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The fate of a population of the endemic frog *Leiopelma pakeka* (Anura: Leiopelmatidae) translocated to restored habitat on Maud Island, New Zealand

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Abstract We assess the fate of 100 *Leiopelma pakeka* transferred in two batches from remnant forest on Maud Island to a new site at Boat Bay, 0.5 km away, in 1984–85. Seventy of the original 100 individual frogs were recaptured, plus 35 young recruits into the population. The 43 frogs released in 1984 settled closer to the release site than did the 57 released a year later, suggesting that many of the later arrivals avoided sites already occupied by frogs. Boat Bay frogs became heavier than frogs in the source population, presumably a reflection of lower population density and greater per capita food supply. Numbers declined initially, but the frog population remained relatively stable after losses of founder individuals began to be offset by local recruitment. The mean annual survival rate after initial settlement was high (97%), indicating an average life expectancy of 33 years.

Keywords *Leiopelma pakeka*; capture-recapture; translocation; conservation; demography; frogs

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INTRODUCTION

The Maud Island frog *Leiopelma pakeka* is a threatened New Zealand endemic, classified as Nationally Vulnerable under the New Zealand threat classification system (Hitchmough 2002). It was formerly included with Hamilton's frog *L. hamiltoni*, but was later described as a new cryptic species, *L. pakeka*, based on allozyme and morphometric differences (Bell et al. 1998). However, Holyoake et al. (1999, 2001), using partial 12s RNA and Cyt b sequences, found little variation between the two taxa (<1% for Cyt b) and favour keeping them as one species. This and associated questions of the taxonomy of allopatric populations of New Zealand herpetofauna, and the conflicting datasets derived from them, is an issue of on-going debate yet to be resolved (Bell et al. 2004).

As a prelude to future island-to-island translocations aimed at increasing the range of endemic frog species, we undertook a trial translocation of 100 frogs within Maud Island in 1984 and 1985 with New Zealand Wildlife Service approval (Bell 1994, 1996, 1997; Bell et al. 1998; Bell & Pledger 2001; Dewhurst & Bell 2004). The New Zealand Department of Conservation carried out the first island-to-island translocation of *L. pakeka* in 1997 when 300 frogs were moved from Maud Island to Motuara Island, 33 km SE in Queen Charlotte Sound (Tocher & Newman 1997), plus a within-island translocation of *L. hamiltoni* on Stephens Island in 1992 (Brown 1994, 2002). This paper reports on the outcome of the initial Maud Island translocation covering a 20-year period (1984–2003) and describes the demographic responses of the new frog population living at reduced density.

STUDY AREAS

Source habitat

Maud Island is located in the central Marlborough Sounds (New Zealand). It is a relatively sheltered island consisting of 309 ha of moderate to steep hill

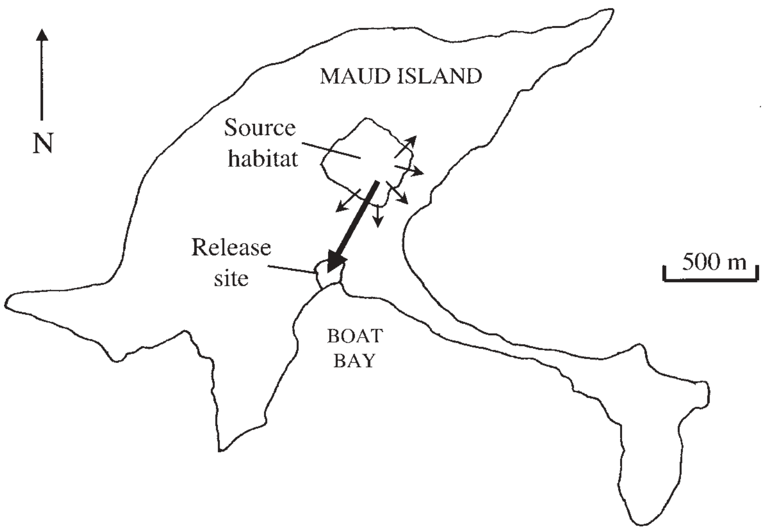

Fig. 1 Location of the source population and the Boat Bay translocation site on Maud Island. Large arrow indicates the translocation, small arrows indicate short-distance dispersal of frogs from the source population.

country, gazetted as a reserve in 1975. Over the past 100 years, Maud has been highly modified by farming and had retained little natural vegetation other than a 16-ha remnant bush stand, fenced off to exclude stock in 1965 (Bell 1995). The source population frogs survived in this stand, mostly on the lower, rocky slopes (Bell & Bell 1994). The forest remnant is a broadleaf stand dominated by kohekohe (*Dysoxylum spectabile*) and mahoe (*Melicytus ramiflorus*) except above an altitude of 200 m where kamahi (*Weinmannia racemosa*), hinau (*Elaeocarpus dentatus*), and miro (*Podocarpus ferrugineus*) are more common. When this frog population was first reported in 1958 (Stephenson 1961), the main stand of bush was quite isolated, but forest restoration has proceeded rapidly over the last 30 years, and now extensive regenerating forest covers adjacent slopes. The estimated size of the source population is at least 19 000 individuals (Bell & Bell 1994).

Choice of release site

A 2-ha forest remnant in a coastal gulley at Boat Bay, 0.5 km south-west of the source population (Fig. 1), was chosen as the release site, after all potentially suitable sites on Maud Island were surveyed (by BDB) in 1983–84.

Dominating the forest vegetation at Boat Bay were kohekohe, mahoe, pukatea (*Laurelia novae-zelandiae*) and rewarewa (*Knightia excelsa*). The ground under the forest had been heavily grazed by domestic stock until fenced by the mid 1970s. The forest floor was open and dry, and areas of rocky boulder bank that would have provided important retreat sites for any frogs, were trampled, disturbed and unstable. Under conservation management, stock were excluded from the site, as well as from other areas on Maud Island, allowing substantial forest regeneration that continues to the present day. Over 1974–84, a regenerating scrub layer dominated by kawakawa (*Macropiper excelsa*) became dominant in the understorey at Boat Bay, although patches of rocky boulder bank remained relatively free of vegetation (BDB pers. obs.). One such boulder bank site (area 150 m^2) was chosen for the release of translocated frogs. Day and night searches over 1983–84 had confirmed that there were no frogs there. Meteorological data (temperature, relative humidity) collected on data-loggers at the intended release site in 1984 confirmed that the microenvironment suited *L. pakeka* (Bell 1994).

METHODS

Transfer of frogs

Over 1984–85, 100 individually marked frogs were captured during day and night searches in the source habitat. Each frog was weighed, measured (snout-vent length, tibiofibula length, body girth), toe-clipped (for individual identification), and coded for colour pattern before being translocated to Boat Bay, as described by Bell (1994). Frogs chosen for

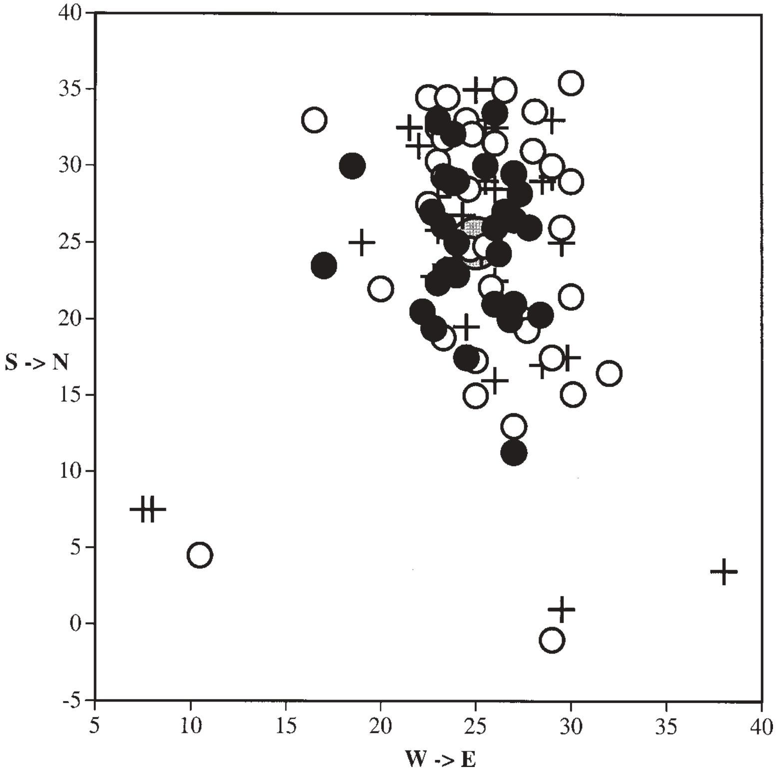

Fig. 2 Centres of activity of individual ranges of frogs relocated at Boat Bay following release there. The grid scales are in metres and the release point (grey circle) was at grid position 25–25. Three categories of frog are shown—the first cohort (black circles) released in May 1984, the second cohort (white circles) released in May 1985 and locally-recruited young frogs (crosses).

translocation included all age and size classes, although the sample was biased in favour of frogs in the adult size range (>33 mm snout-vent length). Frogs over 40 mm snout-vent are more likely to be females (Bell 1978), and those smaller than that (in the 34–40 mm range) either males, or young females.

The first 43 frogs were moved in May 1984. After confirming in December 1984 that frogs were surviving, a further 57 were transferred in May 1985. The frogs were released during daytime, all at the same site in a rocky boulder bank at Boat Bay (grid co-ordinates 25–25 in Fig. 2). Being nocturnal (Bell 1978), the frogs immediately sought shelter beneath the rocks. Follow-up night searches at Boat Bay were made at least twice annually until 1994, and then mostly annually thereafter up to March 2003. On each visit to the island, 1 to 2-h searches were usually made over 4–5 successive nights, generally over 600 m^2 around the release site (Fig. 2). Searches over more successive nights were made in 1993 (E. A. Bell), 2000 (R. Blacken), and 2002 (P. Dewhurst & S. Rowe), and on occasion these extended beyond the immediate vicinity of the release site to cover up to 0.25 ha of the Boat Bay gulley. Each marked frog caught was identified, measured and described, as on its initial capture. Unmarked frogs were also measured and described, and then toe-clipped for individual identification, under New Zealand Wildlife Service and Department of Conservation permits and Victoria University Animal Ethics Committee approval. Frogs previously caught in a given sampling visit were simply identified and re-weighed. After examination, frogs were released at their sites of capture (marked by a numbered peg), and these sites were mapped as grid co-ordinates to the nearest 0.5 m (Fig. 2).

Capture-recapture analysis

The mark-recapture analysis used the Cormack-Jolly-Seber model (Lebreton et al. 1992) and the package MARK (http://www.cnr.colostate.deu/~gwhite/mark/mark.htm). Survival and capture rates were compared for dependence on time, group (release 1, release 2 or new animals), and time since release. Model selection used Akaike's information criterion (AIC, see e.g., Burnham & Anderson 1998). Assuming random sampling, estimates of abundance Nj were obtained from nj/estimated pj, where nj is

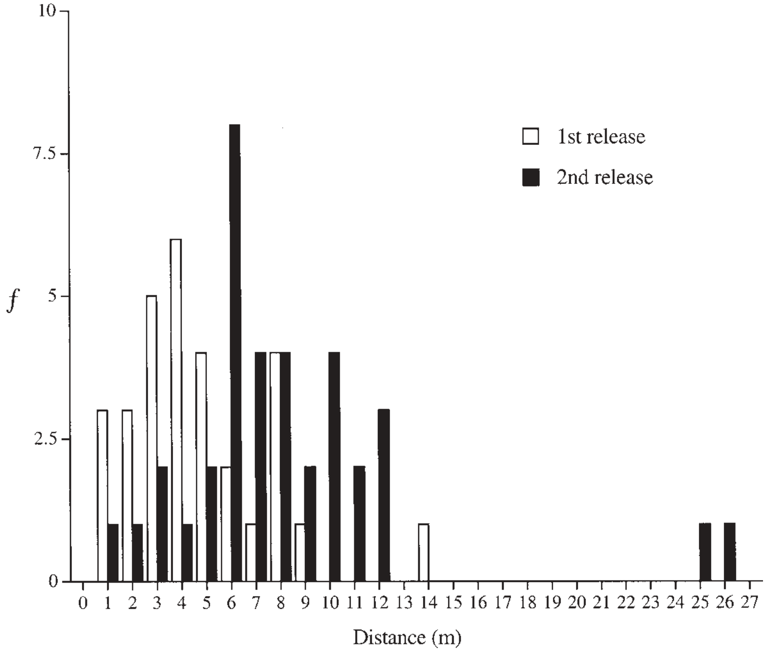

Fig. 3 The distance from the point of release to the centre of activity of the new home range in frogs translocated to Boat Bay. Note the difference between the first and second releases.

the number caught and *pj* is the probability of capture at sample *j*. A 95% confidence interval for *Nj* is obtained from MARK's confidence interval for *pj*, using the formula (*nj*/*p*(upper), *nj*/*p*(lower)), and an approximate standard error for the *Nj* estimate is *nj* * SE(*p* estimate)/square of *p* estimate, obtained from a delta theorem (Seber 1973).

RESULTS

Spatial distribution around release site

Seventy of the 100 frogs released were subsequently recaptured at Boat Bay over 1986–2003, while 35 locally bred frogs had been captured by 2003. Centres of activity of individual ranges of frogs relocated at Boat Bay show that most settled in the general region of the release site, although a few dispersed further, some up to 25–26 m (Fig. 2, 3). If a frog was recaptured only once, then its capture location was taken as the centre of its individual range.

The two releases a year apart allow comparison between the two cohorts of translocated frogs. The average distance from the point of release to their new centres of activity is significantly less for the first cohort (4.8 m) than for the second cohort (8.0 m; Mann-Whitney test, U = 289, $P = 0.001$). New recruits settled on average 7.9 m from the release point of their parents, significantly different from the first but not second cohort of releases (Mann-Whitney tests, U = 353, $P = 0.035$ and U = 539.5, $P = 0.305$ respectively).

The mean range area (11.6 m^2) and length (2.4 m) for Boat Bay frogs returning sufficient data were not significantly different from those of frogs in the source population (means 8.6–16.9 m^2 (area) and 1.8–2.2 m (length). The probability values from Mann-Whitney tests between Boat Bay and the source population sites were $P = 0.20–0.39$ for mean range area, and $P = 0.13–0.75$ for mean range length).

Relative weight of translocated frogs

Boat Bay frogs became relatively heavier (per unit length) than the frogs remaining in the source population. When the first and last measurements of frogs captured at Boat Bay are compared (Fig. 4), weight for a given length had mostly increased and the difference between the curves was highly significant (linear mixed effects model, $P < 0.001$). To compare relative weights in relation to lengths, the following condition index was used: (log weight/log snout-vent length) × 100. For 60 frogs for which more data were available, the mean condition index at release was 45.6, compared with a mean of 55.5 at last capture (difference highly significant,

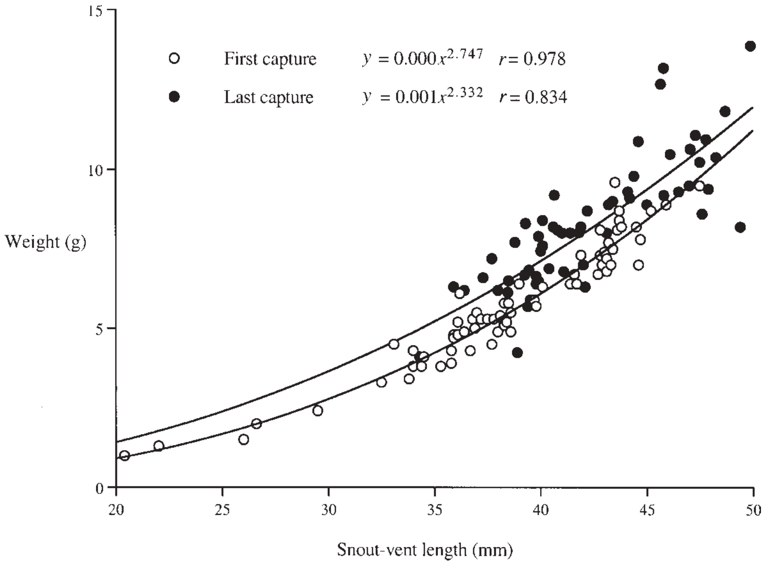

Fig. 4 The first and last snout-vent and weight measurements of translocated Maud Island frogs at Boat Bay. Power curves are fitted. A shift to the right due to growth (x-axis) is evident, as well as an increase in relative weight (y-axis).

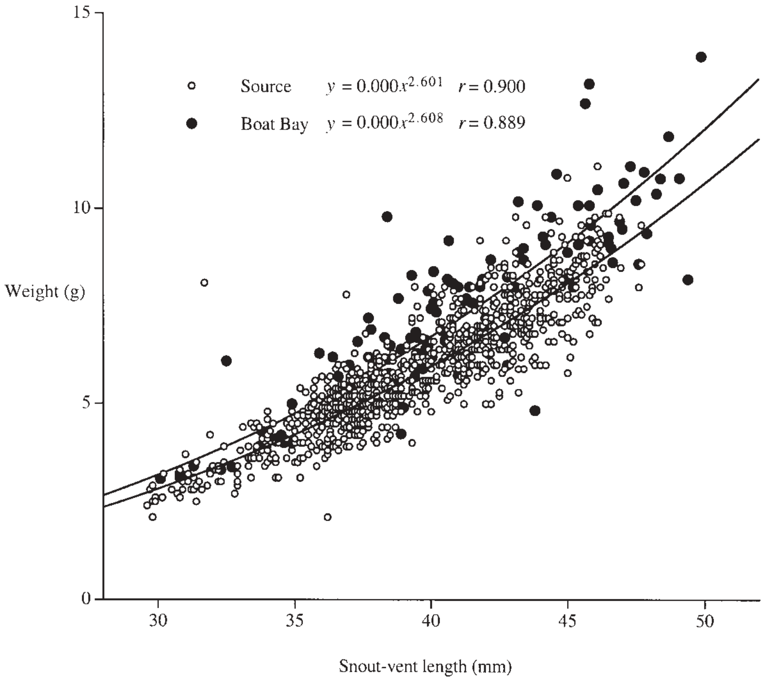

Fig. 5 The snout-vent and weight measurements of frogs >29 mm snout-vent length captured at Boat Bay compared with those in the source population (based on measurements at last capture). Power curves are fitted.

Wilcoxon signed rank test for paired data, $P < 0.001$).

That Boat Bay frogs tend to be heavier for a given length than those in the source population is also evident from comparison of weights and snout-vent lengths between the two sites (Fig. 5). An analysis of covariance on y = log(weight) and x = log(SVL), with "frog" as a random effect to allow for repeated measures, had $P < 0.001$ when the locations were contrasted.

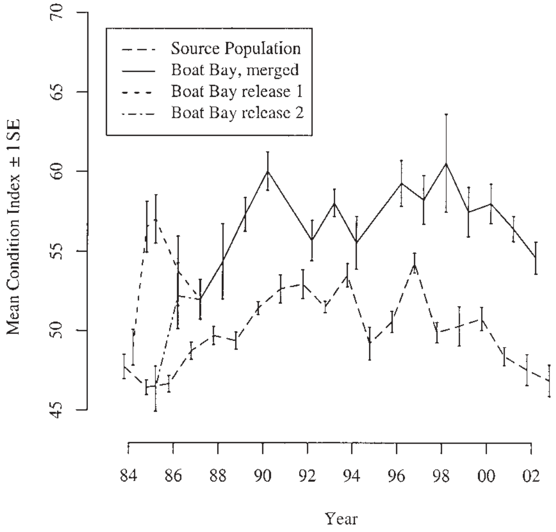

Fig. 6 Annual means (±1 SE) of condition indices over 1984–2003 for frogs >29 mm snout-vent caught at Boat Bay (solid line) and at two sites for the source population (dashed line). Data for the two Boat Bay releases in 1984 and 1985 are merged in 1987. The curves are slightly offset to illustrate standard error bars more readily. Only samples >2 are included.

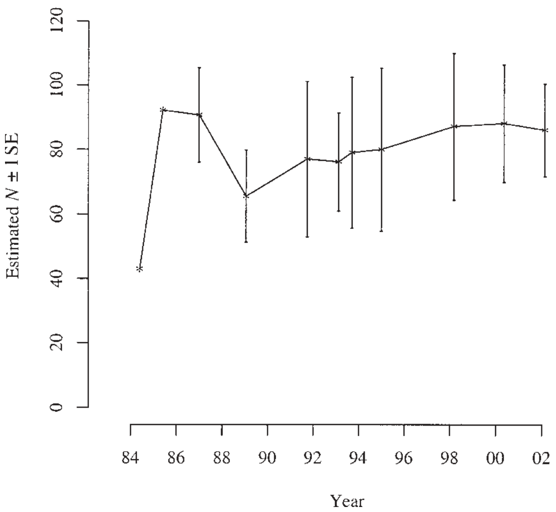

Fig. 7 Jolly-Seber estimates (±1 SE) of the Maud Island frog population at Boat Bay from 1984–85 to 2003.

Temporal changes in the frog condition index at Boat Bay are compared with an equivalent sample marked in the source population in 1984–85 in Fig. 6. Early condition (at release time for translocated frogs, at first capture in 1984–85 for the source population) versus later condition depended on population (interaction test, $P < 0.001$, with "frog" as a random effect to allow for repeated measures). In the source population, the average condition rose from 47.2 to 49.9, while in translocated frogs in Boat Bay it rose from 47.1 to 56.1.

While small sample sizes ($n < 5$) at Boat Bay resulted in marked fluctuations in some years, the condition index otherwise remained greater there. The two cohorts released in 1984 and 1985 both increased in mean condition immediately after release. Both Boat Bay and source population frogs have declined in condition in recent years.

Survival and population trends at Boat Bay

The estimates of overall population trends at Boat Bay from 1984–85 to 2003 are given in Fig. 7, using pooling of some adjacent samples to increase the numbers caught per sample to a minimum of three. This pooling is justified when annual survival rates are so high. The *N* estimates using the model parameters, subdivided into the three groups, are shown in Fig. 8.

The AIC criterion selected a model in which capture probabilities varied through time but not by group. The annual survival rate (of frogs that neither died nor dispersed off the grid) was found to take one of three values: 0.642 (SE 0.086) for each translocated group just after release; 0.970 (SE 0.007) for these groups subsequently, with no difference of rates between the two groups; and a constant annual survival rate of 0.803 (SE 0.069) for the local recruits, with no evidence of variation over time. Models with survival completely constant, or fully time-varying, or varying among all three groups, had AIC values higher than the chosen model by 15.7, 75.2, and 8.8 respectively, and were therefore less valid.

The selected model also showed the population of local recruits increasing after February 1990 (when the first such recruit was found), as seen in the widening band between the two top lines in Fig. 8. The apparent reduction in total population in 2003, driven by a lower estimate in the first cohort only, is likely to be caused by the negative bias in the final population estimate, which is a common feature of Jolly-Seber models. Overall, the evidence seems to point to a slow regular increase of recruits, which is now offsetting the slow decline of the original translocated animals.

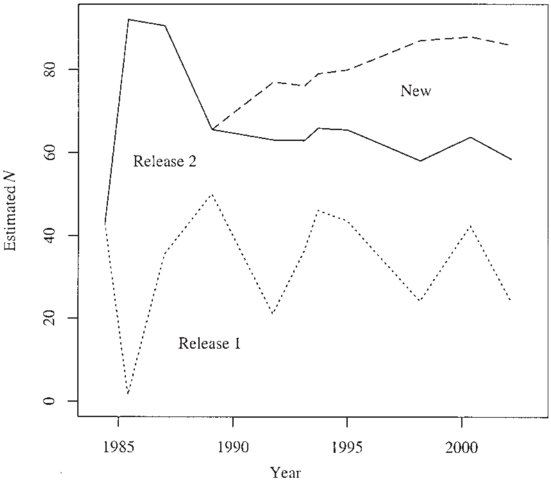

Fig. 8 Estimated population size (*N*) of the three cohorts at Boat Bay up to 2003. The addition of new recruits broadly offsets losses of frogs released in 1984–85.

The 95% confidence interval for the post-release annual survival rate of 0.64 is 0.475–0.810, while that for the continuing survival rate of 0.97 is 0.958–0.988. This ongoing survival rate exceeds that of the source population (Bell & Pledger in prep.), and translates into an average life expectancy of 33 years. The new recruits had a lower survival rate of 0.80 with a 95% confidence interval of 0.680–0.922.

DISCUSSION

This trial has demonstrated that *L. pakeka* can be successfully translocated. The first two propagules have survived well at Boat Bay for up to 20 years. To have recaptured 70% of the translocated frogs, and to have found an additional 35 local recruits, is an encouraging outcome. This result is an improvement on earlier findings (Bell 1994, 1997) mostly because more frogs were found by deliberately increasing search effort at Boat Bay in recent years. The ongoing annual survival rate of the released frogs is high (0.97), exceeding that of the source population (Bell & Pledger in prep.), and translates into an average life expectancy of 33 years. New recruits had a lower survival rate of 0.80, perhaps correlated with dispersal amongst sub-adults, or with greater mortality amongst younger and smaller frogs.

Leiopelma pakeka is a K-selected species with small clutch size, parental care, slow development, delayed maturity and great longevity (34+ years) for a frog (Bell 1994, 1997; Bell & Wassersug 2003). K-selection does not favour rapid population growth, and this was not observed at Boat Bay. Translocated populations typically suffer losses (mortality or emigration) immediately after arriving in a new habitat, but those remaining tend to fare well if the environment is suitable, as was observed at Boat Bay. The translocated frogs came from a higher density population at the main site, and benefited from intraspecific competitive release with higher per *capita* food availability, so developed better body condition (heavier per unit length) than frogs in the source population (Fig. 4–6). On the other hand, the weight of a frog may be affected by a range of factors, including level of food reserves, water retention, and gravidity (females) and the condition index does not discriminate between these.

Both Boat Bay and source population frogs have declined in condition in recent years (Fig. 6), suggesting an environmental factor common to both sites. An effect of age seems less likely, as another younger cohort of source population frogs marked 10 years later (1994–95) also declined in mean annual condition over 1999–2003: their successive mean condition indices (±SE) were 47.37 (1.05), 48.55 (0.59), 47.99 (0.46), 45.79 (0.57) and 45.75 (0.52). One noteworthy environmental event was a drought early in 2001 that was followed by reduced weight and condition in both the Boat Bay and source populations.

While the Maud Island translocation trial has been successful over the short-term, the demographic and genetic risks inherent in small populations make its longer-term future uncertain (Ballou 1995). We hope that the population increases over time so that such risks diminish. One potential threat to *L. pakeka* (and *L. hamiltoni*) is disease, which has been associated with major declines in the related *L. archeyi* in recent years (Bell 1999, 2004; Waldman et al. 2001). Little is known about the likely mechanisms of disease transmission between frog populations, but it is possible that *L. pakeka* was more vulnerable to disease when confined to the 16-ha remnant patch of forest on Maud Island, and this risk may have been reduced by creating new populations at Boat Bay and on Motuara Island. This meta-population could be further extended through more translocations of *L. pakeka* while the source population remains substantial.

Could frogs have been at Boat Bay prior to the translocation, only to appear as unmarked "recruits" after the 1984–85 releases? Observations at Boat Bay before the translocation were thorough, conducted by day and night, yet no frogs were found. This supports the view that no frogs were there, although before human disturbance on the island they were probably distributed not only at Boat Bay but also in suitable habitat across the island. Unmarked frogs caught since 1990 are therefore assumed to be descendants of the translocated frogs, and available evidence supports this: most of the first 10 unmarked frogs captured were small, i.e., sub-adults, with snout-vent lengths at first capture of 31, 14, 25, 36, 27, 31, 35, 34, 29 and 40 mm (mean 30.2 mm), and none were too large to be progeny of marked frogs released in 1984–85. In more recent years (1997–2003), many unmarked frogs were not caught until they had reached adult size—particularly those found in peripheral areas at Boat Bay, which were not searched as regularly as the area around the release point.

Could unmarked frogs have dispersed to Boat Bay from the source population? Frogs have colonised suitable patches of habitat close to the source population (Fig. 1), and have moved up to 26 m within Boat Bay (Fig. 3), but dispersal from the source population to Boat Bay (500 m) is most unlikely as the habitat in the intervening zone is too dry. Two study plots approx. 150 m apart have been used to monitor the source population since 1976 (Newman 1990; Bell 1994), yet no marked frogs have dispersed between the two sites over that time. Indeed, adult frogs have been found to have relatively small home ranges of only a few m^2 (Bell 1994, 1997, unpubl.).

CONCLUSIONS

The Boat Bay trial has allowed us to examine spatial and demographic relationships in a pioneering population. The staggered releases a year apart (1984–85) enabled comparison between the two propagules, and provided evidence for possible competition and avoidance behaviour in the new population. Frogs from the first release settled significantly closer to the release point than did those from the second release, suggesting that intraspecific competition may have induced the latter to move further away. These frogs are known to occupy discrete home ranges (Bell 1994, 1997), to shelter in specific retreat sites (Bell 1978), and to respond to chemical cues in their environment (Lee & Waldman 2002).

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