

BULLETIN

of the
FLORIDA STATE MUSEUM
Biological Sciences

Volume 31

1987

Number 3

THE ECOLOGY OF THE STOCK ISLAND TREE SNAIL
ORTHALICUS RESES RESES (SAY)

JANE DEISLER



UNIVERSITY OF FLORIDA

GAINESVILLE

Numbers of the BULLETIN OF THE FLORIDA STATE MUSEUM, BIOLOGICAL SCIENCES, are published at irregular intervals. Volumes contain about 300 pages and are not necessarily completed in any one calendar year.

OLIVER L. AUSTIN, JR., *Editor*
S. DAVID WEBB, *Associate Editor*
RHODA J. BRYANT, *Managing Editor*

Consultants for this issue:

WALTER B. MILLER
FRED G. THOMPSON

Communications concerning purchase or exchange of the publications and all manuscripts should be addressed to: Managing Editor, Bulletin; Florida State Museum; University of Florida; Gainesville FL 32611; U.S.A.

This public document was promulgated at an annual cost of \$2280.00 or \$2.28 per copy. It makes available to libraries, scholars, and all interested persons the results of researches in the natural sciences, emphasizing the circum-Caribbean region.

THE ECOLOGY OF THE STOCK ISLAND TREE SNAIL, *ORTHALICUS RESES RESES* (SAY)

JANE DEISLER*

ABSTRACT

A study to determine the life history and behavior of the Stock Island Tree Snail, *Orthalicus reses reses* (Say) (Pulmonata: Bulimulidae), was conducted during May-August 1981 and August-October 1982 in the southern Florida Keys. A follow-up assessment of these populations was conducted in July 1986. The activity of the snail was found to be linked to rainfall patterns. Statistical analysis indicated that population size was not limited by species of tree available for colonization. The diet of the snail was determined by stomach content analysis and substrate examination and was found to consist of epiphytic growths on tree surfaces. Reproductive events were observed and growth rate and sources of mortality were examined. The density and composition of a population on Stock Island were determined. Human activity was determined to have a negative impact on the Stock Island populations. Comparative data for *O. floridensis* and *O. reses nesodryas* were included where they were available.

RESUMEN

Se efectuó un estudio de la historia natural y comportamiento del caracol arborícola de la Isla Stock, *Orthalicus reses reses* (Say) (Pulmonata: Bulimulidae) en los cayos del sur de Florida, entre mayo-agosto de 1981 y entre agosto octubre de 1982. Una evaluación, a continuación, de estas poblaciones fue conducida en Julio 1986. Se determinó que la actividad del caracol está en relación con los patrones de precipitación.

*The author is Curator of Natural History at the Corpus Christi Museum, 1900 N. Chaparral, Corpus Christi, Texas 78401.

El análisis estadístico indicó que el tamaño de la población no está limitada por el número de especies de árboles disponibles para la colonización. La dieta del caracol se determinó mediante el análisis del contenido estomacal y examen del sustrato. La dieta consiste de crecimientos epifíticos sobre los árboles. También se hicieron observaciones reproductivas y se estudiaron las tasas de crecimiento y las principales fuentes de mortalidad. Asimismo, se determinó la densidad y composición de una población en la Isla Stock. Finalmente, se incluye datos comparativos acerca de *O. floridensis* and *O. reses nesodryas*, en la medida de su disponibilidad.

TABLE OF CONTENTS

INTRODUCTION	108
ACKNOWLEDGEMENTS	112
ENVIRONMENT	112
Plant Associations	112
Habitat Preferences	118
Climate	120
BEHAVIOR	121
Activity Patterns	121
Foraging Behavior and Food.....	124
Reproduction	127
DEMOGRAPHY	131
Growth Rates	131
Mortality	135
Effects of Human Activity	139
Population Density and Composition	140
CONCLUSIONS	141
LITERATURE CITED	143

INTRODUCTION

The genus *Orthalicus* is a group of large, arboreal pulmonate snails in the family Bulimulidae. The genus is distributed primarily in tropical Central and South America. The two species that occur in North America, *Orthalicus floridensis* Pilsbry (Fig. 1A) and *O. reses* (Say) (Figs. 1B, C), are restricted to southern Florida. The latter species is divided into two subspecies: *O. r. reses* (Say) (Fig. 1B) and *O. r. nesodryas* Pilsbry (Fig. 1C).

O. r. reses, also known as the Stock Island Tree Snail, is the primary subject of this study.

O. reses reses historically has been restricted to its type locality on Stock Island, but apparently now it has been introduced into Key Largo and mainland Florida (Fig. 2). Its restricted range and lack of columellar and apical pigmentation serve to set it apart from *O. reses nesodryas*. The latter snail historically has been distributed over a broader range in the Florida Keys, exclusive of Stock Island (Fig. 2). Both subspecies of *O. reses* bear distinctive flame-like vertical brown stripes on the shell. These color characters separate them externally from *O. floridensis*, which lacks this pigmentation. *O. floridensis* is also the only one of these snails to occur naturally on the mainland of Florida (Fig. 2). The systematic relationships of these animals have been examined in detail elsewhere (Deisler, in prep.).

The purpose of this study is to provide data on plant associations, habitat preferences, foraging, and activity patterns of *Orthalicus* in Florida and to determine the life history of the Florida species. This project focuses on *O. reses reses*, the Stock Island Tree Snail, in its type locality in the southern Florida Keys because of its status as a threatened species. This snail has been included on the U.S. Fish and Wildlife Service list because of severe reduction in its population size and near elimination of its habitat. One purpose of studying its life history is to develop a recovery plan. Past studies (Craig 1972) have dealt primarily with *O. floridensis* in its range on the mainland of Florida. Data from this mainland taxon are probably not applicable to populations in the Keys, as the much lower rainfall in the Keys radically affects these tree snails. Nevertheless, comparative data for *O. floridensis* and *O. reses nesodryas* will be included in this study wherever they are known.

Very little information has been compiled on the life history, behavior, and ecology of *Orthalicus*. Most authors on the subject deal briefly with the appearance of the eggs, the estivation habits of the snail, and the production of the shell varices (Binney and Bland 1869:216-218, Binney 1885:439, Pilsbry 1899:102-103, 1912:443-444, 1946:29-31). Several authors have commented on the effect of cold on these animals, specifically on *O. floridensis* (von Martens 1893:179, McGinty 1936:2, Clency 1940:122). Two papers have dealt with growth rates in *O. floridensis* (Simpson 1923:111-112, Craig 1972:16-20) and two on probable diet in that animal (Pilsbry 1912:443, Craig 1972:16-20). Some of this ecological information was extracted from studies of the related tree snail, *Liguus fasciatus* (Müller), and is not the result of direct study of *Orthalicus* (Pilsbry 1912:443-444).

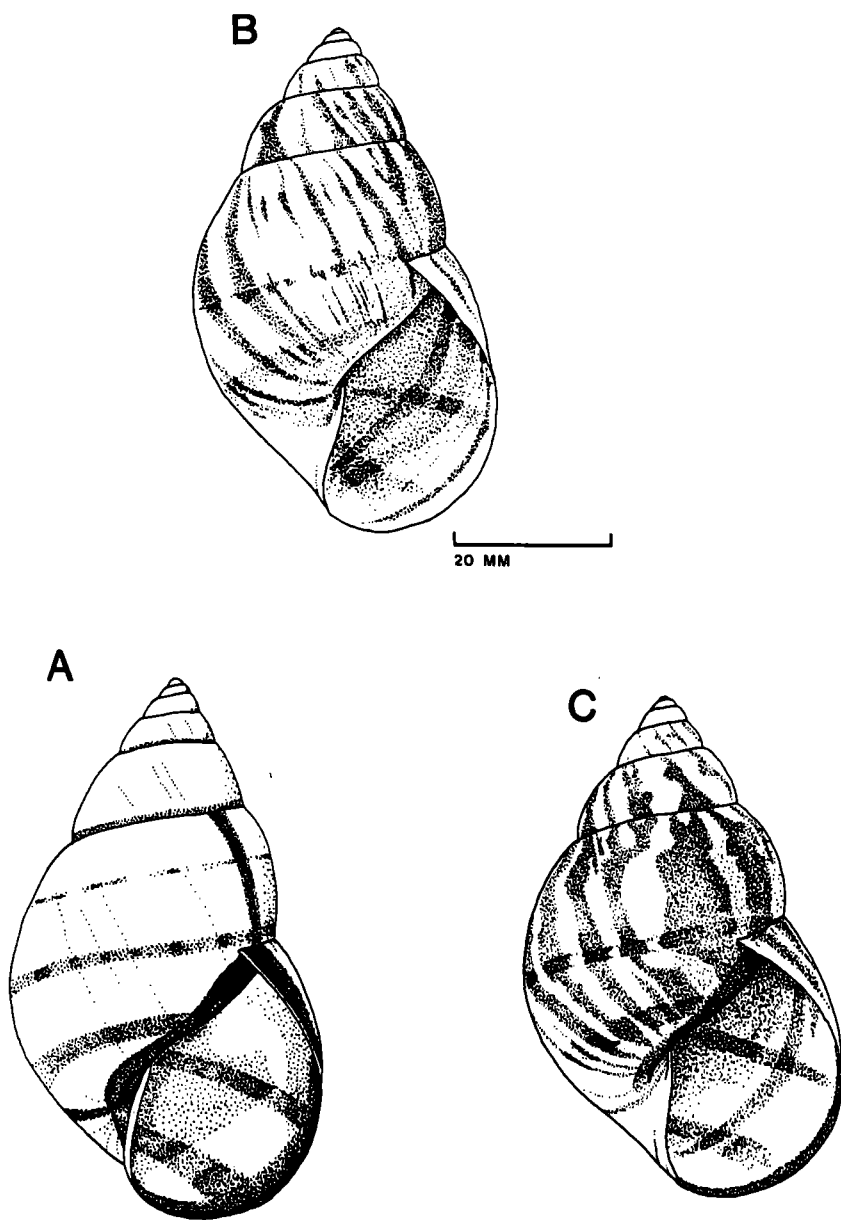


Figure 1. Shells of (A) *Orthalicus floridensis* Pilsbry, (B) *Orthalicus reses reses* (Say), and (C) *Orthalicus reses nesodryas* Pilsbry.

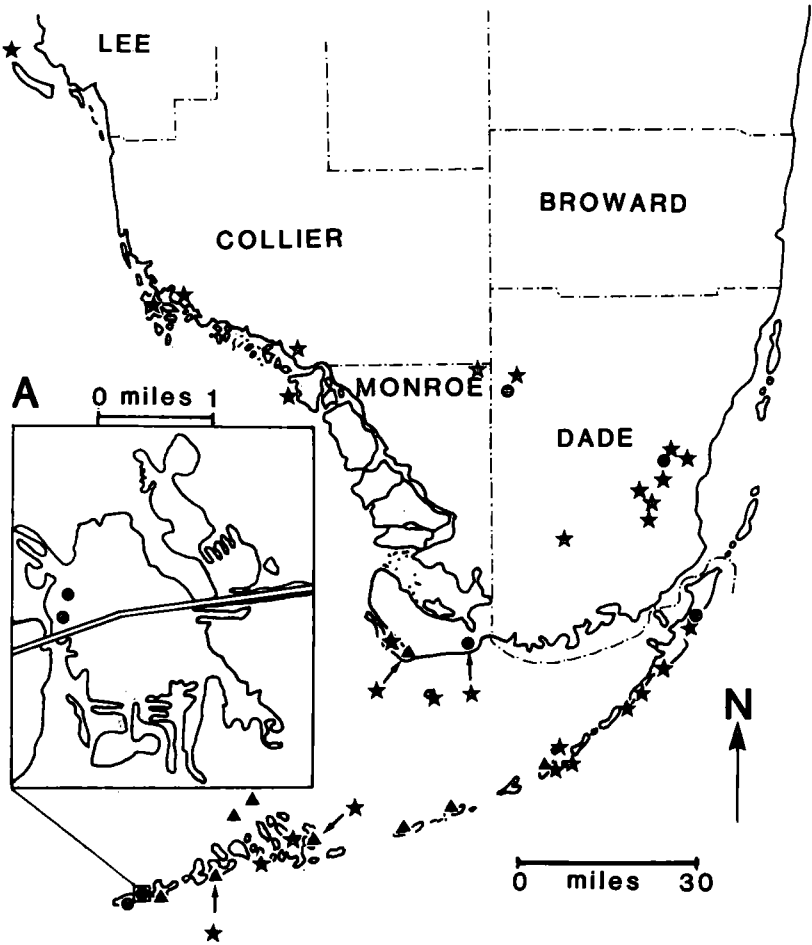


Figure 2. Distribution of *O. r. reses* ● (A = location of colonies on Stock Island, Monroe County), *O. r. nesodryas* ▲, and *O. floridensis* *.

ACKNOWLEDGEMENTS

I would like to express my gratitude for the assistance given to me by a number of people at the University of Florida. I greatly appreciate the time and effort invested in this project by Fred G. Thompson, under whose supervision this study was conducted. I am also grateful for the encouragement given to me by Martha Crump and Jonathan Reiskind. Stephen Bloom and Carmine Lanciani assisted me with statistical methods and computer analysis. The following people assisted me with identifications: James Kimbrough and Jack Gibson (mycology), Joseph Davis (phycology), Mike Thomas (entomology), and David Hall and William Stern (vascular plants). I would especially like to thank Shirley Taylor, Louisiana State University, for her timely identification of my crustose lichen samples.

I am grateful for the loan of material from collections of the Field Museum of Natural History (FMNH), Chicago; The Museum of Comparative Zoology (MCZ), Harvard University; and The Academy of Natural Sciences (ANSP), Philadelphia. I am deeply appreciative for the assistance and hospitality offered to me by George M. Davis, Robert Dillon, and Arthur and Cindy Bogan at the Academy of Natural Sciences, Philadelphia, and Richard Houbick at the National Museum of Natural History (USNM), Washington, D.C., when I visited those institutions.

I would particularly like to thank the people too numerous to list who gave of their time and energy to help me in the field, including the staffs of the following organizations who allowed me to examine the snail colonies in their localities: IFAS extension office in Key West, Key Deer Wildlife Refuge on Big Pine Key, the National Weather Service at the Key West Airport, the Fruit and Spice Park in Homestead, and Monkey Jungle in Miami.

This research was supported by funding from the U.S. Fish and Wildlife Service (Contract No. 85910-0759) and the Division of Sponsored Research, University of Florida (DSR Seed Grant A-I-26), extended to Fred G. Thompson as the principle investigator.

Finally, this study could not have been undertaken without the aid of the late Howard W. ("Duke") Campbell of the U.S. Fish and Wildlife Service, to whom I owe a great deal.

ENVIRONMENT PLANT ASSOCIATIONS

Only one previous study has attempted to identify the host trees of *Orthalicus* in Florida. Craig (1972) observed *O. floridensis* feeding actively on *Forestiera segregata* (Florida privet), *Piscidia piscipula* (Jamaica dogwood), *Carica papaya* (wild papaya), *Eugenia axillaris* (white stopper), and *Ficus aurea* (strangler fig). He ranked these plants in order of preference but gave no criteria for the order. Craig also noted these snails on *Sansevieria thyrsiflora* (African bowstring hemp), *Hymenocallis keyensis*

(Key lily), *Rhizophora mangle* (red mangrove), *Conocarpus erectus* (buttonwood), and *Agave decipiens* (agave), but did not directly observe them feeding.

During the current investigations both species of Florida *Orthalicus*, *O. floridensis* and *O. reses*, were observed feeding and estivating on a large variety of native and introduced trees (Table 1).

The occurrence of *Orthalicus* on host-tree species was examined at three sites in 1981 to determine if the snails demonstrated a preference for any of the tree species at those sites (Table 2). At each site the number of trees of each species and the number of snails inhabiting each tree species were counted. The percentage of the flora that each tree species represented was calculated, as was the percentage of the total snail population that was found on each tree species. The tree species were classified by bark type: either rough or smooth.

At sites where the trees are approximately equal in size, the percentages calculated for tree frequency and snail occurrence should be similar if snail distribution is random. When graphed these points should lie close to the line $y = x$ (Fig. 3). Points lying above the line indicate tree species inhabited by fewer snails than expected, while points lying below the line indicate tree species inhabited by more snails than expected.

At site 1 the trees were similar in size, with trunk diameters averaging 15 cm and tree height 4.5 m. The calculated percentages of snails inhabiting a tree species conformed with the abundance of that tree species in the flora. This can be seen graphically in Figure 4 but was not tested statistically because of the small size of the samples. Figure 3A shows that the points for site 1 fall fairly close to the line $y = x$, an indication that *O. reses* does not show a strong preference for any of the host-tree species at this site.

A situation similar to that at site 1 prevails at site 3 where all of the trees are also approximately the same size. The points in Figure 3C lie extremely close to the line $y = x$, indicating a very strong correlation between the frequency of a tree species and the number of snails that inhabit it. At site 3 also, *O. r. nesodryas* shows no preference for any particular tree species present (Fig. 4).

Site 2 shows a pattern that is similar to those at sites 1 and 3, but with more variation (Fig. 4). The two apparent exceptions to the random distribution of snails on tree species are the unexpectedly high frequencies on *Ficus citrifolia* (shortleaf fig) and *Piscidia piscipula* (Jamaica dogwood). These exceptions may be explained by the exceptional sizes of trees of these species.

As snails are distributed over the surface of a tree, a larger tree with more surface area can be inhabited by a greater number of snails. Most of the trees at site 2 are approximately the same size, with a trunk diameter of about 45 cm and height of roughly 6 m. The two exceptional

Table 1. Trees on which *Orthalicus* have been found in South Florida. Nomenclature is from Little (1979) and identification from Long and Lakela (1971), Little (1979), and Tomlinson (1980). E = exotic species, N = native species.

Tree species	Common name	<i>floridensis</i>	<i>reeses</i> <i>reeses</i>	<i>reeses</i> <i>nesodryas</i>
<i>Annona globifera</i>		X		
<i>A. reticulata</i> E	custard apple	X		
<i>Bischofia javanica</i> E	bishopwood	X		
<i>Broussonetia papyrifera</i> E	paper mulberry	X		
<i>Bumelia celastrina</i> N	saffron plum			X
<i>Bursera simaruba</i> N	gumbolambo		X	
<i>Byrsonima lucida</i> N	locustberry, Key byrsonima		X	
<i>Cassia</i> sp.		X		
<i>Chrysalidocarpus lutescens</i> E	areca palm	X		
<i>Chrysophyllum cainito</i> E	star apple	X		
<i>Citrus aurantifolia</i> E	lime	X		
<i>Coccoloba diversifolia</i> N	pigeon plum		X	
<i>C. uvifera</i> N	sea grape	X		X
<i>Conocarpus erectus</i>	silver buttonwood,			X
var. <i>sericeus</i> N	button mangrove			
<i>Delonix regia</i> N	poinciana		X	
<i>Eriobotrya japonica</i> E	loquat	X		
<i>Eugenia foetida</i>	Spanish stopper,		X	
(= <i>myrtilloides</i>) N	boxleaf stopper			
<i>E. axillaris</i> N	white stopper		X	
<i>E. uniflora</i> E	Surinam cherry	X		
<i>Ficus aurea</i> N	strangler fig		X	
<i>F. citrifolia</i> N	shortleaf fig			
<i>Gymnanthes lucida</i> N	crabwood, oysterwood			X
<i>Jacquinia keyensis</i> N	joewood, cudjowood			X
<i>Lysiloma bahamensis</i>	wild tamarind,	X	X	X
(= <i>latissiquim</i>) N	Bahama lysiloma			
<i>Malpigia glabra</i> E	Barbados cherry	X		
<i>Mangifera indica</i> E	mango	X		
<i>Manikara bahamensis</i>	wild dilly			X
(= <i>Achras emarginata</i>) N				
<i>Metopium toxiferum</i> N	poisonwood		X	X
<i>Morus rubra</i> N	red mulberry	X		
<i>Murraya koenigii</i> E	curry leaf	X		
<i>Piscidia piscipula</i> N	Jamaica dogwood, fish-poison tree		X	X
<i>Pisonia discolor</i> N	biolly		X	X
<i>Pithecellobium guadelupense</i> N	Guadeloup blackbead			X
<i>Pouteria campechiana</i> E	canistel	X		
<i>Psidium guajava</i> E	guava	X	X	
<i>Reymosia septentrionalis</i> N	darling plum		X	X
<i>Roystonea</i> sp. N	royal palm	X	X	
<i>Schinus terebinthifolia</i> E	Brazilian pepper, Florida holly		X	
<i>Syzygium jambos</i> E	rose apple	X		
<i>Thrinax radiata</i>	Florida thatch			X
(= <i>floridana</i>) N	palm			

Table 2. Percent occurrence of *Orthalicus* on host trees at three sites.

Tree species	Bark	Number Trees	Percent Flora	Number Snails	Percent Population
SITE 1: <i>O. reses reses</i> , Stock Island, golf course, June 1981					
<i>Metopium toxiferum</i>	s	11	22.45	5	20.00
<i>Eugenia</i> sp.	s	9	18.37	3	12.00
<i>Pisonia discolor</i>	s	8	16.32	6	24.00
<i>Thrinax radiata</i>	s	6	12.25	0	0.00
<i>Bursera simaruba</i>	s	4	8.16	3	12.00
<i>Byrsonima lucida</i>	s	3	6.12	4	16.00
<i>Coccoloba diversifolia</i>	s	3	6.12	1	4.00
<i>Ficus citrifolia</i>	s	2	4.08	2	8.00
<i>Reynosia septentrionalis</i>	s	2	4.08	0	0.00
<i>Schinus terebinthefolia</i>	r	1	2.04	1	4.00
TOTALS		49		25	
SITE 2: <i>O. reses reses</i> , Stock Island, county home, September 1982					
<i>Bursera simaruba</i>	s	4	23.53	15	26.79
<i>Swietenia mahogani</i>	r	3	17.65	8	14.29
<i>Ficus citrifolia</i>	s	1	5.88	10	17.86
<i>Piscidia piscipula</i>	s	1	5.88	14	25.00
<i>Coccoloba diversifolia</i>	s	1	5.88	5	8.93
<i>Schinus terebinthefolia</i>	r	1	5.88	1	1.78
<i>Pisidium guajava</i>	s	1	5.88	1	1.78
<i>Pisonia discolor</i>	s	1	5.88	1	1.78
<i>Delonix regia</i>	s	1	5.88	1	1.78
<i>Melaleuca leucadendra</i>	r	1	5.88	0	0.00
<i>Citrus aurantifolia</i>	s	1	5.88	0	0.00
<i>Cordia dentata</i>	s	1	5.88	0	0.00
TOTALS		16		36	
SITE 3: <i>O. reses nesodryas</i> , Johnston Key, July 1981					
<i>Conocarpus erectus</i>	r	7	36.84	5	27.78
<i>Manilkara bahamensis</i>	s	4	21.05	5	27.78
<i>Gymnanthes lucida</i>	s	3	15.79	3	16.67
<i>Thrinax radiata</i>	s	2	10.53	2	11.11
<i>Pithecellobium guadalupense</i>	s	1	5.26	1	5.56
<i>Metopium toxiferum</i>	s	1	5.26	1	5.56
<i>Pisonia discolor</i>	s	1	5.26	1	5.56
TOTALS		19		18	

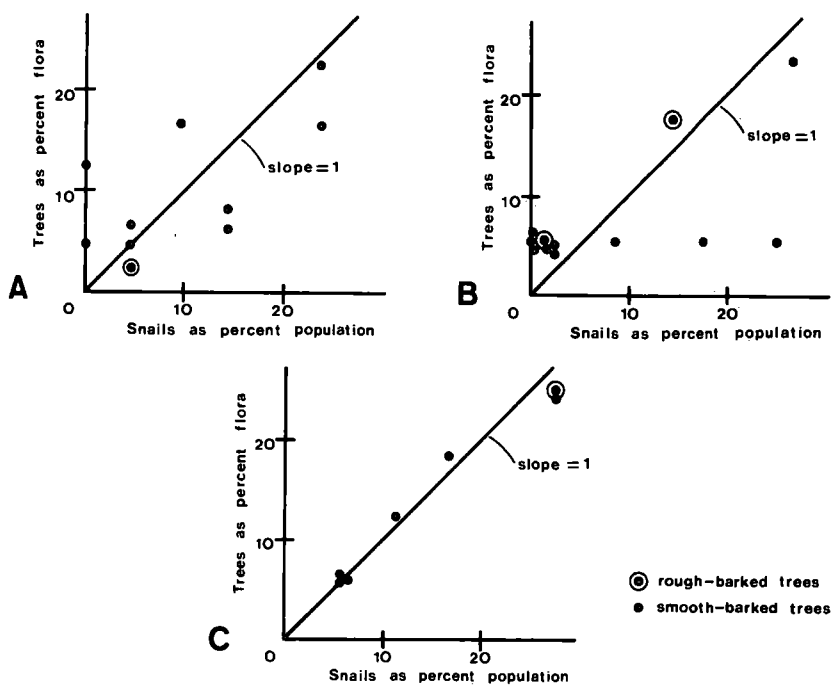


Figure 3. Distribution of *Q. reses* on tree species at three sites in the Florida Keys.

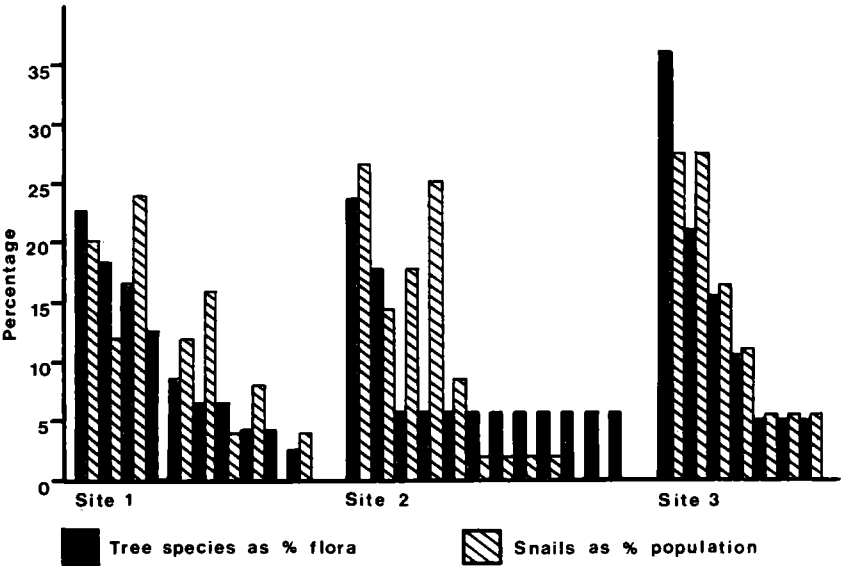


Figure 4. Percent occurrence of *O. reses* compared to percent occurrence of host-tree species at three sites.

trees are much larger: *Ficus citrifolia* measures 1.2 m by 12 m and *Piscidia piscipula* 0.75 m by 10.5 m. These trees have more surface area and therefore have more snails inhabiting them.

Voss (1976:68) stated that bulimuline tree snails prefer trees with smooth bark over those with rough bark, because smooth bark theoretically allows the snails to expend less energy when crawling over the surface and to gather more food because of fewer obstructions to the movement of the snails or of their radulae. Hypothetically, it also seems reasonable that smooth bark should be advantageous because it is easier for an estivating tree snail to form a secure mucous seal on a smooth surface. Mortality from dehydration or accidental dislodgement should be lower.

The first step in examining this situation is to test statistically the hypothesis that tree snails prefer one type of bark over the other (H_1). With the data for *O. reses* from all three sites (Table 2), a Chi-squared test was used to examine the distribution of snails on trees with rough bark in comparison with the distribution of snails on trees with smooth bark (Fig. 5). The resulting X^2 value, 0.012, indicates that the null hypothesis should not be rejected. *O. reses reses* shows no preference for either smooth-barked trees or rough-barked trees. In view of these data, no further experiments were performed to test hypothetical advantages conferred by smooth bark.

HABITAT PREFERENCE

Early authors reported merely that *Orthalicus* is found in trees (Say 1830:39, Binney 1858:39, 1885:439, Binney and Bland 1869:216-218) and sometimes on "dyewoods" (von Martens 1893:179). Pilsbry (1912:443-444) stated that *Orthalicus* has the same habits as *Liguus*. He reported that the latter lives in dense, shady woods on well-drained soil, and that the snail is never found on pines and mangroves but only on hardwood trees. Later authors concurred with this, specifically reporting on *O. floridensis* in the Cape Sable area (Simpson 1923:111-115, McGinty 1936:2) and *O. reses nesodryas* on Key Vaca and Sugarloaf Key (Pilsbry and Grimshawe 1936:19). Craig (1972:16-17) noted that *O. floridensis* on Pavilion Key occurs primarily in areas that are similar to true tropical hammock, and that it usually avoids the mangroves on the leeward side of the island and the growth near the beach. When occasionally found in these areas, it was always in estivation.

Populations of *Orthalicus* appear to be most dense in the true mainland hardwood hammock such as that found in the Pinecrest region of the Everglades. In the Keys, *Orthalicus* is also found in hardwood

	rough bark	smooth bark	row totals
number of trees with snails	O = 6 E = 5.833	O = 29 E = 29.167	35
number of trees without snails	O = 5 E = 5.167	O = 26 E = 25.833	31
column totals	11	55	N = 66

$$\chi^2 = \frac{(O-E)^2}{E} = 0.0122145; \text{d.f.} = 1; p = 0.05; H_0 \text{ not rejected.}$$

Figure 5. Chi-squared 2 x 2 contingency table for bark-type preference in *O. reses* (Siegal 1976:104-111). $H_0 = O. reses$ shows no preference for bark-type. $H_1 = O. reses$ prefers one bark-type over the other. O = observed values, E = (column total x row total) - N, N = column total sum = row total sum, d.f. = (rows - 1) x (columns - 1).

hammocks, but appears to be limited to the portions of the islands that are relatively high, with minimum altitudes of 5-11 feet.

The hardwood hammock is not the only habitat in which *Orthalicus* can be found in Florida. On the mainland, *O. floridensis* is frequently found in ornamental and fruit trees in parks and backyards in the southern portions of Dade County. In some cases these populations can be traced to introductions made as long as 30 years ago by local residents. The trees in which the snails occur are generally more isolated than trees in a true hammock and often are non-native species. An important limiting criterion may be the use of pesticides on the host trees (Craig 1972:19).

O. r. nesodryas also can be found in trees planted as landscaping, but such situations are rarer in the range of this animal. The relatively recent development of the keys on which this animal occurs has eliminated much of the native hammock habitat without enough elapsed time for replacement landscaping trees to have attained the size needed to support breeding colonies of the snail.

At its type locality, *O. reses reses* is found in the scrubby remnants of native hammock on the golf course on Stock Island. However, it occurs with more frequency on the native and exotic trees planted in isolated pockets between the fairways and in the parking area around the county buildings. Museum collections indicate that *O. reses* once was found in Key West proper, but development, the presence of *Rattus rattus* (black rat), and mosquito fogging may have combined to eliminate any populations on that island. *O. reses reses* also appears to have been introduced to two sites on the mainland and one on Key Largo. The mainland sites consist of hardwood hammock made up largely of *Lysiloma bahamensis* (wild tamarind), and also some *Ficus*. The Key Largo site is mixed hardwood hammock.

CLIMATE

Few comments appear in the literature on the climate inhabited by *Orthalicus* species. Von Martens (1893:179) wrote that the snail was confined to hot regions of America. McGinty (1936:2) reported that large specimens of *O. floridensis* were killed by frosts at Cape Sable. On the other hand, Clench (1940:122) noted that a colony of *O. floridensis* introduced to Sanibel Island north of its natural range survived 19 years of normal temperatures for that area, but that an extremely low temperature might kill them. Pilsbry (1946:37) reported that this colony was still present in 1945.

The typical climatic pattern for south Florida is one of a dry season alternating with a wet season. The dry season extends from November to approximately April or June and the wet season coincides with the warmer

months of the year. Rainfall data from the National Climatic Center shows that timing of the seasons is the same in Key West and the mainland (Fig. 6). However, the total amount of rain for the year is less in Key West than on the mainland, as is the amount of rain received in any given month.

Similar mean temperature patterns are shown for the two sites (Fig. 7). In each location, the coldest months are December, January, and February, June through September the warmest. The mainland site experiences the greatest extremes, with a 3-year range of -0.6 - 38.9°C . The 3-year range for Key West is 5.0 - 33.9°C . The range during the active season in Key West is given by the Climatic Center as 15.6 - 33.9°C over a 3-year span, with the range for June-July being 28.7 - 33.9°C . The latter compares favorably with the values measured at the study site on Stock Island, which were 29 - 33°C for the same months. The temperature range for the active season on the mainland is given by the Climatic Center as 18.3 - 38.9°C , somewhat higher than for Key West.

BEHAVIOR

ACTIVITY PATTERNS

Individuals in the Stock Island colony of *Orthalicus reses reses* began moving and feeding at various times during mid-June and early July in 1982. During a 2-week dry period in mid-July the snails resumed estivation. A mucus seal was formed, but was not as thick as those formed in the winter.

During June and early July the snails moved primarily during actual rainfall. They moved infrequently at night when it was not raining, and they never moved during a dry day. In late August and September, however, the animals remained extended for periods of up to 8 hours during daylight hours, even when no rain was falling.

Evidently water is an important stimulus to activity. At 11:55 a.m. on 7 July 1981, 250 ml of distilled water at 21°C was slowly poured over a snail in estivation. The water dissolved the mucus seal, and the snail emerged from its shell within 9 minutes. When water was similarly applied to each of five individuals that were withdrawn into their shells but not estivating, the snails emerged from their shells and began to move within 25 seconds to 20 minutes. They continued moving and feeding for 5-21 minutes. A similar experiment on 12 September 1982 resulted in activity lasting up to 8 hours.

In contrast, artificial darkness showed no effect. On 7 July 1981, at the same time as the water experiments, artificial darkness was applied to three snails. This was done by placing a light-colored box over their perches. The temperature was monitored to ensure that it remained with

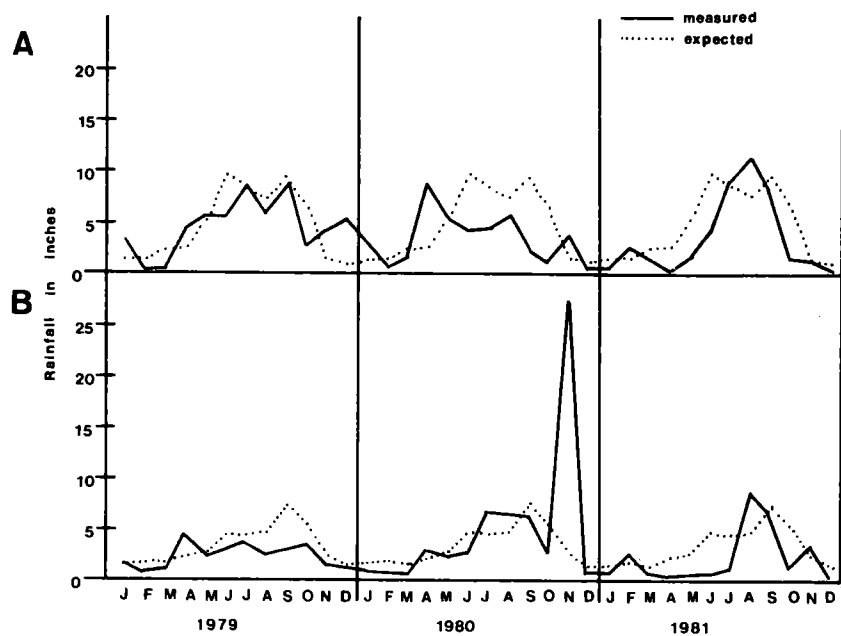


Figure 6. Monthly rainfall at (A) Forty-mile Bend in the Tamiami Trail and (B) Key West Airport. Expected values = 50-year average.

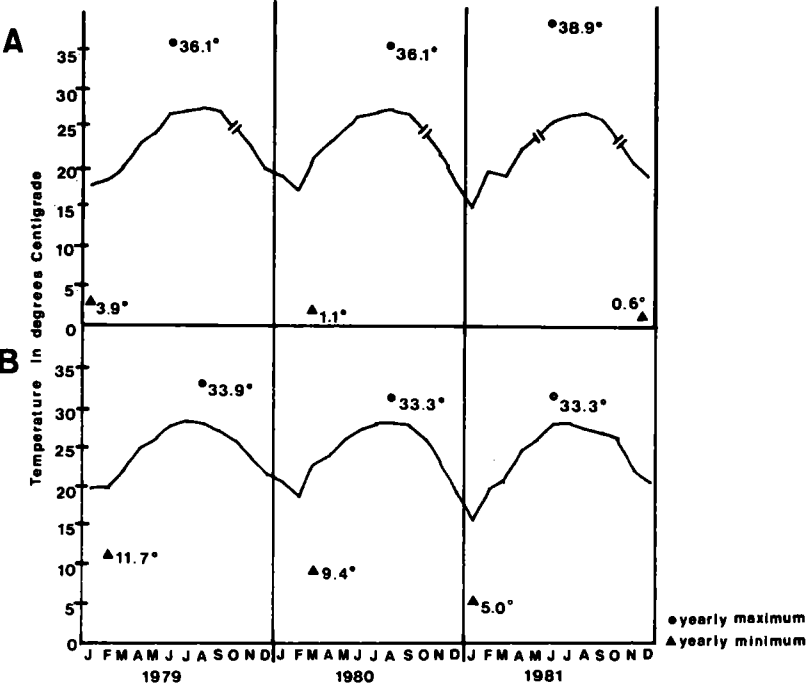


Figure 7. Average monthly temperature at (A) Forty-mile Bend in the Tamiami Trail and (B) Key West Airport .

the normal daytime range (29-33°C). The snails did not respond within a period of 2 hours. Snails were seen to move within 2 hours after nightfall on dry days.

The rate at which *Orthalicus* moves ranges from 38.1 cm to 95 cm per hour, measured over 5-minute intervals in the range of 29-33°C. Rapid movement is generally in a straight line and occurs when heavy rainfall is present or the tree surface is very wet after heavy rain. When the surface over which the snail is moving begins to dry, movement becomes irregular and slow. The snail frequently follows a curved path, with apparently random changes in direction.

Movement from tree to tree is infrequent and was noted to occur under two circumstances. Snails will occasionally cross from one tree to another in the course of feeding if the branches of the trees are interlocked. This was seen twice on the Stock Island golf course site over a period of 63 days. Snails were also seen to change trees after egg-laying. Most snails returned to the tree they had been on before nesting, but three did not return to their original trees and were found as far as 3 m away from the bases of those trees. In one case, a snail climbed a bus bench instead of a tree after nesting. Craig (1972:19) reported an instance of movement across a lawn from trees apparently when food was lacking. This was not seen in the Stock Island colonies.

Estivation generally begins in December, but can start earlier if rainfall ceases. *O. floridensis* on the mainland finds hollows in the host tree either at the base of the trunk or in the crotch of a major branch. In large populations as many as 20-30 individuals were found in one hollow. *O. reses reses* was also found estivating in hollows in the host tree as a general rule, but *Orthalicus* often estivates anywhere in the tree, frequently in exposed sites on the limbs. These are commonly attacked by predators and killed, with the crushed shell often remaining glued to the tree. Other estivation sites include the crevices between rocks in ornamental walls, the eaves of houses, the underside of bird-baths and bird-feeders, the spaces under piles of discarded sheets of plywood, and the hollows among above-ground roots. Estivation continues until movement is stimulated by rainfall during the following year, between May and August.

FORAGING BEHAVIOR AND FOOD

In June and July 1981, individuals of populations of *O. reses reses* fed during the day while it was raining, immediately after rainfall, and at night. By late August and September feeding was seen all times of day and night. Maximum activity was noted from late afternoon through the night

to mid-morning, and during rainfall. Mainland populations of *Orthalicus* fed in this pattern as early as July in the Everglades-Pinecrest region.

Feeding activity is indicated by a series of muscular contractions in the head. This reflects the movement of the buccal mass and the repeated passage of the radula over the bark surface. Feeding snails often follow a random twisting path that covers the entire bark surface. As noted above, they move in a straight line if surface moisture is abundant.

Pilsbry (1912:444) reported that *Liguus* fed mostly or entirely on minute fungi from the bark of trees, judged on the basis of stomach contents, and that *Orthalicus* has the same habits as *Liguus*. Craig (1972:18) examined the substrate on which individuals of *O. floridensis* were feeding and reported that the probable foods for *O. floridensis* on Pavilion Key are a variety of algae and fungi on tree surfaces. He made tentative identifications of these growths on *Piscidia piscipula* (Jamaica dogwood) and found that most of the fungi were common and widespread.

Examination of the stomach contents of *O. reses reses* from Stock Island reveals that the animals feed primarily on fungi, with some algae and lichens. The stomach contents of *O. r. nesodryas* from Johnston Key are similar, but the stomach contents of a mainland population of *Orthalicus* showed a predominance of algae, reflecting a similar predominance of algae on the trees at that time. Specific items identified from gut contents included basidiospores, *Aureobasidium*-fungus, mycelial fragments, algae, and large quantities of bacteria (J. Kimbrough, pers. comm.). The bacteria could be normal gut contents or a result of the relaxation and preservation procedure. They are probably not a food item.

Host trees were surveyed for possible food items. This was done because of the difficulty of identifying gut contents after partial digestion. Samples of tree bark were gathered and either incubated under moist conditions for 5-10 days for identification of algae and fungi, or dried for lichen identification.

A large variety of fungi, algae, and lichens were found on the various host trees (Table 3). Some mixobacteria also were seen, as were some mites, both of which may serve secondarily as food for *Orthalicus*. Neither mites nor mixobacteria were found in the gut contents of the snails examined. However, the snails show no sign of selective feeding behavior and may occasionally consume bacteria and mites inadvertently.

None of the epiphytes identified is specific to any particular species of tree, and many are widely distributed and common. It is unlikely that the type of food-growths present should be a factor in the absence of snails from otherwise suitable trees.

Table 3. Epiphytic growths found on the bark of host trees of *Orthalicus reses reses*.

Tree Species	Fungi	Lichens	Algae
<i>Bursera simaruba</i>	<i>Mortierella</i> sp.	<i>Opegrapha</i> sp. <i>Pyrenula</i> sp.	Coccoid green
<i>Byrsanina lucida</i>	<i>Orbidia</i> sp.	<i>Trypethelium</i> cf. <i>elcutteriae</i> <i>Phaeographis</i> sp. <i>Phaeographina</i> spp. (2) <i>Anthracotheicum ochraceoflavum</i> <i>Pyrenula</i> sp.	
<i>Coccoloba uvifera</i> <i>C. diversifolia</i>	<i>Hysterium</i> sp. <i>Graphis</i> sp.* <i>Pertusaria</i> sp.*	<i>Lecanora chlorotera</i>	<i>Leptosira</i> sp.
<i>Eugenia</i> sp.	<i>Pertusaria</i> sp.* <i>Staurothela</i> sp.* <i>Verticillium</i> sp.*	<i>Arthopyrenia hyrata</i> <i>Arthopyrenia</i> sp. <i>Anthracotheicum ochraceoflavum</i> <i>Pyrenula</i> sp. <i>Arthonia</i> sp. <i>Arthonia rubella</i> <i>Lecanora chlorotera</i>	<i>Leptosira</i> sp. Coccoid green
<i>Ficus</i> sp.	<i>Chaetomium</i> sp.	<i>Lecanora chlorotera</i> <i>Anthracotheicum ochraceoflavum</i> <i>Pyrenula</i> sp. <i>Pyxine cocoes</i> <i>Physcia crispa</i> <i>Ocellularia</i> sp.	Coccoid green
<i>Piscidia piscipula</i>	<i>Echinostelium minutum</i> <i>Macbrida decapillata</i> <i>Licea tenera</i>	<i>Graphina</i> sp. <i>Arthonia rubella</i> <i>Arthothelium</i> sp. (?)	<i>Tolypothrix</i> sp. <i>Entophysalis</i> sp. <i>Phormidium</i>
<i>Pisonia discolor</i>	<i>Pestalotia</i> sp. <i>Pertusaria</i> sp.	<i>Lecanora chlorotera</i> <i>Arthonia rubella</i> <i>Anthracotheicum</i> sp.	<i>Leptosira</i> sp. Coccoid green
<i>Swietenia mahogani</i> **	Pyrenomycete	<i>Anthracotheicum ochraceoflavum</i> <i>Arthonia</i> sp. <i>Bacidia</i> sp.	
<i>Thrynax radiata</i>	<i>Pestalotia</i> sp. <i>Libertella</i> sp.		Coccoid green

* Fungus represented as part of a lichen.

** Myxobacteria also found on this tree species.

REPRODUCTION

Previous information about reproduction in *Orthalicus* concerns only size, appearance, and number of eggs that the Florida species lay (Binney and Bland 1869:216, 218, Binney 1885:439, Pilsbry 1899:102-103, 1946:29-31). Reproductive activities of *Liguus fasciatus* were recorded by Pilsbry (1912:443-444, 1946:38), Davidson (1965:382, 387), and Voss (1976:66), but were not known for *Orthalicus*.

In this study mating was observed in *O. reses reses* on Stock Island in mid-September 1982 and in August and September 1986 (F. Ford, pers. comm.). Furthermore, snails that were not then mating were induced to mate by applying either distilled water or tap water to them. Mating was not so induced in July 1982, although application of water stimulated them to move and to feed. It is possible that water, in the form of rainfall, could be the cue that induces mating in physiologically ready individuals.

The means by which two snails find each other for mating was not noted, nor was any sort of courtship behavior seen. Voss (1976:66) observed that *Liguus* tree snails follow the mucus tracks of other snails, and this is probably the means by which *Orthalicus* individuals find their mates.

Copulation was observed only in the trees. Fertilization in these hermaphroditic snails was seen to be reciprocal and sequential. The events involved in copulation were witnessed as follows: two 3-year-old snails were found in coitus on a branch 14 feet above the ground in a large Jamaica dogwood tree (*Piscidia piscipula*) at 10:45 a.m., 13 September 1982. Snail A was clinging to the underside of the branch. Snail B was clinging to the shell of snail A at a 45° angle, with the anterior portion of the body of snail B twisted so that the genital pore was adjacent to the genital pore of snail A (Fig. 8). Snail B was serving as the male. After 10 minutes the snails separated slightly but remained clinging to the same locations, no longer in coitus. They did not move for 5 minutes. Then coitus resumed with snail A as the male. The two snails remained linked for 38 minutes. After unlinking, the snails separated slightly as before and remained without motion for the rest of the period of observation, which ended at 12:25 p.m. that same day.

No other actual instance of copulation was witnessed, though several pairs of snails were seen clinging to each other as if coitus had occurred recently. This sort of positioning was not seen at any other time during the active season. Additional occurrences of copulation events were reported in this population during August and September 1986.

Nesting occurred in 1982 two weeks after the observed coitus. Rain was frequent and heavy during this time, and both the tree bark and the ground were very moist. In the colony of 25 adult snails under observation on 24 September 1982, I saw 13 descend the tree trunks in

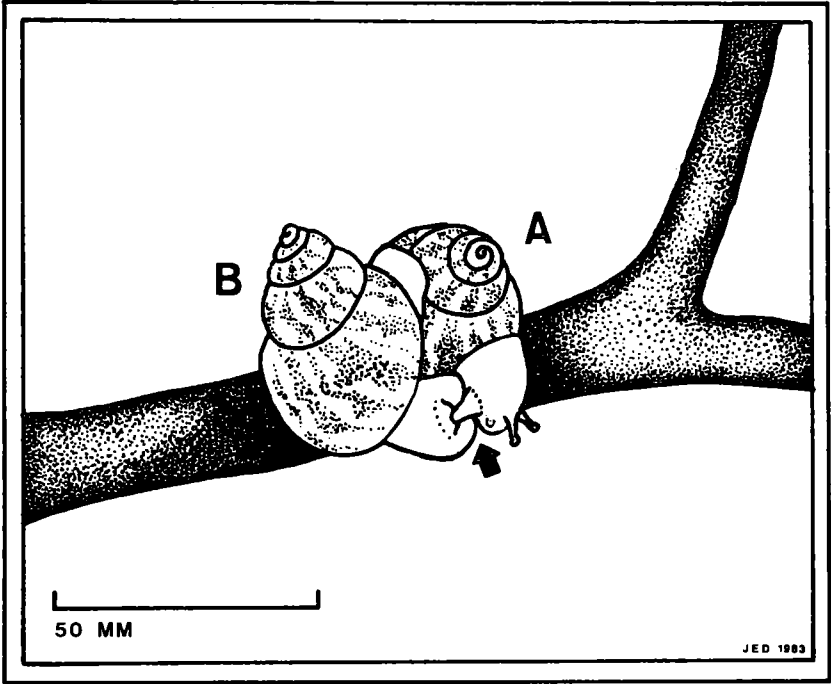


Figure 8. Mating in O. reses reses on Stock Island (everted genitalia indicated by arrow).

straight-line paths at a relatively rapid rate. There was no sign of cephalic muscular contractions, showing that the animals were not feeding as they moved.

As each snail reached the base of its host tree it either crawled along the junction of the tree and the ground, hesitantly left the tree and moved onto the leaf-mold, or moved rapidly from the tree to the soil without hesitation. Some snails were seen to "test" the soil by pausing to dig shallow nests, but moving on before completing construction or laying eggs. Others went directly to areas of soft dirt and leaf-mold and proceeded to dig a deep nest (40-50 mm deep).

Excavation of the nest was carried out first by the posterior portion of the foot (Fig. 9A). It was twisted and flexed repeatedly in order to push dirt aside. When the hole was approximately 20 mm deep, the snail turned in place and withdrew its head and the anterior portion of its foot as far as possible into the shell and continued to dig until most of the shell was below the surface (Fig. 9B). At this point the nest was approximately 50 mm deep. This procedure required a variable amount of time, from 1 to 12 hours. As many as 14 snails from a population of 25 adults were seen nesting at any one time.

Once the nest was deep enough so that only the apex of the shell was above the surface of the soil, the snail began to lay eggs (Fig. 9C). The actual process of egg-laying lasted from 24 to over 96 hours. It also required enlargement of the nest as the egg mass becomes larger. The eggs are oval and calcareous as reported for the genus in Florida by other authors (Binney and Bland 1869:216, 218, Binney 1885:439, Pilsbry 1899:102-103, 1946:29-31). They are tan when newly laid and measure 6 by 5 mm.

Most snails remained in one nest for at least 48 hours and layed from 8 to 21 eggs. Most of these nests contained at least 15 eggs. A few snails made more than one nest, depositing only a few eggs in each. Once egg-laying had ended, the eggs were covered over by the efforts of the snail to move back to the soil surface. In some cases a snail was not successful in this effort and died while still in the nest.

Nests were located in areas of soft soil or leaf-litter, either directly at the base of the host tree or up to 2 m from it. Nests were also located in cavities beneath above-ground roots that were filled with leaf-mold.

Certain sites appear to be preferred for nesting. As many as six different snails, three at a time, were seen to nest in a space measuring 10 cm on a side at the base of a Jamaica dogwood tree. This area consisted of soft soil and leaf-mold that was kept damp by the presence of a large, overhanging root extension. This tendency for multiple use of the same nest site makes it necessary to exercise caution in estimating maximum individual clutch size in *O. reses reses*.

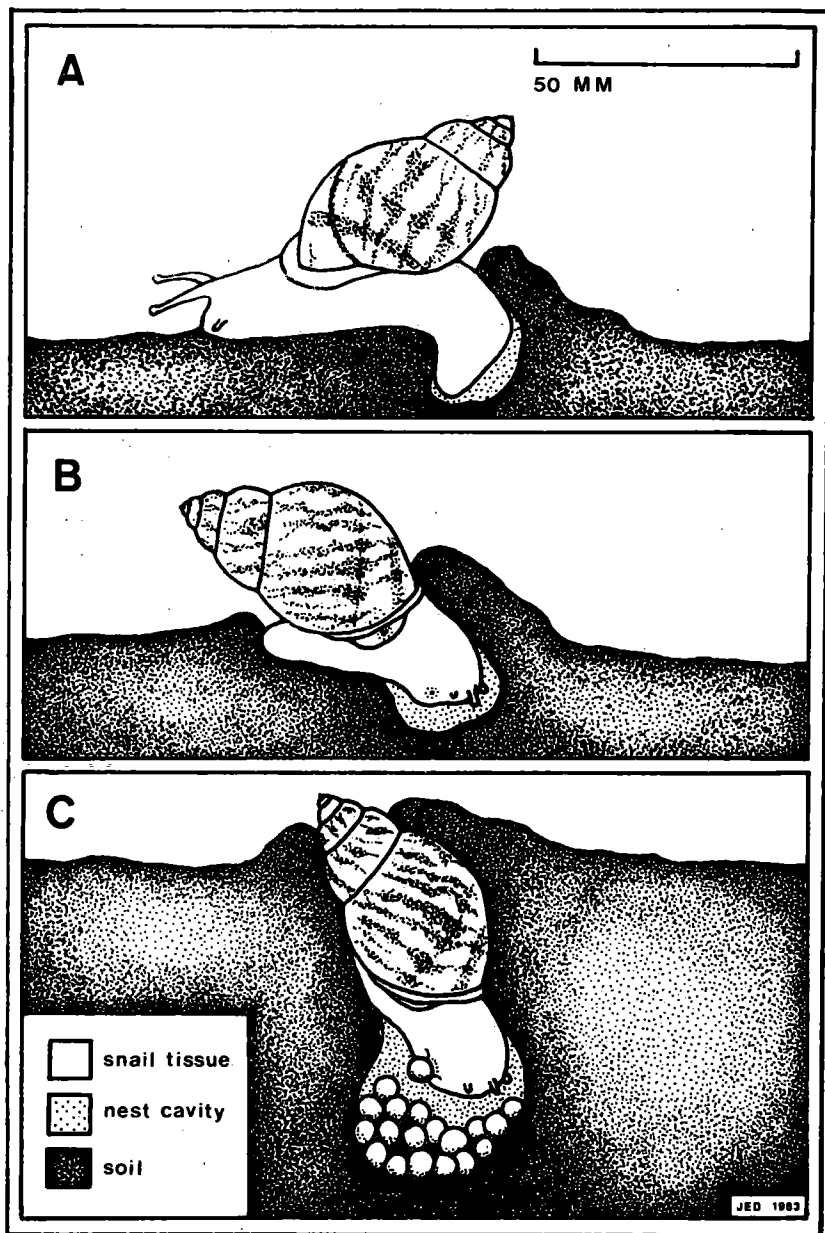


Figure 9. Nidification and ovulation in *O. reses reses* on Stock Island. (A) Preliminary nest-building with posterior portion of foot. (B) Excavation with head and anterior portion of foot. (C) Completed nest with snail in position for ovulation.

Most nesting snails were 2 to 3 years old. One snail with four estivation varices was seen nesting and laying eggs. A single 1-year-old also was seen nesting, but it died while still in the nest. It had laid at least 10 eggs before dying and had six more eggs inside its body at the time of death. Several juveniles less than a year old were in the colony, but they were not seen to descend to the ground at any time, although they were actively crawling on the trees.

Young snails were seen hatching 19 June 1982, one day after the first two consecutive days of measurable rain since February of that year. A total of 21 hatchlings emerged from the soil at the base of a poisonwood tree (*Metopium toxiferum*). It was not possible to determine if these young snails were from the same clutch or not because of the tendency for *O. reses* adults to lay eggs in sites where other clutches already have been deposited. However, the hatchlings emerged from the same spot at the base of the tree, and only one nest was found. No unhatched eggs remained in the nest, indicating 100 percent of the clutch hatched. In a second nest found at the base of a Jamaica dogwood tree, 4 of 18 eggs hatched. Thus the hatching rate appears to be extremely variable.

Immediately upon hatching, the young snails began climbing the nearest tree and feeding. They had fragile, brown shells that were transparent and showed no signs of pigmentation. The shells were 6-7 mm long and consisted of approximately three whorls. The animals were grey with some of the internal organs visible externally as darker parts of the body. The first fecal pellets were produced about 6 hours after hatching.

DEMOGRAPHY

GROWTH RATES

Pilsbry (1899:102-103, 1946:29-31) was the first author to discuss the formation of growth varices by *Orthalicus*. He noted that these dark brown lines are due to resting periods induced by climate, when shell growth is halted but pigment deposition is not. The spacing and number of these varices are dependent on the rate of growth of the individual snail and the frequency of the dry weather that induces estivation.

Varices are also affected by the duration of estivation. The darkest and widest growth lines are produced by the long annual period of estivation that occurs in the winter. It is possible to estimate the age of a snail from the number of these major varices on the shell. Simpson (1923:111-112, 115) used varices in this way to comment on the age distribution of a population of *O. floridensis* on Cape Sable.

Craig (1972:18-19) also used varices to determine age. He conducted a statistical age-growth study on *O. floridensis* on Pavilion Key.

He found that the largest number of major varices was seven and estimated the maximum age of the species to be seven years. He compared the length of the shell with the age estimated from the number of varices and calculated a mean age of 3.36 for the population and determined a mean shell height of 51.6 mm.

Using the number of major shell varices as the criterion, specimens of *O. reses reses* were separated by age class. The shell heights were measured, and mean height for each age class was calculated. These values were plotted on a graph with 95% confidence intervals indicated for each class (Fig. 10). Figure 10 shows that shell height increases most during the first growing season, with average amounts of growth as follows: 16.06 mm the first year, 5.16 mm the second year, 4.5 mm the third year, 1.73 mm the fourth year, 2.1 mm the fifth year, and 3.04 mm the sixth year. Individuals varied greatly, which was reflected in the high values calculated for standard deviation. Calculated mean age for these snails was 2.11 years and mean shell height 43.06 mm.

Another way to examine growth rate is to look at the yearly rate of shell deposition. Shells of *O. reses reses* were sorted by varix number into age classes and weighed. The average weights were calculated for each age class and plotted with 95% confidence intervals for each class (Fig. 11). In the first year the amount of shell produced is less than in most succeeding years. However, the actual amount of shell production per year follows a linear pattern, with average grams of shell material deposited as follows: 0.80 gm in the first year, 1.03 gm in the second year, 2.13 gm in the third year, 0.30 gm the fourth year, 0.81 gm the fifth year, and 2.67 gm in the sixth year. On the basis of the increase in shell weight, growth is constant from year to year. The slope of the regression line for the weight values is 1.22, representing an average yearly increase of shell material of 1.22 gm.

The large amount of variation within the age classes is due to variation in individual growth rates. These rates were measured in the two most common age classes in populations of *O. reses reses* on Stock Island by marking and recapturing individual snails during the active season. Juvenile snails showed rates of shell height increase of 0.019-0.340 mm/day over a 53-day period in the summer. Snails with two varices (those in the third growth season) showed rates of addition to the shell lip of 0.07-0.52 mm/day over a concurrent 56-day period.

Variability in individual growth rates is most likely caused by differential food intake. Snails that are estivating in sites protected from direct rainfall start feeding later than those in more exposed positions. Therefore they also begin to grow later in the season, reducing the yearly measurement. Although individual metabolism also may be a factor, causing variable efficiency in converting food energy to growth, exposure to rainfall is probably the most important factor.

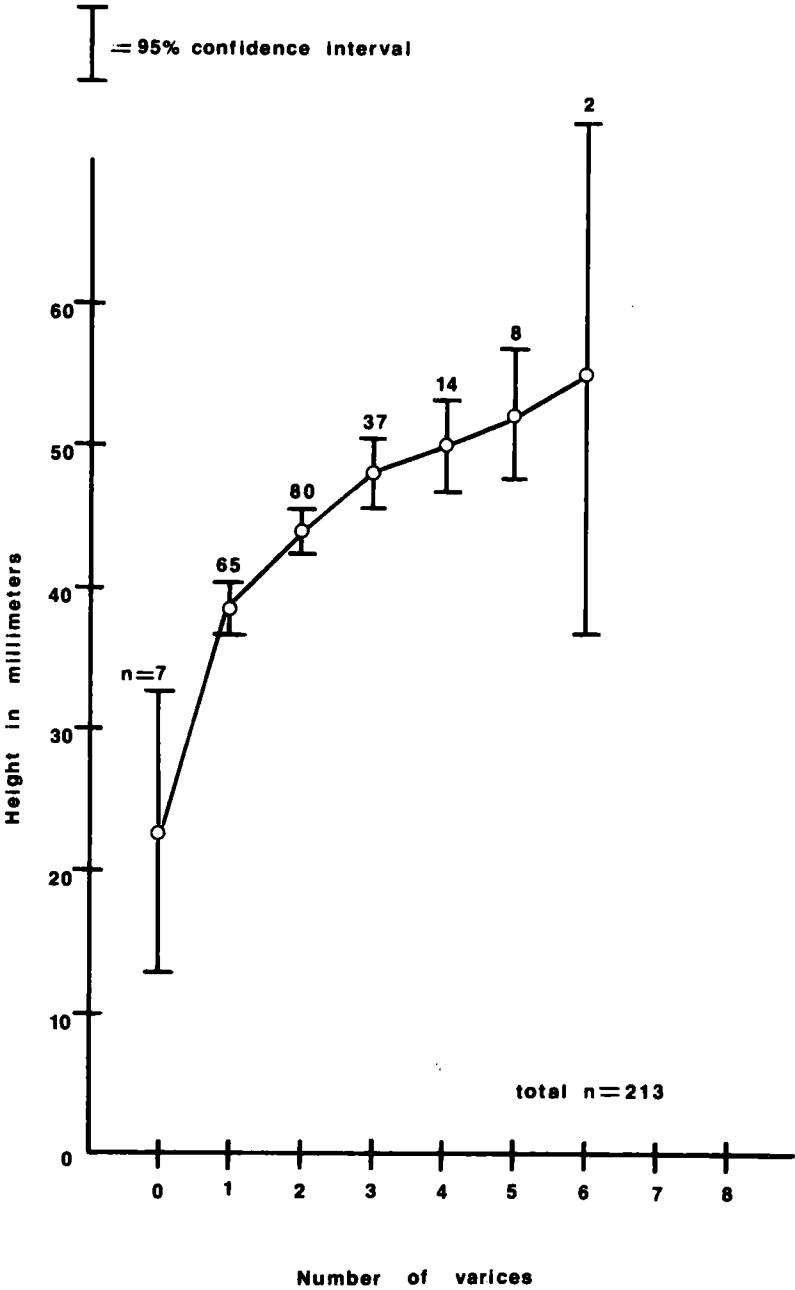


Figure 10. Growth rate in *Q. reses reses* (mm of shell height added per year).

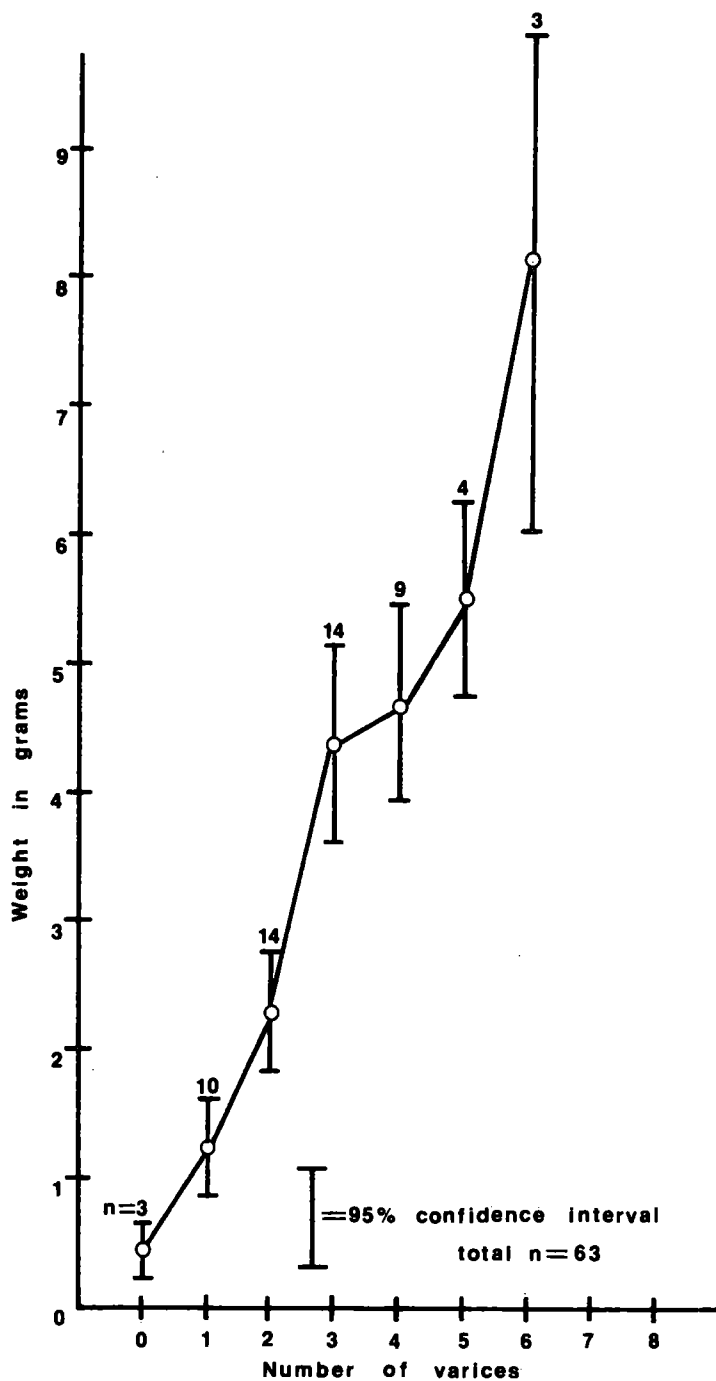


Figure 11. Growth rate in *Q. reses reses* (g of shell deposited per year).

MORTALITY

Mortality in *Orthalicus* stems from a number of causes. Some of these causes can be determined after death by the condition and location of the shells. One cause of death that can be determined in this manner is mammalian predation.

Predation by carnivorous or omnivorous mammals leaves characteristic patterns of shell damage. These predators generally crush the smaller and weaker upper whorls of the shell with their teeth. They also may gnaw on the shell. The shells generally have little organic matter left in them after a mammal has fed on the snail.

The raccoon (*Procyon lotor*) may be a frequent predator of *Orthalicus* and has been reported to prey on *Liguus fasciatus* on Lignumvitae Key (Tuskes 1981:167). Raccoons are present throughout the range of *Orthalicus* in Florida and are active climbers that can reach tree snails easily throughout the year. Experiments with naive animals showed that raccoons manipulate *Orthalicus* and *Liguus* shells in preference to more customary food items. They typically bite the upper whorls from the shells and consume the entire soft body.

The southern opossum (*Didelphis virginiana pigra*) also feeds on tree snails and, like the raccoon, is an active climber. This animal is more numerous in the mainland range of *Orthalicus* than in the Keys, but has been reported from Key Largo, Key Vaca, Big Pine Key and Key West (Layne 1974:387).

The black rat (*Rattus rattus*) is a foreign species abundant throughout South Florida and the Keys, including Key West (Layne 1974:390). Because it is smaller than either the raccoon or the opossum, the black rat may be limited to preying on younger and smaller snails.

Thompson (1980:5) listed the Norwegian rat (*Rattus norvegicus*) as a possible predator of *O. reses reses* on Stock Island. However, this species is apparently limited to the Miami residential area (Layne 1974:390). It probably does feed on *Orthalicus*, but only where the ranges of the two taxa coincide, which limits predation primarily to *O. floridensis*, the only member of the genus to occur naturally in Miami. The introduced colony of *O. reses* in Cox's Hammock, Goulds, also may be affected by the Norwegian rat.

The grey squirrel (*Sciurus carolinensis*) was seen feeding on *Liguus fasciatus*, the other large arboreal snail in South Florida, in the Miami area (Thompson, pers. comm.). Squirrels are known to augment their diet with other arboreal invertebrates, such as beetles, ants, and caterpillars (Martin et al. 1951:232). This animal is probably an occasional predator on *Orthalicus* as well as *Liguus* where its range overlaps that of the snails. This squirrel has been reported in South Florida throughout most of the mainland range of *O. floridensis* as well as on Key Largo, Plantation Key,

and Lower Matecumbe Key (Layne 1974:390). *Sciurus* is not found in the southern Keys and therefore is not a factor in the mortality of *O. reses reses* on Stock Island.

The eastern woodrat (*Neotoma floridana*) is represented in South Florida by the subspecies *N. f. smalli*, the Key Largo woodrat. It is found only on Key Largo and Lignumvitae Key (L.N. Brown 1978:11-12). The woodrat is reported to be primarily a vegetarian but occasionally has been observed to eat snails and insects (Lowry 1974:258). It may be a predator on tree snails, including *O. reses* and *Liguus fasciatus*, but, like the woodrat, it may be restricted to feeding on smaller and younger snails by size limitations. The woodrat is also known as the packrat because of its tendency to carry bright or shiny objects to its nest. Empty snail shells sometimes found in woodrat nests may only represent this collecting tendency and not true predation.

There are unsubstantiated reports by local residents that house cats (*Felis catus*) feed on *O. reses reses* on Stock Island (Thompson 1980:5). There are a large number of semi-feral cats in the area where the tree snail colonies are found. However, these cats refused snails offered them in place of their regular food. The cats washed vigorously after contact with the snails and showed signs of distaste. Therefore, it is doubtful that house cats prey on the snails.

Birds, such as blue jays (*Cyanocitta cristae*), contribute to the mortality of tree snails and, like mammalian predators, leave characteristic patterns of shell damage (Voss 1976:68, Tuskes 1981:167). The birds peck at the shells of exposed animals, usually while the snails are in estivation. These attacks leave distinct radiating cracks in the body whorl of the shell. Sometimes the damage to the shell is enough to produce a depressed area or even a hole. The birds are then able to attack the flesh of the snail. Unlike mammalian attacks, however, such avian attacks leave a considerable quantity of flesh in the shell. Sometimes the snails are uninjured by these attacks despite the damage done to the shell, in which case some snails are able to repair the shell, leaving a scar. Other snails appear to die of dehydration following breakage of the shell.

Observers in Dade County have seen blue jays (*Cyanocitta cristae*) attack *O. floridensis*. On Stock Island, Monroe County, local observers report that a large black bird that they termed a "crow" carried out attacks on *Orthalicus reses reses*. It has not been possible to identify this bird more specifically. However, the following avian species occurring in the Key West area are potential predators: common grackle (*Quiscalus quiscula*), red-winged blackbird (*Agelaius phoeniceus*), smooth-billed ani (*Crotophaga ani*), and starling (*Sturnus vulgaris*) (M. Brown, pers. comm.). Bird-caused shell damage was found in the colonies of *O. reses reses* on Stock Island, but such damage and mortality was particularly high in a large colony of *O. floridensis* in Homestead. The density of the population at this

site forces many snails to estivate in exposed situations, where they are vulnerable to avian attack.

Unlike mammalian and avian predation, attacks by the two known invertebrate predators on *Orthalicus* do not damage the shell. It is therefore difficult to estimate the impact that such predation has on the tree snails.

The predatory gastropod *Euglandina rosea* is one of the invertebrates known to feed on *Orthalicus* (Baker 1903:51, Voss 1976:68). *Euglandina* is found throughout the range of the Florida *Orthalicus*. This carnivore is often considered to be terrestrial, but it is frequently found in the same trees inhabited by *Orthalicus*.

The second invertebrate predator known to feed on *Orthalicus* is the larva of a click beetle, probably *Aleus* sp., identified by M. Thomas of the Department of Entomology at the University of Florida. This sizeable larva (25-35 mm long) lives in the leaf-mold and feeds on any organism with which it comes in contact. A specimen was found actively consuming a nesting *O. reses reses* on Stock Island.

Ants are commonly found in trees throughout the range of *Orthalicus*, but it is not known if they attack and feed on the snails. Eisner and Wilson (1970:14) reported that ants do not consume the related snail, *Liguus fasciatus*, because of what appeared to them to be the discharge of a defensive fluid that repelled the ants. However, Tuskes (1982:168) reported that fire ants (*Solonopsis geminata*) do attack *Liguus*. Ants were seen walking over the shell and extended foot of *O. reses reses* on Stock Island, without harming the snail, as they moved up the tree on which it lived. Ants also were seen consuming the flesh of dead and rotting specimens of *O. reses* and *O. floridensis*.

Flies of the family Sarcophagidae may contribute to mortality of *O. reses reses*. Two species, tentatively identified at the University of Florida by M. Thomas as *Sarcodexia sternodontis* and *Helicobia rapax*, were reared from recently dead snails collected on Stock Island. Muma (1954:8-9) reported four parasitic sarcophagids causing death in *Drymaeus dormani* (Binney), a small bulimulid tree snail distributed in northern and central Florida. Stegmaier (1972:237-241) reared seven species of sarcophagid flies from snails collected in Dade County. He wrote that most flies in this family are saprophagous rather than parasitic, but did not indicate which mode of life was followed by *S. sternodontis* or *H. rapax*, both of which he reared from *Marisa cornu-arietis* (Linné). Stegmaier reports that both species of fly have been reared from a large variety of invertebrates in North and South America, including a number of terrestrial pulmonate snails. It was not determined whether the eggs of these flies were laid on the flesh of *O. reses reses* before death of the snail or after.

The land hermit crab (*Coenobita clypeatus*) has been reported as a possible predator on tree snails (Davidson 1965:386, Voss 1976:69). Hermit

crabs do occupy the shells of *O. floridensis* on Big Pine Key, but this is not proof of predation. These crustaceans will inhabit any suitable containers they find, usually gastropod shells, but can include small bottles.

A number of other predacious invertebrates may feed on *Orthalicus*, but have not yet been reported doing so. Muma (1967:3-10) indicated that two species of scorpion present within the range of *Orthalicus* were large and aggressive enough to pose a possible threat to nesting tree snails. These scorpions are *Centuroides keysi* (36-73 mm) and *C. gracilis* (70-110 mm). Muma (1967:21-25) also recorded several whip-scorpions within the range of the Florida *Orthalicus*: *Mastigoproctus giganteus* (38-50 mm), *Tarantula marginemaculata* (10.5-17 mm), and *Paraphrynus raptator* (= *T. fuscimana* [Koch] [Franz 1982:130]) (17.5-24 mm). Like scorpions, these arachnids are secretive ground-dwellers and therefore would pose a possible threat to nesting snails. Large centipedes of the genus *Scolopendra* also may be possible predators of nesting *Orthalicus* (F. Thompson and R. Franz, pers. comm.).

Several "lightning bugs" from the family Lampyridae are present within the range of the Florida *Orthalicus* and may prey on the snails (J. Lloyd, pers. comm.). Several climbing species in the genus *Pyraclomena* are found in Key West, as well as representatives of the non-climbing genus *Photurus*. *Pyraclomena* is believed to be a snail specialist, while *Photurus* will feed on snails if they are present but feeds on other prey more commonly. A summary of the feeding behavior of several prominent snail-eating lampyrids is presented by Mead (1961:106-109).

In an effort to estimate minimum predation rates, all empty shells seen in populations of *O. reses nesodryas* on Johnston Key and *O. reses reses* on Stock Island were collected. Of 327 *O. r. nesodryas* specimens collected, 80% of the shells were whole, indicating death due to invertebrate predation, cold, dehydration, old age, disease, or some other factor that does not damage the shell. Only 3% showed signs of mammalian predation, with 0.6% showing predation of undeterminable type. However, 16% of the shells showed scars of past injury that had been repaired and was not the apparent cause of death.

In the more restricted population of *O. reses reses*, only 35 empty shells were recovered. Of these 63% showed no signs of damage, while 20% showed indications of death by predation (17% mammalian and 3% avian). Shells that showed scars of injuries not causing death made up 17% of the sample.

If these samples are representative, then predation rates vary greatly from colony to colony, with up to 20% of mortality attributable to vertebrate predation. Since the act of predation often crushes the shell beyond recovery, this is a minimum estimate. Some larger predators, such as raccoons, may remove their prey from the area entirely. Invertebrate predation that does not damage the shell cannot be distinguished from non-

predatory causes of death, and therefore also may exceed estimated predation rates. Predation by vertebrates and invertebrates must be a very important factor in controlling populations of *Orthalicus* in South Florida.

EFFECTS OF HUMAN ACTIVITY

Numerous museum lots (containing 30-60 or more specimens each) of live-taken *Orthalicus reses reses* shells exist. Most of these were collected during the 1930s and a few during the 1940s. Collection pressure was severe at that time and appears to have had a negative effect on population size. Not since the 1950s has it been possible to collect such sizeable lots, because the animals were not present in sufficient density. This evident decline in population density of the Stock Island snails also was effected through habitat loss as a result of real estate development.

During the 1981-1982 surveys on Stock Island it could be seen that the snail was undergoing loss of habitat. Redevelopment of the golf course was planned, though not completed. The county land population was isolated in a parking lot area where nesting snails were subject to great mortality through crushing. In 1986, reports were received by the Nature Conservancy that the snail population was declining. On 2-3 July 1986 my field investigation confirmed a reduction in the population.

In June 1981 I observed 25 adults in the golf course population (Table 2) and 6 adults in August 1982, and J. Young (pers. comm.) saw 3 adults in September 1986. No empty shells were discovered, with the exception of one specimen collected in 1982 by a golf course employee. The dearth of empty shells and the observations made by local residents indicate that this reduction is possibly due to human collecting activities.

The county land population is faring better than the one on the golf course, but it also is showing a reduction in numbers. In August 1981, 36 adults were seen living at that site (Table 2). Approximately the same number were present in August 1982 when the observable population was estimated to be 30-40 adults and 67 hatchlings and juveniles, or a total of 107 snails. However, in multiple independent surveys of the same site in during June through August 1986, all surveyers reported 21-25 adult snails and 1 hatchling (J. Young, K. Sunderland, A. Hooten, F. Ford, pers. comm.). Two adult snails were seen in the Botanical Garden (M. Huckel, pers. comm.), making a total of 28 snails observed in the area.

Human collecting of the live snails has been reported by a resident of the area (H. Schiller, pers. comm.). Approximately 10 specimens were removed from a hibiscus bush (*Hibiscus rosasinensis*) early in 1986. Since that time no specimens have been found on that host plant.

Habitat degradation is also a factor in the reduction of the county land population. In several instances, cement and gravel have been dumped at the base of host trees. This effectively destroys the nesting grounds for both *Orthalicus reses reses* and *Drymaeus multilineatus*, by making the soft leaf mold and dirt inaccessible. In addition, because many of the host trees are located in the parking lot, vehicles are being parked on the dirt immediately at the base of these trees, thereby packing the soil and making it unsuitable for nesting. These vehicles also pose a potential threat to those individuals who are able to nest, because they remain in the nest for 72-96 hours and are extremely susceptible to crushing.

POPULATION DENSITY AND COMPOSITION

On Stock Island there are generally 1-4 snails per inhabited tree. A maximum of 13 snails was found in a large Jamaica dogwood tree (*Piscidia piscipula*) approximately 10 m tall. Similar densities were found in a colony of *O. reses nesodryas* on Johnston Key.

Population densities on the mainland were higher. *O. floridensis* in the Pinecrest region of the Everglades generally was found in numbers of 30-40 snails per inhabited tree. Similar densities were seen in a colony of *O. floridensis* in the Fruit and Spice Park in Homestead, Dade County. Densities of approximately 4-8 snails per inhabited tree were seen in a mixed colony of *O. floridensis*, *O. reses reses*, and *Liguus fasciatus* in Goulds, Dade County.

Calculation of a Lincoln Index for the population of *O. reses reses* on the golf course on Stock Island is inappropriate because of the disturbance of the habitat by man and because the snails do not represent a randomly mixing population. A census of an area of 0.33 acres produced 17 snails, which is a crude density of 510 snails per acre of uniform habitat. If the entire 20-acre course were so populated, it could support approximately 10,200 snails. But a survey of the area showed the snail to be highly restricted in its distribution in the suitable habitat. Only two places appear to be well-colonized at this time. The total population actually may number fewer than 200 snails.

Among the factors that may affect population density are quantity of food available, size and density of habitable trees, presence of suitable nesting and estivation sites, and rates of predation. The results of human activity include both directly and indirectly causes of mortality. Density is also affected by the climate, including the quantity and regularity of rainfall, and the frequency of freezing temperatures. The large numbers of specimens in museum lots indicate that human collecting of adult snails may

be responsible to a great degree for the low densities seen on Stock Island at the present time.

An attempt was made to establish the age distribution of *O. reses* on Stock Island (Fig. 12). A detailed count of all snails present, including hatchlings, resulted in a total of 107 individuals. When the snails were sorted by age class, the following percentages resulted: 66% of the population were hatchlings or juveniles of less than 1-year old, 6% were 1-year-olds, 14% were 2-year-olds, 11% were 3-year-olds, 3% were 4-year-olds, and 1% were 5-year-olds. No snails were found during the survey that were more than 5 years old.

Error is most likely to occur in the counts of the hatchlings, juveniles, and 1-year-old snails. They are relatively small (6-35 mm generally) and can be overlooked easily. Therefore, young snails may comprise more of the population than this study indicates. The counts for the adult (2 years old and older) snails are more certain and give results that are consistent with those from tracking marked animals.

In general, reproduction was found to begin when snails had attained 2 years of age. On this basis, reproductive individuals comprise 29% of the Stock Island population. No difference was noted in the number of eggs laid by individuals of different age classes.

Simpson (1923:111-112) examined the age distribution of a colony of estivating *O. floridensis* on Cape Sable. He found that of a colony of approximately 500 snails, very few were "adult" (with three growth varices), 5% were 2-year olds, and over 90% were 1-year olds. However he indicated that this was an unusual distribution, with many more "yearlings" than normal. No other studies have been conducted on the age distribution within colonies of *Orthalicus*, although several have been carried out on the related snail, *Liguus fasciatus* (Brown 1978:39-59, Tuskes 1981:166-167).

CONCLUSIONS

This study of the ecology of the Stock Island tree snail, *Orthalicus reses* (Say), was undertaken to facilitate the development of a recovery plan for this federally listed, threatened species. Little was known about the life history and ecological requirements of *O. reses*. Information about these subjects was required in order to be able to reverse the reduction in population size and enlarge the habitat required by the snail.

The results of this study indicate that *Orthalicus reses* is not as specialized as has been thought. This snail is not limited by species of tree available for colonization and can be found on both native and introduced trees with either rough or smooth bark. It feeds, apparently without

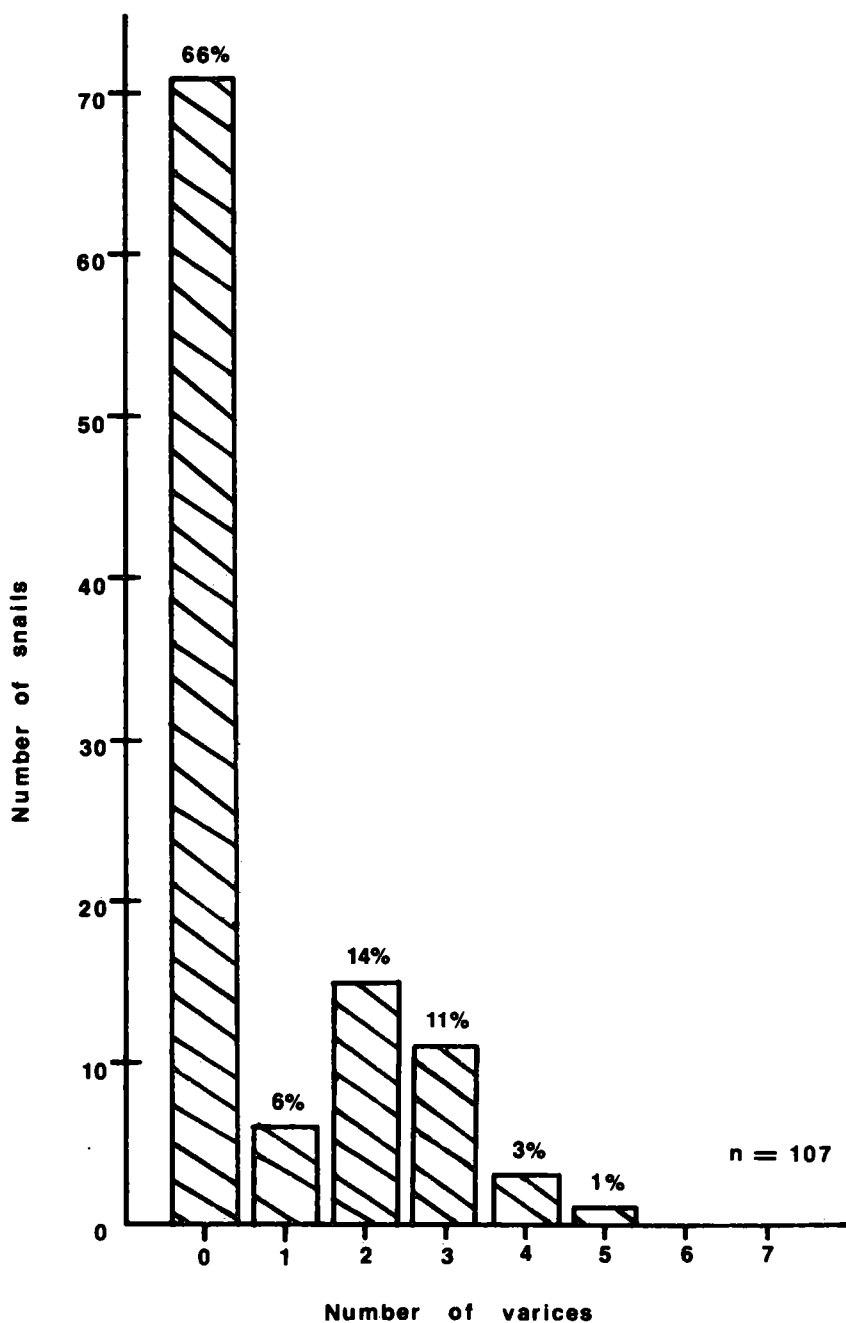


Figure 12. Age class distribution of *O. reses reses* on Stock Island.

discrimination, on epiphytic lichens, fungi, and algae on tree surfaces. *O. reses* most generally is found in hardwood hammock or remnants of such hammock, but appears able to survive in landscaped areas of sufficient maturity. Most nests are constructed in soft soil and leaf-mold, but some have been found in lawns as well. Activity (feeding and reproductive events) is stimulated by rainfall. However, *O. reses* is capable of surviving long periods (6-9 months) of drought routinely by estivating. The discovery of two recently established colonies of *O. reses reses*, one in the Everglades and one on Key Largo, indicates that it is possible to transplant the snail successfully.

Several factors limit the population of *O. reses reses*. These include predation, destruction and degradation of habitat, and temperatures near or below the freezing point. Vertebrate predation, which can account for up to 20% of mortality, can be reduced by trapping programs. Such a program for trapping raccoons (*Procyon lotor incautus*) in the area has been planned by Monroe County in an effort to reduce the decline of the county land population on Stock Island (A. Hooten, pers. comm.). Destruction of habitat can be limited by legal means. Degradation of the nesting grounds on the county property is being reversed by the county through the construction of protective, leaf-mould-containing nesting boxes at the base of host trees in and near the parking lot. These are planned to reduce vehicle-related problems, as well as to prevent the dumping of unsuitable substrates on the nesting grounds. Curtailment of collecting by humans would greatly increase the size of the type population on Stock Island.

The effects of habitat degradation can be ameliorated by the establishment of transplanted colonies in areas unlikely to be disturbed by man's activities. These areas can be only in the most southern portions of the State of Florida, where the winter temperatures only rarely drop to the freezing point. The minimum number of snails that could be transplanted to form these colonies would be two sexually mature adults, i.e. snails of at least 2 years of age. A search for suitable transfer sites has been undertaken jointly by Monroe County and the State of Florida, with the cooperation of the U.S. Fish and Wildlife Service (D. Wesley, pers. comm.). Further studies on the life history of the Stock Island Tree Snail are being carried out by the Florida Game and Freshwater Fish Commission in cooperation with Monroe County (J. Hovis, pers. comm.).

LITERATURE CITED

- Baker, F.C. 1903. Shells of land and water. A.W. Mumford, Chicago. 175 pp.
Binney, W.G. 1858. The complete writings of Thomas Say on the conchology of the United States. H. Baillere, New York. 249 pp.

- _____. 1885. A manual of American land shells. Bull. U.S. Nat. Mus. 38th ser. 28:1-528.
- _____, and T. Bland. 1869. Land and freshwater shells of North America. Part I: Pulmonata Geophila. Smithsonian Misc. Contr. 8(194):1-316.
- Brown, C.A. 1978. Demography, dispersal, and microdistribution of a population of the Florida tree snail, Liguus fasciatus. M.S. thesis, Univ. Florida, Gainesville. 135 pp., 17 figs.
- Brown, L.N. 1978. Key Largo woodrat. Pp. 11-12 in Rare and Endangered Biota of Florida: Vol. One, Mammals. J.N. Layne (vol. ed.), P.C.H. Pritchard (ser. ed.). Univ. Presses Florida, Gainesville. 52 pp.
- Clench, W.J. 1940. Oxystyla on Sanibel Island, Florida. Nautilus 53(4):122-123.
- Craig, A.K. 1972. Observations on the arboreal snail Orthalicus floridensis. Quart. J. Florida Acad. Sci. 35(1):15-20.
- Davidson, T. 1965. Tree snails, gems of the Everglades. Nat. Geogr. 127(3):372-387.
- Eisner, T., and E.O. Wilson. 1970. Defensive liquid discharge in Florida tree snails (Liguus fasciatus). Nautilus 84(1):14.
- Layne, J.N. 1974. Land mammals of South Florida. Pp. 386-412 in Environments of South Florida: Past and present. P.J. Gleason (ed.). Miami Geol. Soc. Memoirs 2.
- Little, E., Jr. 1979. Checklist of United States trees. USDA, Forest Service, Agric. Hndbk. 541. 375 pp.
- Long, R.W., and O. Lakela. 1971. A flora of tropical Florida. Univ. Miami Press, Coral Gables. 962 pp.
- Lowry, G.H. 1974. The mammals of Louisiana and its adjacent waters. Louisiana State Univ. Press, Baton Rouge. 565 pp.
- Martin, A.C., H.S. Zim, and A.L. Nelson. 1951. American wildlife and plants: A guide to wildlife food habits. Dover Publications, New York. 500 pp.
- McGinty, P.L. 1936. A canoe trip in the Ten Thousand Islands to collect Liguus. Nautilus 50(1):1-8.
- Mead, A.R. 1961. The giant African snail: A problem in economic malacology. Univ. Chicago Press, Chicago. 257 pp.
- Muma, M.H. 1954. Predators and parasites of the citrus tree snail. Citrus Mag. 16(10):8-9.
- _____. 1967. Scorpions, whip scorpions and wind scorpions of Florida. Arthropods of Florida 4:1-28.
- National Oceanic and Atmospheric Administration. 1979. Climatological data annual summary: Florida 83(13):1-10.
- _____. 1980. Climatological data annual summary: Florida. 84(13):1-10.
- _____. 1981. Climatological data annual summary: Florida. 85(13):1-10.
- Pilsbry, H.A. 1899. American Bulimulidae: North American and Antillean Drymaeus, Leiostracus, Orthalicinae and Amphibulimulinae. Man. Conch. 2nd ser. 12:1-258.
- _____. 1912. A study of the variation and zoogeography of Liguus in Florida. J. Acad. Nat. Sci., Philadelphia, 2nd ser. 15:429-470.
- _____. 1946. Land Mollusca of North American (north of Mexico). Monogr. Acad. Nat. Sci., Philadelphia 3[2(1)]:1-520.
- _____, and C.N. Grimshawe. 1936. Oxystyla undata undata in Florida. Nautilus 50(1):19-20.

- Say, T. 1830. Descriptions of some new terrestrial and fluviatile shells of North America. *New Harmony Dissem.*, Dec. 28.
- Siegal, S. 1976. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., New York. 312 pp.
- Simpson, C.T. 1923. An expedition that failed. *Nautilus* 36(4):109-115.
- Stegmaier, C.E., Jr. 1972. Notes on some Sarcophagidae (Diptera) reared from snails (Mollusca) in Florida. *Florida Entomol.* 55(4):237-242.
- Thompson, F.G. 1980. Proposed technical review draft of the recovery plan for: Stock Island Tree Snail. U.S. Fish Wildl. Serv., unpubl. rept., pp. 1-5.
- Tomlinson, P.B. 1980. Trees native to tropical Florida. Harvard Univ. Printing Ofc., Allston MA. 480 pp.
- Tuskes, P.M. 1981. Population structure and biology of Liguus tree snails on Lignumvitae Key, Florida. *Nautilus* 95(4):162-169.
- Von Martens, E. 1893. Land and freshwater Mollusca. Pp. 177-248 in *Biologia Centrali-Americana*. F.D. Godman and O. Salvin (eds.).
- Voss, R.S. 1976. Observations on the ecology of the Florida tree snail, Liguus fasciatus (Müller). *Nautilus* 90(2):65-69.
- Weems, H.V., Jr., and C.M. Tibbets. 1982. Dusky-handed tailies whip scorpion. Pp. 130-131 in *Rare and Endangered Biota of Florida: Vol. Six, Invertebrates*. R. Franz (vol. ed.), P.C.H. Pritchard (ser. ed.). Univ. Presses Florida, Gainesville. 131 pp.

Contributions to the BULLETIN OF THE FLORIDA STATE MUSEUM, BIOLOGICAL SCIENCES SERIES, may be in any field of biology. Manuscripts dealing with natural history of systematic problems involving the southeastern United States or the New World tropics are solicited especially. Manuscripts should be of medium length—circa 35 to 200 pages (10,500-60,000 words). Examination for suitability is made by an Editorial Board.

The BULLETIN is distributed worldwide through institutional subscriptions and exchanges. It is considered the responsibility of the author to distribute his paper to all interested individuals. To aid in this the author(s) receive(s) 50 copies free, and he(they) may purchase additional separates at cost if ordered when page proof is returned. The author is also responsible for any charges incurred for alterations made by him on galley or page proofs. The Museum will send an invoice to the author for this amount upon completion of publication.

PREPARATION OF MANUSCRIPT

Contributors should consult recent numbers of the BULLETIN for preferred style and format. Highly recommended as a guide is the CBE Style Manual, 3rd Edition, 1972 (American Institute of Biological Sciences, Washington, D.C.).

Manuscripts must be submitted in duplicate and satisfy the following minimal requirements. Please submit duplicate copies of manuscripts. They must be double-spaced throughout, including tables, figure captions, and literature citations. Figure legends and tables should be typed on separate sheets. Also, please submit a copy of the complete text and tables on one or more 5¼" flexible diskettes from (1) IBM or compatible microcomputer with Microsoft WORD; or (2) Apple microcomputer with Applewriter submit document files. If that is not possible, the editors will have such diskettes prepared commercially at author's expense upon acceptance of the manuscript.

All illustrations are referred to as figures. They must comply with the following standards: Photographs should be sharp, with good contrast, and printed on glossy paper. If the background of photographs (especially those of specimens) is not desired, amberlith should be cut out and used to cover the background. Drawings should be made with dense black waterproof ink on quality paper or illustration board. All illustrations should have a cover sheet. All lettering will be medium weight, sans-serif type (e.g. Futura Medium, News Gothic) in cutout, dry transfer, or lettering guide letters. Make allowance so that after reduction no lower case letter will be less than 1 mm high (2 mm is preferred) nor any capital letter greater than 5 mm high. The maximum size for illustrations is 9" x 14" (twice BULLETIN typepage size); illustrations should not be less than typepage width (4½"). With soft lead pencil on the back of each illustration, designate the top and identify each by author's name, manuscript title, and figure number.

All manuscripts not submitted in BULLETIN format will be returned to the author for retyping.

Manuscripts and all editorial matters should be addressed to:

Managing Editor of the BULLETIN
Florida State Museum
University of Florida
Gainesville FL 32611
U.S.A.