# Capture-recapture Monitoring of Native Snail Populations in Abel Tasman National Park, 2016–2021

Two *Rhytida oconnori* seeking shelter (or trying to) in a *Powelliphanta hochstetteri* shell (photo R. Bollongino)

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# ABSTRACT

Capture-recapture methods were used to monitor populations of two threatened species of land snails, *Powelliphanta hochstetteri* and *Rhytida oconnori*, at two sites in Abel Tasman National Park, New Zealand, between 2016 and 2021. One site is within an area where both snap-trapping and intermittent aerial broadcast 1080 poison are being used to control alien mammalian species and restore native biodiversity in the park. The other site is within the trapping network, but outside of the area subject to aerial broadcast poison. During the first monitoring sessions capture-recapture density estimates for each the four snail populations were between 540 and 900 snails/ha. At the site where both pest control methods were used populations of the two snail species declined, whereas outside the area subject to aerial broadcast poison populations first increased and then started to decline.

Evidence from damaged shells show that the decline in the *P. hochstetteri* population at the site subject to both control methods was mainly a result of predation by a burgeoning population of weka (*Gallirallus australis*), an indigenous large flightless rail. Previously rare, or possibly absent before translocations in 2006, weka numbers in the park began increasing soon after pest control began in 2013, presumably as a result of reductions in numbers of their main predator stoat (*Mustela ermine*). Predation by ship rats (*Rattus rattus*) is considered to be the main threat to NZ's native land snails, but despite a major rat irruption during an interval between monitoring sessions, there was little evidence of rat predation on *P. hochstetter* at either site. Because shells of *R. oconnori* are fragile, they are rarely found, consequently there is no direct evidence of the cause of the *R. oconnori* population decline. However, simultaneous and similar declines in both snail species at the same site indicate that weka predation also caused declines in *R. oconnori*. The snail populations outside of the main pest control area showed initial resilience, despite the presence of weka and ship rats. The delay in weka-induced decline is probably a consequence of protection from predation afforded by the karren substrate at the site. In addition to predation, snail mortality increased due to two exceptionally dry summers in 2019 and 2020, illustrating the vulnerability of terrestrial gastropods to climate change.

Results from the capture-recapture monitoring site outside of the main pest control area were compared to snail count indices from sub-surface searches of ten nearby permanent snail monitoring plots. For population trend monitoring and comparisons between different populations, index methods rely on the assumption that the indices are proportional to the actual population levels, otherwise results are of dubious value and can be misleading. The relationship between capture-recapture population estimates and snail count indices from three monitoring seasons were inconsistent for both snail species. Population trends inferred from the two methods were very different. Our results show that snail count indices are not proportional to population levels and that samples of live snails found during sub-surface searches were unrepresentative, heavily skewed towards small snails. It is possible that the karren substrate in the area around the snail monitoring plots used in this comparison might have confounded the sub-surface search method. The capture-recapture method should be used to validate the sub-surface plot search method at a number of sites with typical forest habitats for the snail species.

The results of this study underline the crucial role of adequate monitoring for informing conservation managers about pest control outcomes and for providing early warning of unexpected and undesirable developments.

# INTRODUCTION

Two of New Zealand's large carnivorous land snails, *Powelliphanta hochstetteri hochstetteri* and *Rhytida oconnori* (Fig. 1), are found in Abel Tasman National Park (Fig. 2). Both occur sympatrically throughout wide areas of unmodified, mid-elevation (>700 m a.s.l.) indigenous forest in the southwest of the park [1, 2]. *P. h. hochstetteri* is also found in nearby Kahurangi National Park [3]. *R. oconnori* might also occur at Parapara Peak, Kaihoka Lakes and other sites in Golden Bay [4]. There are currently four described species of *Rhytida* in Abel Tasman National Park: *R. oconnori*, *R. patula, R. perampla* and *R. webbi* [4-6]. *R. oconnori* is the largest of the four species, with its maximum diameter at maturity (>25 mm) being a reliable species identification criterion (Kerry Walton pers. comm.).

In currently available Department of Conservation (DOC) threat classification lists, *P. h. hochstetteri* is ranked as in Gradual Decline, with the qualifier Conservation Dependent [7], while *R. oconnori* is ranked as Nationally Critical, with the qualifier Conservation Dependent [8]. These rankings are because of threats from habitat degradation and predation by introduced species: feral pig (*Sus scrofula*), rats (*Rattus rattus* and *R. norvegicus*), brushtail possum (*Trichosurus vulpecula*), European hedgehog (*Erinaceus europaeus occidentalis*), song thrush (*Turdus philomelos*) and blackbird (*T. merula*) [3, 9].

DOC has been monitoring populations of the two snail species at Canaan, in the south-west of Abel Tasman National Park, since 2000 [10] with biennial sub-surface searches of permanent plots, as described by Walker (2003) [11]. The sub-surface search method is the standard method to monitor populations of New Zealand's threatened land snail species and entails daytime searches of permanent 100 $m^2$ or 25 $m^2$ plots for live snails and shells. While some shells may be found on the plot surface, most live snails are found by searching under vegetative ground-cover, leaf litter, and coarse woody debris, or in cavities and cracks in the ground [11]. Results from the snail monitoring programme at Canaan indicate that there have been substantial declines in the populations of both species since the programme began in 2000 [12]. The declines have occurred despite pest control undertaken in the area during that time.

Effective and robust monitoring of the responses of threatened taxa to conservation management is an essential part of the ecological restoration process undertaken since 2012 by Project Janszoon in Abel Tasman National Park. In recent years, capture-recapture methods have been developed to overcome deficiencies in the standard method for monitoring *Powelliphanta* snail populations [13-15]. Consequently, concern about the low reliability and limited nature of information obtained from daytime sub-surface plot searches led Project Janszoon to investigate the use of the capture-recapture method to obtain reliable and detailed information on threatened snail populations in the park to assist in their conservation.

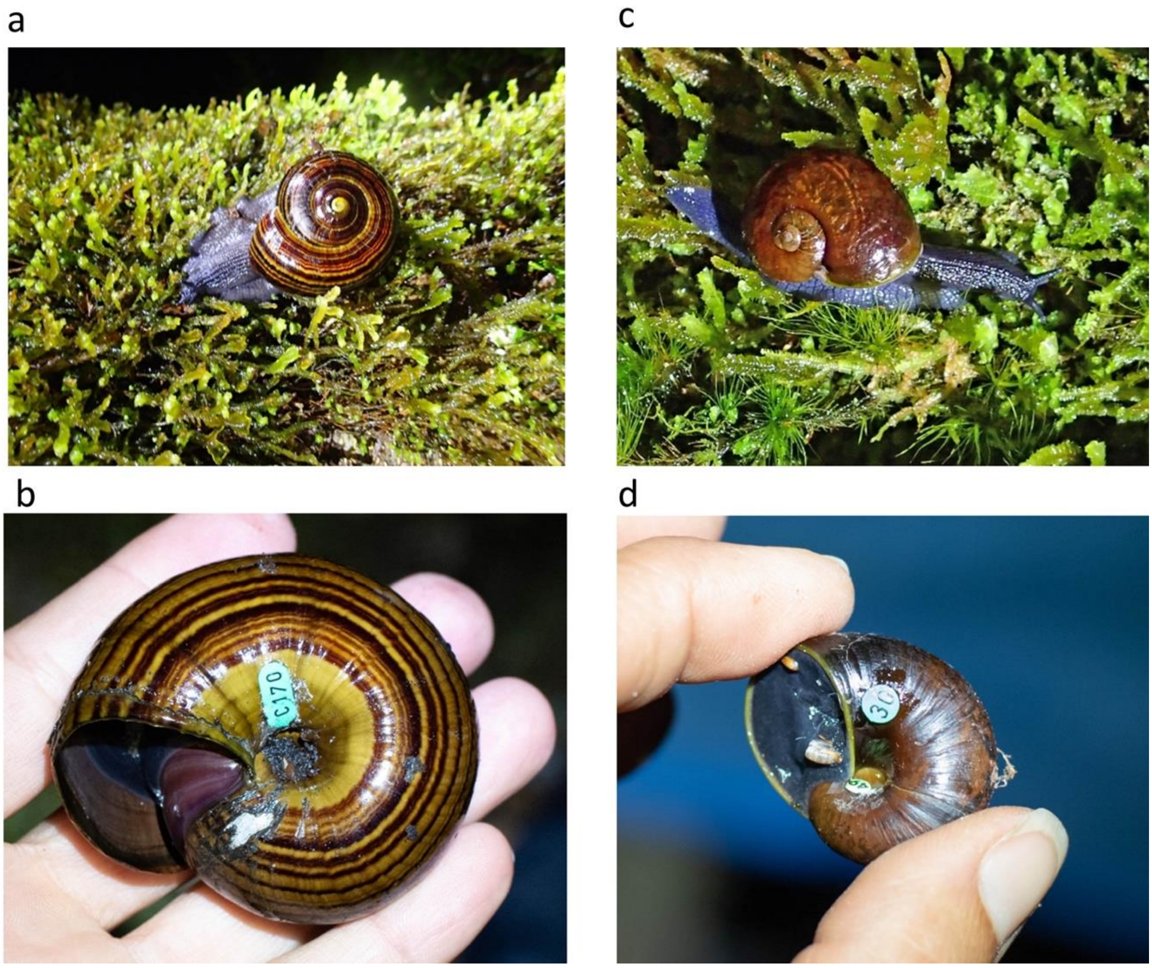

Figure 1. *Powelliphanta hochstetteri* (a,b) and *Rhytida oconnori* (c,d)

Capture-recapture, or mark-recapture, is a method for obtaining population estimates when counting the number of individuals in a population is impracticable [16]. Capture-recapture entails the repeated capture, marking, and release of samples of individuals from a population. Capture-recapture monitoring of *Powelliphanta* and *Rhytida* snail populations entails repeated nocturnal searches for snails active on the surface of a 70 m square plot during a period of three to five weeks [14, 15, 17]. Snails found in the plot are individually marked with numbered identification tags (Fig. 1) 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 capture-recapture analytic methods [18-21]. When capture-recapture sessions are repeated at regular intervals, the method also provides valuable demographic information on survival, recruitment, growth and age structure. Capture-recapture surveys were complemented by searches for shells in the plots to collect information on mortality and predation.

Two capture-recapture plots (Fig. 2) were established in Abel Tasman National Park to assess abundance of the two snail species and monitor trends in their populations. One of the plots (the Wainui plot) lies within a >12,000 ha area of intensive pest control undertaken using both snap-trapping and aerial broadcast cereal pellets containing the poison sodium fluoroacetate, i.e. compound 1080 [22], while the other plot (the Canaan plot) is >2 km outside the area of intensive pest control area with 1080, but within the snap-trapping grid (Fig. 2). Thus, monitoring the two plots should also provide information on the effects of intensive pest control on populations of the two snail species. The Canaan capture-recapture plot is within 200 m of ten of DOC's sub-surface snail-monitoring plots, providing the opportunity to compare results from the two snail monitoring methods.

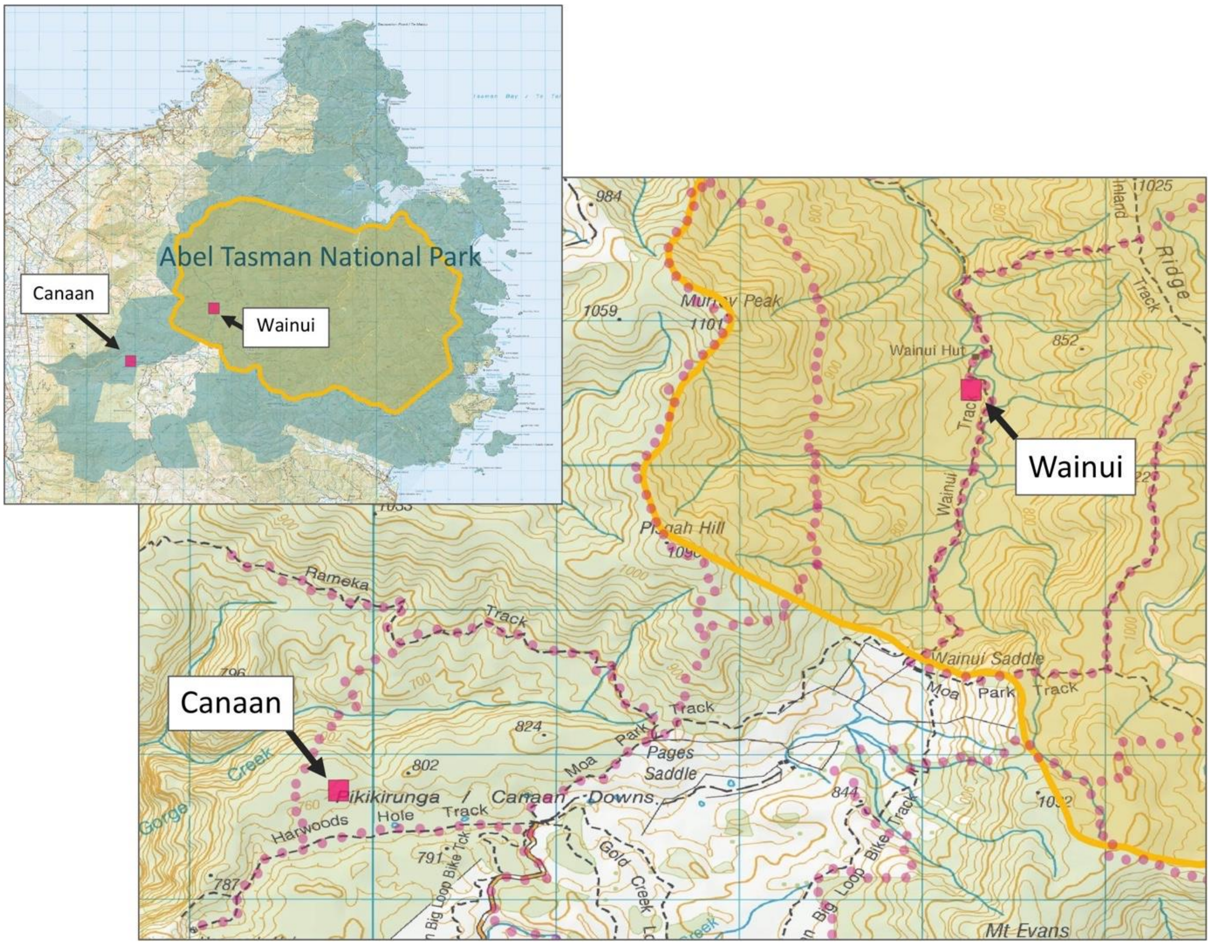

Figure 2. Maps showing the location of the Abel Tasman National Park and the two capture-recapture plots (pink squares). The orange shaded area is subject to aerial broadcast 1080 operations. Pink dots represent stoat traps.

# METHODS

## Study Areas

Two capture-recapture plots were established in the south-west of the park within areas of mid-elevation mixed-beech forest (>700 m a.s.l.) where *P. hochstetteri* and *R. oconnori* were both abundant [1]. The first plot, established in 2016, is at Canaan Downs near Harwoods Hole, and the other, established in 2018, is in the upper Wainui Valley, 4.4 kilometers to the north-east of the Canaan plot. Capture-recapture surveys were undertaken at the Canaan plot during four summers: 2016–17, 2018–19, 2019–20 and 2020–21; and at the Wainui plot during three summers 2018–19, 2019–20 and 2020–21.

The plot locations were chosen because nocturnal searches for snails during spring 2016 and summer 2017–2018 [1, 17] found abundant and widespread populations of both *P. hochstetteri* and *R. oconnori* in them. Although the general locations of the two plots were chosen to be representative of the areas, the final plot locations were dictated by the need for easy access to the plot, while not attracting attention from users of nearby walking tracks, and to avoid hazards, such as cliffs or streams, and obstructions, such as tree-falls or dense patches of bush lawyer (*Rubus cissoides*).

The Canaan plot lies on a south-east facing, 10° upper slope between 755–775 m above sea level (a.s.l.), whereas the Wainui plot is on a gentle east-west terraced foot-slope on the valley bottom between 720–735 m a.s.l.. Although ground cover in the two plots is generally similar, with moss and deep layers of humus, the underlying-rock types are very different. The Canaan plot is on marble karst with intricate karren formations and numerous underground crevices, whereas the Wainui plot is on a smooth bed of granite classified as equigranular hornblende-biotite granodorite and diorite [23]. A distinctive feature of ground cover in the Wainui plot, but not Canaan is thick patches of pinetree moss (*Dendrologotrichum dendroides*). The forest canopy in and around the two plots is similar with 20 to 30 m high closed canopy dominated by silver beech *Lophozonia menziesii*) and red beech (*Fuscospora fusca*). The Canaan plot has a moderately dense understorey, which includes broadleaf (*Griselinia littoralis*), kamahi (*Weinmannia racemosa*), mahoe (*Melicytus ramiflorus*) and soft mingimingi (*Leucopogon fasciculatus*). The understorey in the Wainui plot is less dense, but more diverse including: broadleaf, celery pine (*Phyllocladus alpinus*), *Coprosma linariifolia*, *C. tayloriae* and *C. colensoi*, horopito *(Pseudowintera colorata*), the divaricating shrubs *Raukaua anomalus* and the porcupine shrub (*Melicytus obovatus*), and a trunkless tree fern (*Cyathea colensoi*).

Temperature and relative humidity were recorded at ten minute intervals on data-loggers (Onset Hobo Pro v2 temp/RH Logger) placed 300 mm above the ground in forest a few metres outside of the capture-recapture plots.

## Pest Control and Monitoring

Both the Wainui and Canaan plots are in areas where stoats are being trapped and rat abundance monitored. However, the Wainui plot is within a 12,000 ha area of intensive but intermittent pest control using aerial broadcast cereal pellets containing the poison 1080 [22], whereas the Canaan plot lies in a non-treatment area >2 km outside of the intensive pest control area (Fig. 2). Stoat trapping has been underway since 2013 on a dense network of stoat trap-lines extending throughout 15,000 ha of Abel Tasman National Park [22]. Rat populations in the park are being monitored quarterly using tracking tunnels [24, 25], which provide an index of relative rat abundance: the proportion of baited tunnels visited by rats during one fine night. The rat tracking index is not a direct measure of population density, because it is affected by variation in rat activity levels. Although there are two species of rats in the park: ship rats or black rats (*R. rattus*) and Norway rats (*R. norvegicus*); only ship rats are likely to be present in the high altitude areas and around the plots.

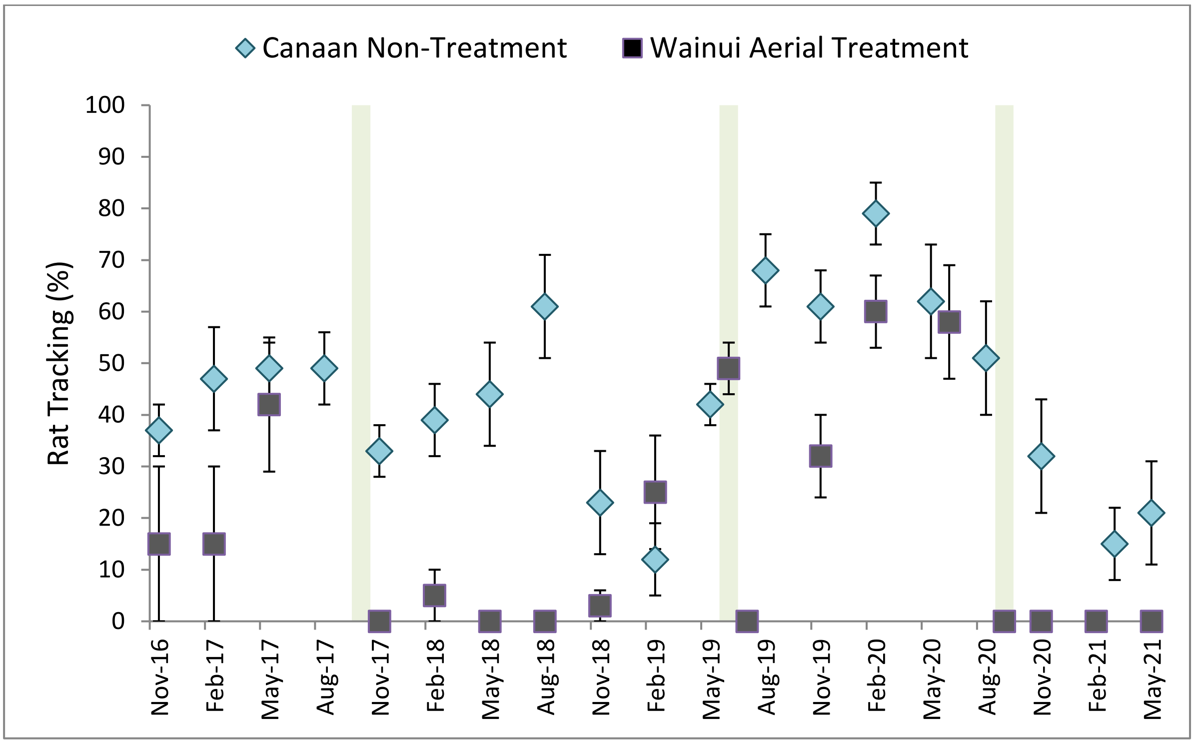

Figure 3. Quarterly rat tracking indices from footprint tracking tunnels (FTT) in the non-treatment area around Canaan (blue diamonds) and the treatment area around Wainui (grey squares). Green bars indicate the timing of aerial 1080 operations. At this elevation, rat numbers usually remain low for approximately one year after 1080 operations before increasing again. The unusually strong mast year in 2020 was an exception as rat tracking index were high three months after the aerial 1080operations.

Aerial broadcast of 1080 in the intensive pest control area (including the Wainui plot) was undertaken during 2014, 2017 2019 and 2020, when rat tracking indices exceeded critical levels [22]. Aerial broadcast 1080 operations reduce rat (Fig. 3) populations to low levels and also reduce numbers of other vertebrate pest species such as brushtail possum and, by secondary poisoning, stoats. Immediately after each aerial broadcast operation, rat tracking rates in the pest control area were close to zero, but increased when rat populations irrupted in response to prolific seed-fall (i.e. mast event) by southern beech trees. In 2020 an unusually strong mast was observed. During the period 2016 to 2021, the mean rat tracking rates were 18% (range 0–58%) in the intensive pest control area and 45% (range 15–79%) in the non-treatment area around the Canaan plot (Fig. 3).

## Capture-recapture Field Method

The capture-recapture field method used in this study is based on the method developed for monitoring of population trends in *Powelliphanta* affected by mining disturbance [13, 14, 26] with modifications described in Lloyd (2017) [17]. The plot boundaries and 10 m wide lanes across the dominant slope of the plot were delineated with Gallagher Poly Wire (a long-lasting polyethylene farm fencing materials) anchored on 300 mm metal standards. A single capture-recapture survey, or primary session, entails between three and seven successive nocturnal searches of a 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. Ideally each survey comprises five or more nocturnal plot searches, but results of a simulation study [27] showed that when nightly capture probabilities are ≥0.20 good population estimates can be obtained with as few as three nocturnal searches. Capture probabilities are inferred after each search night by calculating the percentage of caught snails from the current population size estimate. Reducing the number of searches in a survey from five or more, to only three provides a major reduction in the cost and complexity of capture-recapture surveys. To achieve high capture probabilities, searches are best undertaken on nights when weather conditions favour snail movement (i.e. ideally temperatures >10°C and humidity at, or close to, 100%). For both species, snail numbers are highest on damp nights following a long dry period. *P. hochstetteri* prefer warmer conditions and remain active during heavy rain, whereas *R. oconnori* activity declines markedly during rain.

Each search entailed a single complete search of the entire plot for live snails visible on the surface during the period of darkness. Typically, searches began 30 minutes after dusk and finished no later than 30 minutes before dawn. 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 metres 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 a search, its capture location was marked temporarily so that snails could be released at its original capture site after processing.

On first capture, snails were weighed, their maximum diameter measured and their general condition recorded. To achieve consistent, repeatable snail maximum diameter measurements digital callipers were used with the snail placed in the callipers as described in Meads et al. (1984) [28] (Fig. 4) The snail was then gently rotated until the jaws of the callipers were pushed out to a maximum dimension. Finally the snail was moved up and down in the callipers to find the extreme point on the curved side of the shell where the maximum diameter was measured.

All snails with maximum diameter >15 mm were tagged and included in subsequent capture-recapture analyses. Snails were marked using the standard method developed for tagging *Powelliphanta* snails [13]. A numbered polyethylene tag was glued to the ventral surface of the snail's shell immediately behind the aperture (Figs. 1 b & d) with Selley's Quick Fix Non-Drip Supa Glue™. 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).

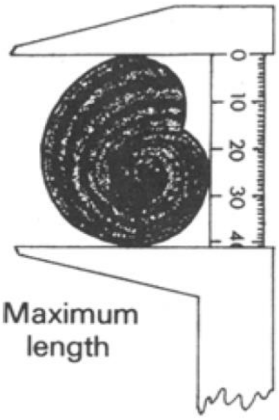

Figure 4. Illustration of how to measure the maximum diameter of a shell from Meads et al. 1984.

The four-digit tags were used on larger snails (>30 mm diameter), while two-digit tags were used on smaller snails (18–30 mm) and queen-bee tags were used on the smallest snails (15–18 mm diameter). When previously tagged snails were recaptured during the same year, only their tag number and general condition were recorded, whereas previously tagged snails recaptured during succeeding years were re-measured, reweighed, tags checked and, if necessary, when overgrown or damaged, replaced. A sample of thirty-eight snails was double tagged during 2016 to investigate tag-loss.

## Snail Shell Surveys

During the summers 2018–19 to 2020–21, daytime searches for snail shells visible on the surface of the two plots were undertaken. Details of the size and condition of shells found on the plots were recorded. Damaged shells were photographed, damage patterns documented and, when possible, the probable predator attributed from the damage pattern [28]. The identities of tagged shells were noted for inclusion in the capture-recapture database. After examination, shells were marked with small coloured polythene tags glued on with Supa Glue$^{TM}$ and usually left *in situ* to provide micronutrients and microhabitats for other snails. To investigate shell decay rates and the prevalence post-mortem damage by predators, a sample of twenty-seven undamaged, tagged *P. hochstetteri* shells was deposited just outside of the Canaan plot and routinely re-examined and photographed.

## Growth Rate Analyses

To investigate age-related demographic processes the von Bertalanffy growth equation [29] was used investigate age-related demographic processes. This equation is commonly used to model growth rates of a range of species, including snails and shellfish [30-34]. Estimates for the growth rate parameters *K* for the growth equations for each of the two species were obtained from successive diameter measurements of tagged snails caught during successive surveys.

In temperate regions, terrestrial snails typically use diapause (winter hibernation and summer aestivation) to withstand unsuitable environmental conditions [35]. Winter hibernation occurs in response to short photo-periods and cool temperatures, while summer aestivation avoids desiccation during dry periods. Although there is no published information on whether snails belonging to the family Rhytididae use diapauses, it seems likely. Observed activity levels of *P. hochstetteri* and *R. oconnori* are both highest during warm moist periods [17, 36]. There will be little or no growth during periods of diapause. Temperate region land snails grow most rapidly during the summer months in response to longer photo-periods and warmer temperatures [34, 37, 38]. Consequently, the time interval $\Delta t$ between paired measurements used to calculate growth rate excluded time outside the six month summer period: 16 October to 15 April.

Values of the slope coefficients from the regression analyses of summer growth rate ($\Delta D/\Delta t$) against initial diameter were used as the observed growth rate parameter $K_{Obs}$ in equation 4 (below) to estimate the instantaneous growth rate parameter $K$ for von Bertalanffy growth curves. Two other growth parameters used for von Bertalanffy growth curves were the minimum and asymptotic maximum diameters ($D_0$ and $D_{Max}$) observed during the study: 12 mm and 74 mm for *P. hochstetteri*; and 10.5 mm and 36 mm for *R. oconnori*. Estimated values for the three growth parameters $D_0$, $D_{Max}$ and $K$ were used in Equation 2 to generate von Bertalanffy growth curves for *P. hochstetteri* and *R. oconnori*.

Equation 1 is the general form of the von Bertalanffy growth equation, with diameter $D_t$ at age $t$ estimated from age $t$. $D_{Max}$ is the asymptotic or maximum diameter attained by the snails, $K$ is a growth parameter and $t_0$ is the constant of integration. Equation 2 is the reciprocal form of general equation, allowing age $t$ to be estimated from $D_t$. The value of the constant $t_0$ was estimated using Equation 2 with $D_0$ being snail diameter at hatching when age $t = 0$. Values of the growth parameters $D_0$ and $D_{Max}$ for the two species were the minimum and maximum diameters observed in captured snails during the study.

Equation 1: $D_t = D_{max}\left(1 - e^{-K(t+t_0)}\right)$

Equation 2: $t = \left[-log\left(1 - {}^{D_t}/_{D_{Max}}\right)/K\right] - t_0$

Equation 3: $\frac{dD_t}{dt} = K(D_{Max} - D_t)$

Equation 4: $K = \frac{-log(1-\Delta t K_{Obs})}{\overline{\Delta t}}$

The instantaneous growth rate for the von Bertalanffy growth curve is a linear function of size (Equation 3) with slope $K$. The observed growth rate parameter obtained from capture-recapture data $K_{Obs}$ is estimated as the slope of the regression $\Delta D/\Delta t$ against $D_{Max} - D_{t1}$, where $\Delta D = D_{t2} - D_{t1}$. However, because of the time interval $\Delta t$ between successive diameter measurements, $K_{Obs}$ underestimate the instantaneous growth rate. The magnitude of underestimation increases with the length of the time interval $\Delta t$. A good approximation of $K$ can be obtained from $K_{Obs}$ using Equation 4 [33].

This is a deterministic approach to estimating the growth curve without regard to variations in the growth parameters $K$, $D_0$ and $D_{Max}$ in response to individual genotypes and varying environmental conditions. More sophisticated analyses have been developed to model individual variation in growth curves obtained from capture-recapture observations [30, 31], but these require more data than are available and are unnecessary for this study.

To estimate instantaneous growth rates, growth between each pair of repeat diameter measurements ($\Delta D$) was calculated as $D_{t2}$ - $D_{t1}$, the difference between diameter measurements at times $t_1$ and $t_2$, the times of first and second measurements respectively. Growth rate between paired measurements was then calculated as $\Delta D/\Delta t$, where $\Delta t$ is the time interval between paired measurements (i.e. $t_2$ - $t_1$). Observed growth rate parameters ($K_{Obs}$) for von Bertalanffy growth are estimated as the slope of the regression of the growth rate ($\Delta D$ /$\Delta t$) against $D_{Max}$ - $D_{t1}$, the asymptotic or maximum diameter ($D_{Max}$) minus the initial diameter ($D_{t1}$).

## Snail Condition Indices

Condition indices (analogous to the body-mass index used for humans) for the two snail species were created using diameter and weight measurements for all snails caught and measured during the capture-recapture surveys. The dataset included measurements from snails not included in the mark-recapture analyses, such as small snails with diameter <15 mm, and snails caught in the plot but outside of a formal search. The condition index used for each species was calculated as weight (W) divided by a simple volumetric size function of snail diameter selected to have zero correlation with snail weight. The volumetric size function was in the form $D_i^k$, where Di are individual snail diameters. Thus, condition indices (Ci) for individuals of the two snail species were calculated as:

$$C_i = W_i/D_i^k \ .$$

Values of the exponent $k$ for the two species were selected by iteration of correlation analyses of the relationship between weight and $D_i^k$ with changing values of $k$. The selected value of $k$ was the iteration where Pearson’s correlation coefficient equalled zero. Units for the indices are g/unit volume, but the size of the unit volume is unknown and will be different for the two species.

## Capture-recapture Analyses

### *Estimating Plot Population Sizes*

The numbers of snails present in the plot during of each survey were estimated using closed capture-recapture models, which are based on the assumptions that there are no births or deaths, and no immigration into, or emigration out of, the plot population during the sampling period. These assumptions seem reasonable for capture-recapture assessments of *Powelliphanta* and *Rhytida* snail populations. *Powelliphanta* snails are slow breeding and long-lived [3], consequently there will be negligible recruitment or natural mortality during the 20- to 30-day capture-recapture sampling period.

The relatively small home ranges (mean Minimum Convex Polygon home range of 16.6 m$^2$) for radio-tagged *P. hochstetteri* [36] during a 45 day monitoring period indicates that although snails with home ranges 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. There are currently no data on home-range size or demography of *R. oconnori*.

Analyses of the capture-recapture data to obtain plot population estimates were undertaken using the R-package RMark [39] as an interface for the software MARK [19, 40] and the R-package Rcapture [41, 42], which uses loglinear models for capture-recapture analyses. Population sizes for surveys in each plot were estimated separately using a closed population capture-recapture model in RMark [16, 20] with a conditional likelihood model [43]: Huggins Closed Population Estimation (*Huggins*). The conditional likelihood model has 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 $t$. Although six models can be fitted to the capture-recapture data using the two encounter parameters, the only useful model for analyses of the snail data is ($p_t = c_t$). In this time-only model ($T$), the probabilities of first capture and recapture are the same on any search night, but vary between nights. Models with snail diameter included as a covariate were used to investigate whether size, or its corollary age, affected capture probabilities.

The R-package Rcapture [41] was also used to estimate plot population sizes. Rcapture fits a variety of closed population models to estimate population size using three basic types of closed population models: temporal models (*Mt*) where capture probabilities vary among capture occasions; heterogeneity models (*Mh*) where capture probabilities vary between animals; and behavioral models (*Mb*) where capture probability differs before and after the first capture. Rcapture also fits more complex models where capture probabilities affected by two factors simultaneously (i.e. *Mth* and *Mbh*). None of the models in Rcapture can be used to fit individual covariates such as snail size diameter, but heterogeneity models should detect heterogeneity, if size affects capture probability. Because snail capture probabilities vary greatly among capture occasions in response to environmental conditions, only models with a temporal component (i.e. *Mt*, and *Mth*) were considered as realistic models when the best fit-models were selected.

### *Estimating the Edge Effect Bias in Population Estimates*

Simulations were used to estimate the effect of heterogeneity due to individual's locations, known as the edge effect bias [27]. Although long-term immigration and emigration will be insignificant during a capture-recapture session, snails with home ranges straddling the plot boundary will spend some of their time during capture-recapture session outside of the plot, where they are not available for capture. The resulting lower capture probabilities for these snails inflate population estimates. This systematic upward bias in plot population estimates obtained using closed capture-recapture methods is referred to as the "edge effect". Although spatially explicit capture-recapture methods have been developed to overcome the edge effect, their current implementation in *secr* [44] is not effective for analyses of snail capture-recapture data [17]. There were also logistical difficulties in obtaining the spatial resolution required for spatially explicit analyses. Using a handheld gps unit with sub-metre accuracy proved time-consuming, compromising our ability to complete a plot search in one night. Additionally, when damp, the dense overhead forest canopy degraded the gps signal and decreased location estimate precision markedly.

In this study, population estimates for *P. hochstetteri* obtained using closed capture-recapture methods were adjusted downwards to compensate for the edge effect bias using a correction factor obtained from simulations using a random-walk to model snail movements during each capture-recapture survey [45]. Parameter estimates used for the model were obtained from a radiotelemetry study of the movements of ten radio-tagged *P. hochstetteri* snails [36] caught and radiotagged in the Canaan capture-recapture plot during the last few days of the Canaan 2016 capture-recapture survey. Simulations using a random-walk model with a gamma distribution [27] were undertaken separately for each of the seven capture-recapture surveys using the schedule of search nights and the total numbers of captures on each night during each of the actual surveys. Each simulation began with snails randomly distributed across the plot and surrounds. Successive locations for the snails were generated using a random-walk model, where the probability of movement on a night was 0.56, and the distances moved followed the gamma distribution with shape and rate parameters of 1.55 and 1.17, respectively.

A total of 1300 simulations were undertaken for each capture-recapture survey, with 100 simulations at each of thirteen simulated plot population sizes ranged around the actual capture-recapture population estimates. Plot population estimates for the simulations were obtained using Huggins Closed Population Estimation with the time only model. Simulations were not used to estimate correction factors for analyses with the time and diameter model or for *R. oconnori*, because radiotelemetry [36] did not provide information on size-related differences in *P. hochstetteri* movement behaviour or on *R. oconnori* movement behaviour.

### ***Robust Analyses to Obtain Demographic Parameters***

Robust design models [46-48] combining closed and open populations models were used to estimate survival and recruitment rates for the intervals between successive surveys. Three robust design models were used. Two implemented in Rmark: Robust Design with Huggins' Estimator (*RDHuggins*) and Robust Design Pradel Recruitment Huggins' Closed Populations (*RDPdfHuggins*) [47]; and a third using the robust function *robustd.t* in Rcapture [42, 49]. Analyses were repeated using all plausible combinations of model parameter specifications for the each of three models types.

Survival estimates obtained from analyses using the Robust Huggins model are true survival rate ($S$), whereas survival estimates from robust Pradel and Rcapture analyses are the apparent survival rate (φ), the product of the true survival rate and study area fidelity ($\varphi = S \times F$). Only robust Rcapture analyses provide estimates of recruitment rate ($R$), the number of new individuals in the plot during the interval as a result of both breeding in the plot and immigration into the plot. Recruitment rates were reported as both per capita and per adult snail in the population at the start of the interval. Adult *P. hochstetteri* were defined as having maximum diameter ≥55 mm, while adult *R. oconnori* had maximum diameter ≥30 mm.

Population trajectories were obtained from the demographic estimates using the discrete time-form of the population transition equation [50]: $N_t = N_0(1 + r)^t$ where $N_0$ is the starting population, $N_t$ is the population after $t$ years, and $r$ is the population growth rate estimated as $R - m$, where $R$ is the per-capita recruitment rate and $m$ is the annual mortality rate calculated as $1 - \varphi$, with values of $R$ and $\varphi$ obtained from analyses with Rcapture. The proportions of *P. hochstetteri* shells with evidence of predation by weka (*Gallirallus australis*) $p_{weka}$ were used to partition between-surveys mortality estimates for *P. hochstetteri* into mortality from weka predation ($m_{weka}$) and other mortality ($m_{other}$), i.e. $m_{weka} = m.p_{weka}$ and $m_{other} = m.(1\text{-}p_{weka})$. The partitioned estimates were used to compare population trajectories with and without weka predation for between-survey intervals for the two plots

The numbers of *P. hochstetteri* snails in each of the two plots dying between successive capture-recapture surveys were estimated as the product of mortality for the interval between surveys ($m_{i \to i+1}$) and capture-recapture estimates of the numbers of snails in the plots at the time of the first survey ($N_i$). Mortality for intervals was estimated using $1\text{-}\varphi_{i \to i+1}$, where $\varphi_{i \to\text{-} i+1}$ is the apparent mortality for the interval obtained from robust analyses in Rcapture. Plot population estimates ($N_i$) are from Huggins closed analyses using the time only model with adjustments for edge-effect bias.

***Best-fit models***

Akaike's Information Criterion with a correction for small sample size (AICc) was used to assist model selection among differently parameterised, but nested models, for each of the model types [51]. In general, models with the smallest AICc value were selected as the most parsimonious, or best-fit, models. However, models with standard errors for parameter estimates either close to zero or very large were dismissed, because the model parameters were not individually-identifiable. Non-identifiable parameters can result from: incorrect model structure, inadequate data, or parameter values being close to the 0 or 1 boundaries [19].

## Comparisons of the Capture-recapture and Sub-surface Search Methods

Ten of twenty-one permanent sub-surface search plots used by DOC to monitor snail populations in the Abel Tasman National Park are randomly distributed throughout 6 ha on the hill slope around, and less than 200 m from, the Canaan capture-recapture plot (Fig. 5). The ten sub-surface search plots and the capture-recapture plot are all located within similar forest type, with similar terrain and aspect. Results from sub-surface searches of the ten plots undertaken during summers 2016–17, 2018–19 and 2020–21 [52] were compared with results from capture-recapture sessions at Canaan during the same summers. Snail counts from sub-surface searches and population estimates from capture-recapture sessions were converted to density estimates (snails$^{-1}$ 100 m$^2$) using total plot areas. The total area of the sub-surface search plots is 475 m$^2$, comprising three 100 m$^2$ plots and seven are 25 m$^2$ plots, while the capture-recapture plot is 4900 m$^2$. Because of the two different sizes of ten sub-surface plots, snail counts from them were pooled for estimating confidence interval around density estimates. During capture-recapture surveys, snails <15 mm diameter were not tagged and are therefore not included in population estimates. Consequently, for direct comparison, snails <15 mm diameter were excluded from the sub-surface data set.

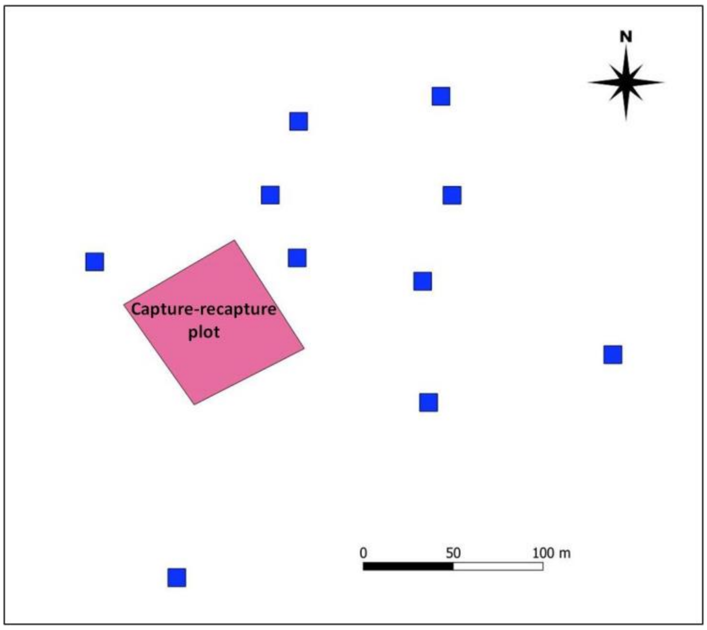

Figure 5. Location of the Canaan capture-recapture plot (pink rectangle) with respect to ten closest sub-surface plots (blue rectangles). Note that the sub-surface plots vary in size and are not to scale.

## General Statistical Methods

Standard errors (SE) for derived estimates were calculated using standard error propagation methods [53]. The 95% confidence intervals (CI95%) around estimates were calculated as: Mean Estimate ±1.96SE. A variety of statistical test were used for testing hypotheses. Binomial logistic regressions were used for comparisons of proportional data (e.g. the proportions of shells with and without evidence of predation by weka). General linear models (GLM) with Poisson error distributions were used for comparing count data (e.g. the numbers of snails found in plots). Student *t*-tests were used for comparing parameter estimates accompanied by standard errors (e.g. population estimates from capture-recapture analyses). Empirical cumulative distribution functions (ECDF) of the maximum diameters of samples of snails and, or shells were plotted to provide visual comparisons of the size distributions in the samples. Kolmogorov-Smirnov goodness-of-fit tests were used to test for significant differences between the empirical cumulative distributions of diameters from the different samples.

# RESULTS

## Capture-recapture Survey Summary

Capture-recapture surveys were undertaken during four summers at Canaan (2016–17, 2018–19, 2019–20 and 2020–21) and three summers at Wainui (2018–19, 2019–20 and 2020–21). The first survey (Canaan 2016–17) was undertaken during October (Table 1). However, results from that session and a concurrent radio-telemetry study of *P. hochstetteri* activity [17, 36] showed snail activity increased with increasing night-time temperatures. Consequently, subsequent survey sessions were scheduled for later in summer (Table 1). There were five nocturnal searches during the Canaan 2016–17 surveys and the first two Wainui surveys, but only three nocturnal searches during each of the other two Canaan surveys and four during the last Canaan survey (Table 1). Surveys extended over periods of between twenty-one and forty nights, with the intervals between successive nocturnal searches within surveys ranging between two and twenty-eight nights.

Table 1. Schedule of capture-recapture surveys.

| Plot | Survey | | Survey Length (Nights) | Intervals Between: | | | | |
|---|---|---|---|---|---|---|---|---|
| | Summer | Dates | | Surveys (Years) | Searches (Nights) | | | |
| | | | | | 1–2 | 2–3 | 3–4 | 4–5 |
| Canaan | 2016–17 | 5 Oct 16 – 25 Oct 16 | 21 | | 5 | 3 | 5 | 7 |
| | 2018–19 | 12 Mar 19 – 10 Apr 19 | 30 | 2.38 | 15 | 14 | | |
| | 2019–20 | 7 Dec 19 – 12 Jan 20 | 37 | 0.66 | 8 | 28 | | |
| | 2020–21 | 29 Nov 20 –7 Jan 21 | 40 | 0.88 | 8 | 15 | 16 | |
| Wainui | 2018–19 | 10 Nov 18 – 13 Dec 18 | 34 | | 14 | 3 | 6 | 10 |
| | 2019–20 | 8 Nov 19 – 4 Dec 19 | 27 | 0.90 | 2 | 6 | 3 | 15 |
| | 2020–21 | 26 Oct 20 – 17 Nov 20 | 23 | | 4 | 5 | 13 | |

All *Rhytida* snails captured during the capture-recapture surveys resembled known *R. oconnori* snails, with diameters >25 mm, and were therefore identified as *R. oconnori*.

There were 2614 captures of snails during the seven capture-recapture surveys (Table 2), with: 1165 and 801 captures of *P. hochstetteri*; and 330 and 318 captures of *R. oconnori*, at Canaan and Wainui respectively. The 2614 captures resulted in 1667 snails being tagged: 677 *P. hochstetteri* and 278 *R. oconnori* on the Canaan plot, and 479 *P. hochstetteri* and 236 *R. oconnori* on the Wainui Plot (Table 2). Nightly capture rates (i.e. the proportion of the estimated population caught) for the two species varied among surveys (Table 2), with higher rates for *P. hochstetteri* (mean 0.274: range 0.16–0.29) than *R. oconnori* (0.156: 0.05–0.16), and at Wainui than Canaan (mean capture rates 0.323 *cf.* 0.236 and 0.217 *cf.* 0.110 for *P. hochstetteri* and *R. oconnori* respectively).

Table 2. The numbers of first-captures and recaptures of *P. hochstetteri* and *Rhytida oconnori* snails during search nights of the seven capture-recapture surveys. The *Capture Rate* for each survey is the average of nightly capture rate from capture-recapture analyses using population estimates shown in Table 3.

a) Canaan

| Species | Summer | Capture | Search Night | | | | | Total | Capture Rate |
|---|---|---|---|---|---|---|---|---|---|
| | | | 1 | 2 | 3 | 4 | 5 | | |
| *Powelliphanta* | 2016–17 | First-capture | 53 | 13 | 21 | 12 | 73 | 172 | 0.173 |
| | | Recapture | 0 | 7 | 8 | 5 | 40 | 60 | |
| | 2018–19 | First-capture | 112 | 53 | 64 | | | 229 | 0.198 |
| | | Recapture | 0 | 17 | 34 | | | 51 | |
| | 2019–20 | First-capture | 118 | 82 | 56 | | | 256 | 0.193 |
| | | Recapture | 0 | 27 | 29 | | | 56 | |
| | 2020–21 | First-capture | 59 | 66 | 52 | 53 | | 230 | 0.262 |
| | | Recapture | 0 | 17 | 35 | 59 | | 111 | |
| *Rhytida* | 2016–17 | First-capture | 16 | 5 | 8 | 14 | 17 | 60 | 0.050 |
| | | Recapture | 0 | 0 | 0 | 2 | 4 | 6 | |
| | 2018–19 | First-capture | 8 | 21 | 36 | | | 65 | 0.135 |
| | | Recapture | 0 | 2 | 6 | | | 8 | |
| | 2019–20 | First Capture | 26 | 36 | 61 | | | 123 | 0.122 |
| | | Recapture | 0 | 7 | 8 | | | 15 | |
| | 2020–21 | First Capture | 9 | 14 | 11 | 12 | | 46 | 0.095 |
| | | Recapture | 0 | 0 | 4 | 3 | | 7 | |

b) Wainui

| Species | Summer | Capture | Search Night | | | | | Total | Rate |
|---|---|---|---|---|---|---|---|---|---|
| | | | 1 | 2 | 3 | 4 | 5 | | |
| *Powelliphanta* | 2018–19 | First-capture | 14 | 95 | 32 | 56 | 67 | 264 | 0.156 |
| | | Recapture | 0 | 4 | 13 | 23 | 50 | 90 | |
| | 2019–20 | First-capture | 84 | 41 | 45 | 34 | 29 | 233 | 0.230 |
| | | Recapture | 0 | 26 | 35 | 36 | 37 | 134 | |
| | 2020–21 | First-capture | 30 | 11 | 8 | 5 | | 54 | 0.292 |
| | | Recapture | 0 | 8 | 10 | 11 | | 29 | |
| *Rhytida* | 2018–19 | First-capture | 23 | 17 | 33 | 18 | 29 | 120 | 0.128 |
| | | Recapture | 0 | 3 | 8 | 9 | 14 | 34 | |
| | 2019–20 | First-capture | 25 | 13 | 13 | 11 | 15 | 77 | 0.162 |
| | | Recapture | 0 | 5 | 5 | 7 | 12 | 29 | |
| | 2020–21 | First-capture | 13 | 15 | 3 | 18 | | 49 | 0.121 |
| | | Recapture | 0 | 4 | 0 | 5 | | 9 | |

## Tag Loss and Re-tagging

Thirteen of the 38 *P. hochstetteri* snails double-tagged during the 2016–17 survey at Canaan were recaptured: 12 during the 2018–19 survey and two during the 2019–20 survey, including one snail previously recaptured during the 2018–19 survey. Tags were still in place and readable on all 13 recaptured double-tagged snails, but in three cases one of the tags was partly overgrown by new shell. Partly overgrown tags were also observed on two single-tagged snails: the tag on a *P. hochstetteri* was partly overgrown, but readable, after 2.5 yrs, and the tag on a single tagged *R. oconnori* was overgrown and unreadable after one year. The *P. hochstetteri* snails with partly overgrown tags were all tagged ≥2.5 years before recapture and were <37 mm diameter when originally tagged. The *R. oconnori* with the unreadable overgrown tag was 23.6 mm diameter on recapture. The tag on one *P. hochstetteri* at Canaan was scratched and the numbers unreadable after one year. Cyano-acrylate glue is extremely persistent on snail shells and glue remnants would remain visible on the shell for a long period, probably several years, after a tag fell off. Glue remnants where a tag was previously attached were only observed on one *P. hochstetteri*.

To avoid tags becoming unreadable the tags on forty-one snails were replaced, with intervals between initial tagging and retagging varying between one and four years. Thirty-three *P. hochstetteri* and one *R. oconnori* were retagged in the Canaan plot. Two *P. hochstetteri* and five *R. oconnori* were retagged in the Wainui plot.

## Closed Population Estimates

### *Best-fit models*

There was no support for behavioral models (i.e. models where animals avoid or seek recapture), indicating that capture and tagging a snail has no effect on the likelihood of future recaptures. There was also no support for models used to detect other hidden sources of heterogeneity in the snail capture probabilities. However, there was strong support for models with size as a covariate (i.e. *T+D* models) for both species (Figs. 6a–d and Tables 3a & b), indicating that size does affect capture probability, with higher capture probabilities for larger snails.

The *T+D* model with snail diameter as an individual covariate was the best fitting model of the two nested Huggins models for ten of the fourteen analyses undertaken using RMark (Table 3 & Fig. 6). The time-only model *T*, which does not include snail diameter as a covariate, was the best fitting Huggins’ model for four analyses of survey data from Canaan: *P. hochstetteri* in 2018–19 and *R. oconnori* in 2016–17, 2019–20 and 2020–21.

Population estimates from analyses with the *T+D* model were similar or slightly higher than those from the *T* model, but had wider confidence intervals, especially for *R. oconnori*. Among analyses undertaken using Rcapture, the temporal model (*Mt*) was the best fitting model with little support for models that include heterogeneity. Population estimates and confidence intervals from Rcapture’s temporal model were very similar to those from analyses undertaken using time-only model in RMark (Table 3 & Fig. 6).

Table 3. Population estimates for *P. hochstetteri* and *Rhytida oconnori* present on the Canaan and Wainui plots during capture-recapture surveys, obtained using three closed population capture-recapture analyses: Huggins closed population analyses in Rmark with *Time*, *Time Diameter* models (a & b) and using *Rcapture* (c). Bold font is used to identify estimates from the best-fitting of the nested Huggins models for each survey session and snail species. Population estimate are accompanied by the 95% confidence interval (CI95%) and the width of CI95% as a percentage of the population estimate.

| a) Time model | *Powelliphanta* | | | *Rhytida* | | |
|---|---|---|---|---|---|---|
| | N. | *CI95%* | | N. | *CI95%* | |
| Canaan | | | | | | |
| 2016-17 | 269 | *(234 – 323)* | *33%* | **264** | ***(144 – 554)*** | ***155%*** |
| 2018-19 | **471** | ***(393 – 588)*** | ***41%*** | 180 | *(115 – 332)* | *120%* |
| 2019-20 | 538 | *(450 – 665)* | *40%* | **378** | ***(261 – 594)*** | ***88%*** |
| 2020-21 | 325 | *(295 – 369)* | *22%* | **140** | ***(85 – 274)*** | ***135%*** |
| Wainui | | | | | | |
| 2018-19 | 454 | *(399 – 531)* | *29%* | 241 | *(194 – 319)* | *52%* |
| 2019-20 | 319 | *(293 – 358)* | *20%* | 131 | *(107 – 176)* | *53%* |
| 2020-21 | 73 | *(63 – 94)* | *42%* | 120 | *(80 – 213)* | *111%* |

| b) Time+Diam. model | *Powelliphanta* | | | *Rhytida* | | |
|---|---|---|---|---|---|---|
| | N. | *CI95%* | | N. | CI95% | |
| Canaan | | | | | | |
| 2016-17 | **295** | ***(242 – 388)*** | ***49%*** | 351 | (124 – 1,377) | *357%* |
| 2018-19 | 473 | *(393 – 591)* | *42%* | **292** | **(117 – 1,058)** | ***322%*** |
| 2019-20 | **628** | ***(482 – 868)*** | ***61%*** | 382 | (262 – 607) | *90%* |
| 2020-21 | **334** | ***(300 – 385)*** | ***25%*** | 224 | (93 – 721) | *281%* |
| Wainui | | | | | | |
| 2018-19 | **491** | ***(418 – 599)*** | ***37%*** | **316** | **(214 – 528)** | ***99%*** |
| 2019-20 | **387** | ***(331 – 472)*** | ***36%*** | **179** | **(121 – 318)** | ***110%*** |
| 2020-21 | **102** | ***(71 – 189)*** | ***115%*** | **138** | **(82 – 290)** | ***150%*** |

| c) Rcapture | *Powelliphanta* | | | *Rhytida* | | |
|---|---|---|---|---|---|---|
| | N. | *CI95%* | | N. | *CI95%* | |
| Canaan | | | | | | |
| 2016-17 | 269 | *(225 – 312)* | *33%* | 264 | *(74 – 454)* | 144% |
| 2018-19 | 471 | *(375 – 568)* | *41%* | 180 | *(79 – 282)* | 113% |
| 2019-20 | 538 | *(432 – 644)* | *39%* | 378 | *(218 – 539)* | 85% |
| 2020-21 | 325 | *(289 – 361)* | *22%* | 140 | *(052 – 227)* | 125% |
| Wainui | | | | | | |
| 2018-19 | 454 | *(389 – 519)* | *29%* | 241 | *(180 – 303)* | 51% |
| 2019-20 | 319 | *(287 – 351)* | *20%* | 131 | *(98 – 164)* | 51% |
| 2020-21 | 73 | *(58 – 87)* | *39%* | 120 | *(58 – 182)* | 104% |

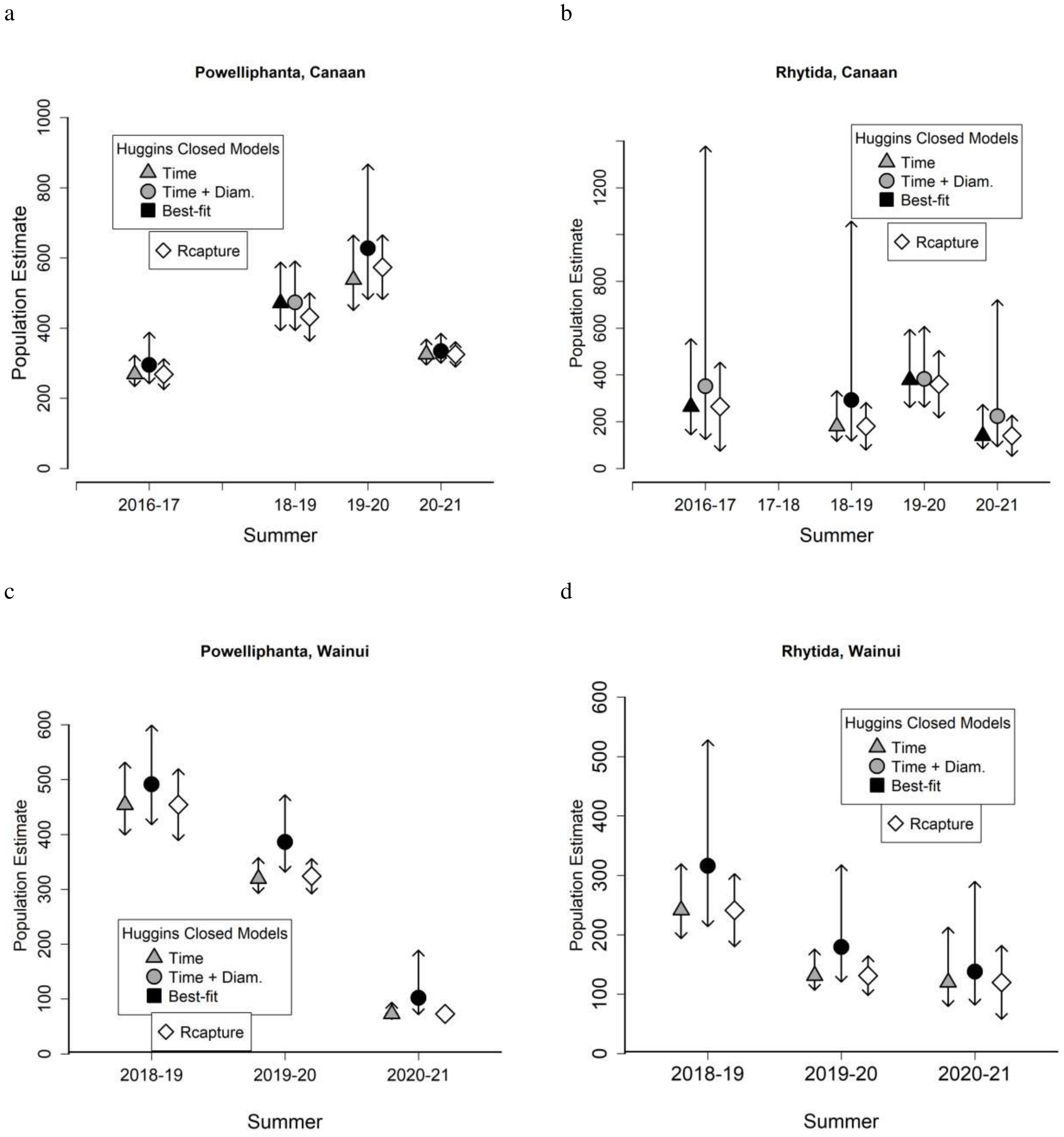

Figure 6. Plot population estimates for *P. hochstetteri* and *Rhytida oconnori* at Canaan (a & b) and Wainui (c & d) from capture-recapture analyses using Rcapture and Huggins estimator for closed population with both time (*T*) and time and diameter (*T+D*) models.

The results of random-walk simulations for each the five survey sessions indicate that the edge-effect bias in the closed capture-recapture analyses using the *T* model resulted in over-estimating actual *P. hochstetteri* population sizes by between 6.7% and 12.1%, requiring downward adjustments in the population estimates of between 6.3% and 10.8% (Table 4).

Table 4. Estimates of the edge-effect bias (percentage over-estimate) in Huggins' population estimates with the Time only model for *P. hochstetteri* during the seven surveys. Adjust is the percentage subtracted from the original population estimates

| | Edge Effect | | | Population Estimates | | | |
|---|---|---|---|---|---|---|---|
| | | | | Original | | Adjusted | |
| | Mean | *(CI95%)* | Adjust | N. | *(CI95%)* | N. | *(CI95%)* |
| Canaan | | | | | | | |
| 2016–17 | 8.26% | *(7.6% – 8.9%)* | -7.63% | 269 | *(234 – 323)* | 248 | *(216 – 298)* |
| 2018–19 | 11.43% | *(10.7% – 12.2%)* | -10.26% | 471 | *(393 – 588)* | 423 | *(352 – 528)* |
| 2019–20 | 11.32% | *(10.6% – 12.0%)* | -10.17% | 538 | *(450 – 665)* | 483 | *(405 – 597)* |
| 2020–21 | 12.11% | *(10.9% – 13.4%)* | -10.80% | 325 | *(295 – 369)* | 290 | *(264 – 329)* |
| Wainui | | | | | | | |
| 2018–19 | 8.01% | *(7.5% – 8.5%)* | -7.42% | 454 | *(399 – 531)* | 421 | *(370 – 492)* |
| 2019–20 | 7.34% | *(6.9% – 7.8%)* | -6.84% | 319 | *(293 – 358)* | 297 | *(273 – 333)* |
| 2020–21 | 6.74% | *(5.9% – 7.6%)* | -6.31% | 73 | *(063 – 094)* | 68 | *(059 – 088)* |

### *Population change*

Population changes between successive surveys estimated from analyses with the *T* and *T+D* models are generally similar (Table 5a & b), but with wider confidence intervals around population estimates from the *T+D* model, especially for *R. oconnori*, resulting in few of the population changes obtained from the *T+D* models being significant. Four of the five population changes between surveys for *P. hochstetteri* estimated from the *T* model are significant ($p$<0.10), whereas only two of the five population changes from the *T+D* model are significant. None of the population changes for *R. oconnori* are significant at $p<0.1$ for either model, although two are significant at $p<0.15$.

All three estimation methods show the Canaan *P. hochstetteri* population increased during the intervals between the first three surveys (2016–17, 2018–19 and 2019–20), but then declined markedly between the 2019–20 and 2020–21 surveys. Estimates from the *T* model show annualised increases of 20% and 26% per annum during the first two intervals followed, by a decline of 40% per annum during the last interval. All three estimation methods show the Wainui *P. hochstetteri* population decreased during both intervals between the three surveys (2018–19, 2019–20, and 2020–21), with estimates from the *T* model showing annualised decreases of 30% and 77% per annum during the two intervals. The only non-significant population change for *P. hochstetteri* was for the interval between 2018–19 and 2019–20 surveys at Canaan.

Edge-effect adjustment for estimates of *P. hochstetteri* population size from the *T* model only has a minor influence on estimated total population change between surveys (Tables 4 & 5). With edge-effect adjustment estimates of total changes in *P. hochstetteri* populations between surveys went from 76%, 14% and -40% to 71%, 14% and -40% in the Canaan plot, and from -30% and -77%, to -29% and -77% in the Wainui plot.

Table 5. Percentage population changes with CI95% between surveys obtained from closed population estimates using Huggins' models with (a) time only (*Time*) and (b) time and diameter (*T+D*). Significant population changes ($p < 0.1$) are identified with bold font, negative changes are red font. *Annual* is the population change annualized. Population changes are shown excluding edge effect corrections.

| a) Time Model | *Powelliphanta* | | | *Rhytida* | | |
|---|---|---|---|---|---|---|
| Interval | Change | *(CI95%)* | Annual | Change | *(CI95%)* | Annual |
| Canaan | | | | | | |
| 2016-17 to 2018-19 | **76%*** | ***(34% to 117%)*** | **26%** | -32% | *(-116% to 53%)* | -14% |
| 2018-19 to 2019-20 | 14% | *(-16% to 45%)* | 20% | 110% | *(-12% to 232%)* | 173% |
| 2019-20 to 2020-21 | **-40%*** | ***(-62% to -17%)*** | **-40%** | -63%† | *(-118% to -8%)* | -63% |
| Wainui | | | | | | |
| 2018-19 to 2019-20 | **-30%*** | ***(-46% to -13%)*** | **-31%** | -46%† | *(-77% to -14%)* | -47% |
| 2019-20 to 2020-21 | **-77%**** | ***(-91% to -64%)*** | **-78%** | -9% | *(-63% to 45%)* | -9% |

** ~ $p$<0.05; * ~ $p$<0.10; †~ $p$<0.15

| b) Time + Diameter Model | *Powelliphanta* | | | *Rhytida* | | |
|---|---|---|---|---|---|---|
| Interval | Change | *(CI95%)* | Annual | Change | *(CI95%)* | Annual |
| Canaan | | | | | | |
| 2016-17 to 2018-19 | **60%*** | ***(17% to 104%)*** | **21%** | -17% | *(-202% to 168%)* | -7% |
| 2018-19 to 2019-20 | 33% | *(-13% to 78%)* | 47% | 31% | *(-119% to 181%)* | 44% |
| 2019-20 to 2020-21 | **-47%*** | ***(-81% to -13%)*** | **-47%** | -41% | *(-126% to 43%)* | -42% |
| Wainui | | | | | | |
| 2018-19 to 2019-20 | -21% | *(-45% to 2%)* | -22% | -43% | *(-102% to 16%)* | -45% |
| 2019-20 to 2020-21 | -74%† | *(-100% to -48%)* | -75% | -23% | *(-97% to 51%)* | -24% |

* ~ $p$<0.10; †~ $p$<0.15

Changes in the *R. oconnori* population on the Canaan plot fluctuated with population estimates from the *T* model showing annualised decreases of 14% and 63% in the first and third interval but a 173% annualised increase during the middle interval between the 2018–19 and 2019–20 surveys. The *R. oconnori* population in the Wainui plot declined during both intervals between surveys with annualised decreases of 47% and 9%.

## Demographic Parameters from Robust Analyses

Annualised estimates of the true survival rate ($S$) and apparent survival rate ($\varphi$) from the three robust analyses show generally similar patterns (Table 6). The one exception is for *P. hochstetteri* in the Canaan plot between the second and third surveys (i.e. 2018–19 to 2019–20). The estimate of the true survival rate from analysis with the Huggins' Estimator was much higher (0.975) than the apparent survival estimates from Pradel and Recapture analyses (0.537 and 0.652). As apparent survival rate is the product of the true survival rate and fidelity ($\varphi = S \times F$), the difference could reflect low site fidelity during the interval between the second and third surveys at Canaan.

Apparent survival rates for *P. hochstetteri* declined over time in both plots. Estimates for apparent annual survival rates between the last two surveys in the Wainui plot were low ($\varphi$ = 0.091 and 0.085 for estimates from Pradel and Rcapture analyses respectively). Estimates of survival rates for *R. oconnori* (Table 6) were much lower than for *P. hochstetteri*, presumably because *R. oconnori* are shorter lived than *P. hochstetteri*. The highest survival rates for *R.*

*oconnori* were for the interval between the second and third surveys (i.e. 2018–19 to 2019–20) in the Canaan plot, when $S = 0.36$ and $\varphi = 0.28$ and 0.36. Estimated survival rates for *R. oconnori* were especially low for the interval between the first two surveys in the Canaan plot and the final two surveys in the Wainui plot.

Table 6. Survival ($S$) and apparent survival ($\varphi$) parameter estimates from three robust analyses: Robust Design with Huggins' Estimator (R-Hug.), Robust Design Pradel Recruitment Huggins' Closed Populations (Pradel) and Rcapture (Rcap.).

| | | *Powelliphanta* | | | *Rhytida* | | |
|---|---|---|---|---|---|---|---|
| Plot | Interval | $S$ | $\varphi$ | | $S$ | $\varphi$ | |
| | | R-Hug. | Pradel | Rcap. | R-Hug. | Pradel | Rcap. |
| Canaan | | | | | | | |
| | 2016 to 2018 | 0.756 | 0.698 | 0.670 | 0.000 | 0.103 | 0.000 |
| | 2018 to 2019 | 0.975 | 0.537 | 0.652 | 0.358 | 0.280 | 0.357 |
| | 2019 to 2020 | 0.472 | 0.373 | 0.354 | 0.102 | 0.179 | 0.106 |
| Wainui | | | | | | | |
| | 2018 to 2019 | 0.365 | 0.300 | 0.281 | 0.140 | 0.156 | 0.131 |
| | 2019 to 2020 | 0.102 | 0.091 | 0.085 | 0.000 | 0.000 | 0.000 |

Table 7. Annual recruitment rates per capita and per adult from robust analyses using Rcapture. The column *% adults* is the percentage of adult snails in the population at the start of the interval between surveys.

| | | *Powelliphanta* | | | *Rhytida* | | |
|---|---|---|---|---|---|---|---|
| Plot | Interval | % adults | Recruitment rate | | % adults | Recruitment rate | |
| | | | Per capita | Per adult | | Per capita | Per adult |
| Canaan | | | | | | | |
| | 2016 to 2018 | 55% | 1.089 | 1.979 | 66% | 0.856 | 1.296 |
| | 2018 to 2019 | 54% | 0.500 | 0.922 | 32% | 1.782 | 5.583 |
| | 2019 to 2020 | 31% | 0.210 | 0.672 | 49% | 0.279 | 0.567 |
| Wainui | | | | | | | |
| | 2018 to 2019 | 19% | 0.403 | 2.099 | 42% | 0.387 | 0.921 |
| | 2019 to 2020 | 13% | 0.123 | 0.918 | 9% | 0.910 | 9.968 |

Annual recruitment rates for *P. hochstetteri* declined over time in both plots (Table 7), with greater declines in the per capita recruitment rate than the per adult recruitment rate reflecting increases in the proportions of small snails found in the plot during later surveys. There was large variation in estimates of annual recruitment rates for *R. oconnori* (Table 7), especially the per adult recruitment rate. Recruitment per adult in the Canaan plot increased from 1.30 during the first interval between surveys to 5.58 during the second interval and then dropped to 0.57 during the third and final interval. Recruitment per adult in the Wainui plot increased dramatically from 0.92 to 9.97 during the two intervals between surveys. Analogous increases in per capita recruitment during the two intervals were less dramatic, going from 0.39 to 0.91.

## Growth Curves

Two hundred and forty-six pairs of repeat diameter measurements from individual *P. hochstetteri* snails caught and measured during successive surveys on the two plots (Table 8) were used to estimate instantaneous growth parameters for von Bertalanffy growth curves for intervals between surveys for the two plots separately (Table 9). There were only twenty-six repeat diameter measurements for *R. oconnori* from both sites and all surveys in both plots (Table 8). These measurements were pooled to estimate a single instantaneous growth rate for *R. oconnori* in both plots and all intervals between surveys.

Table 8. Summary of the numbers of pairs of repeat diameter measurements during successive surveys used to estimate snail growth rates.

| Measurement Session | | *Powelliphanta* | | *Rhytida* | |
|---|---|---|---|---|---|
| 1st | 2cnd | Canaan | Wainui | Canaan | Wainui |
| 2016-17 | 2018-19 | 67 | . | 0 | . |
| 2018-19 | 2019-20 | 66 | 55 | 11 | 10 |
| 2019-20 | 2020-21 | 46 | 12 | 5 | 0 |
| | | 179 | 67 | 16 | 10 |

Regression analyses of summer growth rate ($\Delta D/\Delta t$) against initial maximum diameter showed significant ($p<0.05$) relationships between growth rate and initial diameter for *P. hochstetteri* from Canaan during all intervals between surveys and for Wainui during the last interval between surveys (Table 9). Moderate $R^2$ values of 0.70, 0.42 and 0.43 for the regressions for Canaan for the first two intervals and Wainui for the last interval indicate that initial diameter explains much of the variation in growth rates between individual snails during these intervals. However, the low $R^2$ values of 0.08 and 0.05 for the regression of growth and diameter measurements for the final interval between surveys at Canaan (2019–20 to 2020–21) and the first interval at Wainui (2018–19 to 2019–20) indicate that initial diameter has little explanatory power for *P. hochstetteri* growth rates during these intervals, with individual snails exhibiting different growth rates not related to their initial diameters.

The growth curves for *P. hochstetteri* at Canaan during the first two intervals between surveys (i.e. 2016–17 to 2018–19 and 2018–19 to 2019–20 were similar, but growth curves for the final interval between surveys at Canaan (2019–20 to 2020–21) and for the both intervals between surveys at Wainui are very different (Fig. 7a). Large differences between the five growth curves for different intervals and plots indicate that growth rates for *P. hochstetteri* are variable, with low growth rates during the intervals between the three surveys at Wainui and between the last two surveys at Canaan (2019–20 to 2020–21). As a consequence, snail maximum diameter is not a reliable predictor of age for *P. hochstetteri* and cohort analysis based on snail size is not possible.

Regression analyses of summer growth rate against initial maximum diameter for *R. oconnori* in both plots and all intervals between surveys (Table 9) was significant ($p<0.001$) with a moderate $R^2$ value of 0.6 indicating that initial diameter explains much of the variation in growth rates between individual snails. The growth rate curve for *R. oconnori* (Fig. 7b) shows *R. oconnori* take only three years of growth to approach their asymptotic maximum diameter of 36 mm, whereas even during the intervals with fastest growth *P. hochstetteri* took fifteen years to approach their asymptotic maximum diameter of 74 mm (Fig. 7a). This figure is comparable to other growth estimates for *Powelliphanta*. A study of growth in captive *P. augusta* indicate that they reach maximum diameter 20 years after hatching [54, 55]. Free living tagged *P. h. bicolor* and *P. lignaria johnstoni* have average life spans of 12 to 14 years, with some individuals living up to 20 years [3].

Table 9. Estimates of growth parameters for *P. hochstetteri* and *Rhytida oconnori* over the intervals between successive surveys. Estimates are coefficients are from the model: *Summer Growth ~ Initial Diameter*. Adjusted Rsq is the percentage of variation explained by the model.

| Plot | Interval | N | Intercept | | Slope | | *P*-value | Adjusted |
|---|---|---|---|---|---|---|---|---|
| | | | Estimate | SE | Estimate | SE | | Rsq |
| *Powelliphanta* | | | | | | | | |
| Canaan | | | | | | | | |
| | 2016 to 2018 | 70 | 10.3 | 0.68 | -0.155 | 0.012 | <0.001 | 0.70 |
| | 2018 to 2019 | 78 | 12.6 | 1.25 | -0.171 | 0.023 | <0.001 | 0.42 |
| | 2019 to 2020 | 66 | 5.0 | 0.97 | -0.045 | 0.018 | <0.05 | *0.08* |
| Wainui | | | | | | | | |
| | 2018 to 2019 | 57 | 6.5 | 1.76 | -0.068 | 0.035 | 0.058 | *0.05* |
| | 2019 to 2020 | 17 | 6.6 | 1.31 | -0.091 | 0.025 | <0.01 | 0.43 |
| *Rhytida* | | | | | | | | |
| | All plots & years | 26 | 25.5 | 2.86 | -0.695 | 0.110 | <0.001 | 0.60 |

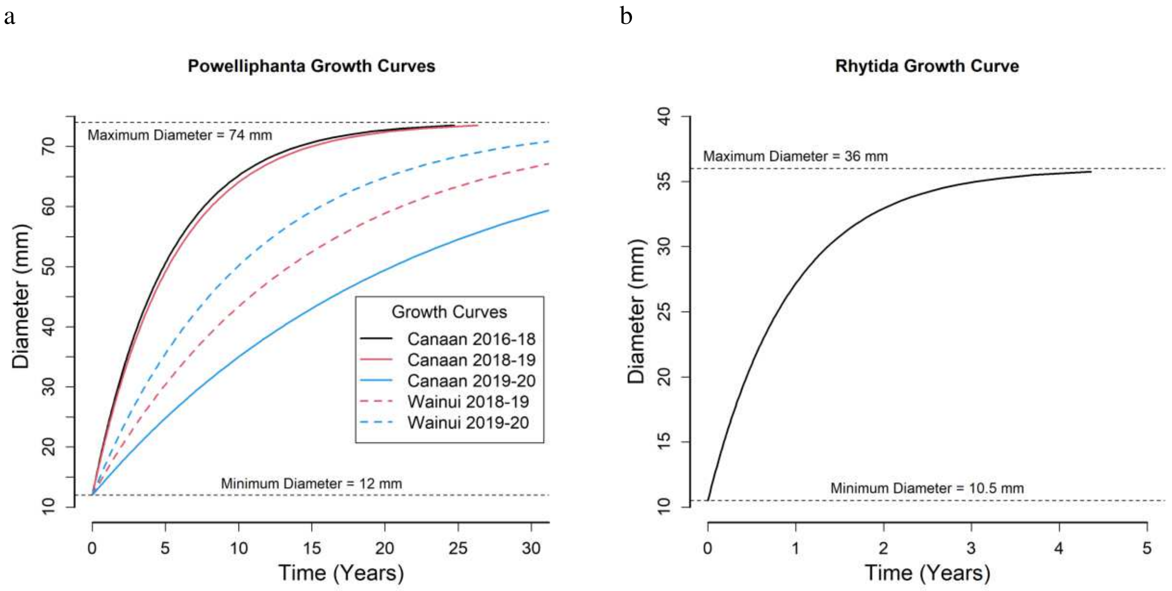

Figure 7. Growth curves for *P. hochstetteri* (a) and *Rhytida oconnori* (b) obtained using von Bertalanffy growth equation.

## Snail Condition Indices

Snail condition indices for *P. hochstetteri* varied between surveys (Fig. 8a & Table 10). At Canaan, snail condition indices for *P. hochstetteri* were highest during the first survey (2016–17) and lowest during the second survey (2018–19), taking mid-range values in the two most recent surveys (2019–2020 and 2020–21).

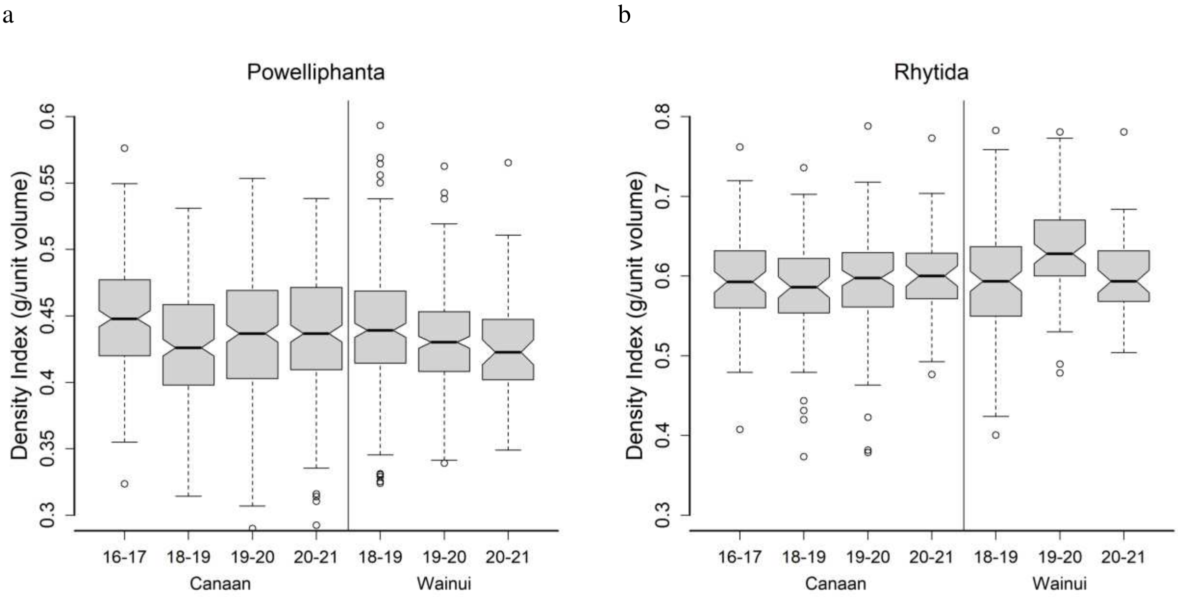

Figure 8. Boxplots of snail density indices to compare the condition of *P. hochstetteri* (a) and *Rhytida oconnori* (b) snails during different capture-recapture surveys.

Table 10. Condition indices for snails weighed and measured during the seven capture-recapture surveys, with the results of pair-wise tests comparing snail conditions during different surveys. Significant pair-wise differences are shown in bold.

| Species | Plot | Summer | N. | Mean | *(CI95%)* | *P*-val. for pair-wise tests Reference summer | | |
|---|---|---|---|---|---|---|---|---|
| | | | | | | 2016–17 | 2018–19 | 2019–20 |
| *Powelliphanta*: | | | | | | | | |
| | Canaan | 2016–17 | 215 | 0.448 | *(0.44–0.45)* | | | |
| | | 2018–19 | 229 | 0.428 | *(0.42–0.43)* | **0.000** | | |
| | | 2019–20 | 262 | 0.436 | *(0.43–0.44)* | **0.003** | **0.053** | |
| | | 2020–21 | 235 | 0.438 | *(0.43–0.44)* | **0.021** | **0.013** | 0.531 |
| | Wainui | 2018–19 | 263 | 0.445 | *(0.44–0.45)* | | | |
| | | 2019–20 | 235 | 0.432 | *(0.43–0.44)* | | **0.003** | |
| | | 2020–21 | 59 | 0.427 | *(0.42–0.44)* | | **0.013** | 0.510 |
| *Rhytida*: | | | | | | | | |
| | Canaan | 2016–17 | 74 | 0.594 | *(0.58–0.61)* | | | |
| | | 2018–19 | 66 | 0.583 | *(0.57–0.60)* | 0.298 | | |
| | | 2019–20 | 125 | 0.595 | *(0.58–0.61)* | 0.945 | 0.221 | |
| | | 2020–21 | 48 | 0.593 | *(0.57–0.62)* | 0.960 | 0.379 | 0.909 |
| | Wainui | 2018–19 | 122 | 0.600 | *(0.59–0.61)* | | | |
| | | 2019–20 | 83 | 0.633 | *(0.62–0.65)* | | **0.001** | |
| | | 2020–21 | 49 | 0.598 | *(0.58–0.61)* | | 0.839 | 0.005 |

In pair-wise tests comparing condition indices for the four Canaan surveys, the 2019–2020 and 2020–21 surveys were not significantly different from one another, but all other pair-wise comparison were significant (*$p<0.1$*). At Wainui, snail condition indices for *P. hochstetteri* were highest during the first survey (2018–19) and declined during the following two surveys. In pair-wise tests comparing condition indices for the three Wainui surveys, the 2019–2020 and 2020–21 surveys were not significantly different from one another, but other pair-wise comparison were significant ($p<0.05$).

Differences between snail condition indices for *R. oconnori* caught during the four Canaan surveys (Fig. 8b & Table 10) were not significant ($p>0.1$). However, there were significant differences ($p<0.001$) between condition indices for *R. oconnori* caught during the first and second Wainui surveys (2018–2019 and 2019–20), but not for other pair-wise comparisons.

## Size Distributions of Live Snails

Plots of the empirical cumulative distribution functions (ECDF) of the maximum diameters snails provide visual comparisons of the size distributions of snail populations on the plots during the seven surveys (Figs. 9a–c). ECDFs for *P. hochstetteri* in the Canaan plot (Fig. 9a) during the last two surveys are to the left of ECDFs for the first two surveys indicating that higher proportions of small snails were found during the more recent surveys (2019–20 and 2020–21). There is a similar shift to the left in the ECDF for *P. hochstetteri* in the Wainui plot between the 2018–19 and 2019–20 surveys (Fig. 9b). A discontinuity in the ECDF between 30 and 50 mm diameter snails for *P. hochstetteri* in the Wainui plot during the 2020–21 survey is evidence of a decline in the proportion of mid-sized snails prior to this survey. ECDFs for *R. oconnori* in both plots (Fig. 9c & d) show a leftward shift over time indicating that there was an increase in the proportions of small snails found during more recent surveys.

Results from Kolmogorov-Smirnov goodness-of-fit tests for comparisons of the ECDF's for live snail diameters from different surveys on each of the plots were significant ($p<0.05$) for fifteen of the eighteen comparisons. Differences between ECDFs for *P. hochstetteri* during the 2019–20 and 2020–21 surveys in the Wainui plot were only significant at $p<0.1$. Differences between ECDFs were not significant ($p>0.1$) for comparisons of *P. hochstetteri* in the Canaan plot during the 2019–20 and 2020–21 surveys and for comparisons of *R. oconnori* in the Canaan plot during the 2018–19 and 2019–20 surveys.

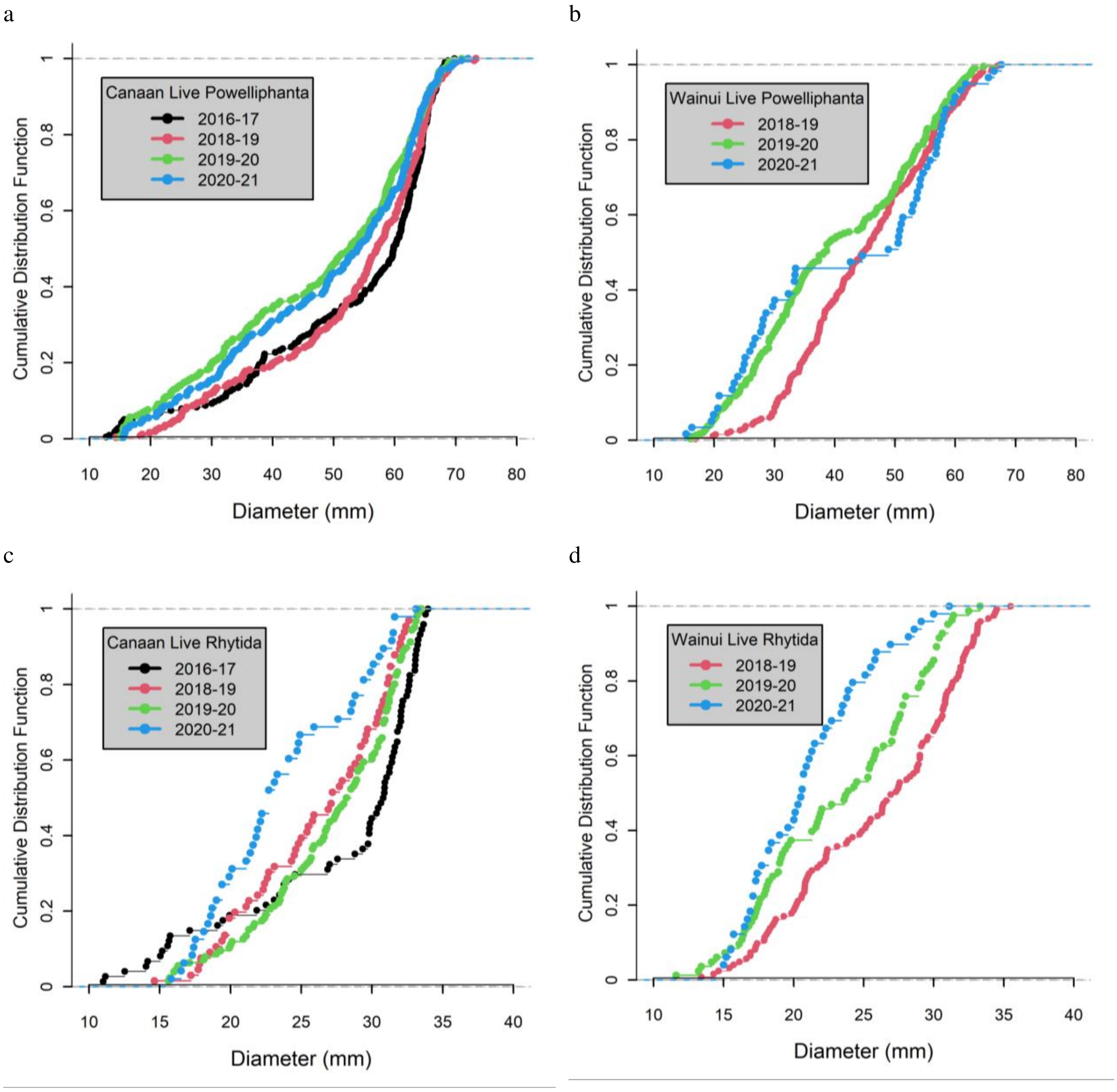

Figure 9. Empirical cumulative distribution plots to compare the size distributions of live *P. hochstetteri* snails found during capture-recapture surveys at Canaan (a) and Wainui (b) and of live *Rhytida oconneri* at Canaan (c) and Wainui (d).

## Shell Surveys

A total of 878 *P. hochstetteri* shells were found in the two plots over the three summers (2018–19, 2019–2020 and 2020–21) with 208 shells found in the Canaan plot and 670 in the Wainui plot. *R. oconnori* shells are rarely found and were therefore excluded from the shell survey data analyses. Seventy-seven of 208 shells (37.0%) found at Canaan and 96 of 670 shells (14.3%) found at Wainui were individually tagged. By the time of the last shell search during summer 2020–21, there had been 726 and 479 *P. hochstetteri* snails tagged in the Canaan and Wainui plots respectively. Thus the tag recovery rates on shells at the two plots were 10.6% and 20.0% respectively.

Only three distinctive damage patterns were observed: shells preyed on by weka, shells preyed on by rodents and trampled shells. Shells preyed on by weka (Fig. 10a–c) were characterised by puncture holes with sharp and fractured edges, presumably created when the snails were stabbed by the weka's dagger-shaped beak. Weka-inflicted puncture holes were usually on the side of the shell, close to the aperture, and often extended into the internal whorls of the shell. The damage pattern on shells preyed on by rats was very different, with obvious rodent teeth-marks evident along the edges of the holes (Fig. 10d). Trampled shells were flattened, with numerous cracks, but no holes.

Figure 10. Predator identification based on shell damage patterns: a to c) Weka: puncture holes with sharp edges, usually close to the aperture but sometimes near the apex; punctures often penetrate to the inside whorls. d) Rat: although the hole is at a similar location to weka puncture holes, the rim of the hole shows tooth-marks and jagged edges.

Most of the *P. hochstetteri* shells found in the Canaan plot during the three summers were undamaged (77%, 66% and 53%), whereas only 48%, 32% and 31% of the shells found in the Wainui plot were undamaged (Table 11). The damage patterns on damaged shells found in both plots indicated that most had been preyed on by weka. The proportion of shells with evidence of predation by weka was significantly ($p<0.001$) lower in the Canaan plot than the Wainui plot (31.3% cf. 58.4%). At Canaan, there was no significant difference ($p>0.1$) between the proportions of shells with evidence of weka predation during the first two summers (22% and 24%), but the proportion of shells with evidence of weka predation increased significantly ($p<0.05$) during the third summer to 41% (Table 12). In pair-wise comparisons of the proportions of shells found with evidence of weka predation at Wainui during the three summers, there were significant difference ($p<0.05$) between the proportions of shells with evidence of weka predation during the first summer and the other two summers

(46% c.f. 63% and 59%), but differences were not significant (*p>0.10*) for shells found during the last two summers.

Table 11. Probable fate of *P. hochstetteri* snails found dead during shell surveys.

| | Canaan | | | Wainui | | |
|---|---|---|---|---|---|---|
| | 2018–19 | 2019–20 | 2020–21 | 2018–19 | 2019–20 | 2020–21 |
| Undamaged | 75% | 66% | 53% | 49% | 32% | 31% |
| Trampled | 0% | 2% | 0% | 5% | 2% | 0% |
| Unknown predator | 4% | 9% | 4% | 0% | 2% | 9% |
| Rodent | 0% | 0% | 2% | 0% | 1% | 2% |
| Weka | 22% | 24% | 41% | 46% | 63% | 59% |
| Total N. of Shells | 55 | 58 | 95 | 134 | 330 | 206 |

Table 12. The proportions of *P. hochstetteri* shells with evidence of predation by weka found during three summers. The *p*-values are for pair-wise comparisons between summers and for the model comparing all summers. Significant pair-wise differences are shown on bold.

| | | | | | *p*-values | | |
|---|---|---|---|---|---|---|---|
| Plot | Summer | N. Weka | Total N. | % Weka | Pair-wise References: *2018-19* | *2019-20* | Model |
| Canaan | 2018-19 | 12 | 55 | 22% | . | | **0.019** |
| | 2019-20 | 14 | 58 | 24% | *0.770* | | |
| | 2020-21 | 39 | 95 | 41% | ***0.018*** | ***0.035*** | |
| Wainui | 2018-19 | 61 | 134 | 46% | . | | ***0.002*** |
| | 2019-20 | 209 | 330 | 63% | ***0.000*** | | |
| | 2020-21 | 121 | 206 | 59% | ***0.017*** | *0.288* | |

Evidence of predation by rodents was seen on only nine of the 878 shells: two shells found in the Canaan plot during summer 2020-21, three shells found in the Wainui plot during summer 2019–20 and four shells during summer 2020-21. Trampling was evident on one shell found at Canaan, and thirteen shells found at Wainui during summers 2018–19 and 2019–20 (seven and six shells, respectively).

The proportions of tagged and untagged shells with evidence of predation by weka were not significantly different (*p>0.10*) at Canaan (Table 13). No tagged shells were found in the Wainui plot during summer 2018–19, because shell searches were undertaken before tagging for capture-recapture monitoring began. Evidence of predation by weka was observed on a significantly (*p<0.05*) higher proportion of tagged shells (80%) than untagged shells (61%), found during the summer 2019–20. Although evidence of predation by weka was also observed on a higher proportion of tagged shells (72%) than untagged shells (56%) found during summer 2020–21 the difference was not significant (*p>0.10*).

Table 13. Comparisons of the proportions of tagged and untagged *P. hochstetteri* shells with evidence of predation by weka.

| Plot | Summer | Tagged | N. Shells | | % Weka | $p$-values | |
|---|---|---|---|---|---|---|---|
| | | | Weka | Not Weka | | Summer | Plot |
| Canaan | 2018–19 | Untagged | 6 | 21 | 22% | *0.943* | *0.742* |
| | | Tagged | 6 | 22 | 21% | | |
| | 2019–20 | Untagged | 11 | 26 | 30% | *0.196* | |
| | | Tagged | 3 | 18 | 14% | | |
| | 2020–21 | Untagged | 25 | 42 | 37% | *0.254* | |
| | | Tagged | 14 | 14 | 50% | | |
| Wainui | 2018–19 | Untagged | 59 | 68 | 46% | *Na* | |
| | | Tagged | 0 | 0 | 0% | | |
| | 2019–20 | Untagged | 163 | 110 | 60% | *<0.005* | *<0.001* |
| | | Tagged | 46 | 11 | 81% | | |
| | 2020–21 | Untagged | 98 | 76 | 56% | *0.105* | |
| | | Tagged | 23 | 9 | 72% | | |

Only two *R. oconnori* shells were found, both in the Wainui plot: an untagged shell preyed on by weka found during summer 2018–19 and a tagged shell with evidence of predation by an unidentified predator found during summer 2019–20.

Twenty-seven undamaged *P. hochstetteri* shells were placed outside of the Canaan plot to investigate shell decay rates and post-mortem damage patterns. Three of the shells disappeared during the ten month monitoring period. As weka were seen investigating the shells, it seems likely that the shells were removed by weka. Only one of the remaining shells showed any additional damage: a hole and cracks that might have been caused by a weka.

### *Comparing Size Distributions of Shells and Live Snails*

Comparisons of the size distributions of live snails and shells with and without evidence of weka predation (Fig. 11) show large differences in the patterns of *P. hochstetteri* mortality for different snail sizes in the two plots during different monitoring intervals. The size distribution of all shells found in the Canaan plot during summer 2018–19 is to right of the size distribution of live snails (Fig. 11a) indicating that mortality was highest in larger snails. The pattern is very different for shells collected during summers 2019–20 and 2020–21 (Figs. 11b & c). In both summers, a higher proportion of shells preyed on by weka were in the 30–40 mm size range and a lower proportion of undamaged shells in the 25–54 mm range. This indicates that weka preferentially preyed on middle sized snails, while mortality from other sources was highest for both small snails <25 mm and large snails >54mm.

During summer 2018–19, the size distribution of all shells found in Wainui plot (Fig. 11d) was similar to that in the Canaan plot: to right of the size distribution of live snails, indicating that mortality was highest in larger snails. The pattern was different in summer 2019–20 (Fig. 11e) with shells preyed on by weka having the same size distribution as live snails while the size distribution of undamaged shells was to right of the size distribution of live snails with few undamaged shells <48 mm. These size distribution patterns indicate weka were preying

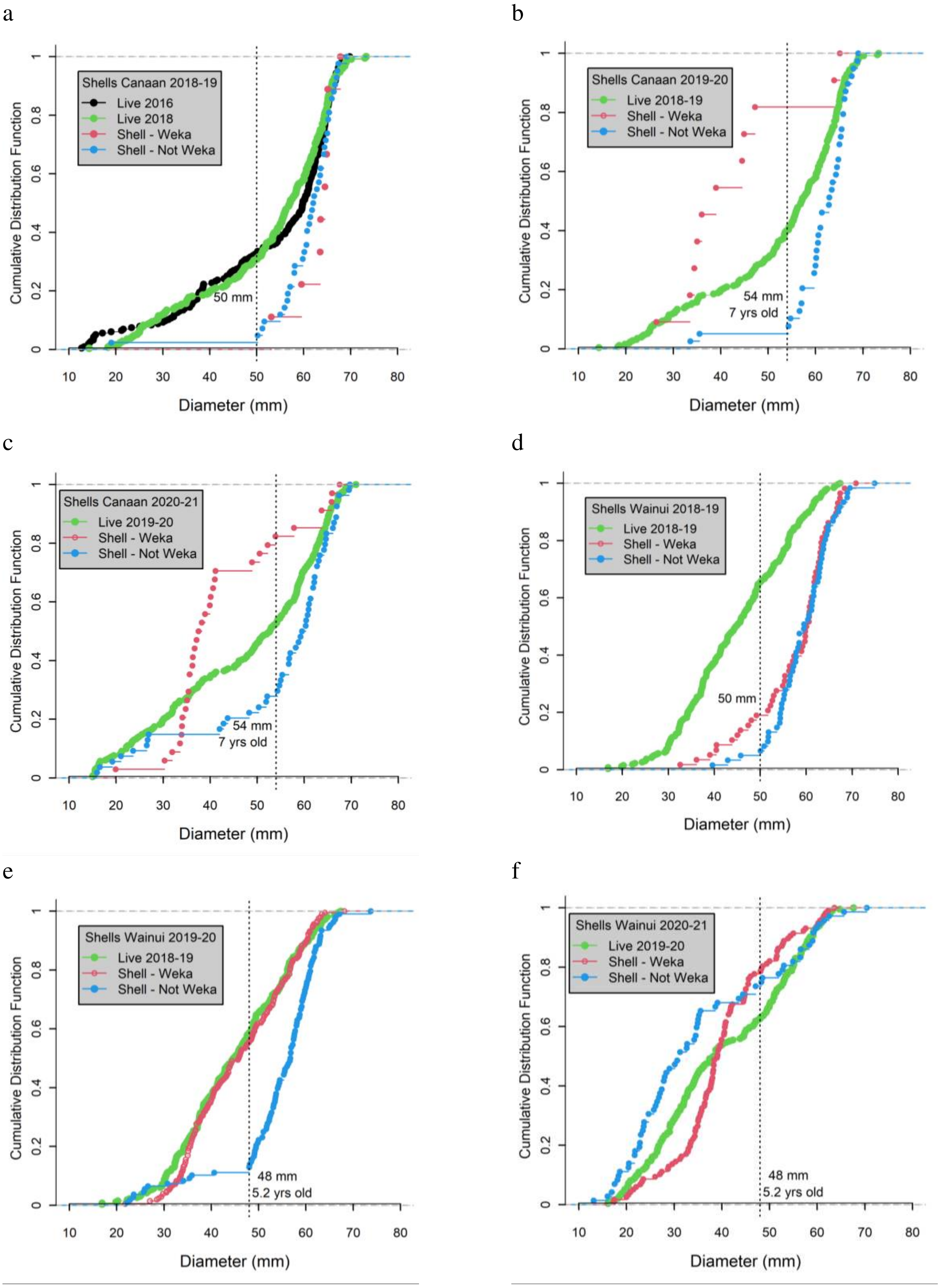

Figure 11. Empirical cumulative distribution (ECDF) plots comparing the size distributions of P. hochstetteri shells, with and without evidence of predation by weka, with the size distributions of live P. hochstetteri snails during the previous capture- recapture survey for different seasons. A-C= Canaan, D-F= Wainui.

on all sizes of snails equally while non-weka mortality was highest for large snails >48 mm. The pattern was different again in summer 2020–21 (Fig. 11f) with the size distribution of all shells close to the size distribution for live snails. The size distribution for weka preyed on shells is slightly to the left of live snails, while the highest proportion of undamaged shells is in the 30–40 mm size range.

### *Mortality Estimates*

At Canaan, annual mortality rates during the first two intervals between surveys (2016–2018 and 2018–2019) were 0.33 and 0.35, comprising weka induced mortality rates of 0.07 and 0.08, and a non-weka mortality rate of 0.26 during both intervals (Table 14). During the third interval between surveys (2019-2020), weka induced annual mortality increased by a factor of 3.2 from 0.08 to 0.27, while non-weka mortality increased by a factor of 1.44 from 0.26 to 0.38, increasing the overall annual mortality by a factor of 1.86 from 0.35 to 0.65. At Wainui, annual mortality rates were high during both intervals between monitoring seasons, with 0.72 annual mortality between 2018 and 2019, and 0.92 between 2019 and 2020 (Table 14). Annual mortality attributed to weka increased by a factor of 1.17, from 0.46 to 0.54, while mortality from other causes increased by a factor of 1.46 from 0.26 to 0.38. Changes in the non-weka mortality rates in the Wainui and Canaan plots during the 2018–2019 and 2019–2020 intervals were almost identical.

Table 14. Mortality estimates for *P. hochstetteri* calculated as ($1-\varphi$) with $\varphi$ values from Rcapture (Table 6). Mortality estimates are separated into mortality from weka predation and other mortality, using the proportion shells with evidence of predation by weka (*% Weka* ) from Table 12.

| Plot | Between-survey Period | % Weka | Annual Mortality Rate | | |
|---|---|---|---|---|---|
| | | | All | Weka | Not Weka |
| Canaan | 2016 to 2018 | 22% | 0.330 | 0.072 | 0.258 |
| | 2018 to 2019 | 24% | 0.348 | 0.084 | 0.264 |
| | 2019 to 2020 | 41% | 0.646 | 0.265 | 0.381 |
| Wainui | 2018 to 2019 | 63% | 0.719 | 0.455 | 0.263 |
| | 2019 to 2020 | 59% | 0.915 | 0.537 | 0.377 |

### *Comparing the Numbers of Shells Found and Predicted Numbers of Snails Dying*

Comparisons of the numbers of *P. hochstetteri* shells found in the plots during shell surveys (Table 11) with estimates of the number of snails that died or left the plot during the interval since the previous capture-recapture survey (Table 15) revealed a much lower detection rate of shells at Canaan (31–51%) than at Wainui (76 & 111%). The large increase in the number of shell found at Canaan at the end of the last interval (2019–20) reflects the higher mortality during the interval. At Wainui, more shells than expected deaths (111%) were found at the end of the first interval (2018–19), whereas the number of shells found at the end of the last interval (2019–20) is 76% of the expected deaths.

Table 15. Comparisons of the numbers of *P. hochstetteri* shells found in the plots during shell surveys with estimates of the number of expected deaths of *P. hochstetteri* snails during the interval since the previous capture-recapture survey. Estimates of mortality for the intervals are from robust analyses in Rcapture. Plot population estimates are from Huggins closed population analyses using the time only model with adjustments for edge-effect bias.

| Plot Interval | Initial Plot Population | | Mortality | | Expected Deaths | | Shells found | | |
|---|---|---|---|---|---|---|---|---|---|
| | N. | *(CI95%)* | *m* | *SE* | N. | *(CI95%)* | N. | % of Expected Dead | |
| Canaan | | | | | | | | | |
| 2016–2018 | 248 | *(216 – 298)* | 0.376 | *0.049* | 155 | *(120 – 190)* | 55 | 36% | *(29% – 46%)* |
| 2018–2019 | 423 | *(352 – 528)* | 0.729 | *0.068* | 115 | *(053 – 176)* | 58 | 51% | *(33% – 109%)* |
| 2019–2020 | 483 | *(405 – 597)* | 0.356 | *0.039* | 311 | *(239 – 383)* | 95 | 31% | *(25% – 40%)* |
| Wainui | | | | | | | | | |
| 2018–2019 | 421 | *(370 – 492)* | 0.296 | *0.036* | 296 | *(244 – 348)* | 330 | 111% | *(95% – 135%)* |
| 2019–2020 | 297 | *(273 – 333)* | 0.093 | *0.022* | 270 | *(240 – 300)* | 206 | 76% | *(69% – 86%)* |

## Population Trajectories

Population trajectories for *P. hochstetteri* populations in the Canaan and Wainui capture-recapture plots modelled using demographic estimates for different intervals during the study vary greatly (Figs. 12a & b). During the 2016–2018 interval, the population trajectory for the Canaan plot showed a dramatic annual population increase of 76% driven by a combination of high annual recruitment rates (1.1 per capita or 1.98 and per adult) and relatively low mortality from all sources (0.33). Weka had little effect on the trajectory: removing weka mortality only changed the annual rate of increase by 9% from 76% to 83%. Much lower annual recruitment (0.50 per capita or 0.92 and per adult) and a slightly higher mortality estimate of 0.35 for the 2018–2019 interval decreased the annual population increase in the Canaan plot to 15%. Removing weka changed the annual rate of increase by 55% from 15% to 24%. Using parameter estimates from the same 2018–2019 interval for the Wainui plot showed weka had a major effect on the population trajectory. With weka there is a 32% annual decline in the plot population trajectory, whereas without weka there is a 14% annual increase in the population. Trajectories using parameter estimates from the most recent interval (2019–2020) show annual declines populations in the Canaan and Wainui plots of 44% and 79% respectively. Removing weka predation reduces these annual declines to 17% and 25% respectively. With the levels of weka predation observed during the most recent interval (2019–2020), trajectories for the *P. hochstetteri* population in the Canaan plot show it declining to extinction within five years while the Wainui plot population will decline to extinction within two years. In the absence of weka the Canaan plot population could persist for eleven or twelve years and the Wainui population for eight or nine years.

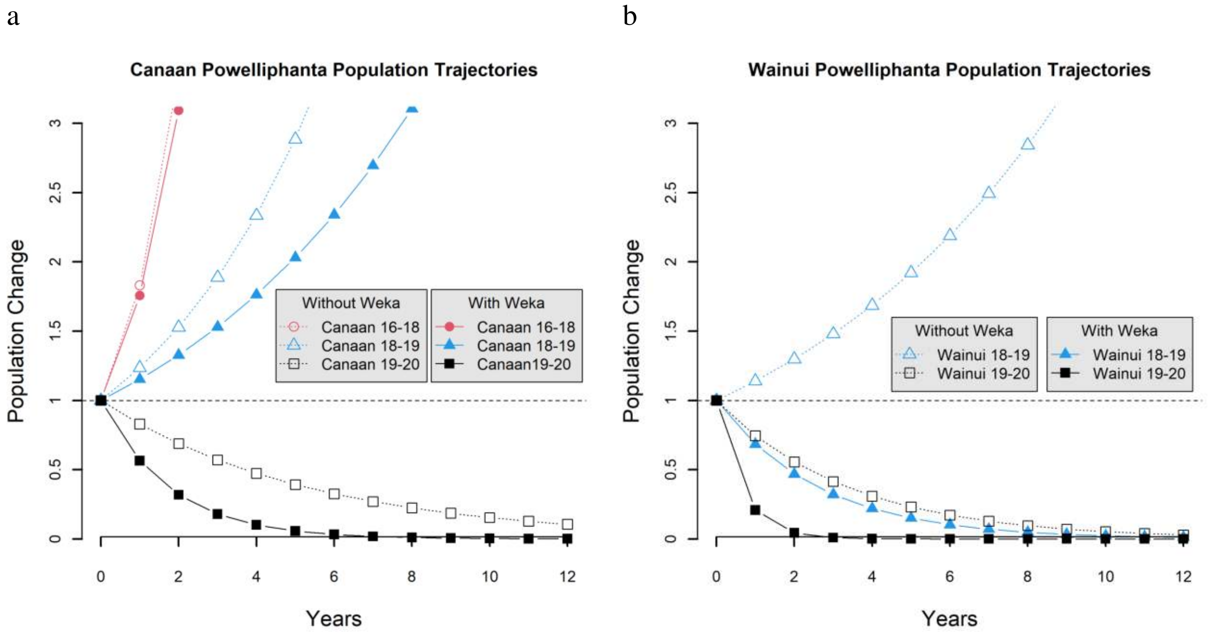

Figure 12. Population trajectories for populations of *P. hochstetteri* , with and without weka predation. The different trajectories are estimated using annual mortality and recruitment parameter estimates from Rcapture for the intervals between capture-recapture surveys in the Canaan (a) and Wainui (b) plots.

## Comparing Capture-recapture and Sub-surface Search Results

Snail density estimates from the ten sub-surface search plots near the Canaan capture-recapture plot, were significantly lower ($p<0.05$) than those from capture-recapture surveys in the plot (Figs. 13a & b and Table 16). *P. hochstetteri* density estimates from the sub-surface search method were 12%, 39% and 11% of estimates obtained using capture-recapture with the time only model adjusted for the edge effect (Table 16). *R. oconnori* density estimates from sub-surface searches during summers 2016–17 and 2018–19 were 8% and 23% of the capture-recapture estimates. During summer 2020–21, no *R. oconnori* ≥15 mm were found during sub-surface searches, whereas the capture-recapture estimate for *R. oconnori* was 2.85 snails$^{-1}$ 100m$^{2}$. Including snails <15 mm in density estimates from the sub-surface search method only reduced the differences between density estimates slightly to 25%, 44% and 18% for *P. hochstetteri* and 8%, 29% and 7% for *R. oconnori*.

Population trends obtained using the two methods were very different (Fig. 13 & Table 17). Sub-surface trend estimates with snails ≥15 mm diameter were 614% (2016–18) and 258% (2018–20) of capture-recapture estimates for *P. hochstetteri*, and -316% (2016–18) and 444% (2018–20) for *R. oconnori*. With snails <15 mm diameter included in the sub-surface search results, sub-surface trend estimates were 283% and 230% of capture-recapture estimates for *P. hochstetteri*, and 473% and 355% for *R. oconnori*.

Comparisons of the size distributions of live snails found using the two methods (Figs. 14a & b) show that the two methods sampled very different size components of the snail population, with significantly higher proportions of large snails of both species caught during capture-recapture surveys than during sub-surface searches. Significance levels were $p<0.001$ for *P. hochstetteri* and $p<0.05$ for *R. oconnori*. The effect is more pronounced for *P. hochstetteri* with 79% (557 of 704) of snails caught during the three capture-recapture sessions had diameters >37 mm at first capture, compared to 21% (6 out of 29) of snails found during sub-surface searches in summers 2016–17 and 2018–19.

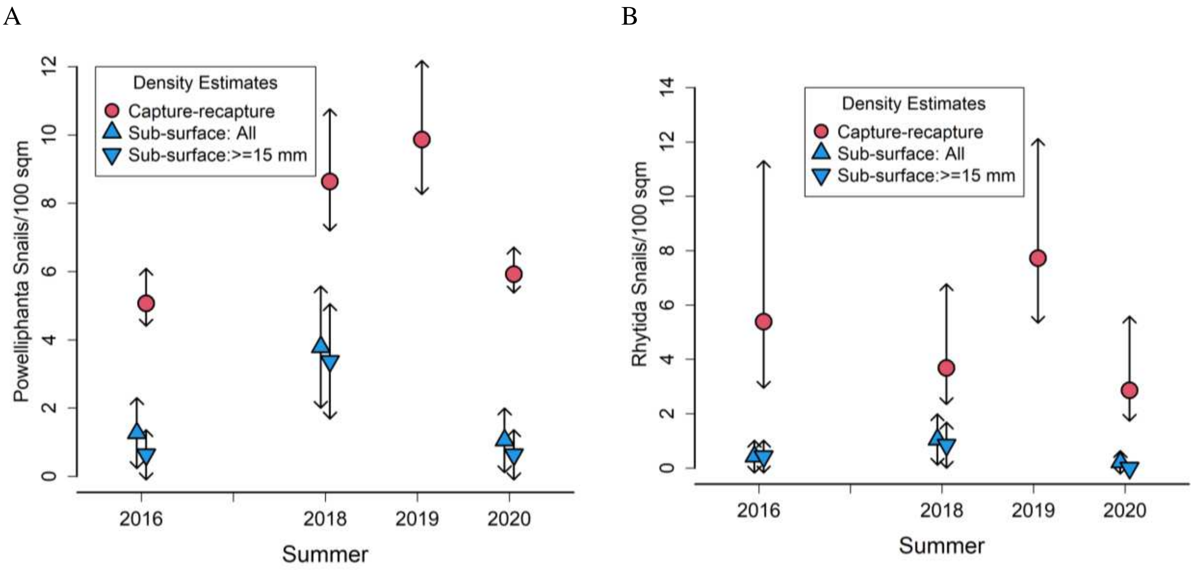

Figure 13. Comparisons of density estimates of *P. hochstetteri* (a) and *Rhytida oconnori* (b) at Canaan obtained using capture-recapture and sub-surface search methods. Capture-recapture estimates are from the 4,900 $m^2$ capture-recapture plot, while estimates from the sub-surface search method are from ten nearby sub-surface search plots, which have a combined area of 475 $m^2$. Density estimates for *P. hochstetteri* are adjusted using the edge-effect adjustment.

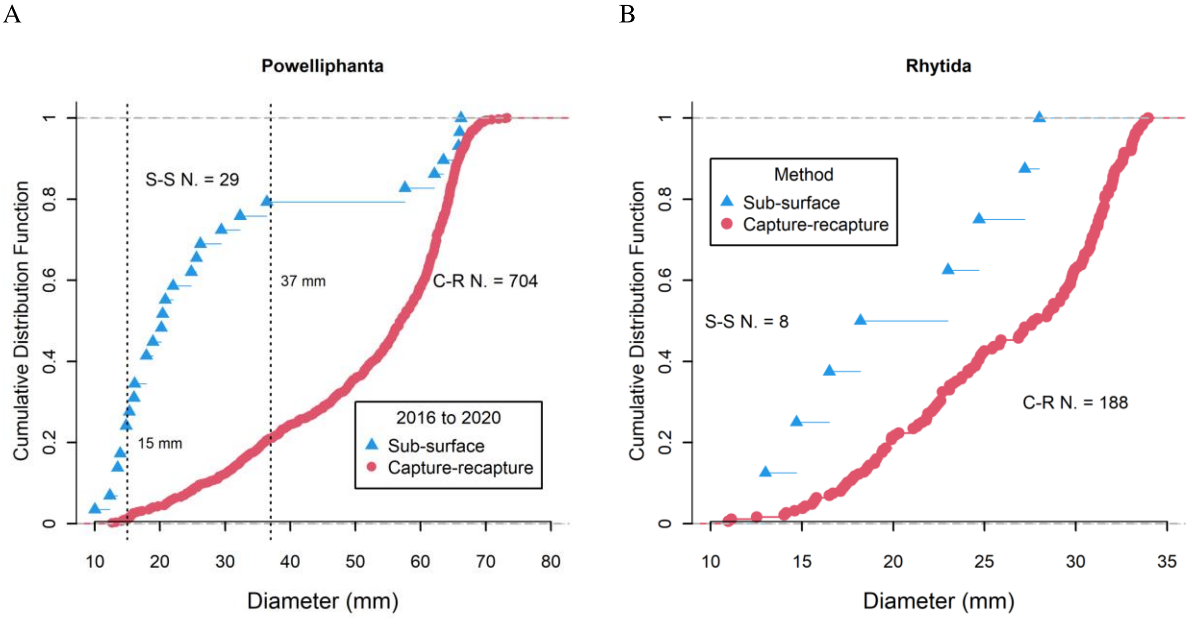

Figure 14. Empirical cumulative distribution plots comparing the size distributions of live *Powelliphanta* (a) and *Rhytida* (b) snails found in the course of capture-recapture surveys at Canaan and sub-surface searches of ten nearby plots during summers 2016-17, 2018-19 and 2020-21.

Table 16. Comparisons of population density estimates from capture-recapture surveys at Canaan with the results of sub-surface searches in ten nearby plots during three summers: 2016-17, 2018-19 and 2020-21. The results of sub-surface searches are presented with snails <15mm diameter both excluded and included. Density estimates for *P. hochstetteri* from capture-recapture surveys are adjusted using the edge-effect adjustment. The estimate *CI/Est.* is the width of *CI95%* as a percent of the density estimate and estimate *Ratio SS/CR* is the ratio of density estimates from subsurface searches and capture-recapture.

| | Density Estimate (Snails$^{-1}$ 100m$^2$) | | | | | | | Difference (SS/CR) |
|---|---|---|---|---|---|---|---|---|
| | Sub-surface Search (SS) | | | | Capture-recapture (CR) | | | |
| | N | Est. | *(CI95%)* | CI/Est. | Est. | *(CI95%)* | CI/Est. | |
| *Powelliphanta* | | | | | | | | |
| Excl. <15mm | | | | | | | | |
| 2016-17 | 3 | 0.63 | *(-0.1 – 1.4)* | 231% | 5.06 | *(4.4 – 6.1)* | 33% | 12% |
| 2018-19 | 16 | 3.37 | *(1.7 – 5.1)* | 100% | 8.64 | *(7.2 – 10.8)* | 41% | 39% |
| 2020-21 | 3 | 0.63 | *(-0.1 – 1.4)* | 231% | 5.92 | *(5.4 – 6.7)* | 22% | 11% |
| All sizes | | | | | | | | |
| 2016-17 | 6 | 1.26 | *(0.23 - 2.29)* | 163% | | | | 25% |
| 2018-19 | 18 | 3.79 | *(2.00 - 5.58)* | 94% | | | | 44% |
| 2020-21 | 5 | 1.05 | *(0.11 - 1.99)* | 179% | | | | 18% |
| *Rhytida* | | | | | | | | |
| Excl. <15mm | | | | | | | | |
| 2016-17 | 2 | 0.42 | *(-0.2 – 1.0)* | 283% | 5.39 | *(2.9 – 11.3)* | 155% | 8% |
| 2018-19 | 4 | 0.84 | *(0.0 – 1.7)* | 200% | 3.68 | *(2.3 – 6.8)* | 120% | 23% |
| 2020-21 | 0 | 0.00 | *(0.0 – 0.0)* | | 2.85 | *(1.7 – 5.6)* | 135% | 0% |
| All sizes | | | | | | | | |
| 2016-17 | 2 | 0.42 | *(-0.17 – 1.02)* | 283% | | | | 8% |
| 2018-19 | 5 | 1.05 | *(0.11 – 1.99)* | 179% | | | | 29% |
| 2020-21 | 1 | 0.21 | *(-0.21 – 0.63)* | 400% | | | | 7% |

Table 17. Comparisons of population trends estimated from capture-recapture surveys at Canaan and sub-surface searches in ten nearby plots for the two intervals between summers 2016–2017, 2018–2019 and 2020–2021. Population trends are estimated as: $(N_{t+1} / N_t) - 1$.

| Interval | Estimates of Population Trends | | | | Diff SS/CR |
|---|---|---|---|---|---|
| | Sub-surface Search (SS) | | Capture-recapture (CR) | | |
| | Est. | *(CI95%)* | Est. | *(CI95%)* | |
| *Powelliphanta* | | | | | |
| Excl. <15mm | | | | | |
| 2016 to 2018 | 433% | *(310% – 557%)* | 71% | *(34% – 117%)* | 614% |
| 2018 to 2020 | -81% | *(-205% – 42%)* | -31% | *(-54% – -09%)* | 258% |
| All sizes | | | | | |
| 2016 to 2018 | 200% | *(108% – 292%)* | | | 283% |
| 2018 to 2020 | -72% | *(-171% - -27%)* | | | 230% |
| *Rhytida* | | | | | |
| Excl. <15mm | | | | | |
| 2016 to 2018 | 100% | *(-70% – 270%)* | -32% | *(-123% – 60%)* | -316% |
| 2018 to 2020 | -100% | | -23% | *(-107% – 62%)* | 444% |
| All sizes | | | | | |
| 2016 to 2018 | 150% | *(-14% - -314%)* | | | -473% |
| 2018 to 2020 | -80% | *(-295% - 135%)* | | | 355% |

# DISCUSSION

## Discussion of Methods

### *The Impact of Capture-recapture Field Work on Snails*

Ecological research can have detrimental effects on the study subjects especially when research involves capture and marking of individuals [56-59]. A study of the impact of different marking techniques on hard-shelled gastropods [59] concluded that marking gastropods with plastic tags attached using cyano-acrylate glue had no effect on their life history traits. However, it has been reported that using cyano-acrylate glue to attach tags to *Powelliphanta* snails increases the risk of tagged snails being preyed on by rats [60]. In our study, cyano-acrylate glue was used to attach tags to 1700 snails (i.e. more than 20% of the snails present in the plots during the study). Despite relative high rat abundance index levels during the study period (Fig. 3) only five *P. hochstetteri* shells out of 878 (including 180 tagged shells) showed evidence of predation by rodents (Table 11). Because so few snails were preyed on by rats, our study results does not provide conclusive information on whether using cyano-acrylate glue to tag snails increases the risk of rat predation.

The proportions of tagged and untagged shells with evidence of predation by weka were not significantly different ($p>0.1$) at Canaan, but were significantly different ($p<0.001$) at Wainui (Table 13). The significantly higher proportion of tagged shells with evidence of weka predation at Wainui indicates that tagging might have increased the risk of predation by weka at Wainui. This could be because the tags disrupt crypsis, but this seems unlikely as the tags are attached to the snail's ventral surface, which is not visible during daytime when snails are sheltering below ground cover, and will not be visible in the dark when the snails are active on the surface. Concurrent, but coincidental, increases in weka predation pressure and the proportion of tagged shells at Wainui during the period between the 2018–19 and 2020–21 provides a more plausible explanation for the higher proportion of tagged shells with evidence of weka predation found at Wainui. Some of the untagged shells in the collection will be from snails that died before or just after tagging began in summer 2018–19 when fewer shells showed evidence of weka predation (i.e. 46% *cf.* 63% and 59%). Their presence will depress the proportion of untagged shells with evidence of weka predation compared to tagged shells which will have all died recently, during a period with a high weka predation rate.

There has been controversy over the use of the capture-recapture method to monitor snail populations, because it was thought that there is more risk of field workers trampling snails during nocturnal capture-recapture surveys population surveys than during the standard sub-surface searches [10]. Results of a radio-tracking study of *P. hochstetteri* [36] indicate that this is not the case, as the greatest risk of trampling by field workers is during the daytime, when many snails are hidden under a light covering of leaf litter or moss. However, repeated searches during capture-recapture field work coupled with daytime searches for shells on the plots provide opportunities to detect and document trampling by field workers not provided by the sub-surface search method. Only one of 208 shells found at Canaan (0.5%) and 13 of 670 shells (2%) found at Wainui showed evidence of trampling (Table 11), with many of the trampled shells looking old and decayed. Three live snails at Wainui showed fresh cracks in their shells, which may been a result of trampling. Trampling could have been by field workers, during either night-time or daytime searches, or by ungulates. Although the impact of trampling is minor it is undesirable, but unavoidable whenever field work is undertaken in areas with snails. Trampling also has a detrimental effect on vegetation and habitat quality, which can reduce snail populations [61].

### *Tag Loss*

Absence of tag loss is a fundamental assumption in capture-recapture analyses. If the assumption is violated, parameter and standard error estimates will be biased [59, 62, 63]. In the context of capture-recapture studies, tag loss is loss of a marked individual's identity. In this study tag loss can occur in three ways: the tag dropping off; the tags being damaged and becoming unreadable; and the tag being overgrown as a new shell whorl overlays the tag. Information collected to date indicates that tag loss caused by tags dropping off or being damaged is extremely rare even over long periods of several years, whereas tag loss caused by tags being overgrown over a period of years as new shell whorl overlay the tag is inevitable for snails that are tagged while they are still growing rapidly (i.e. <60 mm diameter for *P. hochstetteri* and <30 mm diameter for *R. oconnori*).

Tag loss from tags being overgrown will be a serious issue for open-population analyses using information from multiple capture-recapture sessions, where there may be several years between recaptures of tagged individuals. In open-population analyses and robust analyses, undetected tag loss from overgrown tags will lead to inflated between-session mortality estimates.

Population size estimates in this study are from closed population analyses, using information from individual capture-recapture surveys. These estimates will not be affected by tag loss, because tag loss during the three to five weeks of capture-recapture surveys will be negligible or non-existent. Similarly, demographic estimates from robust population analyses used in this study are unlikely to be significantly affected by the low level of tag loss likely during the intervals between successive surveys, which ranged between 0.7 and 2.4 years.

Information from double tagging can be used during capture-recapture analyses to correct for tag loss [63-65]. Unfortunately, the sample of recaptured double tagged snails during this study (13 out of 38) is too small to provide quantitative estimates of tag loss required for correcting parameter estimates. However, there is no evidence of tag loss to date. During future capture-recapture sessions, random samples of individual snails should be double tagged to obtain reliable quantitative information on rates of tag loss, especially tag overgrowth. Double tagging should be both at first-capture and on recapture by adding extra tags to previously tagged snails. When snails are double tagged, the tags should be attached at slightly different distances from the aperture. Tags on single tagged snails should be attached as close as possible to the aperture, to delay tag overgrowth. The use of miniature passive radio-frequency identification (RFID) tags [66] instead of numbered plastic tags should be investigated, as RFID tags would remain readable when overgrown. However, no suitable RFID tags have been identified yet.

### *Influence of Capture Probabilities on Capture-recapture Population Estimates*

A simulation study investigating the influence of different factors on the precision and accuracy of *P. hochstetteri* population estimates from open population capture-recapture analyses with the time only model concluded that capture probability had the largest influence on precision and accuracy of population estimates [27]. Results from capture-recapture sessions at Canaan and Wainui confirm the importance of achieving high capture-probabilities for obtaining precise population estimates of both species (Tables 2 & 3). The the precision of population estimates[1] declined rapidly when session capture probabilities dropped below 0.20. The precision of nine of the 14 population estimate were acceptable, with CI95% widths ≤53% of the population estimates, but precision of *R. oconnori* population estimates from all four sessions at Canaan and the last session at Wainui were poor, with CI95% widths between 88% and 155% of the population estimates (Table 3). Presumably this is a consequence of low capture probabilities (0.05 – 0.12) for *R. oconnori* during these sessions (Table 2).

Results of a radiotelemetry study of *P. hochstetteri* [36] and an analysis of the influence of environmental factors on *P. hochstetteri* and *R. oconnori* capture probabilities during the first capture-recapture session at Canaan [17] show, for both species, surface activity, and hence capture probabilities, are highest on warm moist nights with temperatures >8°C and relative humidity >90%. More recent observations indicate that activity levels of both species are highest immediately after the onset of suitable conditions following a period of adverse conditions. Also, while *P. hochstetteri* remain active during heavy rain, *R. oconnori* surface activity declines markedly at the onset of rain. Consistently low capture probabilities for *R. oconnori* at Canaan might be a consequence of the plot habitat, not environmental conditions, with some *R. oconnori* active in the karren where they cannot be found.

The relationship between the precision of population estimates and capture probabilities [27] underscores the importance of scheduling capture-recapture searches for nights when snail activity levels are high. This requires both identifying suitable environmental conditions and predicting nights when they are likely to occur.

### *Selecting Best-fit Models for Growth Curves*

A study comparing how three different growth models (logistic, Gompertz and von Bertalanffy) fitted growth data in captive *P. augusta* [54] concluded that the logistic model was the best-fit model, followed by the Gompertz model, and that the von Bertalanffy model was the poorest fit. Their conclusion is flawed because the regression being modeled should be instantaneous growth rate versus size, not observed growth between two size measurements. The time intervals between successive diameter measurements are finite, consequently the observed growth between pairs of size measurements used in the regressions underestimates the instantaneous growth rate [33]. The magnitude of underestimation increases with the length of the time interval between measurements, but is largest when the first diameter measurement is small. The main difference between the three

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[1] Precision expressed as the width of CI95% around a population estimate as a percentage of the estimate.

growth models in the comparison is that smaller individuals grow more slowly with the logistic and Gompertz models than the von Bertalanffy model [67]. Thus, better fit of the logistic and Gompertz models is because underestimation of the instantaneous growth rate is most severe for small snails. To overcome this problem, we used Equation 4 from Yagamuchi (1975) [33] to obtain an estimate of the actual growth-rate parameter ($K$) from the observed growth rate parameter ($K_{Obs}$) provided by the regression of observed growth rate versus initial diameter. Another source of error in the study [54] was introduced by using the regressions for the three growth models to estimate asymptotic size separately for the three models [54], instead of using the observed asymptotic size. None of the asymptotic size estimates obtained from the regressions (logistic 38.7 mm; Gompertz 40.9 mm; & von Bertalanffy 48.4 mm) are close to the observed maximum diameter size of 44.3 mm in *P. augusta* [68]. Our own comparisons of the three growth models showed that differences between them were insignificant when the same parameter values were used in all three models.

### *Shell Surveys and Mortality Estimates*

It is unrealistic to expect to find the shells of all snails that die between capture-recapture surveys: snails can die underground, shells can wash away, small shells will decay rapidly, and shells may be hidden under windfalls. However, at Wainui, more shells than expected were found at the end of the first interval between capture-recapture surveys (Table 15). This is probably because some of the shells from snails that died before the first capture-recapture survey were not found during the first shell survey, but were subsequently found during the second shell survey. At Canaan many fewer shells than expected were found during all three shell surveys (Table 15). It is likely that the many snails die underground in the karst crevices, where they cannot be found. If this is the case, weka predation rates in the Canaan plot might be overestimated, as shells preyed on by weka will be on the plot surface, where they can be found easily.

## Population Trends

Results from the study provide comprehensive and reliable information on snail population trends in the two capture-recapture plots during the monitoring periods. Population estimates from time only models with edge-effect adjustment are used for *P. hochstetteri* (Table 4), but estimates without edge effect adjustment are used for *R. oconnori* (Table 3).

The *P. hochstetteri* population in the Canaan plot increased by ≥20% per annum during the first three years of the study, rising from an estimated 248 snails (CI95%: 216–298) in 2016 to 483 (CI95%: 405–597) in summer 2019–20 (Table 46). However during the final year of the study, the plot population declined by 40% to 290 (CI95%: 264–329) in summer 2020–21. The population decline was a consequence of significant reductions in both survival and recruitment rates (Table 6 & 7). Information from shell surveys indicate that the reduction in the survival rate is a result of large increases in both weka induced mortality, from 0.07 and 0.08 to 0.27, and non-weka mortality, from 0.26 to 0.34 (Table 14). The overall annual mortality rates went from 0.33 and 0.35 to 0.65 during the last year of the study. The size distribution of live *P. hochstetteri* found during the first survey at Canaan, showed an even spread of all sizes (Fig. 9a), consistent with a stable population. Over the next three years, there was a shift in the size distribution with a greater proportion of smaller snails present in the plot, presumably as a result of young snails being recruited to the expanding population. During the final year of the study, recruitment declined (Table 7) and the size distribution shifted very slightly towards a higher proportion of large snails.

To what extend karst might provide protection for snails needs further investigation. The steep decline of snail populations at Canaan during the last interval and the results from the shell survey suggest that weka predation is drawing level with Wainui. However, as discussed above, it is yet unclear if weka predation rates are over estimated due to the karst environment.

The population estimate for *P. hochstetteri* snails in the Wainui plot during the first capture-recapture survey in summer 2018–19 was 421 (CI95%: 370–492). The high numbers of *P. hochstetteri* snails and relatively high proportion of smaller snails (Fig. 9b) in the Wainui plot during summer 2018–19 indicate that the *P. hochstetteri* population had been increasing during the preceding four to five years. As this corresponds to the period when Project Janszoon's intensive pest control began, it seems likely that the population increase was a response to the success of pest control in reducing densities of two major predators of land snails: possums and rats. During the two years since the first survey of the Wainui plot, there have been annual declines of 30% and 77% in the *P. hochstetteri* population, resulting in the most recent plot population estimate of only 68 snails (CI95%: 59–88) for summer 2020–21. Information from shell surveys indicate that the declining population is primarily driven by high levels of weka predation, with weka induced annual mortality rates of 0.45 and 0.54 during the two intervals between surveys of the Wainui plot (Table 14). However, effect of weka predation was augmented by relatively high levels of annual mortality from other sources (i.e. 0.26 and 0.38) leading overall annual mortality rates of 0.72 and 0.92 during the last two years.

Modelled population trajectories for *P. hochstetteri* populations in both plots show that with current demographic trends both populations will decline to extinction within a few years (Figs. 12 a & b). At Canaan the plot population will approach extinction within 5 years, while at Wainui the plot population will approach extinction within two years.

Because of wide confidence intervals around population estimates for *R. oconnori* at Canaan, there is considerable uncertainty about population trends in *R. oconnori* at Canaan (Fig. 6b and Table 3a). Population estimates for *R. oconnori* at Canaan fluctuated widely during the monitoring period, decreasing from 264 (CI95%: 144–554) in 2016, to 180 in 20018–19, then increasing to 378 in 2019–20, before decreasing again to 140 (CI95%: 85–274) in the final 2020–21 survey. There appears to be rapid turnover in *R. oconnori* at Canaan with high annual adult mortality (Table 6) in most intervals and high recruitment rates during some intervals

The population estimates for *R. oconnori* in the Wainui plot declined during both intervals between surveys; declining from 241 (CI95%: 194–319) in 2018–19, to 131 (CI95%: 107–176) in 2019–20 and then 120 (CI95%: 80–213) in 2020–21. During the last interval between surveys, low survival rates were partly offset by a high recruitment rate (10 snails per adult) reducing the magnitude of the decline. Although there is no direct evidence for the cause of the decline in *R. oconnori* in the Wainui plot, because of the similarity with the decline in the *P. hochstetteri* plot population, it seems likely that it is also a consequence of predation by weka.

## Weka as a Threat to Conservation Objectives

Weka, a large (700–1000g) indigenous flightless rail, are a known predator of *Powelliphanta* and, in pre-human NZ, were probably the taxon's main predator [3]. Results from this study suggest that the burgeoning weka population in Abel Tasman National Park constitute a major threat to populations of *P. hochstetteri* and *R. oconnori* snails in the park.

Weka populations are subject to dramatic fluctuations [69]. A range of factors have been implicated as contributing to declines in weka populations, including: disease, competition, non-target poisoning, drought and starvation [70]. But predation by introduced mammalian predators, in particular stoats and ferrets, appears to be the main cause of the declines [69, 71-74]. There were catastrophic declines in weka populations in Abel Tasman National Park and surrounding regions during the late 1980's and early 1990's [69]. Weka numbers in the region remained low for many years, but have increased markedly in recent years. Bird distribution monitoring carried out over a large area of the park suggests that weka expanded their distribution rapidly and are now present all over the park (Fig. 15). Results from annual bird counts along line transects in the Wainui area of Abel Tasman National Park during the period 2013–16 (Peter Gaze unpublished) show that weka were absent from the Wainui valley during 2013 & 2014; first appeared in 2015 and were widespread by 2016. Bird surveys elsewhere in Abel Tasman National Park showed the area occupied by weka tripled over a three year period (2016–18). Weka counts undertaken during 2020 using call playbacks showed no difference between weka densities at Canaan and Wainui (R. Bollongino unpublished), but no information is available about weka numbers at Canaan from previous years.

Although weka were translocated to the Abel Tasman National Park in 2006, the burgeoning weka populations in the park and surrounding areas is probably a response to reduced mustelid numbers resulting from increased predator control in the park and surrounding areas. Intensive mustelid control throughout Abel Tasman National Park began in 2013 with establishment of an extensive stoat trapping network throughout the park. Since 2014, there have also been regular pest control operations with aerial broadcast 1080 poison in cereal baits across large areas of the park to reduce numbers of possums and rats. Broadcast 1080 poison also reduce mustelid numbers by secondary poisoning [75]. Over the same period, there has also been a proliferation of local site-based pest control projects in the wider region around the park.

The results of recent *Powelliphanta* snail surveys in the Golden Bay region [52] show that weka are now the snail's main predator over a much wide area than Abel Tasman National Park. Ogle (2019) [52] reported that 14% of 814 shells found during searches of 20 plots in 2018 showed evidence of predation by weka, compared to 10% with evidence of predation by rats. Detailed examination of the results shows that weka predation pressure is higher in snail plots away from the west coast. With results from west coast plots removed from the data, 32% of 358 shells showed evidence of predation by weka, compared to 20% with evidence of predation by rats. The proportion of shells with evidence of weka predation tended to be highest in areas with predator control, with the proportion of weka damaged shells reaching 77% of 26 and 78% of 18 shells on two plots.

When food is plentiful and in the absence of predation, weka populations can increase rapidly, raising four clutches a year, with up to 6 eggs per clutch, and young can breed at 5-months old [70]. It is possible that the current abundance of weka is temporary, part of normal population cycle, but this seems unlikely as there is no reason to expect local weka population will collapse as long as mustelid numbers are being controlled effectively.

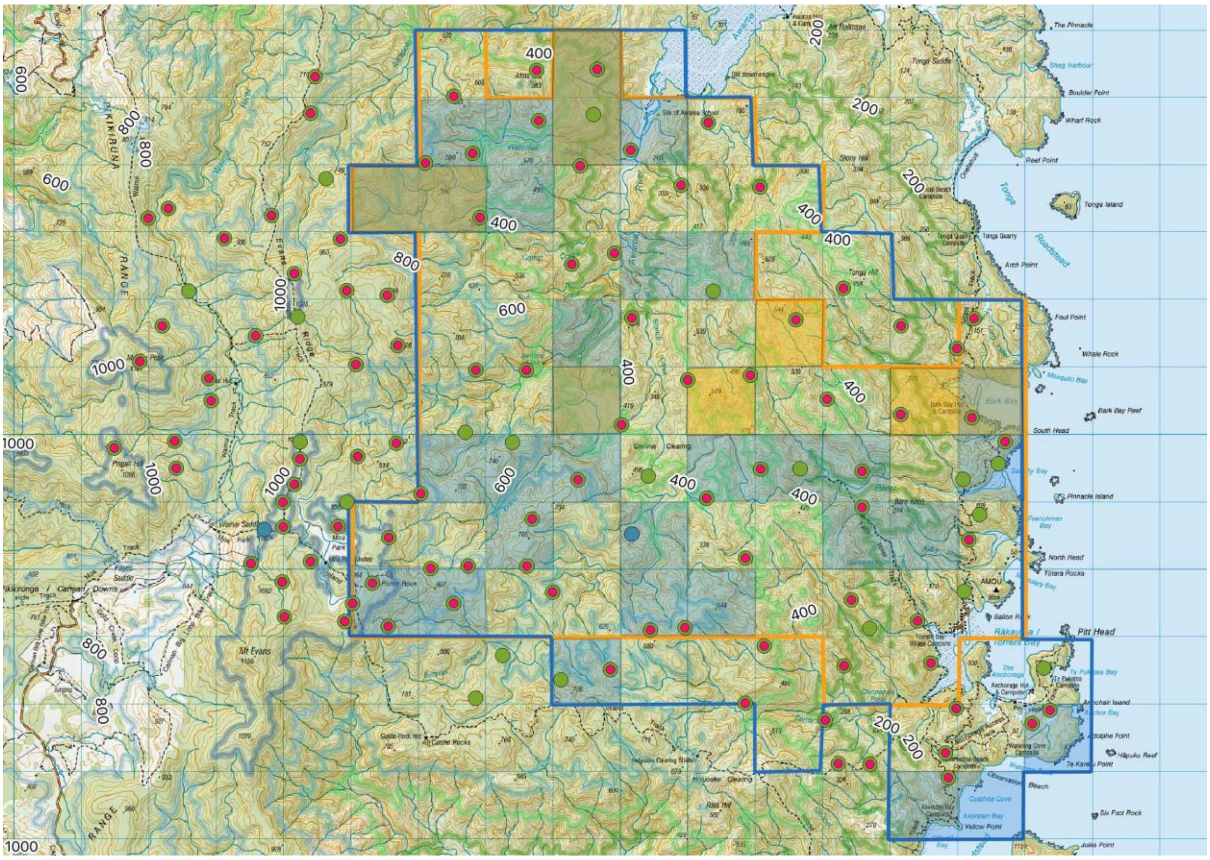

Figure 15. Minimal distribution monitoring of weka in the Abel Tasman National Park 2015-2019. Initially, walk-through surveys were carried out in 2015 and 2018 (orange and blue outlines, respectively). Observers spent app. one hour within each 1km square grid. Squares in which weka were detected are highlighted in orange (2015) and blue (2018). Monitoring shifted to acoustic recording in 2019. Recorder locations are shown as green dots, red dots indicate locations were weka were detected (listening to 45 secs in the morning and 45 secs in the evening over a 2-week period, Bollongino in prep.). The map shows that weka recolonized the are completely within a few years.

Weka are omnivorous and predatory. Their diet consists mostly of fruit and ground-dwelling invertebrates, but includes reptiles, small mammals and the eggs and young of ground nesting birds [70]. The species plays important roles in ecosystems, as a predator and seed disperser [76]. However, it is generally accepted that weka's predatory behaviour can compromise conservation of other threatened species [69, 77, 78] and as a consequence have been removed from several offshore island nature reserves. In the absence of predators, weka densities can reach more than one bird per hectare [69]. If weka reach this density throughout Abel Tasman National Park, they will have profound effects on range of native species currently in the park and compromise future translocations to the park. Species likely to be affected by weka depredations include: ground-dwelling invertebrates, reptiles, ground-nesting birds (e.g. kiwi *Apteryx sp*., kea *Nestor notabilis*, seabirds, waterfowl like whio *Hymenolaimus malacorhynchos* and pāteke *Anas chlorotis* and species with pre-fledging young that spend time on the ground (e.g. kaka *N. meridionalis*, parakeets *Cyanoramphus sp.* and short-tailed bats *Mystacina tuberculata*).

It can be argued that weka and *Powelliphanta* coexisted in pre-human New Zealand. However, it seems likely that in the absence of predation by mustelids contemporary weka populations can reach higher densities than in pre-human New Zealand, because native species that preyed on, or competed with, weka are now extinct. Also rodents now provide a substantial additional food source not present in pre-human New Zealand. The impact of weka is also exacerbated by predation pressure from exotic animal species (possums, rodents, hedgehogs, pigs, thrush and blackbirds) and habitat degradation as a result of both browsing by introduced mammals and climate change.

In the Weka Recovery Plan [69], it is suggested that problem weka populations should be managed in the interests of both weka and other threatened species, without providing strategies or examples, other than removing weka from offshore islands. Options for managing weka in Able Tasman National Park are limited. Controlling weka numbers by trapping, shooting or poisoning is likely to be unpalatable to broad sections of the community, and will need to be ongoing because of reinvasion and high recruitment rates. A number of fenced weka exclusion plots spread across ATNP could provide a temporary solution to ensure survival of representative samples of the park’s snail populations.

## Rats as Predators of Snails

Rats are another known introduced predator of *Powelliphanta* and *Rhytida* snails [3, 9, 28, 52]. The rarity of live snails in low altitude (<600 m) areas of Abel Tasman National Park, where rats are most abundant, and high incidence of shells with evidence of rat predation at mid-altitudes, has been interpreted as evidence that rats are suppressing snail populations in these areas [1, 2]. However, there was negligible evidence of rat predation on the *P. hochstetteri* shells found in the two capture-recapture plots (Table 11). The small numbers of *R. oconnori* shells found provide no information on rat predation, but there is no reason to expect major differences between rat predation on the two snail species. It is possible that rats and mice (*Mus musculus*) prey on snail eggs and very young snails, leaving no trace, but if this is the case snail recruitment rates could be expected to be lower than observed (Table 7). The low level of rat predation observed in the two plots, despite relatively high rat index levels (Fig. 3) is unexpected and difficult to explain. This is especially true because our monitoring included the period following a rat irruption when beech seed, the staple food fuelling rat irruptions, germinate and rats are left hungry. The current lack of evidence for rat predation does not exclude that this behaviour will change in the future.

## Other Factors Contributing to the Decline of the Snail Populations

Increases in non-weka induced mortality during the interval between last two surveys (2019–20 and 2020–21) at both sites indicate that factors other than weka have contributed to recent snail population declines. The most likely factor is drought. The last three summers in Abel Tasman National Park have been exceptionally dry, with the highest values for soil moisture deficit (Fig. 15) since data collection began in 1995.

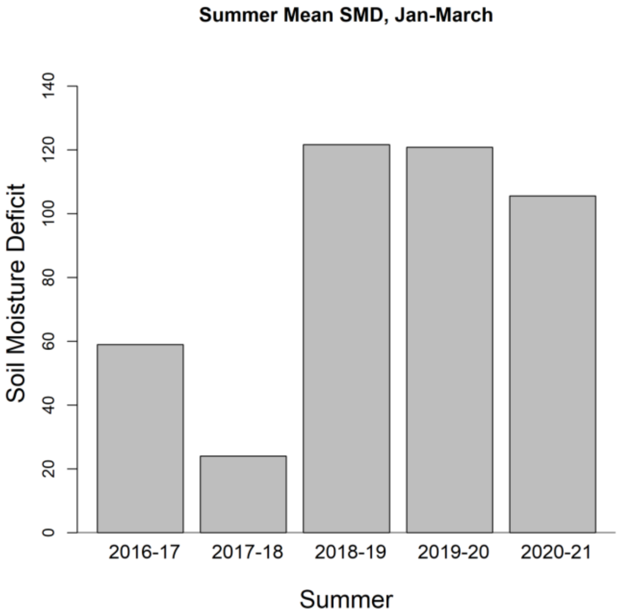

Figure 16. Mean Soil Moisture Deficits (SMD) for summers (January to March) since capture-recapture surveys began at Canaan (based on data retrieved from NIWA).

Summer rainfall, is crucial for the activity and growth of terrestrial snails. During dry periods, terrestrial snails pause their activity and go into aestivation to retain body moisture [35]. Extended aestivation during long dry periods can result in death due to starvation or desiccation. Other observations consistent with the negative impact of recent summer droughts on *P. hochstetteri* are:

- The observed slower snail growth rates for *P. hochstetteri* at Wainui and during the last interval at Canaan (2019–20 to 2020–21) compared to growth during the first two intervals at Canaan (i.e. from 2016–18 to 2019–20). Growth in terrestrial snails varies adaptively and is a plastic trait with growth rates affected by a range of factors including: temperature, moisture, nutrition and population density [34, 37, 79-82].
- Declines in condition indices for *P. hochstetteri* over time (Fig. 8a & Table 10).
- Increased numbers of snails with growth abnormalities found during recent surveys (R. Bollongino pers. obs.).
- Increases in the proportions of small shells found with no sign of predation. Small snails have a lower resilience to drought [83], because they have lower volume to surface ratio than large snails.

Although extreme drought events have always occurred occasionally it seems likely that the recent dry periods is a result of climate change as the recent prolonged summer drought conditions are unprecedented during the 35 years since conditions have been recorded.

## Comparing Capture-recapture and Sub-surface Search Methods

There were large differences between estimates of population densities and population trends obtained from capture-recapture and the sub-surface search method in the Canaan plots. Density estimates from sub-surface searches carried out during three summers were all considerably lower than those from capture-recapture for both species and in all years (Figs. 13a & b, and Tables 16 & 17). Including snails <15 mm in the sub-surface density estimates only reduced differences between estimates slightly.

Differences between estimates from the two methods are to be expected, because the sub-surface search method does not provide actual density estimates, it provides indices in the form of snail counts per plot. Index methods rely on the assumption that the indices are proportional to actual population densities for comparisons between populations and for population trend monitoring [84]. Results from this study indicate the assumption is not warranted, as indices from the sub-surface methods ranged between 11% and 39% of population estimates for *P. hochstetteri* and 0% and 23% for *R. oconnori*. The results of a study using repeated destructive plot searches [85] also indicate that the assumption that snail counts from sub-surface searches and population densities are correlated is flawed. In destructive searches of fourteen ten-meter square plots, the proportions of snails found during standard sub-surface searches of the plots and the final tally of snail found in the plots ranged widely between 8% and 56%. This range is likely to be an underestimate the extent of variability, as population indices from the sub-surface search method will be subject to biases from numerous sources including local habitat structure, current and previous weather conditions, seasonal changes in snails' behaviour and the skill and motivation of field workers. The destructive searches in the study were undertaken by a single team of searchers, in a narrow range of habitats, during a short period with little variation in weather conditions, thus the results probably underestimate the range of the differences between snail counts and number of snails in a plot likely to be encountered when sub-surface searches are used as wide-scale monitoring method.

Differences between size distributions of the snails found using capture-recapture and the sub-surface search method in the Canaan plots (Figs. 14a & b) is more concerning than the discrepancies between density and trend estimates from the two methods because age distributions derived from size distributions provide crucial demographic insights into a population's status. In the absence of information from other sites, it is unclear whether the bias towards finding smaller snails is a common feature of the sub-surface search method or is a local phenomena resulting from the habitat structure in the Canaan plots. The deep rocky crevices in the karren at Canaan might well provide daytime refugia for large snails where they cannot be found by daytime searchers.

The sub-surface search method [11] has been promoted as providing reliable estimate of live snail density to monitor trends over time and compare densities in different locations [3, 11]. The method has been adopted as the standard method for monitoring populations of threatened snails and is used widely throughout NZ, consuming substantial conservation resources [3]. However if index methods, such as the sub-surface search method, are used without validating the relationship between the index and actual population densities, index methods can provide misleading results [84].

In the Powelliphanta Recovery Plan [3] the long-term recovery goal for many taxa includes a target population density in terms of snails$^{-1}$100 m$^2$. Presumably target densities are measured using the sub-surface search method, as this is the only population monitoring method discussed in the plan. For *P. hochstetteri*, the long-term recovery goal sets a target population densities of >12 snails$^{-1}$100 m$^2$. In this study, sub-surface density estimates were between 11% and 39% of actual population density estimates from capture-recapture, thus the target density for *P. hochstetteri* becomes actual densities either >31 or >109 snails$^{-1}$100 m$^2$. Both figures seem unrealistically high.

The sub-surface search method for monitoring snail populations has some advantages over the capture-recapture method used in this study. It is easier to achieve wide geographical spread, is logistically relatively straightforward and requires fewer resources. However, information from this and two other studies [15, 85] indicate that, contrary to Walker [3, 11], the sub-surface search method does not provide reliable estimates of live snail densities or population trends. Information on snail populations gained from sub-surface searches is likely to be misleading and not provide a reliable basis for sound conservation management.

There has been a major investment in a *Powelliphanta* snail monitoring programme using sub-surface plot searches. In the Golden Bay region alone, biennial monitoring of permanent snail plots has been underway for nearly thirty years, and there are now 166 permanent snail monitoring plots at 22 locations in the region [52]. Unless it can be demonstrated that snail counts from sub-surface plot searches are proportional to the actual population densities and that the snails found during searches are an unbiased representative sample of snails present in the plot, information from the snail monitoring programme is of dubious value and could be misleading. Capture-recapture provides a way to validate the sub-surface search method and determine how reliable its results are. This could be done by establishing a number of capture- recapture plots alongside a selection of the existing permanent sub-surface plots and monitoring the two types of plots concurrently.

## Monitoring Conservation Management Outcomes

One of the principal objectives of the pest control undertaken in Abel Tasman National Park is to maintain and improve densities of two species of native land snails *P. hochstetteri* and *R. oconnori* and restore viable populations of them [3, 22]. The results of snail monitoring within the intensive pest control area at Wainui indicate that currently this is not being achieved. Facilitated by mesopredator release, weka numbers are increasing and may be endangering the survival of populations of both snail species. Similar examples of the unforeseen and undesirable consequences of pest control are well documented [86-88].

Although better appreciation and understanding of the complexities of ecosystems being managed will assist prediction of the most likely consequences of management actions such as pest control [89], our ability to predict consequences is limited. NZ ecosystems are now dominated by multiple invasive alien species over a range of trophic levels. The resulting assemblages of invasive alien and indigenous species are novel and unstable. Conservation management aimed at changing the species composition of these assemblages (e.g. species removal by pest control, species reintroductions or reforestation) is likely to result in complex and unexpected changes in the assemblages [87, 90-93].

The low predictability of the response of NZ's novel species assemblages to conservation management makes monitoring of threatened or otherwise important species within these assemblages a crucial component of conservation management programmes. Monitoring must provide reliable comprehensive information on the status and trends of the species being monitored in a timely manner to allow adaptive changes in management regimes to overcome undesired and previously unforeseen outcomes. The results of this study demonstrate that the capture-recapture method provided timely, reliable and comprehensive information on the effect of pest control on populations of two species of threatened land snails, whereas NZ's standard land snail monitoring method of diurnal sub-surface plot searches did not.

# CONCLUSIONS

Capture-recapture monitoring provided comprehensive evidence that populations of two species of native terrestrial snails are severely threatened by a burgeoning weka population and face local extinction within a period of only a few years. Although weka are a natural predator of snails and have an important role in a healthy native ecosystem, the predator-prey balance is disturbed in Abel Tasman National Park's heavily modified ecosystems. Weka might also affect other species of conservation interest such as ground-breeding waterfowl. Predator release, lack of competition, habitat change and increased food abundance are all factors that favour weka population growth, whereas snail populations are facing pressures from exotic and native predators, and habitat degradation through browsing as well as increasing drought events as a consequence of global climate change. Currently, there is no evidence that rats are a significant snail predator within the study areas. The results of this study demonstrate how quickly population trends in a recovering population can reverse. The results also underline the crucial role of adequate monitoring for informing conservation managers about pest control outcomes and for providing early warning of unexpected and undesirable developments.

Potential measures for improving snail populations are:

- controlling weka numbers;
- creating fenced weka exclusion areas of an ecologically meaningful size;
- controlling browsing mammals so that understorey vegetation and ground cover can recover to provide shelter for invertebrates and improve soil moisture.

# SYNOPSIS

- Weka are the main predators of *P. hochstetteri* and *R. oconnori* in Able Tasman National Park, threatening their survival in the park and surrounding areas.
- Further investigations are needed to specify if and to what degree karst habitat provides protection for snails from weka predation.
- Mesopredator release as a result of stoat control has allowed weka populations to reach high densities that threaten other conservation values as well as snails.
- Although weka was a natural predator of snails in pre-human NZ, the ecological balance between snails and weka has been disturbed by several factors including: the presence of introduced predators of snails, habitat degradation from browsing and trampling by introduced mammals and extreme climatic events due to climate change.
- Increase in the frequency and severity of droughts as a consequence of climate change is putting additional pressure on snail populations.
- The results of this study demonstrates the instability of species assemblages in contemporary NZ and underlines the need for high quality outcome monitoring programmes to deliver timely, reliable and comprehensive information to conservation managers so they can avoid unexpected and undesired outcomes.

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