Using Simulations to Improve the Mark-recapture Method for Monitoring Native Snail Populations

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ABSTRACT

Two mathematical models of snail movements during mark-recapture surveys were developed using information from a study of the movements of ten radio-tagged *P. hochstetteri* snails (Lloyd, 2017b). One model used a bivariate normal distribution of locations around randomly distributed home range centers, while the other used a random-walk with individual snails starting at random locations at the beginning of the surveys. The distances and travel speeds between successive capture locations generated by simulations using the two movement models were compared to those observed during an actual mark-recapture survey. The random-walk model provided a better fit to the observed data and was used to estimate correction factors to compensate for bias in mark-recapture population estimates resulting from the edge effect and to investigate the influence on accuracy and precision of mark-recapture estimates of snail populations of three different factors: number of surveys, capture probability and plot population size. All three factors affected the accuracy and precision of mark-recapture simulated population estimates, however nightly capture probability had the largest influence. With nightly capture probabilities ≥0.20 and plot population sizes ≥200, good population estimates can be obtained with as few as three night-time surveys. Reducing the number of night-time surveys from five, or more, to only three provides a major reduction in the cost and complexity of a mark-recapture surveys.

INTRODUCTION

Diurnal sub-surface searches of 100 m^2 plots (Walker 1997) are the standard method for monitoring populations of New Zealand's threatened snails. However, concern about deficiencies in data from the standard method (Hamilton, 2015a; Lloyd, 2017a; McLennan, 2005) have led to the development of a mark-recapture method for monitoring threatened snail populations (Gruner, Weston, & Hamilton, 2011; Hamilton, 2015b; Lloyd, 2017a; Lloyd, Hamilton, & Blakely, 2014). Mark-recapture (Williams, Nichols, & Conroy, 2001), also known as capture-recapture, entails the repeated capture, marking, and release of samples of individuals within a plot. The total population size in the plot is then estimated from the capture histories of tagged individuals using established mark-recapture analytic methods (Borcher, Buckland, & Zucchini, 2002; Cooch & White, 2014; Lukacs, 2014; White, Anderson, Burnham, & Otis, 1982).

The mark-recapture method provides estimates of snail populations and when mark-recapture surveys are repeated at regular annual or biannual intervals the method can also provide demographic information on recruitment and survival. By contrast, the standard diurnal sub-surface search method for monitoring threatened snail populations only provides population indices in the form of snail counts per 100 m^2 plot. These indices are assumed to be proportional to actual population densities, but recent work indicates that this assumption is unsound (Hamilton, 2015a; Lloyd, 2017a; McLennan, 2005). In addition, because of low numbers of snails found during searches of sub-surface plots and inherent variability in these numbers, snail count indices are often imprecise. Typically the 95% confidence intervals around population indices are wide, often extending from less than 50% to more than 200% of the population indices e.g. (Lloyd, 2011; Ogle, 2012). The width of these confidence intervals means that information from sub-surface plot searches has little statistical power and can only detect massive population changes, such as catastrophic declines of more than 50%, or increases greater than 100%. Smaller changes will not be statistically significant.

Although mark-recapture estimates of snail population sizes are more robust than snail counts from sub-surface plot searches, they are affected by a systematic bias, referred to as the "edge effect", which occurs because populations of snails within the mark-recapture plot are not entirely closed. For example, although *Powelliphanta hochstetteri* are relatively sedentary, with individuals only moving short distances overnight (Mean: 1.32 m; Range: 0–3.3) compared to the 70 m square plot size used for mark-recapture surveys, snails with home ranges straddling the boundary of a plot will spend some of their time outside of the plot, where they are not available for capture. The resulting lower capture probabilities for these snails inflate mark-recapture population estimates creating a systematic upwards bias, or edge effect. Although frequently ignored or dismissed as negligible, the edge effect is a widely recognised problem in mark-recapture population estimation and a variety of strategies have been developed to deal with it. Spatially explicit capture-recapture methods have been developed to overcome the edge effect by using the exact locations of captures during mark-recapture studies to estimate population density (Royle et al. 2013). However, the only available implementation of spatially explicit capture-recapture analyses, the R-package *secr* (Efford, 2017), performed poorly in a mark-recapture study of *P. hochstetteri* (Lloyd, 2017a), providing snail density estimates 30 to 40 % higher than density estimates from standard mark-recapture methods. This result is implausible, because the edge effect biases standard mark-recapture estimates upwards. The *secr* package also performed poorly in a simulation study using a bivariate normal model of snail movements based on information from a radio-telemetry study of *P. hochstetteri* (Lloyd, 2017b). In the simulation study, density estimates from *secr* were between 29% and 60% higher than the simulated population density (Lloyd, 2017a). Consequently, Lloyd (2017a) used Monte Carlo simulations with the bivariate normal model of snail movements to estimate a correction factor to compensate for the edge-effect bias in a population estimate from a mark recapture survey of *P. hochstetteri* at Canaan in the Abel Tasman National Park during 2016. In the current study, a more realistic random-walk model of snail movements was developed. Location data generated from simulations using each of the two snail movement models were compared to location data from the Canaan 2016 mark-recapture survey to select the best movement model. Simulations with the best of the two movement models were then used to estimate correction factors to compensate for the edge effect bias and produce reliable mark-recapture population estimates from the results of three mark-recapture surveys (Lloyd, Bollongino, & Overmar, 2019). After correction for the edge effect, the mark-recapture method provides reliable estimates of snail populations.

Despite the mark-recapture method providing significant improvements in both quality and type of information compared to the standard diurnal sub-surface search method, uptake of the mark-recapture method for monitoring threatened snail populations has been disappointing. Reluctance to adopt the mark-recapture method is primarily because the method is expensive and logistically demanding. Currently, a single mark-recapture survey for *Powelliphanta* and, or *Rhytida* snails entails a team of six field workers undertaking at least five nocturnal searches for snails active on the surface of a 70 m square plot during a period of three to four weeks (Lloyd, 2015, 2017a). Successive searches must be spaced at least two nights apart to ensure independence, and less than two weeks apart to minimise snail dispersal and mortality between surveys. An extra difficulty is that to achieve good results, searches must be undertaken when weather conditions favour snail movements (i.e. temperatures > 8°C and humidity at or close to 100%), which can be difficult to predict and plan for. Any reductions in the scale and complexity of mark-recapture surveys will make the method a more attractive proposition for conservation managers.

In an attempt to improve the efficiency of mark-recapture surveys and thereby reduce their scale and complexity, simulations were used to investigate the influence on accuracy and precision of mark-recapture estimates of snail populations of three different factors: number of surveys, capture probability and plot population size.

METHODS

Models of Snail Movements

Two snail movement models were used for simulations: a model assuming a bivariate normal distribution of locations around randomly distributed home range centers (Lloyd, 2017a); and a random-walk model with individual snails starting at random locations. Parameter estimates used for the models were obtained from a radiotelemetry study of the movements of ten radio-tagged *P. hochstetteri* snails (Lloyd 2017) caught and radiotagged in the Canaan mark-recapture plot during the last few days of the Canaan 2016 mark-recapture survey period.

In the bivariate model, the covariance matrix for the bivariate normal distribution of the location coordinates is:

$$\begin{bmatrix} \sigma_X^2 & 0 \\ 0 & \sigma_Y^2 \end{bmatrix},$$

with X and Y values of the coordinates having equal variance σ^2 and being uncorrelated. For each simulated mark-recapture survey in the bivariate model a set of randomly distributed home range centres was obtained using the R-function *runif* to generate random X and Y coordinate pairs throughout a 200 m square region centered on the 70 m square plot. Random locations around these simulated home range centres were calculated for each simulated survey night (k) using random values of azimuth (α_k between 0 and π radians) and distance (D_k metres) from the home range centres: $X_k = D_k \times \sin \alpha_k$; and $Y_k = D_k \times \cos \alpha_k$. Random values for azimuth were generated using the R-function *runif*. Random values for distance were generated using the R-function *rnorm* with mean equal to zero and standard deviation estimates for a radiotelemetry monitoring period similar to the length of the simulated mark-recapture study (Table 1).

Table 1. Standard deviation of distances from home range centre of ten radio-tagged snails for observation periods ranging from 10 to 45 days.

Observation Period (Days)	10	15	20	25	30	35	40	45
N. Obs.	103	152	197	236	260	286	300	302
SD (m)	1.45	1.54	1.73	2.05	2.35	2.55	2.61	2.64

In the random-walk models, each simulation began with snails randomly distributed throughout a 200 m square region centered on the 70 m square plot, with snail starting location generated using the R-function *runif*. Successive locations of each simulated snail for each night of the simulated mark-recapture survey period were generated using a random-walk model. Nights when the simulated snails moved were selected randomly using the R-function *rbinom* with the probability of movement (0.56) obtained from the radiotelemetry study (Lloyd, 2017b). On nights when a simulated snails moved, the directions they moved in were random, with values of azimuth (α_k between 0 and 2π radians) generated using the R-function *runif*, and the distances moved (D_k) generated using the R-function *rgamma,* with shape and rate parameter estimates for the gamma distribution obtained using the R-function *fitdistr* in the R-library *MASS* to fit a gamma distribution to the distances radio-tagged snails moved overnight (Figures 1 & 2). The location of simulated snails at the end of night k (X_k, Y_k) was calculated from its location at the end of the previous night (X_{k-1}, Y_{k-1}): $X_k = X_{k-1} + (D_k \times \sin \alpha_k)$; and $Y_k = Y_{k-1} + (D_k \times \cos \alpha_k)$.

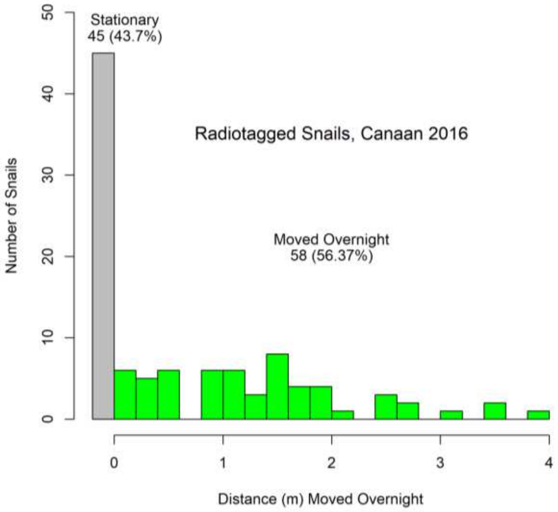

Figure 1. Histogram of distances moved overnight by *P. hochstetteri* snail. Data from a study of the movements of ten radio-tagged *P. hochstetteri* snails in the Canaan mark-recapture plot during spring 2016 (Figure 10. In: Lloyd 2017b. *A radio-tracking study of Powelliphanta hochstetteri*)

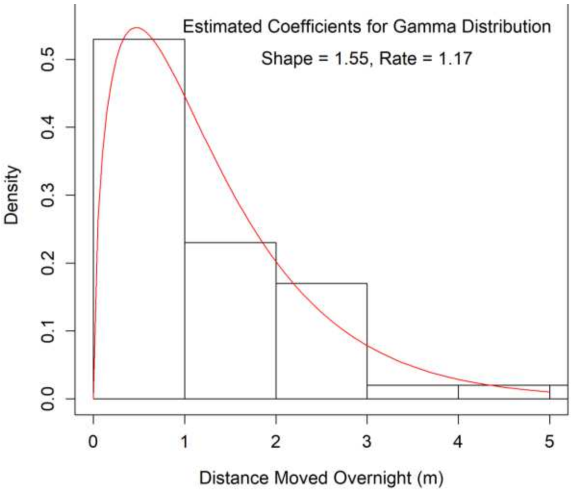

Figure 2. Gamma density function fitted to the overnight distances moved by radio-tagged *P. hochstetteri* snails at Canaan in 2016. Gamma coefficients for the fitted distribution are: Shape = 1.55 and Rate = 1.17.

In both models, a random sample of snails for a simulated survey night was drawn from snails located within 70 m square plot on the night using the R-function *sample* without replacement and sample size set as required for the simulations (Table 2). Samples from survey nights for each simulated mark-recapture survey period were then compiled to provide capture histories for all snails sampled during the simulations.

Table 2. Summary of the numbers of *P. hochstetteri* snails caught and capture probabilities (P. Capture) on survey nights during three mark-recapture surveys: Canaan 2016 & 2019, and Wainui 2018.

Canaan 2016 (Pop. 264)	*Night*	*1*	*6*	*9*	*14*	*21*
	N. Caught	51	19	28	16	111
	P. Capture	0.19	0.07	0.11	0.06	0.42
Canaan 2019 (Pop. 451)	*Night*	*1*	*16*	*30*		
	N. Caught	112	70	101		
	P. Capture	0.25	0.16	0.22		
Wainui 2018 (Pop. 453)	*Night*	*1*	*15*	*18*	*24*	*34*
	N. Caught	14	99	45	79	117
	P. Capture	0.03	0.22	0.10	0.17	0.26

Determining the Best-fit Movement Model

To determine which of the two snail movement models provide the best fit to data from actual mark-recapture surveys, distances and travel speeds between successive capture locations generated by the simulation models were compared to those observed during the mark-recapture survey undertaken at Canaan during 2016 (Lloyd, 2017a). Snail locations during the Canaan survey were recorded to sub-metre accuracy on a handheld gps unit (Trimble Geoexplorer 6000 Series).

Both simulation models were run with 1000 simulations, using the total numbers of capture in the observed data at Canaan on each survey night (Table 2) and simulated plot populations of 250 snails, which is close to the estimated plot population during the Canaan mark-recapture survey in 2016 (Lloyd, 2017a). The Kolomogorov-Smirnov test (implemented using the R-function *ks.test*) was used to compare the empirical cumulative distribution functions of the distances moved and the average speed of travel between successive capture locations in simulated and observed data.

Simulations to Obtain Edge Effect Correction Factors

Simulations were used to obtain correction factors to adjust for the edge effect bias in *P. hochstetteri* population estimates obtained from the three mark-recapture surveys undertaken in Abel Tasman between 2016 and 2019 (Lloyd, 2017a; Lloyd et al., 2019). Mark-recapture population estimates from the three surveys and simulations of the surveys were all obtained using RMark (Laake, 2013) with the same mark-recapture analytic method using a closed capture-recapture full likelihood model (Otis, Burnham, White, & Anderson, 1978) with the probabilities of first capture (p) and recapture (c) being the same, but varying between nights (i.e. $p_t = c_t$).

Simulations using the random-walk model with a gamma distribution were undertaken separately for each of the three mark-recapture surveys using the schedule of survey nights and the total numbers of capture on each night during each of the three actual surveys (Table 2). A total of 1000 simulations were undertaken for each mark-recapture survey, with 100 simulations at ten simulated plot population sizes. For each survey, the simulated plot population sizes ranged around the actual mark-recapture population estimates. Thus, mark-recapture population estimates from the three surveys were 264, 453 and 451 for Canaan 2016, Wainui 2018 and Canaan 2019 respectively, and the ranges of simulated plot population sizes used for the simulations were 200–290 by 10, 340–520 by 20, and 340–520 by 20.

Correction factors (Equation 1a) for each of the three mark-recapture surveys were estimated and used to adjust mark-recapture population estimates from the surveys for edge effect bias (Equation 1b).

Equations 1 a & b.

a) $Correction\ Factor = Mean\left(\frac{Simulated\ \ Plot\ Population}{MR\ Population\ \ Estimate\ for\ the\ Simulation}\right)$

b) $Corrected\ MR\ Estimate = Correction\ Factor\ \times Original\ MR\ Estimate$

Simulations to Investigate Factors Affecting the Accuracy and Precision of Mark Recapture Population Estimates

Simulations using the random-walk model with a gamma distribution were used to investigate the relative effects of capture probability, population density and the numbers of surveys on accuracy and precision of simulated population estimates obtained from RMark. There were 100 simulations at each combination of a range of capture probabilities (0.05, 0.1, 0.2, 0.3, and 0.4) and population densities (100, 200, 300 400 and 500 snails in the plot). Each simulation included five survey nights, with survey nights on every fourth night (i.e. nights 1, 5, 9, 13 and 17). For each simulation, population estimates were obtained from RMark using the results of two, three, four and five survey nights. *Accuracy* and *Precision* estimates for each simulation were respectively: the mark-recapture population estimate as a percent of the simulated plot population size (Equation 2a), and the width of the confidence interval around the mark-recapture population estimate as a percentage of the simulated plot population size (Equation 2b).

Equations 2 a & b.

a) $$Accuracy = 100 \times \frac{MR\ Population\ Estimate}{Simulated\ plot\ population\ Size}$$

b) $$Precision = 100 \times \frac{(Upper\ Confidence\ Limit - Lower\ Confidence\ Limit)}{Simulated\ Plot\ Population\ Size}$$

Simulations are most accurate when the *Accuracy* value is 100%; this is when the mark-recapture population estimate is equal to simulated plot population size. When *Accuracy* values are less than 100% population estimates are underestimates, whereas when *Accuracy* values are greater than 100% population estimates are overestimates. Precision improves as *Precision* values decline.

Box-and-whisker plots with logarithmic scales on the vertical axes were used to visualise the influence of numbers of surveys, capture probabilities and plot population size on the *Accuracy* and *Precision* values for simulations. Box-and-whisker plots are a non-parametric method to display dispersion and skewness in samples of a variable without assumptions about its underlying statistical distribution. The central hinge on a box plot depicts the median, while the top and bottom of the box depict the first and third quartiles respectively (i.e. enclosing 25% and 75% of the range of values). Whiskers on the plot depict the range of values outside the upper and lower quartiles, with outlying values plotted as individual points beyond the whiskers. Notches on the sides of a box provide approximately 95% confidence intervals around the medians. Thus, when notches of box plots from different samples do not overlap, it is likely that medians of the samples are significantly different.

RESULTS

Determining the Best-fit Movement Model

The mean numbers of observations of successive captures per simulation with the random-walk and bivariate normal models were 56.5 and 57.7 respectively. These values are similar to the 60 observations of successive captures of *P. hochstetteri* during the Canaan 2016 mark recapture survey.

The empirical cumulative distribution functions (ECDF) for distances moved and speeds of movements between successive captures (Figure 3) during the mark-recapture survey were not significantly different from ECDFs generated using simulations with the random-walk model (two-sided Kolomogorov-Smirnov test: $p = 0.33$ & $p = 0.37$ respectively), but were significantly different from those generated using simulations with the bivariate normal model (two-sided Kolomogorov-Smirnov test: $p < 0.0001$).

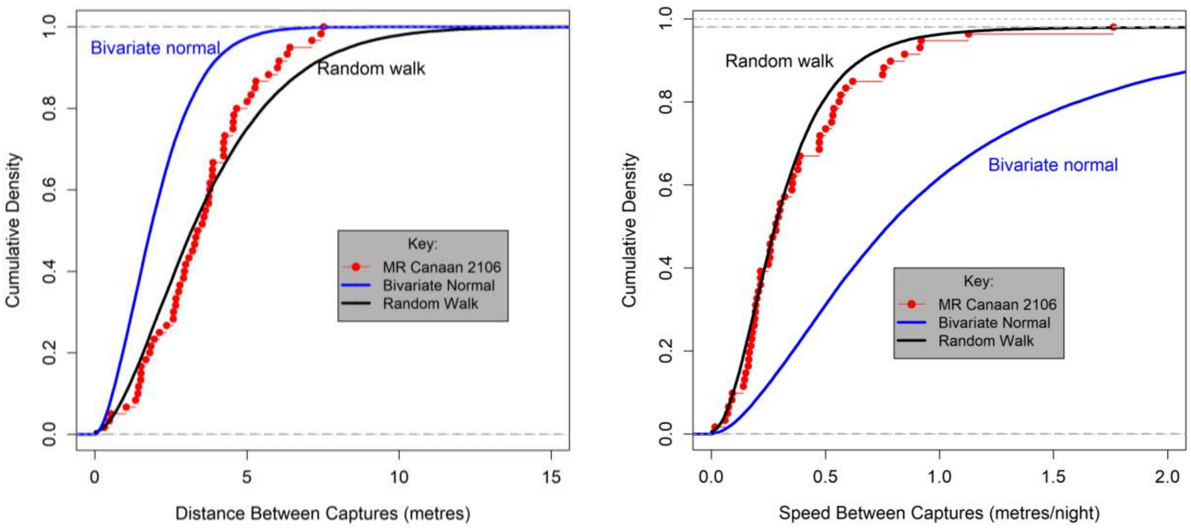

Figure 3. Comparisons of the empirical cumulative distribution functions of the distances moved and the average speed of movements between successive capture locations for *P. hochstetteri* snails (red) captured on more than one survey night during mark-recapture surveys of the Canaan plot during 2016 and from simulations using two models for snail movement: bivariate normal (blue) and random-walk (black).

Differences between the ECDF generated with the bivariate normal model and the other two ECDFs are far greater for speed than for distance (Figure 3). This is because, there is no correlation between the distances moved and time between successive captures in the bivariate model (Pearson's correlation coefficient = 0.003), whereas there is a positive correlation between distance moved and time between captures both during the actual mark-recapture survey and in simulations using the random-walk model (Pearson's correlation coefficient = 0.175 and 0.385 respectively). The increased proportion of faster movements in the bivariate model is apparent in histograms comparing speed between captures for the mark-recapture survey and the two simulation models (Figure 4).

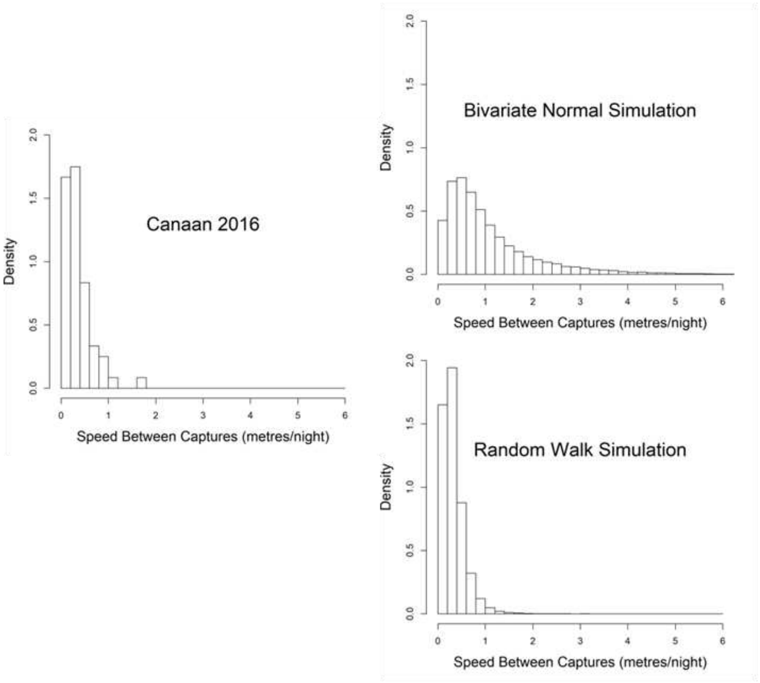

Figure 4. Histograms showing the distributions of the average speed of movements between successive capture locations for *P. hochstetteri* snails captured on more than one survey night during mark-recapture surveys of the Canaan plot during 2016 and from simulations using two models for snail movement: bivariate normal and random-walk.

Correcting mark-recapture Population Estimates for the Edge Effect

Correction factors for population estimates from Canaan 2016 and 2019, and Wainui 2018 mark recapture surveys were respectively 0.931, 0.916 and 0.935 (Table 3). Thus, because of edge-effect bias, mark-recapture population estimates are respectively 7.4%, 9.2% and 7.0% greater than the actual population sizes. The sizes of the edge effect are likely to be affected by a variety of factors. However the primary factor influencing the magnitude of overestimates is probably the length of intervals between night-time searches because snails are more likely to move in or out of the plot during longer intervals between searches. Mean intervals between night-time searches were 5, 14.5, and 8.25 days respectively for the Canaan 2016 and 2019, and Wainui 2018 surveys. Other factors that might affect the edge effect are the number of night-time surveys (5, 3 and 5), numbers of snails captured and distribution of nightly capture rates among nights during the course of a survey (Table 2).

Table 3. Estimated correction factor to compensate for the edge effect bias in mark-recapture population estimates from three mark-recapture surveys for *P. hochstetteri* snails. Confidence limits (CI95%) for the original MR population estimate are from MR analyses using R-Mark.

MR Plot	Year	Corr. Factor	Population Estimate				Size of Bias
			Original		Corrected		
			N.	*(CI95%)*	N.	*(CI95%)*	
Canaan	2016	0.931	264	*(23 0 – 317)*	246	*(214 – 295)*	7.4%
	2019	0.916	451	*(379 – 557)*	413	*(347 – 510)*	9.2%
Wainu	2018	0.935	453	*(398 – 529)*	423	*(372 – 495)*	7.0%

Factors Affecting the Accuracy and Precision of Mark-Recapture Population Estimates

Mark-recapture population estimation was considered to have failed for simulations where either the standard error around the population estimate was zero, or the population estimate or width of the confidence interval around it, were one hundred times larger than the simulated population size. Mark-recapture population estimation for many of the simulations with nightly capture probabilities less than 0.2 failed (Table 4). Highest failure rates were for simulations with only two simulated survey nights and low simulated population sizes. There was only one failure among the 2000 simulations with nightly capture probabilities of 0.2. This simulation had the lowest simulated population size of 100 individuals and only two survey nights. There were no population estimation failures in simulations with nightly capture probabilities greater than 0.2.

Table 4. Proportions of simulations where mark-recapture population estimation failed. There were no failures in simulations with nightly capture probabilities greater than 0.2.

	Nightly Capture Probability											
	0.05				0.1				0.2			
N. Surveys	2	3	4	5	2	3	4	5	2	3	4	5
Pop. size												
100	0.79	0.47	0.19	0.07	0.27	0.10	0	0	0.01	0	0	0
200	0.56	0.24	0.07	0.01	0.10	0	0	0	0	0	0	0
300	0.50	0.09	0	0	0.06	0	0	0	0	0	0	0
400	0.32	0.06	0	0	0.03	0	0	0	0	0	0	0
500	0.31	0.02	0	0	0	0	0	0	0	0	0	0

All three factors modeled in the simulations affected the *Accuracy* and *Precision* values of mark-recapture population estimates (Figures 5–8), however nightly capture probability had the largest influence. The *Accuracy* values for simulations with capture probabilities of 0.05 generally had range widths equal to more than 100% of the plot population size (Figure 5a) and *Precision* rarely dropped below 100% of the population size (Figure 5b). Increasing capture probabilities to 0.10 reduced the range of *Accuracy* values (Figures 6a) and reduced *Precision* values somewhat (Figures 6b), but the reductions were only significant for simulations with four or five survey nights and simulated plot population sizes of 300 or 400 individuals.

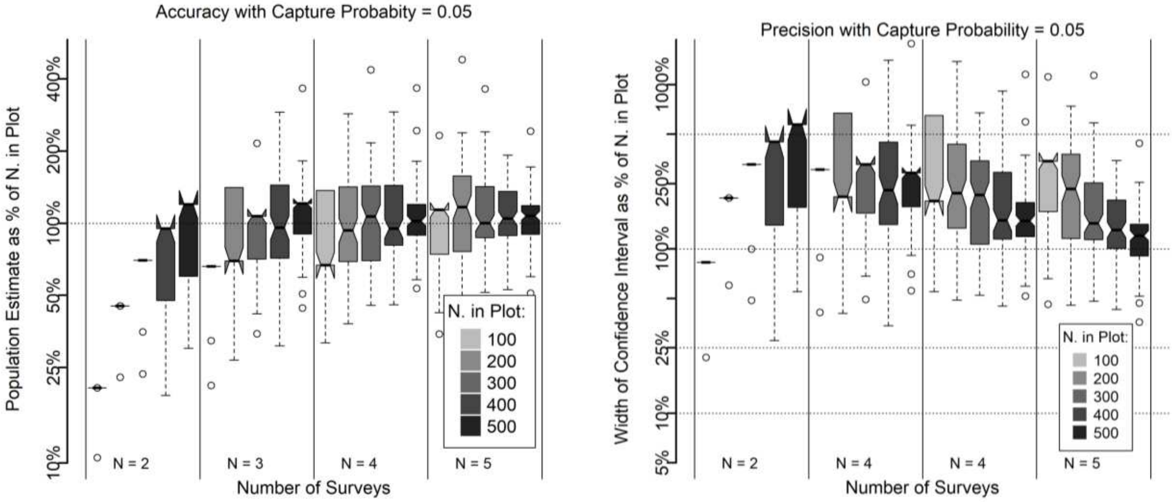

Figure 5. Box plots showing the relative influences of the number of surveys and population size on the accuracy and precision of mark-recapture population estimates in simulations with nightly capture probabilities of 0.05.

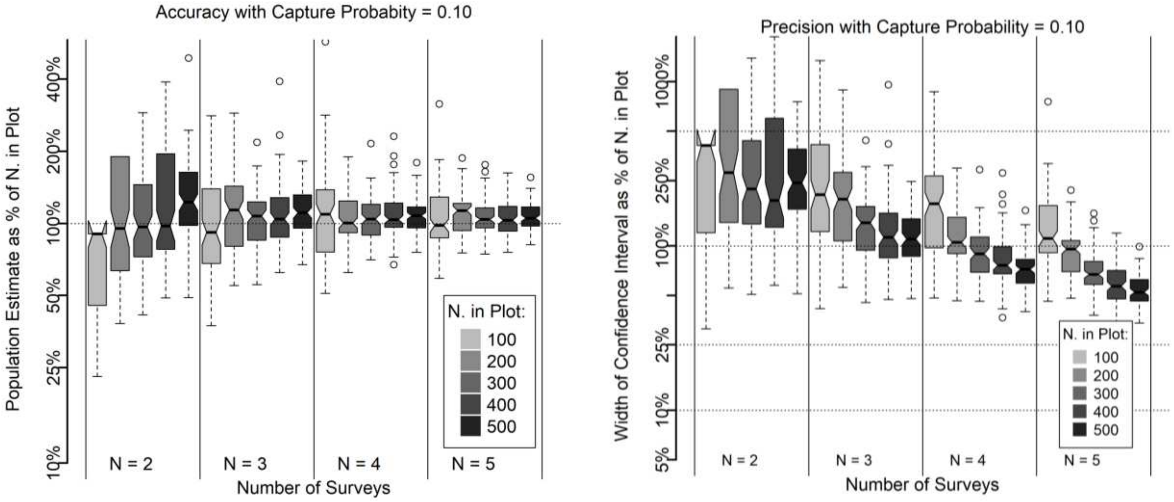

Figure 6. Box plots showing the relative influences of the number of surveys and population size on accuracy (a) and precision (b) of mark-recapture population estimates in simulations with nightly capture probabilities of 0.10.

For simulations with capture probabilities ≥0.2 and more than 2 survey nights, the mean and median *Accuracy* values show relatively little change with plot population size or numbers of survey nights Figure (7). Mean *Accuracy* values ranged between 5% and 9 %, which is within the range of values expected as a consequence of the edge effect bias resulting from using a closed mark-recapture method. However, the range of *Accuracy* values declined with increasing numbers of survey nights and plot population size. *Precision* values for simulations with capture probabilities ≥0.2 showed much greater response (Figure 8) than *Accuracy* values to changes in all three factors modeled in the simulations. The median and range of *Precision* values declined steadily with increases in all three of the modeled factors. For example, the median and maximum *Precision* values were 167% and 1800% for simulations with 2 survey nights, capture probabilities = 0.2 and plot population size = 100, compared to 7.5% and 9.2% for simulations with 5 survey nights, capture probabilities = 0.4 and plot population size = 500.

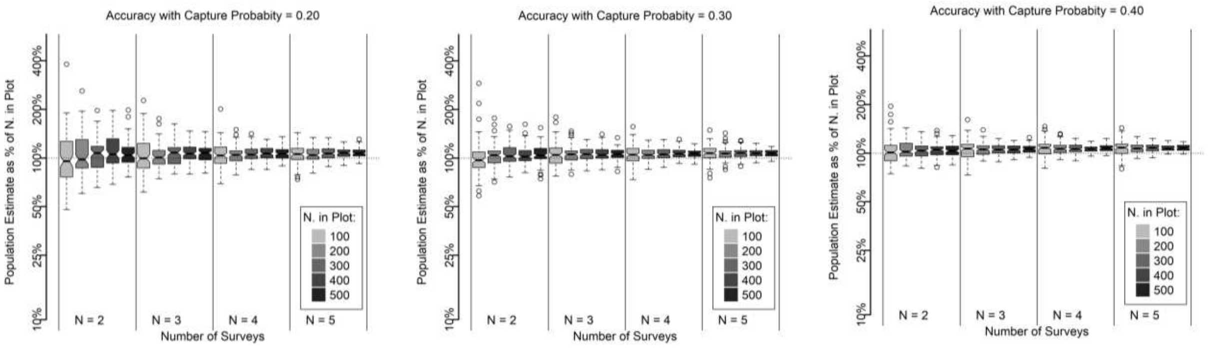

Figure 7. Box plots showing the relative influences of the number of surveys and population size on the accuracy of mark-recapture population estimates in simulations with nightly capture probabilities of 0.20, 0.30 and 0.40.

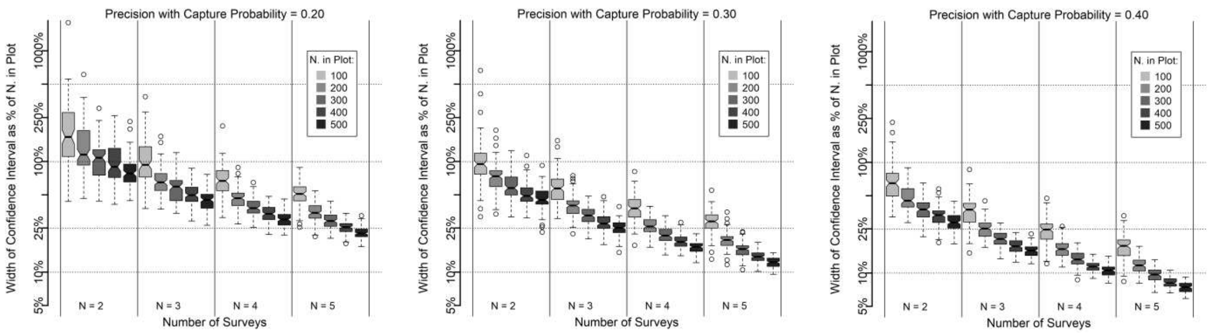

Figure 8. Box plots showing the relative influences of the number of surveys and population size on the precision of mark-recapture population estimates in simulations with nightly capture probabilities of 0.20, 0.30 and 0.40.

DISCUSSION

Movement Models

The results indicate that the random-walk model provides a good model of snail movements during mark-recapture surveys for *P. hochstetteri* snails, whereas the bivariate normal model performs poorly (Figure 3). In this study, failure of the bivariate normal model probably stems from the lack of correlation between the distances moved and time between successive captures. The random-walk model fits the observed location data during a mark-recapture survey well. The random-walk model also provides a better description of the snail movements observed during a radiotelemetry study of *P. hochstetteri* snails (Lloyd, 2017b). During the three to five weeks of the radiotelemetry study, there was no indication that any of the ten radio-tagged snails had core home ranges, which would be expected if snail movements followed a bivariate normal model.

Although the random-walk model used in this study provides a good model for snail movements during the relatively short duration of a typical mark-recapture survey (i.e. 3–4 weeks), it is unlikely that it will be a good model for describing snail movements over longer periods as it does not incorporate site fidelity. In the real world, a significant proportion of individual snails remain within a plot over a period of years (Lloyd et al., 2019), whereas with the random-walk model used in this study most simulated snails will eventually leave the simulated plot.

Correcting for the Edge Effect

Simulations with the random-walk model indicate that the edge-effect bias in mark-recapture population estimates for *P. hochstetteri* in the three surveys considered here is relatively small, with mark-recapture population estimate between 7 & 9% higher than actual population size (Table 3). The correction factors obtained from these simulations will not be valid for population estimates from other mark-recapture surveys of *P. hochstetteri* as the simulations were customized to the results of each individual mark-recapture survey by using the numbers of snails caught each survey night and the schedule of survey nights. Parameter estimates used to model snail movements were obtained from a radiotelemetry study of *P. hochstetteri* snails movements undertaken in the Canaan mark-recapture plot (Lloyd, 2017b) close to the end of the 2016 mark-recapture survey (Lloyd, 2017a). Consequently the parameter estimates are well suited to modelling movements during the Canaan 2016 survey, however their validity for the other two mark-recapture surveys for *P. hochstetteri* is less certain.

Although snail activity levels are strongly influenced by environmental conditions (Lloyd, 2017a, 2017b), differences between surveys are minimised by scheduling search nights for nights with conditions that favour snail movements (i.e. temperatures > 8°C and humidity at or close to

100%). Additionally, in simulations of the surveys differences in activity levels in response to environmental conditions are modelled by snail capture numbers on each survey night.

There is no information on how differences between habitats will affect snail movement. Habitats in the Canaan and Wainui plots are superficially similar. Both plots are between 700 and 800 m asl, under closed canopy mixed beech forest, with deep humus layer on the forest floor. However, there are major differences in the compositions of undergrowth, ground cover and underlying rock in the two plots.

In the absence of realistic alternatives, the simulation method using parameter estimates from the radiotelemetry study at Canaan in 2016 provides the best method to obtain correction factors for population estimates from other mark-recapture surveys for *P. hochstetteri*. Because other snail species are likely to have very different movement behaviors to *P. hochstetteri*, radiotelemetry studies will be required to obtain parameter estimates describing their movement behaviour will be required to use the method to correct mark-recapture estimates for other snail species.

Factors Affecting the Accuracy and Precision

All three of the factors modeled in the simulations affected the accuracy and precision of mark-recapture population estimates, but nightly capture probability had the largest influence. Simulation results show that as long as nightly capture probabilities approach, or exceed, 0.20 (Figures 7 & 8), good population estimates can be obtained with four or more surveys, even with the lowest plot population size of 100 snails. When plot population sizes are ≥200 and capture probabilities are ≥0.20 only three night-time surveys should provide reasonably good population estimates. This reduction in the number of night-time surveys from five, or more, to only three provides a major reduction in the cost and complexity of a mark-recapture survey. However to achieve nightly capture probabilities ≥0.20 survey nights must be selected carefully to ensure that environmental conditions suit high levels of above-ground activity by the snail species being targeted. Surveying on only three nights within the three to four week long period that a mark-recapture survey should be completed in makes it easier to schedule survey nights on nights with good conditions for above-ground snail activity.

Modifications to the mark-recapture survey field method since the original protocol was developed (Gruner et al., 2011) have also improved survey efficiency: reducing the time taken to search a plot, the number of field workers required and the amount of habitat disturbance. The original protocol (Gruner et al., 2011) required four searchers to search unmarked swathes going up the dominant slope and return to the bottom edge of the plot between uphill searches of succesive swathes. Searching along 10 m wide lanes marked across the dominant slope of the plot with permanent lines (Lloyd, 2017a) has proved more efficient. In the original protocol, all captured snails were transported to a site outside of the mark-recapture plot for processing and then returned to their capture location after processing. However, it is more efficient to record details of snails that are already tagged at their capture location without transferring them to the processing site. In addition, on dry nights with relatively few (≤20) snails to tag, untagged snails can be tagged at their capture sites as they are found (Lloyd et al., 2019). An established processing site is only required on wet nights or on nights when large numbers (>20) of snails must be tagged.

One obstacle to the uptake of the mark-recapture method is the belief that the method is only useful in areas with high densities of snails. Comparisons between snail counts from diurnal sub-surface searches of 100 m^2 plots and population estimates obtained using either mark-recapture (Lloyd, 2015, 2017a), or repeated destructive plot sampling (Hamilton, 2015a) show that on average only 20%–25% of powelliphanta snails (*P. hochstetteri*, *P. augusta* and *P. patrickensis*) present in a plot are likely to be found during a sub-surface search. Thus, although a population of 100 powelliphanta snails in a 70 m square mark-recapture plot corresponds to 2.04 snails per 100 m^2 plot, the probable snail count from diurnal sub-surface searches will only be 0.41–0.51 snails. Sub-surface searches for *R. oconnori* are probably less effective than searches for powelliphanta snails, with as few as 8% of the rhytida snails present in a plot being found in the one available comparison (Lloyd, 2017a). Thus, a population of 100 rhytida snails in a 70 m square mark-recapture plot could correspond to a snail count of only 0.16 from a diurnal sub-surface search of a 100 m^2 plot. When the diurnal sub-surface search method is used, populations with snail counts of less than one snail per 100 m^2 plot are generally considered low density populations, but the results of the simulations indicate that even at these densities good population estimates can be obtained using the mark-recapture method.

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