

**LIFE HISTORY OF THE KANAB AMBERSNAIL  
ON NATIVE AND NON-NATIVE HOST PLANTS  
IN GRAND CANYON, ARIZONA**

by Clay B. Nelson

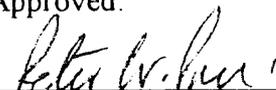
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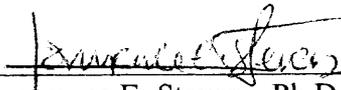
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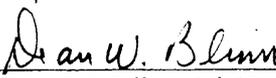
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**ABSTRACT**

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Clay B. Nelson

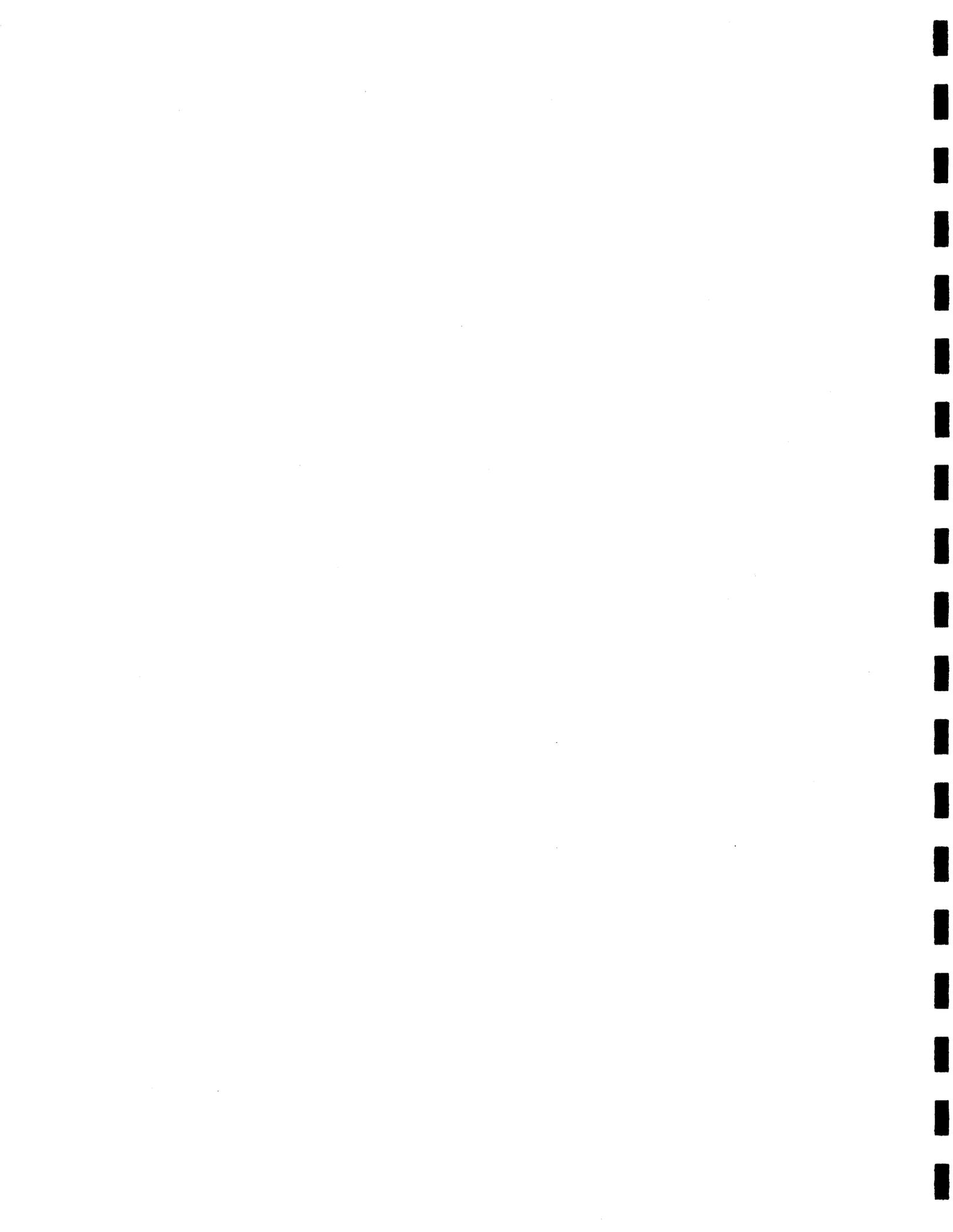
The endangered Kanab ambersnail (Succineidae: *Oxyloma haydeni kanabensis* Pilsbry) is a terrestrial snail that occurs at two locations, both of which are located in the Southwestern United States. Like many endangered species, the Kanab ambersnail was listed due to realized and potential threats to its populations stemming from adverse modification or loss of its wetland habitat. One of these populations exists at a spring in Grand Canyon, Arizona, and is susceptible to habitat loss from the scouring effects of fluctuating flows of the Colorado River released from Glen Canyon Dam. As a result, this population has become the focus of several research, monitoring, and conservation projects with the common goal of balancing species recovery with resource management.

Field investigations have determined that this population occurs primarily on two host plant species, native *Mimulus cardinalis*, and non-native *Nasturtium officinale*. Ecological studies have revealed that snail densities on non-native *Nasturtium* are typically higher than those on *Mimulus* throughout much of the year. Therefore, I studied a population of Kanab ambersnails reared exclusively on each host plant species in a laboratory environment to determine if a shift in host plant utilization to *Nasturtium* has an affect on the life history traits of the snail.

Through the construction of a cohort life table for Kanab ambersnail populations on each host plant species, I found a clear trend of increased performance in the snails

reared on *Nasturtium*. The *Nasturtium* population had faster growth rates, and produced significantly more offspring than those on *Mimulus*. As a result, population densities on *Nasturtium* were also significantly greater than those on *Mimulus*, as observed in the field. However, host plant utilization did not influence hatching success, survivorship, or hatching time. Using lifetime fecundity and survivorship estimates to project population sizes over a 50-year period, the intrinsic rate of increase ( $r$ ) for the population on *Mimulus* was  $< 1$  (indicating a decreasing population) and  $> 1$  on *Nasturtium* (indicating a population increase).

These data are important for future captive population establishment and monitoring techniques for succineid species, and represent the first account of the Kanab ambersnails life history. In addition, this information can be coupled with long-term population and habitat monitoring to more accurately, and less intrusively estimate population dynamics in the field.



## CHAPTER I

### BACKGROUND

Early studies of snail ecology often focused on the impacts snails can inflict on crops (Godan 1983, Villalobos et al. 1995). More recently, snails have become the focus of studies involving anatomy and physiology, genetics, ecology, habitat restoration, and conservation of rare or endangered species (Miller et al. 2000, Daniell 1994, Molloy 1995, Pearce-Kelly et al. 1995). Although this research has contributed a great deal of knowledge to our understanding of the biology and ecology of snails in general, studies concerning the family Succineidae have been few. Consequently, it is not surprising that very little information exists on *Oxyloma*, and even less is available on KAS. Here, I summarize available background information pertaining to the biology, conservation, research, and management of KAS.

### Distribution

Gastropods are the most successful group of mollusks in terms of diversity and niche breadth, with representatives in numerous habitats. The Succineidae is a morphologically diverse group of pulmonate landsnails with worldwide distribution (Patterson 1971). This family is represented by the genera *Oxyloma* Westerlund, *Succinea* Draparnaud, and *Catinella* Pease (Pilsbry 1948). *Oxyloma* occurs throughout the Northern Hemisphere and in South Africa (Pilsbry and Ferris 1911 and Spamer and Bogan 1995). Although the succineids are terrestrial, they are restricted to moist habitats, and are often associated with wetlands, ponds, lakes, rivers, and springs (Harris and Hubricht 1982). *Oxyloma haydeni* has been collected throughout the U.S. and Canada.

However, only two populations of *Oxyloma haydeni kanabensis* are known to exist, both of which are located in the Southwestern United States. These two populations are believed to be Pleistocene relicts of formerly more widespread populations that are now restricted to small wetland and spring fed habitat (Spamer 1993, Spamer and Bogan 1993).

James H. Ferris first collected KAS in 1909 at “the Greens” near Kanab Creek, Utah, but the snail did not receive sub-specific taxonomic status until H.A. Pilsbry revised succineid taxonomy in 1948. By the 1920’s, another population of KAS had been discovered at Three Lakes (3L), approximately 8 km east of the type locality in an adjacent canyon. In the early 1990’s, a malacological survey of the state of Utah determined that the “Greens” type locality population had been extirpated due to water development, and no live KAS were reported from the area (USFWS 1995a). At this time the 3L population was also surveyed and estimated to contain approximately 100,000 individuals. The only other currently known population of KAS was discovered at VP in Grand Canyon in 1991 (Blinn et al. 1992), although no surveys of this population or its habitat occurred until after the species was listed as endangered in 1992 (Fig. 1).

Recent investigations on the distribution of the Succineidae throughout the United States and Canada have revealed several unidentified ambersnail populations in the Southwest and one reported KAS population in Alberta (Harris and Hubricht 1982, Meretsky 2000, Meretsky and North 2000). However, the occurrence of these populations raises concerns about identification methods, and questions the validity and location of the KAS type locality. While the Canada population was identified through

dissection, a re-examination of this population and a thorough identification of the newly discovered (possibly rediscovered) Utah populations are needed to accurately describe and clarify the taxonomy and distribution of this genus and species.

### **Taxonomy**

The limited literature available on *Oxyloma* taxonomy may be partly due to the potential for cryptic evaluation in this family. In general, the Succineidae are referred to as “ambersnails”, due to the amber color of their shells, after death, which are characteristically fragile, have a large aperture to shell length ratio, and are ovate with decreasing whorls coming to a point (Molloy 1995). KAS observed in the field exhibit many of these attributes, but their shells may vary in color from black to yellowish-brown (Fig. 2). Also, some variation in shell shape has been observed throughout developmental stages, causing difficulties in identification of younger snails (personal observation). As a result, members of this family presently require not only anatomical analysis of genital structure, but also the proportion and arrangement of organs, pigmentation of tissue, shape and color of shell, sculpture, whorls, and habitat analysis for identification (Hoagland and Davis 1987). However, substantial variation within populations, potential anatomical change over the lifetime of the individuals, and limited reliability in the differentiation of anatomical structures limit taxonomic resolution in this genus (Franzen 1964), elevating the need for genetic analysis.

## Genetic Taxonomy

Significant genetic differentiation exists among many common and widespread terrestrial mollusk species (Daniell 1994). Uncertainty surrounding the taxonomy of this genus has also become apparent through genetic analyses, which strongly contradict morphological findings. In particular, *Oxyloma* have been found to be more genetically diverse than their morphology suggests, further complicating the identification, and therefore the management of this genus (Stevens et al. 2000).

During an attempt to locate other populations of KAS, two populations of the Niobrara ambersnail (NAS, *O. h. haydeni* Pilsbry) were discovered within Glen and Grand Canyons. One NAS population occurs at -9 Mile in Glen Canyon, approximately 9.5 km downstream from GCD on the Colorado River. The other population occurs at Indian Garden (IG) at 1100 m elevation on the Bright Angel trail in Grand Canyon, approximately 135 km downstream of GCD. Inter and intrataxon genetic analysis of the NAS populations at -9 Mile and IG and the previously known KAS populations at VP and 3L using amplified fragment length polymorphism (AFLP) techniques revealed, "all four locations contain genetically distinct and unique populations... and statistical analysis indicate that this differentiation is highly significant." (Miller et al. 1997 and 2000). Furthermore, this analysis revealed no evidence of recent bottlenecks in the populations, suggesting that the individual populations have occurred at their localities for prolonged periods.

In an effort to further clarify genetic and morphological discrepancies, Stevens et al. (2000) performed a "double-blind" analysis of mitochondrial DNA in conjunction with traditional morphological taxonomic identification methods on a suite of *Oxyloma*

and other succineid populations from the United States and Canada, including specimens from VP, 3L, -9 mile, IG, and the previously identified KAS populations in Canada. Results from these analyses support Miller et al's. (2000) findings, and reveal that the VP population is genetically unique compared to the other *Oxyloma* populations, including the other known KAS population at 3L. However, morphologically, it is indistinguishable from 3L. Specimens collected from the location in Alberta and previously identified as KAS by Harris and Hubricht (1982) were morphologically and genetically identified as NAS. Moreover, specimens collected from another location in Alberta were morphologically identified as KAS, but were determined to be genetically distinct from both the VP and 3L populations. Possible explanations for such discrepancies could be attributed to an increase in the range of the species causing an overlap, or a misidentification of the original species collected from the Canada site (Stevens et al. 2000). Also, specimens collected by Meretsky (2000), at what is believed to be the "Greens" type locality were morphologically and genetically identified as NAS, although further investigation of this site is needed to determine if KAS and NAS co-occur there, or if the population is exclusively NAS (Stevens et al. 2000).

In summary, the current status of *Oxyloma* taxonomy and genetics is in a state of confusion. While recent analyses have addressed the amount of genetic differentiation among some ambersnail populations, they have also revealed contradictions between morphological and genetic taxonomy. However, it appears that the KAS population at VP is unique, even with respect to the KAS population at 3L. These findings validate present concerns regarding the protection of the KAS population at VP, and also warrant

further morphological and genetic investigations of other *Oxyloma* populations throughout the United States and Canada.

### Study Areas

Habitat has been characterized for both the 3L and VP KAS populations, although little research has been conducted at 3L due to its location on private land. Habitat at this site is composed of marshland dominated with sedges (*Juncus* spp.) and large cattails (*Typha domingensis*) interspersed around several small ponds. Surveys of this population have been conducted intermittently throughout the late 1990's and reveal a large, relatively stable population of KAS (V. Meretsky, pers. comm.). Potential disturbances to this population include livestock grazing, water development, and flash flooding (V. Meretsky, pers. comm.).

Vaseys Paradise is a cool dolomitic spring that flows directly from the Mississippian Redwall limestone into the Colorado River, approximately 53 km downstream of Lees Ferry, Arizona (Fig. 3). The nearly uni-thermal water issued from the spring forms several small rivulets that flow approximately 100 m down a steep gradient covered with patches of lush vegetation to the mainstem of the Colorado River. Threats to this population include fluctuations of the Colorado River, as well as disturbance from human visitors, freezing in harsh winters, and falling debris from the talus slope above.

Dense patches of native monkeyflower (*Mimulus cardinalis*) and non-native watercress (*Nasturtium officinale*) characterize the majority of VP habitat. Poison ivy (*Toxicodendron rydbergii*), common reed (*Phragmites australis*), horsetail (*Equisetum*

spp.), water sedge (*Carex aquatilis*), maidenhair fern (*Adiantum capillus-veneris*), and lesser amounts of rushes, grasses, trees, herbs, and mosses also occur throughout the site (Stevens et al. 1997a).

Native *Mimulus* is distributed throughout the Southwestern United States and is commonly associated with wet habitats. It is a perennial herb with creeping rhizomes that reproduce vegetatively, but also has been observed reproducing by seed. These plants grow to over 1 m in height, producing long sticky stems and leaves covered with dense trichomes. Dead *Mimulus* leaves and stems remain somewhat intact and provide feeding and overwintering substrates for KAS.

Non-native *Nasturtium* is an aquatic annual herb native to Europe and widely naturalized in the United States. Historical recordings of *Nasturtium* in Grand Canyon date back to Clover and Jotters 1938 expedition (Clover and Jotter 1944). *Nasturtium* is found at many springs in Grand Canyon and makes up about 15% of the overall habitat at VP, forming large rootmats that cover saturated bedrock and soils (L. Stevens, pers. comm.). *Nasturtium* is known to contain anti-herbivore secondary chemistry, consisting of several compounds that deter feeding insects and animals when the plant tissue is damaged (Newman et al. 1992). *Nasturtium* is susceptible to frost, although any portion of the plant remaining submerged may survive if the water remains unfrozen (Simon et al. 1984).

Air temperature at VP range from  $< -10^{\circ}\text{C}$  in winter to  $> 45^{\circ}\text{C}$  in the summer, with a bimodal precipitation pattern. The east facing aspect of the spring allows for relatively quick thawing in winter and protects the site from extremely hot temperatures during summer afternoons. Spring outflow and temperatures have been measured during

field monitoring and range from: 14.5 °C, 0.02 m<sup>3</sup>/s in April, 14.5 °C, 0.18 m<sup>3</sup>/s in May, 17 °C, 0.07 m<sup>3</sup>/s in July, to 16.5 °C, 0.02 m<sup>3</sup>/s in September.

## **Ecology**

Monitoring of the VP population has occurred quarterly since March 1995 and has provided valuable information regarding KAS ecology and population dynamics. The following information is a summary, derived from the ecological report by Stevens et al. (1997a). Monitoring efforts at VP include surveying patches of host plant vegetation for overall patch size and snail densities. In addition, each vegetation patch is topographically mapped using a total station survey instrument and data recorders to determine patch area. Each patch is haphazardly sub-sampled by researchers using a 20-cm diameter ring and recording vegetation type, height, coverage, distance to patch perimeter, duff and litter depth, soil type, soil moisture, and soil depth. Snails are sought in each plot and their length and location are recorded. Snail densities from plots are bootstrapped to estimate the mean density within each patch, and totaled to estimate overall KAS population size at VP (Efron and Tibshirani 1993). Repeated surveys are used to track changes in habitat size and composition through time. The population estimate is coupled to a stage to discharge relationship model (Randle and Pemberton 1988), and used to predict the number of snails and area of habitat threatened by inundation at various river discharges from GCD. Using these methods, estimates of the KAS population at VP has ranged from 104,004 individuals in September, to as few as 18, 476 individuals in March 1995. Analysis of KAS densities on each host plant type reveal no significant differences were found between *Nasturtium* and *Mimulus* in March

and June 1995. However, KAS densities were significantly higher on *Nasturtium* in August (205.5 snail/m<sup>2</sup>, SD = 211.8, n = 11; 44.1 snails/m<sup>2</sup>, SD = 6.94, n = 13, Mann-Whitney U = 35.5, P = 0.03, DF = 1; respectively) and September 1995 (356.8 snails/m<sup>2</sup>, SD = 314.89, n = 45; 84.9 snails/m<sup>2</sup>, SD = 34.14, n = 34, Mann-Whitney U = 284.5, P < 0.0001, DF = 1; respectively). It should be noted that variability in sampling exists throughout the VP site due to the fragile nature of the habitat and possible sampling error among researchers. In addition, the cryptic nature of KAS makes finding and identifying snails in some vegetation very difficult. Therefore many vegetation patches are only surveyed around the perimeter to avoid trampling habitat, which falsely assumes that snails are distributed evenly throughout each patch.

Analysis of size class distributions from these studies indicated that KAS live from between 12 and 15 months, with peak reproduction occurring in mid-summer. KAS have been observed producing gelatinous egg masses containing up to 25 eggs, typically depositing them on the underside of host plant stems and leaves. Winter dormancy is initiated in October and emergence from dormancy typically occurs in March. Dormant KAS have been observed withdrawn into their shells and sealed to a firm substrate. Although the causes for such large seasonal differences in population size are currently unknown, high mortality attributed to unsuccessful winter dormancy has been suggested.

### **Parasitism**

While monitoring the KAS population at VP, researchers have periodically observed snails parasitized by the flatworm trematode *Leucochloridium cyanocittae* (Stevens et al. 1997b). Parasitism rates have ranged between 1% and 10% since 1995 and are determined by dividing the total number of parasitized snails by the total number of mature (> 10 mm)

KAS surveyed during each monitoring trip (Stevens et al. 1997a). Parasitism has not been observed in snails < 10 mm in length, or in other snail species found at VP, including *Catinella*. Monitoring of the KAS population at 3L reveals that parasitism also occurs at this site.

The life cycle of the genus *Leucochloridium* is especially adapted for intermediate infestation of a succineid species with final infestation of a passerine host (Baer 1971). Parasitized snails are visually identified by the presence of one or two large pink and green sporocysts clearly visible in the snail's body and eyestalks. Each sporocyst contains numerous metacercariae, up to 100 individual wormlike cercariae packed together in a protein covering known as a brood sac. The pink and green-banded metacercaria-filled sporocysts can grow to a length of 12 mm, and pulsate rhythmically through the snail's eyestalk when exposed to light (Fig. 4). It is thought that this motion attracts birds. The snail's eyestalk only needs to be touched by a bird's beak or leaf to eject the sporocyst, which is subsequently eaten by the bird. The trematodes develop in the bird's gut and produce eggs, which are expelled in the bird's feces. If ingested by another intermediate mollusk host, the process may start all over again. The presence of a parasite may damage the snail's eyestalk, but it does not necessarily kill the host snail. Live KAS have been observed at VP with damaged eyestalks, presumably resulting from sporocyst expulsion. Observances of a parasitized snail reveal that they are also capable of reproduction, although fecundity is likely reduced (Esch and Fernandez 1994).

### **Predators**

Landsnails have numerous predators including insects, mammals, birds, and other snails (Godan 1983). Possible KAS predators at VP include several bird species, mice,

and possibly carabid beetles. However, during the past five years, direct observations of snail predation are limited to a single case involving a deer mouse (*Peromyscus* sp.) (V. Meretsky, pers. comm.). Further studies on the VP *Peromyscus* population have shown that these mice do occur throughout the year, and may potentially affect the size of the KAS population (V. Meretsky, pers. comm.). Experiments conducted by Nelson (unpublished) failed to reveal any intact portions of a snail's hard body parts (shell or radulae) in feces collected from the *Peromyscus* population at VP. A number of bird species also occur at VP and could be potential KAS predators, including Common Ravens (*Corvus corax*), American dippers (*Cinclus mexicanus*), and various flycatchers although no direct observations of snail predation have been confirmed. Predation of snails at the 3L population by birds has been observed, but identification of the snail species was unknown.

### **Management**

Management for individual species often conflicts with ecosystem management (Stevens and Wegner 1995). Although ecosystem management is intended to consider all physical, chemical, and biological components of a system, it has been criticized for neglecting individual species (Meretsky et al. 2000). As more ecosystems are manipulated by human activities, management practices are required that integrate human uses and ecosystem functions (Vogt et al. 1997). Depending upon the ecosystem, habitat types, species, and range of human uses, such decisions may become exceedingly complicated. This dilemma is exemplified in the management of the Colorado River through Grand Canyon and the conservation of KAS.

The U.S. Fish and Wildlife Service (USFWS) federally listed KAS as endangered in 1992. As a result, the USFWS drafted a recovery plan outlining several recovery objectives to assist in the downlisting of KAS, including: 1) reduced human impacts on known KAS populations, 2) protection of currently known populations, 3) inventory of suitable habitat, 4) ecological studies, 5) establishment of a captive population, and 6) improved communication and education.

In 1995, an Environmental Impact Statement on the Operation of GCD recommended that the flow regime be altered to include Beach/Habitat Building Flows (BHBF) aimed at restoring the Colorado River back to a more natural ecosystem. In March 1996, the hydrograph of the Colorado River was increased to 45,000 cfs; increasing sediment transport in the water column that settled out in eddies with the intent of enhancing beaches and backwaters. However, the BHBF flows were determined to conflict with the conservation of the KAS population at VP by inundating and scouring away snails and habitat.

In an effort to mitigate the effects of the BHBF on the KAS population at VP, the USFWS also issued two Biological Opinions (BO's) in 1995 and 1998, which advocated: 1) limits on incidental take of snails and habitat at VP, 2) additional surveys and monitoring, 3) the establishment of a refugia population, and 4) the discovery or establishment of a secondary population of KAS in Arizona (USFWS 1995b and 1998). Collectively the Recovery Plan and BO's have defined the direction of research, monitoring and conservation for KAS, leading to more informed decisions regarding dam operations and the management of the Colorado River Ecosystem.

Bureau of Reclamation-sponsored monitoring of the KAS population at VP has been the main source of information on KAS ecology and population dynamics. Also, an interagency team consisting of several cooperators has conducted surveys of 150 springs in the Southwestern United States in an effort to locate other populations of KAS and evaluate potential secondary population establishment sites (Sorensen and Kubly 1997 and 1998). Since September 1998, the Arizona Game and Fish Department (AGFD) has translocated 900 snails from VP to three separate sites throughout Grand Canyon in an attempt to establish a secondary population within the state of Arizona. Monitoring of these sites has continued since this time and has included the addition of approximately 50 snails per location to ensure genetic variability and increased sustainability. To date, one site has shown positive results, with reproduction and successful over wintering occurring (Sorensen and Nelson 2000). The other two sites have not been successful, which may be attributed to low population stock sizes (150 snails), difficulties in sampling, and sensitivity of snails to slight changes in environmental conditions (Sorensen and Nelson 2000).

Following the successful establishment of two experimental captive populations of KAS for research reported in this study, the AGFD partnered with The Phoenix Zoo (TPZ) to establish a fully protected, non-experimental refugium population of KAS on zoo grounds. On May 27, 1999, 50 KAS of various size classes were collected from VP and released in the Phoenix Zoo refugium. On April 28, 2000, an additional 50 KAS were collected from VP and added to the refugium to maintain adequate population size and genetic diversity. However, since September 2000, no KAS have been located in the enclosure, and it is assumed that the population has expired. Reasons for the

unsuccessful long-term establishment of this population may be attributed to a small initial stock size and high ambient air temperature coupled with low humidity during summer months, creating less than optimal environmental conditions (Nelson and Sorensen 2000).

While these projects provided managers and scientists with important information regarding KAS, uncertainty pertaining to management practices and future conservation needs still exist. To resolve some of these issues, an expert panel was convened in December 1999 to review the current body of knowledge surrounding KAS and provide possible recommendations for future research, monitoring and conservation of KAS. Panel members included conservationists, malacologists, geneticists, and population biologists. The review panel ultimately produced a report consisting of general conclusions and recommendations (Noss et al. 1999). These recommendations include 1) additional genetic and morphological studies, 2) additional habitat studies, 3) no more translocations, 4) encouragement of artificial "floods" up to historical levels (> 45 K cfs), 5) minimally invasive monitoring of VP, 6) no active mitigation necessary for VP population, and 7) a re-assessment of the current recovery plan and inclusion of new information.

## **DISCUSSION**

Since KAS was listed as endangered in 1992, great progress has been made toward better understanding this species and the issues that surround it. However, finding a balance between the conservation of KAS and the management of the Colorado River Corridor continues to be an enlightening challenge. While efforts have focused on

the recovery process, many uncertainties regarding the conservation of KAS continue to hinder the implementation of a management plan. Long term trends in population dynamics, minimum viable population size, distribution, life history, and genetics and taxonomy of this genus all need to be addressed in order to prioritize management and conservation objectives.

The successful establishment of a second population of snails from VP to another location within the Grand Canyon was a major step in the management and conservation of this species. However, the ethics involved in the establishment of this population has been a point of contention among managers and scientists alike. While the establishment of this population accomplished recovery objectives and relieved some management pressures from the VP population, the introduction of a species to "new" areas always brings scrutiny. Although all environmental compliance needs were met before translocations occurred, the historic range of the species, competition, predation, and the potential for the introduction of parasites and diseases into a new area have all been questioned. These are valid concerns, the co-occurrence of KAS and other species at VP, relatively low potential for competition or species displacement, ambiguity surrounding its taxonomy, and benefits to management and conservation in an continuously altered environment definitely cloud the line between conservational ethics and management. Nonetheless, it has been concluded that no further translocations will take place, although the continued need to augment the population for genetic viability will likely become another point of discussion.

It has been suggested that a less intensive management approach be taken in the future regarding the KAS population at VP. Using monitoring data collected over the

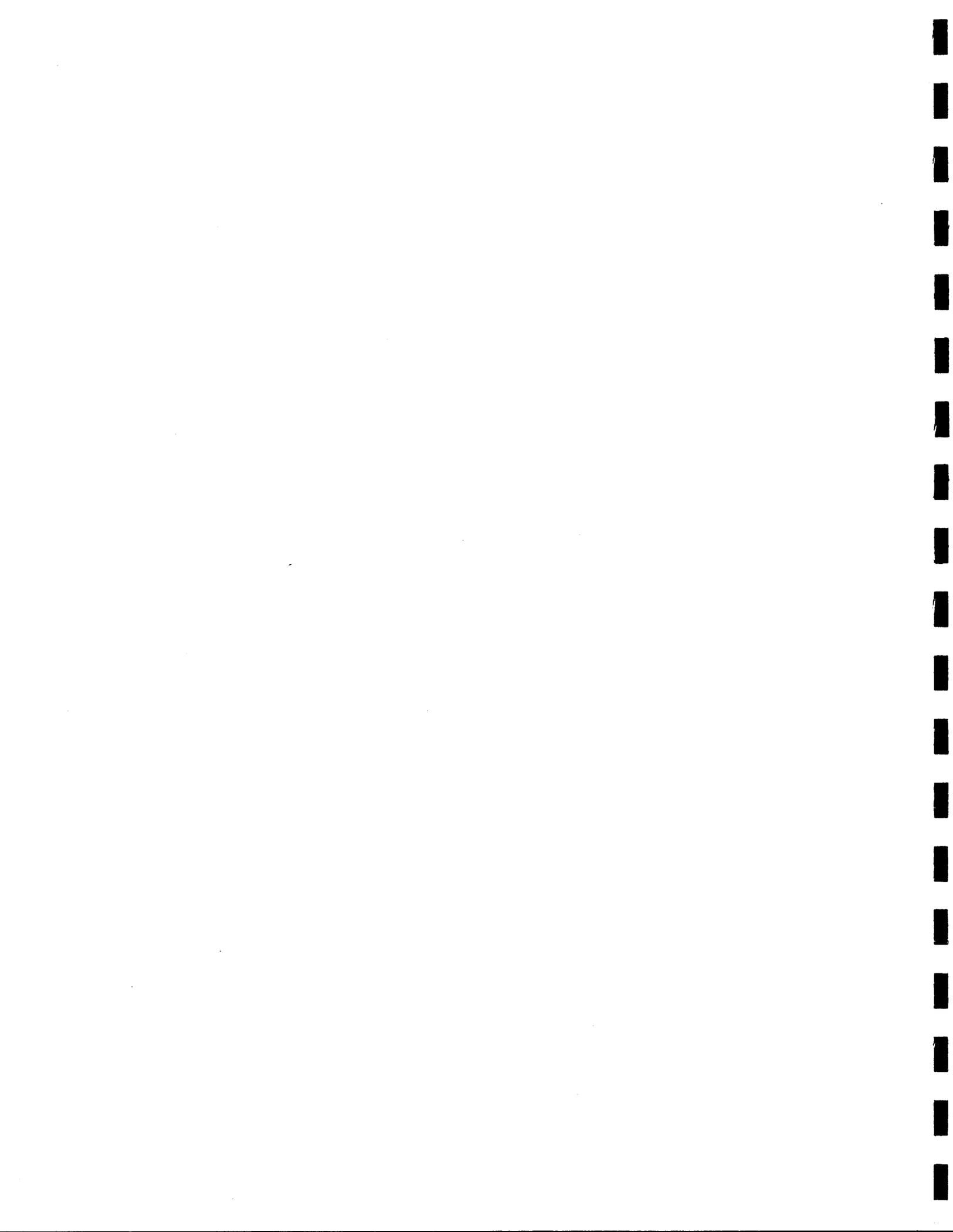
past half decade, coupled with life history data presented in this thesis and new analysis on sampling error and design (Sorensen 2001), a less intrusive population-monitoring program may be used. This approach is further supported by the assumption that this population has persisted at this site through historic floods that are much greater than what the population and habitat are now experiencing. However, many unknowns still exist with respect to the KAS population at VP. For these reasons, it is in our best interest to error on the side of caution when it comes to the management and conservation practices that will affect this population.

For instance, we currently do not know how KAS at VP are distributed throughout the habitat, nor do we know how much habitat and/or how many snails can be lost before extinction at this site occurs. Thus far, decisions have been made based on the assumption that pre-dam conditions were much like the conditions today. It is likely that climatic conditions have remained relatively similar throughout the past century, but other processes interrupted by the dam may have more serious implications that cannot be resolved. Potential source populations of snails may have existed in Glen Canyon, which dispersed to VP during large flood events. These same events may have also allowed for snails to be dispersed from VP to other locations throughout the Colorado River corridor by floating on vegetation that was scoured from the site.

Possibly the most notable reason for taking a conservative approach with respect to the management of the KAS population at VP is the current state of confusion regarding the taxonomy and genetics of this genus. Clarification of this taxon may have serious implications regarding the management and conservation of several currently protected and unprotected populations of ambersnails, although all indications suggest

that the VP population is entirely unique, and should therefore be managed accordingly. As the taxonomy and genetics of other ambersnail populations throughout the Southwest are examined, the classification of each population will ultimately need to be determined by a standard method, with an outcome that will need to be accepted by scientists and managers alike.

The challenge remains in the ability of special interest groups, managers, and scientists to incorporate new information into their decisions as it becomes available, and to make compromises based on evidence at hand. Through this process, the conservation of KAS and management of the Colorado River ecosystem can both be achieved. Although the public does not regard snails as "heroic" species, the story of KAS in Grand Canyon is noteworthy. The importance of this species and the issues that surround it have implications that extend far beyond the realm of Grand Canyon, setting a precedent for the conservation, research and monitoring of numerous snail species and their habitats in arid regions.



## CHAPTER II

### ESTABLISHMENT AND MONITORING OF CAPTIVE KAS POPULATIONS

#### INTRODUCTION

An important component for the research and recovery of some species is the establishment of captive populations. These populations provide unique opportunities for research on various life history traits and ecological responses in a controlled environment. For endangered species, captive populations may serve as refugia for furthering research, conservation, and recovery efforts. For KAS, the establishment of a captive population is a primary objective for its recovery, and also allows for more specific research on population dynamics and life history traits.

Here, I summarize the establishment and monitoring of two captive populations of KAS and native and non-native host plant material. Propagation and maintenance techniques, plant phenology, and general snail population dynamics on both plants are also examined. The establishment of a captive population is a delicate and sometimes controversial process. Nevertheless, captive population establishment has become a common tool for the research, conservation, and reintroduction of many species. Captive populations have been established for several species, including black footed ferrets, California condors, and several endangered fish species. However, this process can pose difficulties such as inadequate construction and maintenance of habitat and environmental conditions, resulting in captive reared species failing to reproduce or survive a second generation. Furthermore, successfully reared captive populations often have problems assimilating back into their natural environments due to human influences, and changing environmental conditions. (e.g. California condor, wolves, ferrets, etc.)

Captive colonies have been successfully established for several invertebrate species with the intent of research rather than conservation and reintroduction. More recently, the population establishment of several species of rare or endangered snails has been attempted for research and conservation purposes. However, rearing land snails in artificial environments has proved difficult, mainly due to the sensitivity of snails to small changes in temperature, humidity, diet, and damage related to habitat sampling and monitoring (Pearce-Kelly et al. 1995). Other concerns for rearing snails include density dependant changes in population size and structure, including differences in growth rate, altered competitive hierarchies, lowered fecundity, reduced movement rates, genetic constraints, and adaptation to artificial conditions (Pearce-Kelly et al. 1995, Stiven and Foster 1996, Foster and Stiven 1996a and 1996b). However, if the habitat is adequate, and the founding stock of snails is an appropriate size, population establishment and regeneration can be accomplished. Molloy (1995) successfully propagated several generations of the of the endangered Chittenango ovate ambersnail (*Novisuccinea chittenangoensis*) and several captive breeding programs for the endangered Polynesian tree snail (*Partula* spp.) have produced over 24 populations at zoos and laboratories across Europe and North America (Tonge and Bloxam 1991, Pearce-Kelley et al. 1995).

Due to the endangered status of KAS, the susceptibility of its habitat to human caused impacts (i.e., commercial and water development projects in Utah, high flow releases from GCD in Arizona, recreational visitation impacts), and the difficulty of sampling in the field, creation of a captive population was recognized as an important step in learning more about this taxon. While the primary purpose of these populations is to facilitate research on KAS life history and population dynamics on native and non-

native host plant species, they also provide important information on establishment and monitoring of future populations of endangered snails. In addition, captive populations serve as sources of public education on biological research, endangered species conservation, and ecosystem management. This research was conducted with permission from the U.S. Fish and Wildlife Service and the Arizona Game and Fish Department.

## **METHODS**

Captive populations of KAS were established at two locations. The first population was established at an indoor greenhouse facility at Northern Arizona University (NAU), in Flagstaff, Arizona (elevation 2133 m). This facility provided a secure environment in which to rear KAS and allowed for the manipulation of environmental variables for experimentation. The second population was established at the base of GCD in Page, Arizona. Although this population is contained within enclosures, photoperiod and other environmental conditions were found to be similar to those measured at VP, and are therefore considered to be a semi-natural environment.

### **Enclosure Design**

KAS enclosures at the NAU greenhouse facility were designed and constructed to isolate groups of snails on each host plant species for general monitoring of population dynamics, and to provide a parent population for life history studies. Enclosures needed to hold gravel, soil, vegetation, and prevent snails from escaping. Four enclosures were constructed from 5 mm thick Plexiglas welded together to form a long narrow chamber (150 cm long x 30 cm wide x 30 cm tall). Each chamber was sub-divided into five

separate cells approximately 30 x 30 x 30 cm in size. Each enclosure has a series of small holes in the bottom for drainage, and a 0.5 mm mesh screen top sealed with a re-sealable non-toxic adhesive (Fig. 5). Temperature and humidity are continually regulated and were kept at a relatively constant 20<sup>0</sup> C and 30% humidity. Photoperiod was maintained using natural light and increased to 14 h of light/d in the spring and summer to induce reproduction.

Preliminary surveys of the GCD compound were conducted to evaluate the solar energy budget, water quality, protection from natural and human disturbances, and ease of viewing for public tours. A Solar Pathfinder™ was used to measure the amount of direct solar radiation at the dam in relation to that at VP. With these considerations in mind, a site was chosen in the sluiceway at the base of the dam. This site closely matched the photoperiod at VP, required minimal maintenance, and provided a protected location for monitoring. An educational panel describing KAS natural history and management concerns was developed and placed near the site.

Due to the location of the GCD site, enclosures were constructed for ease of sampling and to endure outdoor conditions. A total of nine enclosures were built of 5 mm Plexiglas (1m long x 1.5 m tall x 0.5 m wide). The enclosures were covered with 1 cm mesh hardware cloth to protect the snails from predation and falling debris from the face of the dam. Under the hardware cloth was a fine (0.5 mm) mesh screen, which provides slight shade and keeps snails from escaping. Each enclosure was raised on cinder blocks to allow water fluctuations in the sluiceway to flow through holes in the bottoms and sides, saturating the lower gravel-soil layer and provide soil moisture for host plant roots (Fig. 6).

### **Host Plant Propagation at NAU**

In September 1996 both KAS primary host plants (*Nasturtium* and *Mimulus*) were collected from VP and transported to the NAU laboratory facility. Two enclosures were stocked with *Nasturtium*, and two were stocked with *Mimulus*. Plants were placed on a base of 2 cm gravel and 2 cm potting soil in all five individual 30 x 30 x 30 cm cells within each enclosure and several rocks and sticks were added to provide habitat. All enclosures were watered daily by drip system using city water and fertilized monthly with Miracle Grow™ commercial fertilizer, using the manufacturers recommended quantity. All plants were monitored on a biweekly basis for health, growth, and seed production. Plant growth rates were obtained by randomly selecting plants from each cell and measuring the distance from the base to the terminal apex on a bimonthly basis. Flowering plants were sampled to determine mean seed production. Seed viability was examined by collecting seeds from each plant type and storing them for up to six months. At monthly intervals, seeds were removed from storage and placed in wetted petri dishes and germination success was recorded.

### **Host Plant Propagation at GCD**

In May 1998, host plants were introduced into a prototype enclosure at GCD. Plants were monitored for survival, potential inundation, predation, and other disturbances for 3 mths. Once the propagation of host plants in the prototype was deemed a success, eight more enclosures were constructed and placed in the sluiceway in the same manner. Three enclosures were propagated with *Nasturtium*, three with *Mimulus*, and three contained 50% *Mimulus* and 50% *Nasturtium* (mixed vegetation).

All enclosures were stocked with bark, branches and rocks as substrata for overwintering snails.

### **Snail Propagation and Monitoring at NAU**

In August 1997, 248 KAS were collected from VP and placed in Tupperware™ containers with small amounts of host plant material and moist paper towels to maintain humidity. The containers were placed in a cooler and monitored to ensure proper temperature during transport to the NAU facility. In the laboratory, snails were equally distributed into each of the 20 cells containing their respective host plants in each of the two enclosures, averaging approximately 12 snails per cell. All snails collected were < 4 mm in length to limit the extent of possible trematode parasitism.

Snails were initially measured during collection in the field, and again as they were placed on their respective host plants in the laboratory. Measurements were obtained by placing the snail on a ruler and recording the length of the shell from the apex whorl to the front of the shell. All measurements were taken to the nearest 0.5 mm. When snails reached a minimum size class of 5 mm, approximately 100 snails on each host plant were marked using small color coded number tags, fixed to their shells with a minute amount of non toxic adhesive. At biweekly intervals, marked snails were collected from each cell, measured to the nearest 0.5 mm and placed back into their cells. Because damage to host plant vegetation was kept at a minimum, all snails were not relocated during each census. However, snails that were missed during one census were often located in a subsequent census. The difference in shell length was divided by the time between measurements to produce an average growth rate per day for snails on each

host plant species. A two-sample t-test was performed on these rates to determine if a significant difference exists.

A census of the entire population of snails was taken each month. Each census consisted of a ten-min search for snails in each host plant cell. This period was determined by searching cells for all snails and timing the effort. After a ten minute search, the rate of discovering new snails decreased markedly and was not worth further effort. All snails found during each census were measured and placed back on their respective host plants in each cell from which they were removed. Mortality was recorded by measuring and removing all dead snails from each host plant cell. However, shells were removed at irregular intervals and did not coincide with growth measurements or population censuses. When photoperiod began to decrease in the fall, all enclosures were moved to a greenhouse with a mean temperature of 15 °C and 75 % humidity to more closely represent dormancy conditions found in the field. As photoperiod increased in the spring, enclosures were moved back to the original greenhouse. In an effort to minimize disturbance, snails were not sampled during the dormancy period of late October through early March 1998. A surplus of KAS was created by farming an equal amount snails from both host plant enclosures in the laboratory at times when both populations were experiencing new recruitment. These snails were placed in an extra enclosure containing a mixture of both host plant species and maintained for future population establishment at GCD.

## **Snail Propagation and Monitoring at GCD**

On September 24, 1998, a total of 450 KAS were collected from the surplus created by the previously established NAU captive population and introduced to each of the nine enclosures at GCD. Fifty KAS were placed in each of the nine enclosures containing the three host plant assemblages. Due to the larger size of the enclosures at GCD, monitoring occurred on a monthly basis and consisted of a qualitative assessment of vegetation composition and health. Censuses of each enclosure were conducted for 15 minutes using previously established timing criteria from the NAU population. All snails found during each census were measured to the nearest 0.5 mm and returned to their enclosures. All dead snails were measured and removed from the enclosures during each census. Percent mortality was calculated by dividing all dead snails by the total number of live snails found in each plant enclosure during each census. Dormant snails were typically measured, but not removed from their dormancy location. Snail densities within each enclosure were lower than densities found in the field over a similar area and habitat type, and were therefore not believed to have had an influence on the overall population dynamics within each enclosure.

## **RESULTS**

### **Host Plant Propagation at NAU**

Host plant propagation at NAU was successfully accomplished. Conditions in the laboratory were conducive to plant growth, and plants flourished within days of being transplanted. *Nasturtium* growth rates varied throughout plant development. Plants grew approximately 15 cm high, and then began to spread out. Mean stem growth was 0.97

cm/month ( $SE \pm 0.33$ ,  $n = 14$ ) under a natural light regime from August to March.

Younger plant tissue was often softer and lighter in color, but leaves and stems became thicker and darker as the plant matured. Reproduction occurred when the natural photoperiod increased to that of spring and summer conditions. Plants produced several seedpods each containing an average of 30 seeds ( $SE \pm 8.7$ ,  $n = 30$ ). Seeds stored at laboratory conditions ( $20^{\circ} C$  and 30% humidity) remained viable for up to six months, and readily germinated in wet conditions.

Growth rates for *Mimulus* also varied throughout plant development. As plant growth decreased, stems became more structurally supportive. Mean growth rate for *Mimulus* was 1.84 cm/month ( $SE \pm 0.35$ ,  $n = 28$ ) under a natural light regime from August to March. *Mimulus* flowered and produced seedpods throughout the experiment. New shoots continually germinated from existing root masses and produced viable seeds through cross and self-pollination. Seeds stored for six months in laboratory conditions ( $20^{\circ} C$  and 30% humidity) also germinated, though not to the extent of the *Nasturtium* seeds.

#### **Host Plant Propagation at GCD**

The establishment of host plant vegetation in the captive breeding enclosures at GCD was also highly successful. Within the first month, vegetation in all nine enclosures flourished and required only thinning as maintenance. The root masses of all host plant vegetation successfully tapped into the water table created in the base of each enclosure and therefore negated the need for watering by hand. Although plant phenology was not

recorded for vegetation at GCD, it was observed that neither host plant species died back over the 1998 winter season as often observed at VP.

### **Snail Propagation and Monitoring at NAU**

Laboratory experiments revealed KAS growth rates differ significantly between non-native *Nasturtium* and native *Mimulus* ( $t = 0.954$ ,  $P = 0.026$ ; Fig. 8). The mean growth rate for KAS on *Nasturtium* was 0.109 mm/day, (SE  $\pm$  0.008,  $n = 78$ ), while KAS on *Mimulus* grew an average of and 0.088 mm/day (SE  $\pm$  0.007,  $n = 84$ ). Initial sizes of KAS used for growth measurements ranged from 7 mm to 12 mm, and excluded juvenile snails that could not be individually marked (Fig. 7).

A monthly census of the population on both host plants revealed that the mean population size for KAS on *Nasturtium* was significantly greater than on *Mimulus* for most samples (sign test,  $P = 0.001$ ) (Fig. 8). After the initial release of snails into all enclosure cells, an immediate decrease in population size occurred in September 1997 and continued through winter dormancy in October 1997. A post dormancy census in March 1998 revealed a large peak in population size on *Nasturtium* (mean 53.8, SE  $\pm$  25.56) followed by a smaller peak in the *Mimulus* population (mean = 14.3, SE  $\pm$  1.63) in April 1998. Reproduction in the *Nasturtium* population occurred earlier and produced more juveniles than the *Mimulus* population ( $t = 1.92$ ,  $P < 0.05$ ). However, mortality in the *Nasturtium* population was disproportionately higher than on *Mimulus*, resulting in almost equal population sizes by September 1998 (mean 7.2, SE  $\pm$  1.31 and 4.7, SE  $\pm$  1.15, respectively). A second, smaller reproductive pulse was observed in both

populations, although its magnitude was much smaller on *Nasturtium* than the previous pulse, and was similar in size to the population on *Mimulus* (Fig. 9a and b).

Due to the length of time between each census, it was difficult to relocate egg masses for continued monitoring. Egg masses were consistently found in moist areas on the underside of leaves and stems of both host plants, though number of egg masses, eggs per mass, time to hatching, and hatching success were not recorded during this phase of the research (See Chapter 3).

Mortality size-class frequencies were similar for snails on both host plant species, although the overall size-class distribution of dead snails on both host plants differed significantly (Chi Square = 19.5,  $n = 366$ ,  $P < 0.05$ ). Overall mean size class of dead snails collected from both host plants also differed ( $t = -4.12$ ,  $P < 0.0001$ ). Dead KAS collected from *Nasturtium* totaled 213 individuals and had a mean length of 8.2 mm (SE  $\pm 0.16$ ), totaling approximately 37% of the dead KAS on this plant. Dead KAS collected from *Mimulus* totaled 153 individuals with a mean length of 9.2 mm (SE  $\pm 0.19$ ). Approximately 38% of dead KAS collected from *Mimulus* were also in the 8 to 10 mm size class range (Fig. 10). Both populations exhibit a linear increase in mortality frequency in relation to size until 8 to 10 mm, followed by a decrease in mortality frequency with increasing size.

### **Snail Propagation and Monitoring at GCD**

Captive population dynamics did not differ between plant assemblages at GCD, except for slight variations in recruitment and mortality, likely attributed to sampling error. Approximately one month after the initial release of 450 snails at GCD, a 70%

decrease in population size was observed, which continued in subsequent surveys through November. However, in late November, populations on all host plant assemblages increased slightly due to new recruitment. However, by December 1998, the population decreased and stabilized at approximately 10 individuals per host plant through February 1999. After the January 1998 to March 1998 dormancy, populations on all host plant assemblages increased to approximately 20 individuals as a result of new recruitment in the spring (Fig. 11).

Percent mortality also did not differ among plant types. Although mortality increased markedly, from the initial release of snails and reached a maximum during December 1998. From January 1999 through the last survey in June 1999, mortality slowly decreased until it was less than 30% of the total population on all plant types (Fig 12). The observed pattern of increased mortality during the winter months closely resembles field observation up to 80% over-wintering mortality (Stevens et al. 1997a).

Percent dormancy was related to the percent mortality. Dormancy was first observed in October 1998 but was not common until November of that year, when 30 to 40 % of all snails sampled were dormant (Fig. 13). Sampling during winter months was curtailed to reduce the possibility of dislodging dormant snails. After sampling resumed again in May 1999, no dormant snails were located. Population samples in May and June also revealed juvenile snails on all host plant assemblages indicating a portion of the snails had survived winter dormancy and successfully reproduced.

Size class histograms for active snails show similar distributions on all plant assemblages through time, with juveniles occurring on *Nasturtium* and mixed plants in November 1998. Dormancy was not restricted to any particular size class or plant

assemblage. Mortality size class distributions reflect the general distribution of the live population, with slightly more snails found in the 7 to 11 mm size class range, although small shells are less likely to be located during sampling due to decomposition and fragility, and may therefore not be fully represented in the mortality histograms.

## DISCUSSION

### Host Plant Propagation at NAU

*Nasturtium* growth in the laboratory may have been restricted by cell size, given that no plants grew past the height of the cell or obtained sizes comparable to unconstrained plants observed in the field. The availability of water may also have been a factor in plant growth. Although plants received adequate water, those exposed to additional water did grow more vigorously. *Mimulus* was less restricted by the enclosures and required trimming. Plant trimmings were placed back in the enclosures to provide a layer of duff and litter that was readily utilized by snails in those cells. *Mimulus* in the laboratory were similar to those observed in the field and flowered several times throughout the year under a natural photoperiod. Seed viability experiments did not involve counting successful germination and were simply presence or absence observations, however, seeds from both plants successfully germinated after six months. The ideal growing conditions within the laboratory facilitated plant growth, which is likely to be much greater than what is observed in the field.

## Snail Propagation and Monitoring at NAU

Since its establishment, the KAS population at NAU had produced at least four generations of viable snails on both host plant species and completed one simulated winter dormancy period (September 1997 to March 1998). This population had also remained free of parasitic trematodes. Tests of mitochondrial DNA have not detected significant genetic changes between generations (M. Miller, pers. comm.).

In the laboratory, KAS reared on *Nasturtium* exhibit different population dynamics than those reared on *Mimulus*. Among these differences, were faster growth rates and higher reproductive output on *Nasturtium*. Although these differences led to a large increase in the KAS population on *Nasturtium*, this population experienced high mortality, returning it to a level comparable to the *Mimulus* population. Possible explanations may include density dependant changes in population size such as self-regulation and resource competition.

Differences in host plant and habitat use among snails has been shown to influence growth and fecundity (Spelke et al. 1995). Results from this study are consistent with this relationship, and reveal a significant difference in population sizes due to host plant use. Faster growth of snails on *Nasturtium* has allowed this population to reproduce slightly earlier, and accounts for the month of lag time between reproduction occurring on each host plant species. Furthermore, faster growth may also allow the KAS population on *Nasturtium* to reproduce more often during each season if juvenile snails are able to reach maturity before the initiation of winter dormancy. Fecundity of KAS on *Nasturtium* was significantly greater, resulting in a nearly 3-fold difference in population size between the two host plants. However, much of the difference occurred

in only a few of the cells containing *Nasturtium*, leading to large standard error for samples collected during those times. Some cells contained over 250 snails, while others remained relatively constant for both host plants, averaging approximately 12 snails.

Consequently, a disproportionate amount of mortality occurred in these high-density cells, returning the population back to a size comparable to the *Mimulus* population. Density dependant changes in growth, fecundity, and mortality have been observed in several populations of snails (Foster and Stiven 1996b) and are considered to be some of the most important factors influencing their population dynamics. While food availability in the cells containing high snail densities was never in short supply, other density dependant factors such as mucus effects, and competitive aggressiveness may be contributing to high mortality (Williamson and Cameron 1976). Also, high juvenile mortality may simply be a direct response to high density as a regulatory component of population size (Foster and Stiven 1996b).

Although this research provided important information pertaining to KAS population dynamics on native and non-native host plant species, a more specific study of the effects of this host plant shift is warranted. Chapter three addresses these concerns and builds upon this information to examine the more fundamental differences in life history characteristics between KAS populations on each host plant species to determine the life history traits that influence differences in population dynamics on each host plant.

### **Snail Propagation and Monitoring at GCD**

The primary objective of creating a semi-natural captive population and increasing public education was accomplished through the establishment of the GCD

population. Although, sampling was less frequent, and overall sample sizes were relatively small, this population has provided valuable supplemental information on population establishment and KAS population dynamics and life history traits.

A large decrease in population size immediately following the initial release of snails was observed in this population as well as NAU, and is most likely due to sampling inefficiency since mortalities did not account for the difference between the expected population sizes and the observed size. Also, low sample sizes during winter months limits interpretation of those data; however, recruitment occurred on all host plant types and was greatest in the enclosures that contained only *Nasturtium*. The fall and early winter of 1998 were mild, which may explain the late fall reproduction. This is important because it indicates that mature KAS at VP may be able to reproduce more or less continually through the summer and fall if conditions are mild.

Dormancy was first observed for snails on all host plant assemblages on 1 November 1998, and continued into April 1999. By 14 April 1999 no dormant KAS were observed. Most dormant snails were found on firm surfaces such as sticks, rocks, leaves, and the sides of the Plexiglas enclosures. Snails dislodged from dormancy typically emerged within a matter of minutes and began moving. Thus, if weather conditions permit, KAS at VP may enter and exit dormancy several times throughout the winter to feed and possibly reproduce. Because the 1998-1999 winter was very mild, no host plants in our enclosures died back, providing a continued source of food and shelter for snails emerging from dormancy. The availability of food late in the season may also be a major factor in determining the survival of juvenile snails hatched late in the season at VP.

Although temperatures were relatively mild, KAS did initiate dormancy. This has also been observed in the NAU population and at TPZ, and corroborates past research suggesting that the initiation of dormancy is largely controlled by photoperiod, with emergence related to a combination of both photoperiod and temperature (Bailey 1981 and 1983). KAS at VP also appear to undergo dormancy in October each year, but more variability exists in the emergence dates. This strategy allows snails to initiate dormancy before freezing temperatures, but also allows them to take advantage of mild winter or early spring conditions if temperatures and host plant availability permit. If temperatures remain warm when the photoperiod cues them into dormancy, KAS metabolism may continue to remain high, consuming winter food reserves and potentially increasing winter mortality.

Peak mortality occurred in early January, a period that also corresponded with peak dormancy. Percent mortality was similar on all host plants assemblages through time. Mortality size class distributions were also similar on all host plants and followed the same trend as the greenhouse population, with the greatest percent of dead snails found in the 8 to 10 mm size class. This size class range is also where KAS may begin to allocate energy to reproductive organs and egg development. If KAS hatched during peak reproduction times observed in the field (June and July) they would be approximately this size at the onset of winter.

The GCD enclosures were not affected by falling debris and showed no evidence of predation. However, a torrential rain in July 1998 dislodged several enclosures in the sluice way, compromising their integrity and possibly allowing the unintentional release

of snails. This disturbance concluded the initial experiment, and initiated a second monitoring effort of the population and habitat on an irregular basis.

### **Management Implications**

The establishment of both of these populations accomplishes objectives in the KAS Recovery Plan and Biological opinions. Together, they represent the first captive populations of this species, and have provided invaluable information concerning KAS ecology, and captive rearing methods. In addition, the GCD population has served as a source of public education, informing over 1,000,000 people about KAS ecology, management concerns, and the importance of riparian communities in the Southwest.

Additional research on the NAU population may involve using specimens for genetics and taxonomy, and examining the effects of temperature and photoperiod on KAS dormancy. Research on the GCD population is warranted to further explore winter mortality, but we do not recommend maintaining the experiment at the dam perpetually. Both of these populations have been virtually self-sustained through the year 2000. Plans to transport the GCD population to an aquarium that has a special exhibit devoted to the Colorado River and its species have been made, and will allow other researchers to study KAS host plant interactions and further public education efforts.

## CHAPTER III

# KANAB AMBERSNAIL LIFE HISTORY ON NATIVE AND NON-NATIVE HOST PLANT SPECIES

## INTRODUCTION

The interactions between an organism and its food resources are a fundamental component of ecology, and are essential for understanding the mechanisms that determine a species' life history traits (Stearns 1976 and 1992). Therefore, shifts in host preference to a novel or introduced plant may lead to significant changes in a species' growth, reproduction, survivorship, and genetics, with implications that span from distribution and population dynamics, to evolutionary ecology and speciation (Bush 1969, Heed 1971, Price 1997). Although most studies concerning shifts in host plant use involve specialized insect taxa, these same mechanisms may also influence the ecology, life history, and population dynamics of mollusks.

Here, I experimentally examine how a shift in host plant use from native *Mimulus cardinalis* to non-native *Nasturtium officinale* influences the life history of the endangered Kanab ambersnail (KAS; Succineidae: *Oxyloma haydeni kanabensis* Pilsbry). Although field studies reveal that KAS densities are typically higher on *Nasturtium* than on *Mimulus* throughout much of the year, it is difficult to determine if these differences are the result of variation in life history traits, and if the source of such variation is due to a shift in host plant use.

In terms of host plant use, many species are either characterized as generalists or specialists. Trade-offs exist under both feeding regimes, and several other factors may contribute to such distinct patterns of resource utilization. For example, host plant use may be determined by competitive interactions, plant distribution and quality,

palatability, secondary plant defenses, associated physical conditions, or phylogenetic constraints from past evolutionary history. However, many of these factors may also facilitate a shift in host plant utilization.

Typically, snails exhibit a generalist feeding habit, although strong preferences for particular host plants among a variety of available resources has been observed (Cowie 1984, Wolda and Krueger 1973). Grime et al. (1968) demonstrated that strong associations between snail species and vegetation assemblages are most likely attributed to palatability though moisture, light intensity, and nutrition. However, the fact that KAS has shifted host plant use to *Nasturtium* is unusual because of the glucosinolate-myrosinase secondary chemical compound that the plant contains as a feeding deterrent (Newman et al. 1992 and 1996). Although some examples of snails feeding on *Nasturtium* are known because of the commercial value of the plant, and high nitrogen content (Godan 1983, Newman et al 1992 and 1996), studies indicated that most herbivory occurs when the plant is in a senescent stage and the secondary compounds are beginning to deactivate (Newman et al. 1990). However, If KAS is able to cope with the secondary compounds in *Nasturtium*, the benefits of higher nitrogen content may result in increased performance through variability in life history traits.

Variation among life history traits has been observed among several species of terrestrial and aquatic snails, but is typically attributed to differences in proximate factors. Baur and Raboud (1988) found that the life history of the polymorphic landsnail *Arianta arbustorum* differed significantly along an altitudinal gradient, leading to significant differences in size at maturity, reproductive output, and survivorship. Three populations of the aquatic snail *Lymnaea peregra* reared in three separate habitat types also showed

variation in life history traits including, size at maturity, and fecundity (Lam and Calow 1989). Other factors such as population density may also lead to variability among growth rates, reproduction, and survivorship (Cameron and Carter 1979, Chaundhry and Morgan 1987, Foster and Stiven 1996a, Stiven and Foster 1996b). However, few studies on mollusks address intraspecific and intrapopulational variation in life history traits due to a shift in host plant use.

Past methods of examining variation among life history traits incorporated a comparative approach, which used broad comparisons of traits between several species at higher taxonomic levels (Stearns 1976). However, when comparing higher taxonomic levels, by definition we are considering organisms that are inherently different, and it should be expected to find more variation in their life history traits (Brown 1983). In addition, these organisms often occur in different environments and are exposed to different selection pressures. Therefore, studies that address intraspecific variation control for many differences by examining the same organism. However, intraspecific differences in life histories may become more difficult to detect due to genetic constraints, and complex interactions with environmental, physiological, and developmental variables (Stearns 1980). Moreover, analysis of intrapopulational life history variation further limits the sources of variation because differences in environmental factors associated with different habitat types are also controlled. In this study, I investigate variation in life history traits at an intraspecific and intrapopulational level, and control for differences in environmental factors by conducting this research in a laboratory environment, which attributes differences in life history variation to host plant use, as suspected in the field.

## **METHODS**

### **Life History Traits**

To determine KAS life history traits on *Nasturtium* and *Mimulus*, age-specific life tables were constructed for cohorts of snails reared on each host plant species. Each cohort was produced by collecting 20 mature ( $\geq 10$  mm) snails from each host plant enclosure, and isolating them in groups of two, in small 15 x 15 x 15 cm reproductive enclosures containing their respective host plant vegetation. Each of the 20 reproductive enclosures was monitored on a biweekly basis for size at first reproduction of the parent snails, number of egg masses produced, number of eggs per mass, hatching success, time to hatching, and oviposition site. Age at death was also recorded for all snails in each cohort, as well as for the parent snails. This process was repeated three times for a total of 30 separate reproductive enclosures for each host plant type. Comparison of life history traits was performed using non-parametric Mann-Whitney U Tests and linear regression comparisons, in Statistica (Statsoft, Inc. 2000; **Table 1**). All reproductive enclosures were kept in the laboratory at a relatively constant 20<sup>0</sup> C and 30% humidity, and exposed to a 14 h photoperiod. Enclosures were restocked with ample amounts of host plant vegetation as necessary.

### **Growth**

When cohorts of snails reached a minimum size of 5 mm they were marked with B dots™ using the manufacturer's recommended adhesive. In order to decrease densities in the reproductive enclosures and allow for easier monitoring of newly produced egg masses, the marked snails were moved to larger 30 x 30 x 30 cm cells containing each

host plant type for the duration of the experiment. All marked snails were individually located and measured on a biweekly basis by placing them on a ruler and recording the distance from the apex whorl to the aperture. Mean and median growth rates derived from these experiments were analyzed using linear regression analysis (**Table 1**). Differences in growth rates were analyzed using slope comparison analysis (Zar 1996).

### **Life Table**

Data collected from all three cohorts of KAS on each host plant species was pooled for the construction and analysis of the age specific life tables. Standard error, variance, and 95 % confidence intervals for survivorship curves ( $l_x$ ), probability of death ( $d_x$ ) during time period  $x$  to  $x + 1$ , and the intrinsic rate of natural increase ( $r$ ), for KAS on each host plant were calculated using the methods of Ebert (1999).

All snails older than 154 days were not followed through death. Therefore, the mean size at death for the parent snails was used as a maximum size obtainable for cohorts on each host plant. A mean death rate calculated from all previous time intervals and was applied to snails surviving 154 d, until they obtained their projected size of death, at which time a 100% death rate was applied. However, due to the small number of snails surviving past 154 d, this method was only used for 12 snails on *Nasturtium* and 5 snails on *Mimulus*. Population projections for years 1 through 5, and 51 through 52 using an initial number of 1000 snails of age  $x$  were calculated using survivorship ( $l_x$ ) and fecundity data ( $m_x$ ) in Populus 5.0 (Alstad et al. 2000).

## **Population Dynamics**

Mean population size in the reproductive enclosures was pooled for each biweekly sample through 154 ( $x = 11$ ) days on each host plant species. Differences in these population sizes were tested using a t-test with the appropriate Bonferroni adjustment for total tests performed (Zar 1996). The total number of snails in size class ranges representing juvenile (1 to 5 mm), pre-reproductive (5 to 10 mm), and reproductive ( $> 10$  mm) size classes were plotted as a qualitative representation of population size and distribution structure through time.

## **Feeding Preference**

Using the methods of Szlavec (1986) food preference experiments were conducted using 30 individual snails ranging from 2 mm to 10 mm. Snails were collected from each host plant species and placed in small plastic containers (15 x 15 x 15 cm) that included a choice of five different feeding substrata: 1) live *Mimulus* leaves, 2) live *Nasturtium* leaves, 3) dead *Mimulus* stems, 4) moist soil, 5) and no preference = plastic. All KAS were isolated without food for 72 h prior to the experiment to starve the snails and clear their digestive tracts of any material eaten prior to the experiment. Snails were placed in individual containers misted with water to moisten the substrata, and observed every 20 min from 1900 to 0500 h. Each time snails were observed; their position in the container was noted, as well as any movement that had taken place since the last observation.

## **Fecal Analysis**

Diet of KAS was determined by fecal analysis using the methods of Williamson and Cameron (1976). Ten snails were randomly selected from each host plant contained in the 30 x 30 x 30 cm cells and placed on a moist white paper towel in two separate 15 x 15 x 15 cm enclosures according to host plant type. Feces were collected from snails in each group, mixed with a small amount of glycerin and mounted on a slide. Slides were examined under a microscope at 40 x magnification and feces were analyzed to determine their composition. A qualitative identification of live plant material, dead plant materials, soil, and other unidentifiable materials was performed.

## **Selfing**

Selfing was examined by isolating 20 KAS per host plant type in small plastic boxes (selfing enclosures) secured with a screen top. The selfing enclosures were placed firmly into the substrate of each of the host plant cells and contained host plant material. Isolated snails were monitored on a monthly basis for egg mass production, oviposition site, and hatching success.

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## RESULTS

### Life History Traits

Mean size at first reproduction was similar for parent snails on both host plant species. KAS on *Nasturtium* first reproduced at an average size of 11.5 mm (SE  $\pm$  0.51, n = 36), while KAS on *Mimulus* reproduced at 11.65 mm (SE  $\pm$  0.20, n = 30). The influence of adult snail size on both the number of clutches laid, and eggs per clutch among host plants was tested using regression comparison, although no significant relationship was found (Table 2). However, once reproduction occurred, snails on both plants continually produced eggs throughout their life span.

KAS reared on *Nasturtium* had a greater overall reproductive output than those on *Mimulus*. Although not significant, KAS on *Nasturtium* produced an average of 1.6 egg masses (SE  $\pm$  0.4, n = 30), whereas KAS on *Mimulus* produced 0.9 (SE  $\pm$  0.2, n = 30; Table 2). However, the mean number of eggs produced per mass was significantly different between KAS populations on the two host plants (Mann Whitney U, U = 300, DF = 2, P = 0.00016). The number of eggs per mass on *Nasturtium* ranged from 7 to 27 with a mean of 14.19 (SE  $\pm$  0.78, n = 47), while eggs per mass on *Mimulus* ranged from 4 to 20, with a mean of 9.7 (SE  $\pm$  0.7, n = 27; Fig. 14).

Hatching success was similar for egg masses produced on both host plants. Approximately 51.6% of eggs successfully hatched on *Nasturtium* (SE  $\pm$  5.6, n = 47) and 55.8 % on *Mimulus* (SE  $\pm$  10.3, n = 27; Table 2). Time to hatching was also similar among host plants, ranging from 14 to 35 d on *Nasturtium* with a mean of 26 d (SE  $\pm$  1.1, n = 32) and 21 to 35 days on *Mimulus* with a mean of 28 d (SE  $\pm$  1.43, n = 8; Table 2). Upon hatching, juvenile snails were approximately 1 to 2 mm in length. Most newly

hatched snails were mobile and readily dispersed, although many remained in a single location for extended amounts of time (d). Egg mass deposition occurred in moist areas generally out of the direct light, including the undersides of host plant leaves, stems, soil, and on the sides of the experimental enclosures. All egg masses consisted of transparent gelatinous eggs which became opaque as they developed. On *Nasturtium* oviposition sites included the underside of leaves or in the root masses. Oviposition on *Mimulus* occurred only on the underside dead leaves, and litter. Several egg masses were oviposited on the sides of the plastic reproductive enclosures, which often dried out, and failed to hatch. Consequently, the overall hatching success for KAS populations on both host plants would have been considerably higher if the un-natural plastic substrate was not available for oviposition.

Size at death for parent snails was similar on both host plant species. The mean size at death was calculated for only those snails that reproduced successfully, and was approximately 16 mm ( $SE \pm 0.30$ ,  $n = 30$ , and  $SE \pm 0.30$ ,  $n = 32$ ; on *Nasturtium* and *Mimulus*, respectively). This size was larger than expected, due to the high death rate of individuals throughout their lifetime. It is possible, that by selecting reproductively mature snails from the general population, we inadvertently selected more fit snails that had survived the period of highest mortality. However, many snails within the general population at GCD, VP, NAU, and The Phoenix Zoo have been found in the 18 mm or greater size class range.

## Growth

Growth rates for KAS reared on *Nasturtium* had a mean of 0.11 mm/d (SE  $\pm$  0.030, n = 1037) whereas KAS on *Mimulus* averaged 0.092 mm/day (SE  $\pm$  0.026, n = 411). Mean growth was greater for KAS on *Nasturtium* throughout the experiment, and was slightly faster in younger size classes, and slowed before reproductive maturity on both host plants. However, a test for differences in slope regressions of growth rate revealed no significant difference (Fig. 15).

## Life Table

Each life table is age structured in two week intervals (x), and represents a schedule of the probabilities that a snail of age x will survive to a certain age (x + 1). However, this basic component of the life table is expanded upon to include conditional probabilities for survival and death, as well as rates of fecundity, to provide a more accurate depiction of how these traits differ between the two KAS populations.

The initial count of snails ( $n_x$ ), includes only those individuals that had successfully hatched. Although hatching success was relatively low on *Nasturtium* and *Mimulus* (51.7% and 55.8%, respectively), considerable variation in initial population sizes on each host plant can be attributed to significantly higher fecundity observed in the KAS population on *Nasturtium*. The probability that an individual (age x), dies during the time interval x + 1 follows a similar overall pattern for each population (Tables 3 and 7). However, differences existed with respect to the amount of variation among these probabilities between populations. The probability of death for individuals at each age decreases between the interval x = 0 to 5. During this time, KAS on *Mimulus* had a

greater probability of dying than do KAS on *Nasturtium*. From interval  $x = 5$  to 9, the probability of mortality increased steadily as snails reached reproductive maturity. During this interval, KAS on *Nasturtium* experienced a higher rate of mortality than those on *Mimulus*, and the mean probability of death to this age was 0.275 for both populations, resulting in 5 survivors on *Mimulus*, and 12 on *Nasturtium* (Fig. 16).

Due to the small number of snails surviving on each host plant at  $x = 10$ , mean growth rates, size at death for parent snails, and probability of death were calculated from both populations and used to extrapolate life history traits for the interval  $x = 11$  to  $x = 13$  on *Nasturtium*, and  $x = 14$  on *Mimulus* (due to slower growth). Although snails greater than 14 mm had often been observed in the field and lab on both host plants, this size was used as the maximum size obtainable by snails on either host plant. Therefore, snails that reach this size have a 100% probability of death (Tables 3 and 7).

Two additional tables and graphs were created for both KAS populations to calculate the variance, standard error, and 95 % confidence intervals for the probability that a new individual (age 0) dies during the time period  $x$  to  $x + 1$  ( $d_x$ ), and the probability that a new individual (age 0) is alive at the beginning of age  $x$  ( $l_x$ ) (Tables 3,4,5 and 7,8,9). As would be expected, young individuals are more likely to die, and the probability of death for a newly born individual decreases with time, because their chance of survival to that time has continuously decreased. Confidence intervals are large at younger stages of life, revealing high variance among these probabilities (Fig. 17 a and b). The probability of survival from  $x = 0$  is also similar for KAS on each host plant, and decreases exponentially with time, similar to a type III survivorship curve representative of most  $r$  strategist species (Deevey 1947; Fig. 18 a and b).

The number of offspring produced by a female at age  $x$  ( $m_x$ ) was also calculated using the rates of fecundity for the parent snails isolated in each reproductive enclosure. Since all KAS are simultaneously hermaphroditic, all individuals are considered as potential females. Since growth rates for KAS on *Nasturtium* were faster, these snails were able to reach reproductive maturity at  $x = 9$ , while KAS on *Mimulus* did not reach a comparable size until time  $x = 10$ . Therefore, KAS on *Nasturtium* not only had a higher fecundity, and were able to reproduce earlier, they were also able to reproduce more often than on *Mimulus*.

Using this information, population projections for KAS on both host plant species revealed significant differences in growth. Using an arbitrary number of 1000 initial snails at age  $x = 0$ , less than one snail remained after 5 years, and long term projections revealed a population growth rate per individual ( $r$ ) of 0.92, which indicates a decreasing trend of population size (Table 6). However, using these same methods, 1000 KAS on *Nasturtium* reach over 8500 individuals after 5 years, and the population continued to grow exponentially. Population growth rate per individual for this population is  $r = 1.06$ , revealing a trend of population growth (Table 10).

### Population Dynamics

The mean number of snails produced in each reproductive enclosure was greater for KAS reared on *Nasturtium* than on *Mimulus* for every biweekly survey (Fig. 19). Significant differences in population size occurred on days 0, 42, 56, 70, and 84 after hatching (Bonferroni adjustment to  $P < 0.004$ ,  $n = 25$  for all;  $t = 2.9$ ;  $t = 3.0$ ;  $t = 4.3$ ,  $t = 1.7$ ,  $t = 3.5$ , respectively).

Analysis of size class distributions through time showed a similar patterns for both populations of KAS, although their magnitudes are quite different. On *Nasturtium*, KAS in the 1 to 5 mm size class range are initially abundant, although their frequency decreases exponentially due to high mortality and growth beyond the 5 mm size class. As early as day 28, snails in the 5 to 10 mm size class range are observed, and continue to increase in frequency as snails in the 1 to 5 mm range decrease. This relationship reaches its maximum on day 56, where all snails recorded are in the 5 to 10 mm range. As snails in this size class range continue to grow, some reach the 10 to 15 mm size class (day 98), although their frequency is very low due to the cumulative effects of high mortality occurring in the previous size classes (Fig. 20a).

The initial number of KAS in the 1 to 5 mm size class was much less than observed on *Nasturtium* due to lower fecundity. Through time, these snails also decreased in frequency due to mortality and growth beyond this size class. A noticeable difference in the rate of decrease for snails in the 1 to 5 mm size class on both host plants between days 14 and 28 revealed a much slower mortality rate for KAS on *Mimulus* during this time. In addition, differences in growth rate between snails on the two host plants was apparent during this time due to the presence of snails in the 5 to 10 mm size class range only occurring on *Nasturtium*. Differences in growth were also observed in the first observation of snails in the 10 to 15 mm size class appearing approximately four weeks earlier on *Nasturtium* (d 84) than on *Mimulus* (d 112). However, the influence of high mortality is apparent for both populations, as seen in the low numbers of snails existing in the 5 to 10 mm size class (Fig. 20b).

## Feeding Preference

Feeding preference experiments revealed no preference among the choices provided. KAS overwhelmingly stayed on the plastic 63%, 23% preferred *Nasturtium*, 10% on *Mimulus*, and 3.3% chose soil ( $n = 30$ ). However, this experiment was conducted during the night when activity was highest in the field, although the laboratory population may have altered its feeding activity since captivity.

## Fecal Analysis

A total of 20 samples of feces were examined for snails from each host plant. Analysis shows that 80% of the snail's feces on *Nasturtium* consisted of live plant material and 20% was soil and decomposed vegetation. On the other hand, 70% of the feces from snails on *Mimulus* contained dead plant material, 20% contained live material, and 10% contained a combination of live, dead, and soil.

## Setting

Snails isolated before reproductive maturity resulted in a 100% setting rate on each host plant species. Mean egg mass size was  $6.3$  ( $SE \pm 0.7$ ,  $n = 20$ ) on *Nasturtium* and  $5.9$  ( $SE \pm 0.7$ ,  $n = 20$ ) on *Mimulus*. Reduced fecundity was apparent with a 56% reduction in eggs per mass on *Nasturtium* and a 40% reduction on *Mimulus*.

## DISCUSSION

Laboratory experiments conducted on KAS reveal that intraspecific variation in life history traits existed between snails reared on native *Mimulus cardinalis* and non native *Nasturtium officinale*. Although some variation among individual life history traits existed, both populations exhibited the same overall life history strategy of early reproduction, high fecundity, and high mortality associated with an r-strategists and type III survival curve (Deevey 1947). However, KAS on *Nasturtium* do grow faster, lay more egg masses, and have a larger average clutch size than KAS on *Mimulus*. As a result, KAS on *Nasturtium* are able to reproduce earlier in the season, and thus, produce more cohorts throughout their life cycle. Although not all differences are significant, a distinct trend of increased performance for snails on *Nasturtium* is apparent, which leads to a positive rate of increase for the KAS population on *Nasturtium*. Furthermore, since all environmental factors were maintained at a similar level for both populations in the laboratory, variation in life history traits is likely due to differences in host plant use.

Since KAS at the field site are able to freely move among host plant species across a relatively homogeneous set of environmental variables, selection pressures for traits influenced by proximate environmental factors are equal throughout the entire population. Therefore, the variation observed in this population is likely the result of phenotypic plasticity, induced by specific host plant use. Although this may seem like a relatively expensive trait to maintain (Caswell 1983), natural selection will favor organisms capable of adapting their life history traits to track environmental changes (DeWitt 1998). This plasticity may be maintained as a trait in itself (Caswell 1983), allowing KAS to incorporate several different food resources in its feeding regime with

varying degrees of success through variability in life history traits. This is important because it enables KAS to more readily colonize a variety of habitat types, consistent with life history strategies observed in other snails that rely on the colonization of new habitat for survival and population persistence.

Food preference experiments in the laboratory reveal no preference exists between live *Nasturtium*, dead *Mimulus*, live *Mimulus*, soil, and plastic. However, these experiments were conducted during night hours based on peak foraging observed in the field population. Since this population had been maintained in constant laboratory conditions, including a 14-hour photoperiod and nearly uniform temperature regime, feeding patterns may have changed. It is possible that KAS in the field merely come across *Nasturtium* during random foraging of available food resources, and unwittingly benefit from the consequences. However, field data suggest that densities between the two host plants are consistently different throughout much of the year, which would not be expected if the probability of KAS on either host plant were equal. In addition, increased performance or fitness linked with a preference for *Nasturtium* is an evolutionarily valid reason for a shift in host plant use.

In the field, host plant preference may be influenced for a variety of different reasons. In addition to containing glucosinolates that act as a feeding deterrent to many herbivores, green *Nasturtium* also possess relatively high amounts of nitrogen, which has been found to be a key factor in feeding preferences and increased growth among several groups of shredders, including aquatic snails (Mattson 1980, Newman 1990, Newman et al. 1992 and 1996). Furthermore, fecal analysis revealed that KAS on *Nasturtium* are eating live plant tissue, while KAS on *Mimulus* are typically ingesting dead materials.

which likely have lower nitrogen content. Although *Mimulus* also contains nitrogen, it may not be as accessible due to the thick trichomes and tough texture of its leaves. Moisture is also a key factor in determining the distribution of several species of snails and may be the single most important variable influencing oviposition (Godan 1983). Since *Nasturtium* is typically found in or near, or highly saturated soils, KAS may initially be attracted to a moisture gradient, and increased probability of hatching success associated with moist root masses found on *Nasturtium*. Other potential reasons for host plant shifts may be the incorporation of secondary compounds in snail tissue as a deterrent for predators, or competitive exclusion, which prompts a change in niche utilization. However, both of these seem unlikely due to minimal evidence of predation and competition observed in the VP population. A possible genetic link may also exist between KAS and *Nasturtium* since both are old world species, and mollusk damage on *Nasturtium* crops in Europe has been recorded for centuries (Godan 1983). However, it would be difficult to determine if any genetic predisposition for one host plant over another exists in a species with such a general overall feeding habit.

Growth rates for KAS on *Nasturtium* were consistently faster than on *Mimulus*, which would be expected, given other increases in performance in this population. Although growth is not significantly faster, the cumulative effect allows KAS on *Nasturtium* to reach reproductive maturity at an earlier time. Growth rate trends were similar for both KAS populations, with KAS exhibiting faster growth in earlier stages, which slows during reproductive maturity due to a shift in allocation energy. Overall growth rates may be slightly faster than those observed in the field due to ideal laboratory conditions. However, KAS in the field that presumably hatched in mid summer, have

reproduced by fall, which would be congruent with growth rates and sizes at maturity observed in the lab.

Differences in fecundity between KAS reared on *Nasturtium* and *Mimulus* is likely the most important factor contributing to overall differences in population dynamics. Since hatching success and survivorship were similar between the two populations, the greater initial number of KAS produced on *Nasturtium* ultimately yields a greater number of reproductively mature snails, which increases population size. In the field, survivorship due to winter mortality and other factors may play a more important role in population regulation. Wolda and Kreulen (1973) found that juvenile survivorship was the leading factor in population regulation of *Cepea nemoralis*.

Reproduction occurred for KAS on both host plant species when photoperiod was increased to 14 hours, which is similar to the photoperiod experienced by reproductively mature snails in the field. Although a positive correlation between increased growth and size at reproduction has been observed in other snails, size at first reproduction seems to be constrained by developmental maturity in KAS because snails on both host plants did not reproduce until a minimum size of 11 mm was obtained. However, once snails reached reproductive maturity, snails on *Nasturtium* did produce more egg masses and significantly more eggs per mass than snails on *Mimulus*.

Oviposition preference has been associated with increased performance in several insect taxa (Price 1997). Among mollusks, oviposition site can be governed by substrate availability, light intensity, and moisture. KAS in the reproductive enclosures oviposited in similar areas to those observed in the field (i.e. undersides of leaves, duff, litter, and soil). However, a large portion of KAS in both host plant enclosures oviposited eggs on

the plastic containers. The majority of these eggs became desiccated and dried out, resulting in 100% mortality. Therefore, it is possible that overall population sizes in the field may be considerably larger than in the laboratory because this circumstance would not be encountered.

Mortality between the two populations was high during hatching and juvenile stages, and suggests that juveniles are more vulnerable than adults (Lam and Calow 1989). Few snails achieved reproductive maturity, which is a limiting factor of population growth. However, those snails that did reproduce were considerably larger than expected. This may have been due to artificial selection for the fittest snails that were able to survive past reproductive maturity. Furthermore, the rearing regime used also excluded several mortality factors, such as possible predation, and fluctuations in temperature and humidity. However, fine adjustments in microhabitat that may have provided KAS in the field with more ideal conditions may not have been reproduced in the laboratory.

Dormancy may be an important component in the regulation of this population in the field, and was not examined in this study. Field studies indicate that KAS initiates dormancy during the fall as temperatures and photoperiod decrease. During this time, KAS are retracted in their shells and do not feed. Therefore, physiological processes are slowed until environmental conditions cue emergence. However, field data suggest that unsuccessful winter dormancy may attribute up to 80 % of observed mortality. I suggest further work be conducted in this area to determine the exact factors which promote dormancy, and how winter mortality may act as a population regulator. In addition, host

plant use may also influence winter dormancy by providing more suitable dormancy substrata, and foraging material when emergence from dormancy occurs.

### **Selfing**

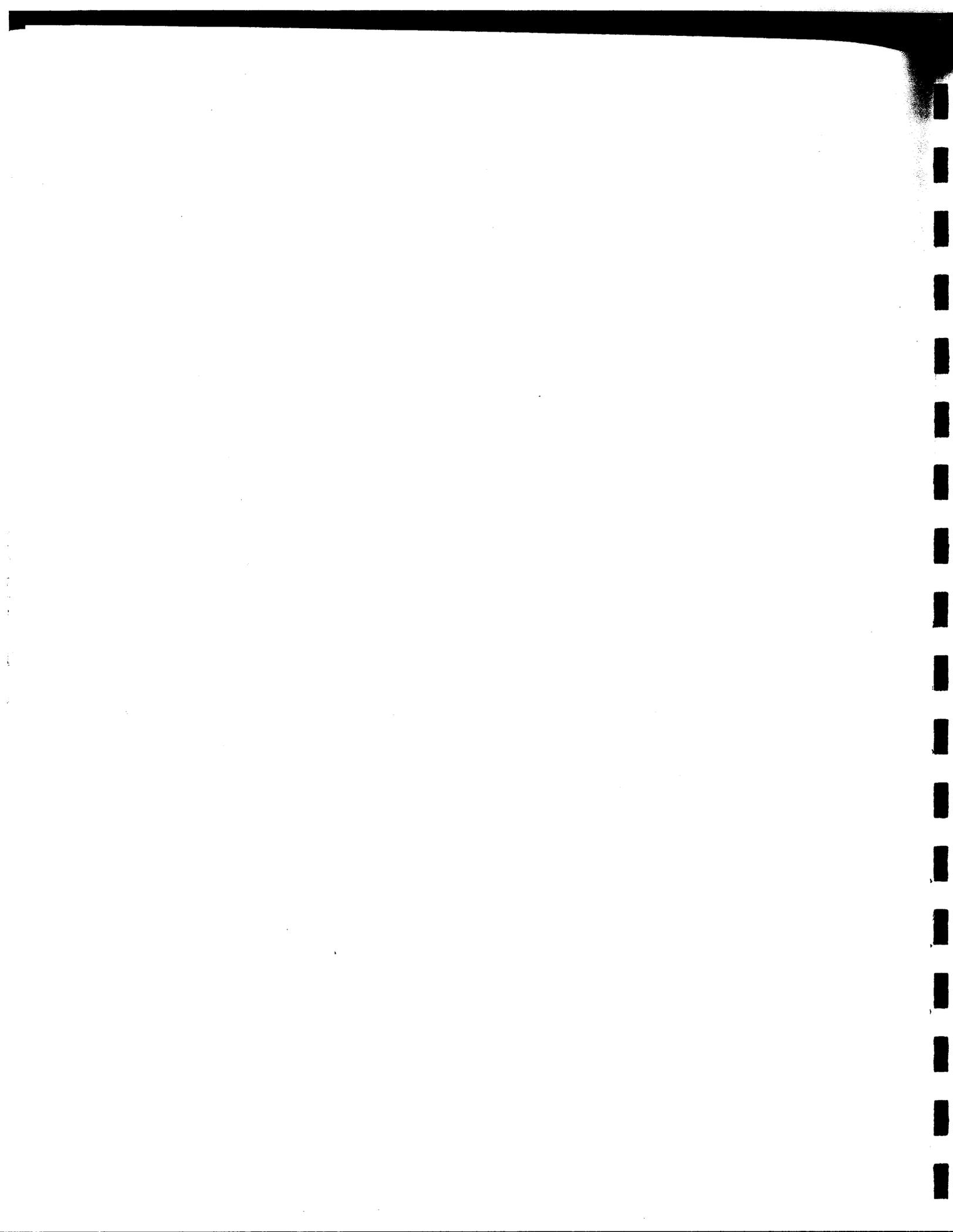
In pulmonates, reciprocal insemination is typically the rule (Barrientos 1998), allowing snails to simultaneously inseminate one another, increasing the production of offspring throughout the population. Observations of mating did not enable us to determine if this was common among our snails. Experimentation also showed that KAS is able to self inseminate. This has also been shown to occur in many Succineidae (Bayne 1973) and allows small, isolated, and slow moving populations to become established. Selfing occurred at a relatively low frequency and did not differ between host plants. Reduced fecundity is often attributed to selfing in many species of Succineidae (Villalobos et al. 1995) and was also apparent in KAS. With this in mind it is possible that some of the egg masses produced in the life history experiments were the result of selfing as opposed to crossing, however, it is not likely that a snail would choose to self if a partner was available in close proximity. Therefore, we assumed that selfing did not contribute to the majority of egg masses produced in those experiments.

### **Management Implications**

Life history analysis is a fundamental component to understanding the ecology of any organism. It lies at the heart of biology, predicting which combinations of traits will evolve in an organism based on its environment (Stearns 1992). In doing so, life history theory encompasses myriad of disciplines including evolution, genetics, physiology,

population dynamics, and ecology. Recently, the importance of understanding a species life history has become apparent for the conservation of endangered species. The proper management and conservation of the endangered Kanab ambersnail depends upon an accurate understanding of its ecological interactions and population dynamics at VP.

Results from this study represent the first account of KAS life history in general, and specifically shed light on how differences in habitat abundance and use at VP may influence the overall population dynamics of KAS at this site. This information is important because current management decisions are based on population estimates of KAS at VP, which cause habitat destruction, are expensive, and may be unreliable. However, it must be noted that decisions influencing the "take" of snails and habitat at VP should not be made solely on any one data set or another, but rather, a combination of all relevant information. Data collected in the laboratory provides excellent information on KAS life history traits; however, artificial conditions can positively influence snail performance, create artificial densities, and do not include changes in the physical conditions, disturbances, or other ecological interactions between KAS and its surrounding environment. Therefore, any speculation regarding the KAS population at VP should incorporate this information, VP monitoring, and other research conducted on this species.



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**Table 1**

<b>QUESTIONS</b>	<b>ANALYSIS</b>
Does the number of egg clutches differ among host plants?	Mann-Whitney U
Does the number of eggs/clutch differ among host plants?	Mann-Whitney U
Does hatch time vary among host plants?	Mann-Whitney U
Is hatching success different among host plants?	Mann-Whitney U
Does snail adult size influence the number of clutch laid among host plants?	Regression comparison
Does snail adult size influence the number of eggs/clutch among host plants?	Regression comparison
Does snail adult size influence hatching success among host plants?	Regression comparison
Does snail adult size influence the percent hatching success among host plants?	Regression comparison
Does mean growth rate differ among host plants?	Regression comparison
Does median growth rate differ among host plants?	Regression comparison

**Table 2**

<b>QUESTIONS</b>	<b>RESULTS</b>
Does the number of egg clutches differ among host plants?	Yes
Does the number of eggs/clutch differ among host plants?	Yes*
Does hatch time vary among host plants?	No
Is hatching success different among host plant?	No
Does snail adult size influence the number of clutched laid among host plants?	No
Does snail adult size influence the number of eggs/clutch among host plants?	No
Does snail adult size influence hatching success among host plants?	No
Does snail adult size influence the percent hatching success among host plants?	No
Does mean growth rate differ among host plants?	Yes
Does median growth rate differ among host plants?	Yes

Table 3

Life Table for KAS on <i>Mimulus</i>								
x	$n_x$	$q_x$	$D_x$	$d_x$	$P_x$	$l_x$	$m_x$	$l_x m_x$
0	143	0.461538	66	0.461538	0.538462	1	0	0
1	77	0.25974	20	0.13986	0.74026	0.538462	0	0
2	57	0.333333	19	0.132867	0.666667	0.398601	0	0
3	38	0.342105	13	0.090909	0.657895	0.265734	0	0
4	25	0.24	6	0.041958	0.76	0.174825	0	0
5	19	0.105263	2	0.013986	0.894737	0.132867	0	0
6	17	0.117647	2	0.013986	0.882353	0.118881	0	0
7	15	0.2	3	0.020979	0.8	0.104895	0	0
8	12	0.25	3	0.020979	0.75	0.083916	0	0
9	9	0.444444	4	0.027972	0.555556	0.062937	0	0
10	5	0	0	0	1	0.034965	0	0
11	5	0.25	1	0.006993	0.8	0.034965	4.28	0.14965
12	4	0.25	1	0.006993	0.75	0.027972	4.28	0.11972
13	3	0.25	1	0.006993	0.666667	0.020979	4.28	0.08979
14	2	1	2	0.013986	0	0.013986	4.28	0.05986

Table 4

Calculation of Variance for $l_x$ for KAS on <i>Mimulus</i>							
x	$\frac{q_x}{n_x p_x}$	$\sum_{j=0}^{x-1} \frac{q_j}{n_j p_j}$	$l_x^2$	$var(l_x)$	$se(l_x)$	+95% interval	-95% interval
0	0.005994	-	1	0	0	1	1
1	0.004557	0.005994006	0.289941	0.001737907	0.041688	0.62017	0.456753
2	0.008772	0.010550853	0.158883	0.001676352	0.040943	0.47885	0.318353
3	0.013684	0.019322782	0.070615	0.001364472	0.036939	0.338134	0.193334
4	0.012632	0.033006993	0.030564	0.001008821	0.031762	0.237079	0.112572
5	0.006192	0.045638572	0.017654	0.000805689	0.028385	0.188501	0.077233
6	0.007843	0.051830522	0.014133	0.000732506	0.027065	0.171928	0.065834
7	0.016667	0.05967366	0.011003	0.000656588	0.025624	0.155118	0.054672
8	0.027778	0.076340326	0.007042	0.000537582	0.023186	0.12936	0.038472
9	0.088889	0.104118104	0.003961	0.00041242	0.020308	0.102741	0.023133
10	0	0.193006993	0.001223	0.000235961	0.015361	0.065073	0.004857
11	0.05	0.193006993	0.001223	0.000235961	0.015361	0.065073	0.004857
12	0.083333	0.25967366	0.000782	0.000190137	0.013789	0.054999	0.000946
13	0.166667	0.343006993	0.00044	0.000143629	0.011985	0.044469	-0.00251
14	-	0.454118104	0.000196	9.64364E-05	0.00982	0.033234	-0.00526

Table 5

Calculation of Variance for $d_x$ for KAS on <i>Mimulus</i>							
$x$	$\frac{p_x}{n_x q_x}$	$\sum_{j=0}^{x-1} \frac{q_j}{n_j p_j} + \frac{p_x}{n_x q_x}$	$d_x^2$	$\text{var}(d_x)$	$\text{se}(d_x)$	+95% Interval	-95% Interval
0	0.008158508	0.008158508	0.213018	0.001738	0.041688	0.543247	0.37983
1	0.037012987	0.043006993	0.019561	0.000841	0.029004	0.196709	0.083012
2	0.035087719	0.045638572	0.017654	0.000806	0.028385	0.188501	0.077233
3	0.050607287	0.06993007	0.008264	0.000578	0.02404	0.138028	0.04379
4	0.126666667	0.15967366	0.00176	0.000281	0.016766	0.07482	0.009097
5	0.447368421	0.493006993	0.000196	9.64E-05	0.00982	0.033234	-0.00526
6	0.441176471	0.493006993	0.000196	9.64E-05	0.00982	0.033234	-0.00526
7	0.266666667	0.326340326	0.00044	0.000144	0.011985	0.044469	-0.00251
8	0.25	0.326340326	0.00044	0.000144	0.011985	0.044469	-0.00251
9	0.138888889	0.243006993	0.000782	0.00019	0.013789	0.054999	0.000946
10	-	-	-	-	-	-	-
11	0.8	0.993006993	4.89E-05	4.86E-05	0.006969	0.020651	-0.00667
12	0.75	0.993006993	4.89E-05	4.86E-05	0.006969	0.020651	-0.00667
13	0.666666667	0.993006993	4.89E-05	4.86E-05	0.006969	0.020651	-0.00667
14	0	0.493006993	0.000196	9.64E-05	0.00982	0.033234	-0.00526

Table 6

Age class	YEAR ( <i>Mimulus</i> )								
	0	1	2	3	4	5	50	51	52
0	1000	42.80	1.83	0.08	0.12	0.15	1.41E-25	1.29E-25	1.18E-25
1	0.00	45.37	3.88	0.25	0.03	0.05	8.17E-26	7.48E-26	6.85E-26
2	0.00	33.38	5.72	0.55	0.04	0.02	6.56E-26	6.01E-26	5.50E-26
3	0.00	33.38	6.67	0.84	0.08	0.01	4.78E-26	4.38E-26	4.01E-26
4	0.00	0.00	4.98	0.10	0.12	0.01	3.41E-26	3.12E-26	2.86E-26
5	0.00	0.00	2.86	0.98	0.16	0.02	2.85E-26	2.61E-26	2.39E-26
6	0.00	0.00	1.81	0.09	0.21	0.03	2.63E-26	2.41E-26	2.21E-26
7	0.00	0.00	0.00	0.71	0.24	0.05	2.61E-26	2.39E-26	2.19E-26
8	0.00	0.00	0.00	0.34	0.20	0.05	2.28E-26	2.09E-26	1.91E-26
9	0.00	0.00	0.00	0.13	0.13	0.05	1.87E-26	1.71E-26	1.57E-26
10	0.00	0.00	0.00	0.00	0.04	0.02	1.02E-26	9.35E-27	8.56E-27
11	0.00	0.00	0.00	0.00	0.02	0.02	1.11E-26	1.02E-26	9.35E-27
12	0.00	0.00	0.00	0.00	0.01	0.01	8.12E-27	7.43E-27	6.80E-27
13	0.00	0.00	0.00	0.00	0.00	0.01	8.86E-27	8.12E-27	7.43E-27
14	0.00	10.00	0.43	0.02	0.00	0.00	4.84E-27	4.43E-27	4.06E-27
Total	1000	164.94	28.18	4.07	1.40	0.50	5.36E-25	4.91E-25	4.49E-25
$r$ ( $N_{T+1}/N_T$ )	0.16	0.17	0.14	0.34	0.36	....	0.92	0.92	0.92

Table 9

Calculation of Variance for $d_x$ for KAS on <i>Nasturtium</i>							
$x$	$\frac{p_x}{n_x q_x}$	$\sum_{j=0}^{x-1} \frac{q_j}{n_j p_j} + \frac{p_x}{n_x q_x}$	$d_x^2$	$\text{var}(d_x)$	$se(d_x)$	+95% interval	-95% interval
0	0.004222347	0.004222347	0.177695	0.00075	0.027391	0.475226	0.367851
1	0.009173605	0.011415831	0.045075	0.000515	0.022684	0.256768	0.167847
2	0.041596639	0.046923077	0.003787	0.000178	0.01333	0.087666	0.035411
3	0.042530569	0.049554656	0.003418	0.000169	0.013014	0.083969	0.032954
4	0.046323529	0.055746606	0.002736	0.000153	0.01235	0.076514	0.028101
5	0.084126984	0.096923077	0.000947	9.18E-05	0.009579	0.049545	0.011994
6	0.058055152	0.073846154	0.0016	0.000118	0.01087	0.061305	0.018695
7	0.058333333	0.08025641	0.001363	0.000109	0.01046	0.057425	0.016421
8	0.089285714	0.121923077	0.000606	7.39E-05	0.008595	0.041462	0.007769
9	0.075	0.121923077	0.000606	7.39E-05	0.008595	0.041462	0.007769
10	0.416666667	0.496923077	3.79E-05	1.88E-05	0.004338	0.014656	-0.00235
11	0.233333333	0.33025641	8.52E-05	2.81E-05	0.005305	0.019628	-0.00117
12	0.357142857	0.496923077	3.79E-05	1.88E-05	0.004338	0.014656	-0.00235
13	0	0.196923077	0.000237	4.66E-05	0.006827	0.028766	0.002004

Table 10

Age class	YEAR ( <i>Nasturtium</i> )								
	0	1	2	3	4	5	50	51	52
0	1000	115.70	13.38	1124.00	1993.05	2501.27	1.48E+17	1.56E+17	1.65E+17
1	0.00	131.90	30.52	468.61	1208.55	1523.27	7.98E+16	8.42E+16	8.88E+16
2	0.00	124.96	48.19	178.92	729.63	1079.36	4.77E+16	5.04E+16	5.32E+16
3	0.00	104.13	72.28	94.29	525.16	983.61	3.77E+16	3.98E+16	4.20E+16
4	0.00	166.61	106.02	43.49	319.65	811.73	2.86E+16	3.01E+16	3.18E+16
5	0.00	0.00	106.82	63.56	177.26	607.84	2.14E+16	2.26E+16	2.39E+16
6	0.00	0.00	96.38	84.75	104.91	442.98	1.71E+16	1.80E+16	1.90E+16
7	0.00	0.00	57.82	85.30	72.24	266.73	1.21E+16	1.28E+16	1.35E+16
8	0.00	0.00	38.55	70.25	55.35	135.63	7.67E+15	8.10E+15	8.55E+15
9	0.00	0.00	0.00	52.69	58.06	81.38	5.45E+15	5.76E+15	6.07E+15
10	0.00	0.00	0.00	22.58	36.28	38.05	2.58E+15	2.73E+15	2.88E+15
11	0.00	0.00	0.00	15.05	10.06	42.85	2.45E+15	2.58E+15	2.73E+15
12	0.00	0.00	0.00	6.69	26.61	33.98	1.55E+15	1.63E+15	1.72E+15
13	0.00	10.00	1.16	0.13	11.24	19.93	7.33E+14	7.73E+14	8.16E+14
Total	1000	653	571	2310	5328	8569	4.13E+17	4.35E+17	4.60E+17
$r$ ( $N_{T+1}$ / $N_T$ )	0.65	0.87	4.05	2.31	1.61	....	1.06	1.06	1.06

Figure 1

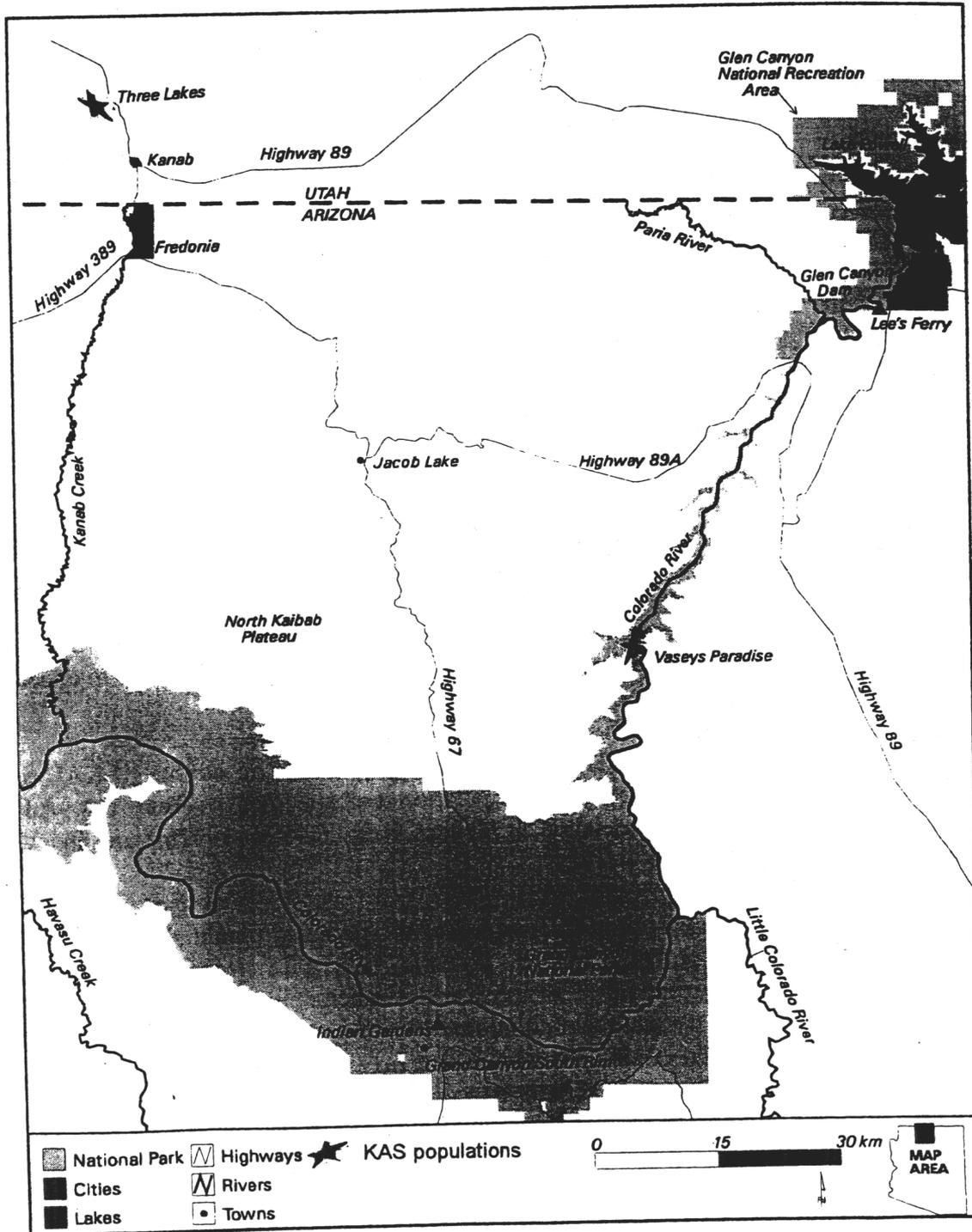


Figure 2



Figure 3

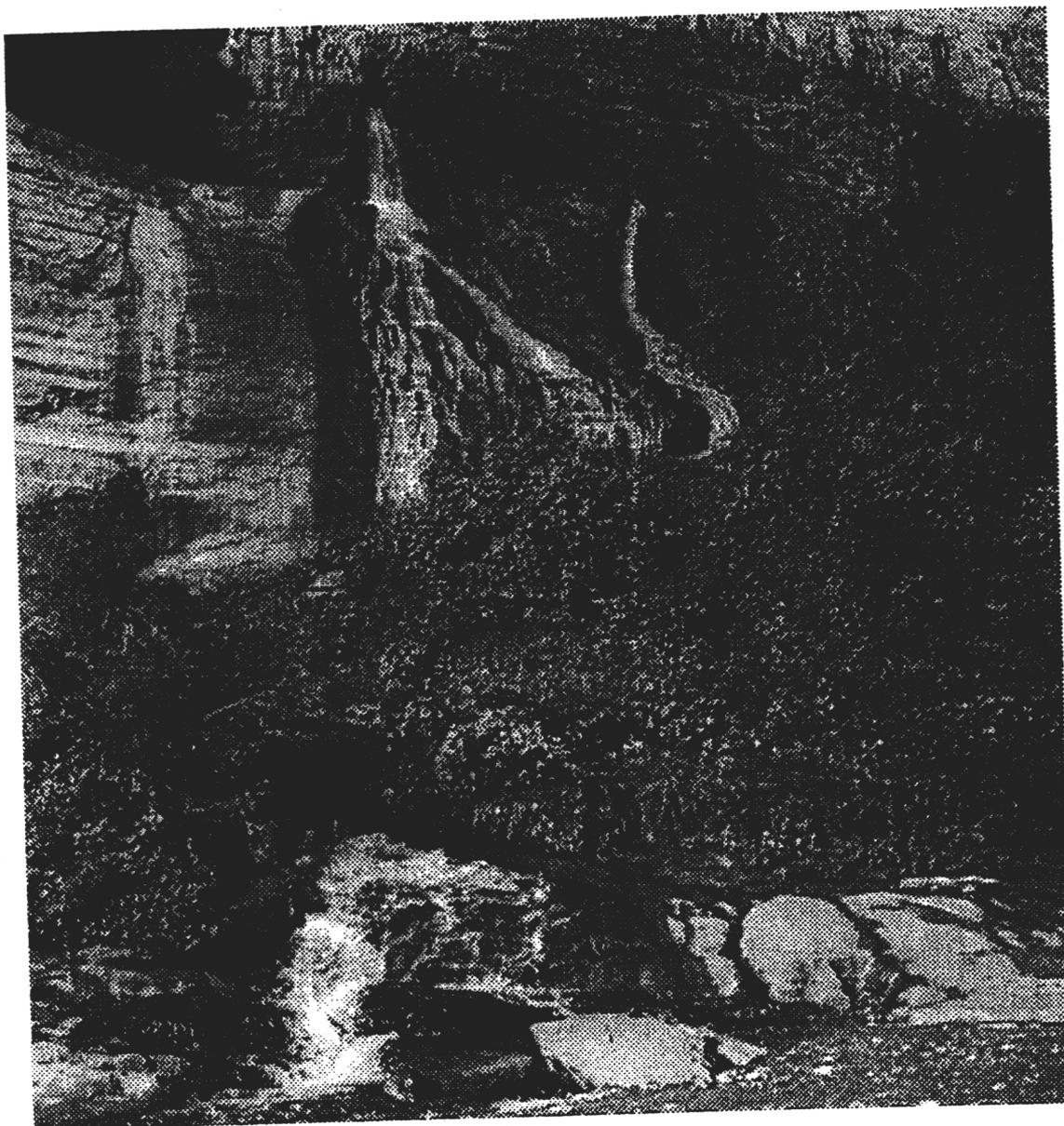


Figure 4

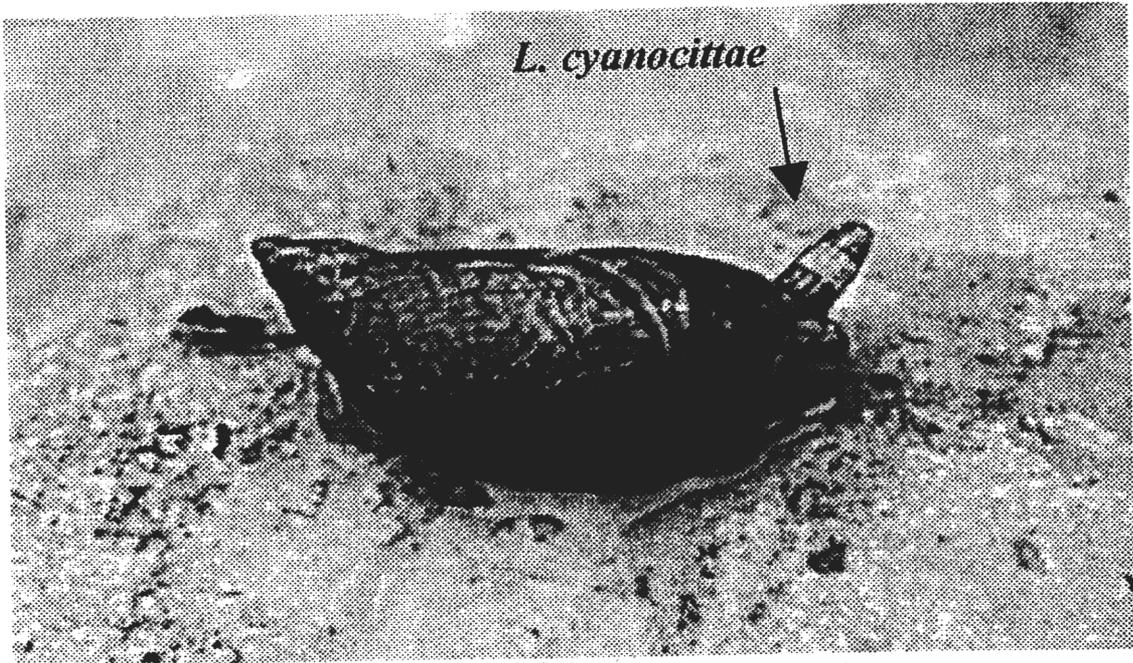
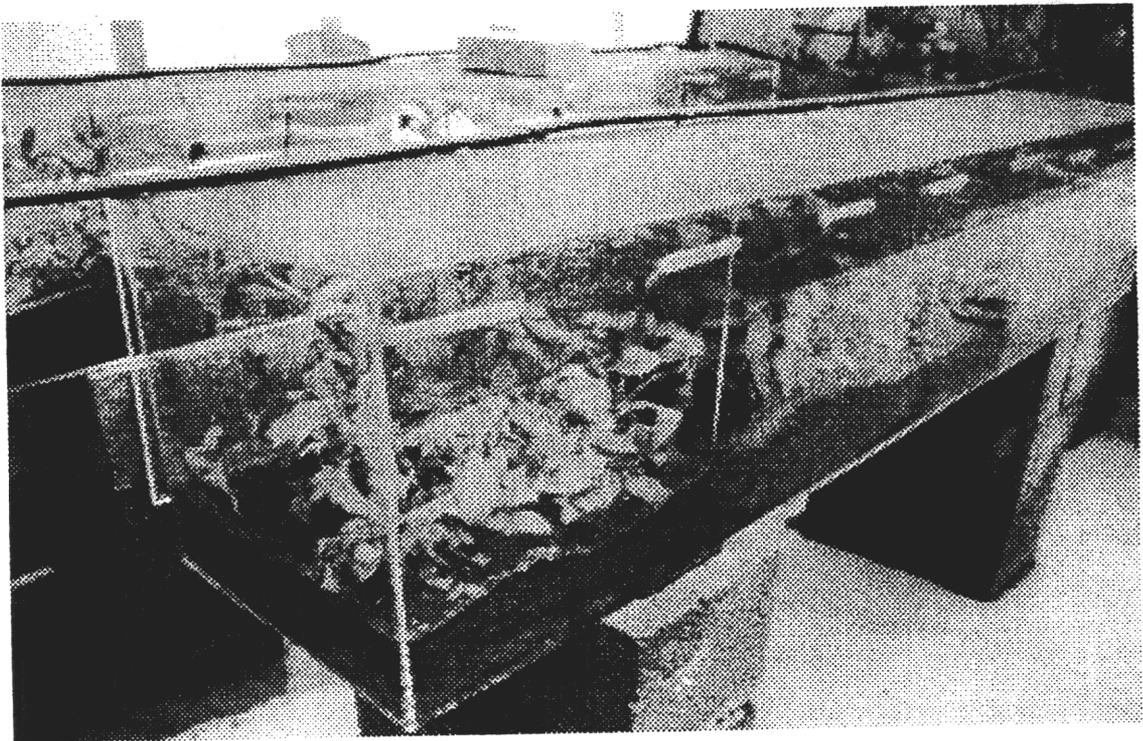


Figure 5



**Figure 6**

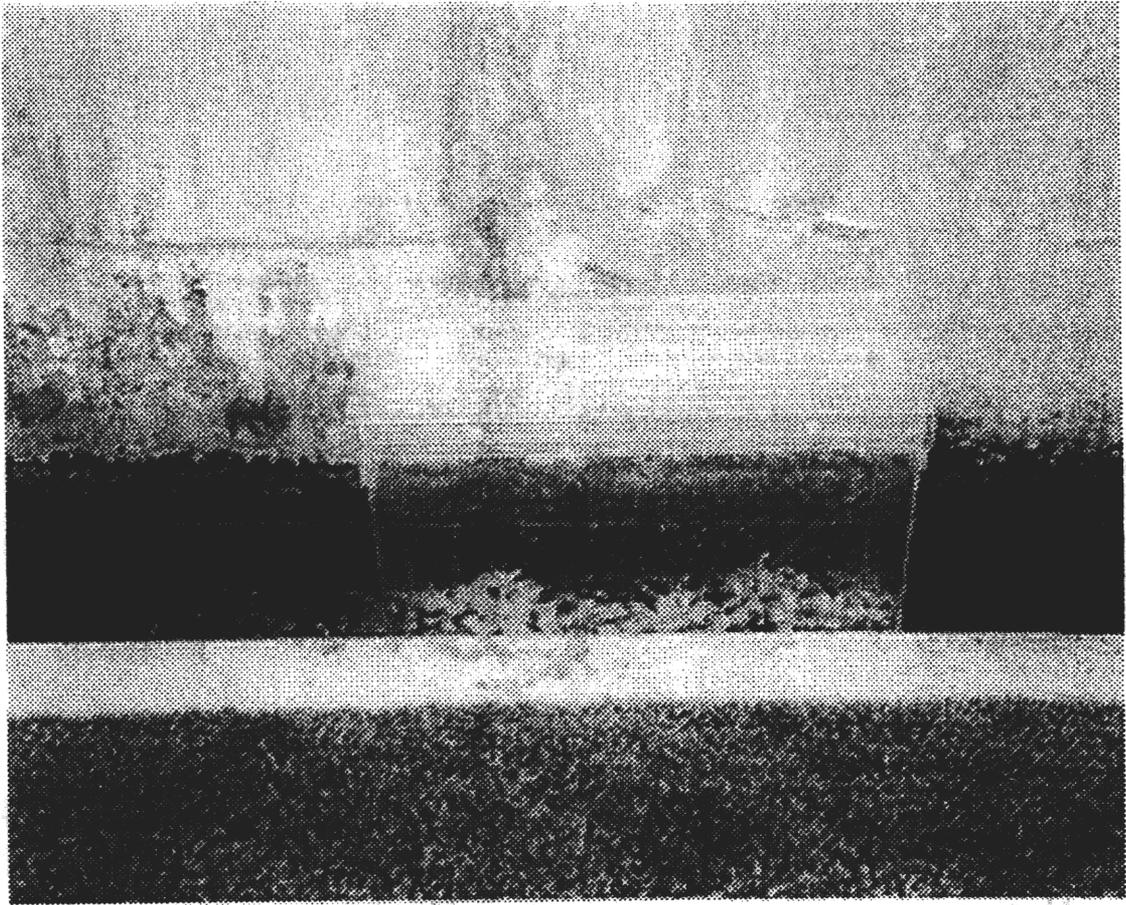


Figure 7

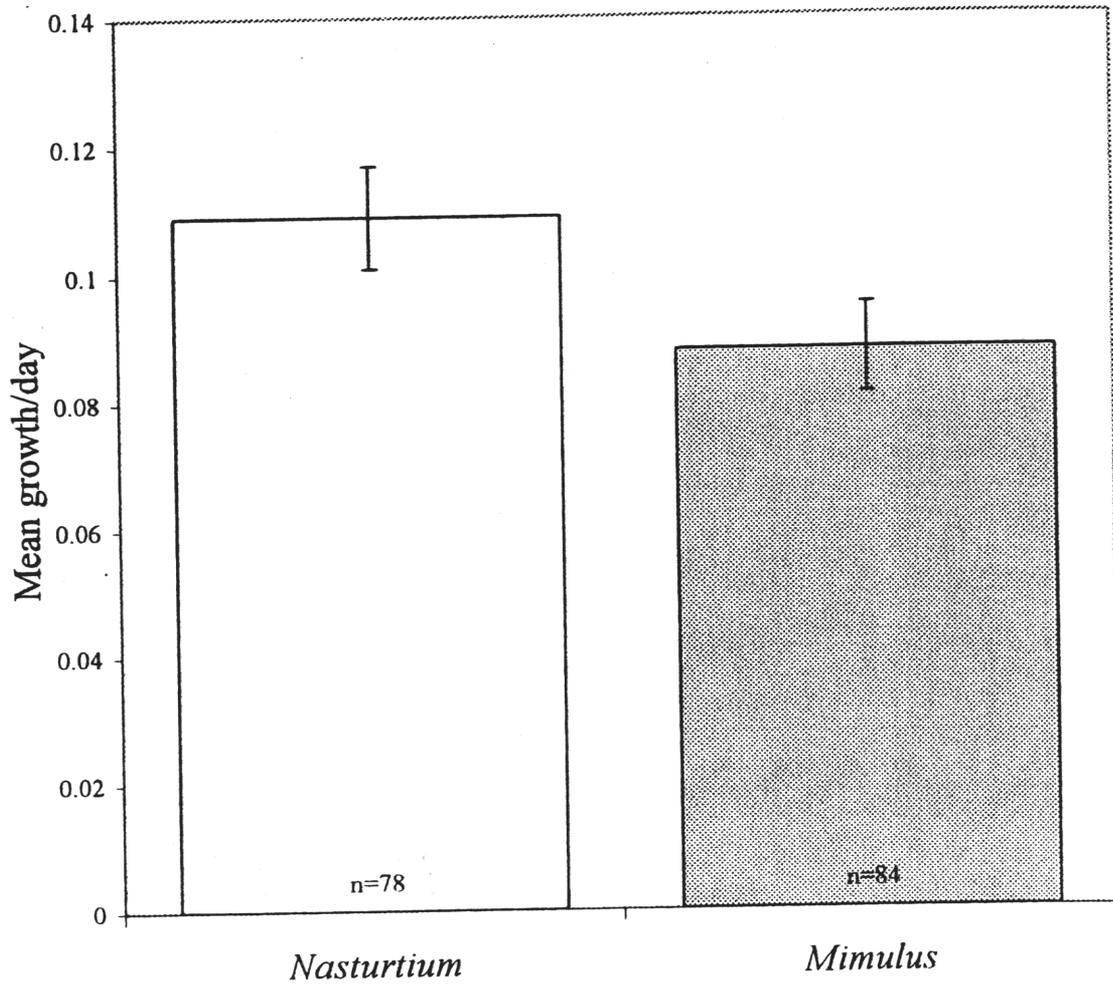


Figure 8

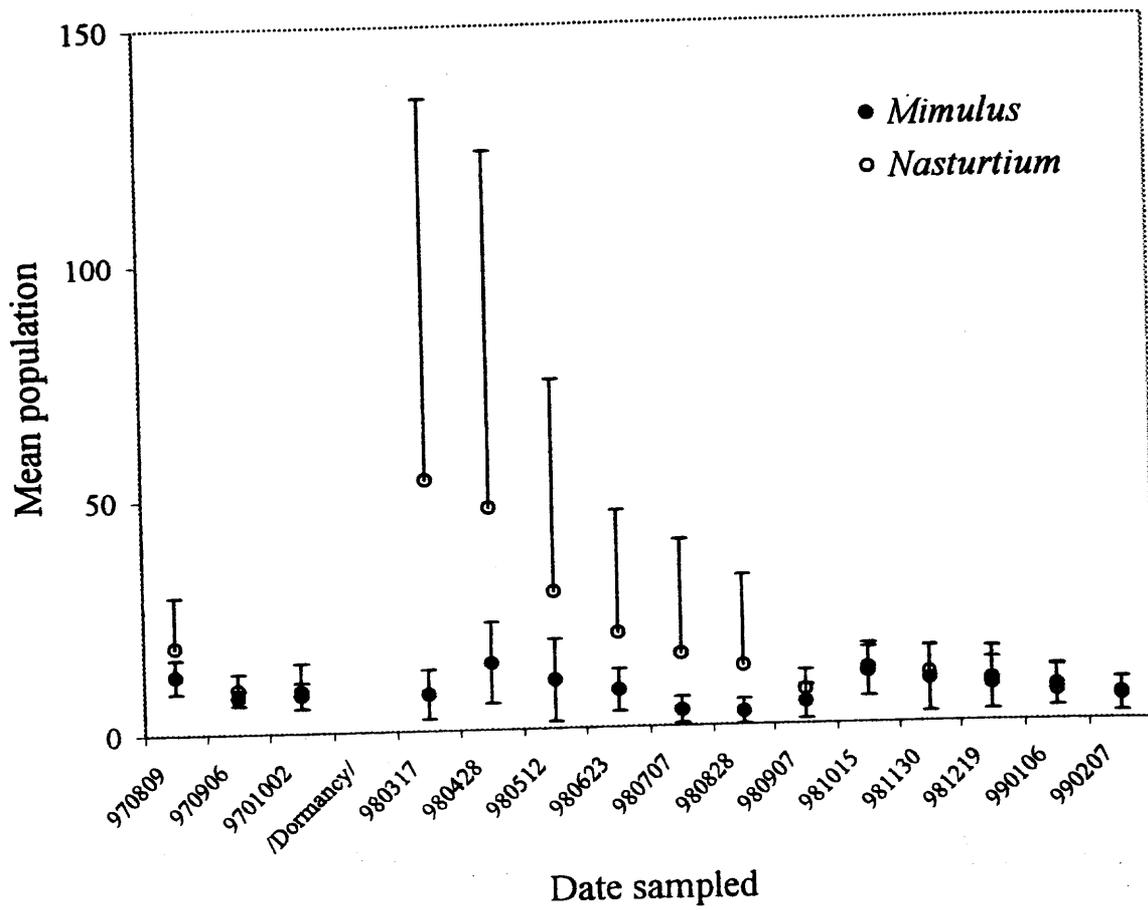


Figure 9a and b

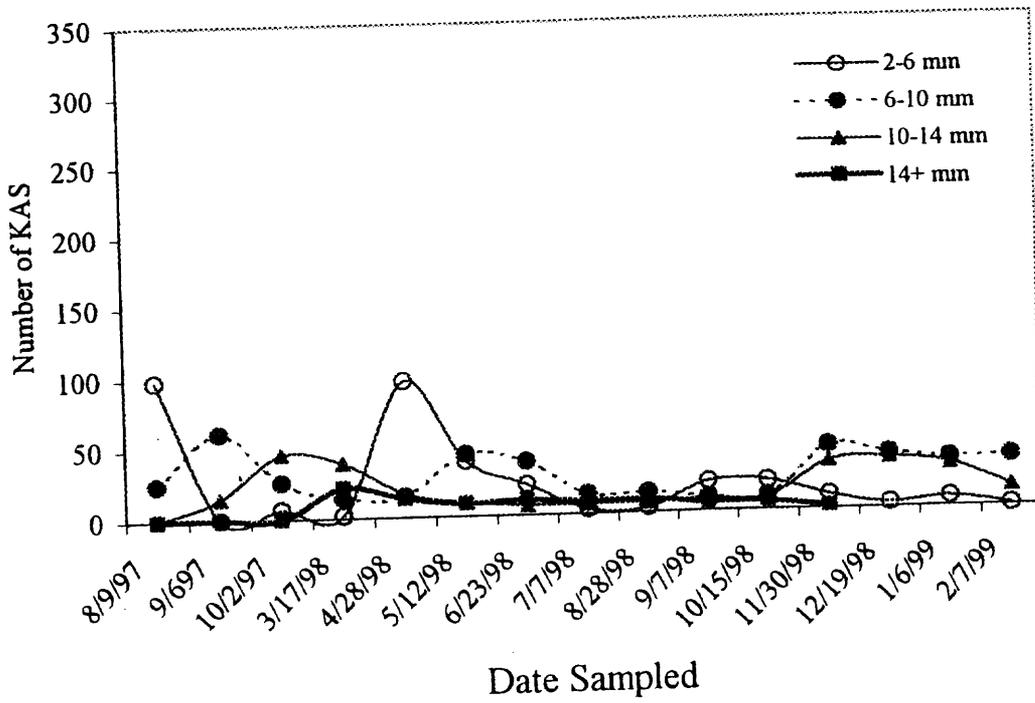
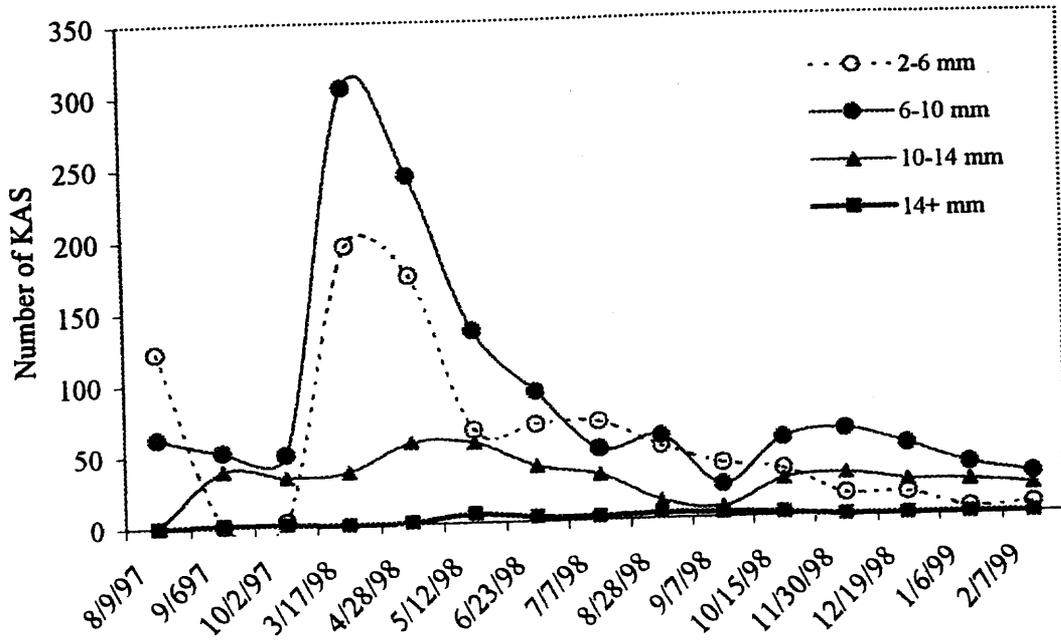


Figure 10

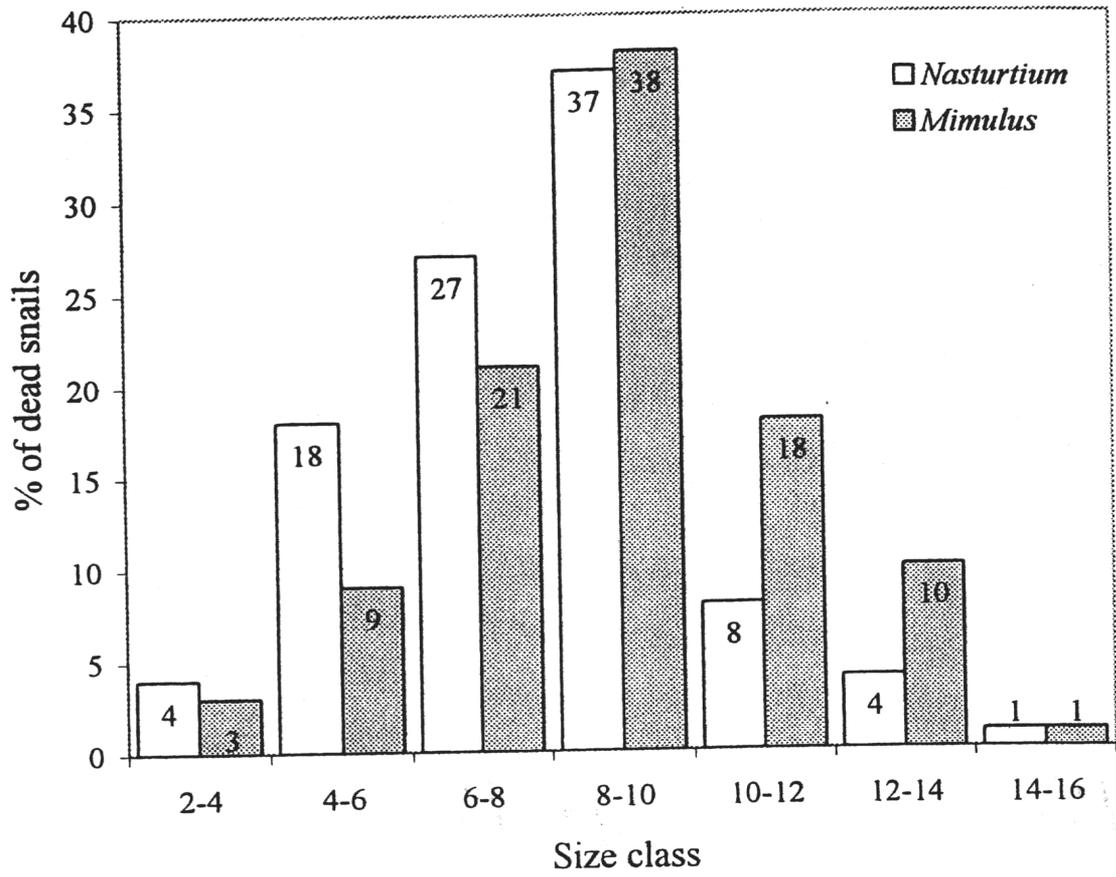


Figure 11

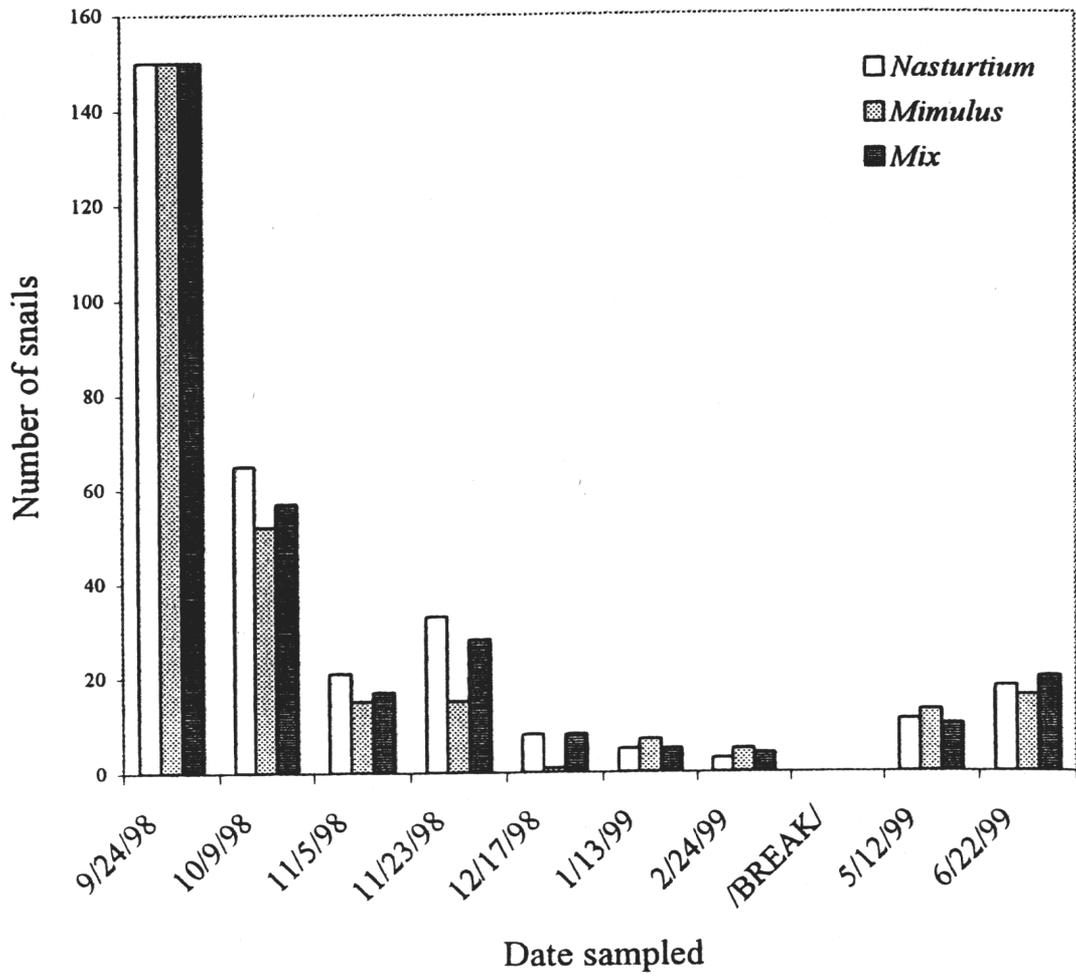


Figure 12

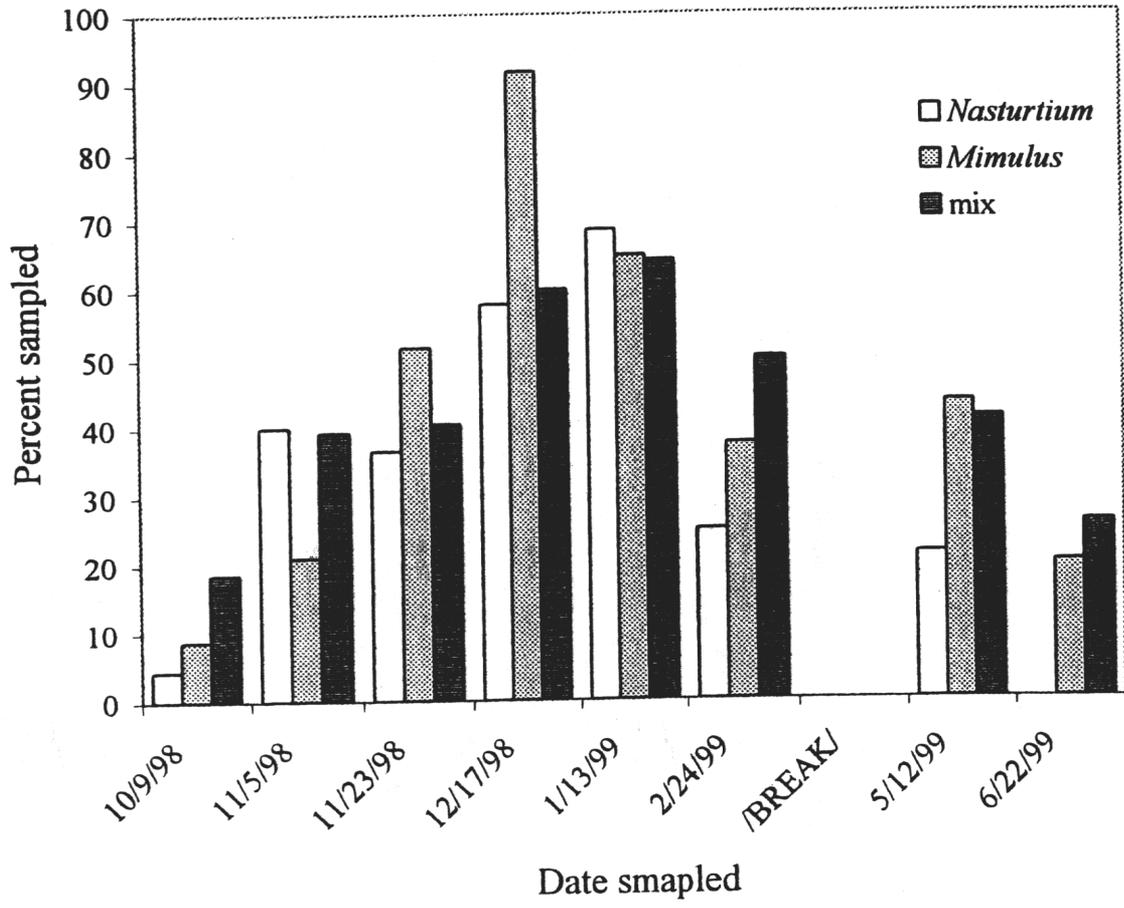


Figure 13

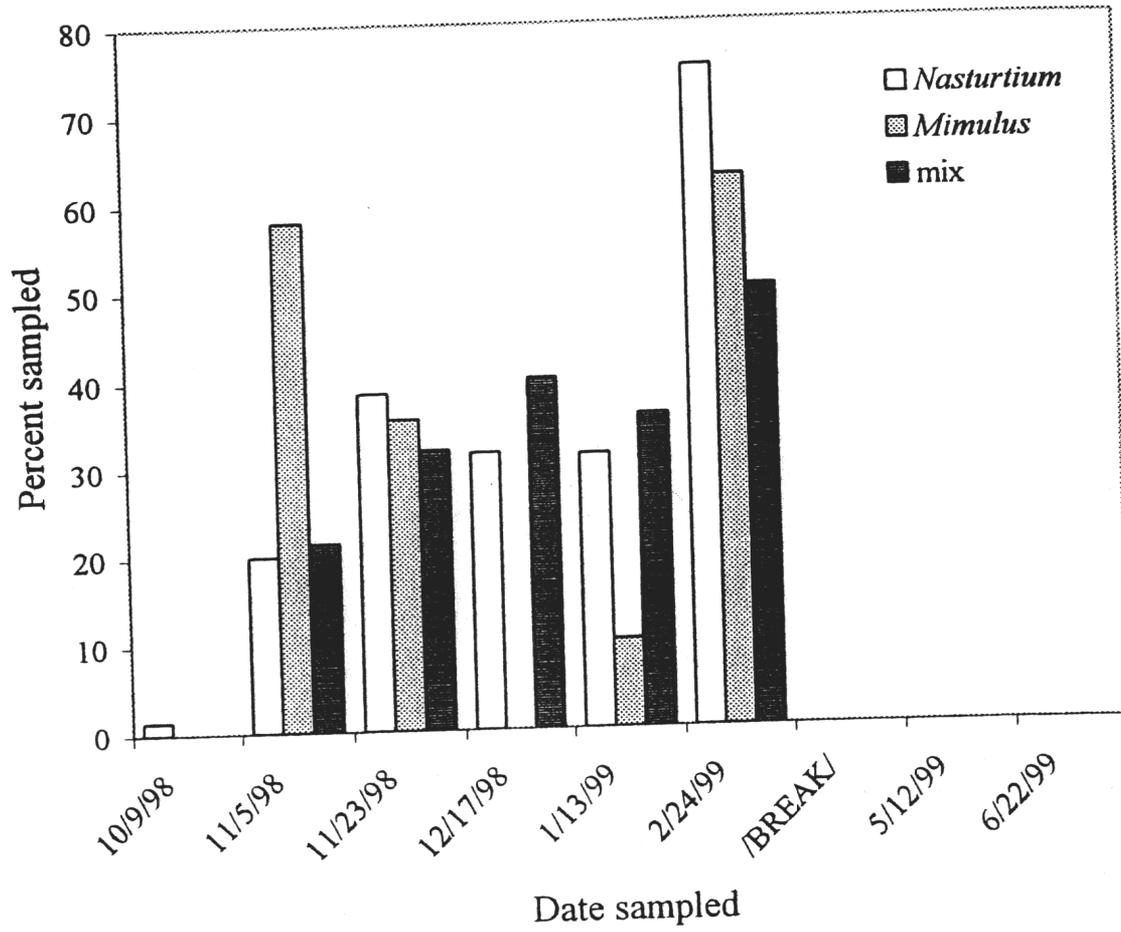


Figure 14

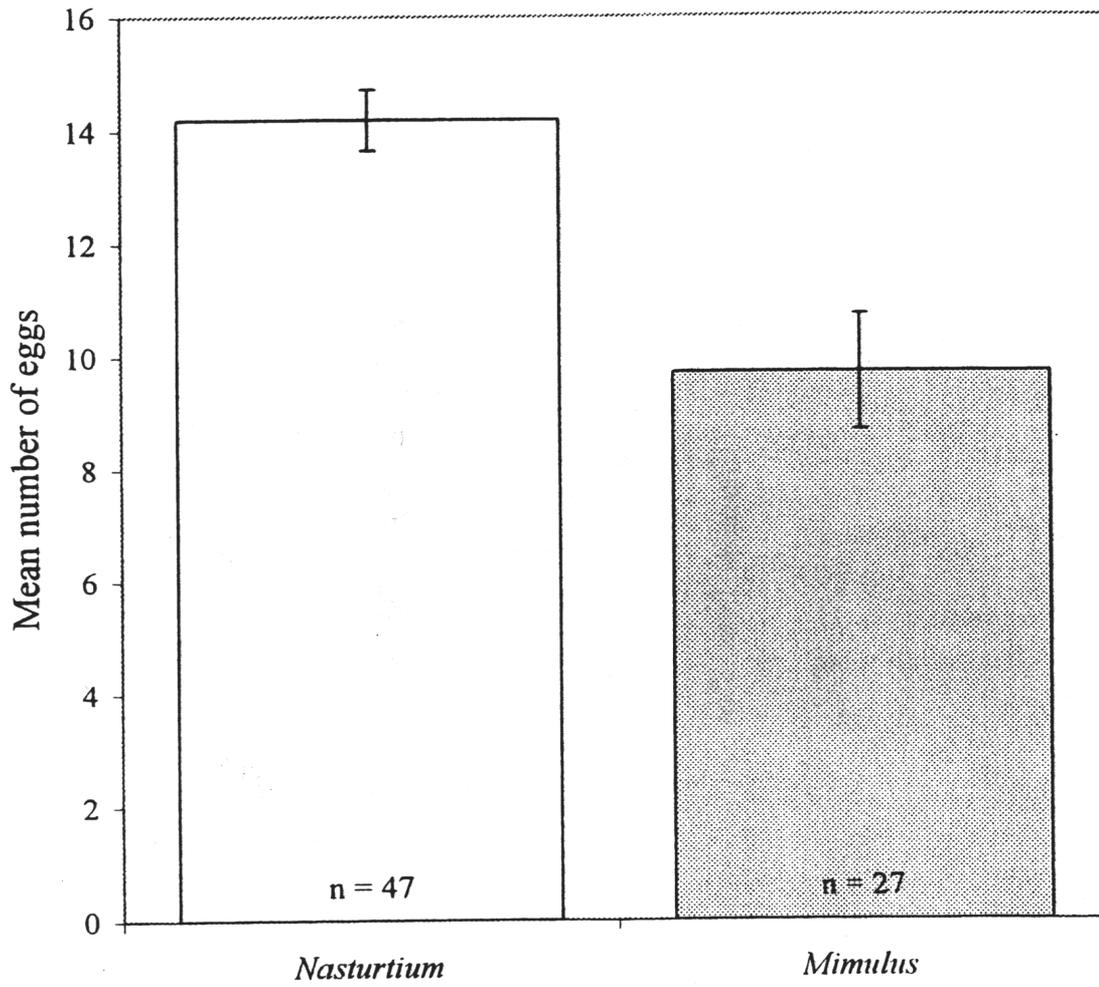


Figure 15

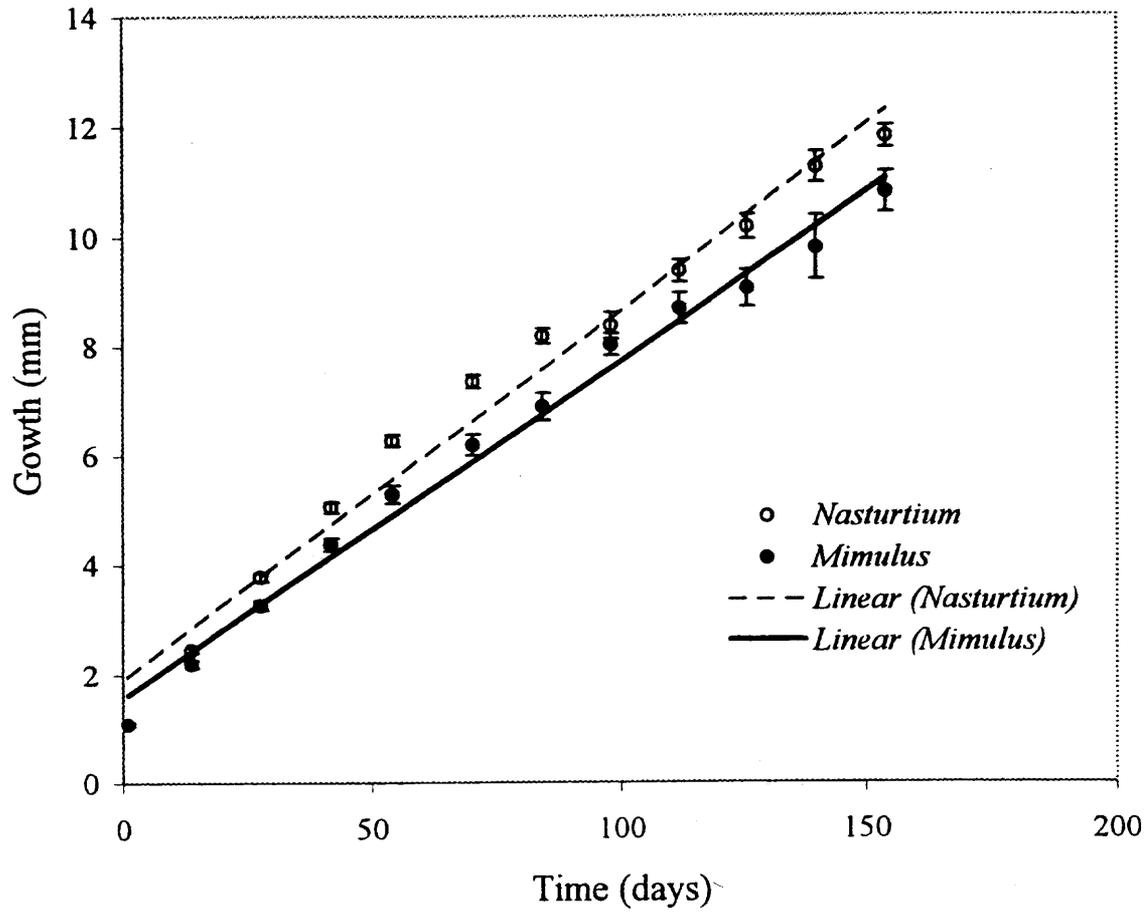


Figure 16

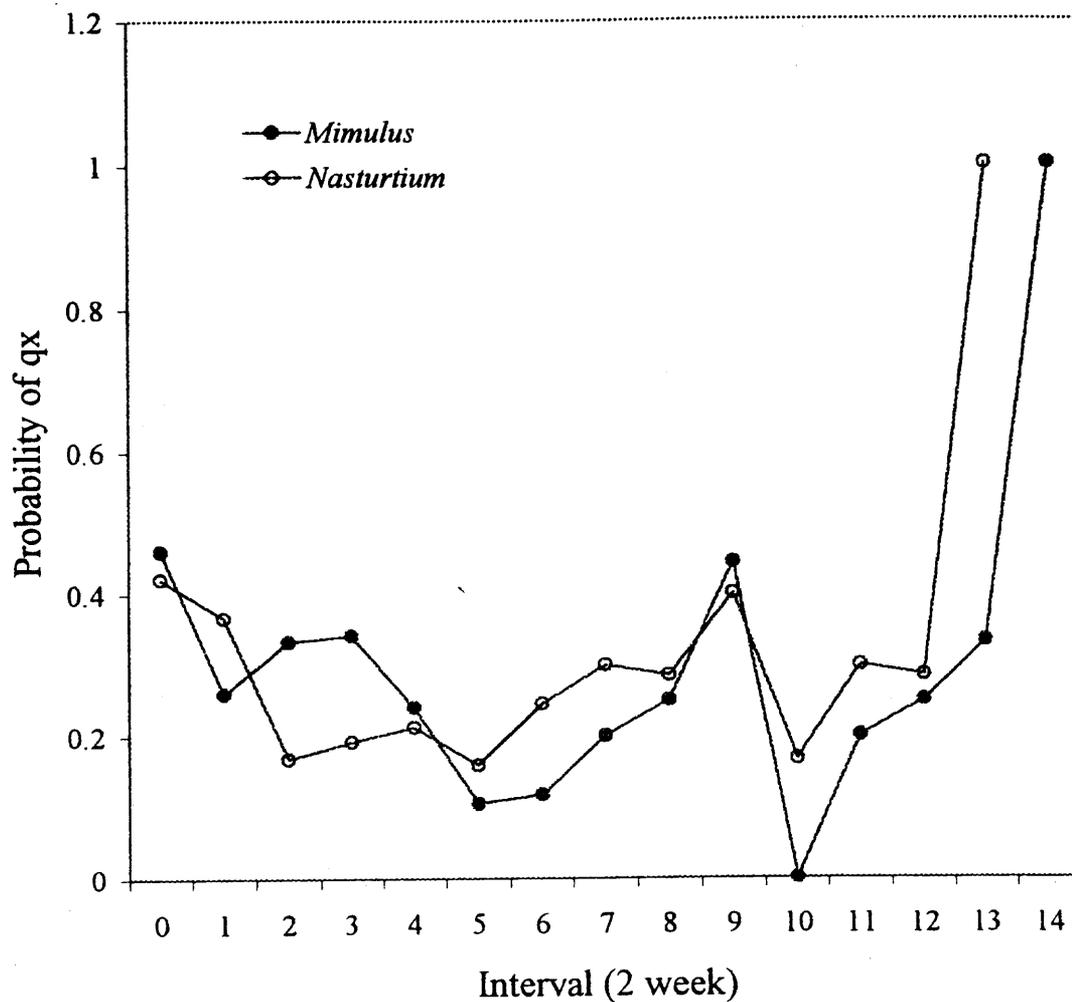


Figure 17a and b

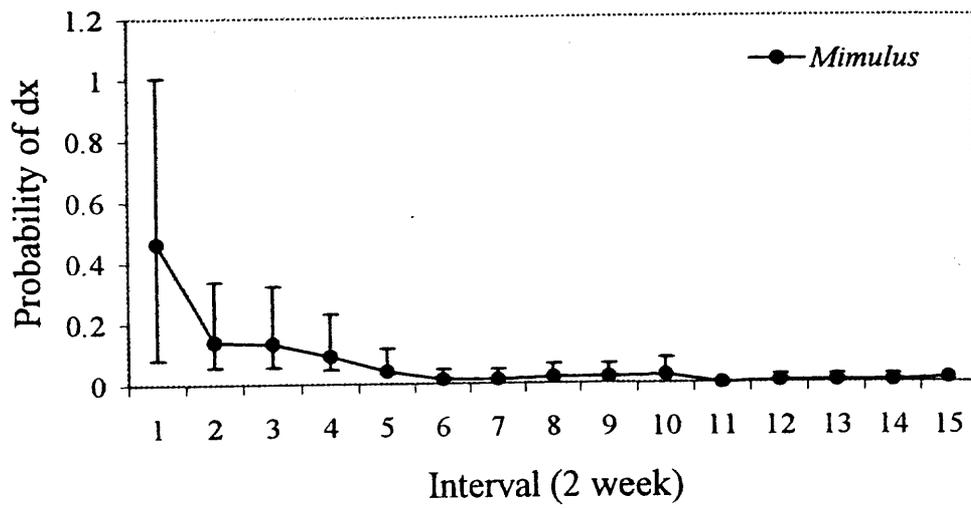
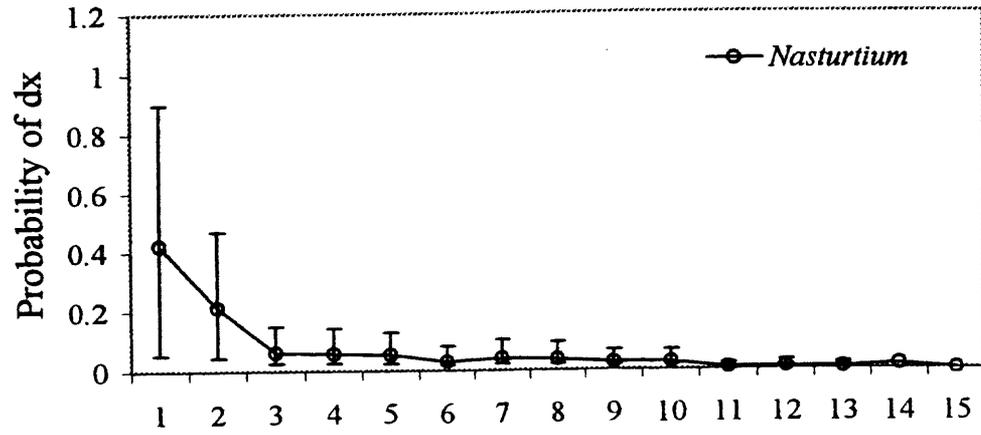


Figure 18a and b

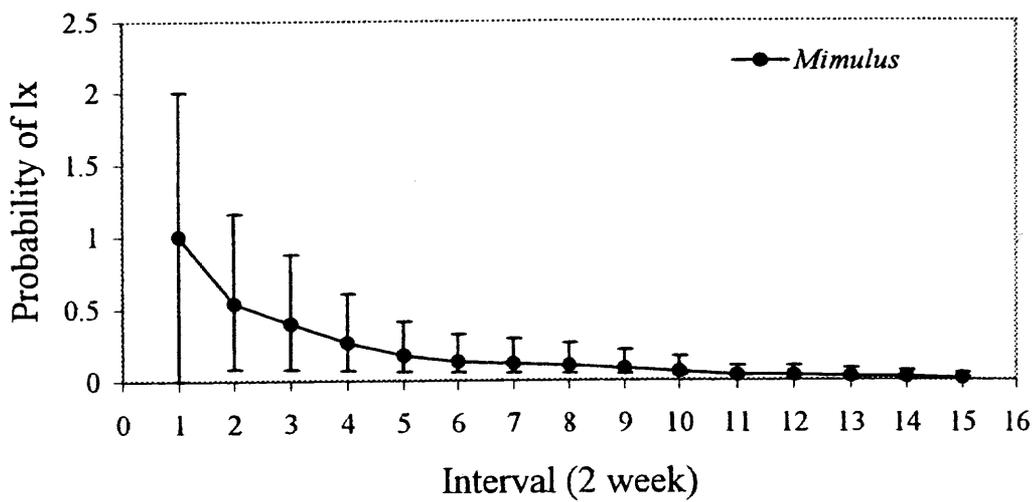
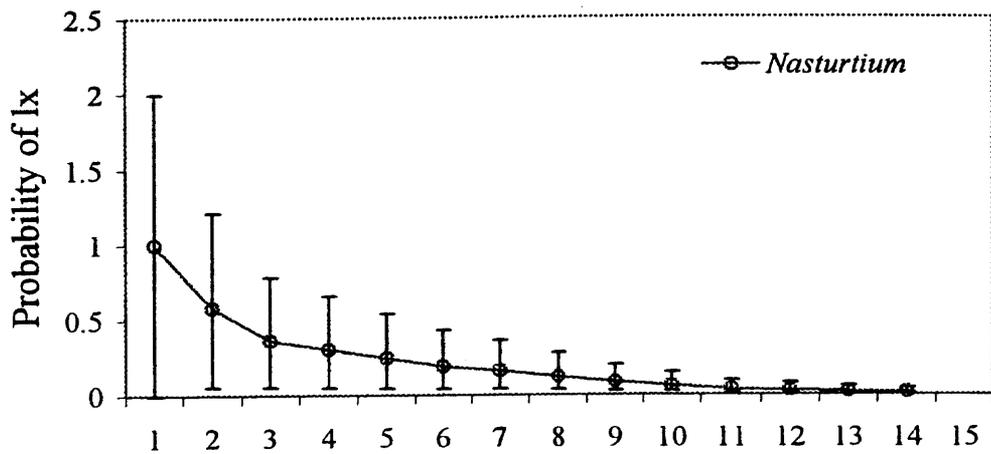


Figure 19

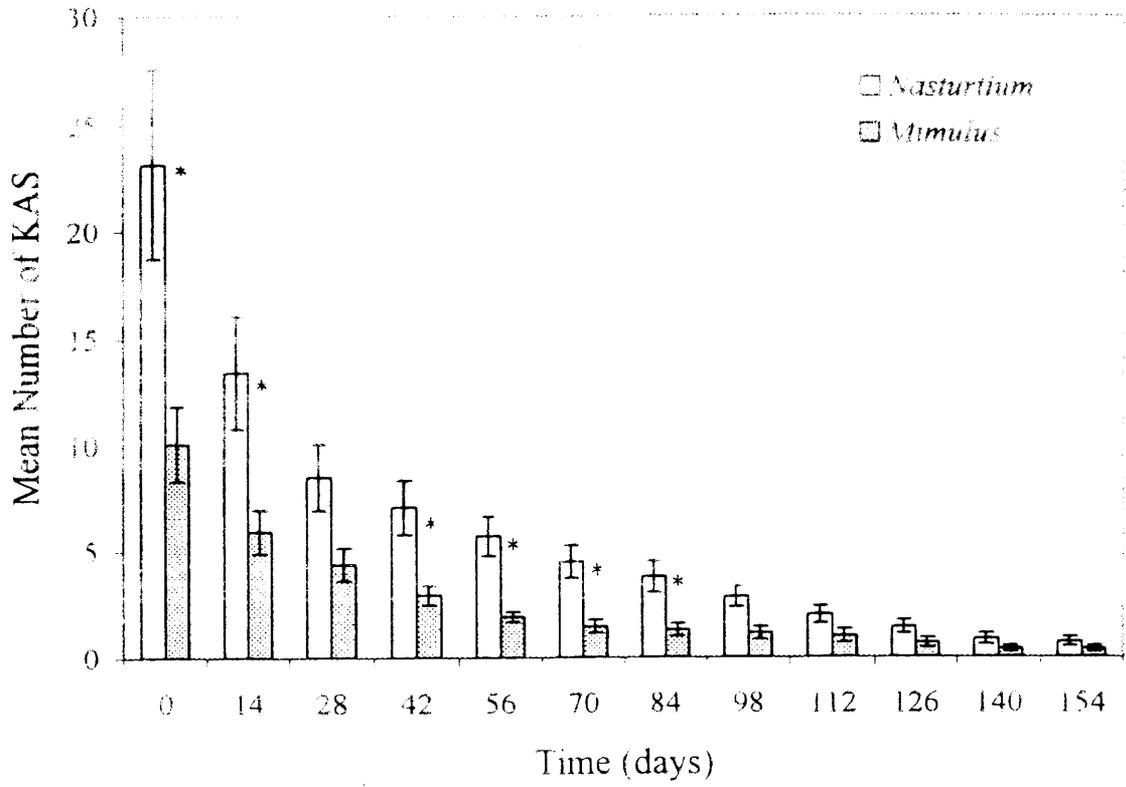
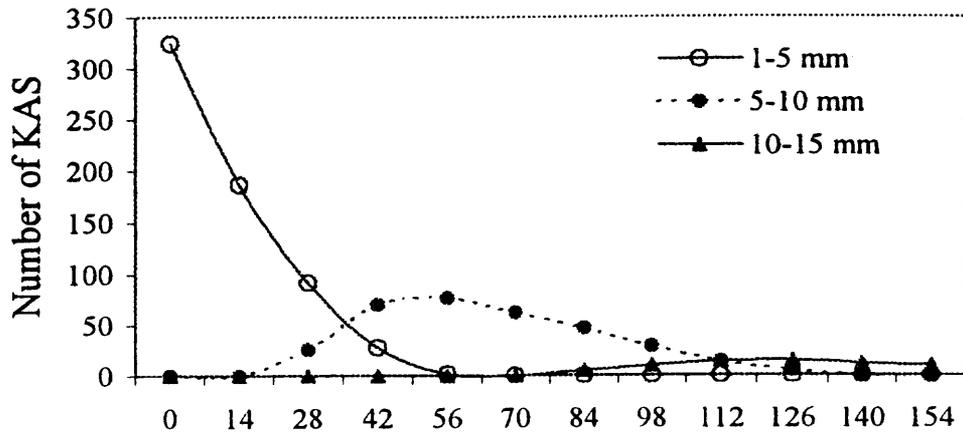


Figure 20a and b

*Nasturtium*



*Mimulus*

