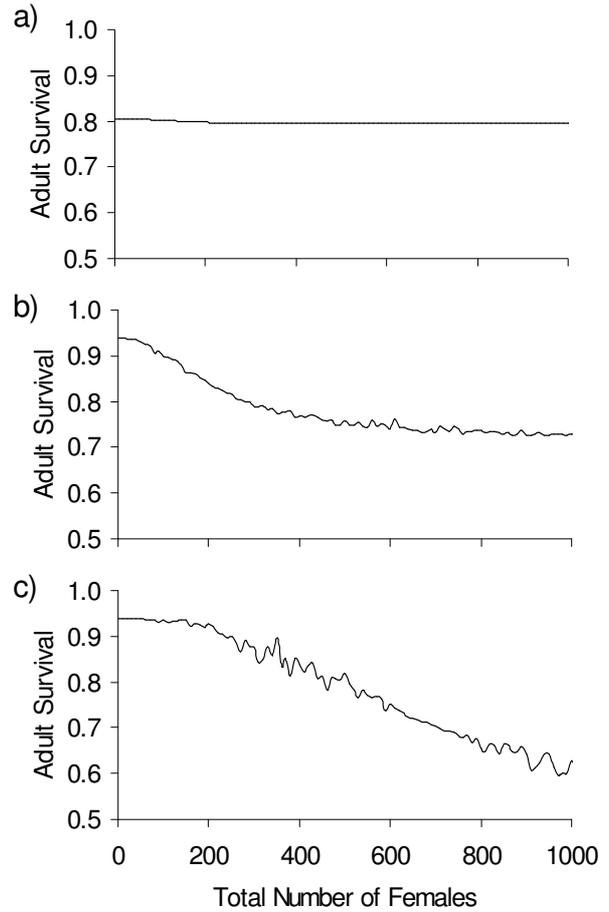


FIG. 1. Illustration of the form of density-dependence in adult survival, with the four parameters set at: a) Low values (current value=0.80, ES=0, N=500, R=0.01); b) Medium values (current value =0.88, ES = 0.1, N=2000, R=0.25; and c) High values (current value=0.93, ES=0.2, N=5000, R=0.5). See Appendix 1 for details of the equation used.

(4) We projected both populations for 30 years and recorded for each whether the population became extinct during that period as well as the annual population growth rates over the period. (5) We repeated Step 4 to obtain two replicate projections for the same translocation scenario. (6) Steps 1-5 were repeated 1000 times in order to evaluate the translocation scenarios across a wide range of possible population dynamics.

MODEL ASSUMPTIONS

Unless otherwise stated, the assumptions detailed here cannot be supported with existing data. One inherent assumption in our discussion of results is that the habitat and environment for population T is at least as good for *L. hamiltoni* as the habitat and environment of population D and that all frogs translocated to popula-

TABLE 2. Nine translocation scenarios for *L. hamiltoni* from frog bank Stephens Island to a new island site. Values represent number of subadult and adult frogs translocated.

Scenario	1	2	3	4	5	6	7	8	9
Subadults	0	0	0	20	20	20	40	40	40
Adults	0	20	40	0	20	40	0	20	40

tion T remain at the release site and become part of the population i.e. no movement away from the release site. Also, we have not allowed for population genetic effects such as inbreeding depression or phenomena that result in population dysfunction at small population sizes (e.g. Allee effects in population T). Similarly, we have assumed that any density dependence in the vital rates acts negatively, and that parameters derived from the frog bank population on Stephens Island, adequately describe population T.

We assume AFR can be lower in population T, and that changes to AFR in *L. hamiltoni* following a translocation are similar to that shown for *L. pakeka* on Maud Island (Ben Bell, Victoria University of Wellington, *pers. comm.* 2001) and Motuara Island (unpublished data). Another major assumption in our model is that the starting number of females available for translocation is 125 and that females breed annually (although we also consider 250 females and a biennial model; see Discussion). This former estimate is conservative given that mean population size from only 93 m<sup>2</sup> of the frog bank is estimated at 205 (Fig. 2).

#### SURVIVAL RATES FOR ADULTS AND SUBADULTS

Three size classes are evident in *L. hamiltoni*. Juveniles are described as frogs <16 mm SVL; subadults were defined as those 16 to 35 mm SVL inclusive, and adults >35 mm SVL (Fig. 3). We were careful to define subadults as those frogs smaller than the maximum body size for a male *L. hamiltoni* (36 to 40 mm SVL; Fig. 3). Because female *L. hamiltoni* reach a larger body size than males, this definition ensured that if a given number of subadults were selected for translocation, the sex ratio should be approximately equal (of 109 adult frogs sampled, 55 were thought to be males and 54 females).

In order to obtain estimates of mean survival rates for adults and subadults, we analysed mark-recapture data

collected from the frog bank, Stephens Island, between July 1997 and July 2003 (27 sessions concentrated over autumn). All analyses were carried out using Program MARK (White & Burnham, 1999). Due to sparseness of the data, we pooled across the sexes and estimated a single survival rate for males and females. We considered four models. In all models, survival rate was constant across time, and was estimated separately for adults and subadults. Capture rate was allowed to be either time-dependent or constant, and either different for subadults and adults or not. The best-fitting model was the one in which capture rate was both time-dependent and the same for subadults and adults (AICc weight=1.000). There was some evidence of lack-of-fit for this model, which we allowed for by inflating the resulting confidence intervals using a bootstrap estimate of overdispersion (White & Burnham, 1999). The estimate of mean adult survival was 0.88 (95% confidence interval: 0.80 to 0.93), while that for subadult survival was 0.73 (95% confidence interval: 0.57 to 0.85). We used these estimates and confidence limits to specify the low, medium and high values for survival.

#### FERTILITY RATE

We decided to choose values for fertility rate so that the mean simulated population growth rate for population D (in the absence of any translocation) would match the current population growth rate. In order to estimate the latter, we used Program MARK to fit a Pradel model (White & Burnham, 1999) to the same mark-recapture data for subadults and adults. In this model, population growth rate was constant across time, and was estimated separately for adults and subadults. Following the results for the survival rate analyses, we made capture rate both time-dependent and the same for subadults and adults. We again allowed for lack-of-fit by inflating the resulting confidence intervals using a bootstrap estimate of

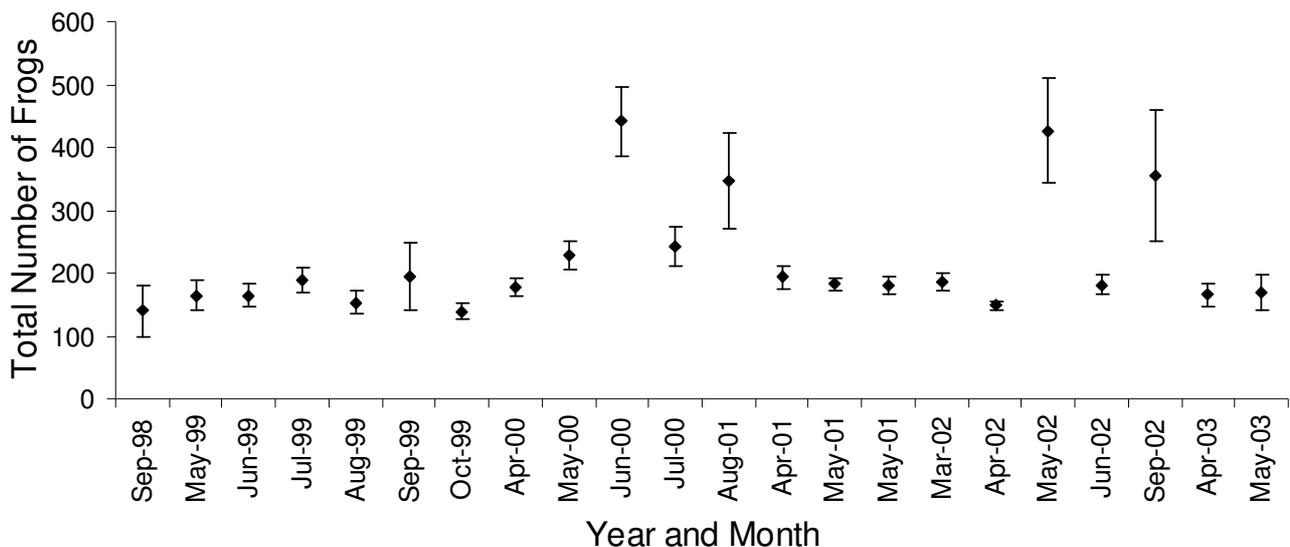


FIG. 2. Jolly-Seber population estimates (mean  $\pm$  SE) for *L. hamiltoni* on Stephens Island over a 93 m<sup>2</sup> search area (total area of habitat for *L. hamiltoni* estimated at 300 m<sup>2</sup>). Note: frogs were sampled twice in May 2001, early in the month, then again late in the month. Frogs < 16 mm SVL were not toe-clipped until session 4 therefore total population estimates were restricted to sessions 4–27 inclusive (Note: Jolly-Seber estimates cannot be calculated for the first (i.e. fourth) and last session (July 2003)).

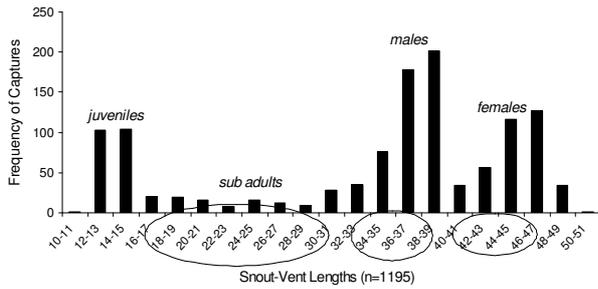


FIG. 3. Size class frequency distribution for *L. hamiltoni* on Stephens Island;  $n = 1195$  frogs captured from 1997 to 2003.

overdispersion. The estimate of mean adult population growth rate was 1.01 (95% confidence interval: 0.85 to 1.21), while that for subadults was 0.95 (95% confidence interval: 0.88 to 1.04). The confidence intervals associated with these estimates were too wide for us to make use of them in setting low and high values for fertility rate. We therefore chose to set the values for fertility rate so that the mean simulated population growth rate for population D would equal 0.95, 1.00 and 1.05. These represent a range of plausible growth rate levels that are consistent with the data. The resulting low, medium and high values for fertility rate were 0.4, 1.2 and 2.0 respectively.

AGE AT FIRST REPRODUCTION

We assumed that individual females do not begin breeding at the same age. We specified the between-individual variation in AFR using a symmetric triangular distribution with a specified mean and an arbitrary range of four years (Fig. 4). Population T was assumed to have a mean AFR that was either zero, one or two years earlier than that for population D, again with a range of four years (Fig. 4 and Table 1). This potential reduction in AFR was considered realistic based on data collected from Motuara Island following the translocation of 300 *L. pakeka*. *L. pakeka* on Motuara Island displayed astonishing individual growth rates following translocation (unpublished data), and a similar result was noted for *L. pakeka* translocated to Boat Bay on Maud Island (Ben Bell, Victoria University of Wellington, *pers. comm.*

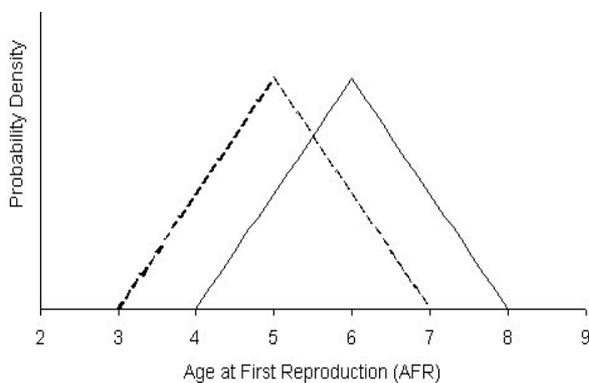


FIG. 4. Example of the triangular distributions used to represent between-individual variation in AFR. The distribution for population D has a mean AFR of six years (solid line), while that for T has a mean of five years (dashed line).

2001). We did not attempt to include environmental stochasticity for AFR, the same triangular distribution being used each year.

STATISTICAL ANALYSES

We summarised the results of the model runs by calculating the mean growth rate for the two populations, both separately and combined (i.e. considered as a single population). We also calculated the probability of extinction for each population. The resulting means and probabilities allow us to make comparisons amongst the different scenarios that should apply generally across a wide range of possibilities (1000 runs, each with two replicates) for the real-life dynamics of the two populations.

In order to calculate 95% confidence limits for these means and probabilities, we performed factorial ANOVAs on each measure of interest. The factors in each of these analyses were Run (1000 runs) and Translocation scenario (the nine combinations in Table 2). In each case, the ANOVA model contained the main effects of these two factors plus their interaction. The confidence intervals were calculated as  $\pm$  twice the standard error of the mean or proportion concerned, with the standard error being provided as part of the ANOVA output.

As a check on the generality of the patterns in the overall means and probabilities, we also performed a sensitivity analysis by re-running the analyses of variance with a slightly different model. This model included the main effect of each model-input parameter, the main effect of the factor translocation scenario, and all possible interactions between the input parameters and this factor. The *P*-value corresponding to each interaction was then used as an indicator of the relative size of that interaction, and therefore of the influence of the corresponding input parameter on the comparisons amongst the translocation scenarios (actual sizes of *P*-values are not relevant in analysing the results of simulation studies, as they can always be “made small” simply by increasing the number of runs of the model).

RESULTS

By considering mean population growth rate over a 30-year period of population D and T combined, the model predicted the best strategies for *L. hamiltoni* involved the translocation of 40 adult (AD) frogs or a combination of 20 AD with 40 subadults (SA; Table 3).

TABLE 3. Mean population growth rate over a 30-year period for the two populations D and T combined, for each of the nine translocation strategies. Each mean has a 95% confidence interval of  $\pm 0.002$ .

	Adults			
	0	20	40	
Subadults	0	0.992	1.019	1.022
	20	1.013	1.021	1.020
	40	1.018	1.022	1.020

TABLE 4. Mean population growth rate over a 30-year period for the two populations considered separately, for each of the nine translocation strategies. Each mean has a 95% confidence interval of  $\pm 0.004$  (population D) and  $\pm 0.006$  (population T). Also shown is the predicted mean size of population T at the end of the 30-year projection period (to the nearest integer).

		Mean population growth rate						Final population size		
		population D Adults			population T Adults			population T Adults		
		0	20	40	0	20	40	0	20	40
Subadults	0	0.992	0.992	0.983		1.066	1.057		136	211
	20	0.996	0.995	0.985	0.994	1.044	1.040	17	146	195
	40	1.002	0.998	0.989	1.007	1.035	1.030	49	168	194

The 95% confidence intervals associated with values in Table 3 indicate that there is little difference in predicted growth rate between combinations involving at least 20 AD frogs. Mean combined population growth rate decreased only when 20 SA frogs alone were used for translocation, and the worst strategy was not removing any frogs at all (Table 3). It is important to note that the comparisons between these means are more robust to model-misspecification than the values themselves. The latter should not be taken as predictions of population growth rates expected for *L. hamiltoni* should each translocation scenario be carried out, as the underlying models are necessarily only approximations to reality.

When the results for the two populations were separated, scenarios involving the removal of 40 SA with 0 and 20 AD yielded the highest predicted population D growth rates (Table 4). A general trend was apparent; when scenarios which removed the same quantity of frogs were compared (across diagonals) population D growth rate decreased as more adult frogs were removed for translocation (Table 4).

For population T, modelling results were greatly dependent on the quantity of frogs translocated (i.e. the size of the founder population) and it is therefore appropriate to consider growth rates in tandem with total population size at the end of the 30-year projection pe-

riod. As an example, although population T founded by 20 AD had a higher predicted population growth rate than population T founded by 40 AD, at the end of the 30-year projection period there were more frogs in population T under the latter scenario because the founder population was larger (Table 4). With this in mind, the highest growth rates were achieved in population T with the combinations that involved 20 and 40 AD (i.e. no subadults translocated to population T), and introducing subadults alone was the worst strategy (20 or 40 SA; Table 4).

Extinction probability of both populations combined was highest under the scenario involving no frogs (Table 5), a result which complements the population growth rate results (Table 3). However, when the 95% confidence intervals were considered all nine scenarios yielded statistically similar extinction probabilities (Table 5).

For populations considered separately, the best strategy for population D, in terms of extinction probability was to remove no adult frogs (Table 6). However, for population T, the more adult frogs introduced the better. The introduction of 40 AD frogs (with any combination of subadults) resulted in the lowest population T extinction probability (Table 6), and combinations involving at least 20 adults produced similar results. Of interest, the addition of 20 or 40 subadults to these 40 AD frogs resulted in no significant lowering of extinction probability. In concurrence with mean population growth results for population T, the worst scenarios in terms of extinction probability involved the introduction of either 20 or 40 SA alone (Table 6).

Sensitivity analyses indicated that population D was far less sensitive to variation in the input parameters than population T. For population T, the largest interaction involved current value for subadult survival, due in

TABLE 5. Proportion of runs that lead to extinction over a 30-year period for the two populations combined, for each of the nine translocation strategies. Each mean has a 95% confidence interval of  $\pm 0.002$ .

		Adults		
		0	20	40
Subadults	0	0.007	0.005	0.004
	20	0.006	0.004	0.006
	40	0.004	0.004	0.006

TABLE 6. Proportion of runs that lead to extinction over a 30-year period for the two populations separately, for each of the nine translocation strategies. Each mean has a 95% confidence interval of  $\pm 0.004$  (population D) and  $\pm 0.006$  (population T).

		Population D Adults			Population T Adults		
		0	20	40	0	20	40
		Subadults	0	0.007	0.010	0.019	
20	0.006		0.010	0.021	0.069	0.011	0.007
40	0.005		0.012	0.024	0.040	0.007	0.007

TABLE 7. Mean population growth rate over a 30-year period for population T, for each of nine translocation scenarios, separately for each of the three current values used for subadult survival. Each mean has a 95% confidence interval of  $\pm 0.01$ .

		Current subadult survival								
		0.57 Adults			0.73 Adults			0.85 Adults		
		0	20	40	0	20	40	0	20	40
Subadults	0		1.014	1.014		1.082	1.067		1.104	1.089
	20	0.838	0.992	0.994	1.054	1.060	1.052	1.090	1.080	1.074
	40	0.893	0.990	0.984	1.052	1.047	1.042	1.076	1.068	1.063

part to our wide range of values tested (Table 7). When subadult survival was low (0.57), it was most beneficial in terms of mean population growth to translocate 20 or 40 AD frogs alone. For higher values of subadult survival (0.73 and 0.85), translocating fewer adults (20 AD) became increasingly preferable, presumably due to the higher rates of subadult survival reducing the need to have such a large founder population of adults; fewer adults in the founder population lessens density dependence on vital rates culminating in an improvement in population growth rate. Overall, however, there was no significant difference between scenarios involving 20 and 40 AD, and patterns across all subadult survival values tested match patterns observed in Table 4; namely the favoured translocation scenarios involve 20 or 40 AD with the least favoured involving 20 or 40 SA alone.

The corresponding summaries for the probability of extinction in population T were similar to those for mean growth rate. Differences between scenarios were most sensitive to current value for subadult survival (Table 8). If subadult survival was low, it was best to increase the number of frogs being translocated to at least 20 AD to minimise extinction probability, with the best scenarios involving the translocation of 40 AD (Table 8). These differences were absent for the higher current values of subadult survival; here extinction probability was very low for all combinations except for 20 SA alone.

Sensitivity analyses for all other input parameters are not presented here given that different values for subadult survival (the parameter which led to the greatest interaction effect) failed to alter conclusions as to which translocation scenario was preferable, both in

terms of population growth rate and extinction probability.

### DISCUSSION

To fully implement the “Native Frog (*Leiopelma* spp.) Recovery Plan” (Newman, 1996), preparations must be made for a translocation of *L. hamiltoni* to another island, free of introduced mammalian predators. An appropriate island in the vicinity of Stephens Island has already been selected (Mike Aviss, Department of Conservation, *pers. comm.* 2004). To aid in preparation for a translocation we have used a tailored, species-specific simulation model, providing the degree of model complexity that is supported with available data, to choose an optimal translocation strategy for *L. hamiltoni*. The strength of our approach is that we have evaluated translocation scenarios across a wide range of possible population dynamics, and have considered risk in terms of both population growth rate and extinction.

From a choice of nine hypothetical translocation scenarios (including the “no translocation at all” option) we believe the best strategy for *L. hamiltoni* is to translocate 20 adult female frogs to a new population (with 20 adult males). Supplementing these adult frogs with 20 subadult females (with 20 subadult males) seems reasonable given that (1) subadults may be more likely to remain at the translocation site (Tocher & Brown, 2004); (2) the removal of up to 20 subadult females does not significantly impact on the population growth and extinction probability of the donor (frog bank) population; and (3) supplementing 40 translocated adult frogs with a selection of subadults improves the total number of female frogs expected in population T after 30 years, and increases the size of the founder population which

TABLE 8. Proportion of runs that lead to extinction over a 30-year period for population T, for each of nine translocation scenarios, separately for each of the three current values used for subadult survival. Each mean has a 95% confidence interval of  $\pm 0.01$ .

		Current subadult survival								
		0.57 Adults			0.73 Adults			0.85 Adults		
		0	20	40	0	20	40	0	20	40
Subadults	0		0.030	0.013		0.000	0.000		0.000	0.000
	20	0.187	0.030	0.021	0.015	0.000	0.000	0.004	0.001	0.000
	40	0.118	0.019	0.021	0.002	0.000	0.000	0.000	0.000	0.000

will lessen the “bottleneck” effect and promote a relatively more diverse genetic makeup within population T.

In practical terms, *L. hamiltoni* are not easily sexed, and targeting certain sexes and ages for translocation will be necessary to ensure 40 adults and 40 subadults of an even sex ratio are translocated. We expect a random sample of frogs within 16–35 mm SVL range (subadults) to have a sex ratio slightly biased towards males (given males have a smaller adult SVL than females). As such only frogs  $\geq 18$  mm and  $\leq 31$  mm SVL should be considered for translocation to minimise a male bias in sex ratio which is most likely to occur in frogs  $> 30$  mm. We suggest a minimum SVL of 18 mm to ensure a frog is in the subadult range (given measurement error likely to occur in SVL measurements of such small frogs; Fig. 3). Likewise for adults the 40–41 mm class is likely to contain the occasional large male, but frogs  $> 42$  mm are highly likely to be female (Bell, 1994). By assuming male and female frogs are equally catchable and have similar survival rates and longevity over our 6-year study the difference between the number of frog captures in the size range 34–39 mm (455 frogs) and 42–47 mm (300 frogs) over the course of this study gives an approximate estimate of the number of females in the 34–39 mm size class range (155 frogs). Using this rough estimation, approximately 34 % of frogs within the 34–39 mm SVL size class are expected to be females. Therefore, a random collection of frogs in this size class will be male biased, and this bias can be rectified by taking frogs from within the 42–47 mm SVL range as follows: for translocation we recommend the removal of 30 adult frogs with SVLs between  $\geq 34$  and  $\leq 39$  mm and 10 adult frogs  $\geq 42$  mm SVL. As well, we recommend the removal of 40 subadult frogs with SVLs  $\geq 18$  mm and  $\leq 31$  mm.

Removal of 80 frogs from the frog bank represents a removal of approximately 27% of the estimated resident frog bank population, yet our modelling suggests a low probability of the donor population going extinct. To test the robustness of our conclusions to the initial size of the donor population, we repeated the full analysis using 250 rather than 125 females (subadults plus adults). This analysis produced the same patterns as those presented here, as did a model which allowed “biennial-breeding”. We modelled biennial breeding because anecdotal data from our monitoring work suggested biennial breeding may indeed occur in the frog bank population with pulses of juveniles noted every second year. The biennial model generated low population growth rates ( $< 1$ ) and as such we considered it inferior when compared to the annual model presented here which matched the observed population growth rate of population D (unpublished data).

Our results are reassuringly robust. Sensitivity analyses showed that the results for population T were most sensitive to the current value of subadult survival. However, the overall outcome (i.e. which translocation scenario is best) was not strongly influenced by this parameter. Mark-recapture survival estimates can be prone

to downward bias caused by capture heterogeneity, and we would therefore consider the medium and high values for subadult survival as more indicative of true subadult survival than the lower value and it is these values that influenced the model outcome the least. For these values the comparisons between translocation scenarios were similar to those obtained overall.

In summary, we consider the most reasonable management strategy, confirmed by the modelling and supporting qualitative data is the translocation of 20 adult and 20 subadult female frogs (with the concurrent translocation of 40 males). This scenario provides a balance between risk of extinction in donor population and probability of success in the translocated population.

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APPENDIX 1

MODEL EQUATIONS

The calculations used to determine the number of females in each stage are summarized in the equations below. Note that these are based on the assumption of a pre-breeding census, and of a variable-stage duration for subadults (Caswell, 2001).

$$n_1(t+1) \sim \text{Poisson}[F(t)n_3(t)] \quad (\text{c.f. p.455 of Caswell, 2001})$$

$$n_2(t+1) \sim \text{Binomial}[n_1(t), S_2(t)] + \text{Binomial}[n_2(t), \{1-\gamma(t)\}S_2(t)]$$

$$n_3(t+1) \sim \text{Binomial}[n_2(t), \gamma(t)S_3(t)] + \text{Binomial}[n_3(t), S_3(t)]$$

where:

$n_1(t)$  = number of juvenile (stage 1) females in year  $t$

$n_2(t)$  = number of subadult (stage 2) females in year  $t$

$n_3(t)$  = number of adult (stage 3) females in year  $t$

$F(t)$  = fertility rate (juvenile females per adult female) for adults present in year  $t$

$S_2(t)$  = survival rate for subadult females from year  $t$  to  $t+1$

$S_3(t)$  = survival rate for adult females from year  $t$  to  $t+1$

$\gamma(t)$  = probability that a juvenile that survives from year  $t$  to  $t+1$  becomes mature in year  $t+1$

$$= \frac{1}{M} \exp \left\{ -\frac{1}{2} \ln \left( \frac{1}{S_2(t)} \right) \left( M - \frac{V}{M} \right) \right\},$$

where  $M$  and  $V$  are the mean and variance of time spent as a subadult (Caswell, 2001). We set  $M = \bar{A} - 1$ , where  $\bar{A}$  is the mean value of AFR (Fig. 1). Using results for the variance of a symmetric triangular distribution with a range of 4 years, we set  $V = 2/3$ .

Density dependence in each of the vital rates ( $F$ ,  $S_2$  and  $S_3$ ) can be modelled as follows. Suppose the rate ( $y$ ) is assumed to decline with population size, from a value of  $y_U$  for a population of containing one female, to a limit of  $y_L$  for an infinite population. We model the rate between the two extremes using a linear-logistic function (Usher, 1972), with the rate in a given year being calculated as:

$$y = y_U - \frac{y_U - y_L}{1 + e^{-x}} \quad (\text{A1})$$

where  $x = a + b \ln(n)$ , for some parameters  $a$  and  $b$ , and  $n$  is the total number of females in the previous year.

We specify the values of  $y_U$  and  $y_L$  as follows. The value for their difference is calculated as:

$$y_U - y_L = R y_0$$

where  $R$  is the specified relative range of values for  $y$  (Table 1). The value for  $y_U$  is then calculated as:

$$y_U = \min \left\{ (1 + \alpha) y_0^H, \left( 1 + \frac{R}{2} \right) y_0 \right\}$$

where  $\alpha$  is an arbitrarily small positive number,  $y_0$  is the current value for  $y$ , and  $y_0^H$  is the highest of the three values specified for  $y_0$  (Table 1). This choice is motivated by wanting  $y_U$  to never exceed  $y_0^H$  by more than a specified small amount, and to otherwise be such that:

$$(y_U - y_0) = (y_0 - y_L) = (y_U - y_L)/2$$

The parameters  $a$  and  $b$  are determined by setting:

(a)  $y_U = y_0$  when  $n = n_0$ , where  $n_0$  is the current total number of females;

(b)  $y = y_L + \delta(y_U - y_L)$  when  $n = N$ , where  $N$  is the total number of females for which the vital rate 'reaches'  $y_L$ , with  $\delta$  being an arbitrarily small positive number.

This leads to:

$$a = \frac{\ln\left(\frac{d}{1-d}\right)\ln(N) + \ln\left(\frac{\delta}{1-\delta}\right)\ln(n_0)}{\ln(N) - \ln(n_0)}$$

and

$$b = -\frac{a + \ln\left(\frac{\delta}{1-\delta}\right)}{\ln(N)}$$

where  $d = (y_U - y_0)/(y_U - y_L)$ .

The function in equation A1 corresponds to a deterministic density-dependent relationship. We add environmental stochasticity to the relationship by redefining  $x$  to be a normal random variable with mean  $m = a + b \log n$ , and standard deviation  $s$ . The latter is specified using the coefficient of variation of  $x$  as a measure of environmental stochasticity ( $ES$ ). Thus  $s$  is the absolute value of  $mES$ , where the value of  $ES$  is specified in Table 1.