To the non-charismatic mesofauna
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# LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>3-1</td>
<td>Estimates of A (± SE) and W (± SE) based on different methods of calculating snail movement</td>
<td>44</td>
</tr>
<tr>
<td>3-2</td>
<td>Snail density ($D$) (snails/m$^2$) calculated using several different methods for estimating snail movement rates and effective sampling area.</td>
<td>45</td>
</tr>
<tr>
<td>3-3</td>
<td>Models representing hypotheses of effects of hydrilla treatment on apple snail distribution in Lake Jackson. Models also test for potential effects of individual and state covariates.</td>
<td>45</td>
</tr>
<tr>
<td>3-4</td>
<td>List of all non-target species trapped in funnel traps between April and June, 2010 in Lake Jackson, Florida.</td>
<td>47</td>
</tr>
</tbody>
</table>
### LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2-1</td>
<td>Wire funnel traps modified with chimneys and widened entry holes.</td>
<td>33</td>
</tr>
<tr>
<td>2-2</td>
<td>Diagram of shell measurements.</td>
<td>34</td>
</tr>
<tr>
<td>2-3</td>
<td>Tag placement on an apple snail shell.</td>
<td>34</td>
</tr>
<tr>
<td>2-4</td>
<td>Trapping grid array, 7 by 7 traps encompassing 441 m².</td>
<td>35</td>
</tr>
<tr>
<td>2-5</td>
<td>Stage one grid locations in Lake Tohopekaliga.</td>
<td>36</td>
</tr>
<tr>
<td>2-6</td>
<td>Stage one grid locations in East Lake Tohopekaliga.</td>
<td>37</td>
</tr>
<tr>
<td>2-7</td>
<td>Stage two grid locations in Lake Jackson, including areas that were treated with endothall.</td>
<td>38</td>
</tr>
<tr>
<td>3-1</td>
<td>Diagram of snail movements. Each color represents the path of an individual snail through time. Looped arrows mean that the individual was caught in the same trap on two consecutive occasions. Snails that were captured on more than three trapping occasions were relatively infrequent. The snails in this depiction were not necessarily found in the same grid or even in the same season.</td>
<td>44</td>
</tr>
<tr>
<td>3-2</td>
<td>Probability for detection ( (p) ) within control plots in Lake Jackson grids. These values were estimated by averaging most parsimonious CJS models.</td>
<td>48</td>
</tr>
<tr>
<td>3-3</td>
<td>Probability for detection ( (p) ) within treatment plots in Lake Jackson grids. These values were estimated by averaging most parsimonious CJS models.</td>
<td>48</td>
</tr>
<tr>
<td>3-4</td>
<td>Snail apparent survival ( (\phi) ) of control plots in Lake Jackson grids. These values were estimated by averaging most parsimonious CJS models.</td>
<td>49</td>
</tr>
<tr>
<td>3-5</td>
<td>Snail apparent survival ( (\phi) ) of treated plots in Lake Jackson grids. These values were estimated by averaging most parsimonious CJS models.</td>
<td>49</td>
</tr>
<tr>
<td>3-6</td>
<td>Snail apparent survival ( (\phi) ) response to hydrilla treatment in Lake Jackson. Values based on results from model ( \Phi(t) ) ((\text{before, (immediate effect, delayed effect)* treatment}) ) ( p(\text{(before, after treatment)*grid}) ).</td>
<td>50</td>
</tr>
<tr>
<td>3-7</td>
<td>Apparent survival ( (\phi) ) as a function of shell size.</td>
<td>51</td>
</tr>
<tr>
<td>3-8</td>
<td>Snail abundance ( (N) ) in response to hydrilla treatment in Lake Jackson grids. These values were estimated by averaging most parsimonious POPAN models. Each estimate applies to three grids, areas totalling approximately 9000 m².</td>
<td>52</td>
</tr>
</tbody>
</table>
Snail density ($D$) in response to hydrilla treatment in Lake Jackson grids. These values were calculated using the effective sampling areas based on $\frac{1}{2}$ MMDM (see Table 3-1) and abundance estimates from model averaging top POPAN models. .......................... 53

Proportion of snails smaller than 60 mm captured in treated versus control plots. .......................... 54

The mean snail weight increased over time but was similar in treatment and control plots. ................................................................. 55

The mean snail height also increased over time but was similar in treatment and control plots ................................................................. 55

Percentage of snails captured within each size class on Lake Jackson in the 2010 trapping season. Since 98.5% of native apple snails are no greater than 60 mm in height, snails measuring less than 60 mm should be easily consumed by all kites, but those snails larger than 60 mm are expected to be more difficult for juveniles to handle. ................................................................. 56

Number of snails captured within each size class on Lake Jackson in the 2010 trapping season. Herbicide treatments took place between surveys 7 and 8 and the time period separating those two trapping occasions was roughly three weeks as opposed to three to four days as between each of the other surveys. .......................... 57

Summary of snail sizes captured in control plots throughout the sampling seasons. ........ 58

Summary of snail sizes captured in treated plots throughout the sampling seasons. ........ 58
ASPECTS OF THE ABUNDANCE, DENSITY, AND MOVEMENT OF APPLE SNAILS RELATIVE TO INVASIVE SUBMERGED AQUATIC PLANTS IN A CENTRAL FLORIDA LAKE

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The apple snails of Florida, both native (Pomacea paludosa) and exotic (Pomacea insularum), have proven to be important prey items for the endangered Everglade snail kite (Rostrhamus sociabilis plumbeus) that relies on them nearly exclusively for food. Although native snail populations have diminished in recent years throughout the kites’ range, the availability of the exotics has offered a temporary source of sustenance for these otherwise extreme dietary specialists. The majority of remaining kites are thought to inhabit one area, over 20 lakes that comprise the Kissimmee Chain of Lakes in central Florida. Researchers have suggested that the adult kites may be attracted to this area because of the abundance of large exotics which are known to utilize hydrilla (Hydrilla verticillata), an invasive submerged aquatic plant that dominates throughout many of the lakes. In this study, several areas of Lake Jackson were randomly selected and both species of snail were trapped as part of a mark-recapture study to determine the effects of herbicide treatments on snail movement, abundance, and density. Average snail movement rates were used to determine the effective trapping area, and the superpopulation approach was used to estimate snail abundance within each area.
Over 8,000 apple snails were captured in Lake Jackson between April and June of 2010. Modeling results suggest that these snails did not colonize or emigrate from an area in response to the hydrilla treatments. Overall, snail abundance sharply increased over the course of the sampling period. Density increased to a greater degree in the control plots, from 2.04 to 5.86 snails/m². Initial estimates were slightly lower in treated plots but increased from 1.84 to 4.97 snails/m². We concluded that attention to timing of sampling events used for estimating lake-wide or even site abundance could be very critical to the overall reliability of the estimates. The superpopulation approach proved to be very useful and appropriate for this kind of sampling in which timing was an important element and is recommended for future studies.

Because smaller snails were thought to be protected from predation by the dense patches of hydrilla, we expected to find them to be smaller on average in the plots that were not treated. However, we found no support for this hypothesis. When comparing the difference in the number of non-target individuals trapped among treated and non-treated plots, there was no indication that vegetative density prevented predatory fish from entering, and thick mats of hydrilla may actually provide support structure for other avian predators.
Before human settlement and manipulation, Florida was a vast series of interconnected wetlands, receiving and storing rainfall by flooding the extensive system of marshlands and shallow lakes. Endemic flora and fauna are adapted to the seasonal inundations and fluctuating habitats and have grown to depend on the large quantities of water during a portion of the year. Unfortunately for many species, anthropogenic alterations to wetlands in peninsular Florida have caused the degradation of habitat quality (Acosta and Perry 2001, Lorenz 2000). The establishment of water control structures caused innumerable unintended consequences including increased eutrophy and lake succession, diminished water quality, decreased plant diversity, dense vegetation growth, and loss of habitat for wildlife. Government initiated projects such as the Kissimmee River Restoration Project and the Comprehensive Everglades Restoration Plan have been in progress for almost 20 years and researchers have been committed to monitoring changes in wildlife populations in response to restoration efforts (NAS 2003).

The Florida apple snail (*Pomacea paludosa*) has been identified as one indicator of potential restoration success in the Everglades (Darby et al. 1999, Kitchens et al. 2002). It is an important prey item for numerous wetland species, including alligators, redear sunfish, and limpkins (Turner and Mikkelsen 2004). However, interest in the species is largely due to the snail’s most famous predator – the endangered snail kite of Florida (*Rostrhamus sociabilis plumbeus*) – that relies on them nearly exclusively for food (Howell 1932, Cottam and Knappen 1939, Stieglitz and Thompson 1967). The snail kite is a wetland-dependent raptor that inhabits a fragmented series of freshwater wetlands and shallow lakes scattered throughout central and southern Florida (Bennetts and Kitchens 1997). The historical range of the kite once included over 4000 km² that included a portion of the panhandle (Davis and Ogden 1994, Sykes et al.
1995), but they are now restricted to small areas within the Everglades, Lake Okeechobee, Loxahatchee Slough, the Kissimmee River, and the Upper St. Johns River (Reichert et al. 2011). Their population has been reduced from an estimated 3400 individuals in 1999 to roughly 826 in 2010 (Reichert et al. 2011). Many potential causes have been implicated in this decline, but each is related back to one of three important habitat features: distribution of emergent vegetation, nesting substrate, or apple snail presence.

Researchers believe that snail density estimates are an essential component of understanding kite demography and habitat use. They calculate that a snail density of 0.14 individuals per m$^2$ is the minimum needed to support foraging snail kites (Darby et al. 2006). Observations suggest that snail density is correlated with foraging success rates, but a lack of kite presence does not necessarily imply a lack of snails (Darby et al. 2006). Kites are nomadic creatures that move frequently in search of a more abundant and available food supply (Bennetts and Kitchens 2000). Collins and Rawlings have noticed an apparent decline or even disappearance of native apple snails in some Florida wetlands (Rawlings et al. 2007). DeSa (2008), however, noted an increase in snail occupancy after restoration efforts on Lake Tohopekaliga (from here on referred to as Lake Toho). Apple snails are very susceptible to changes in habitat such as extended dry downs (Kushlan 1975, Turner and McCaffree 1994), exposure to agricultural chemicals (Hoang and Rand 2009, Rogevich et al. 2009), and the removal of invasive plants (Corrao et al. 2006). Because the snail kite population is tightly linked to apple snail abundance and availability to kites, factors that negatively affect the snail population could increase the risk of extinction of the snail kite.
Apple Snails of Florida

The Florida apple snail is the largest freshwater snail native to North America (Pennak 1989) and can be found in lakes, rivers, and swamps in Florida, Georgia (Thompson 1984), and Alabama (Hubricht 1962). Its distribution throughout this area makes it the northernmost species in the *Pomacea* genus, while the other members are found naturally distributed in South and Central America and parts of the Caribbean (Haldeman 1845). Unnaturally, however, many of these other species have escaped and become established in parts of Southeast Asia, Sri Lanka, Guam, Papua New Guinea, the Dominican Republic, Hawaii, and the mainland U.S. (Cowie 2002, Lai et al. 2004, Joshi and Sebastian 2006). The Florida apple snail is the only member of the apple snail family (Ampullariidae) that is native to this continent (Burch 1982), but at least three other species of *Pomacea* have become established in Florida: *P. diffusa* (Thompson 1984, Rawlings et al. 2007), *P. haustrum* (Winner 1991), and *P. insularum* (Rawlings et al. 2007). For the purposes of this study, I will be focusing on *P. paludosa* and *P. insularum* as both are important food sources for the Florida population of snail kites.

The Ampullariidae family refers to those freshwater snails that are capable of aestivation. They are distinguished from other families by the presence of both a ctenidium (gill-like structure) and a lung for respiration (Little 1983). Both species, *P. paludosa* and *P. insularum*, are found in a wide range of wetland habitats including graminoid marshes, sloughs, and lake littoral zones, and the dual respiratory system is a necessary adaptation for surviving seasonal fluctuations in water depth as well as dissolved oxygen content (McClary 1964). The lung is also used when the snails leave the water to deposit egg masses on emergent vegetation (Winner 1989) and other non-living strata (Wallace et al. 1956). Similarities end there, however, as the exotic *P. insularum* is significantly larger. *P. paludosa* adults reach approximately 40-70 mm in
length (Thompson 1984) and the exotics grow about three times longer and four to five times the mass (Darby et al. 2007). Additionally, the exotic lays clutches consisting of approximately 1,600 to 2000 eggs (Boland et al. 2007, Barnes et al. 2008) while the native typically lays an average of 30 eggs per mass (Hanning 1979). Since P. insularum are able to lay eggs weekly throughout the breeding season, Barnes et al. (2007) estimates that a single female, even with a conservative 1% hatchling success rate, could produce 252 viable hatchlings each reproductive season. The lifespan of P. insularum is unknown but it is thought to be similar to that of P. canaliculata which live 3 to 6 years (Estebenet and Martin 2002). P. paludosa live a year to a year and a half (Hanning 1979, Ferrer et al. 1990) and generally die post-reproduction in May and June (Darby et al. 2003).

Native to South America, the exotic P. insularum snails (known as island apple snails) were introduced to Florida possibly as early as 1991 (Winner 1991) or earlier (Thompson 1997) through the aquarium and ornamental trade (Britton 1991, Howells 2002), industries which are considered responsible for introducing a third of the world’s most destructive aquatic invasive species (Padilla and Williams 2004). In the mid-1900s, Florida began development of its fish farm culture, producing tropical aquarium fishes, mollusks, and plants easily in the warm subtropical climate (Howells et al. 2006). During this same time period, aquarium trade experimentation with the various exotic snails dramatically increased and the term “mystery snail” was invented to describe all of them. Snail testing involved numerous ampullariids as well as vivaparids which are a related family of operculate freshwater snails that bear live young instead, several of which have also been found released in wetlands within the state (USGS 2009). Gastropods represent 4% of the exotic aquatic species that have been introduced to Florida making it the fourth largest group after fish, plants, and turtles (USGS 2011).
Until genetic analyses were conducted, *P. insularum* snails were incorrectly referred to as channeled apple snails, *P. canaliculata* (Rawlings et al. 2007). We now know that although the two snails have similar shell morphologies, they should be considered separate species, and they are lumped into a group of monophyletic sisters with channeled sutures called the *Pomacea canaliculata* complex (Howells et al. 2006). In other countries where members of this group have been introduced, especially within southern and eastern Asia, major agricultural losses have resulted (Anderson 1993, Naylor 1996, Cowie 2002), but researchers have found it much more difficult to estimate their ecological impacts (Hayes et al. 2008). In wetlands in Thailand, Carlsson et al. (2004) found that the presence of more than two *P. canaliculata* per m² resulted in a decrease in macrophytes and vegetative diversity and an increase in nutrients and algal blooms. Wood et al. (2005) discovered that these snails graze selectively on freshwater bryozoans in Southeast Asia and they have caused the bryozoans to become so rare that they are now only able to exist on floating structures that do not come in contact with the shore or bottom sediment. Halwart (1994) blamed them for the decline of native ampullariids in the Philippines. It has also been suggested that they be introduced as a biocontrol agent against invasive planorbid snails due to their effectiveness at consuming eggs and young (Cazzaniga 1990). However, it has been well established that their voracious appetites are troublesome at best. They were listed among the world’s 100 most invasive species in 2000 (Lowe et al. 2000).

Within the United States, *P. insularum* has also been found established in Texas and Georgia and the number of invaded states may increase as more people are reportedly seeing snails with channeled sutures each year, particularly in Louisiana, Mississippi, Alabama, Georgia, and South Carolina (Rawlings et al. 2007, USGS 2009). The potential impacts of these snails are numerous. It has been suggested that further spread of *P. insularum* may facilitate the
spread of vertebrate parasites like *Parastongylus* spp. which can cause eosinophilic
meningoencephalitis and abdominal angiostrongyliasis, both treatable diseases that infect
humans (Hollingsworth and Cowie 2006) and are known to be present in Florida already (Duffy
et al. 2004, Miller et al. 2006). Burlakova et al. (2009) suspects that *P. insularum* can impact
wetland restoration efforts because of specific feeding preferences for plants such as
*Hymenocallis* and *Sagitaria* spp. Others wonder if the decline in abundance of *P. paludosa*
individuals following *P. insularum* introduction is a direct result of egg consumption by the
exotics (Rawlings et al. 2007) as occurred when *P. bridgesi* was introduced to a congeneric
species (Aditya and Raut 2001, 2002). Rawlings et al. (2007) even hypothesize extinction of *P.
paludosa* by hybridization since the two snails are so closely related phylogenetically. Perhaps
the most disturbing effect is the potential for this exotic to cause the extinction of the already
endangered snail kite.

Despite the substantial difference in size, adult snail kites successfully forage for and
consume both species of snail (Darby et al. 2007, Cattau et al. 2009). This has been fortunate for
the kites as native snail populations have diminished in recent years throughout the kites’ range
(Darby et al. 2005, Rawlings et al. 2007) and the availability of the exotics has offered a
temporary source of sustenance for these otherwise extreme dietary specialists (Bennetts et al.
2000). Unfortunately, juvenile kites struggle to handle the larger snails and waste a high amount
of energy on snails they are never able to consume (Cattau et al. 2009). Despite this fact, the
majority of remaining kites are thought to inhabit one area, over 20 lakes that comprise the
Kissimmee Chain of Lakes area (KCOL) in central Florida (Cattau et al. 2009), where the exotic
snails proliferate (DeSa 2008). In 2010, 51% of successful nesting attempts range-wide occurred
in the KCOL, two thirds of those on Lake Toho alone (Reichert et al. 2011). This dependence on
Lake Toho is disconcerting. Juvenile kites that fledge in the KCOL will be forced to feed on the exotic snails and their inefficiency in doing so may negatively impact their survival (Cattau et al. 2010). Researchers suggest that the adult kites may be attracted to this area because of the abundance of large exotics which are known to utilize hydriilla (*Hydrilla verticillata*) (Reichert et al. 2011), an aquatic invasive plant that dominates throughout many of the lakes (Howells 2002, Gettys et al. 2008, Baker et al. 2010).

**The Hydriilla Invasion**

Native to the warmer regions of Asia (Cook and Lüönd 1982), hydriilla has been recognized as a major submersed aquatic weed in Florida since 1967 (Mackenzie and Hall 1967). It was planted by aquatic plant dealers in the southeast in 1959 (Blackburn et al. 1969) and is now found in at least seventy percent of Florida's freshwater drainage basins, including the KCOL (FLDEP 1988-94). Hydriilla is an extremely competitive colonizer of aquatic habitats and is known to displace important native aquatic plants such as eelgrass (*Vallisneria americana*) once established (Langeland 1996). It can grow to such high densities that it reduces flow in drainage canals and around water control structures (Blackburn et al. 1969, Langeland 1996). Additionally, fishermen and other recreational boaters find that hydriilla can greatly limit the areas where they are able to navigate (Langeland 1996).

It is for these reasons that 174 million dollars were spent to control the noxious weed in Florida from 1980 to 2005 and it continues to be a pressing issue (Schmitz 2007). Corrao et al. (2006) discovered that herbicide applications to water lettuce in Wacissa Springs resulted in drowned snail eggs, but hydriilla treatments in the KCOL are considered to be fairly harmless when conducted properly. Two different herbicides are currently used to control the hydriilla in Osceola County: endothall and imazamox (Interagency Aquatic Plant Management 2011).
Endothall is the preferred herbicide and is sprayed as a liquid or distributed in pellet form to selectively target and eliminate hydrilla without damaging other aquatic plant species. Imazamox is sometimes added to the entire body of water after the endothall treatment to limit excessive regrowth and produce longer lasting results. Within the KCOL, approximately 5700 acres were planned for treatment by one or both herbicides in 2010 (Interagency Aquatic Plant Management 2011 and Zach Welch, pers. comm.). This is a decrease from over 8000 acres that were treated in 2009 (Interagency Aquatic Plant Management 2011), but Lake Toho was responsible for the bulk of that decrease because the hydrilla there did not expand to the same extent as in previous years (Ed Harris, pers. comm.).

Little is known about the nutritional requirements and feeding behavior of apple snails, but both species are known to consume a variety of macrophytes (Howells et al. 2006, Baker et al. 2010) and macrophyte assemblages (Sharfstein and Steinman 2001). The exotic snails have been found to flourish within submerged hydrilla, feeding on the leaves and stems (Howells et al. 2006; Baker et al. 2010), whereas the natives appear to simply graze the epiphytic complexes attached to the surface of the plant eating very little of the actual hydrilla (pers. obs.). Aquarium observations suggest that the two species are equally attracted to hydrilla especially when other food sources are limited suggesting that it is likely that they would be attracted to specific areas where hydrilla is present in natural systems as well. Cattau et al. (Appendix D and E, 2009) observed kites successfully foraging in areas of dense hydrilla and suggested that they may be able to capture smaller size classes in those areas. Because of its ability to serve as a refuge from aquatic predators, thick mats of hydrilla might be able to concentrate higher density populations of younger exotic snails that would be more suitable for juvenile kites to handle. Therefore, by altering an important food source and climbing structure required for breathing, herbicide
treatments could profoundly affect snail distributions, potentially decreasing their availability to the kites. This study addresses these issues and it is hoped that an improved management strategy for invasive plants in the KCOL and the apple snail will be produced as a result.

**Study Objectives**

This study was intended to answer the following research questions and hypotheses.

1.) What is the efficacy of deploying grid arrays of snail traps to determine the snail presence, occupancy, and densities in deeper water habitats typically or routinely dominated by hydriilla in areas of historical kite nesting?

**Hypothesis 1:** Snail densities will be lower in the deeper lacustrine habitats than in shallow wetlands sampled by Valentine-Darby et al. (2008). Telemetry research suggests that snails tend to move toward shallower areas when they reach depths greater than 50 cm (Darby et al. 2002). Biologists who have caught apple snails in the past have limited their sampling to water that is no deeper than 60 cm.

2.) What is the effect of herbicide treatment on apparent snail densities in the vicinity of historically high-use nesting sites?

**Hypothesis 2:** Apparent snail survival (the probability that the snail is alive and remains on the study area, referred to as phi or \( \phi \)) will decrease in treatment plots after herbicide treatments have been completed. Since we believe that the snails are attracted to the hydriilla as a food source, removing it should cause them to disperse to the surrounding area.

**Hypothesis 3:** Grids with hydriilla will yield smaller than average size classes of exotic snails. Because smaller snails should be provided refugia by dense hydriilla, they are
expected to be smaller on average due to decreased predation. In areas without hydrilla, only those larger snails that are no longer vulnerable to so many aquatic predators will be present in high abundance. Once the treatment grids are treated, we expect to the average snail size to increase.

3.) Can the superpopulation approach to estimating abundance be used to determine density for species such as aquatic snails? This method has been discussed as an option in other trapping grid studies (Conroy et al. 2008), but, to my knowledge, has not been attempted.

4.) What are the differential distributions of native and exotic apple snails in these locations?

**Hypothesis 4:** The number of exotics will greatly exceed that of the native snails.

Although both species are likely to be found among the hydrilla, researchers have been observing the expansion of the exotic snails in the area for at least ten years (Rawlings et al 2007, DeSa 2008, Cattau et al. 2010).

5.) What additional faunal species are attracted to the funnel traps and are these species associated with snail captures? Will they be affected by the elimination of the hydrilla?

**Hypothesis 5:** Snails will not be attracted to the traps due the presence of non-target species and detection rates will not be influenced as a result. In a pilot study conducted by Darby et al. (2001), similar funnel traps were baited with and without dead fish and snail capture rates were unaffected.
CHAPTER 2
METHODS

Trap Description

Wire funnel traps like those used in Darby et al. (2001) and Cattau et al. (2010) were modified and used to capture the apple snails. Such traps are sold commercially for catching crayfish. They have also been used in numerous field studies for capturing other aquatic fauna such as sirens, amphiumas, and small turtles (Johnson and Barichivich 2004). The funnel traps are made from green vinyl-coated hardware cloth with ½” by ½” square mesh and have three funnels at the base where individuals can enter but are unable to exit (Fig. 2-1). In order to catch the much larger invasive snails in a lacustrine habitat, two modifications were made to each trap:

(1) The tapered ends of the funnels were cut and widened from 5 cm to approximately 8 cm in diameter. *P. insularum* can sometimes exceed 9 cm in height (Darby et al. 2007), but in an effort to decrease the likelihood for smaller snails to escape, we chose to exclude the very largest snails. It is not known what portion of the population exceed 9 cm, but judging from empty shells that can be found along the shoreline of lakes in the KCOL, the number of these snails is thought be negligible. Due to the design of the trap, we do not expect to see higher escape rates than previously experienced with smaller holes.

(2) “Chimneys”, three foot tall vinyl-coated wire extensions, were attached to existing traps in order to allow the snails and other non-target species access to the water surface for aerial respiration. Modified traps stand approximately 1.5 m, capable of sampling more than two times the depth of other sampling methods.

Traps will not be baited, but trapped females may attract additional males (Darby 1998). Snails may inadvertently be attracted to bycatch as well as some species (Florida and Longnose gar in
particular) occasionally become injured and die while trapped. However, Darby et al. (2001) found that dead fish did not help to attract snails.

**Snail Handling Procedures**

Each apple snail obtained from a trap was identified as native or exotic and then measured and tagged. Four measurements were collected from each individual every time it was captured. Wet weight was measured using one of a series of spring scales (all Pescola® brand). Because of the drastic difference in snail sizes and our desire to achieve the most accurate reading, maximum capacities ranged from 10 g for the very smallest snails up to 200 g for the largest. Shells were also measured for total height, aperture height, and width using vernier calipers. Total height was measured linearly along the spiral axis from the apex to the outer edge of the aperture lip while aperture height was measured from the top of the aperture to the same outer edge of the aperture (Fig 2-2). Width was measured perpendicular to the axis from the edge of the aperture to the opposite side of the shell body.

Upon initial capture, we individually marked each snail with a laminated 3 mm by 5 mm plastic tag (Floy Tag & Manufacturing, Inc., Seattle, WA) applied with marine epoxy glue (Evercoat®) that is formulated to resist damage from exposure to water, sun, chemicals, and fuels and sets in less than 10 minutes. Tags were attached to the shell approximately 15 mm up from the aperture on the right side of the body whorl adjacent to the suture (Fig. 2-3). Prior to attaching each tag, snail shells were dried and then lightly sanded to ensure a tight bond. After allowing epoxy adequate drying time, snails were measured and released within a meter of the trap where discovered. Recaptures were noted, measured, and rereleased as well.
Grid Arrays and Study Sites

Valentine-Darby et al. (2008) deployed and tested trap grid arrays to estimate snail densities in the Everglades. For this study, we used a similar capture technique. Reproductive behaviors and egg production peak between April and May in South Florida wetlands (Darby et al. 1999). Cooler temperatures in central Florida cause this peak to extend into June (Stevens et al. 2002). For that reason, a series of similar grid arrays were used to determine snail presence, abundance, and densities between April and June of 2009 and 2010. The objectives were addressed in two stages.

Stage 1: Grids for the first stage included 64 funnel traps spaced 3.5 m apart (8 by 8 square) covering an area of 600 m². Traps were held in place with PVC poles which were pounded into the substrate. Vegetation was pushed aside to allow traps to come in contact with the lake bottom but none was removed. Traps were checked and emptied every three to four days, the period used by Valentine-Darby et al. (2008), to ensure adequate capture rates for statistical analysis. As Otis et al. (1978) recommends that sampling take place no fewer than five separate occasions, grids were checked a minimum of six times. Trapping took place in March through June 2009.

The first stage was a preliminary test that allowed us to determine the effectiveness of using funnel traps to sample for apple snails in deeper water (greater than 60 cm) and took place in Lake Toho (Fig. 2-5) and East Lake Toho (Fig. 2-6). Lake Toho is frequently foraged by snail kites and known to support a high number of invasive apple snails (Cattau et al. 2009) while containing dense mats of hydrilla (pers. obs.). East Lake Toho is one of the few lakes in the KCOL to maintain a healthy population of native apple snails—despite invasion by the larger exotic snails—and allowed us to determine whether the modified traps were capable of catching smaller snails. This stage also tested the efficiency of using the grid array formation as opposed
to other arrangements such as transects (DeSa 2008, Muench 2004) or randomly scattering traps throughout the study area (Cattau 2008).

**Stage 2:** The second stage took place at six sites randomly selected from the littoral zone of Lake Jackson (Fig. 2-7) in May and June 2010. Lake Jackson is a much smaller lake (413 ha) just east of Lake Kissimmee that is frequented by a relatively high number of snail kites and has also been invaded by hydrilla. Just prior to sampling in Lake Jackson, kite surveys revealed that the number of kites on the lake had increased from zero in March to 14 individuals in April 2010.\(^1\)

From 1992 to 1997, Lake Jackson underwent a large-scale habitat enhancement project that involved three extreme drawdowns and several phases of muck removal and mechanical extraction of vegetation – mostly cattails (Hulon et al. 1999). Lake Toho went through a similar process in 2004 and it resulted in the exotic snails spreading from one small cove (Cattau 2010) to 83% of the entire lake (DeSa 2008). Fish, birds, mammals, reptiles, and amphibians were sampled and surveyed for before and after the Lake Jackson Habitat Enhancement Project (Hulon et al. 1999). 94 species were discovered in all but mollusks were entirely forgotten, so we have no record of changes to the apple snail populations or species present. However, no snail kites were found on the lake during that time period suggesting that the snails may have only been present at very low densities.

Sampling in Lake Jackson required slight changes to the sampling protocol established the year before. 7 by 7 square grids were used rather than 8 by 8 in order to allow us to set up a greater number of sampling grids with the limited number of traps (300), encompassing areas 441 m\(^2\) instead (Fig. 2-4). We continued to check and empty the traps twice a week for two

\(^1\) These numbers are based purely on field observations and have not been corrected for detection probability.
months. After four weeks of trapping, three of the six sites were chosen at random to be treated with endothall, applied as aquatic herbicide Aquathol®. Two weeks after the application, trapping resumed for an additional four weeks in all six of the grid arrays after the hydrilla had dropped. All non-target species were identified and counted during snail sampling as well.

A water depth was collected from each trap point. Water temperatures were taken twice a week throughout the sampling period. Three temperatures were recorded from 0.5 m below the surface of the water in random locations throughout each of the grids using a waterproof digital thermometer with a plumb-bob. The temperatures were then averaged.

Vegetation sampling was completed before and after the herbicide treatment to determine the extent of changes in the density of hydrilla present in all of the grids. Twelve 0.25 m² samples were taken from each of the grids. We chose to limit the sampling size to decrease the potential effects of our plant sampling on apple snail occupancy. Sample locations were stratified to three samples per quarter of each grid and randomly selected. Vegetation was cut at the ground level for those species that were rooted mostly belowground such as Egyptian panicgrass (Paspalidium geminatum). These species were included based on their root locations as opposed to where their stems protruded from the water surface. Floating and mat-forming species like waterlettuce (Pistia stratiotes) and alligatorweed (Alternanthera philoxeroides) were included if they were found at the surface within the quadrat, but their roots were removed prior to being weighed. Submerged species like hydrilla and Utricularia spp. were cut and collected from the entire water column within the square. All species were identified in the field and weighed wet. For species like Egyptian panicgrass or alligatorweed with adequate structure (unlike hydrilla), stems were also counted.
Data Analyses

Estimating Apparent Survival

The statistical modeling program, Program MARK (Cooch and White 2010), was used to analyze the mark-recapture data for snail detection rates and survival. Each time the grids were checked and emptied—even though it took two full days to process all six of the grids—is referred to as a single survey. The before and after treatment periods were considered two separate seasons. To determine survival, Program MARK uses a list of encounter histories for each individual where each number in the series of values corresponds with a survey. If a particular snail was discovered during a survey, then a 1 was recorded. If not, then 0. Had we been unable to complete a survey or the data was otherwise lost, a dash (“-“) would have been recorded. For example, an encounter history for a snail on Lake Jackson on which we completed 14 surveys (7 before treatment and 7 after) would look something like this: 0000100 0011000. This would indicate that the snail was first captured in the first season during the fifth survey and then recaptured on the third and fourth surveys of the second season. Encounter histories for all individuals that were given a unique tag identification number were entered into Microsoft Excel and then transported into Program MARK as an .inp file.

Extensions of the Cormack-Jolly-Seber (CJS) model (Cormack 1964, Jolly 1965, Seber 1965) that are time-specific and control for treatment were used to estimate apparent survival (ϕ) and detection rates (p). Estimating detection—the probability a snail was present but not detected—is an extremely important step in the process. By ignoring detection probabilities, we would be unable to produce accurate estimates for any of the other variables. Apparent survival or “local survival” differs from “true survival” in that it includes mortality as well as emigration from the population. Apparent survival is an important factor because it allows us to test for
demographic closure within the grids. A closed population is one that is free of unknown changes in abundance, particularly births, deaths, immigration, and emigration. If a population can be proven to be closed, then it is possible to account for known changes and estimate occupancy. In planning this study, a variety of options were discussed but we decided to not attempt to achieve within-grid population closure physically because it was deemed contrary to our goal of observing immigration or emigration in response to herbicide treatments. Since the results of the CJS model showed that the apparent survival was not equal to 1 (meaning that the assumption of closure had been violated) an occupancy model could not be completed.

**Covariates and Model Selection**

Variables in sampling or in the environment that might potentially influence detection probabilities, colonization, and extinction rates are called covariates. The CJS model discussed above was used to test for potential effects of covariates. Site covariates that were considered are grid number (location on the lake), trap location within the grid, and water depth at each trap. Sample covariates included water temperature and dead fish presence. Continuous covariates that can vary widely like water depth and temperature were standardized to perform more efficiently in Program MARK. The categorical covariates were coded with ones and zeros so that each had a unique sequence. Covariates were included in the models to determine if apparent survival and detection were significantly affected by these other variables.

Models were chosen based on the Akaike Information Criterion (AIC) method. This method determines the likelihood of each model and applies penalties for including too many parameters and covariates (MacKenzie et al. 2006). Simple yet parsimonious are the ultimate goals for model selection. The differences between resulting AIC values (ΔAIC) were examined. Generally, those ΔAICs that fall within 2 of the top model (that which has the lowest AIC) are
considered and the one that makes the most biological sense is chosen (Burnham and Anderson 2002). However, it is not always necessary to make this choice. Model averaging takes the top competing models and weights them according to their AIC values. This method was used to calculate estimates of abundance described in greater detail below.

**Effective Trapping Area**

The naïve density estimator, where density ($D$) is a function of abundance ($N$) divided by the area ($A$) of the trapping grid, is recognized as a biased method of calculating density because it implies that there is no “edge effect” (Dice 1938, Seber 1982, Stickel 1954). Edge effect can be caused by two potential sources: (1) animals outside of the grid being attracted to the grid and (2) by animals near the edge whose home ranges include a portion of the boundary of the grid thereby increasing the trapping area (Dice 1938, Tanaka 1972). Darby (1998) found that the idea of a well-defined home range does not apply to apple snails, but since we are unsure of what does motivate the snails to climb inside the traps, the first source could be an issue. Animal density is now estimated using the following equation (1):

$$\hat{D} = \frac{\hat{N}}{A(W)}$$

where $W$ represents the width of an additional boundary strip (Wilson and Anderson 1985).

To estimate $W$, Valentine-Darby et al. (2008) attempt to use $\frac{1}{2}$ the mean distance moved (MDM) by snails between trap occasions. This was contrary to the method developed by Wilson and Anderson (1985) in which half of the maximum mean distance moved (MMDM) was used instead. Valentine-Darby et al. (2008) were concerned that the MMDM estimate would be inflated because they had noticed a small portion of snails traveling extraordinary distances in a separate study. However, they compared the two methods and reported that the adjustment resulted in only small differences in density estimations. Since there was no way on knowing
true snail density within their grids, they recommend reporting both types of adjusted density estimates. In this study, the MMDM (± SE) was calculated based on only those snails that were captured on two or more occasions, but only the distance between the site of the initial capture and the trap located the greatest distance away were used to calculate the mean. Each measurement was divided by the total number of days from first to last encounter. The mean net distance moved (MNDM) was also included for comparison. This refers to the distance between the trap where the individual was first encountered and the trap where it was last encountered.

**Superpopulation Estimator and Density**

The superpopulation approach (Crosbie and Manly 1985, Schwartz and Arnason 1996) was used to estimate snail abundance within each of the grids, both before and after herbicide treatments. This is a robust design method which allows for movement between surveys and has been applied to snail kites in previous studies (see Dreitz et al. 2002, Martin et al. 2007). A “superpopulation” is defined as the source of individuals for the population of interest (Williams et al. 2002). Abundance is the total number of snails available for capture at any time during the study with \( B_i \), the number of newly recruited individuals in the population at period \( i + 1 \) that were not present at time \( i \), as in the following equation (2):

\[
\hat{N} = \sum_{i=0}^{K-1} \hat{B}_t
\]

Using this method, the abundance at the first sampling occasion is equal to just those “new” individuals captured, i.e. \( B_0 = N_i \). A multinomial distribution is used to model the random variables, \( B_i \), in which individuals from the superpopulation are assumed to enter the sampled population at different times according to entry parameters, \( \beta_i \). In other words, recruitment \( (B_0, \ldots, B_{K-1}) \) over the course of the season is distributed as a multinomial with parameters \( (N, \beta_0, \ldots, \beta_{K-1}) \).
The superpopulation model makes two assumptions (Williams et al. 2002). First, there must be homogeneity among probabilities of entry. In other words, all members of the superpopulation that have been unavailable for capture during one sampling occasion at time $i$ are assumed to have the same probability of capture as other snails at time $i + 1$. It is also assumed that there is an independence of fates. The term “fate” is used to describe captures and survival as well as entry of additional individuals into the sampling area population. These assumptions can be tested using a goodness-of-fit test for homogeneity of survival, detection, and lack of independence between survival and capture events (Williams et al. 2002).

Snail encounter histories were entered into Program MARK using the POPAN model which emulates the Jolly-Seber model to estimate apparent survival ($\phi$) and probability of capture ($p$), but then provides additional estimates for the probability of new individuals entering the population for each occasion ($pent$) and superpopulation size ($N$) (Schwartz and Arnason 1996). While it is capable of calculating estimates that the CJS model cannot, the POPAN model is incapable of utilizing individual covariates. Because it includes individuals that were never captured, it does not have covariate measurements for each of the animals and therefore cannot model population size as a function of those covariates.

Several different link functions were necessary to estimate the parameters using the POPAN model. Link functions are used to take the beta values provided by the model and transform them into real parameter estimates. Logit was used to estimate $\phi$ and $p$ which means that the parameter probabilities were constrained to fall between 0 and 1. Mlogit links were used for $pent$ so that the sum of the $pents$ from each group (before and after hydrilla treatment within control and treated plots) would total 1. To constrain estimates of $N$ to be positive, the log link function was used. The most parsimonious POPAN models were averaged to determine values of
N for treated and control plots which were then used to estimate snail densities with equation (1) discussed earlier. The effect size of the abundance estimates was also determined to indicate the strength of the relationship between the variables tested.

**Delineating Size Classes**

Since juvenile kites struggle to handle the larger exotic snails, size classes were considered to be a very important factor of this study. Snails were grouped into five different size classes ranging from “too small” to “too large”. The “too small” group included those snails which measured less than 30 mm and would most likely be ignored by foraging snail kites (Sykes 1987) but could potentially be even more susceptible to aquatic predators. Snails that fell between 30 and 45 mm were defined as “small natives” while snails between 46 and 60 mm were “large natives”, meaning that all kites, including juveniles, would be able to successfully handle snails in both of these groups. The term “natives” is used loosely here to describe only the size class in which both species of snail, native and exotic, overlap.

Sixty mm was used as a cutoff for juvenile kite accessibility. Since 98.5% of native apple snails selected by kites are no greater than 60 mm in height (Sykes 1987), snails measuring less than 60 mm should be easily consumed by all kites, but those snails larger than 60 mm are expected to be more difficult for juveniles to handle. Snails measuring between 61 and 75 mm were defined as “large exotics”. The largest snail ever documented to be extracted by an adult snail kite was 75 mm (Kyle Pias, pers. comm.). For this reason, those snails that measured greater than 75 mm were considered to be “too large”, inaccessible to all kites.
Figure 2-1. Wire funnel traps modified with chimneys and widened entry holes.
Figure 2-2. Diagram of shell measurements.

Figure 2-3. Tag placement on an apple snail shell.
Figure 2-4. Trapping grid array, 7 by 7 traps encompassing 441 m$^2$. 
Figure 2-5. Stage one grid locations in Lake Tohopekaliga.
Figure 2-6. Stage one grid locations in East Lake Tohopekaliga.
Figure 2-7. Stage two grid locations in Lake Jackson, including areas that were treated with endothall.
CHAPTER 3
RESULTS

Snail Movement and Effective Trapping Area

Apple snails were observed moving between 1.45 and 1.63 meters per day. Movements appeared random and varied widely (Fig. 3-1). Two individuals actually switched grids over the course of the sampling period. Both were recaptured about a month after their initial capture. One was found in Grid #6 after being caught in Grid #1 originally, a distance of 0.84 km. The other was found in Grid #5 after being caught in Grid #4, a distance of 0.61 km. Excluding those two outliers, the maximum speed observed for an individual was 7.47 m/day. This was consistent with telemetry data published by Darby et al. (2002) in which they observed that several snails travelled approximately 50 m in a week. The values for the width of the boundary strip (W) and the total area sampled (A) which resulted from the various methods of determining snail movement rates did not differ significantly (Table 3-1). This was expected based on results found in Valentine-Darby et al. (2008). Because the majority of marked snails that were recaptured were caught only one additional time, many of the movement rates that went into calculating the means were the same for each method. By excluding those snails which were only recaptured once, the MMDM would have decreased to 1.07 m/day instead.

The naïve trapping area which represents only the space covered by the grid array is 441 m$^2$. Because the calculations for MDM, MMDM, and MNMD indicated that snails could potentially travel 33 to 37 m during the sampling period, the effective trapping area was estimated to be 3091 to 3286 m$^2$ (Table 3-1).
Analysis of Response to Hydrilla Treatment

Apparent Survival and Detection Probabilities

Models that ignored treatment effects but constrained detection probabilities by season (before or after hydrilla treatment) and grid number (location on the lake) outperformed those which held detection constant or were constrained only by season and treatment (Table 3-3). Model selection based on AIC value comparisons suggested that grid-specific characteristics (such as vegetation density or water depth) may explain more variation in detection probabilities than hydrilla presence or absence. Detection probabilities were relatively low in general, ranging from 3 to 14% (Figs. 3-2 and 3-3). Detection in two of the three grids in which the hydrilla was not treated appears to have decreased over the course of the sampling period (Fig. 3-2), whereas detection in all of the treated grids showed a slight increase over time (Fig. 3-3).

When modeling to best estimate apparent survival, model selection suggested similar preferences as for detection probabilities. Analyzing each grid separately always resulted in more parsimonious models than grouping according to treatment (see models #8 and #12). Apparent survival rates were estimated to range between 83 and 98% (Figs. 3-4 and 3-5). Since these estimates fell short of 100%, indicating that the assumption of population closure had been violated, snail occupancy could not be modeled. The results of these analyses indicated that apparent snail survival decreased to a greater extent in treatment plots after herbicide treatments had been completed (Fig. 3-6). However, the confidence intervals of these estimates overlapped to some degree and the results cannot be considered significant.

The most parsimonious model that had the lowest AIC value included snail shell height as an additive individual covariate affecting apparent survival rates (Table 3-3). This model received 41% of the AICc weight versus 16% model weight which was given to the interactive
snail size model (model #3). Models which incorporated shell size represented 93% of the total model weight. The top model was 8.50 ΔAIC points lower than the model which ignored grid and time factors (model #8). A difference of 4 points or more is considered significant (Burnham and Anderson 2002). Analyzing the beta parameters revealed a significantly negative additive relationship between apparent survival and snail size (β\text{SEASON}×\text{GRID}+\text{SIZE} = -0.0070, 95% CI = -0.0127 to -0.0012). This indicates that apparent survival decreased as size increased (Fig. 3-7), contrary to what might be expected. The smallest snails (14 mm) had a 5.79% greater chance of “surviving” or remaining within the grids than the largest snails (89 mm). Snail location within the grid (models #2, 5, 10) and average grid water depth (models #4, 7) had no significant effect on detection probability or survival. Models which tested for the influence of temperature and the presence of dead fish consistently resulted in much higher AIC values and were therefore excluded from the table of resulting models.

**Snail Abundance**

Snail abundance during the second “season” (after hydrilla treatment) of sampling was roughly three times what it was estimated to be during the first “season”. Model averaging of the most parsimonious POPAN models revealed that abundance was higher in the grids which were not treated both before and after treatment \(N_{\text{CONTROL}×\text{BEFORE}} = 6,359; \quad N_{\text{CONTROL}×\text{AFTER}} = 18,291\). However, these results are again insignificant due to overlapping confidence intervals (Fig. 3-8) and an insignificant effect size \(0.00006 ± 0.02782\). Snail abundance estimates for treated plots were only slightly lower \(N_{\text{TREATED}×\text{BEFORE}} = 5,752; \quad N_{\text{TREATED}×\text{AFTER}} = 15,514\).

**Snail Density**

Similar to the changes noticed in abundance, snail density sharply increased between April and June sampling (Fig. 3-9). Using the MMDM method for calculating snail movement,
density appears to have increased to a greater degree in the control plots, from 2.04 to 5.86 snails/m$^2$ (see Table 3-2 for a complete list). Initial estimates were slightly lower in treated plots but increased from 1.84 to 4.97 snails/m$^2$.

**Size Classes**

Researchers have suggested that the presence of hydrilla may protect the smaller snails from predation, but the results gathered from trapping in Lake Jackson did not support that hypothesis. The proportion of snails that were smaller than 60 mm in height –the cutoff between the size classes that were defined as “large natives” and “large exotics”– did not differ significantly between the treated and control plots. If anything, grids in which the hydrilla was removed actually supported a greater percentage of smaller size classes in the later sampling occasions (Fig. 3-10). Mean snail shell heights and wet weights increased over time but did not differ significantly between treated and control plots either (Figs. 3-11 and 3-12). Excluding snails that were “too small”, the proportion of snails that would be small enough for juvenile kites to handle decreased from 42.4 to 13.6% between the end of April and the end of June (Fig. 3-13).

Although the proportion of small snails dropped, in general the number of snails captured greatly increased over the course of the sampling period. The number of snails that were captured that would be suitable for juvenile kites increased from 50 individuals in the initial trapping occasion to 124 individuals in the final occasion (Fig. 3-14). The category of “large exotics” captured, which included snails that would be unsuitable for juvenile kites, grew by nearly 1000% while the category of snails that were presumably “too large” for any kites to extract increased by even more. The quantity of snails captured was higher in the treated plots
(Fig. 3-16) than in the control plots (Fig. 3-15), but relative proportions among size classes did not differ significantly.

8,261 unique individuals were captured in all. Exotic snails represent 99.75% of that number as only 22 native snails were found. Exactly half of all native snails were captured in Grid #5. The rest were caught randomly in each of the five other grids.

**Non-Target Species**

A number of fish species were regularly found in the funnel traps on Lake Jackson, especially blue spotted sunfish (*Enneacanthus gloriosus*), warmouths (*Lepomis gulosus*), and bluegills (*Lepomis macrochirus*) (Table 3-4). Fish represented 96.1% of the non-target species captured. The list of other notable non-fish species trapped includes sirens, frogs, snakes, and crayfish. The number of non-target species captured greatly decreased over the course of the sampling period by 88.6%. Differences between the numbers of individuals caught in the treated and control plots were insignificant. Of the 75 individual gar that were captured, 84% suffered mortalities, by far the highest mortality rate seen among any of the non-target species. Snails were frequently found in traps alongside the decomposing fish, but results from the CJS model showed that the presence of dead fish did not correlate with detection and unintentional baiting was not a significant issue.
Table 3-1. Estimates of A (± SE) and W (± SE) based on different methods of calculating snail movement.

<table>
<thead>
<tr>
<th>Method</th>
<th>Mean Movement (m/day)</th>
<th>Boundary Width (W)</th>
<th>Total Area Sampled (m²) (A)</th>
</tr>
</thead>
<tbody>
<tr>
<td>MDM</td>
<td>1.58 ± 0.049</td>
<td>36.33 ± 1.13</td>
<td>3286.95 ± 133.58</td>
</tr>
<tr>
<td>MMDM</td>
<td>1.52 ± 0.051</td>
<td>34.86 ± 1.17</td>
<td>3120.79 ± 134.93</td>
</tr>
<tr>
<td>MNDM</td>
<td>1.50 ± 0.051</td>
<td>34.60 ± 1.17</td>
<td>3091.41 ± 134.51</td>
</tr>
</tbody>
</table>

Figure 3-1. Diagram of snail movements. Each color represents the path of an individual snail through time. Looped arrows mean that the individual was caught in the same trap on two consecutive occasions. Snails that were captured on more than three trapping occasions were relatively infrequent. The snails in this depiction were not necessarily found in the same grid or even in the same season.
Table 3-2. Snail density \(D\) (snails/m\(^2\)) calculated using several different methods for estimating snail movement rates and effective sampling area.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Sampling Period</th>
<th>MDM</th>
<th>MMDM</th>
<th>MNDM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control Grids</td>
<td>Before Treatment</td>
<td>1.9347</td>
<td>2.0377</td>
<td>2.0571</td>
</tr>
<tr>
<td></td>
<td>After Treatment</td>
<td>5.5648</td>
<td>5.8610</td>
<td>5.9167</td>
</tr>
<tr>
<td>Treated Grids</td>
<td>Before Treatment</td>
<td>1.7501</td>
<td>1.8433</td>
<td>1.8608</td>
</tr>
<tr>
<td></td>
<td>After Treatment</td>
<td>4.7200</td>
<td>4.9713</td>
<td>5.0185</td>
</tr>
</tbody>
</table>

Table 3-3. Models representing hypotheses of effects of hydrilla treatment on apple snail distribution in Lake Jackson. Models also test for potential effects of individual and state covariates.

<table>
<thead>
<tr>
<th>#</th>
<th>Model</th>
<th># Parm</th>
<th>Δ AICc</th>
<th>Weight</th>
<th>Biological Hypothesis</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1)</td>
<td>(\text{Phi}(t(b, d, a)^*g + Size)) (p(t(b, a)^*g))</td>
<td>31</td>
<td>0</td>
<td>0.41</td>
<td>Apparent survival varies by sampling period (before, immediately following, and after hydrilla treatment) and location on the lake (grid #) with an additive effect for snail shell size; detection probabilities vary by sampling period (before and after hydrilla treatment) and location on the lake.</td>
</tr>
<tr>
<td>(2)</td>
<td>(\text{Phi}(t(b, d, a)^*g + Size)) (p(t(b, a)^*g + Loc))</td>
<td>32</td>
<td>1.66</td>
<td>0.18</td>
<td>Apparent survival varies by sampling period (before, immediately following, and after hydrilla treatment) and location on the lake with an additive effect for snail shell size; detection probabilities vary by sampling period (before and after hydrilla treatment) and location on the lake with an additive effect for trap location within each grid.</td>
</tr>
<tr>
<td>(3)</td>
<td>(\text{Phi}(t(b, d, a)^<em>g</em>Size)) (p(t(b, a)^*g))</td>
<td>45</td>
<td>1.85</td>
<td>0.16</td>
<td>Apparent survival varies by sampling period (before, immediately following, and after hydrilla treatment) and location on the lake with an interactive effect for snail shell size; detection probabilities vary by sampling period (before and after hydrilla treatment) and location on the lake.</td>
</tr>
<tr>
<td>(4)</td>
<td>(\text{Phi}(t(b, d, a)^*g + Size)) (p(t(b, a)^*g + Depth))</td>
<td>32</td>
<td>2.02</td>
<td>0.15</td>
<td>Apparent survival varies by sampling period (before, immediately following, and after hydrilla treatment) and location on the lake with an additive effect for snail shell size; detection probabilities vary by sampling period (before and after hydrilla treatment) and location on the lake with an additive effect for the mean water depth of each grid.</td>
</tr>
<tr>
<td>(5)</td>
<td>(\text{Phi}(t(b, d, a)^*g)) (p(t(b, a)^*g + Loc))</td>
<td>31</td>
<td>5.23</td>
<td>0.03</td>
<td>Apparent survival varies by sampling period (before, immediately following, and after hydrilla treatment) and location on the lake; detection probabilities vary by sampling period (before and after hydrilla treatment) and location on the lake with an additive effect for trap location within each grid.</td>
</tr>
<tr>
<td>#</td>
<td>Model</td>
<td># Parm</td>
<td>Δ AICc</td>
<td>Akaike Weight</td>
<td>Biological Hypothesis</td>
</tr>
<tr>
<td>----</td>
<td>------------------------------------------------------------------------</td>
<td>--------</td>
<td>--------</td>
<td>---------------</td>
<td>-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>6</td>
<td>( \Phi(t(b, d, a)*g) p(t(b, a)*g + Size) )</td>
<td>31</td>
<td>5.48</td>
<td>0.03</td>
<td>Apparent survival varies by sampling period (before, immediately following, and after hydrilla treatment) and location on the lake; detection probabilities vary by sampling period (before and after hydrilla treatment) and location on the lake with an additive effect for snail shell size.</td>
</tr>
<tr>
<td>7</td>
<td>( \Phi(t(b, d, a)*g) p(t(b, a)*g + Depth) )</td>
<td>31</td>
<td>5.58</td>
<td>0.03</td>
<td>Apparent survival varies by sampling period (before, immediately following, and after hydrilla treatment) and location on the lake; detection probabilities vary by sampling period (before and after hydrilla treatment) and location on the lake with an additive effect for the mean water depth of each grid.</td>
</tr>
<tr>
<td>8</td>
<td>( \Phi(t(b, d, a)*g) p(t(b, a)*g) )</td>
<td>29</td>
<td>8.50</td>
<td>0.01</td>
<td>Apparent survival varies by sampling period (before, immediately following, and after hydrilla treatment) and location on the lake; detection probabilities vary by sampling period (before and after hydrilla treatment) and location on the lake. (This is the top model excluding covariates.)</td>
</tr>
<tr>
<td>9</td>
<td>( \Phi(t(b, d, a)*g) p(t(b, d, a)*g) )</td>
<td>36</td>
<td>8.85</td>
<td>0.01</td>
<td>Apparent survival varies by sampling period (before, immediately following, and after hydrilla treatment) and location on the lake; detection probabilities vary by sampling period (before, immediately following, and after hydrilla treatment) and location on the lake.</td>
</tr>
<tr>
<td>10</td>
<td>( \Phi(t(b, d, a)*g) p(t(b, a)<em>g</em>Loc) )</td>
<td>42</td>
<td>14.69</td>
<td>0.00</td>
<td>Apparent survival varies by sampling period (before, immediately following, and after hydrilla treatment) and location on the lake; detection probabilities vary by sampling period (before and after hydrilla treatment) and location on the lake with an interactive effect for trap location within each grid.</td>
</tr>
<tr>
<td>11</td>
<td>( \Phi(g) p(t(b, a)*g) )</td>
<td>18</td>
<td>17.78</td>
<td>0.00</td>
<td>Apparent survival varies by location on the lake (grid); detection probabilities vary by sampling period (before and after hydrilla treatment) and location on the lake.</td>
</tr>
<tr>
<td>12</td>
<td>( \Phi((t(b); t(d, a)*Trt) + Size) p(t(b, a)*g) )</td>
<td>18</td>
<td>32.35</td>
<td>0</td>
<td>Apparent survival varies by sampling period (immediately following hydrilla treatment or surveys after that, before-treatment surveys are held constant among all sites) and treatment (either treated or control plots) with an additive effect for snail shell size; detection probabilities vary by sampling period (before and after hydrilla treatment) and location on the lake.</td>
</tr>
</tbody>
</table>
Table 3-3. Continued

<table>
<thead>
<tr>
<th>#</th>
<th>Model</th>
<th># Parm</th>
<th>Δ AICc</th>
<th>Akaike Weight</th>
<th>Biological Hypothesis</th>
</tr>
</thead>
<tbody>
<tr>
<td>(13)</td>
<td>Phi(t(b, d, a)*Trt) p(t(b, a)*g)</td>
<td>18</td>
<td>41.92</td>
<td>0</td>
<td>Apparent survival varies by sampling period (before, immediately following, and after hydrilla treatment) and treatment (either treated or control plots); detection probabilities vary by sampling period (before and after hydrilla treatment) and location on the lake.</td>
</tr>
<tr>
<td>(14)</td>
<td>Phi(Size) p(t(b, a)*g)</td>
<td>14</td>
<td>43.50</td>
<td>0</td>
<td>Apparent survival varies by snail shell size; detection probabilities vary by sampling period (before and after hydrilla treatment) and location on the lake.</td>
</tr>
</tbody>
</table>

Table 3-4. List of all non-target species trapped in funnel traps between April and June, 2010 in Lake Jackson, Florida.

<table>
<thead>
<tr>
<th>Scientific Name</th>
<th>Common Name</th>
<th>Total Number Trapped</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Enneacanthus gloriosus</em></td>
<td>Blue Spotted Sunfish</td>
<td>2475</td>
</tr>
<tr>
<td><em>Lepomis gulosus</em></td>
<td>Warmouth</td>
<td>786</td>
</tr>
<tr>
<td><em>Lepomis macrochirus</em></td>
<td>Bluegill</td>
<td>251</td>
</tr>
<tr>
<td><em>Astacoidea spp.</em></td>
<td>Crayfish</td>
<td>91</td>
</tr>
<tr>
<td><em>Lepisosteus spp.</em></td>
<td>Gar (Florida &amp; Alligator)</td>
<td>75</td>
</tr>
<tr>
<td><em>Lepomis microlophus</em></td>
<td>Redear Sunfish</td>
<td>73</td>
</tr>
<tr>
<td><em>Lepomis punctatus</em></td>
<td>Spotted Sunfish</td>
<td>70</td>
</tr>
<tr>
<td><em>Ameiurus nebulosus</em></td>
<td>Brown Bullhead Catfish</td>
<td>58</td>
</tr>
<tr>
<td><em>Lepomis marginatus</em></td>
<td>Dollar Sunfish</td>
<td>41</td>
</tr>
<tr>
<td><em>Erimyzon succetta</em></td>
<td>Chubsucker</td>
<td>37</td>
</tr>
<tr>
<td><em>Vivaparous georganus</em></td>
<td>Banded Mysterysnail</td>
<td>25</td>
</tr>
<tr>
<td><em>Dytiscidae spp.</em></td>
<td>Predaceous Diving Beetle</td>
<td>23</td>
</tr>
<tr>
<td><em>Notemigonus crysoleucas</em></td>
<td>Golden Shiner</td>
<td>22</td>
</tr>
<tr>
<td><em>Esox niger</em></td>
<td>Chain Pickerel</td>
<td>20</td>
</tr>
<tr>
<td><em>Hoplosternum littorale</em></td>
<td>Armored Catfish</td>
<td>12</td>
</tr>
<tr>
<td><em>Siren lacertina</em></td>
<td>Greater Siren</td>
<td>10</td>
</tr>
<tr>
<td><em>Micropterus salmoides</em></td>
<td>Largemouth Bass</td>
<td>9</td>
</tr>
<tr>
<td><em>Nerodia floridana</em></td>
<td>Florida Green Watersnake</td>
<td>9</td>
</tr>
<tr>
<td><em>Amia calva</em></td>
<td>Bowfin</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Unknown Tadpole</td>
<td>4</td>
</tr>
<tr>
<td><em>Rana grylio</em></td>
<td>Pig Frog</td>
<td>3</td>
</tr>
<tr>
<td><em>Poecilia latipinna</em></td>
<td>Sailfin Molly</td>
<td>3</td>
</tr>
<tr>
<td><em>Fundulus chrysotus</em></td>
<td>Golden Topminnow</td>
<td>2</td>
</tr>
<tr>
<td><em>Nerodia fasciata</em></td>
<td>Banded Water Snake</td>
<td>2</td>
</tr>
<tr>
<td><em>Hyla cineria</em></td>
<td>Green Tree Frog</td>
<td>1</td>
</tr>
</tbody>
</table>
Figure 3-2. Probability for detection ($p$) ($\pm SE$) within control plots in Lake Jackson grids. These values were estimated by averaging most parsimonious CJS models.

Figure 3-3. Probability for detection ($p$) ($\pm SE$) within treatment plots in Lake Jackson grids. These values were estimated by averaging most parsimonious CJS models.
Figure 3-4. Snail apparent survival ($\phi$) ($\pm SE$) of control plots in Lake Jackson grids. These values were estimated by averaging most parsimonious CJS models.

Figure 3-5. Snail apparent survival ($\phi$) ($\pm SE$) of treated plots in Lake Jackson grids. These values were estimated by averaging most parsimonious CJS models.
Figure 3-6. Snail apparent survival ($\phi$) ($\pm$SE) response to hydrilla treatment in Lake Jackson. Values based on results from model $\Phi i(t_{before}, (immediate\ effect, delayed\ effect) \times treatment) \ p((before, after\ treatment) \times grid)$. 
Figure 3-7. Apparent survival ($\phi$) as a function of shell size.
Figure 3-8. Snail abundance (N) (±SE) in response to hydrilla treatment in Lake Jackson grids. These values were estimated by averaging most parsimonious POPAN models. Each estimate applies to three grids, areas totalling approximately 9000 m².
Figure 3-9. Snail density ($D$) ($\pm SE$) in response to hydrilla treatment in Lake Jackson grids. These values were calculated using the effective sampling areas based on $\frac{1}{2}$ MMDM (see Table 3-1) and abundance estimates from model averaging top POPAN models.
Figure 3-10. Proportion of snails smaller than 60 mm captured in treated versus control plots.
Figure 3-11. The mean snail weight increased over time but was similar in treatment and control plots.

Figure 3-12. The mean snail height also increased over time but was similar in treatment and control plots.
Figure 3-13. Percentage of snails captured within each size class on Lake Jackson in the 2010 trapping season. Since 98.5% of native apple snails are no greater than 60 mm in height, snails measuring less than 60 mm should be easily consumed by all kites, but those snails larger than 60 mm are expected to be more difficult for juveniles to handle.
Figure 3-14. Number of snails captured within each size class on Lake Jackson in the 2010 trapping season. Herbicide treatments took place between surveys 7 and 8 and the time period separating those two trapping occasions was roughly three weeks as opposed to three to four days as between each of the other surveys.
Figure 3-15. Summary of snail sizes captured in control plots throughout the sampling seasons.

Figure 3-16. Summary of snail sizes captured in treated plots throughout the sampling seasons.
CHAPTER 4
DISCUSSION

Sampling Grid Efficacy

Logistically, the use of grid arrays to conduct a mark-recapture study of apple snails in central Florida lakes infested with hydrilla was very effective. The modifications made to each trap to sample the larger exotic species did appear to successfully trap smaller snails. The chimney extensions proved to be extremely necessary. The only fatalities seen among amphibians and reptiles occurred when water levels on Lake Toho rose very suddenly covering several traps located in an especially deep area of the lake and one stinkpot turtle (*Sternotherus odoratus*) and a greater siren (*Siren lacertina*) drowned as a result. Snails captured during the same time period were found plastered to the mesh lids, attempting to escape through the exit in the top, but were not harmed.

Physically, the amount of time required to collect, measure, and mark trapped snails greatly exceeded what was expected. Sampling similar grid arrays in shallow wetland habitats, Valentine-Darby et al. (2008) estimated that a team of two was able to set up and process a 100-trap grid array in approximately 15 to 40 hours over the course of 21 to 28 days. Preliminary sampling in Lake Toho and East Lake Toho verified this estimate. During the second half of the sampling season in Lake Jackson when catching upwards of 300 snails each day, a single grid consisting of 49 traps took between 40 and 60 hours over a 23 day period. The drastic difference in snail abundance between the various sites sampled was the primary factor causing this disparity. The only problem with the number of hours required is that trapping is difficult to stop once it has begun. Problems such as inclement weather or mechanical failures can result in loss of data and greater mortality among non-target species (see Desa 2008). Care should be taken to
avoid deploying so many traps that they become unmanageable when snail abundance increases as the season progresses.

Despite potential issues, the trapping grid array should be considered the best viable option for determining snail abundance and density in lacustrine habitats. Deploying a full grid array to determine only snail presence would be unnecessary. Trapping transects, like those used in Muench (2004) and DeSa (2008), would provide equally valuable data but would be much less time consuming. Unless a physical barrier is constructed to maintain the assumption of geographic closure, the grid array design would not be recommended for estimating occupancy either.

The results of this study were unable to support Hypothesis 1 which predicted that snail densities would be lower in the deeper lacustrine habitats than in shallow wetlands sampled by Valentine-Darby et al. (2008). Using the MMDM method for determining the effective sampling area, they calculated densities of native snails in southern Florida wetlands to be no greater than 0.32 snails/m². The lowest density of exotics observed in this study was 1.84 snails/m². Considering that the difference in water depth which suggests that a density that takes the cubic nature of the environment into consideration may be more appropriate, these estimates may not actually be that different. The depth of their traps was unknown but they state that the funnel traps may be used in water that is at least 15 cm. Assuming that their traps were located in 16 cm of water and adjusting the vertical depth to equal the mean of Lake Jackson grids would increase the density of snails per m³ to approximately 1.8.

Of course, this adjustment ignores obvious biological differences between the two species. As mentioned previously, telemetry research suggests that native snails tend to move toward shallower areas when they reach depths greater than 50 cm (Darby et al. 2002). Trapping
in Lake Jackson has suggested that this is not true for exotic snails. Densities of natives in shallower littoral regions of Lake Jackson may be similar to those in shallow wetlands, but further trapping would be required to determine that.

**Extreme Movements Observed**

The two snails that were observed in different grids are thought to be anomalies. For a snail to simply use pedal wave locomotion, the stand method of movement, to travel from one grid to another is considered impossible. Judging by the large size of the snails’ shells, it would be conceivable for an avian predator to carry them from one grid to another and then discard them after failing to remove the operculum. Adult snail kites frequently perched on poles in the grids, favoring the larger diameter poles that were often used for the corners. It would not be unreasonable for a kite to catch a snail in or near one grid and then fly to another to extract and consume it.

Human error is another option for the snail that moved from Grid #4 to #5. It is possible, although unlikely, that a switch was made during sampling. The snails were held in water in lidded plastic containers while waiting to be processed, and containers from each grid were kept in different areas on the boat to avoid confusion. When outdoor temperatures got very warm, we kept the containers open slightly to prevent the snails from overheating in the sun. Snails often tried to escape the containers and had to be watched at all times. The “click” of a snail shell hitting the bottom of the boat worked like an alarm to summon immediate attention, but a mix up would not have been impossible. However, this explanation is not an option for the snail that moved from Grid #1 to #6 because those grids were always sampled on different days.

Snails have also been observed in aquariums travelling by suctioning to the surface tension of the water and floating upside-down from one side of the tank to the other, allowing
their body to be pushed by the current and sometimes undulating to propel their bodies further. This method has been observed in other aquatic snails (see Lee et al. 2008), but has never before been reported in reference to apple snails. This could have been another way for a snail to travel from Grid #1 to #6, but it would be extremely unlikely for a snail to use this method to cross the center of a lake. Maintaining suction through even slight wave action would be nearly impossible over such a great distance. It would be even less likely for a snail to travel using this method between Grids #4 and #5 because there was fairly dense vegetation between the two grids and a spoil island.

**The Effects of Herbicide Treatment**

**Apparent Survival and Abundance**

Apparent survival did seem to decrease to a greater extent in treated plots than control plots, but according to model variances, the differences were insignificant. *Hypothesis 2* which stated that apparent snail survival would decrease in treatment plots after herbicide treatments had been completed could be neither confirmed nor denied. Grids #1 and #2, both control plots on the eastern side of the lake, showed no obvious differences throughout the season. Temperature readings, water depths, and vegetation samples all appeared to be similar, yet $\phi$ increased in Grid #1 and decreased in Grid #2 while the opposite was observed for $p$ in both grids (Figs. 3-2 and 3-4). All of the treated grids showed a slight decrease in $\phi$ but the confidence intervals indicate that there is little reason to believe that those values are exact. There may or may not be an explanation for the changes in apparent survival but they cannot be attributed to treatment effects in this study.

The rationale for believing that snails would leave the treated grids post-treatment was based on the assumption that hydrilla is a major factor attracting snails to a particular area and
removing it should cause snail dispersion. However, the exotic snails are generalists known for their voracious appetites. The limited number of vegetation samples indicated an increase in biomass (both hydrilla and non-hydrilla species) over time. Removing the hydrilla would not necessarily have caused the snails to starve or seek nourishment elsewhere. However, without the structural lofting quality provided by the hydrilla which would allow the snails to spend more time near the water surface, it may be true that they were less available to snail kites. Bennetts et al. (2005) observed kites catching snails more frequently in areas of South Florida with more abundant submersed macrophytes and sparse emergent vegetation. Future studies may want to include an aspect of kite foraging observations within each grid to confirm the lofting hypothesis.

The relationship between apparent survival and snail shell size was unexpected but not unreasonable. Apparent survival includes all changes in the observed population, incorporating births, deaths, immigrants and emigrants. Although true survival was probably very low for small snails, apparent survival was estimated to be lowest among the largest snails. This observation was most likely a response to the ability of the large snails to move at a faster pace. Simply put, they more frequently emigrated from the sampling grids. Further analyses to verify and support this hypothesis are being conducted.

Speculations about snail abundance or density throughout the entire lake should be avoided. Snail distribution is known to be patchy in general (Darby et al. 2001). Very early preliminary sampling in Lake Jackson yielded zero captures in other areas. Kite behavior also supports this concept. If they locate an extremely good foraging patch, snail kites will focus their efforts on that one area continuously and may even exhibit territorial behavior to defend it (Snyder and Snyder 1970, Bennetts and Kitchens 2000). Apple snails are not known to be
extremely mobile but they have shown a propensity to move in search of more favorable habitat (Darby et al. 2002). A study which spans several years and includes larger treatment areas may produce more definitive results as the long-term presence or absence of hydrilla could have a greater effect on snail abundance.

Small Size Classes

There was no evidence to support Hypothesis 3 which predicted that the proportion of smaller snails would be lower in the treated grids post-treatment. The smallest snails became almost non-existent in all of the grids in the last sampling occasions. Adult snails continued to lay egg clusters throughout the entire season and although most of the observed difference was due to the fact that the snails were continuing to grow, individuals in the smaller size classes were not being replaced. Hydrilla may not provide protection from predators as expected. When comparing the difference in the number of non-target individuals trapped among treated and non-treated plots, there was no indication that vegetative density prevented predatory fish from entering. Thick mats of hydrilla may actually provide support structure upon which other avian predators (e.g. boat-tailed grackles (Quiscalus major) and limpkins (Aramus guarauna)) might perch and utilize to forage. Since snail activity and rates of surface inspiration increase as temperatures increase (McClary 1964), foraging would not be difficult for these species even with limited water depth capabilities.

Additionally, it is suspected that the design of this study may have created a bias against the smaller size classes that cannot be ignored. As mentioned earlier, apple snails deposit their egg masses on emergent vegetation (Winner 1989) and other non-living strata (Wallace et al. 1956). Throughout the entire season, the snails displayed an obvious preference for the PVC poles which were used to hold the traps in place. Farmers in the Philippines place stakes near
drainage canals which invasive *P. canaliculata* snails use for egg deposition and the farmers can then collect large batches of egg clusters with little physical exertion (Halwart 1994). It does not eliminate the snails, but it is one of many control methods employed. While we were not intentionally trying to influence snail demographics, scraping fresh egg clusters from the sides of the poles as we pulled each trap out of the water was unavoidable. However, clusters were also attached to nearby emergent vegetation and care was taken to avoid disturbing them when maneuvering the airboat, so a proportion of young snails still should have still been entering the population. It is recommended that future studies take this speculation into consideration, especially if sampling is planned to continue for more than a few weeks.

**Proportion of Native Snails to Exotics**

As expected, the *P. insularum* individuals greatly outnumbered *P. paludosa*. The actual difference was 375 to 1. This supported *Hypothesis 4* which stated that the number of the exotics would exceed that of the native snails. Researchers have been observing the expansion of the exotic snails in the KCOL for at least ten years (Rawlings et al. 2007, DeSa 2008, Cattau et al. 2010). It has been suggested that kites are attracted to Lake Toho specifically because of the presence of exotics (Cattau 2008). Considering the increase of kites nesting on Lake Jackson in recent years, the same is likely to be true there.

**Non-Target Fauna and Unintentional Baiting**

Model results showed that there was no strong correlation between non-target species captures and apple snails. This supported *Hypothesis 5* which stated that snails would not be attracted to the traps due to the presence of non-target species and detection rates would not be influenced as a result. Of the three most common by-catch species, only bluegills (*Lepomis macrochirus*) have been known to consume juvenile snails (less than 10 mm) (Darby et al.
It is assumed that adult bluegills were predating small snails within the grids, but most of the bluegills captured were small juveniles themselves and would not have capable of consuming such large prey within the traps, thereby affecting detection.

Trapped apple snails, the obvious target species, greatly outnumbered the non-target species. Darby et al. (2001) suggested that funnel traps may be effective in capturing other species commonly found in Florida wetlands, but such a projection would not apply to the lacustrine habitats sampled in Lake Jackson. Preliminary sampling on Lake Toho and East Lake Toho did yield a more diverse list of by-catch that included striped mud turtles (Kinosternon bauri), stinkpots (Sternotherus odoratus), and much more numerous greater sirens (Siren lacertina) and banded mystery snails (Vivaparous georgianus) suggesting that those species were just not abundant on Lake Jackson or perhaps they prefer different habitat qualities such as shallower areas or different vegetative structure. However, even in the preliminary plots, apple snails were still the most frequent species encountered. Using modified funnel traps could be a useful tool for determining the presence of other species, but unless the species is known to be have a high abundance or limited home range, the funnel traps may not be recommended for a mark-recapture study as small sample size could prove to be a serious issue.

**Conclusion**

Given then obvious trends in abundance estimated in this study, attention to timing of sampling events used for estimating lake-wide or even site abundance could be very critical to the overall reliability of the estimates. The accuracy of abundance estimates depends entirely on trapping success which is a result of snail movements. Snail activity has been shown to be random (also see Darby 1998) and changes in habitat such as the vegetation structure, water depth, and food availability are only part of the equation. Stevens et al. (2003) argue that
attempts to compare relative snail abundance will be confounded if temperatures vary between sampling sites. Temperature is known to play a major role in snail activity, but it can differ according to habitat type. Shallow wetlands in which thick vegetation restricts water current will generally be warmer than the littoral zone of an open lake. Temporal scale should be greatly considered when conducting range-wide surveys for apple snails in central and southern Florida. Any comparisons of snail abundance or density are meaningless if care is not taken to adjust sampling in accordance with these other factors.

We have developed a process for determining more accurate estimates of snail abundance. Previous grid-based studies have estimated $N$ by obtaining the mean number of captured individuals per trapping occasion and dividing by the detection probability (Valentine-Darby 2008). This method is oversimplified and ignores the recruitment variable $B_i$ and instead conditions on just the number of unmarked individuals trapped at each sampling occasion. The superpopulation approach provides an explicit link between the observable data and unknown parameters thought to be important. It was designed to be a generalization and reparameterization of the Jolly-Seber model that takes the complex structure of open populations into account, incorporating births, deaths, emigration, and immigration (Crosbie and Manly 1985). Using Program MARK, the POPAN model quickly transformed this issue of complexity into simple and straightforward results. The superpopulation approach proved to be very useful and appropriate for this kind of sampling in which timing was an important element. It is highly recommended for future grid-based studies.

Unfortunately, the effects of hydrilla treatment on apple snail abundance yielded inconclusive results. As discussed earlier, more significant evidence may be produced from a study which spans several years and includes larger treatment areas. It is still unclear whether
apple snails show a preference for areas dominated by the invasive submerged aquatic plant species. We know only that the snail kites have been observed foraging successfully in hydrilla-dominated habitats and that this behavior could have negative consequences for the future health of the snail kite population in Florida.
LIST OF REFERENCES


BIOGRAPHICAL SKETCH

Lara Kristen Drizd was born in St. Petersburg, Florida in 1982. The younger of two children, she grew up in the Tampa Bay area, graduating from Countryside High School in 2001. She obtained a Bachelor of Arts in environmental studies at New College of Florida in 2005 after completing a thesis entitled “The Natural History of Florida Tree Snails (Liguus fasciatus) in the Everglades.” In 2006, Lara began working in the Everglades as a field technician for Florida Atlantic University, Davie on several projects including the investigations into: the growth and expansion of *Lygodium microphyllum* into the Everglades, determining the hydrology of tree islands in South Florida, and crayfish population dynamics in response to hydrological influences. A year later, she moved to Gainesville to work for the Florida Fish and Wildlife Cooperative Research Unit and continued collecting data important to wildlife species endemic to the state by helping to launch a pilot study which established a series of sites to be used to monitor the health of nesting habitat of the Everglade Snail Kite. She was then accepted to the Wildlife Ecology and Conservation Program as a graduate assistant at the University of Florida to pursue research into the species of apple snails which inhabit the Kissimmee Chain of Lakes.