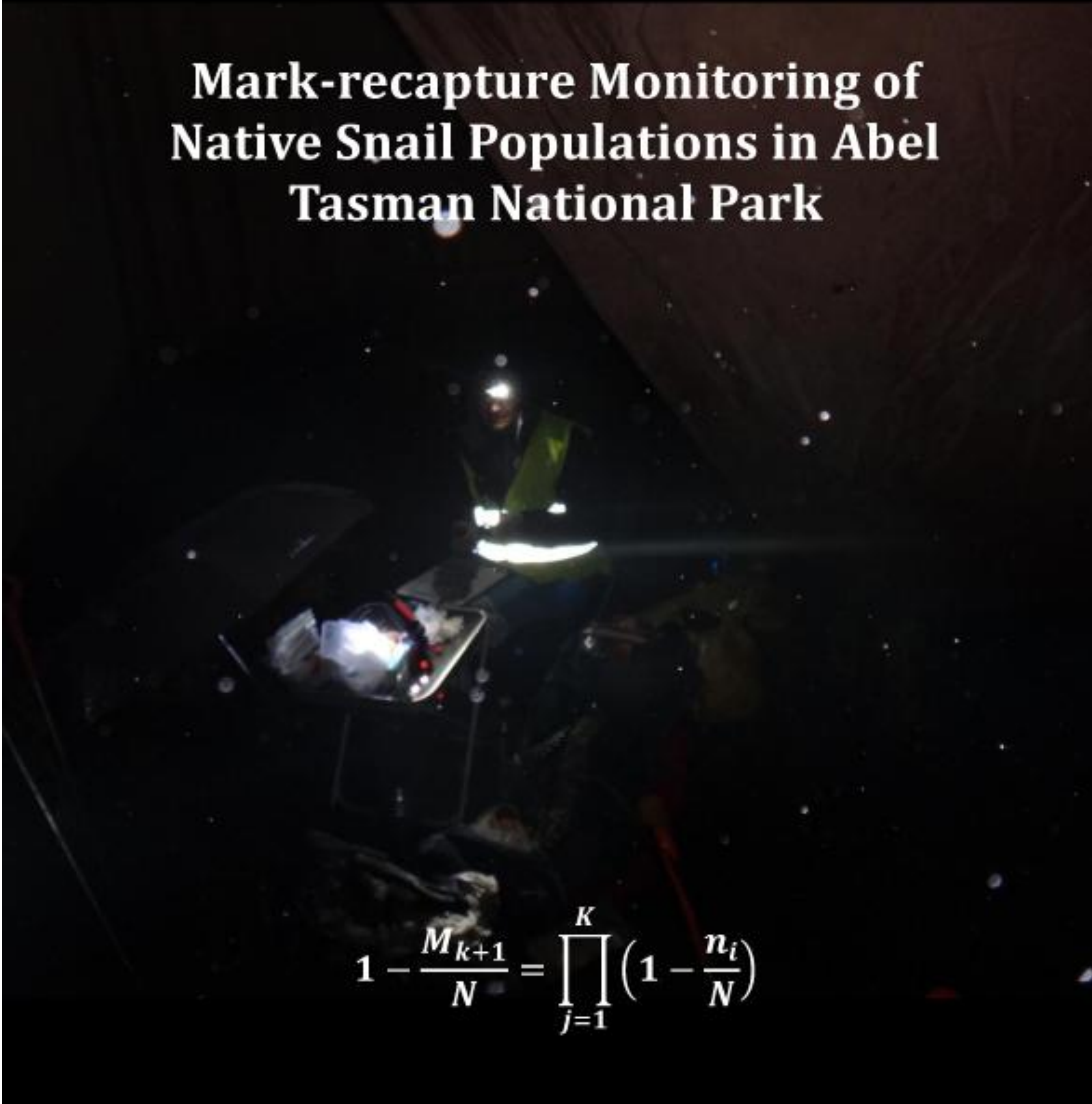
$$P\left(\{x_\omega\}\middle|N,\underline{p}\right)=\frac{N!}{\left[\prod_\omega x_\omega!\right](N-M_{K+1})!}\times\prod_{j=1}^{K}p_j^{nj}\left(1-p_j\right)^{N-nj}$$

Mark-recapture Monitoring of Native Snail Populations in Abel Tasman National Park



$$1-\frac{M_{k+1}}{N}=\prod_{j=1}^{K}\left(1-\frac{n_i}{N}\right)$$

Mark-recapture Monitoring of Native Snail Populations in Abel Tasman National Park

Date: July 2017

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For: Project Janszoon

EXECUTIVE SUMMARY

During spring 2016, a single mark-recapture plot was established in the Canaan Downs area, on the south-west edge of Abel Tasman National Park to establish a long-term monitoring programme using mark-recapture methods to provide reliable and robust information on populations of the endangered carnivorous land snails: *P. hochstetteri* and *R. oconnori*. Mark-recapture monitoring entailed repeated nocturnal searches for snails active on the surface of the 70 m square plot during a 3-week period in October 2016. Snails found in the plot were individually marked with numbered identification tags and the numbers of snails in the plot estimated from the capture histories of individual snails. Mark-recapture estimates of snail densities in the plot are: 555 snails per ha (CI95%: 461−635) for *P. hochstetteri*, and 506 snails per ha (CI95%: 278−1,060) for *R. oconnori*. These are quite different to density estimates derived from snail counts in ten nearby standard snail monitoring plots resurveyed in December 2016: 126 snails per ha (CI95%: 57−196) for *P. hochstetteri*, and 42 snails per ha (CI95%: 2−82) for *R. oconnori*.

Snail counts from DOC's thirteen standard 100 m^2 snail monitoring plots indicate that snail populations in the Canaan area have declined markedly since monitoring began in 2000, with average annual declines of 7.8% for *P. hochstetteri* and 12.2% for *R. oconnori*. However, the size distributions of the 204 live *P. hochstetteri* and 72 live *R. oconnori* caught during nocturnal searches of the mark-recapture plot indicate that the snail populations in the plot are healthy with ongoing high levels of recruitment to populations of both snail species. Because this is the first time mark-recapture monitoring has been used in the area, results from mark-recapture monitoring do not provide any other insight into local snail population trends.

Although mark-recapture monitoring native snails is logistical demanding, it provides reliable unbiased estimates of snail populations and, when repeated at regular intervals, also provides information on recruitment and survival. Mark-recapture monitoring is an important method for validating the existing snail monitoring programme based on snail count indices from sub-surface plot searches. The Canaan mark-recapture monitoring plot should be resurveyed at regular intervals, preferably annually, to get detailed population information and monitor population trends in response to conservation management. If snail population monitoring is to be extended over a wider area of Abel Tasman National Park, the extended monitoring programme should include a small number of mark-recapture snail plots placed in representative habitats with known snail populations to validate information from more widely spread sub-surface searches of 10m square plots.

INTRODUCTION

Ecological restoration of Abel Tasman National Park, in the north of New Zealand's South Island (Figure 1), is being undertaken by Project Janszoon, a privately funded charitable trust, working in partnership with the Department of Conservation. The restoration goal is to transform the park's ecology by a combination of pest control, weed removal, re-forestation and species reintroductions. Increasing populations of endangered native fauna within the park is an important part of the restoration process. To this end, Project Janszoon is considering establishing a snail sanctuary at Canaan Downs, in the south of Abel Tasman National Park, specifically to protect local populations of two endangered carnivorous land snails *Powelliphanta hochstetteri hochstetteri* and *Rhytida oconnori* (Harper and Goodman 2015).

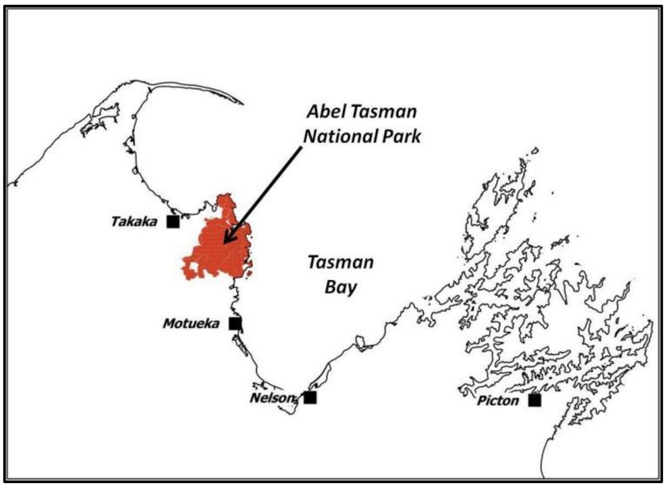


Figure 1. Map of showing the location of Abel Tasman National Park.

P. h. hochstetteri and *R. oconnori* are both endemic to the Abel Tasman region (Efford 1998, Walker 2003) occurring sympatrically in unmodified native forest throughout wide areas of Abel Tasman National Park (Ogle 2016). *P. h. hochstetteri* also occurs in nearby Kahurangi National Park (Walker 2003) and there are reports of *R. oconnori* at Parapara Peak and Kaihoka Lakea, in Golden Bay (pers. comm. Ian Millar). In the Department of Conservation's threat classification lists, *P. h. hochstetteri* and *R. oconnori* are ranked as nationally endangered and nationally critical respectively (Hitchmough et al. 2007). These rankings are because of threats from habitat degradation and predation by introduced species (feral pigs *Sus scrofula*, rats *Rattus sp.*, brushtail possums *Trichosurus vulpecula*, hedgehogs *Erinaceus europaeus occidentalis* and song thrush *Turdus merula*) (Efford 1998, Walker 2003). Native species such as weka *Gallirallus australis*, and kea *Nestor notabilis*, also prey on the two snail species.

Effective and robust monitoring of the responses of threatened taxa to conservation management is an essential part of the ecological restoration process. There has been ongoing monitoring of *P. hochstetteri* and *R. oconnori* in the Canaan region of Abel Tasman National Park since 2000 (Ogle 2012) using the standard method for monitoring populations of New Zealand's threatened snails: diurnal sub-surface searches of 100 m^2 plots (Walker 1997). The diurnal sub-surface search method does not provide population estimates, it provides indices in the form of snail counts per 100 m^2 plot. For the purposes of population monitoring and comparisons between populations, it is assumed that the indices are proportional to the actual population densities. Recent work (McLennan 2006, Hamilton 2015a) indicates that this assumption is flawed. Population indices from the sub-surface search method are subject to biases from a range of sources including local habitat structure, current and previous weather conditions, seasonal changes in snails' behaviour and the skill and motivation of field workers. In addition, because of inherent variability in the numbers of snails found during sub-surface plots, 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 index estimates (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.

In recent years, mark-recapture methods have been developed to overcome deficiencies in the standard method for monitoring *Powelliphanta* snail populations (Gruner et al. 2011, Hamilton 2015b, c, Lloyd 2015). Mark-recapture monitoring of snail populations entails repeated nocturnal searches for snails active on the surface of a 70 m square plot during a period of 3 or 4 weeks. Snails found in the plot are individually marked with numbered identification tags and then released at their capture locations. Estimates of the numbers of snails in the plot are obtained from the capture histories of individual snails using established mark-recapture analytic methods (White et al. 1982, Williams et al. 2001, Borcher et al. 2002, Cooch and White 2014, Lukacs 2014). Estimates of the numbers of snails obtained using the mark-recapture method are not population indices, and are not affected by the wide range of biases that standard snail count indices are prone to. However, the estimates are affected by a systematic bias, referred to as the "edge effect", which occurs because the population of snails in a plot is not entirely closed. Snails with home ranges straddling the plot boundary 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 population estimates, making density estimation from plot population estimates problematic. 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. A common, but simplistic approach, involves making various ad hoc adjustments to the plot population estimates based on estimates of the width of the boundary strip occupied by individuals that move across the plot boundary (Williams et al. 2001). Other workers augment mark-recapture data with radio-telemetry information on animal movements (Ivan 2014). More recently spatially explicit capture- recapture methods have been developed to overcome the edge effect problem by using maximum likelihood methods to estimate population density from information on the exact location of captures during mark-recapture studies (Royle et al. 2013).

The main objective of the work presented in this report is to establish a long-term monitoring programme using mark-recapture methods to provide reliable and robust information on populations of *P. hochstetteri* and *R. oconnori* in Abel Tasman National Park. Although the cost of mark-recapture plots precludes large scale replication of mark-recapture plots over wide geographic areas, information from a small number of mark-recapture plots will be a valuable resource for augmenting and validating the results of ongoing snail population monitoring with sub-surface plot searches.

The report presents population estimates for *P. hochstetteri* and *R. oconnori* obtained from the mark-recapture plot data using two analytic methods: standard mark-recapture analysis for closed populations (White et al. 1982, Huggins 1989, Lukacs 2014) and a spatially explicit capture-recapture method (Borchers and Efford 2008, Royle et al. 2013, Efford 2017). Information on snail home-ranges from a concurrent radio-telemetry study of *P. hochstetteri* movements (Lloyd 2017) was used to simulate *Powelliphanta* snail population distributions. Simulations were then used to evaluate the performance of the two analytic methods, investigate the magnitude of "edge effect" biases in mark-recapture population estimates and develop a method to correct for the bias and achieve unbiased population estimates.

METHODS

The mark-recapture field method was based on the method developed for monitoring of population trends in *Powelliphanta* by Gruner et al. (2011) and described in detail by Lloyd et al. (2014). A single 70 m square mark-recapture plot was established in the Canaan Downs area, on the south-west edge of Abel Tasman National Park (Figure 1). The plot lies within a large tract of unmodified high altitude mixed beech forest, 760–770 m above sea level, on a south-east facing 10° slope, 300 m north of the Harwood's Hole track. Forest in and around the study area has a 20 to 30 m high canopy dominated by silver beech *Lophozonia menziesii* and a moderately dense under-storey including *Griselinea littoralis*, *Weinmannia racemosa*, *Melicytus ramiflorus* and *Leucopogon fasciculatus*. The underlying rock is marble karst, and the ground comprises intricate karren formations with numerous underground crevices, overlaid by layers of moss and deep humus. There was no evidence of trampling by introduced ungulates within the study area, but there was evidence of trampling by wild pigs *Sus scrofa* nearby (<80 m).

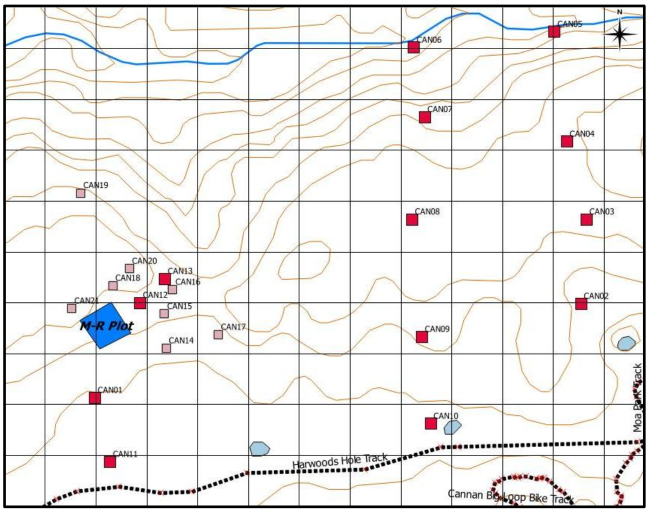


Figure 2. Map with 100 m grid showing the location of the mark-recapture plot (blue) and nearby standard snail monitoring plots. Red squares are standard 100 m^2 snail monitoring plots. Pink squares are 25 m^2 snail monitoring plots.

Before establishing the plot, nocturnal searches for snails were undertaken to identify an area with good populations of both snail species. The actual plot location within the area was relatively random as it was dictated by the need to be close to, but avoid, a surrounding cluster of the Department of Conservation's permanent standard snail monitoring plots (Figure 2). The mark-recapture plot boundaries were delineated with Gallagher Poly Tape and 10 m wide lanes across the dominant slope of the plot were marked with Gallagher Poly Line. (Gallagher Poly Tape and Poly Line are long-lasting polyethylene farm fencing materials.) A single mark-recapture assessment entails between five and seven successive nocturnal searches of the plot. Successive searches are spaced at least two nights apart to ensure independence, and less than two weeks apart to minimise snail dispersal and mortality between surveys. Nocturnal searches are best undertaken on nights when weather conditions favour snail movement (i.e. temperatures > 6°C and humidity at or close to 100%).

Individual mark-recapture search involved a single complete search of the plot for live snails active on the surface. Nocturnal searches were undertaken by a team of at least four people working side by side, along the 10 m wide lanes marked within the plot. Search speed averaged about 5 m per minute. The starting lane and the direction of searches along the lanes were chosen randomly on each search night. When a live snail was found during searches, its capture location was marked temporarily and recorded on a handheld gps unit with sub-metre accuracy (Trimble Geoexplorer 6000 Series), together with the snails' species and any tag numbers. After processing, snails were released at their original capture sites.

On first capture, snails were weighed, their maximum diameter measured and their general condition recorded. Snails were marked using the standard method developed for tagging *Powelliphanta* snails (Grüner, Weston, & Hamilton, 2011) with a numbered polyethylene tag glued to the ventral surface of the snail shells immediately behind the aperture (Figure 3) with Selley's Quick Fix Supa Glue Non-Drip. The tags were attached ventrally to avoid attracting predators to the coloured tags. Three different tag types were used: four-digit and two-digit glue-on shellfish tags (manufactured by Hallprint Pty Ltd, www.hallprint.com) and queen bee tags (obtained from the Bee Works, www.beeworks.com). The four-digit tags were used on larger snails (>30 mm diameter), while two digit tags were used on smaller snails. The queen bee tags were only used on a small sample of very small snails, 15 to 18 mm diameter, but their use was discontinued because of the difficulties experienced gluing them. When previously tagged snails were recaptured, their location, tag number and general condition were recorded.

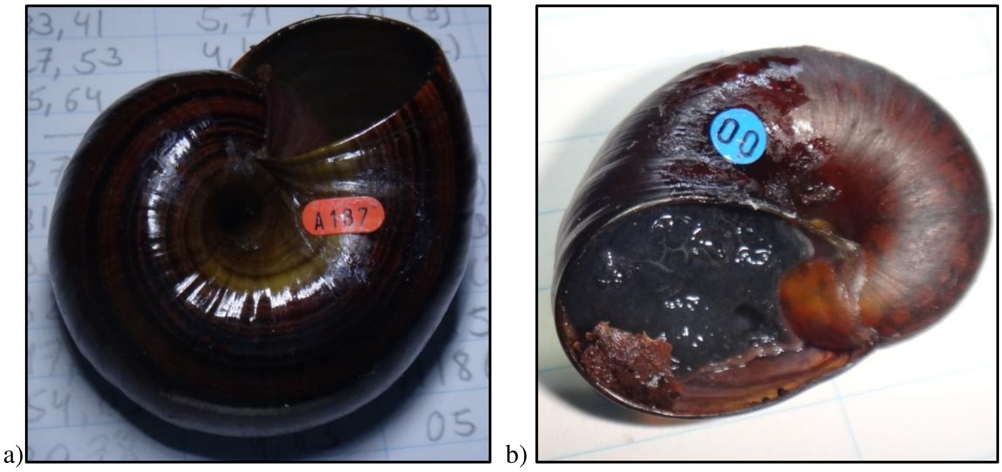


Figure 3. Tagged snails: a) *P. hochstetteri* with a four-digit Hallmark tag and b) *R. oconnori* with a two-digit Hallmark tag.

Environmental Information

Temperature and relative humidity near ground level were recorded at ten minute intervals on a data-logger (Onset Hobo Pro v2 temp/RH Logger) placed 300 mm above the ground attached to a wooden peg in forest 5 m outside the mark recapture plot. Rainfall records with cumulative rainfall over 15 minute intervals were obtained from Tasman District Council's web site (http://www.tasman.govt.nz/environment/water/rainfall/rainfall-433/). The rainfall records are from an automated recording rain gauge situated in open farmland 2.4 km east of the mark-recapture plot and at the same elevation (760 m above sea level). Moon size is the fraction of the moon illuminated, obtained from an electronic astronomical almanac (US Naval Observatory 2001). Dusk and dawn times are the beginning and end of civil twilight, also obtained from an astronomical almanac. Overnight values for climatic variables are values recorded between dusk and dawn times, while daytime values are values recorded between dawn and dusk (i.e. Dusk ≥ Overnight > Dawn ≥ Daytime > Dusk).

Analysis of Mark-recapture Data using MARK

Analyses of the mark-recapture data were undertaken using RMark (Laake 2013) as an interface for the software MARK (White and Burnham 1999, Cooch and White 2014). Closed capture-recapture likelihood-based models (Williams et al. 2001, Lukacs 2014) were used to estimate the numbers of snails in the mark-recapture plot. Closed capture-recapture models are based on the assumptions that there are no births or deaths, and no immigration into, or emigration out of, the population during the sampling period. These assumptions seem reasonable for mark-recapture assessments of *Powelliphanta* snail populations. *Powelliphanta* snails are slow breeding and long-lived (Walker 2003), consequently there will be negligible recruitment or natural mortality during the 20 day mark-recapture sampling period. Evidence from shells found in the study are indicates that snail predation levels are low. The relatively small home ranges (mean MCP home range area of 16.6 m^2) of radio-tagged *P. hochstetteri* (Lloyd 2017) during a 45 day monitoring period indicates that although snails with home range centres close to the plot boundaries may move in and out of the plot, long-term immigration or emigration will be insignificant during the sampling period.

Two families of capture-recapture likelihood models were used to estimate population abundance: full likelihood models (Otis et al. 1978), which have abundance (parameterised as f_0, the number of animals never caught) in the likelihood function; and conditional likelihood models (Huggins 1989), which have abundance conditioned out of the likelihood function. Both types of models have two encounter parameters: p the probability of first capture; and c the probability of recapturing a previously caught and marked individual. Both p and c can have constant values (denoted as p_c and c_c) or be time-specific, taking different values during different sampling sessions (denoted as p_t and c_t). Thus, p_t is the probability of first capture at time t, and c_t is the probability of recapture at time t.

The recapture parameter c is typically used to model behavioral effects following initial capture, such as animals becoming trap-shy or trap-happy. In the case of *Powelliphanta* snails, the recapture parameter is more likely to model temporal autocorrelation in individuals' activity patterns, where the probability of a snail being active on the surface (and consequently available for capture) during a sampling occasion is influenced by whether it was active on the surface during the previous sampling occasion. More complex, heterogeneity models, in which individuals or groups of individuals in the population have different capture probability, were not used.

Six models can be fitted to the mark-recapture data using the two encounter parameters: (p_t c_t); ($p_t = c_t$); (p_c c_t); (p_t c_c); (p_c c_c) and ($p_c = c_c$). However, the models p_tc_t and p_tc_c are not useful, because the final p_t value cannot be estimated; therefore these two models were not used during the analyses. Derived parameters for the models are: N the total number of individuals in the population; M_{t+1} the total number of animals marked; and f_0 the number of animals never caught (i.e. $f_0 = N - M_{t+1}$). Akaike's Information Criterion (AIC_c) was used for model selection for nested models (Burnham and Anderson 2004). The models with the smallest AIC*c* value being accepted as the most parsimonious, or best-fit, models. The likelihood ratio test (LRT) was also used to compare nested models.

Analysis of Mark-recapture Data Using Spatially Explicit Methods

Estimates of the density of the two snail species were also obtained from the mark-recapture data using a spatially explicit capture-recapture method implemented in the R-library *secr* (Efford 2017). Models were fitted to the data using a polygon detector type with the hazard half normal (i.e. HHN) detection function and time dependent probability of detection. The buffer width was set to 4 metres on the basis of information from a concurrent radio-telemetry study of *P. hochstetteri* (Lloyd 2017).

Population Simulations

To simulate the distribution of the *P. hochstetteri* population in, and around, the mark-recapture plots during mark-recapture surveys, it was assumed that individual snail's home range centres were randomly distributed across the area of interest and that individual snails' home ranges were described by the probability distribution of a bivariate normal distribution with the covariance matrix:

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

where X and Y values of the coordinates have equal variance σ^2, but are uncorrelated. For each simulation, a set of randomly distributed home range centres was obtained using the R-function *runif* to generate random X & Y coordinate pairs, and then the R-function *mvrnorm*, from the R-library *mvtnorm*, was used to generate random locations for individual snails around each of these home range centres for each of the five nights of the mark-recapture surveys.

RESULTS

During the 28 day period (27 September to 25 October) of this study, snails were caught during nocturnal searches on eight nights. Only five of the eight nights were formal mark recapture surveys of the entire plot. On the other three nights only parts of the plot were searched. The first night of nocturnal searches (27 September) was a pilot survey to refine the survey method and only two of the seven 10 m wide swathes of the plot were searched. Very limited nocturnal searches were undertaken on another two nights to capture snails for a related radio-telemetry study (Lloyd 2017).

During all these nocturnal searches there were 295 captures of *P. hochstetteri* and 79 captures of *R. oconnori*. Three *P. hochstetteri* and three *R. oconnori* were captured just outside (< 2 m) of the mark-recapture plot. The rest of the snails were captured within the plot. Ten of the *P. hochstetteri* and six of the *R. oconnori* captured were too small to tag, with maximum diameters less than 15.6 mm. All other snails were marked with individual identification tags on first capture. In total, 194 *P. hochstetteri* and 66 *R. oconnori* were tagged. There were 91 recaptures of tagged *P. hochstetteri*, but only 7 recaptures of tagged *R. oconnori*.

Although there was no concerted effort to find and collect snail shells, 24 shells were collected from the plot. Twenty three of the shells were *P. hochstetteri* and one *R. oconnori*. Sixteen of the *P. hochstetteri* shells and the one *R. oconnori* shell were intact. Three of the *P. hochstetteri* shells were old and fragmented and three showed evidence of predation (Meads et al. 1984): two probably by kea *Nestor notablis* and one probably by rodents. One of the *P. hochstetteri* had died recently as a result of trampling. The trampled shell (diameter 34.6 mm) was found on 10 October. Judging from the state of decay, the snail died about 3 weeks before being found; probably during the plot setup phase, before nocturnal searches were begun.

Snail Sizes

The maximum diameters of live *P. hochstetteri* ranged from 12.7 mm to 69.8 mm, with a mode at around 64.5 mm (Figure 4). The size distribution is multi-modal with minor peaks at 15.5, 37.5 and 46.5 mm, which presumably correspond to recent annual cohorts. *R. oconnori* snails were considerably smaller than *P. hochstetteri*, with maximum diameters ranging from 11.0 mm to 34.0 mm, and a mode at around 33.5 mm (Figure 4). The size distribution of *R. oconnori* is also multi-modal with minor peaks at 15.5, 19.5 and 23.5 mm, which probably correspond to recent annual cohorts.

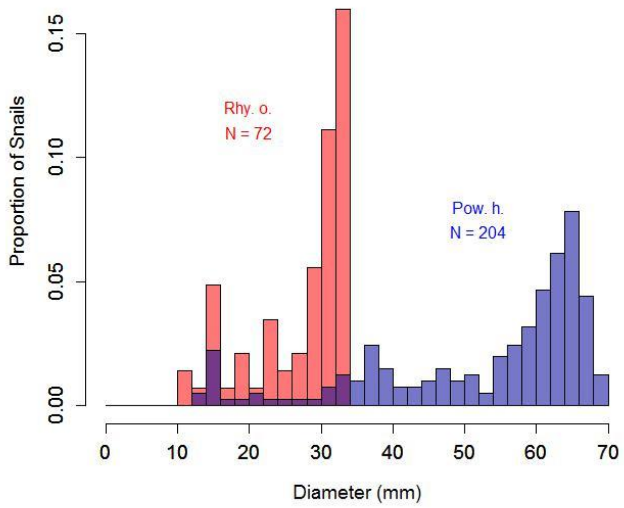


Figure 4. Overlaid histograms showing the distributions of the maximum diameters of the two snail species *P. hochstetteri* and *R. oconnori*.

Comparisons of the size distributions of live *P. hochstetteri* snails and the sample of *P. hochstetteri* shells collected from the plot (Figure 5) using a two-sample Kolmogorov-Smirnov test showed the shells were smaller ($p<0.1$) than the live snails (i.e. their size distribution is to the left of live snails).

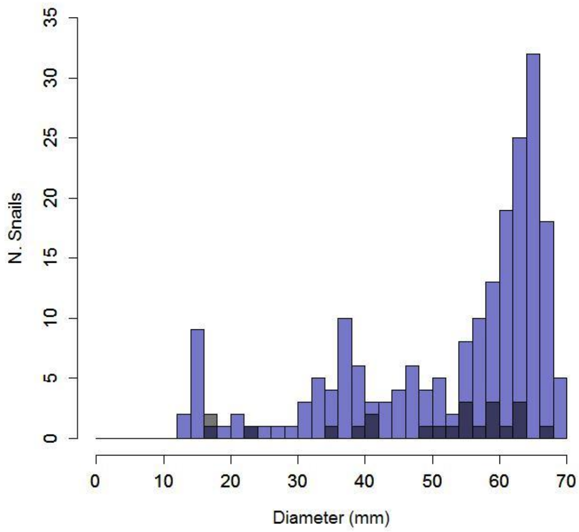


Figure 5. Overlaid histograms comparing the distributions of the maximum diameters of live *P. hochstetteri* and shells collected from the plot.

The relationship between weight and diameter of live snails of the two species fitted polynomial lines with the form $Wgt = \alpha.Diam^{k} + \beta$ (Figures 6 and 7). Coefficient values for the two species are: k = 2.7, α = 0.0006, β = 0.137 for *P. hochstetteri* and k = 2.5, α = 0.0009, β = -0.028 for *R. oconnori*. Significance levels were p<0.0001 for both species. Adjusted R-squared values were 0.97 and 0.95 for *P. hochstetteri* and *R. oconnori*, respectively.

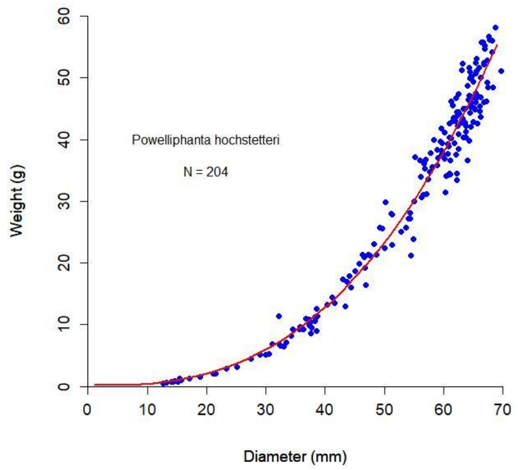


Figure 6. Relationship between weight and maximum diameter for *P. hochstetteri*.

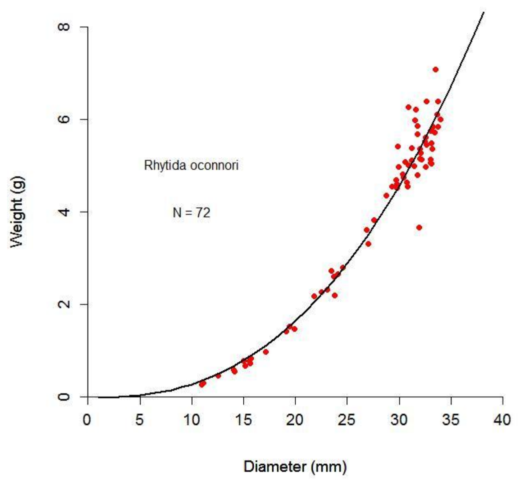


Figure 7. Relationship between weight and maximum diameter for *R. oconnori*.

Effect of Environmental Variables on Snail Activity Levels

The effects of a range of environmental variables on the numbers of snails captured on different nights were investigated using both general linear and general additive modelling (i.e. GLM and GAM). Snail counts were from six nights, which included the five nights when the entire mark-recapture plot was searched as well as the night of the preliminary survey when only two of the seven 10 m wide swathes were searched. An offset term was used in the models to correct for differences in the search effort on the six nights. Values of the offset term for nights when the entire plot was searched were 1 for both species, while values of the offset term used for the night when only part of the plot was searched are the proportions of the species caught in that part of the plot during the five nights when the entire plot was searched (i.e. 0.43 for *P. hochstetteri* and 0.27 for *R. oconnori*). Initial models included: moon size, temperature at dusk, minimum overnight temperature, minimum overnight relative humidity, cumulative overnight rainfall and cumulative rainfall during the previous day.

The results of general linear modelling and general additive modelling were very similar. The minimum significant ($p<0.001$) GLM and GAM models for predicting the numbers of *P. hochstetteri* captured from environmental variables both retained the two variables minimum overnight temperature and minimum overnight relative humidity and an interaction between them. All three terms were significant ($p<0.005$) in both GLM and GAM models. The minimum significant GLM and GAM models ($p<0.001$) for *R. oconnori* only retained minimum overnight temperature ($p<0.01$).

The results of the models are apparent in plots of capture rates for the two species against minimum overnight temperature and relative humidity (Figures 8 and 9). High numbers of *P. hochstetteri* were only caught on warm nights with 100% relative humidity, whereas the numbers of *R. oconnori* caught increased with temperature, but were not influenced by relative humidity values within the range encountered during this work. In plots of the effect of minimum temperature and relative humidity on snail capture rates, the numbers of snails caught on the first night has been adjusted to compensate for reduced search effort by dividing the actual number by the offset term (i.e. 0.43 for *P. hochstetteri* and 0.27 for *R. oconnori*). Thus, actual counts of 38 and 5 for *P. hochstetteri* and *R. oconnori* respectively are adjusted to 88 and 19.

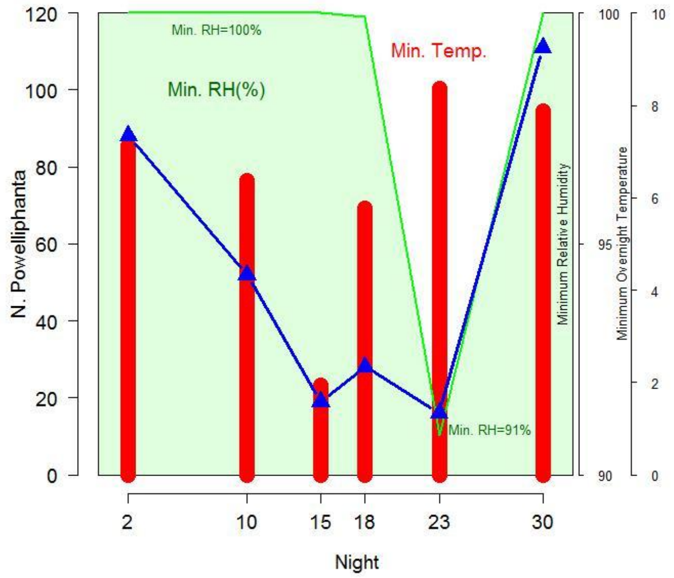


Figure 8. Effect of weather on the numbers of *P. hochstetteri* captured during nocturnal searches. Numbers caught on the first night (Night 2) are adjusted to compensate for reduced search effort.

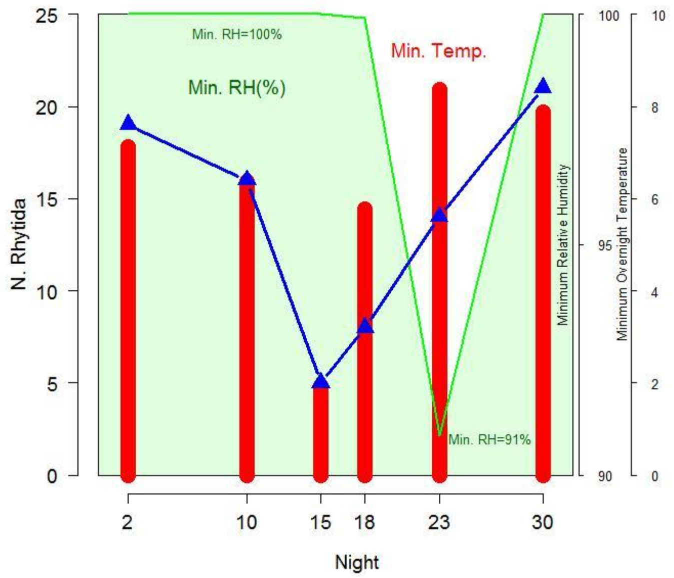
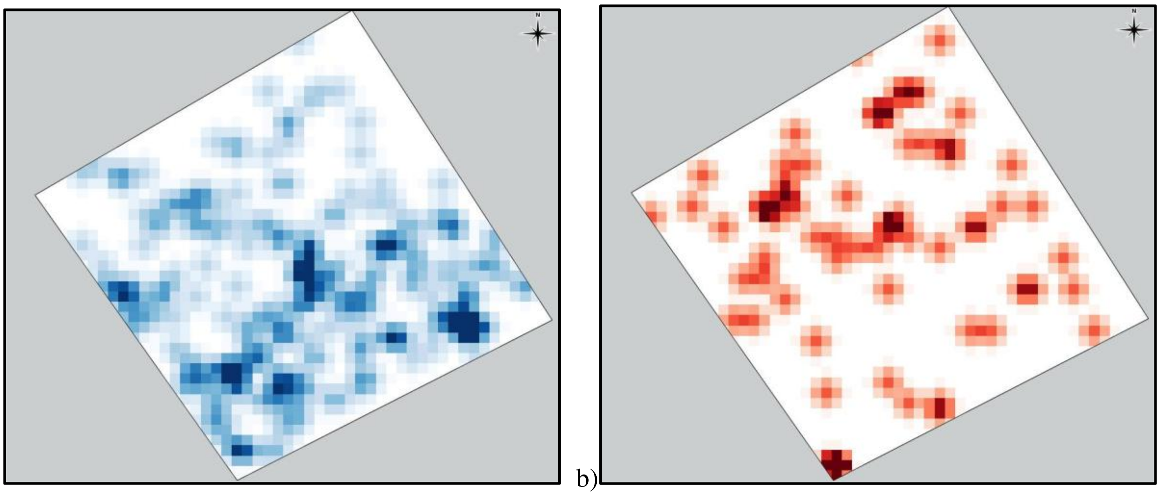


Figure 9. Effect of weather on the numbers of *R. oconnori* captured during nocturnal searches. Numbers caught on the first night (Night 2) are adjusted to compensate for reduced search effort.

Mark Recapture Surveys

Mark-recapture surveys were undertaken on five nights during the 20 day period (5 to 25 October 2016) with intervals of 4, 2, 4 and 7 nights between successive surveys. During the five mark-recapture surveys there were 235 captures of *P. hochstetteri* and 70 captures of *R. oconnori* in the 70 m square plot. Heat maps showing the distributions of all capture location for the two species (Figures 10 a and b) during the five mark recapture surveys were generated using the QGIS plug-in *Heatmap*. Capture locations for *P. hochstetteri* were concentrated in the southern part of the plot whereas capture locations for *R. oconnori* were concentrated in the northern half of the plot. A modified *t*-test (Clifford et al. 1989) to test for spatial association between the two snail species (undertaken using the R-function *modified.ttest* in the R-library *SpatialPack*) showed a strong and significant (p<0.001) negative spatial correlation (-0.92) between the two species. It is not apparent whether this negative correlation is a result of avoidance between the two species or selection for different micro-habitats. It is worth noting that *R. oconnori* were often found off the ground, up to 300 mm up tree trunks, or on low twigs, whereas *P. hochstetteri* were invariably on the ground surface.



a) b)

Figure 10. Heat maps showing the densities of capture locations during the five mark-recapture surveys for a) *P. hochstetteri* and b) *R. oconnori*.

Mark Recapture Analyses

There was a total of 305 snail captures during the five mark-recapture searches. Ten of the *P. hochstetteri* captures and six of the *R. oconnori* captures were of snails that were too small to tag (maximum diameter < 15.6 mm) and were not included in the mark recapture analyses. There were 289 captures of snails large enough to be tagged, these included 225 *P. hochstetteri* and 64 *R. oconnori* (Table 1) with 169 individually identified *P. hochstetteri* and 58 individually identified *R. oconnori*.

Table 1. Summary of the numbers of snails large enough to be tagged that were captured during mark-recapture surveys.

		Night					
		10	**15**	**18**	**23**	**30**	**Total**
P. hochstetteri							
	First captures	51	13	22	11	72	169
	Recaptures	0	6	6	5	39	56
	All captures	51	19	28	16	111	225
R. oconnori							
	First captures	16	5	8	12	17	58
	Recaptures	0	0	0	2	4	6
	All captures	16	5	8	14	21	64

Population Estimates from MARK

Estimates of the numbers of snails present in the plot were obtained from the mark-recapture data using closed population models in the software MARK (White and Burnham 1999) with the R-Mark interface (Laake 2013). Results from the full and conditional likelihood models in MARK were almost identical. The only exception was that snail diameter could not be included as a covariate in the full likelihood models. Therefore, only results from the conditional likelihood models are presented (Table 2). The time-dependent model with equal first-capture and recapture probabilities ($p_t{=}c_t$) model had the lowest AIC*c* value of the four models fitted without the snail diameter covariate (i.e. $p_t = c_t$; $p_c\ c_t$; $p_c\ c_c$ and $p_c = c_c$) for both species. Likelihood ratio testing also showed strong support (p <0.001) for this model compared to other models for both species confirming that it is the most parsimonious, best-fit model for both species. The estimated plot populations for these best fit models are 273 (CI95%: 236–332) for *P. hochstetteri* and 248 (CI95%: 136–519) for *R. oconnori*. These population estimates do not include snails that were too small to tag (< 15.6 mm diameter) which account for 4.3% of *P. hochstetteri* captures during mark-recapture surveys (i.e. 10 of 235) and 8.6% of *R. oconnori* captures (i.e. 6 of 70). To adjust population estimates to include snails < 15.6 mm diameter, population estimates could be increased by 4.4%, i.e. 4.3/(100-4.3), for *P. hochstetteri* captures and 9.4%, i.e. 8.6/(100-8.6), for *R. oconnori*.

Table 2. Plot population estimates and derived density estimates from best-fit models in MARK. The estimates do not include snails that were too small to tag (i.e.< 15.6 mm diameter) and have not been adjusted to compensate for the edge effect. The % value is the size of 95% confidence interval expressed as a percentage of the estimated value. Density estimates are for surface area, not map area.

Species	Model		Plot Population			Density (snails/ha)	
			N	*CI95%*	*CI95% as % of N*	N/ha	*CI95%*
P. hochstetteri							
	Conditional:	$p_t = c_t$	273	*(236–332)*	*(86–121%)*	558	*(482–678)*
		$p_t = c_t$*. Diam*	290	*(241–372)*	*(83–128%)*	592	*(492–759)*
R. oconnori							
	Conditional:	$p_t = c_t$	248	*(136–519)*	*(55–220%)*	506	*(278–1,060)*

Including snail diameter as a covariate in the p_t=c_t models reduced the model's AIC*c* value from 723.2462 to 720.5692 for *P. hochstetteri* and increased the AIC*c* value from 230.2443 to 230.9301 for *R. oconnori*. Thus, including snail diameter as a covariate improved the model fit for *P. hochstetteri*, but gave a poorer fit for *R. oconnori*. Including snail diameter as a covariate in the models increases the estimated plot population in the best-fit model from 273 to 290 (CI95% 241– 290) for *P. hochstetteri* (Table 2).

The 95% confidence intervals around the two population estimates for *P. hochstetteri* are reasonably narrow, extending from 86% to 121% around the estimate for the model without the size covariate; and from 83% to 128% around the estimate for the model with the size covariate. Unfortunately, the 95% confidence interval around the population estimate for *R. oconnori* is considerably wider, extending from 55% to 220% around the estimate. This lack of precision is not surprising, given the low numbers of captures and recaptures for the species.

Table 3. Nightly estimates probability of capture for time-dependent conditional models with equal first-capture and recapture probabilities (p_t=c_t).

	P. hochstetteri		*R. oconnori*	
Night	p	*CI95%*	p	*CI95%*
10	0.190	*(0.14–0.25)*	0.065	*(0.03–0.15)*
15	0.069	*(0.04–0.11)*	0.020	*(0.01–0.06)*
18	0.102	*(0.07–0.15)*	0.032	*(0.01–0.08)*
23	0.059	*(0.04–0.10)*	0.057	*(0.02–0.13)*
30	0.406	*(0.32–0.50)*	0.085	*(0.04–0.19)*

Estimates of the probability of capturing *P. hochstetteri* on the five nights (Table 3) obtained from the time-dependent model (p_t=c_t) ranged from 0.069 on a cool night (i.e. Night 15) to 0.406 on a warm moist night (i.e. Night 30). Estimates of the probabilities of capturing *R.*

oconnori were considerably lower ranging from 0.020 on the cool night to 0.085 on the warm moist night.

In the model for *P. hochstetteri*, including snail diameter as a covariate (Figure 11), average capture probabilities increase with snail size by a factor 3.7, from 0.07 for the smallest snails in the model (15 mm diameter) to 0.25 for the largest (70 mm diameter). The decreases in capture probability with size could reflect the difficulty of seeing small snails active on the surface, but could also be because small snails spend less time active above the ground surface available for capture.

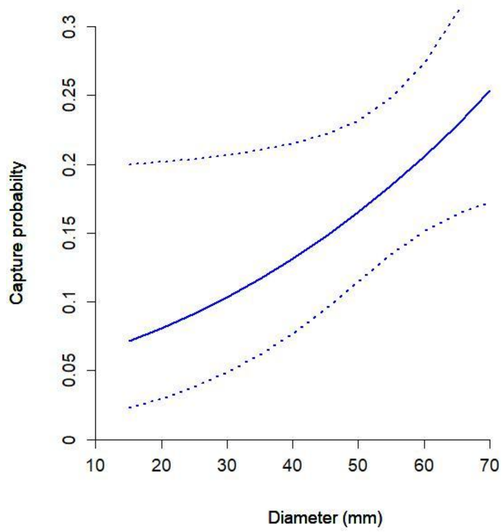


Figure 11. Relationship between diameter and capture probability for *P. hochstetteri*. Dotted lines enclose the 95% confidence interval.

Population Density Estimates Using Spatially Explicit Models

Snail density estimates obtained data using *secr* are in terms of map area whereas those from MARK are in terms of surface area. The surface area of the plot is 4,900 m^2, whereas its map area is 1.8% lower, at 4,814 m^2. To allow direct comparison between snail density estimates from MARK and *secr*, density estimates from *secr* were converted to densities by surface area. Density estimates from *secr* (Table 4) are considerably higher than density estimates from MARK (Table 2). The *secr* density estimate for *P. hochstetteri* is 39% and 31% higher than the two MARK density estimates, while the *secr* density estimate for *R. oconnori* is 154% higher than the MARK density estimate.

The discrepancy between the density estimates for *P. hochstetteri* is not easily dismissed. In this analysis, the reduced capture probabilities of snails with home ranges that straddle the plot boundary (i.e. the edge effect) mean that MARK will overestimate the plot population. Yet density estimates from *secr* are 30 to 40 % higher than estimates from MARK. This seems implausible. A population simulation study was used to investigate which of the two estimation methods provides more credible results.

Table 4. Density estimates for snails obtained using a spatially explicit capture-recapture method implemented in *secr*.

Species	*Map Density*		*Surface Density*	
	N/ha	*CI95%*	N/ha	*CI95%*
P. hochstetteri	761	*(600–966)*	775	*(611–983)*
R. oconnori	1,266	*(422–3,800)*	1,288	*(429–3,868)*

The discrepancy between the density estimates for *R. oconnori* can reasonably be dismissed as a random effect, a consequence of the small sample size and resulting lack of precision in the estimates. Indeed there is considerable overlap between the very wide 95% confidence intervals for both estimates: 278−1,060 for the MARK estimate and 429−3,868 for the *secr* estimate. However, given the size of the discrepancy in estimates for *P. hochstetteri* explaining the discrepancy for *R. oconnori* as small sample size effect is not reassuring.

Simulations to Investigate the Performances of *secr* and MARK

The value for the variance parameter σ^2 used in population simulations was obtained from the results of a concurrent study of the movements of ten radio-tagged *P. hochstetteri* snails in the mark-recapture plot (Lloyd 2017). Individual radio-tagged snail's home range centres were calculated as the mean of the snail's locations for a series of monitoring periods between 10 and 45 days after original radio-tag attachment. The distances between all snails' daytime locations and the centres of their home ranges were then calculated and pooled for each monitoring period. The resulting distributions were unfolded and rotated to provide a density surface describing snail's locations around their home range centres (Figure 12).

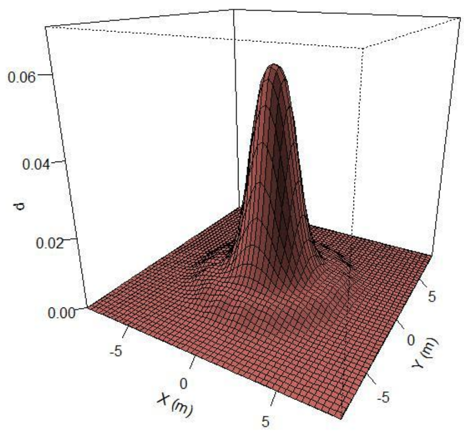


Figure 12. Density surface for the pooled locations of all radio-tagged snail around their home range centres over the 45 day radio-telemetry monitoring period.

The original data for each of the monitoring periods were assumed to follow a half-normal distribution with zero origin. The half-normal distribution was unfolded to create a normal distribution with a zero mean. Home range size is then a function of the dispersion distances of snail locations from home range centres. Measures of the dispersion (i.e. variance, standard deviation or inter-percentile range[1]) all increased steadily with the duration of the monitoring period (Table 5 and Figure 13) indicating snails' home range sizes increased over time. A decline in the rate of increase after about 30 days probably reflects a gradual reduction in the number of snails with functioning radio-transmitters from 30 days onward, rather than the estimates stabilising at the limits of snail's actual home ranges.

Table 5. Estimates of measures of dispersion in the distances of radio-tagged snail locations from their home range centres for difference monitoring periods.

Days	N	Variance	SD (m)	*Inter-percentile Range P2.5–P97.5 (m)*
10	103	2.10	1.45	*2.39*
15	152	2.37	1.54	*2.53*
20	197	3.00	1.73	*2.85*
25	236	4.19	2.05	*3.37*
30	260	5.52	2.35	*3.87*
35	286	6.49	2.55	*4.19*
40	300	6.79	2.61	*4.29*
45	302	6.95	2.64	*4.34*

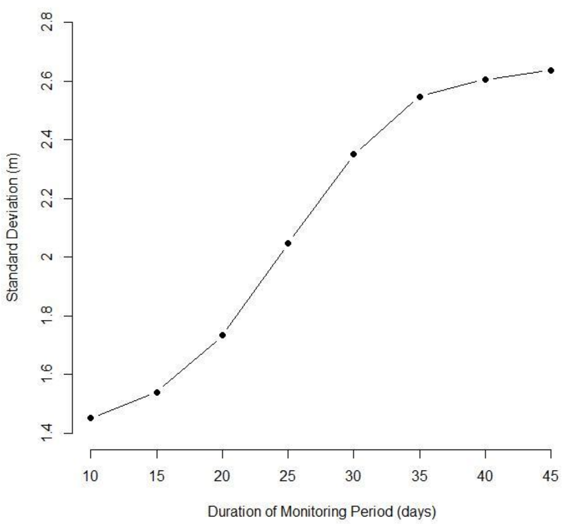


Figure 13. Plot of the standard deviation of the distances of radio-tagged snail locations from their home range centres against the duration of the monitoring period. The plot shows the size of estimated home ranges increases with longer monitoring periods.

[1] An inter-percentile range is the range of values including a specified percentage of the values around the mean value. In this case, P2.5–P97.5, from 2.5% to 97.5% or the central 95% of the distribution.

Univariate normal distribution modelled with variance estimates from three different monitoring periods (Figure 14) show the influence of three different variance estimates on snail distributions within their home ranges. Because mark-recapture survey were undertaken during a 20 day period, the variance estimates from the 20 day monitoring period (i.e. σ^2 = 3.00) was used in the covariance matrix to simulate snail locations during the mark-recapture survey.

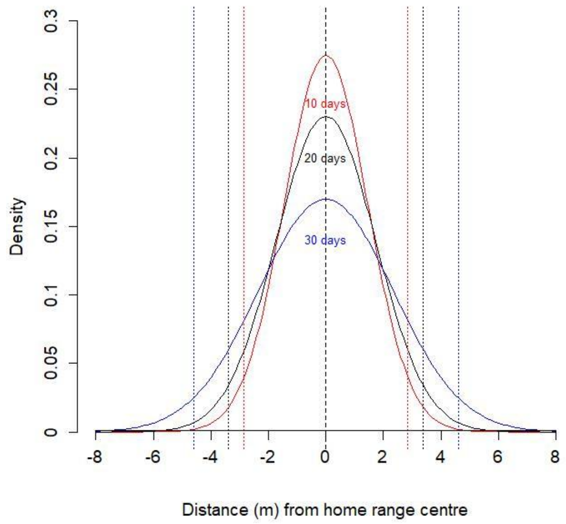


Figure 14. Modelled univariate normal distribution for radio-tagged snail locations around home range centres for three monitoring periods: 10, 20 and 30 days.

Density Estimates for Simulated Populations Obtained Using *secr*

In simulations to investigate the performance of the *secr* analytic package, the simulated 70 m square mark-recapture plot was placed at the centre of a one hectare square (i.e. 100 x 100 m) with the home range centres of 500 snails distributed randomly throughout. The numbers of *P. hochstetteri* snails caught during the five nights of actual mark-recapture surveys (Table 1) was used during the simulations (i.e. 51, 19, 28, 16 and 111). Models were fitted to the simulated data in *secr* using the same settings as used during analysis of the real mark-recapture data: using a polygon detector type, the hazard half normal (i.e. HHN) detection function, time dependent probability of detection and the buffer width of 4 metres. Each analysis of mark-recapture data using *secr* took approximately one hour, consequently only a limited number of simulations (i.e. 10) were undertaken.

Results of the ten simulations (Table 6) showed *secr* performed poorly in estimating the density of the simulated population. Density estimates from *secr* ranged from 647 to 804 with a mean of 724 snails per ha, which is 45% higher than the simulated population density of 500 snails per ha. The simulated density was not enclosed within any of the confidence intervals around the estimates.

Table 6. Density estimates from *secr* for ten simulations of snail populations with 500 snails per ha.

Estimate (snails/ha)	*CI95%*
804	*(616–1,049)*
659	*(512–848)*
647	*(504–831)*
719	*(554–934)*
729	*(560–951)*
664	*(516–854)*
769	*(586–1,008)*
719	*(554–934)*
749	*(573–980)*
779	*(595–1,021)*

Density Estimates for Simulated Populations Obtained Using MARK

The simulations method used to investigate the performance of MARK was similar to the method used for *secr*. As before, the simulated 70 m square mark-recapture plot was placed at the centre of a one hectare square with snail's home range centres distributed randomly throughout the one hectare block. However, simulations for MARK were undertaken for a range of ten different snail densities: from 100 to 1,000 snails per hectare, with 1,000 simulations at each snail density. MARK models were fitted to the simulated data using the best-fit conditional likelihood model for the real data without the snail diameter covariant. This is the model using time-dependent capture probabilities with equal first-capture and recapture probabilities (i.e. p_t=c_t).

On average, the estimated plot populations obtained from MARK were 6.1% above the simulated plot populations. This difference between estimated and simulated plot populations was relatively stable over the range of simulated densities (Table 7 and Figure 15), only varying from 5.8% to 6.7%. However, the spread of differences declined rapidly as simulated snail densities increased, with the P2.5−P97.5 inter-percentile range dropping from 69%−164% of the simulated plot population at 100 snails per ha to 84%−141% of the simulated plot population at 300 snails per ha and decreasing steadily with further increases in the simulated densities (Table 7 and Figure 15).

Table 7. Summary of plot population estimates from MARK for simulations of snail populations with a range of different snail densities. There are 1,000 simulations for each simulated density.

Simulated Density (n /ha)	Simulated Plot Population	Estimated Plot Population		Difference Between Simulated & Estimated Populations	
		Mean	*Inter-percentile P2.5–P97.5*	Mean	*Inter-percentile P2.5–P97.5*
100	49	51.9	*(33.7–80.5)*	1.059	*(0.69–1.64)*
200	98	104.1	*(76.8–148)*	1.062	*(0.78–1.51)*
300	147	156.4	*(123–208)*	1.064	*(0.84–1.41)*
400	196	207.3	*(167–267)*	1.058	*(0.85–1.36)*
500	245	261.4	*(211–333)*	1.067	*(0.86–1.36)*
600	294	312.9	*(256–380)*	1.064	*(0.87–1.29)*
700	343	361.7	*(306–428)*	1.054	*(0.89–1.25)*
800	392	415.0	*(354–489)*	1.059	*(0.90–1.25)*
900	441	467.3	*(399–547)*	1.060	*(0.90–1.24)*
1,000	490	520.0	*(448–617)*	1.061	*(0.91–1.26)*

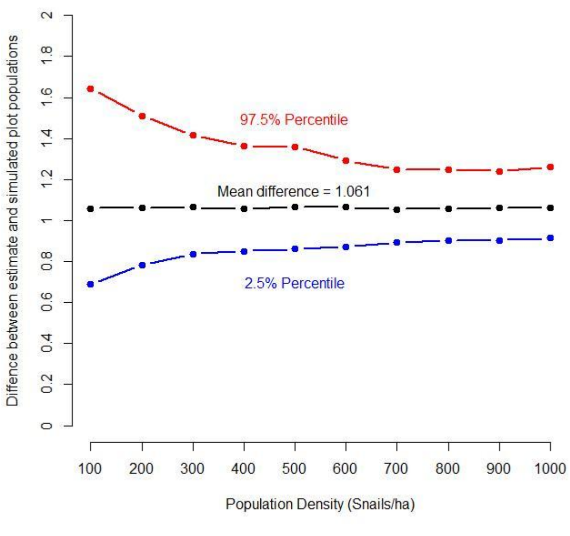


Figure 15. Graph of the mean differences between plot population estimates from MARK and simulated plot populations and over a range of simulated densities from 100 to 1,000 snails per ha.

In analysis of real mark-recapture analyses plot population estimates are primarily informed by the number of snails with home range centres in the mark-recapture plot. Population densities in the wider area outside of the plot have little influence, being limited to the effect of snails with home ranges in the boundary strip surrounding the plot that spend time within the plot. It seems likely that in simulations the numbers of snails with home range centres in the simulated plots will have a major influence on the plot population estimates obtained using MARK. The numbers of home range centres in simulated plots is a random poisson variable with mean equal to the simulated plot population, which is calculated from the simulated density and is constant for each simulated population density.

Linear models were used to investigate the relative influences of the simulated plot population and the numbers of home range centres in the simulated plots on population estimates from MARK. Linear models with population estimates dependant on either simulated plot population size or the number of home range centres in the plot (Figures 16 and 17) were both significant (p<0.001). However, using the extra information from the number of home range centres only improved correlation slightly, with adjusted R-squared value increasing from 0.961 to 0.966. Separate linear models of simulations for the ten single simulated densities showed a similar pattern. The number of home range centres in a simulated plot had a significant (p<0.001) influence on plot population estimates at each of population densities (Figure 18). However, although the relationships between plot estimates and number of home range centres in the simulated plots were significant, correlation between the two variables was weak with mean adjusted R-squared values ranging between 0.104 – 0.169 (mean 0.135).

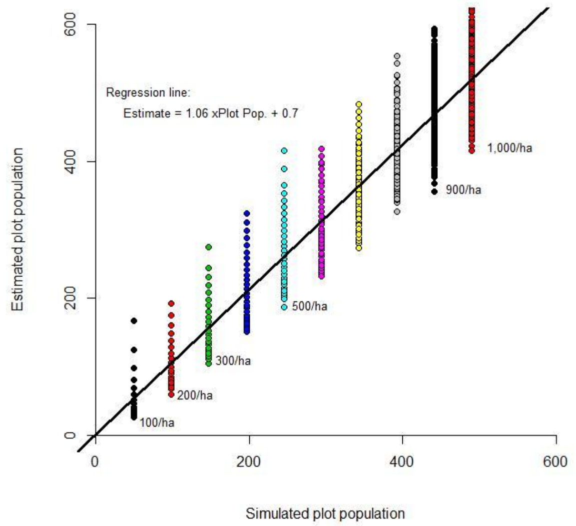


Figure 16. Graph of plot population estimates from MARK against simulated plot populations over a range of modelled densities from 100 to 1,000 snails per ha.

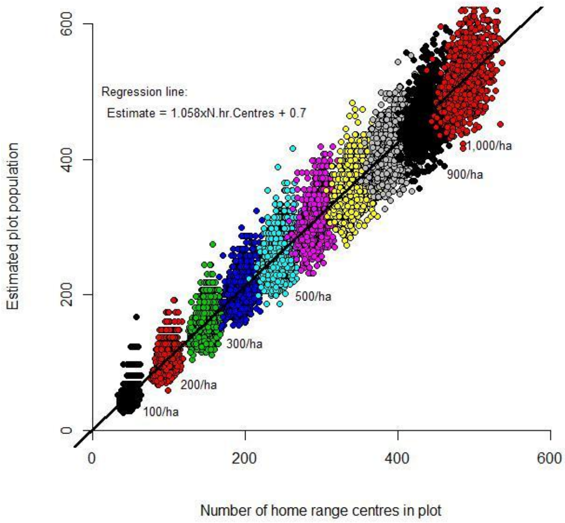


Figure 17. Graph of plot population estimates from MARK against the number of home range centres in the simulated plot over a range of densities from 100 to 1,000 snails per ha.

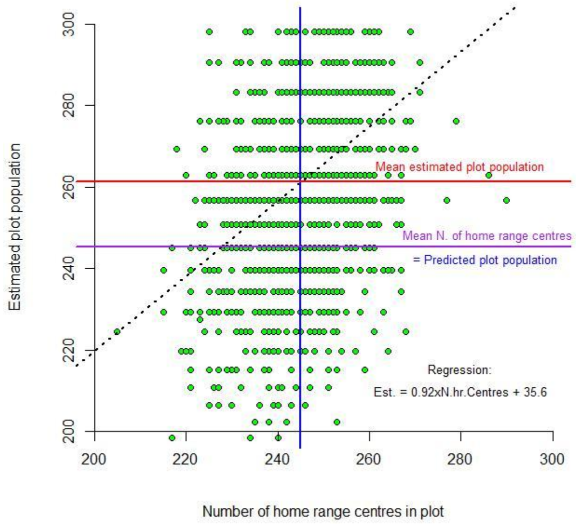


Figure 18. Graph of plot population estimates from MARK against the number of home range centres in the simulated plot for simulations with a densities 500 snails per ha.

Using Simulated Populations to Investigate the "Edge Effect"

Population simulations were also used to gain better insights into the influence of snails with home ranges that straddle the mark-recapture plot boundary. As in previous simulations, the simulated 70 m square mark-recapture plot was placed at the centre of a one hectare square. However, for these simulations home range centres were placed at one metre centres on a lattice across the one hectare area. The actual home range centres were then jittered around the lattice intersections by adding a random deviation ranging between ± 0.5 m to their locations. Individual snail movements around these home range centres were then simulated as before using a bivariate normal distribution with variances equal to 3.000 and zero co-correlation. One hundred population simulations were undertaken providing 1 million simulated locations around 10,000 home range centres. As expected, 49% (490,284) of the one million locations were within the plot. However, although only 49% of the 10,000 simulated snails (i.e. 4,900) had home range centres in the plot, 62 % (6,160) of the simulated snails were in the plot during at least one simulation. This is 25.8% more snails occurring in the plot than had home range centres in the plot. Conversely, 23 % (1,136) of the snails with home-range centres in the plot were outside of the plot during at least one simulation.

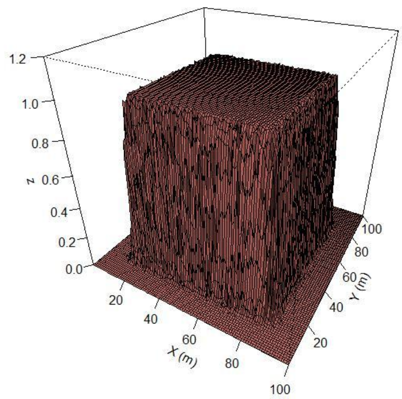


Figure 19. A three dimensional perspective plot mapping the probability of a snail occurring within the mark-recapture plot according to the location of its home range centre.

Figures 19 and 20 illustrate the geometry of this edge effect. Figure 19 is a three dimensional perspective plot mapping the probability of a snail occurring within the mark-recapture plot according to the location of its home range centre. Figure 20 is a cross section through the density surface in Figure 19 at the mark-recapture plot edge showing the linear extent of the edge effect. In these simulations, snails with home range centres inside the plot and more than 3.5 m from the plot boundary will be inside the plot for at least 99% of the simulations whereas snails with home range centres more than 3.5 m outside of the plot will only be in the plot for 1% or less of the simulations (Figure 20). Similarly, a boundary strip extending ±2.6 m from the plot boundary encloses the home range centre of snails that occur in plot for between 5% and 95% of the simulations. Although the 1% –99% boundary strip width ±3.5 m each side of the plot boundary might seem small in comparison to the 70 m plot it is a sizeable area extending over 970 m^2 19.8% of the plot area and increasing the catchment area for snails caught in the plot by 10% from 4,900 m^2 to 5,392 m^2.

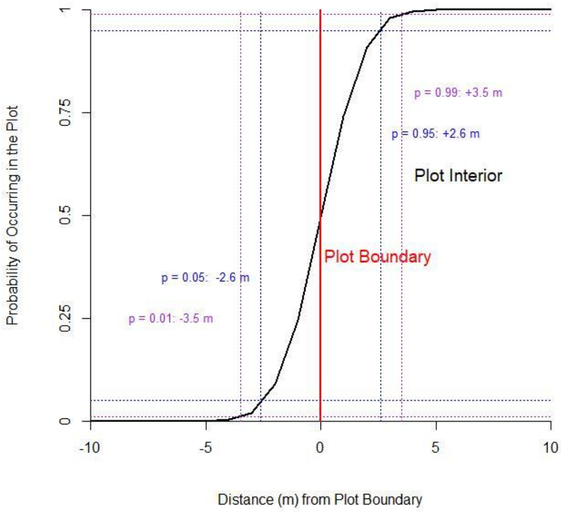


Figure 20. Cross section through density surface in Figure 19 at the mark-recapture plot edge showing the linear extent of the edge effect at the plot boundary.

CONCLUSION AND DISCUSSION

Spatially Explicit Capture-recapture Analyses

The analytic package *secr* used for spatially explicit capture-recapture analyses of the mark-recapture data performed poorly. Density estimates for the *P. hochstetteri* population obtained using *secr* are 30 to 40 % higher than density estimates from MARK using standard mark-recapture methods. This is implausible, because the edge effect biases standard mark-recapture estimates upwards. The *secr* package also performed very poorly in the simulation study (Table 6), producing density estimates between 29% and 60% (mean 45%) higher than the simulated population density of 500 snails per mean ha. None of the confidence intervals around the ten density estimates included the simulated population density. Although spatially explicit capture-recapture analytic methods are theoretically superior to standard mark-recapture methods, their current implementation in *secr* does not provide reliable estimates of snail population densities and should not be used in future analyses of snail mark-recapture data.

Adjusting Population Estimates from MARK

MARK performed well in simulations studies. On average, estimated plot populations obtained from MARK were only 6.1% above the simulated plot population at all ten simulated population densities. The P2.5–P97.5 inter-percentile range enclosing 95% of the 10,000 estimates extended from 16% below to 40% above the simulated plot population at simulated densities > 200 snails per ha. Much of this variation reflects random differences in the numbers of home range centres and snails in plots during the simulations. The relative stability of the differences between the simulated plot population size and estimates from MARK indicates that the 6.1% value may provide a valid correction factor for estimates of the *P. hochstetteri* plot population from MARK, compensating for the edge effect bias. Using the 6.1% correction factor lowers plot population estimates by 6.3%. Best estimates of the *P. hochstetteri* plot population decline from 273 and 290 (Table 2) to 256 and 272 (Table 8), and surface density estimates decline from 558 and 598 snails per ha to 523 and 555 snails per ha. The correction factor is not valid for estimates of the *R. oconnori* plot population.

Table 8.Adjusted plot population estimates and derived density estimates from best-fit models in MARK. The estimates are reduced by 6.3% to compensate for the edge effect bias. The estimates do not include snails that were too small to tag (i.e. <15 mm diameter).

		Plot Population		Density (snails/ha)	
		N	*CI95%*	N/ha	*CI95%*
P. hochstetteri					
Conditional:	$p_t = c_t$	256	*(221–311)*	523	*(451–635)*
	$p_t = c_t.Diam$	272	*(226–349)*	555	*(461–712)*

The correction factor obtained from simulations in this study will not be valid as a correction for edge effect bias in other mark-recapture surveys as the simulations were tailored to the results of this mark-recapture survey, by using the numbers of snails caught and nights surveyed. However, in the absence of better alternatives, the simulation method used in this study does provide a method to obtain correction factors for other mark-recapture surveys by modelling. More sophisticated simulation models could be developed incorporating information on snail's activity periods and using random walks instead of random locations within home ranges. Simulations studies could also provide a tool for investigating the likely effects of different plot sizes and the use of transects instead of square plots.

Comparison with Snail Counts from Standard Sub-surface Searches

Thirteen of Department of Conservation's (DOC) 100 m^2 snail monitoring plots and eight 25 m^2 snail monitoring plots at Canaan (Figure 2) were resurveyed during November and December 2016 (Ogle 2017), shortly after the mark-recapture work described in this report was completed. Three of the 100 m^2 plots and seven of the 25 m^2 plots were within 200 m of the mark-recapture plot (Figure 21). These ten plots are spread over 4.4 ha around the mark-recapture plot and have similar habitat, aspect and terrain to the mark-recapture plot. To allow comparison with density estimates from mark-recapture work, the average of snail counts from the ten DOC plots was converted to density estimates as snails per ha.

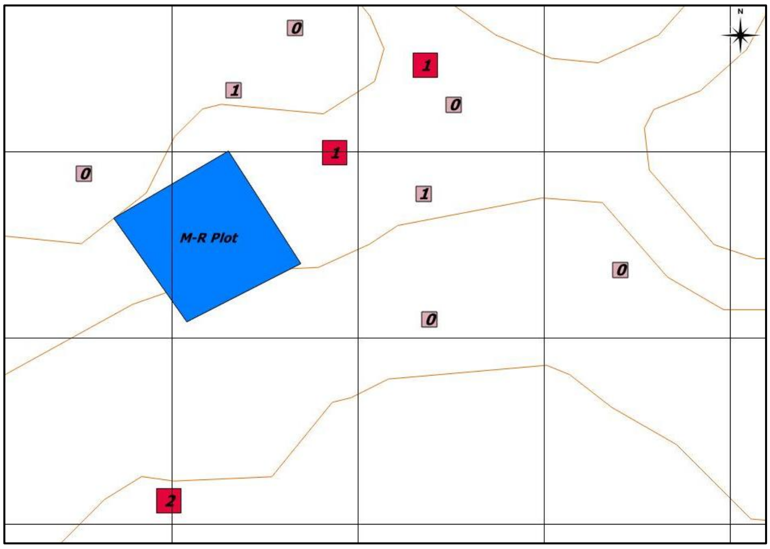


Figure 21. Map showing *Powelliphanta* snail counts for 2016 in the ten DOC snail monitoring plots within 200 m of the mark-recapture plot (blue). Red squares are 100 m^2 snail monitoring plots. Pink squares are 25 m^2 snail monitoring plots.

Counts of *P. hochstetteri* in the 10 nearby DOC plots correspond to 126 snails per ha (CI95%: 57–196), which is only 23% of the density estimate of 555 snails per ha (CI95%: 461–712) obtained using mark-recapture. This difference is consistent with previous comparisons where density estimates for *Powelliphanta* obtained from snail counts have been between 20% and 25% of mark-recapture density estimates (Hamilton 2015c, Lloyd 2015).

Counts of *R. oconnori* in the DOC plots correspond to 42 snails per ha (CI95%: 2−82), which is only 8.3% of the density estimate of 506 snails per ha (CI95%: 278−1,060) obtained using mark-recapture. Although the mark-recapture density estimate for *R. oconnori* is not precise, the massive disparity between density estimates from mark-recapture and the snail count index from sub-surface search method (506 snails per ha cf. 42 snails per ha) indicates that sub-surface searching is not an effective method for finding *R. oconnori*, or monitoring their populations.

Ogle (2017) reports that populations of both snail species in DOC's thirteen standard 100 m^2 snail monitoring plots at Canaan that have been re-surveyed regularly have declined markedly since monitoring began in 2000, with average annual declines of 7.8% for *P. hochstetteri* and 12.2% for *R. oconnori*. Because this is the first time that mark-recapture has been used to estimate population densities of the two snail species in the Canaan area, the mark-recapture estimates do not provide any information on snail population trends. However, the size distributions of the 204 live *P. hochstetteri* and 72 live *R. oconnori* caught during the mark-recapture work (Figure 4) indicate that there are ongoing high levels of recruitment to populations of both snail species in the plot. Before assuming that the decline in snail counts in the thirteen standard snail monitoring plots is evidence of declining population, other explanations for the declining snail counts should be discounted. Possible explanations include systematic changes in capture probabilities as a result of: differences in climatic conditions around the time of the plot searches (i.e. global climate change); differences in the seasonal timing of searches; and changes in the composition, abilities and enthusiasm of the search teams over time. The possibility that plots' habitats have been degraded by repeated biennial sub-surface searches over a 17 year period should also be considered.

A flatworm, probably *Geoplana* sp, preying on a large native earthworm in the mark-recapture plot. Photo by Philip Simpson.

Feral pigs, song thrush and rats are reportedly the most significant predators of snails in the Canaan area (Ogle 2017). There was no evidence of pigs affecting snails in the mark-recapture plot, either by trampling or feeding on them. However, there was pig sign nearby and pig foraging is likely to be localised and catastrophic for snails. Only one of the nineteen *P. hochstetteri* shells collected on the mark-recapture plots and in good enough condition for predator assessment showed evidence of rodent predation. Another two shells showed evidence of predation by kea (Meads et al. 1984), which are common in the area. Surprisingly none showed evidence of predation by weka, which are also common in the area. An interesting and possibly relevant observation during one of the nocturnal searches was of a flatworm, probably *Geoplana* sp, preying on a large native earthworm. Although there are no reports of flatworms preying on terrestrial gastropods in NZ, they do prey on terrestrial gastropods overseas (Barker 1989) without damaging their shells and could be predators of New Zealand's native land snails responsible for the numerous intact empty *Powelliphanta* shells found on the plot.

Conservation Targets for *Powelliphanta*

The target density of 12 *Powelliphanta* snails per 100 m^2 plot (i.e. 1,200 snails per ha) recommended in the *Powelliphanta* recovery plans (Walker 2003) seems unrealistically high. Especially as the target density is in terms of the snail count index, which in the case of the Canaan plots is only 23% of the actual density. Thus, in the Canaan area the recommended target density is actually 5,217 snails per ha, which equates to 0.5 m^2 per snail, or a snail every 1.4 metres in all directions. The recommended area per snail is considerably smaller than the home ranges observed during the radio-tracking study, where the mean minimum convex polygon home range was 16.6 m^2 (CI95%: 9.4–21.0 m^2) and the mean auto-correlated density home ranges was 66.6 m^2 (CI95%: 43.4–81.0). Using the mean weight of *P. hochstetteri* caught during this study (i.e. 31 g), 5,217 snails per ha gives a biomass of 162 kg per ha. Although this biomass is not inconceivable, it seems excessive for a single species inhabiting high altitude forest, especially a carnivorous one occupying a relatively high trophic level. For comparison, in lowland native forest in the south of the North Island the estimated biomass of all species of earth worm combined was 333 kg per ha (Brockie and Moeed,1986).

Improvements to the Mark-recapture Survey Method

There were several successful innovations in the field method used during this mark-recapture work compared to the protocols used in previous *Powelliphanta* mark-recapture monitoring projects e.g. (Gruner et al. 2011, Hamilton 2015b, Lloyd 2015). Searches were undertaken along 10 m wide lanes marked across the slope to improve search efficiency and reduce distance travelled during searches. Smaller two-digit tags were used, allowing tagging of smaller snails to provide crucial information on juvenile and sub-adult snails. Snail handling procedures were improved by the use of triplicate prepared labels to identify captured snails and mark their capture locations. The use of a gps unit with sub-meter accuracy to record accurate location data and other details at the point of capture improved data reliability and allowed the use of spatially explicit capture-recapture analytic methods.

The use of data-loggers deployed on site to record temperature and humidity throughout the mark-recapture period provided a wealth of information on the micro-climate the snails were subject to during the survey period.

The most effective way to improve the precision of snail population estimate from mark-recapture monitoring is to increase capture probabilities. Information from this study and the concurrent radio-telemetry study of *P. hochstetteri* (Lloyd 2017) shows that both snail species are most active on the surface, and available for capture, on warm nights when the minimum night-time temperatures remains above 6°C. *R. oconnori* activity levels are not affected by humidity dropping as low as 90%, whereas *P. hochstetteri* activity levels decline as soon as humidity drops below 100%. Predicting suitable overnight climatic conditions in advance and then organising mark-recapture field teams to survey only on suitable warm and moist nights at short notice is difficult, but should become easier with more experience of local weather conditions in Canaan area.

Trampling

The discovery of a recently trampled *P. hochstetteri* snail during the course of the mark-recapture searched was not surprising. The results of the concurrent radio-telemetry study of *P. hochstetteri* (Lloyd 2017) indicate that there is a risk of *P. hochstetteri* snails being trampled when ever people are working in areas inhabited by *Powelliphanta* snails. Given the state of decomposition when it was found, the snail was probably trampled in the daytime during plot setup, not during nocturnal searches. Repeated searches undertaken during a short period for mark-recapture work mean that if snails are trampled in a mark-recapture plot they will probably be found, whereas this is not the case for other activities in snail areas.

Recommendation for Future Mark-recapture Snail Monitoring

Mark-recapture snail monitoring is expensive and logistically demanding, consequently it is impracticable to have large numbers of mark-recapture plots spread over wide a geographic area. However, mark-recapture monitoring provides reliable unbiased estimates of snail populations to monitor population trends. When repeated at regular intervals mark-recapture surveys also provide information on recruitment and survival. The increased quality, reliability and detail of population information from mark-recapture compared to information from standard sub-surface plot searches more than compensates for the lack of geographical spread. It is worth noting that the area of the single mark-recapture plot (4,900 m^2) at Canaan is 3.8 times greater than the combined area of the 13 standard monitoring plots in the Canaan area (1,300 m^2). Mark-recapture monitoring should be used to augment and validate the existing snail monitoring programme rather than replacing it.

The Canaan mark-recapture monitoring plot should be resurveyed at regular intervals, preferably annually. To facilitate comparisons between the methods and validation off the standard monitoring method, the entire cluster of twelve standard snail monitoring plots (including 25 m^2 plots) within 250 m of the mark-recapture plot (Figure 2) should be resurveyed regularly.

Recent surveys throughout Abel Tasman National Park (Ogle 2016) indicate that both *P. hochstetteri* and *R. oconnori* occur over wide areas of the park, with high concentrations in the Waterfall and Camp Creek catchments, west of the lower reaches of the Awaroa River. If snail population monitoring is to be extended over a wider area of the park beyond Canaan, the monitoring programme should include a small number of mark-recapture snail plots placed in representative habitats with known snail populations to validate information from more widely spread sub-surface search plots.

It would be worthwhile investigating the use of mark-recapture transects with repeated nocturnal searches by two observers along existing stoat traps lines. This would make mark-recapture monitoring less logistically demanding and achieve better geographic spread than the current mark-recapture plot method.

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The 2016 snail team.

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