POPULATION DEMOGRAPHY OF A LAND SNAIL SPECIES OF CONSERVATION CONCERN IN THE BLACK HILLS

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ABSTRACT

Understanding population biology of a species is critical for its successful management. We obtained information on movement, growth, and activity levels from four populations of Cooper's Rocky Mountain snail (*Oreohelix cooperi*) in the Black Hills, South Dakota, during May through September 2005 from a simple mark-recapture set-up. Grid population density estimates for each of the four sites ranged from 145 to 795 individuals. We observed movements up to 7.2 m. Moisture was more important than temperature in determining the presence of Cooper's Rocky Mountain snails within a site. Growth was not continuous across the season, but concentrated in intervals. Different populations maintained distinct differences in shell size. Although we could not statistically explain diameter differences, we hypothesize that population density, range of moisture conditions experienced, or another habitat characteristic, i.e., litter thickness, may influence overall size of individuals. Our results demonstrated that mark-recapture methods can be used for monitoring populations of western land snails as well as answer important demographic, ecological, and life history questions.

Key words: density estimate, growth, mark-recapture, movement, *Oreohelix*, snail

INTRODUCTION

Demography and other ecologically important information are severely lacking for many invertebrates. For those species with management concerns, e.g., land snails, this creates much difficulty for planning. Unfortunately, funding priorities often do not allow for field study to answer the very questions that would make management decisions easier. Thus, we present data to illustrate how even a single-season field study can answer questions vitally important to understanding the ecology of an invertebrate species.

As a case in point, we report on the land snail species, Cooper's Rocky Mountain snail, also known as the Black Hills Mountain snail, (*Oreohelix cooperi* Binney 1858), which resides primarily in the Black Hills of South Dakota and Wyoming although a recent genetic study indicated that isolated populations exist in Montana (Weaver et al. 2006). NatureServe (2006) lists the global status as G5T2Q, meaning they consider it a vulnerable subspecies although they currently list it as *O. strigosa cooperi*. More information on proper taxonomy for this species appears in Weaver et al. (2006) and Weaver (unpublished data). This species is ranked S2 in South Dakota (Nature Serve 2006), meaning it is vulnerable to extinction. Wyoming Game and Fish Department (2005) includes Cooper's Rocky Mountain snails on their list of Wyoming Species of Greatest Conservation Need (2005). The Black Hills National Forest has designated it a management indicator species. The USDI Fish and Wildlife Service was petitioned to include Cooper's Rocky Mountain snail on the threatened or endangered species list and issued a 90-day ruling that scientific information supporting a listing was not presented (USDI Fish and Wildlife Service 2006). Indeed, lack of information is a problem in evaluating many aspects of the biology and ecology of Cooper's Rocky Mountain snail. For example, a species assessment prepared for the USDA Forest Service lists research priorities that include topics ranging from taxonomy to population size to movement (Anderson 2005).

Our work was part of a study designed to identify and develop a practical mark-recapture protocol to monitor populations of Cooper's Rocky Mountain snails in the Black Hills. We present baseline density estimates. In addition, we incorporated other important questions into the study.

Specifically, we address three main questions. First, how does individual shell size vary over the season? Tracking the range of sizes within a population can help determine the age structure of the population. Tracking growth also might determine whether growth is incremental or continuous. In addition, information on shell size allows for comparison among populations. Other studies (Frest and Johannes 2002, Anderson et al. 2007) report differences among populations in the size of the shell. Frest and Johannes (2002) even suggested that these size differences indicate separate species although genetic data presented in Weaver et al. (2006) disputed this. However, these previous studies utilized specimens collected during a short window of time or from different sites at different times of year. The current study provided an opportunity to track size across the summer season to test whether size differences among populations resulted from timing of collections.

Second, how much horizontal movement occurs within populations? Isolation of populations might cause conservation concerns. Genetic results suggest substantial gene flow among populations, even those separated by distance. That is, haplotypes were present in multiple, non-adjacent populations (Weaver et al. 2006). Gene flow suggested that populations are not isolated; however actual migration has not been observed, and field studies have not examined how much movement occurs. We provide data on the mobility of these snails.

Third, how do activity periods vary by season and microclimate? Activity periods are important not only for feeding and breeding of snails but also may influence long-term growth. For example, if snails are more active at moister sites, these sites might produce larger snails. Anderson et al. (2007) were unable to relate temperature or moisture to size differences at particular sites based on soil measurements taken at the time of collection although long-term temperature data indicated a correlation to shell size. Including across-season data from our study may show relationships among temperature, moisture, and size. In addition, understanding when snails are aestivating may help managers identify a timeframe when management activities would be least deleterious to snails.

MATERIALS AND METHODS

We set up grids at four locations (Fig. 1) previously scouted for presence of Cooper's Rocky Mountain snail. Sites included rocky slopes with various amounts of tree cover that included ponderosa pine (*Pinus ponderosa*), spruce (*Picea glauca*), birch (*Betula papyrifera*), and aspen (*Populus tremuloides*). Grids consisted of four rows of five sampling stations placed 2 m apart. At each sampling station, we placed a 0.5- x 0.5-m plywood or pressboard board flat on the ground to function as a "trap." Boards were left in place ≥ 24 hrs before the first trapping session.

At each trapping site, we marked individual snails at initial capture with fingernail polish and an individually numbered bee tag (www.beeworks.com). For each snail, we recorded trap location, number of whorls, and shell diameter using calipers. We also recorded and measured individuals at each subsequent recapture. After marking, we returned snails to the location of capture.

We also recorded soil temperature and moisture at each board using a Weksler soil thermometer and a Quick Draw 2900FI Soil Moisture Probe (SoilMoisture Equipment Corp.). Moisture was measured as the soil suction in centibars, so a lower reading indicated higher soil moisture content. When sites became too dry or were too rocky, the moisture probe could not be inserted and readings were not taken. Late in the season the moisture probe malfunctioned, so readings could not be taken on the last sampling visit at some locations.

We initially visited each site on three consecutive days and then at 2-wk intervals thereafter. Sampling did not begin until we

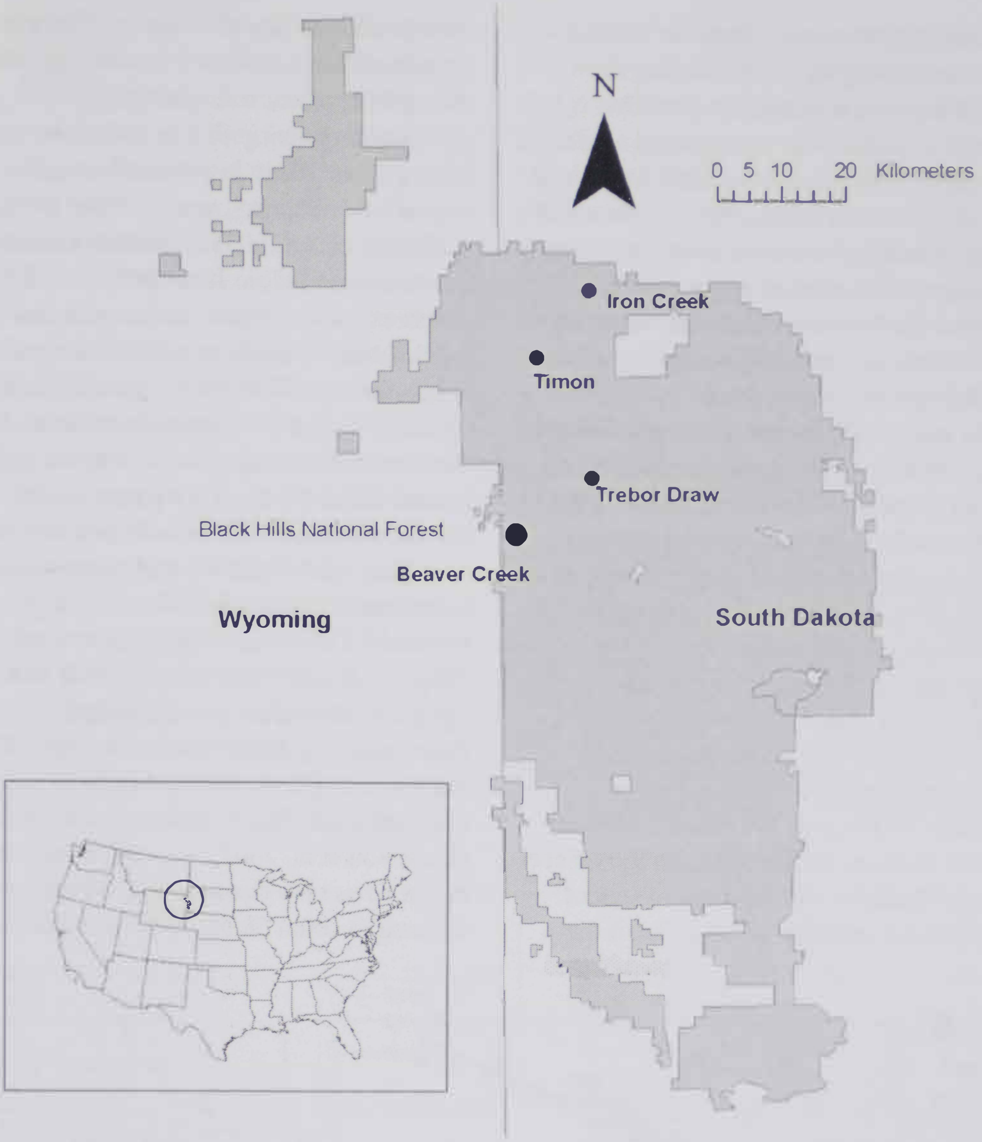

Figure 1. Location of sampling grids used in this study.

observed that snails were "active," i.e., some snails found moving around on the surface or at least extended out of their shells. Due to cold late spring temperatures, we did not observe snail activity until late May and began trapping then. Snow and closed roads also impacted early access to some sites, so initial sampling days were not the same for all sites. For example, the road leading towards Timon Campground was closed for repairs until very late spring, so we did not begin sampling at that site until late June. Sampling continued at all sites through late September.

General assumptions of mark-recapture analyses include (1) marked individuals were representative of the entire population, (2) marks, i.e., bee tags, were not lost and did not affect behavior or spatial arrangement of snails, (3) each marked individual had an equal chance of being recaptured, and (4) study duration was short enough assume closure (White et al. 1982). Although these assumptions were not specifically tested, we found no reason to believe that the animals captured and marked did not represent the population as a whole. We used bee tags in a study of another land snail species (i.e., Anderson 2000) and assumed they would be equally reliable for this study.

The grid density estimates we report used closed population models. These models assume birth, death, immigration, and emigration did not occur during sampling.

Other assumptions were relaxed to varying degrees depending on the model that we selected. Because snails aestivate under unfavorable conditions, we expected models in which capture probability varied with time (t) would fit the data better than models in which capture probability was held constant. Capture probability also varied among individuals, so we also considered models that allowed for behavioral (b) variation to capture and individual snail variation (h).

We analyzed mark-recapture data using program MARK (White and Burnham 1999) to obtain population density estimates. Each trapping session was considered a separate sampling occasion. Model selection criteria in program Mark uses a series of goodness-of-fit tests of these models and provided a way to test appropriateness of models for our data.

Some may argue that open models are more realistic for these populations since we observed some mortality and suspect movement off the grid. We could not obtain estimates from an open model, the Jolly-Seber option in Mark, for this data due to lack of numerical convergence to determine if they were similar to closed estimates. Precedence for using closed models for snail population estimates appears in Anderson (2000). Although some mortality occurred during the study, we likely began sampling after the majority of offspring were born for the year; Anderson et al. (2007) found that most broods were released before June. We also did not observe such extensive surface movement that would indicate snails moved off the grid in large numbers. Therefore, a closed model at this time scale should reliably estimate density. We explored the impact of violations of the closure assumption on the robustness of our density estimates in the discussion section.

Size, whorl number, moisture, and temperature data were analyzed using Microsoft Office Excel 2003 (Microsoft Corp.) and JMP Version 4.0.2 (SAS Institute, Inc.). For individual growth analyses, the first three sampling sessions were lumped. Whorl number and diameter were highly correlated in these samples (Fig. 2) and in a previous study (Anderson et al. 2007), and either measure might be used to examine size. Whorls were difficult to count on the smallest individuals

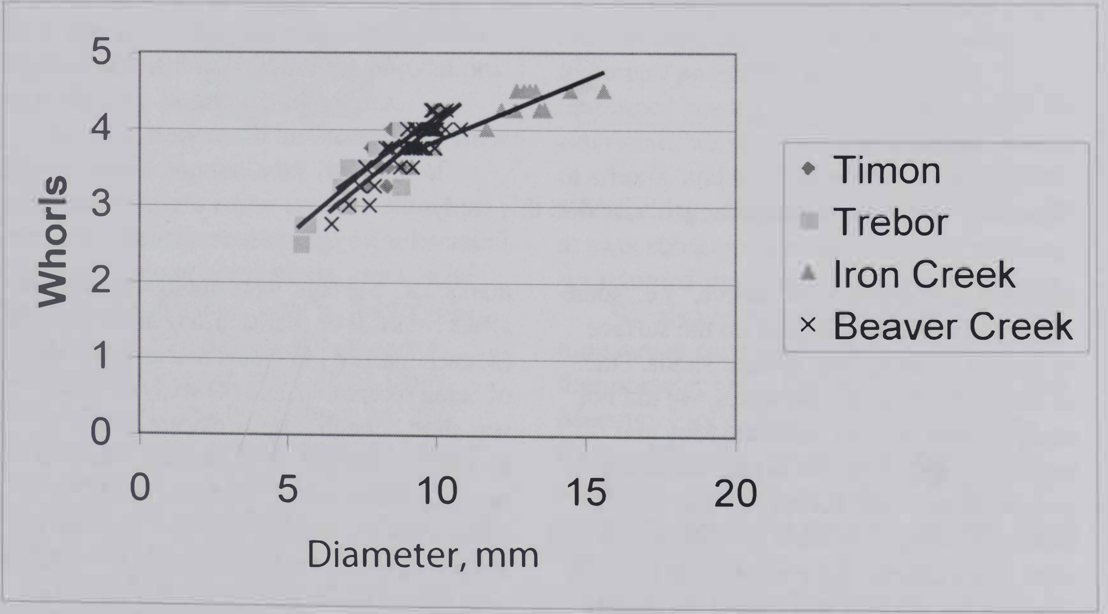

Figure 2. Relationship between number of whorls and shell diameter at each of the sampling locations. Individual snails captured in late June (from sampling dates nearest 23 June from each population) are plotted. Timon (whorls = 0.2842 diameter + 1.2768, $R^2 = 0.66$, $n = 40$), Trebor (whorls = 0.3343 diameter + 0.8746, $R^2 = 0.76$, $n = 12$), and Beaver Creek (whorls = 0.3207 diameter + 0.821, $R^2 = 0.77$, $n = 39$) appear to have a different slope than Iron Creek (whorls = 0.1625 diameter + 2.1862, $R^2 = 0.80$, $n = 14$) although this was not tested due to the small sample size at Iron Creek.

without a microscope without practice. Due to a learning curve for counting whorls, whorl counts during May might be less reliable than those conducted during June or later. Thus, we used diameter for individual growth analyses because it seemed a more precise measure. Some individuals showed negative growth that might have been due to damaged shells, human error, or caliper precision. If the decrease was < 0.1 mm, we assumed it due to caliper precision, and adjusted growth to zero. If the decrease was > 0.1 mm, the cause could not be determined after the fact, so the individual was removed from the individual growth analyses. We examined individual growth in two separate ways. First, average change in diameter of individuals recaptured on subsequent trapping sessions (~ 2 wks apart) was examined for all four sites. At two of the sites that had more recaptures (Beaver and Timon), we plotted total change in diameter of individuals caught at initial capture and subsequently recaptured. Total change in diameter of all recaptures was not subdivided to a weekly rate because we found evidence that growth was not constant across the season.

We evaluated movement from successive locations of recaptured individuals. Since precise pathways of movement were unknown, we estimated movement distances for those individuals recaptured under different boards. These estimates assumed straight-line distances from the mid-point of the board where the snail was originally captured to the mid-point of the board where it was recaptured.

RESULTS

Grid Density Estimates

The original purpose of the study was to determine if our mark-recapture methods might be useful for monitoring, and we obtained estimates of snail density on each grid. Number of captures, recaptures, and grid density varied among sites (Fig. 3, Table 1). The model selection procedure in the

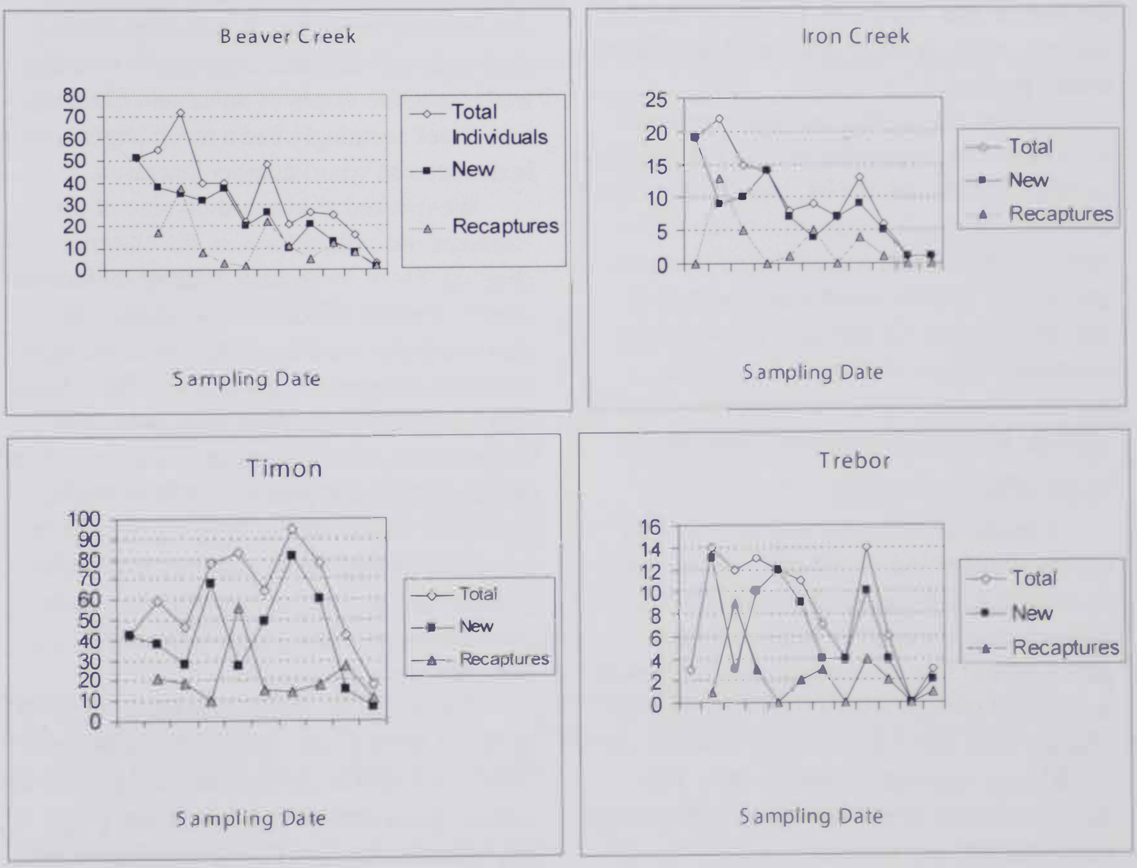

Figure 3. Total individuals captured at each sampling date at each site. Newly captured individuals and recaptured individuals are also shown.

Table 1. Grid density estimates for *Oreohelix cooperi* at four locations.

Site	Estimate (model)	Standard Error	95% confidence interval	Total No. of unique individuals caught	No. of sampling sessions	Date of first sampling session	Recapture rate (No. individuals recaptured/ total ind)	No. of dead recoveries
Beaver Creek	483 (M_{tb})	272	304-1,740	292	12	26 May	29%	18
Iron Creek	153 (M_{tb})	152	90-1,018	86	11	6 Jun	29%	1
Timon Camp	795 (M_{th})	65	687-945	415	10	27 Jun	33%	6
Trebor	145 (M_t)	22	114-202	74	12	26 May	26%	1

CAPTURE option of program MARK chose models that reflected differences in capture rates at different sampling occasions as expected. M_{tb} (Burnham's M_{tb}) was the most appropriate model (model selection criteria = 1.0, with other models at ≤ 0.89) for two of the sites (Iron Creek and Beaver Creek). For the Trebor site, model M_t (Table 1) had the highest selection criteria value (1.0, with all others being ≤ 0.7).

For the Timon site, the density estimate from model M_{th} (selection criteria 0.91) appears in Table 1. Although the M_{tb} model had a higher selection criteria, it produced a much higher estimate (8953) with a much larger standard error (SE = 28,696) than those produced by any other models for this site. These density estimates were most likely to be used as minimum estimates, so we rejected the high M_{tb} estimate in favor of that from model M_{th}.

Individual Growth

Change in diameter was not constant across summer but occurred in spurts (Fig. 4). Average changes in diameter of ~ 0.1 mm occurred in early July among three populations. The Trebor population showed a different pattern with a 0.09-mm average change from late May to early June but only a 0.02-mm average change in early July. Small numbers of recaptures at Trebor might have affected our results.

Time of growth also varied by individual with some recaptured individuals showing virtually no seasonal growth whereas others grew substantially ($\leq$ 0.5 mm; Fig. 5).

Shell Size by Populations

Individuals from all four populations showed a strong correlation between number of whorls and diameter based on analyses of individuals captured at the trapping session closest to 23 June (Fig. 2). Although sample sizes were not similar enough to allow statistical analyses of the slopes of linear relationships, Iron Creek seemingly had a much larger change in diameter as whorl number increased.

We tracked average shell size of all captured individuals across the summer (Fig. 6). From these data, date of collection clearly did not influence our conclusion that shell size varied among populations as similarly reported in previous studies (Frest and Johannes 2002, Anderson et al. 2007). Even if samples were measured at Iron Creek at the point in the season in which average shell size was smallest, they would still be larger on average than samples from other populations at any time during the season, provided more than a small number of samples were measured.

The range in average diameter also differed among populations. We detected only a 0.3-mm difference in average diameter across the season at the Timon site (Fig. 6), whereas the Iron Creek and Trebor sites indicated ranges of > 2.0 mm. A linear regression indicated that average diameter

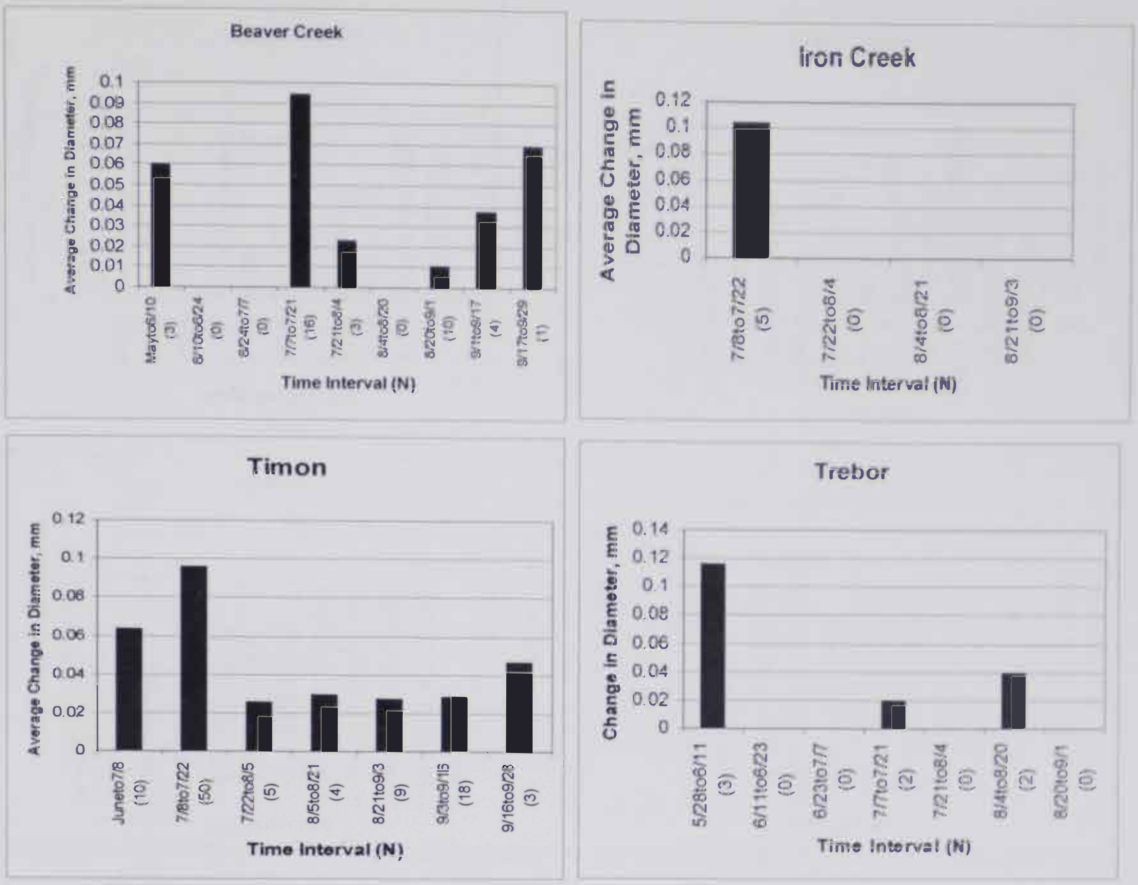

Figure 4. Change in diameter in individual snails captured on subsequent trapping sessions two weeks later. Initial three sampling days are considered one occasion for this chart.

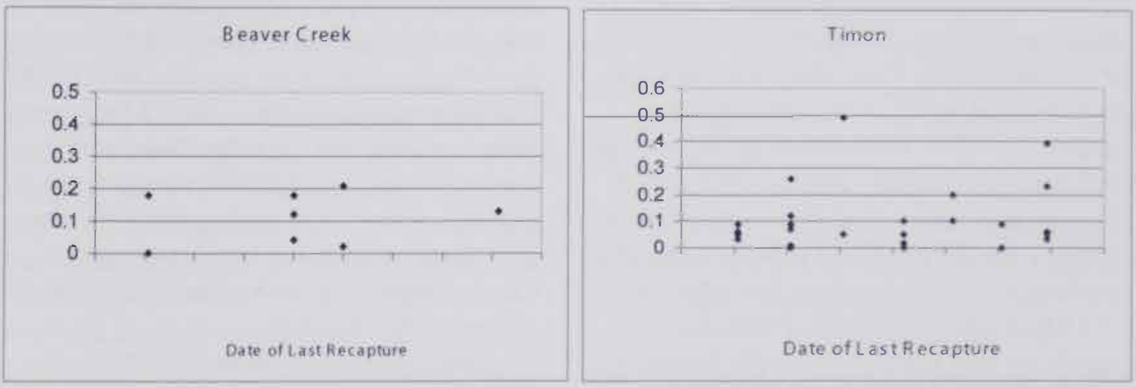

Figure 5. Individual shell growth across the season at the Beaver Creek and Timon sites. Individuals captured on the first day of sampling that were recaptured at any time later in the season are plotted by their change in diameter.

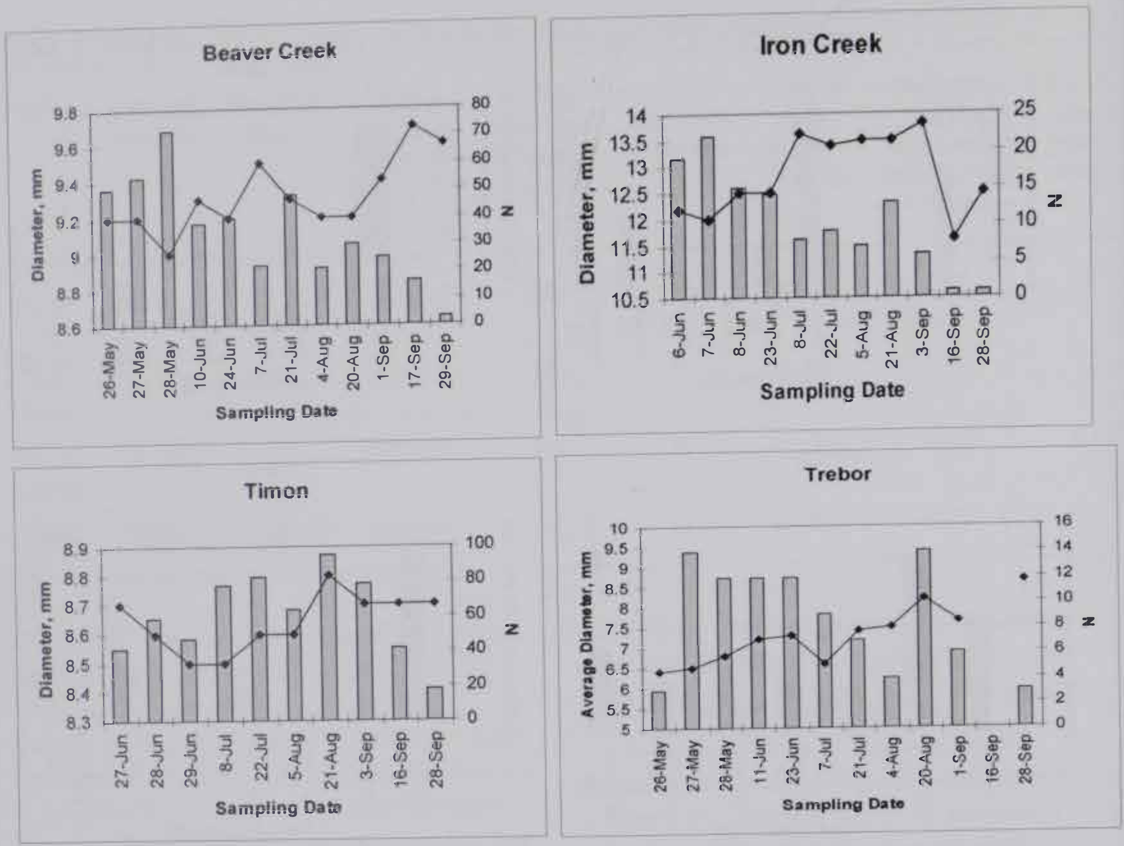

Figure 6. Average diameter of all captured individuals across the season by population. Average diameter is represented by dots and N is represented by columns on each of the graphs. Only individuals with recorded diameter measurements are included, so N may differ than the total number of individuals caught on some occasions.

increased across the summer at Beaver Creek (average diameter = -108 + 3.66e-8 date, $R^2 = 0.52$, $P = 0.0082$) and Trebor (average diameter = -534 + 0.0000002 date, $R^2 = 0.80$, $P = 0.0002$) sites. The Timon site appeared to flatten out during late summer (average diameter = -55 + 1.98e-8 date, r^2=0.38, linear regression P=0.0559). The late start date at this site may have affected the strength of our results. We did not detect a linear increase at the Iron Creek site (average diameter =-112 + 3.88e-8 date, $R^2 = 0.034$, $P = 0.58$). The results on Iron Creek were surely biased by the small sample sizes in September.

Tracking number of whorls of all captured individuals from selected dates also suggested that small individuals became less abundant as the season progressed (Fig. 7). Whorl number suggests that populations shifted towards more mature adults as the season progressed. This provides further evidence that most births occurred early in the season.

Snail Activity

The number of snails caught varied among sampling sessions across the summer (Fig. 3). Snail numbers peaked at all sites in late May or early June except for the Timon Campground site at which we did not begin sampling until late June. Snails apparently became less active as summer progressed although a secondary peak occurred in late July (Beaver Creek) or late August (Iron Creek, Timon, and Trebor) before numbers plummeted in September.

Interpretation of patterns shown by new (unmarked) individuals and recaptured individuals (Fig. 3) was difficult. New snails did not contribute a constant proportion to the population, nor did the percentage of recaptures uniformly increase across the season. Instead some variation in the percentage of new vs. recaptured snails occurred over time.

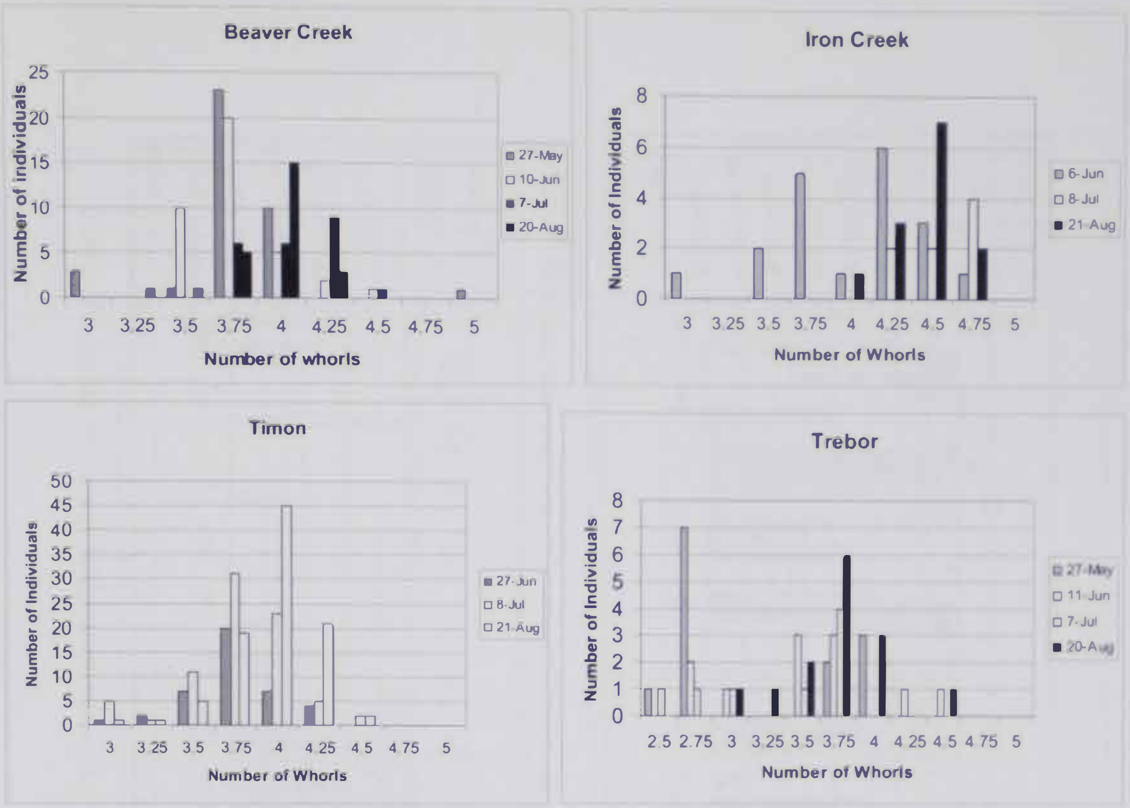

Figure 7. Distribution of whorl number at selected sampling dates. Early, middle, and late summer dates are shown for comparison.

Snails also were not uniformly distributed across a sampling site. Numbers of snails captured differed among the boards on a grid (Fig. 8) that suggested spatial variation. At three sites (Iron Creek, Timon, and Trebor) there were some boards at which we captured no snails on any sampling occasion. This suggested that for some reason, some boards were not as desirable for snail activity as others. Moisture and temperature data provide some insight into this phenomenon as discussed below. Note that at some sampling times, boards were out of place either through animal disturbance or from sliding downhill. When the board had moved, no data were available for that sampling session. Dates and boards affected were 1) Beaver Creek on 24 June (B2 and C2), 4 August (A1, A2, and A3), 20 August (C2), and 29 September (A2), 2) Iron Creek on 8 July (D1), and 3 September (B5), 3) Timon on 27-29 June (B1, C2, D1, and D5), and 4) Trebor on 11 June (C1, D2), 23 June (B1, C1, C2), 7 July (B1, B3), and 20 August (B3).

Movement

Most recaptured individuals remained under the same board as originally captured. However, 20 individuals showed some movement between sampling occasions (Table 2). The number of mobile individuals differed among populations. Percent movement, i.e., number of individuals that moved/total recaptured, ranged from 5 percent at the Timon site to 10 percent at the Iron Creek site.

Observed movements were mostly to adjacent boards, which would be a distance of approximately 2 m. We calculated straight-line distances because the path traveled was not known. We recaptured only six individuals at a board that required movement of a distance > 2 m. The longest movement recorded was by an individual at the Timon site that moved a minimum of 7.2 m between 8 July and 22 July. Interestingly, this individual also showed two other movements > 2 m between other sampling occasions.

Table 2 illustrates horizontal movement, but vertical movement was also likely since

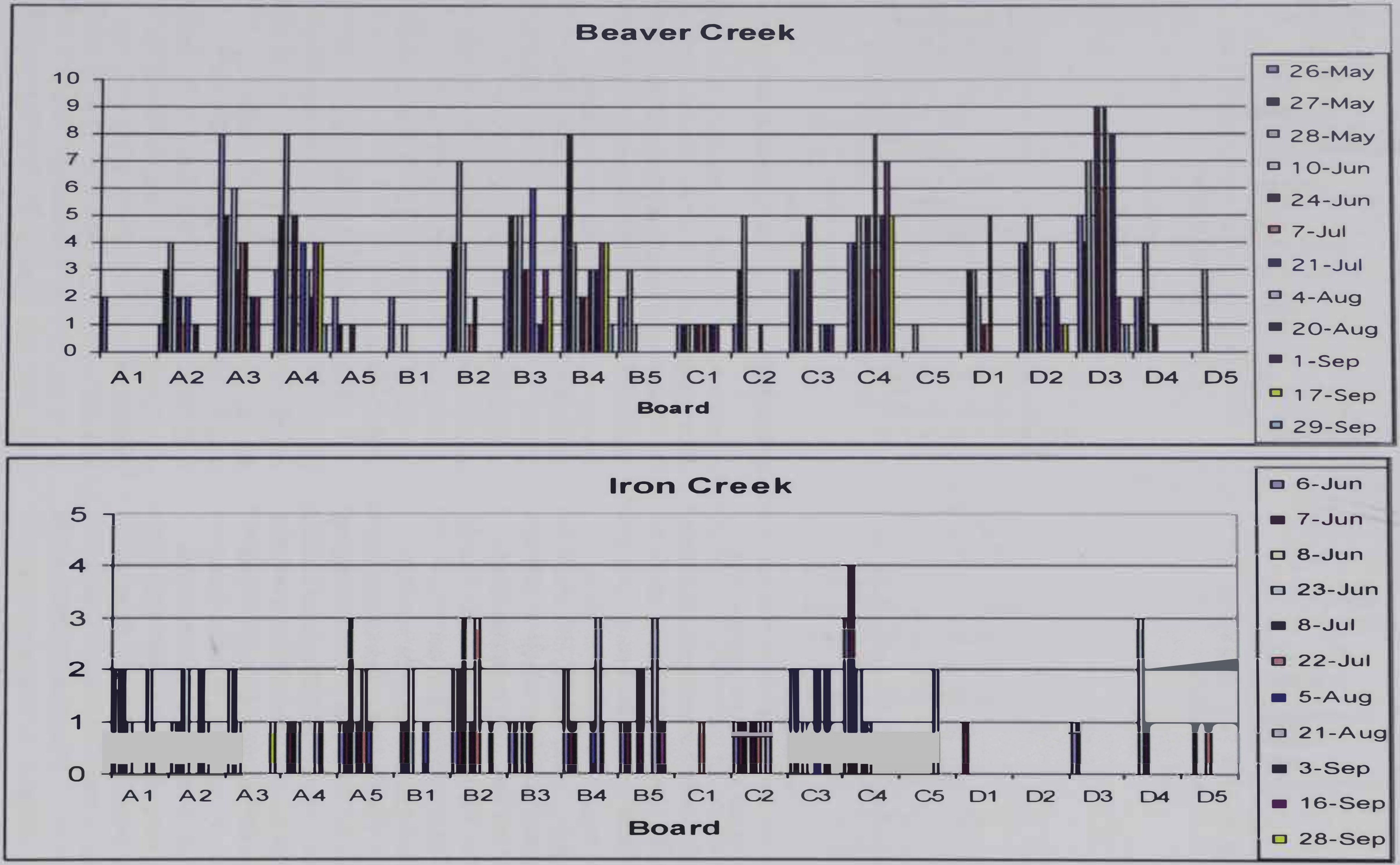

Figure 8. Snails captured at each board on each sampling occasion. Boards were set up in rectangular grids consisting of four rows (A-D) of five boards (1-5), so board A3 refers to the third board in the first row of the grid.

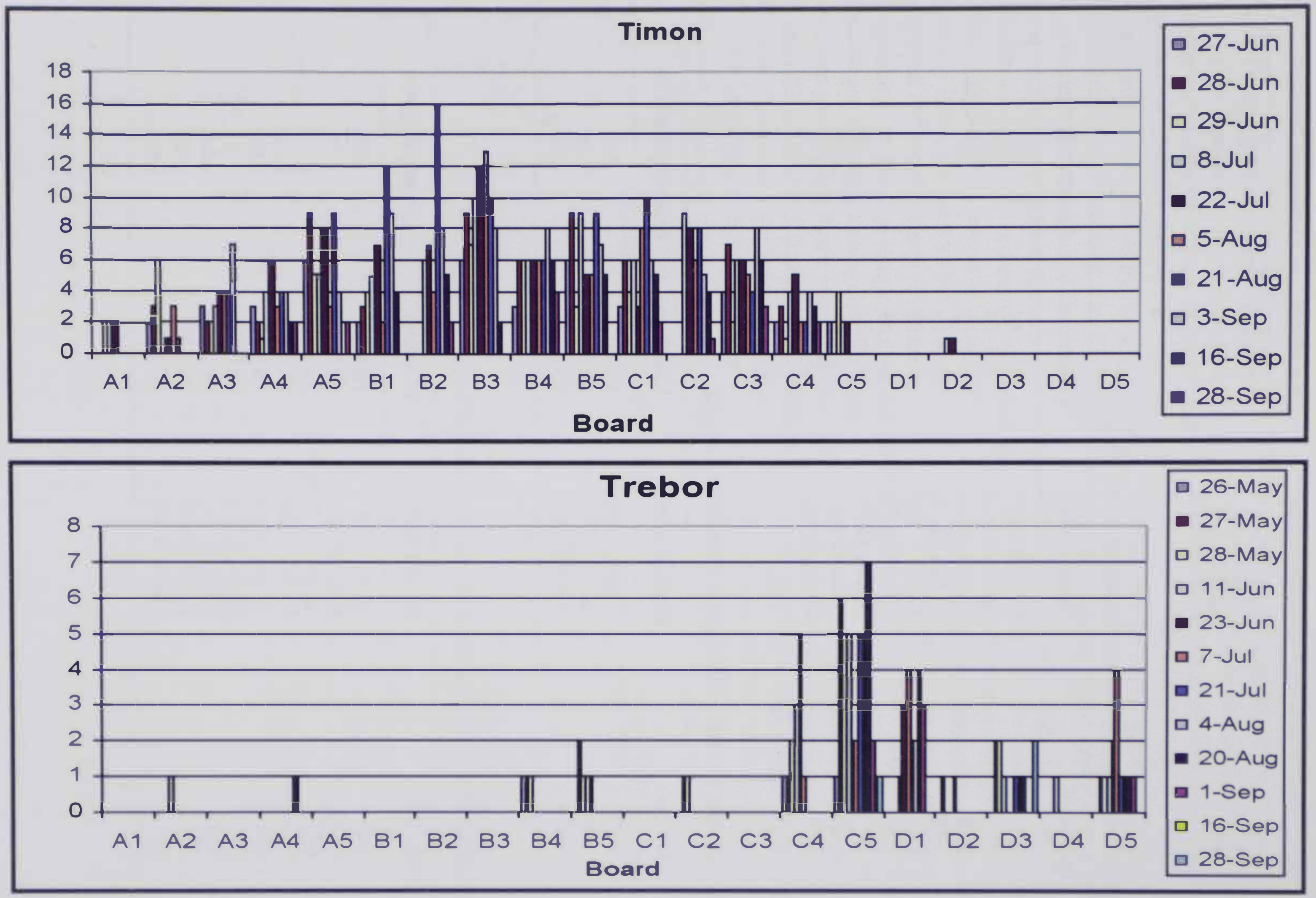

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Table 2. Individuals Recaptured at Different Locations

Trebor Draw (74 total individuals, 25 recapture events, 8% movement)

Individual	Capture Dates	Locations	Estimated Distance
B11	11 Jun, 7 Jul	C5 to D5	2 m
B12	28 May, 7 Jul	C5 to D5	2 m

Beaver Creek (292 total individuals, 127 recapture events, 7%movement)

Individual	Capture Dates	Locations	Estimated Distance
B28	21 Jul, 4 Aug	B2 to A4	4.5 m
O18	26 May, 21 Jul	B5 to C4	2.8 m
O22	27 May, 7 Jul	B4 to C4	2 m
O43	28 May, 24 Jun	D3 to C3	2 m
O43	24 Jun, 17 Sept	C3 to B3	2 m
O59	28 May, 20 Aug (dead)	A4 to B4	2 m
G7	28 May, 21 Jul	C1 to D1	2 m
G42	10 Jun, 4 Aug	B3 to B4	2 m
G73	24 Jun, 4 Aug	B3 to B4	2 m

Iron Creek (86 total individuals, 29 recapture events, 10%movement)

Individual	Capture Dates	Locations	Estimated Distance
G18	7 Jun, 21 Aug	C4 to C5	2 m
G48	23 Jun, 3 Sept	B3 to B4	2 m
G61	8 July, 22 July	D4 to D5	2 m

Timon Campground (415 total individuals,191 recapture events, 5% movement)

Individual	Capture Dates	Locations	Estimated Distance
G19	27 Jun, 8 Jul	B3 to C1	4.5 m
G19b	8 Jul, 22 Jul	C1 to A4	7.2 m
G19c	22 Jul, Aug 5 (dead)	A4 to C1	7.2 m
G23	29 Jun, 22 Jul	B3 to A4	2.8 m
G57	28 Jun, 29 Jun	B3 to A1	4.5 m
G67	28 Jun, 3 Sep	B4 to B3	2 m
B18	22 Jul, 21 Aug	A3 to B2	2.8 m
B81	22 Jul, 3 Sept	C3 to B3	2 m
B97	22 Jul, 21 Aug	D2 to C2	2 m

new snails would appear at a board at a higher rate than one would logically expect if horizontal movement rates of only 5 to 10 percent were the only movements that occurred.

Soil Temperature and Moisture

Soil temperature and moisture varied among and within sites (Figs. 9 and 10). A comparison of sites suggests that the range of temperatures experienced by the snails on the grids varied slightly among sites (Table 3).

A regression analysis of the average temperature/board against the average number of captures/board across all sampling dates suggested that temperature did not strongly influence the number of snails captured (*P* > 0.05) at any of four sites. Regressing the average temperature across boards per sampling date against the total captures gave a significant relationship at the Timon site only (*P* = 0.0140), but combining all sites yielded no significant relationship.

Moisture had a slightly stronger influence than temperature on the number of snails captured. A regression analysis of the average moisture across dates/board against the average number of captures/board was significant only for the Timon site (*P* < 0.0001). Using the average moisture reading across boards/sampling date against the total number of captures per sampling date was not significant for any individual sites. However, when data from all sites were combined, the average moisture reading/sampling date was related to total number of captures/sampling date (*P* = 0.0073). Some of the moisture analyses might have been slightly biased because we did not take moisture readings late in the season after the probe malfunctioned or when sites became too hard to insert the probe. Captures at these times were very low although we might have detected a stronger relationship if these data were available.

The boards provided a slightly cooler and moister microenvironment than the surrounding uncovered habitat. Temperature and moisture readings were taken under and adjacent to board B3 during each sampling

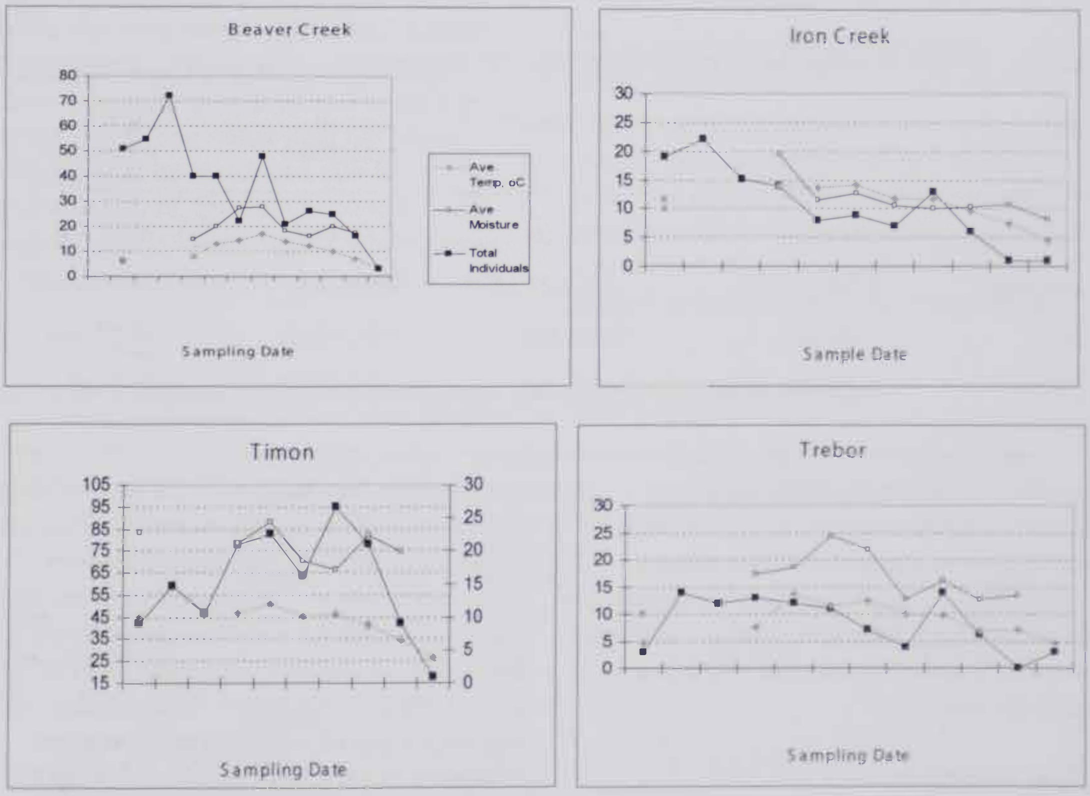

Figure 9. Average temperature and moisture measurements at each location. The plotted points are an average of the measurements across all cover boards on each particular sampling date.

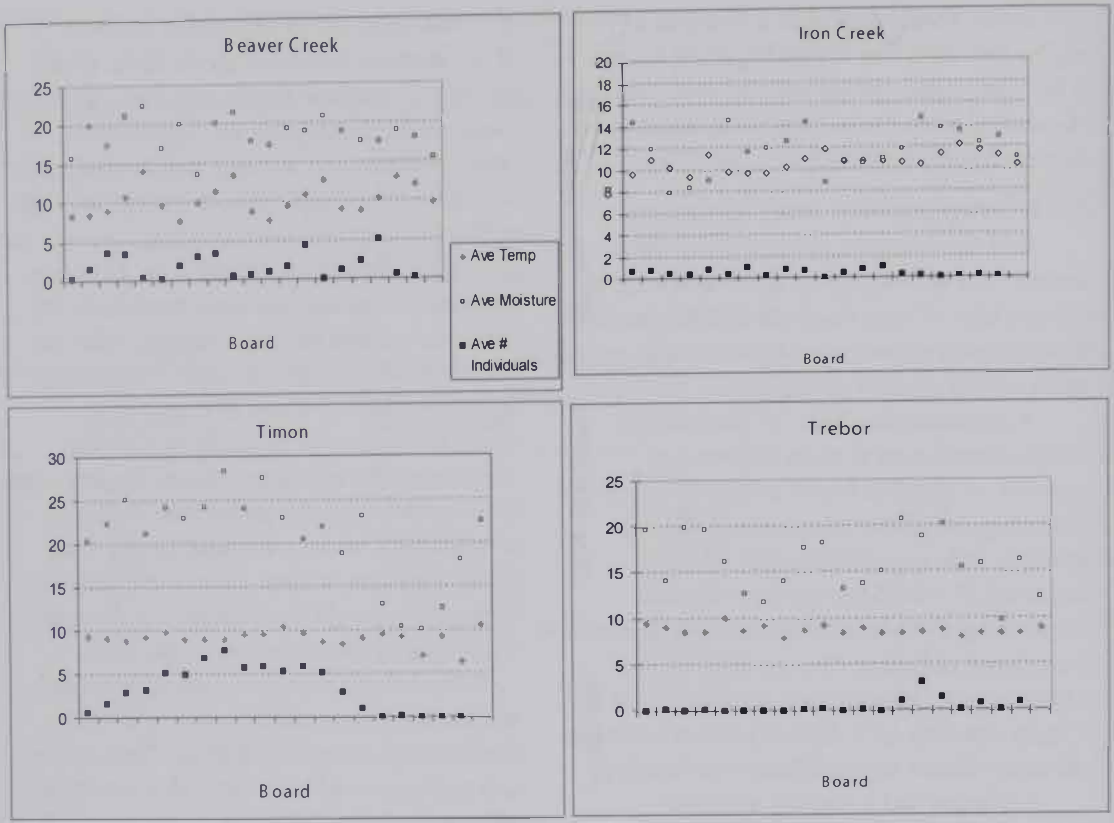

Figure 10. Variation in temperature and moisture within sites. Averages are taken from each board across all the sampling occasions during the summer.

Table 3. Ranges in temperature and moisture by site and date.

Site	Low Temp, °C	High Temp, °C	Moistest, in centibars	Driest, in centibars
Beaver Creek	3 (29 Sep)	17 (21 Jul)	7 (26 May)	28 (21 Jul)
Iron Creek	5 (28 Sep)	14 (8 & 22 Jul)	8 (28 Sep)	19 (23 Jun)
Timon	4 (28 Sep)	12 (22 Jul)	17 (21 Aug)	23 (27 Jun)
Trebor	5 (26 May, 28 Sep)	14 (23 Jun)	10 (26 May)	24 (7 Jul)

occasion. A matched pairs comparison detected a difference ($P < 0$ .05) for both temperature and moisture. Temperature averaged 0.8 °C higher outside the board than under the board. Moisture readings averaged 2 centibars lower outside the board than under the board.

DISCUSSION

Reliability of Density Estimates

The Cooper's Rocky Mountain snail populations technically violated some assumptions for closed population modeling, i.e., no migration and no mortality. However, given that observed migration distances were low compared to the grid size and that observed mortality was low, closed models seemingly provided useful estimates (White et al. 1982). According to White et al. (1982), the coefficient of variation of population estimates (se(N)/N) should be < 20 percent for precise estimates. Two of four coefficients of variation for the estimates (Timon and Trebor) reported in this study fell below 20 percent, so those estimates were presumably realistic. Estimates for the other two sites yielded higher standard errors so may have been less precise. In addition, average estimates of probability of capture (p) at all four sites were low (0.07), which reduced reliability of our models.

It should be noted that these estimates only predicted the number of snails on the trapping grid itself and not the entire population. We did not measure the total area that snails actually inhabit at each site, which indeed was difficult to determine since snails apparently were not always visible; thus, the grid estimate was not extrapolated to a wider area.

Although some sites apparently had denser populations than others, direct comparison among sites from our limited data might be suspect. Sampling sessions were not conducted on the same days although grid sizes were equal at each site. As discussed below, snail activity varied across the summer, and this may have affected the number of snails observed at a particular time.

In addition, grids at all sites may not cover the same amount of "ideal" habitat. For example, grids at some sites, e.g., Trebor, may have been placed at the edge of the population rather than the center, which might have reduced number of snails observed. Spatial variation in snail activity was evident (Fig. 8), which shows how captures varied among boards at each site. Although we attempted to place grids in areas where shells or live snails were observed, precisely predicting snail activity across the entire grid before sampling began was impractical.

Despite the complications surrounding the estimates, this study provided the only repeatable, mark-recapture density estimates for any land snails from the western United States as far as we could determine from searches of published literature. Our results demonstrated that a mark-recapture protocol with grids of cover-board traps can effectively serve as a useful "trap." The protocol described here is repeatable, and, if desired, estimates can be used for comparison in a long-term monitoring program. We suggest that the estimates be used only as density estimates or minimum estimates of populations on the grid and NOT extrapolated as full population estimates. A precedent for such monitoring exists in Iowa where a mark-recapture protocol is being used for monitoring of the federally-endangered Iowa Pleistocene snail, (*Discus macclintocki*; Henry et al. 2003).

Comparison with Previous Estimates

Comparison between these results and density estimates provided by Frest and Johannes (2002) are difficult to interpret (Table 4). Their estimates are based on averaging counts from 0.25-m^2 quadrats randomly placed around a site on one particular day.

Table 4. Comparison to density estimates by Frest and Johannes (2002).

Site	Frest's 1999 estimates of snails/m^2 (nearest Frest location number)	Snails/m^2 derived from the population estimates in this study	Low sample snails/m^2 (date)	High sample snails/m^2 (date)
Beaver Creek	5-10 (82)	4.8	0.6 (29 Sept)	14 (28 May)
	2-10 (83)			
Iron Creek	4 (11)	1.5	0.2 (16 & 28 Sept)	4 (6 June)
Timon	10-15 (19)	8.0	4 (28 Sept)	19 (21 Aug)
Trebor Draw	Up to 20 (87)	1.5	0 (16 Sept)	3 (27 May & 20 Aug)

For comparison with this study, two different calculations were made. First, we used grid population estimates (Table 1). For this purpose, we assumed that the area sampled included not just the area under the boards but also between boards and a slight buffer around the boards, for ~ 10 m x 10 m area. Thus, we divided population estimates by 100 for the number of snails/m^2. Note that density estimates were based on recapture probabilities and not just on numbers of snails from a sample. For perhaps a more direct comparison to Frest and Johannes' methods, numbers from each sampling occasion were examined individually and were divided by 20—number of 0.25-m^2 boards used as traps—then multiplied by four to obtain an estimate/m^2. The lowest and highest of these estimates also appear in the table to illustrate the range.

Exact reasons for differences between these estimates remain unknown, but several methodological possibilities are available. First, collection sites from Frest and Johannes (2002) are not an exact overlay of areas that grids were placed in this study. In fact, in some cases they did their sampling at quite a distance from the sites in this study, i.e., the Beaver Creek site from which Frest and Johannes (2002) had no samples near the campground but provided estimates from other sites along the creek. Since distribution of snails is patchy, it is difficult to make comparisons from different locations.

Second, as can be seen from the low/high estimates, date of sampling can heavily influence results when estimates are based on data from a single day. In addition, it is unknown if the cover boards used in this study would increase the probability of viewing snails across the summer over what would be seen in a quadrat without a cover-board; however, observed recapture rates of 26 to 33 percent suggested some "trap-happy" behavior. These issues illustrated the importance of using a repeatable protocol at a fixed location to monitor the population over time rather than base it on one day's sampling.

Compared to published studies of land snails using similar methods, we provide estimates at least as reliable. A mark-recapture study of the Iowa Pleistocene snail, used a closed model, M(th), to estimate population size (Anderson 2000). In that study, sample sizes were smaller (16-297/site) and using a maximum number of eight sampling sessions compared to 10-12 in this study. Probabilities of capture were low in that study (0.01 to 0.23) as well. Recapture rates for the Iowa Pleistocene snail were generally lower (0- 48%, with seven populations having recapture rates < 10%).

Another snail study of marked copse snails (*Arianta arbustorum*) in roadside areas in Sweden did not use cover-boards, but searched grids by hand (Baur and Baur 1990). Their recapture rates averaged 29.4 percent one month after marking.

Importance of Temperature and Moisture

Moisture apparently was more important than temperature to presence of Cooper's Rocky Mountain snail underneath a board. However, our temperature and moisture measurements were limited because they were only taken at specific times and might vary at other times of the day. Further examination of temperature and moisture across the summer using environmental recorders would be useful.

The range of conditions experienced at a site may be important and should be examined further. For example, we observed the moistest environment overall at Iron Creek where we found the largest individuals.

Movement

Movement rates and distances in this study were comparable to the rates found in other snail studies. Between 0 and 17 percent of Iowa Pleistocene snails migrated between cover boards on different cold-air slopes in Iowa (Anderson 2000). Furthest movement was 8 m. Average linear movement by copse snails along roadside areas ranged from 1.5 to 4.9 m at different sites in Sweden (Baur and Baur 1990). Average distances moved by copse snails in subalpine areas in Sweden ranged from 7 to 12 m/year (Baur 1986). Longer dispersals of ≤ 500 m in 6 months were known from an African giant snail (*Achatina fulica*), which was fitted with a radio-transmitter (Tomiyama and Nakane 1993).

More information is needed to understand dispersal and other movement in this species. Some Cooper's Rocky Mountain snails moved horizontally from underneath the boards, based on observations of marked individuals both on and off the grid that had previously been marked while under a board. Projecting whether active dispersal alone can account for the gene flow evident from genetic studies is difficult (Weaver et al. 2006). Passive movement resulting from human or animal activity or from rolling downhill is probably needed to explain some of the gene flow. Vertical movement was also likely. Snails were probably burrowing into the soil or retreating into crevices more readily than expected.

Although we observed some mortality (Table 1), yielding robust survival rates from our data was impractical. Longer-term monitoring that included some winter sampling would be helpful to better understand survival in this species.

Growth and Size

Individual snails apparently took advantage of microclimate conditions to add to their diameter in spurts during the season. Growth rates in this study appeared to be lower than those reported from a laboratory study of the related subalpine mountain snail (*Oreohelix subrudis*) where growth rates of $\leq$ 1.4 mm occurred over 2-month periods (Beetle 1987). Beetle noted that for subalpine mountain snail to reach its average adult diameter of 20 mm may require 3 years. Using our growth rates, Cooper's Rocky Mountain snail would take 10 years to reach maturity assuming an average four-whorl adult was ~ 8.5 mm in diameter and born at 2.25 whorls and 3.25 mm in diameter. This being unlikely, growth must continue during other parts of the year as was the case for the subalpine mountain snail.

The shift in whorl size to larger classes as summer progresses suggests growth in whorl number to adult size. Not enough data were available to determine if whorl growth reached a maximum number or if growth continued as conditions allowed. We would expect distinct size classes for previous years' cohorts if there was continual, steady increase in whorls, but that did not seem readily apparent. Whorl number was used to identify species for many snails, so our results would be expected either due to die-off of older individuals or slowing of growth after maturity.

Our diameter data supported presence of more than one size morph as described in Anderson et al. (2007). We were unable to conclusively correlate a specific environmental factor to differences in diameter although Anderson et al. (2007) showed that temperature is likely a factor using long-range climate data.

Size data indicated that snails are not "born" at full size but are growing during the season. The range in average size across summer was much narrower in two populations (Timon and Beaver), which also show smaller-diameter individuals. This may suggest interplay between habitat conditions and periods of growth. For example, if conditions suitable for growth are present for shorter time periods at Timon and Beaver sites, they would have had a much narrower opportunity to increase in size.

A complicating factor involved juvenile size. Whether snails in the different populations are born at the same size was unclear since very few juveniles were observed. However, snails in populations of the larger size morph likely were already larger at birth based on findings by Anderson et al. (2007) that indicated larger adults produced larger offspring.

In a study of the rock-dwelling land snail (*Chondrina clienta*) in Sweden, Baur (1988) found shell size was related to density and the amount of plant cover. Although overall density estimates were not related to average mid-season shell diameter ($P > 0.05$) in our study, the difficulties in the precision of density estimates make this difficult to evaluate from this data alone. Anderson et al. (2007) found shell density was a significant factor in adult shell size for Cooper's Rocky Mountain snail. We did not measure thickness of the litter layer on the grids, which would provide a similar variable to plant cover for Cooper's Rocky Mountain snail.

CONCLUSIONS

Our results fill in several gaps in information identified in the species assessment document for the R2 Region of the USDA Forest Service (Anderson 2005) and illustrated the importance of field work in providing information for planning and management of rare invertebrates.

We demonstrated that a mark-recapture protocol is possible to monitor Cooper's Rocky Mountain snail densities. We provided conclusive evidence that size differences observed among populations were not the artifact of the time of season that populations were sampled. We also provided evidence that growth is not continuous but most likely occurs as conditions allow. We also demonstrated snail activity varies over the summer and management activities could be planned around such times. For example, disruptive activities should probably be avoided in May and June and after rainy periods in late July and August, but may have less impact in September. Growth may be occurring at times of the year not covered in this study.

Additional field seasons would greatly increase reliability of population estimates, provide a greater understanding of survival, and possibly increase understanding of movement of these snails. However, that is not possible with current funding and personnel limitations. Should additional field seasons be conducted, or for those setting up similar studies in different systems, a few recommendations follow. Automatic temperature and moisture recorders should be placed at each site to allow a better understanding of the range of conditions experienced by the snails and to more accurately compare conditions between years. Some soil cores should be taken to provide an understanding of whether (and how deep) snails are moving down into the soil and when (presumably when surface conditions are less favorable). Site boundaries should be defined to allow extrapolation of grid population estimates to actual location estimates. In sites that are especially large, secondary grids could be set up to monitor the variation in density across the site as well as allow for more information on movement.

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