BULLETIN

OF THE

FLORIDA STATE MUSEUM

BIOLOGICAL SCIENCES

Volume 14   Number 3

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ON SEA HORSE KEY, FLORIDA

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Gainesville
1969

THE COTTONMOUTH MOCCASIN ON SEA HORSE KEY, FLORIDA

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SYNOPSIS: From 1954 to 1957 the author studied the cottonmouth moccasin (*Agkistrodon piscivorus*) population of the islands near Cedar Key, Levy County, Florida. Sea Horse Key, one of the outer islands, approximately 1 mile long and 7 miles from the mainland, then supported a total population of roughly 600 cottonmouths.

The cottonmouths aggregate under the breeding colonies of cormorants and herons on the outer Cedar Keys and scavenge the fish the birds drop accidentally from their nests. After post-nidal feeding stops in August, they eat birds, rats, and squirrels. An abundant skink is the principal food of young cottonmouths.

The bird rookeries control distribution and food habits of three-fourths of the island's snakes, serving snakes up to 150 meters distant. Activity ranges are remarkably small (males average 0.43 acre, females 0.35 acre). Although the main ridge lacked rookeries, ranges were similar. No evidence of territoriality was found. Snake Key rookeries also support a large population of cottonmouths. Atsena Otie and North Keys have no rookeries and few cottonmouths.

Island snakes den in shallow stump holes and under debris. Frequent warm winter periods make emergency demands on stored fat, and 77 per cent of Sea Horse Key snakes are in danger of starvation during winters with a mean temperature of 16.3°C, compared to 36 per cent of the fatter snakes on Snake Key. The fat bodies of snakes apparently function as reserve food during periods of high temperature. Fat-body weights, length/weight ratios, and feeding behavior suggest that Sea Horse snakes are at a critical survival level. When removed from their winter dens, cottonmouths apparently shun all holes for periods of up to 2 years; a persistant site memory is postulated.

At lowest cloacal temperatures (4.0°C) cottonmouths are passive; they are able to strike at 4.5°C, crawl at 12.5°C, and feed at 14.5°C. Variation in observed rates of heating and cooling suggests some physiological control. Up to 36 per cent of cottonmouths showed aggressive behavior at low temperatures contrasted to 4.1 per cent at high readings (21°C and above).

The major cause of mortality is starvation. Adults have no enemies other than linguatulid parasites and man. Two healthy and apparently genetically eyeless snakes indicate the relative importance of olfaction in the island environment. The ambithermal cottonmouth, with its endogenous biennial sexual cycle, its vagile nature, and its keen olfaction seems well adapted to preempt the island niche of a terrestrial carnivore-scavenger.

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INTRODUCTION

The cottonmouth moccasin, *Agkistrodon piscivorus,* is the domi-
nant terrestrial vertebrate on two islands of the Cedar Keys, Levy
County, Florida (Fig. 1). The present study, made from 1954 to 1957,
sought to discover factors responsible for the high population density
on Sea Horse Key, which offers an environment markedly different
from the species' usual mainland habitats (Wharton, 1958).

This island, lying on an immense sand flat 5 to 7 miles offshore,
is an old, high, sand dune covered with a modified climax forest. Its
lee shores support mostly black mangrove (*Avicennia nitida*) (Fig.
2) with some white mangrove (*Laguncularia racemosa*) and red man-
grove (*Rhizophora mangle*). I have reported elsewhere (1966) on
reproduction and growth of the cottonmouths of the island. The
present study deals principally with the behavior of the snakes in
their adaption to this unusual and seemingly hostile environment,
almost entirely without fresh water.

Arriving by drift or storm, the cottonmouths have adapted sur-
prisingly well to these offshore islands. Some protection is afforded
the snakes by the fact that the three outermost islands, North, Snake,
and Sea Horse, lie within the Cedar Keys National Wildlife Refuge,
established to protect breeding colonies of birds, primarily white ibis
(*Guara alba*), American egret (*Casmerodius albus*), snowy egret
(*Leucophoyx thula*) and several heron species. The islands also
afford protected nesting sites for cormorants (*Phalacrocorax auritus*),
osprey (*Pandion haliaetus*) and bald eagle (*Haliaetus leucocephalus*).
Cormorants and larger herons are especially important provisioners
of the cottonmouth population.

It is generally conceded that on the mainland cottonmouths are
largely aquatic or semi-aquatic. On the Cedar Keys islands they lead
a terrestrial life, seldom, if ever, venturing into the surrounding salt
water. I questioned 14 long term residents and many fishermen at
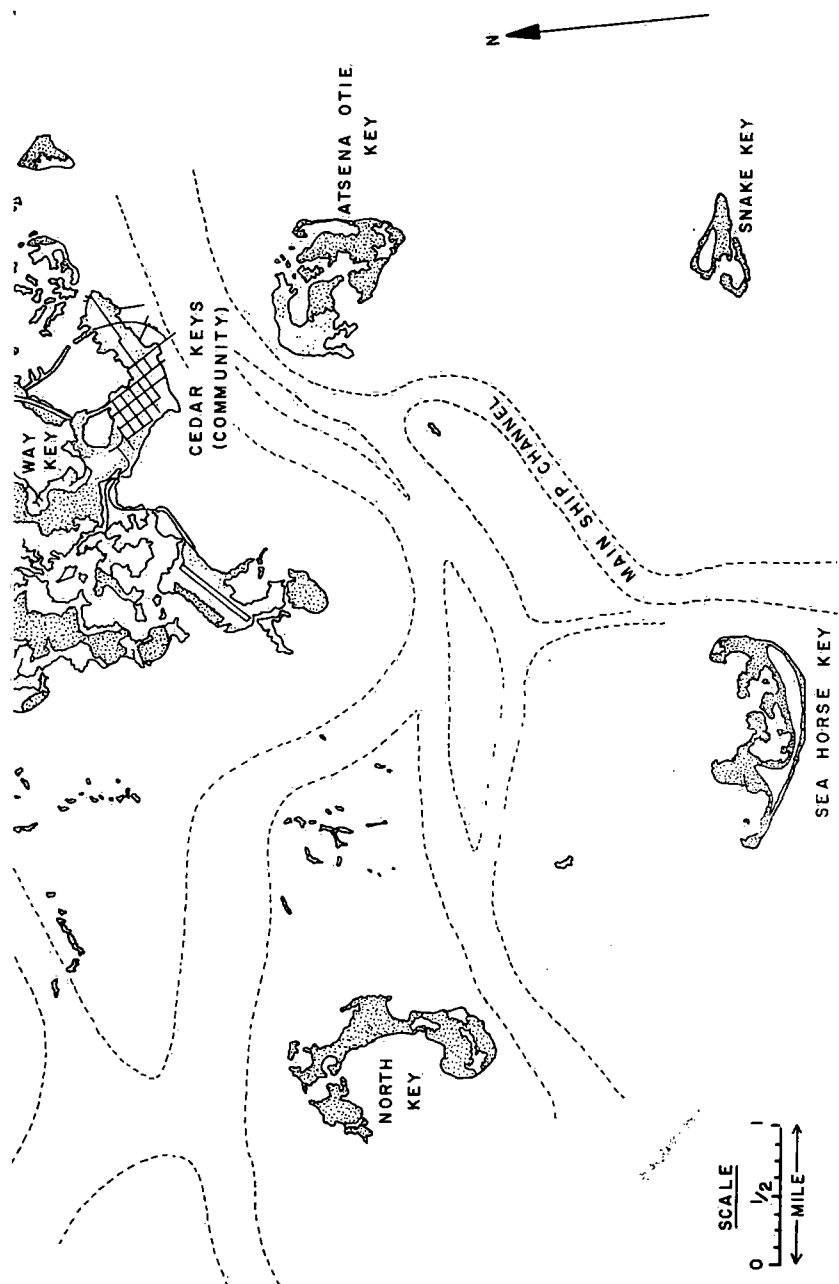Cedar Keys; only one, James Richburg, saw a snake of this species

FIGURE 1. The major islands of the Cedar Keys. Snake, Sea Horse, and North Keys comprise the Cedar Keys National Wildlife Refuge. Dashed lines indicate main ship channels.
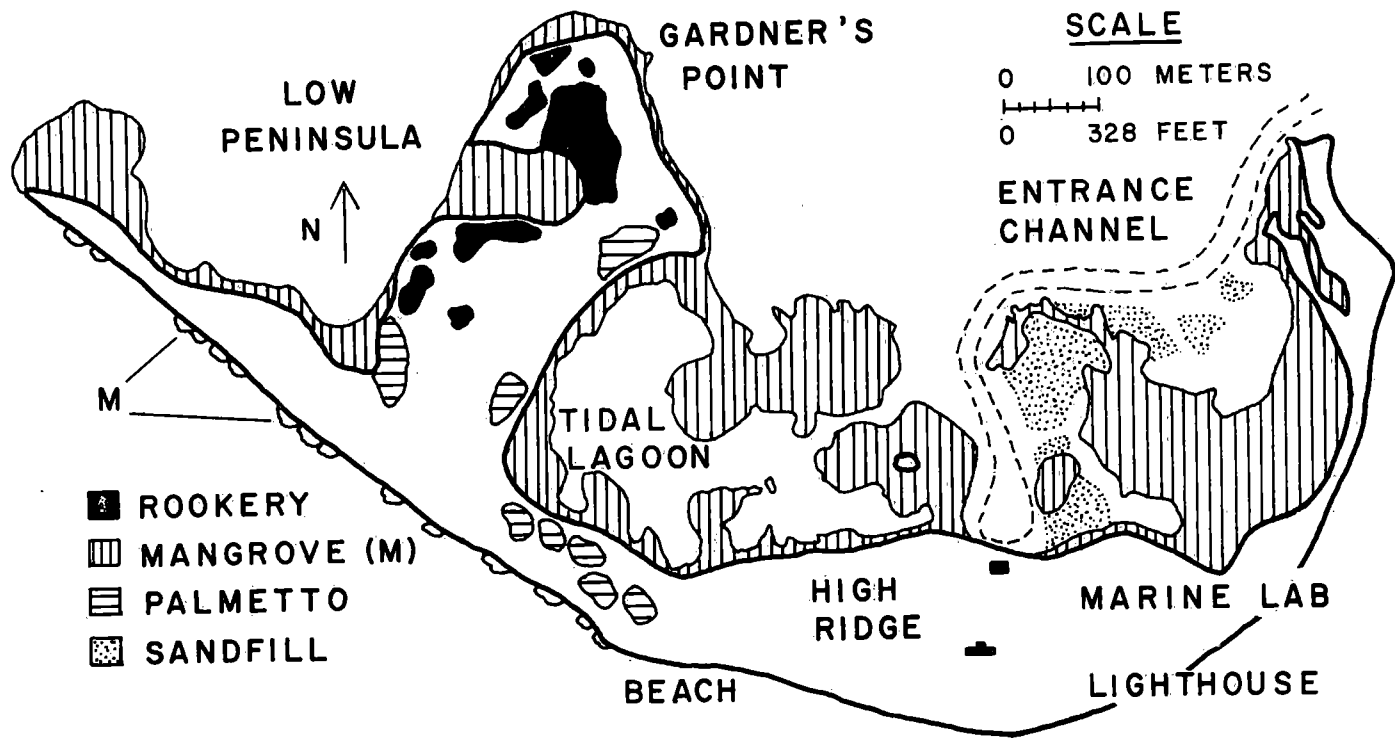
FIGURE 2. Maps of Sea Horse Key showing the extent of rookeries, mangroves, and saw palmetto (*Serenoa repens*).

swimming (at Snake Key). Kirk Strawn, who studied marine life on the flats around Sea Horse Key, never saw a cottonmouth in salt water. I worked the shore of Sea Horse Key many times on foot and by boat, both day and night, and I never saw a cottonmouth swimming in the salt water other than when they were provoked by handling. Nor have I seen any signs of snakes moving to or from the beach. Sometimes cottonmouths coil at the strandline; presence of cover, beach-scavenging rats, or an activity range adjoining the beach may explain these instances. I found no instance of their feeding on fish that could not be attributed to the nesting, feeding, or roosting of birds. That these snakes do not directly exploit the plentiful fish life in the shallow, calm waters of Sea Horse Key is difficult to reconcile with the habits of the cottonmouth on the mainland.

Only a few notes have been published on marine island cottonmouths. Sass (1926) thought that cottonmouths on the Isle of Palms, South Carolina, rarely, if ever, fed on marine fishes. Wood (1954) noted mass migration from Virginia's barrier islands to the mainland. Carr (1936) and Wharton (1958, 1960, 1966) have made the only previous reports dealing directly with the Cedar Keys cottonmouths.

MATERIALS AND METHODS

Most of the cottonmouths occupied the island's western end. The thick vegetation made it necessary to cut trails through this area, and 206 trail stations were designated with stamped aluminum tags nailed on trees at 25 meter intervals (Fig. 3).

Snakes were approached carefully and restrained gently by a leather noose around the neck. By the use of subcaudal scale-clipping, (Blanchard and Finster, 1933), 402 cottonmouths were marked individually. These afforded 510 recaptures, counting dissections, and a total of 545 individuals were handled. Data recorded on

a keysort card for each capture included length, weight, cloacal tem-
perature, and heart rate (if the specimen was quiet). Nearby soil,
air, and leaf mold temperatures, humidity, body position, behavior
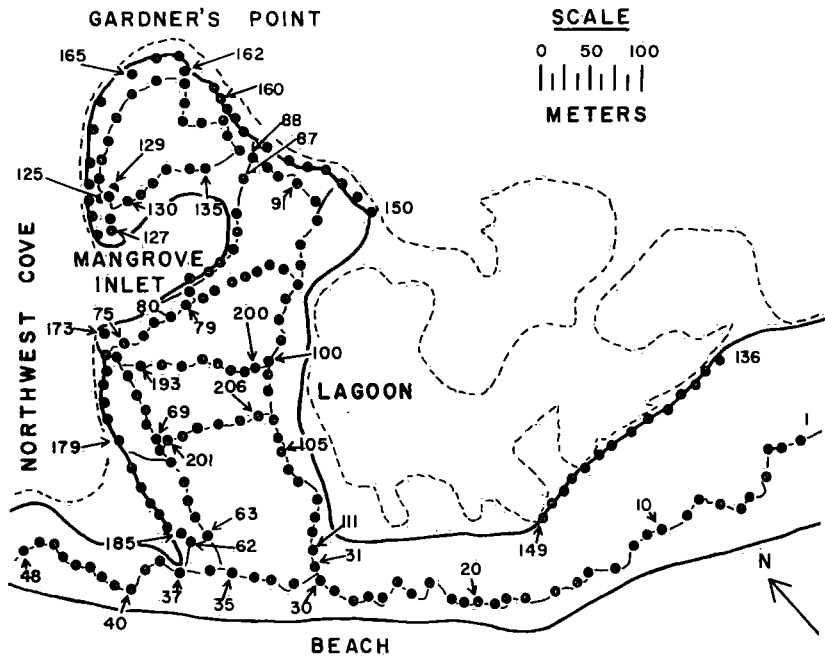
FIGURE 3. Sea Horse Key trail system. Points are stations 25 meters apart.
Stations 1—30, high ridge of island. Dashed line, edge of mangroves.

(activity in which the snake was engaged), and demeanor before
noosing were also noted.

For estimating the size of cottonmouths found dead in the field the
largest vertebrae and ribs were compared with a skeletal series of 33
specimens of known size and weight.

Cloacal temperatures were taken with Schultheis rectal thermom-
eter; soil and air temperatures with either the Schultheis instrument
or a standard mercury thermometer. A maximum-minimum ther-
mometer was kept at ground level in the forest of the central ridge
throughout the study. Temperature and humidity in den cavities
and in adjacent microclimates were taken with a battery-operated
Aminco instrument with a temperature-humidity probe.

AGGREGATION

While records of snake aggregations in the literature apply chiefly

to denning such as the record by Noble and Clausen (1936), or to unusual concentrations of snakes caused by factors such as rising water (Slevin, 1950), one of the most spectacular and seldom documented aggregations of vertebrate life is that brought about by the odorous and noisy bird rookery. With the fragility of the nests of many wading birds and the frequency of dropped eggs, fish, and fallen nestlings, a variety of scavengers and predators find bird colonies a happy hunting ground. Host (1955) reports a gathering of alligators near a large rookery of herons and ibises in the Everglades. Nor is this food source ignored by mammals, including man. I have a report that over 20 jaguars aggregated under a great jabiru stork rookery in central South America in 1955. Austin and Kuroda (1953) describe the remarkable instance of humans subsisting on salmon dropped by cormorants and herons nesting around the Suruga Shrine in Aomori Prefecture, Japan.

The cottonmouth, by virtue of its adaptability to almost any available food source, dead or alive, becomes a resourceful opportunist when bird rookeries are nearby. Here it scavenges beneath the nest trees, apparently attracted by the odor of the excreta and the fish regurgitated by annoyed parent birds or dropped by clumsy nestlings.

Chapman (1908) was one of the first to note what may have been aggregating cottonmouths under a nesting colony of anhingas and herons near St. Lucia, Florida. In the early 1920's, Sass (1926), on the Isle of Palms near Charleston, South Carolina, saw scores of cottonmouths gathered under a great blue heron "village" apparently attracted by dropped fish. Host (1955) noted many cottonmouths beneath a large rookery on the edge of Lake Okeechobee, Florida, and assumed that they were after the eggs and young. Carr (1936) was the first to report aggregations of cottonmouths on the islands of the Cedar Keys group, where he found 11 of 13 captured snakes coiled beneath nest trees. In May 1942 Mr. and Mrs. Allen D. Cruickshank (pers. comm.), encountered a concentration of cottonmouths and banded water snakes, *Natrix fasciata,* under a heron and glossy ibis rookery at King's Bar Reef, Lake Okeechobee, Florida, where 3 to 10 cottonmouths swam in front of the blind constantly during the week they were there. This couple also report seeing from 8 to 12 of these snakes on 20 April 1942 in the vicinity of anhinga and egret nests near the present Anhinga Trail in Everglades National Park, Dade County, Florida. W. T. Neill (pers. comm.) found cottonmouths very common under nests of about 95 little blue herons at McKinney's Mill, a small bonnet-choked cypress pond in Emanuel County, Georgia. Neill had noted that cottonmouths were not nor-

mally abundant there, and believes they came from other nearby
ponds, drawn by the odor of the fish and excreta. John N. Hamlet
(pers. comm.) saw many large cottonmouths in an active anhinga
and heron rookery near Pritchardville, South Carolina, from 1951 to
1953.

On the Florida mainland cottonmouths occur most commonly in
shallow ponds, marshes, and swamps. When water levels drop the
life concentrated in them provides a considerable food supply for the
cottonmouths. Allen and Swindell (1948) report cottonmouth ag-
gregations at pools left in drying marshes. Henry P. Bennett (pers.
comm.) encountered cottonmouth concentrations in 1955 in drying
sloughs and ponds in the Corkscrew Swamp sanctuary, Collier
County, Florida. When such ponds dry completely the cottonmouths
apparently seek out deeper ponds or subsist on dry land until the
water table rises again.

Walter Auffenberg (pers. comm.) collected reptiles from 1949 to
1951 between DeLand and New Smyrna, Volusia County, Florida.
He noted that when water levels fell, aggregations of cottonmouths
fed ravenously on the abundant life concentrated in the remaining
pools of roadside ditches, consuming fish, frogs, rodents, and reptiles.
Sometimes they ingested inanimate objects as well, for the stomachs
of two specimens dissected after death were packed with mud and
some with sticks up to 12 mm in diameter and 75 mm long. Burkett
(1966) remarks on the ingestion of plant material by midwestern
cottonmouths.

Sometimes cottonmouths move considerable distances. Hamilton
and Pollack (1955) record a cottonmouth killed 1 mile from the
nearest water at Fort Benning, Georgia. Probably such overland
journeys are aided by a keen olfactory sense. Noble and Clausen
(1936) have shown that the sense of smell is very important in some
snakes. Fish odor apparently attracts cottonmouths, for Neill (pers.
comm.) noted cottonmouths drawn to a fish-cleaning platform 50 m
from a lakeshore.

I conducted several tests to verify the cottonmouths' scenting
ability on Sea Horse Key. A crushed sardine and oil trail was ineffec-
tive in February. In early March 1967 near Gardner's Point I placed
a known number of pieces of cut mullet at points where no snakes
were present within a radius of 30 m. The next morning three pieces
were missing and I found two snakes in dense cover about 20 m
away; one, a male, contained one piece of mullet; the other, a female,
two. At another locality I caught two snakes, including a 356-mm
juvenile, in a small funnel trap baited with mullet.

O 1955

◑ 1956

● 1957

□ 1955 - 56

▨ 1956 - 57
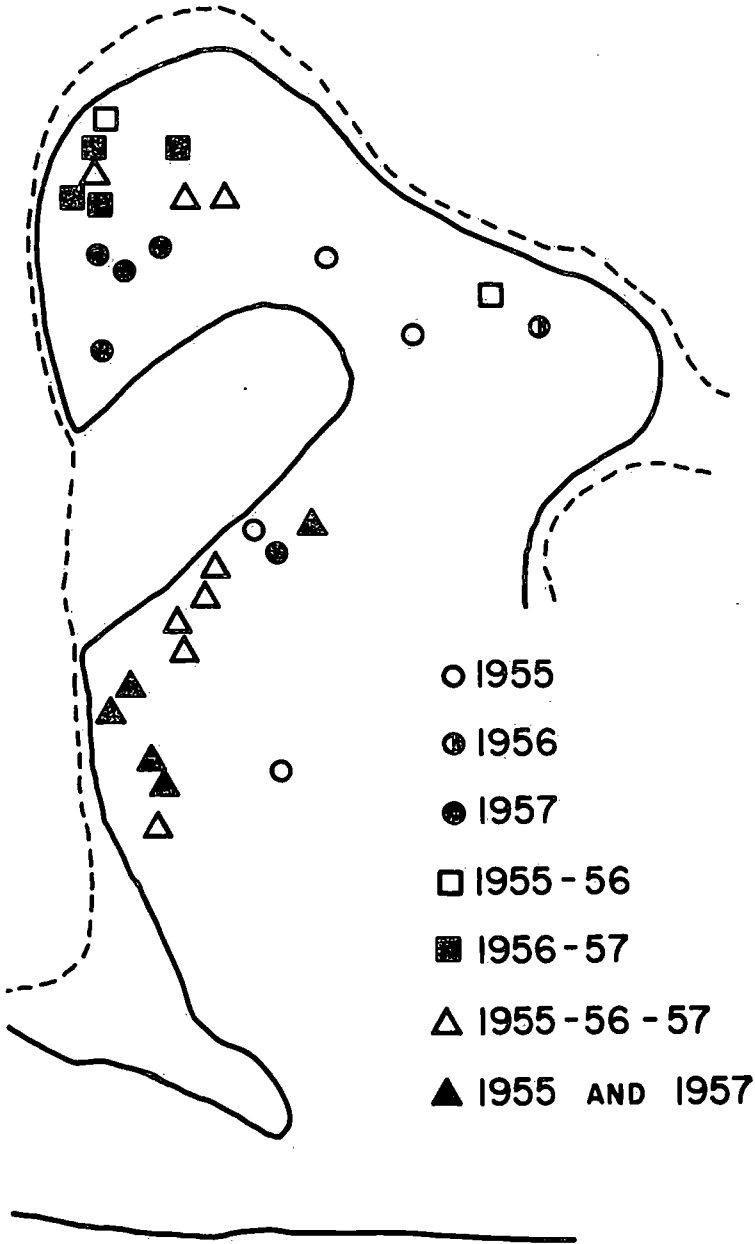
△ 1955 - 56 - 57

▲ 1955 AND 1957

FIGURE 4. Location of nest trees on Sea Horse Key used by birds (principally cormorants). Symbols show years occupied.

In early April I placed five piles of 10 chunks of mullet on the ground at 2100 between Stations 95 and 115 and visited them repeatedly until 2300. A light breeze blew from the east. Shortly after 2100 near Station 115, a snake was seen to eat one piece and crawl away; another snake was discovered swallowing one piece 30 minutes later, and a third snake ate two pieces of fish 1 hour and 20 minutes later. As the last two individuals were spattered with avian excreta, they were presumably drawn a minimum distance of 35 m from the nearest nest tree. It is puzzling that the snakes ate only one or two pieces of cut fish each instead of gorging themselves as they might have.

Effect of Rookeries on
Movement, Abundance, and Distribution

Spring aggregations of cottonmouths beneath nest trees are comprised of individuals arriving from varying distances (Fig. 4). Thirty snakes captured during the previous non-nesting period, 1 September- 28 February, and found beneath active nest trees had moved an average of 62 m. Only two had presumably arrived from distances exceeding 150 m., only five from over 100 m. During the rookery season 16 snakes did not move to a nest tree; the closest point of their activity ranges to an active nest tree averaged 139 m. These data suggest that Sea Horse Key cottonmouths are seldom lured by scent to a nest tree further than 150 m.

Table 1 summarizes the distances between points of capture for 483 snakes and large annually active nest trees (six or more nests per tree). Except for two osprey nests, all trees were cormorant rookeries. Two-thirds of the cottonmouths taken in the nesting season were found within 32 m of an active nest tree; and evidently more than half of the snakes remain within 32 m of these trees during fall and winter months.

Table 1. Numbers of Cottonmouths Recaptured at Varying Distances from Active Nest Trees During Nesting and Non-nesting Seasons

Distance from nest tree (in meters)	Nesting Season April 1-August 31	Non-Nesting season Sept. 1-March 31
0- 16	42	56
17- 32	54	147
32-150	42	142
TOTAL	138	345

Of 402 original captures, 234 snakes were taken on the low peninsula during the nesting season (1 March-31 August). Of these 121
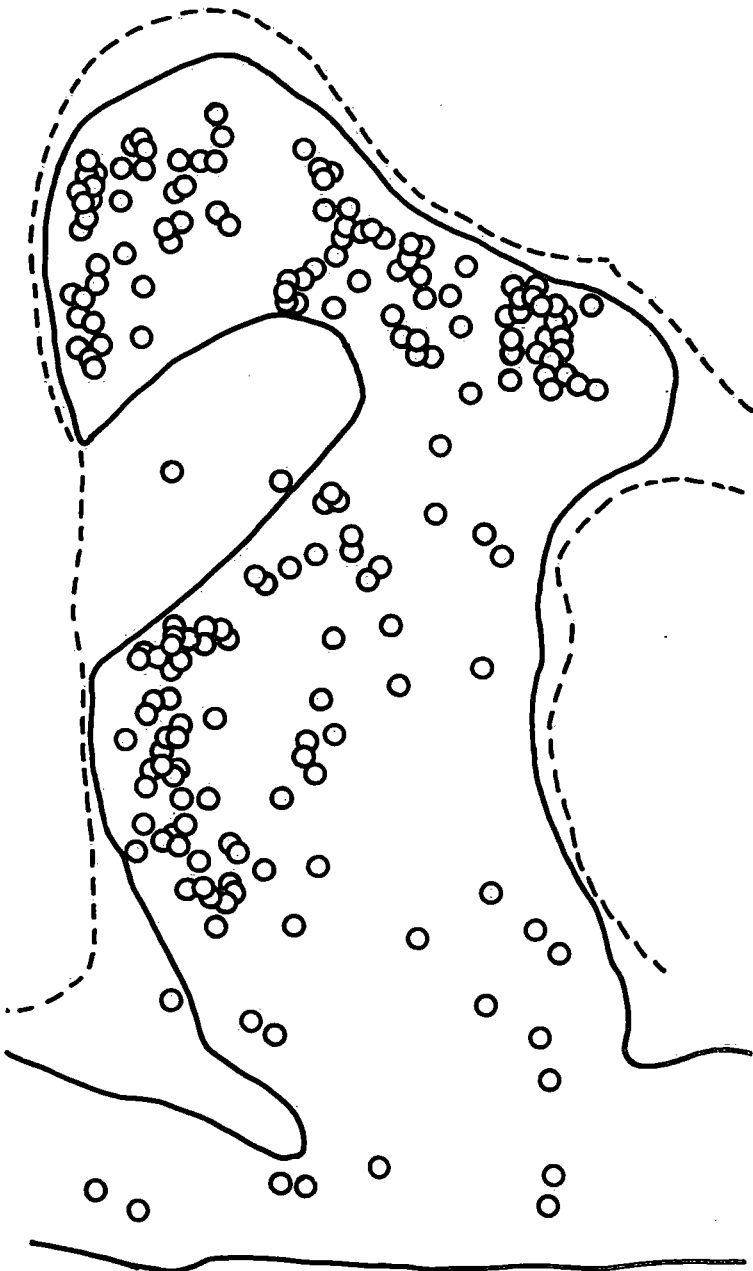
FIGURE 5. Midpoints of cottonmouth activity ranges on the low peninsula of Sea Horse Key.

were taken under, or had been under (bore avian excreta) active nests; 172 (73.5%) captures were within 32 m of the nest trees.

The midpoints of snake activity ranges (Fig. 5) plotted on a map of the low peninsula show that the bulk of the population is concentrated between Stations 68 and 77 on the west side of the peninsula, and from Station 92 west around the entire Gardner's Point area. A 60-m circle (mean distance moved) drawn around each active nest tree excludes only 15 per cent of range midpoints; 8 per cent of the range midpoints are more than 100 m from active nest trees. Evidently most individuals live within the mean distance at which the majority are attracted to nest trees.

Thus the location of rookery trees appears to control the distribution and food habits of almost three-fourths of the Sea Horse Key cottonmouths. With the snakes so dependent on the birds, obviously their nesting habits must effect the welfare of the cottonmouth population.

Well developed olfaction is one facet of a generalized behavior pattern enabling cottonmouths to adapt to the environment of Sea Horse Key. Were it not for their ability to locate the principle food sources of the island from a considerable distance, these snakes would doubtless be far less abundant, and the density (22.27 per acre) would more nearly approach that of the main ridge (1.85 per acre). On the ridge the reptiles apparently feed chiefly on rodents.

During hot summer days cottonmouths are seldom found in the open rookery areas. At these times they remain tightly coiled in the nearest heavy cover, crawling to the nest trees at dusk. Of 232 night captures, 141 were taken under active nest trees, 47 in 1955, 42 in 1956, 52 in 1957, distributed monthly as follows: March 2, April 26, May 43, June 55, July 2. This coincides roughly with the availability of dropped fish.

I have watched 17 different snakes in the act of feeding on fish or fish remains. During April 1955 and May 1956 snakes aggregated under the nest trees about 15 minutes after dark, gliding about, searching and feeding. I have seen their reactions to dropped fish several times. A falling fish instantly alerts them. With the head raised about 125 mm they glide quickly near to where the fish landed, then lower the head and try to locate it, apparently by use of the tongue. The snakes generally find and swallow a fish within 5 to 10 minutes after it falls.

While feeding beneath nest trees cottonmouths are quite active and easily disturbed by the flashlight beam, moving quickly for the nearest cover. By working carefully it is possible to move among a

feeding aggregation, and I have captured as many as 9 individuals beneath a single tree. When beneath active nest trees the snakes are quick to investigate any commotion in the leaves. Sometimes they may be lured by throwing sticks or other objects to simulate falling fish. I once tapped my catch stick on the ground and a snake came forward with upraised head and struck at it.

Young cormorants occasionally fall to the ground. Fallen fledglings I placed near searching cottonmouths were never eaten, though I once found a snake that had swallowed a cormorant leg and another that had ingested a wing, both probably scavenged from a decaying carcass. The remains of many well feathered nestlings are found on the ground where it is apparently difficult or impossible for parent cormorants to feed their young. Carr (1936) reports a portion of an eggshell in a cottonmouth on Snake Key. It is extremely rare to find an unbroken egg on the ground. Fallen nestlings and eggs are undoubtedly insignificant food sources.

The small size of some dropped fish does not deter feeding cottonmouths. Carr (1936) found several tiny fish in a sizable cottonmouth from Snake Key. I once saw a 1422-mm male swallow two fish 50 mm long.

Small cottonmouths may attempt to swallow fish heavier than themselves. I found a 711-mm snake weighing 269 grams attempting to swallow a 305-mm, 354-gram serranid dropped by an osprey. Sometimes parts of fish skeletons are eaten. One small cottonmouth had about 25 mm of the skull of a catfish, *Bagre marinus*, protruding from its body about 100 mm behind the head. A 559-mm male was seen eating the skull of another fish.

Large cottonmouths sometimes eat small and unusual prey. Carr (1936) reported that a 1473-mm specimen from Snake Key had eaten a skink. A 1016-mm specimen from Snake Key that I took had eaten a caterpillar and a 1295-mm snake from North Key had eaten a terrestrial snail about 3 inches long. Burkett (1966) notes that cottonmouths feed on both insects and gastropods. Cottonmouths are occasionally ophiophagous. In the fall of 1955 I saw two water snakes (*Natrix sipedon* ssp.) at Station 160, at Gardner's Point and caught one; a few days later I took a cottonmouth containing a *Natrix* from the same area.

Cottonmouths may compete for food under nest trees. Two snakes were once found engaged in a violent tug-of-war over a 125-mm dogfish, (*Opsanus* sp.). On another occasion I found two large male snakes, both over 1270 mm, struggling over a fledgling crow.

Small cottonmouths are uncommon beneath nest trees and no

newborn snakes were found there. Of 101 original captures taken
beneath these trees, only 4 snakes were under 610 mm, and all con-
tained fish or were feeding when captured; 22 others ranged between
610 and 914 mm, 64 between 914 and 1219 mm, and 11 above 1219
mm.

I think that undisturbed snakes must return to the same nest trees
repeatedly, but my experience suggests that snakes may leave tempo-
rarily the vicinity of capture, very likely because of the shock of the
experience. Both males and females sometimes make a "shock" or
escape run following release. In 9 instances this straight line escape
behavior of large male snakes carried them out into salt water for
about 30 m before each turned back to shore; I never saw a female
enter the sea. On 6 June I captured 4 snakes at Station 92; on the
following night I found 5 different individuals there. I believe that
my handling of the previous night caused the first 4 snakes to leave the
immediate area of the tree

Normally snakes wait for darkness to move into exposed places
under isolated nest trees, although on hot July days they begin to
gather beneath egret and night heron nests in dense canopy by 1700.
Occasionally they feed under nests in the daytime. On 5 April I
watched a 1041-mm female crawl several meters to a dropped fish at
1400. During daylight hours I once slid a white 6-foot carpenter's
rule through the leaves to within 250 mm of a large male snake, which
struck it viciously, perhaps a feeding reaction.

After young cormorants leave the nest tree, they frequently return
to it to be fed by the parents. In late July I took 8 snakes scavenging
at night at Station 120 where young cormorants still perched in their
nest trees. Later (mid-July to early September), these cormorants
leave their nest tree and congregate in certain roost trees. The
snakes seem to leave the nest tree as soon as the cormorants depart.
On 27 June I noted snakes beneath the Station 91 cormorant nest tree
(still occupied by young birds), whereas the Station 86 nest tree had
neither birds or snakes. By 19 July only a few snakes remained in
the area of the nest trees, but I caught two under new roosting trees.

While ospreys are not plentiful enough on Sea Horse Key to be
principal provisioners for snakes living there, they are important as
they start carrying fish before other birds begin nesting. On Snake
Key 24 February, I collected a 350-mm, 681-g mullet one of a pair of
ospreys dropped. Courtship maneuvers of ospreys often involve
carrying fish, which are sometimes dropped from the feeding perch.
One night a perched osprey dropped a 681-g serranid at Station
110, indicating they may go to roost holding a fish. Most osprey-

caught fish were either trout, *Cynoscion* sp., serranids, or mullet, *Mugil* sp. and large enough for a substantial meal. On Snake Key, as on Sea Horse Key, cormorants provide most of the food. Herons and egrets are minor contributors. Ibises, because they feed on small crabs and crayfish, probably contribute little. In 1966 and 1968 a large rookery of white ibis occupied most of the main ridge of Sea Horse, but no increase of cottonmouths was noted beneath the nests while at the same time snakes were markedly numerous beneath small rookeries of the brown pelican, *Pelecanus occidentalis,* a species that had not nested on the island during the initial study.

To ascertain how long individual snakes attended nest trees in consecutive years, 218 captures from Sea Horse Key were plotted by year, month, and capture point. Of 3 individuals captured during 3 consecutive feeding seasons, 1 was taken at the same tree each year and 2 had moved to other trees. Of 15 snakes captured in 2 successive feeding seasons, 7 returned to the same nest trees. Of the other 8, 3 left probably because nesting stopped in the old tree, 4 changed to other nest trees (about 50 m away) even though the original tree was still active, and 1 moved 190 m for no apparent reason.

Station 76 functioned as an active nest tree for 3 consecutive years. Four snakes taken there in the winter of 1954-55 were found there again in the summer of 1955, 1 remained until the winter of 1955-56, and 2 until the summer of 1956. Of 3 more taken initially in the summer of 1955, 3 remained through the following winter, 2 persisted until the summer of 1956, and 1 stayed for the winter of 1956-57. During the same 3 years 16 snakes arrived from other nest trees. The small size of activity ranges seems to preclude a continuous nomadic wandering from tree to tree, although the cottonmouths usually move widely enough to include several active nest trees within their activity ranges.

I conclude that while some snakes may remain at or near a nest tree for 3 consecutive years, the bulk of the population seems divided between those individuals that remain about 2 years at a nest tree and those that move to another site. If disturbance by crows and ospreys should make cormorants regurgitate heavily in a certain area, or if younger birds drop fish more often in certain trees, snakes might be drawn by scent from one nest tree to another. Also a snake on its escape run after the traumatic experience of being handled may approach within smelling range of a different rookery tree.

Fish dropped by birds provide a continuous source of food through the warmer months when reptile metabolism is highest. I believe

the very small number of cottonmouths I encountered on several trips to both Atsena Otie and North Keys can be explained by the absence of large rookeries. Rats and the few fish dropped by the 6 or 8 pairs of ospreys seem to constitute the only food for the cottonmouths on Atsena Otie.

As the welfare of most cottonmouths on Sea Horse and Snake Keys is dependent on the rookeries, the snake population has undoubtedly fluctuated over the years, along with the nesting bird populations. The interrelationship is not entirely one-sided. The legend that the islands swarm with venomous snakes normally protects the rookeries from invasion by man. The presence of snakes near nest trees may also discourage the roof rats that might otherwise prey upon the eggs and nestlings. In 1958, unfortunately, an estimated 400 snakes were removed for venom research at the University of Florida Medical School.

Activity Range and Movements

As cottonmouths on the Florida mainland are chiefly found in aquatic habitats where their normal sphere of activity is influenced by a body of fresh water, it is interesting to examine the movements of cottonmouths in the terrestrial, insular surroundings of Sea Horse Key. Whether they wander at random or favor a circumscribed area has an important bearing on the ability of this limited environment to support a large number of reptiles. Activity range and movement was studied by plotting points where each snake was captured. Provided they were captured more than twice, the area enclosed by lines connecting these points is regarded as an activity range as defined by Carpenter (1952).

The activity ranges established in this study are based on marked and recaptured snakes. Individuals were marked and released at the point of capture. Of these 107 were captured 3 or more times, providing usable (three-dimensional) data. Six snakes were taken 5 to 6 times each, six 7 times, and two 8 times. The mean number of captures, including the initial capture, was 3.8 per snake, and the mean elapsed time between initial capture and the last recapture for each of 107 snakes was 18.6 months. Thirty-five snakes were taken 2 years or more after the initial capture, and one was retaken after 39 months.

Capture-points were plotted on scale maps of the island using compass bearings from the nearest station and station to snake distances. Straight lines connecting the outermost points of capture

were then drawn on the map. The areas of these triangles and poly-gons were measured in acres with a planimeter.

Activity ranges for Sea Horse Key cottonmouths vary from less than 0.11 acre to more than 3 acres. Males seem to have slightly larger ranges than females (M 31 ♂ ♂ = 0.43 acre, M 58 ♀ ♀ = 0.35 acre).

Over 18 per cent (15 ♀ ♀, 5 ♂ ♂) have activity range of less than 0.11 acre. With two exceptions these captures spanned a 7 to 33-month period. Four snakes remained in almost the identical spot for well over 2 years. Small activity ranges were often associated with the presence of nearby winter dens and food sources; half of 20 snakes with limited range lived very near both a den and a food source (usually a rookery tree). Others were reasonably near a den and about 50 meters from a possible food source. Only one snake was not near a den or a food source.

In 16.8% (n = 18) the activity range is greater than one acre; 16 of these were excluded from the calculation of mean range, for most of these longer movements could be accounted for by travels, pre-sumably to wintering areas. Six of the ranges were greatly extended by travel to large palmetto patches, while five of these movements were by snakes that wintered on the wind-shielded east side of the low peninsula with its thicker vegetation. One large male was cap-tured 2 successive summers at the nest tree of Station 76; each year it traveled 295 meters to a wintering area near Station 34. Three other large activity ranges can be explained by the abandonment of Station 92 as a nesting site. Any cessation of nesting at a given site may also cause permanent changes of range.

An example of the complete desertion of a rookery and its effect on the cottonmouths is afforded by the area near Station 36. John D. Kilby (pers. comm.) recalls that around 1934 a large rookery of white wading birds occupied this vicinity. In 1954 the cherry-laurel and bay trees contained old nests probably used for the last time in 1953. During the 3 years following 1954 snakes became progressively less numerous in the vicinity; seven emigrations were noted. It seems reasonable to suppose that the abandonment of the rookery caused these snakes to leave. Most evidently migrated to active nest trees elsewhere; several skeletons attested the fact that some died. The number of individuals remaining approximated that of the normal ridge population where no birds nest.

As the main ridge supports far fewer snakes than the rookery-bearing peninsula, the size of the activity ranges in both habitats might be compared. Only two snakes from the main ridge were

captured three times; one had a range of 0.40 acre, the other 0.11 acre. Ten additional snakes from the main ridge were captured only twice. By measuring the distance between the capture points of
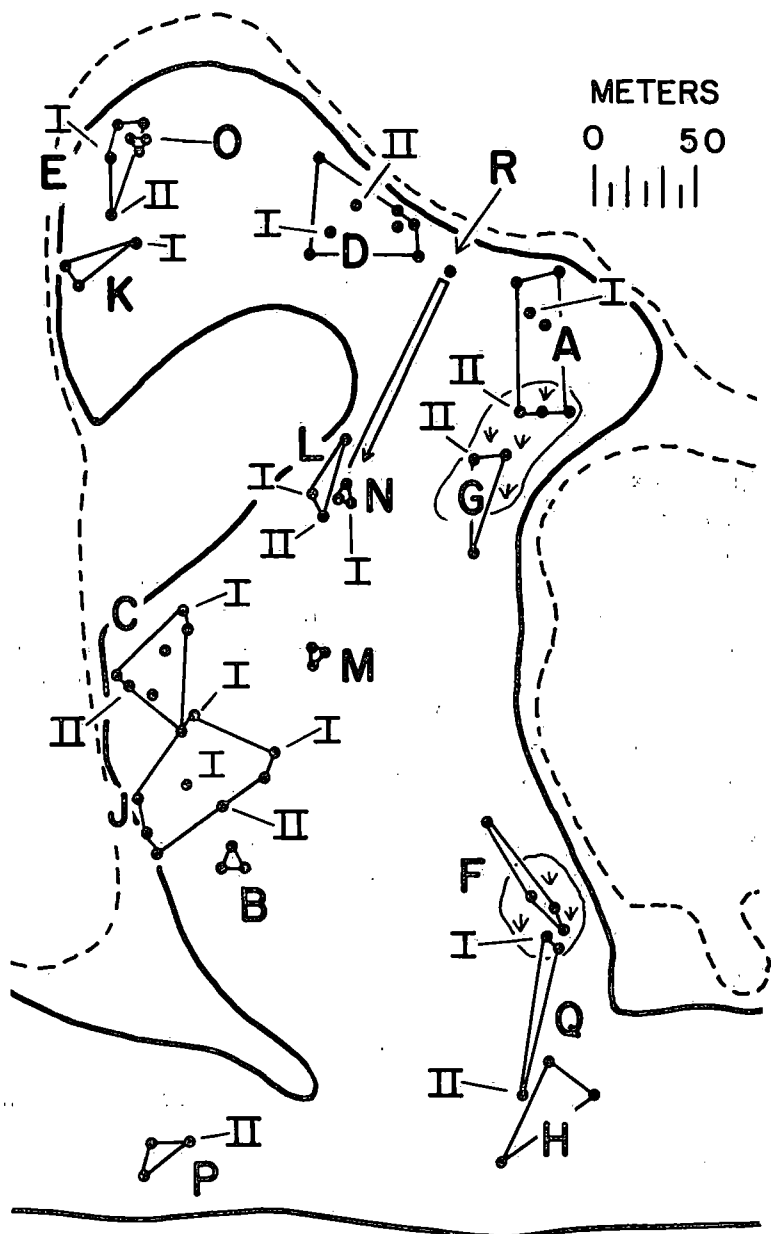
these and a sample of 33 from the peninsula, rough comparisons can be made. The mean distance between capture points for the ridge snakes was 60 m; the peninsular snakes, 71 m. The average number of months covered by the ridge captures was 9.8; for the peninsular snakes, 12.8. If one may draw a conclusion from only 12 captures, the ridge-inhabiting snakes apparently have activity ranges of approximately the same area as those of snakes in the low peninsula.

Figure 6 plots the activity ranges of 16 cottonmouths on Sea Horse Key and shows their proximity to active nest trees, dens, and wintering areas such as saw palmetto patches. The activity ranges B, M, N, and O, are noteworthy for their extremely small size; the snakes apparently remained in a tiny area for nearly 3 years. The activity range of N shows initial escape behavior to point R following capture and exact homing return, a common occurrence among large male snakes. Specimen A illustrates usual behavior; in February 1955 this snake was taken in a den, but spent the next 2 winters in the Palmetto patch at Station 95; in the summer of 1956 it was taken under a nesting tree at Station 92, and it returned to this vicinity in the spring of 1957 though the tree was inactive. Specimens G and F wintered in nearby palmetto patches. Snake Q wintered in the deep leaves about several hickory trees at Station 32. One of these trees formerly had an osprey nest, but it was not in use, and the snake then journeyed to the active osprey nest at Station 107, where it was taken twice.

As stated above, movement to a wintering area greatly increases areal range. Snake 121 fed in the area between Stations 88 and 115 but wintered in the palmettos at Station 95, a movement of 160 meters. Snake 269 wintered in 1955 and 1958 at Station 95, then moved 180 meters to feed at the nest trees of Station 76. Snake 323, originally captured at Station 92, apparently traveled to winter in the palmettos at Station 107, a distance of 300 meters.

FIGURE 6. Activity ranges of 16 cottonmouths on the low peninsula of Sea Horse Key. I, captures under active nest trees; II, captures at or near dens or wintering areas. Each point indicates a single capture. The data below are arranged in the following sequence: Letter designating home range, snake number, sex, activity range in acres (in parenthesis), and number of months over which range was determined. A 26 ♀ (0.66) 25; B 42 ♀ (0.11) 34; C 28 ♀ (0.55) 27; D 261 ♀ (0.66) 7; E 171 ♀ (0.22) 19; F 17 ♂ (0.22) 25; G 280 ♀ (0.24) 27; H 78 ♀ (0.40) 22; J 8 ♂ (0.77) 18; K 227 ♀ (0.15) 29; L 212 ♀ (0.16) 30; M 135 ♀ (0.10) 13; N 293 ♂ (0.11) 10; O 234 ♀ (0.11) 29; P 76 ♂ (0.11) 27; Q 87 ♀ (0.22) 19; Point R is discussed in the text.

Six snakes showed remarkably long movements, which I can not explain. A 1321-mm male, number 50, traveled 320 meters from Station 103 to Station 120 in 27 months. A 635-mm female, number 161, traveled 380 meters in 6 months. Female 270 traveled 450 meters from Station 34 to Station 124 across (or around) the mangrove inlet, and female 332 in 4 months traveled 498 meters from Station 32 to Station 116. Female 237 is unique in ranging for at least 8 months on one side of the mangrove inlet at Station 129, then crossing or circumnavigating the mangroves to establish a new range on the other side.

More remarkably a 1448-mm male, number 238, not only ventured from Gardner's Point to the vicinity of the laboratory on the main ridge, but did it twice, perhaps illustrating a homing tendency. First captured in October 1955 at Station 125, it was taken 12 months later by Doyle Folks at the boat landing; 830 m distant. In July 1957, 11 months later, the snake was retaken 60 m from its original point of capture 2 years before. In February 1958 I was astounded to encounter this snake again coiled near the dock, having in 8 months made its way back 732 m to the vicinity of the laboratory.

A large bi-directional snake trap with drift fences 2 feet high was installed across the entire island from shore to shore at Station 16. No appreciable movement of snakes was noted, for the trap apparently took only those individuals within whose activity range it was located.

Klauber (1956) reviewed marking and recapture studies on crotalid snakes. Fitch (1949) concluded that the Pacific rattlesnake, *Crotalus viridis oreganus*, shows no evidence of a home base and that the ranges of males might be as large as nearly 30 acres, females 16 acres. Fitch (1960) calculated the home range for *Agkistrodon mokeson* males to be 24.4 acres, for females 8.5 acres. Carpenter (1952) found that garter and ribbon snakes, *Thamnophis* sp., have a tendency to remain in a limited area, and he recaptured 42 that had moved an average distance of 81 meters, 85 that moved an average distance of 60 meters. These distances approximate distances moved by cottonmouths at Sea Horse Key. Carpenter gives the maximum activity ranges of *Thamnophis s. sirtalis* as 4.15 acres, the average as 2.07 acres. The average Sea Horse Key cottonmouth has an activity range of less than half an acre, limited indeed, compared to *Agkistrodon mokeson, Crotalus,* and *Thamnophis.* This may be partly due to the birds that bring them food and because rats and lizards are abundant in this environment. I strongly suspect that when food is plentiful cottonmouths are quite sedentary.

The activity ranges of Sea Horse Key cottonmouths are not littoral, nor do they provide an access corridor to the sea. Thus salt water is apparently not a significant factor in their lives. Their ranges for the most part are inland, and their small size enables the low peninsula to support a high population of snakes in a limited area. Snakes do not gather at the trees where nesting begins, but tend to be attracted to the nest tree nearest their range. Thus the available food supply is apportioned more evenly among the total population.

The close proximity of large male cottonmouths may precipitate combat. One actual fight I watched occurred in foxtail grass (*Chaetochloa macrosperma*) in the rookery area of Gardner's Point, at 2230 on 24 June 1956 between two males that measured 1333 mm (2098g) and 1384 mm (1489g). The participants at first eyed each other, heads held 15 cm high, then hooked necks and threw each other to the ground. Combat ended 4 minutes later when one snake suddenly glided directly toward me while the other traveled 2 meters in the opposite direction. The thinner but longer snake was unharmed; its opponent had been bitten in the side at mid-length. A moist, slightly swollen spot was oozing blood, otherwise the snake behaved normally. Possibly I interrupted a battle on 6 April 1957 when I found 2 males of equal size lying across each other, with a female within 0.75 meters. All 3 crawled off after 5 minutes, probably disturbed by my approach.

Jousts between males are a remarkable characteristic of North American crotalids. Ramsey (1948) noted them in *Agkistrodon piscivorous leucostoma*, and Allen and Swindell (1948) watched a "dance" between two captive 4-foot moccasins of the eastern subspecies in September that lasted 4 hours. Shaw (1948) describes the combat dance in the copperhead *Agkistrodon mokasen laticinctus*. Lowe (1948) states that the dance of male North American crotalids, which he calls territorial fights, occurs in both fall and spring in captivity and in the field, and that biting during them is rare.

The first instance of combat (above) on Sea Horse Key seems late in the year to be associated with mating. No female was found nearby. Territoriality is an unsatisfactory explanation when snakes aggregate in rookery areas. This particular fight may have been initiated by an accidental bite. The absence of bites on other cottonmouths seems to support this assumption.

FOOD AND FEEDING

If one generalization can be applied to the cottonmouth, it is that this snake apparently eats whatever animal food is available, from a

decomposing frog in a roadside ditch to a full-grown American egret. This is undoubtedly a highly important factor in allowing the cottonmouth to survive in an island environment such as Sea Horse Key.

Burkett (1966) lists food he examined from 46 cottonmouths from Arkansas, Louisiana, and Texas and summarizes food reported by 17 other authors. Other lists of foods eaten by the adult cottonmouth may be found in Strecker (1926), Allen and Neill (1950), and Wood (1954). In the stomachs of 20 specimens taken in Louisiana Arny (1948) found mammals in 5, reptiles in 9, a caterpillar in 1, and unidentifiable masses in 7.

Schwartz (1952) reports that in the Florida Keys a 12-inch specimen had eaten a shrew, *Blarina brevicauda*, and a rice rat *Oryzomys palustris*, while a 4½-foot snake had consumed a half-grown marsh rabbit, *Sylvilagus palustris*. O'Neil (1949) lists the cottonmouth as seventh ranking predator on the muskrat in Louisiana coastal marshes. Parker (1937) records a juvenile containing a skink, *Eumeces fasciatus*. Peterson, Garrett, and Lantz (1952) captured two cottonmouths on Key Vaca, Monroe County, Florida that in company with several *Natrix sipedon compressicauda*, were apparently feeding on a brackish water breeding aggregation of the giant tree frog, *Hyla septentrionalis*.

Birds and bird eggs are reported eaten by cottonmouths less often than mammals and reptiles. Adams (1955) reported cottonmouths in Louisiana eating a sora rail, *Porzena carolina*, and a seaside sparrow, *Amnospiza maritime*. Leavitt (1956) noted a Pied-billed Grebe, *Podilymbus podiceps*, eaten in the Gulf Hammock area of Florida. Mrs. Allen D. Cruickshank (pers. comm.) reports that at King's Bar Reef, Lake Okeechobee, the cottonmouth swallows the eggs of ibis and other birds whole with the shell intact; in May 1942 she killed a 2803-mm specimen there that contained a glossy ibis egg, three Louisiana heron eggs, a full-grown immature American egret, and an adult glossy ibis. She also noted that when cottonmouths approached the nests, the ibises leaned over and struck at them; a number of dead birds found with peculiar blood clots about the head suggested the snakes may have struck back.

Rhea Warren, who has collected cottonmouths in the Everglades for 12 years, told me (pers. comm.) that on a half dozen occasions he has seen these snakes at night scavenging snakes and frogs killed by automobiles on the black-top pavement of the Tamiami Trail west of Miami. That cottonmouths readily feed on other snakes is well established. A number of authors, Conant (1934), Penn (1943), Allen and Swindell (1948), Smith and List (1955), and Burkett (1966) have reported cottonmouths eating their own kind, both

Table 2. FOOD ITEMS FOUND IN 93 COTTONMOUTHS FROM THE CEDAR KEYS

Food Items	Number Snakes
MAMMALS	
Roof rat, *Rattus rattus*	24
Gray squirrel, *Sciurus carolinensis*	4
BIRDS	
Mourning dove, *Zenaidura macroura*	1
Fish crow (fledgling), *Corvus ossifragus*	1
Towhee, *Pipilo erythrophthalmus*	1
Cormorant (parts), *Phalacrocorax auritus*	3
Unidentified small birds	2
REPTILES	
Little brown skink, *Lygosoma laterale*	1
Florida five-lined skink, *Eumeces inexpectatus*	4
Anole, *Anolis carolinensis*	1
Salt water snake, *Natrix sipedon*	1
Marine Fish[1]	48
ARTHROPODS	
Caterpillar (unidentified)	1
Spider (unidentified)	1
Carapaces of spider crab[1]	2
Remains of shrimp[1]	2
MOLLUSCS	
Carnivorous land snail, *Englandina rosacea*	1
Conch (unidentified)[1]	1
MISCELLANEOUS	
Chicken and turtle bones (discarded refuse)	1

[1] Dropped by nesting birds

young and adult. If Sea Horse Key snakes are indeed at a suboptimum food level, it is surprising that no instance of cannibalism was observed during this study.

The only previous information on the food of the Cedar Key cot-

Table 3. FOOD BY MONTHS OF COTTONMOUTHS FROM SNAKE AND SEA HORSE KEYS

Month	Food Mass		Number of snakes examined	Per cent with food
	Identified	Unidentified[1]		
Jan.	2R, 2S	2	71	8.4
Feb.	1B, 1F	0	78	2.5
Mar.	1B, 1E, 7F, 5R	7	108	18.5
Apr.	11F, 2SH, 1R, 1S	6	115	18.2
May	7F, 1R	10	62	29.0
June	2B, 2CO, 2F, 1R 1SC	12	77	25.9
July	1CH, 1CO, 1E, 11F 1R, 1S	2	81	22.2
Aug.	1A, 1C, 1E, 4F 1R	0	26	30.7
Sept.		3	125	2.4
Oct.	1F	3	57	7.0
Nov.	1B, 2F, 1L, 1N 3R	0	46	17.3
Dec.	1CR, 1E, 4R	1	86	8.1

Key: A-*Anolis*, B-Small Bird, C-Crab, CH-Conch, CR-Caterpillar, CO-Cormorant (Body parts only), E-*Eumeces*, F-Fish, L-*Lygosoma*, N-*Natrix*, R-Rat, S-Squirrel, SH-Shrimp, SC-Refuse.

[1]Probably fish

tonmouths is by Carr (1936), who found food remains in the stomachs of 6 of 13 moccasins from Snake Key. Two of these contained skinks, *Eumeces inexpectatus*, two had ingested heron feathers (probably accidentally), and two contained bird bones of a single limb. Carr discussed the food sources available to the Snake Key cottonmouths and concluded that neither the heron rookery, reptiles present, nor the salt water fish offered adequate nourishment.

The majority (89.5 per cent) of the stomachs of Sea Horse Key cottonmouths I examined were empty, which suggests that the island snakes feed less frequently than those on the mainland. Barbour (1956) found that 25 per cent of the cottonmouths in a Kentucky pond contained food. Hamilton and Pollack (1955) found food in all

Table 4.   NUMBERS OF COTTONMOUTHS CONTAINING FOOD BY MONTH: ORIGINAL
CAPTURES COMPARED WITH RECAPTURES

Month	Original captures		Recaptures	
	Number	% with food	Number	% with food
Jan	29	10	42	7
Feb.	43	2	35	0
Mar.	52	21	56	16
Apr.	56	31	59	8
May	31	29	31	23
June	31	39	46	8
July	35	17	46	5
Aug.	11	18	15	0
Sept.	62	5	63	0
Oct.	29	7	28	4
Nov.	22	18	24	4
Dec.	39	12	47	2

9 of the snakes they examined in Georgia. Army (1948) found food
in all of the 20 specimens he captured in Louisiana.

Table 2 lists food eaten by 93 individual cottonmouths from the
Cedar Keys area. Table 3 lists this food by month, with the per-
centages of snakes containing food. As most palpable, but unidenti-
fied, food masses listed in Table 3 occur during the rookery period in
May and June, they probably represent fish. If a snake contained
what I felt was other than fish, I either gently made it regurgitate, or
else killed and dissected it.

Table 4 shows that the snakes are more likely to contain food
when captured for the first time than when recaptured (original cap-
tures with food, averaged 16.8 per cent; recaptures with food, 6.7
per cent). This seems to be additional evidence that the initial
capture of a crotalid snake produces a profound and lasting effect
on the snake. This phenomenon was first reported by Fitch and
Glading (1947) in Pacific rattlesnakes. Fitch (1949) found that all
his California crotalids lost weight up to 29 months. I showed previ-
ously (Wharton, 1966) that the 47 Cedar Key cottonmouths with
good weight data over a 3-year period lost an average of 86.5 g yearly.
When it is considered that most of these snakes were captured gently,

measured, weighed, and released within 5 minutes, this remarkable reaction is difficult to explain.

The two fish the Sea Horse Key cormorants feed on most often are pinfish, *Lagodon rhomboides*, and Gulf toadfish, *Opsanus beta*. I have seen the snakes eating both. I once found a cottonmouth in the act of eating a spiny boxfish, *Chilomycterus schoepfi*. Between April and September, I collected the following other fish disgorged by cormorants: cod, *Urophycis floridanus*, majarra, *Encinostomus* sp.; leatherfish, *Monocanthus ciliatus*; and whipsnake eel, *Bascanichthys scuticaris*. I have never seen a mullet, *Mugil* sp., or trout, *Cynoscion* sp., disgorged by cormorants, despite contrary statements by local fishermen.

Ospreys are the source of trout, mullet, and grouper, *Mycteroperca* sp., in the cottonmouths' diet before 20 March. I have 8 records of fish consumption between 28 October and 19 March that are probably osprey drops. Between the desertion of rookeries and perch trees in August and the start of nesting in March (Table 3), food intake drops markedly and is principally confined to reptiles and mammals. Rats apparently provide the bulk of nourishment during this period; they probably fall prey to the cottonmouth when searching for acorns in the ground litter in November and December though squirrels, thrashers, towhees, and thrushes are also very active on the ground. The presence of rats in snake stomachs in March suggests that at this time the rats are also feeding on dropped fish scraps in competition with the earliest cottonmouths to visit the nesting areas.

While skinks are eaten only occasionally by adult snakes, they may be the principal food of young cottonmouths in the Cedar Keys. Of the 5 skinks recorded, 2 were from snakes less than 356 mm. The largest snake that had eaten a lizard was 940 mm. One 483 mm young snake contained the primary feathers of a small warbler; 2 others less than 350 mm in length contained bits of shrimp regurgitated by birds. It must be difficult for a small snake to find regurgitated particles small enough to swallow beneath the nest trees. Of 48 snakes found eating food dropped by birds, only 7 measured less than 600 mm, and the mean length of 30 scavenging cottonmouths was 962 mm. Both food particle size and competition from larger snakes probably limit the scavenging activities of the smaller snakes.

Rats appear to be too large for snakes of less than 600 mm to swallow. The smallest snake to have eaten a rodent was a 508 mm specimen that ate two 23 g young rats in December. A 660 mm snake ate two young rats weighing 42 g each. The mean length of

the snakes that had eaten rats was 1046 mm. The four squirrels (Table 3) were taken by snakes over 1200 mm.

Evidently rookery scavenging is about the only source of food for snakes on Snake Key. Rats and other small mammals are either absent or quite rare; I found none in the 88 snakes I examined from this island, nor did I trap any. This absence of mammalian food does not seem to effect the population adversely, for it seems healthier than the one on Sea Horse Key (Wharton, 1966).

Both North and Atsena Otie islands lack communal bird rookeries and rats probably constitute the cottonmouths' major food source. Although 3 of 4 snakes from North Key were taken beneath osprey nests, from the incidence of parasitism by *Porochephalus crotali* in these snakes and bait pilfering, I believe the low snake population there exists primarily on rats. I trapped rats on Atsena Otie, found the same high incidence of parasitism, and concluded that rats are the major food on this island as well.

HIBERNATION

Hibernation and aestivation are common reptilian behavioral responses to temperature extremes. Strecker (1926), Gloyd (1938), Cagle (1942), Arny (1948), Dundee and Burger (1948), and Burkett (1966) have reported on the denning habits of the western cottonmouth, *A. p. leucostoma.* Dundee and Burger found them 1/2 mile from and 36 m above the nearest permanent water. Strecker found them in rotten logs, Dundee and Burger in limestone cliffs, and Gloyd in rock crevices. Neill (1948) found *A. p. piscivorus* in decaying stumps. Alexander Sprunt, Jr. (pers. comm.) poked 15 out of a stump near a cypress swamp on an Edisto River plantation in South Carolina. Neill (1947) suggests the cottonmouth is more cold-tolerant than most snakes in the Richmond County, Georgia area and says it is one of the last to hibernate.

Sea Horse Key cottonmouths seek temporary winter shelter. Specimens have been noted away from dens during warm spells of every month of the year. Numbers found hibernating over the 3-year period are: 4 in November; 16 in December; 25 in January; 10 in February; 1 in March.

While palmetto patches are frequently used, the principal underground refuges were the stump holes of trees blown over in the 1950 hurricane. These trees all lie in the same direction, their trunks aligned almost north-south. The holes are generally shallow, less than 300 mm deep, and the occupants can be located by flashlight. I
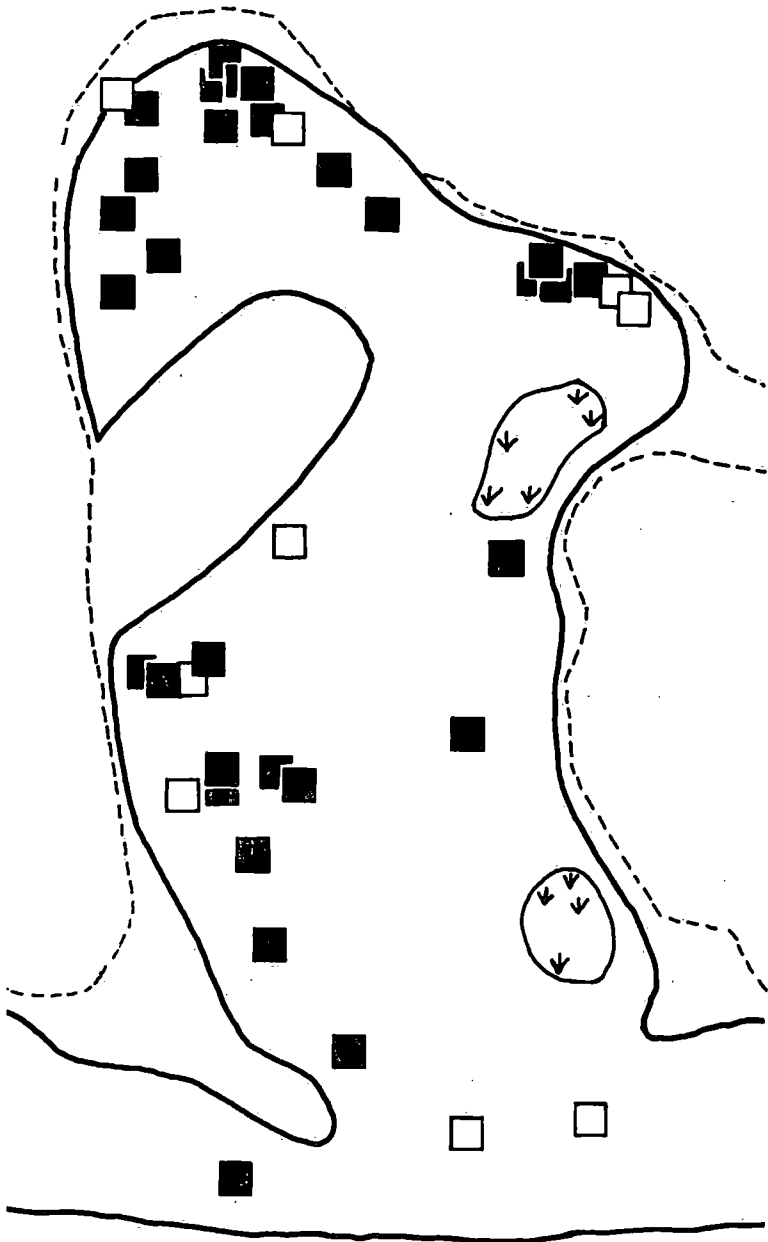
FIGURE 7. Subsurface winter dens and wintering areas (palmetto) of Sea Horse Key cottonmouths on the low peninsula. Solid symbol, occupied dens; open symbol, unoccupied dens. Compare with Fig. 8.

have taken as many as nine from a single den (at station 153 in January 1956), but the usual number is from one to five. Many of these holes seem to provide scant protection, but little is needed against the mild Gulf Coast winters.

Figure 7 maps 30 known active stump-hole dens on the low peninsula and 9 probable ones, most of them around the periphery of Gardner's Point and the western edge of the low peninsula. Snakes also definitely winter in, and travel to and from, areas of thick ground cover such as saw palmetto clumps and thick vines. The grouping of marks on Figure 8 at the Station 95 palmetto patch show the frequency of snakes encountered there between 15 December and 28 February. I worked this patch more extensively than any other and am convinced that it is actively sought in cold weather. Here on 11 January 1956 I kicked out from under dead fronds two males (1134 g each) with cloacal temperatures of 8.0°C while the air temperature was 7.0°C. I believe that some snakes also winter beneath fronds in the low cabbage palm hammock.

One favored winter refuge is the dense growth north of Station 76, with much saw palmetto and heavy leaf mold; another is along the south shore of the sheltered and sunny mangrove inlet. Other denning places include deep accumulations of leaf litter around the bases of trees, the interior of hollow logs, and the stump holes from rotted cabbage palms. I found only two holes of the gopher tortoise (*Gopherus polyphemus*) on Sea Horse; cottonmouths used one as a winter den.

Temperatures at Sea Horse Key are seldom low enough to be fatal. While denning may not be necessary to protect the snakes from extreme cold, the practice is nevertheless important. Normally most snakes den deep beneath ground level during winter and place minimum energy demands on their metabolism. Selection of shallow holes and emergence during winter warm periods by Sea Horse cottonmouths make increased demands on energy reserves. This can be fatal, as winter food is limited.

The earliest I found a snake in a den on Sea Horse Key was 6 November. Its cloacal temperature was 19.0°C, the air was 17.0°C, and I feel that this snake was not hibernating, but either hunting or seeking cover in the den. Normally snakes do not seek dens before mid-December, and 90 per cent of snakes in dens were taken in December, January, and February, the latter month having over 44 per cent of the winter total. Only one denned snake is recorded for March. The latest I have found a snake in an underground refuge

FIGURE 8. Location of 163 cottonmouths captured in fall and winter. Solid symbols, captures 1 Sept.—30 Nov.; open symbols, captures 1 Dec.—28 Feb. Compare with Fig. 7.

was 7 April, with a cloacal temperature of 15.8°C. The highest air temperature recorded during denning was 18.3°C.

On 18 and 19 December 1955 (air temp. 15.6°C.) I took nine snakes from seven sub-surface dens and one from a palmetto patch. Their cloacal temperatures varied from 13.5 to 16.5°C (M = 14.9°C). Three snakes taken near Station 92 on 12 February 1955, had a mean cloacal temperature of 4.2°C (air, 5.6°C), the lowest cloacal temperatures I recorded. These snakes were in a shallow den, and their temperature was lagging well behind that of the air. The cloacal temperatures of nine snakes taken in a den near Station 153 on 10 January 1956 were within 1.2°C (M = 10.7°C) of each other at a soil temperature of 12.8°C and an outside air temperature of 7.8°C. The low of the previous night was 5.0°C, and the highest daytime temperature was 8.9°C. Air temperature within the den was 9.1°C at the time of capture. This suggests that, in this instance, soil temperature kept the snakes at a point about intermediate between soil and air temperatures.

Table 5. DIURNAL TEMPERATURE (°C) AND PER CENT RELATIVE HUMIDITY OF DEN SITES COMPARED WITH GROUND SURFACES

| Date and den number | Temperature | | | Humidity | |
| | Air | | Soil | | |
	Den	Surface	Surface (4" depth)	Den	Surface
18 Dec. 1955, Den 3	13.3	16.7	——	85	70
19 Dec. 1955, Den 3	15.6	17.8	15.0	87	75
10 Jan. 1956, Den 13	9.1	7.8	12.8	—	—
11 Jan. 1956, Den 13	8.9	6.9	12.8	73	68
18 Feb. 1956, Den 3	18.9	21.1	19.5	96	92
4 Mar. 1956, Den 3	17.8	20.0	18.3	90	84
19 Jan. 1957, Den 7	11.3	13.3	12.8	—	—

Table 5 comparing temperature and humidity at ground level and within different dens shows in five of the seven recordings the den was from 1.3° to 3.4°C colder than the outside air. The den air temperature is usually closer to that of the soil. When air temperatures drop the den remains warmer because of the lag of the soil temperatures (10, 11 January 1956). As table 5 shows, den tempera-

tures usually remain colder when air temperatures rise. Dens also have a consistently higher humidity than the surface air. Thus while dens are only shallow, open stump holes, they are deep enough to ameliorate temperatures and maintain a higher humidity. As Benedict (1932) indicates, reptiles may lose heat readily by vaporization of water; higher humidities in dens would tend to favor the conservation of heat.

On 11 December 1955 I found five snakes in a cedar stump-hole near Station 128, which was open and scarcely below ground level. Three snakes were coiled on one another deep in the den, and two towards the entrance. The two outer snakes had cloacal temperatures of 10.0°C, the same as air temperature. The inner three were distinctly warmer, with cloacal temperatures from top to bottom of 11.0°C, 11.3°C, and with the snake next to the soil 12.2°C.

One of the most perplexing wintering problems is den desertion. Of 50 snakes taken in dens, only three were ever retaken again in a den and none of these in the den in which it was originally found, although each snake was released quickly into the opening of its den after weighing. Near Station 92, an area that always yielded a large number of snakes, there were several active nest trees in 1955 and at least one functional nest tree in 1956. In the winter of 1955 I took 10 snakes from three dens near Station 92 and released them near the same dens. They did not return to these dens that winter, and the dens remained deserted the next 2 years. I found two of the snakes in 1956 in a nearby den that had escaped my notice in 1955. This den contained nine snakes in all, which I released at the den mouth; none returned either that winter or the next, although two new snakes appeared there in 1957. Not only were the Station 92 dens deserted, but in 1955 I took snakes from 10 other dens, 8 of which remained deserted by all snakes for the second (1956), and third (1957) winters. On 10 January 1956 I marked nine snakes from a den near Station 153, and released each at the entrance hole. Though the next day was several degrees colder, not a single snake was present in this den. Even though they make an escape run on release, I find it difficult to believe that these serpents could not find their way back to their den.

I conclude that snakes move away from the site of a den disturbance, and do not re-enter the den for at least 2 years. Perhaps they move off in response to the normal shock pattern of behavior and are too cold to return, but this does not explain their absence in subsequent years. It has been suggested (I.L. Brisbin, Jr.—pers. comm.)

that musk sprayed during capture is a warning device. Musk would have to persist for several years to explain den desertion, and this theory does not explain why some dens are re-used by other snakes. Another theory supposes mass movements to winter in other parts of the peninsula, which the general location of winter captures (Fig. 13) does not support. As I found the denning sites of only a small percentage of the total population, I could possibly have overlooked many of them but I felt that I had discovered most of the den sites in the Gardner's Point area where I made these observations.

Published accounts of den re-use are limited and conflicting. Hirth (1966) found that 9 out of 10 *Crotalus viridis* returned to dens after displacement of 50 to 774 m. Den abandonment, or specific crevice abandonment, might be inferred from Fitch's (1960) data an *Agkistrodon mokeson*. Of 492 copperheads Fitch captured during a 10-year period, apparently only 11 were recaptured on the ledge where the original captures were made, and only 3 of these at the exact crevice. It is possible that all the snakes might have returned to the identical crevice had they not been disturbed. Fitch (1949) and Woodbury (1951) note that there may be a difference in whether a snake is allowed to emerge normally to be trapped or caught or whether it is disturbed in situ and physically removed when its instincts direct it to remain underground.

I suggest that some crotalid snakes may have a persistent site memory. Rattlesnakes, successfully adapted to cold climates and large homiotherm prey, have developed the ability to migrate long distances to and from specific dens. Cottonmouths have been known to migrate up to 1/2 mile (Dundee and Burger, 1948) and presumably have the same instincts. If these snakes have a highly developed directional sense, perhaps the site memory is also strong and enables them to avoid disturbed dens. Evidence to support such a theory of den avoidance is weak, but if cottonmouths do have such associative powers, my data suggest that this ability may persist for at least 2 years.

TEMPERATURE AND BEHAVIOR

Cottonmouths appeared disinclined to move at 8.0°C and below, but from 10.0 to 12.0°C followed the usual escape pattern of remaining until one leaves, then moving away. Generally snakes handled with a CT (cloacal temperature) of 8.0—10.0°C were passive and only gaped, though one 1524-mm male with a CT of 9.0°C squirmed continuously on being handled and finally bit itself twice. At the

lowest CTs recorded (4.0, 4.1, and 4.5°C from three snakes 12 February 1955) all were passive and only two sprayed musk—the one with a CT of 4.0°C sprayed musk copiously. A 1118-mm male at CT 4.5°C swelled up and struck several times after being annoyed. Warning by opening the mouth or gaping first occurred at a CT of 6.5°C, with musking and inflation.

In one den three individuals with CTs of 10.0, 11.1 and 11.3°C seemed aggressive towards the snake stick. All three struck it, and two bit the leather noose. Two inflated and one attempted to vibrate the tail, which at this temperature is a feeble and slow movement. These snakes were passive until touched. Two bit the stick while being withdrawn from the den. At 9.0-10°C some snakes partially coiled when touched. One snake with a CT of 11.0°C crawled out of a hole when molested. A 406-mm young, disturbed under a palmetto frond, was violently aggressive at CT 11.4°C. About half the cottonmouths threatened at this temperature.

Of 11 snakes whose demeanor was recorded between 4.5 and 10.0°C, 4 were aggressive and 7 were passive. This high incidence of aggression may be due to rough handling, although aggression would have survival value when snakes are immobilized by cold. I noted a cottonmouth vibrating its tail at a CT of 12.2°C. At 15.0-16.0°C cottonmouths were able to snap into a coil fairly rapidly, and I noted unprovoked crawling at this temperature. Figure 9, showing numbers of snakes captured at each degree of air temperature, shows four snakes captured under nest trees at an air temperature of 14.4°C. These snakes, two of which were actually swallowing fish at the moment of capture, had CT's of 14.5, 15.8, 15.2, and 15.4°C. The leaf mold temperature was 16.8°C and the soil 19.8°C, so the snakes were feeding on a warm substrate. Island cottonmouths may thus feed at 3.8°C below the 18.3°C recorded by Allen and Swindell (1948).

From these observations I conclude that cottonmouths in this area become attracted to food and are able to scavenge at a CT of 14.0°C and are quite active at a CT of 16.0°C. Figure 10 suggests that the optimum temperature for these snakes lies between about 18°C and 29.5°C, somewhat lower than the preferred substrate temperature of 35.34°C mentioned by Bogart (1949).

I have noted sunning activity in November between 10.0 and 20.0°C (Fig. 10). The coldest day on which I captured a cottonmouth sunning was 6.1°C; this snake (CT 10°C) had crawled out of a gopher hole den at Station 40.
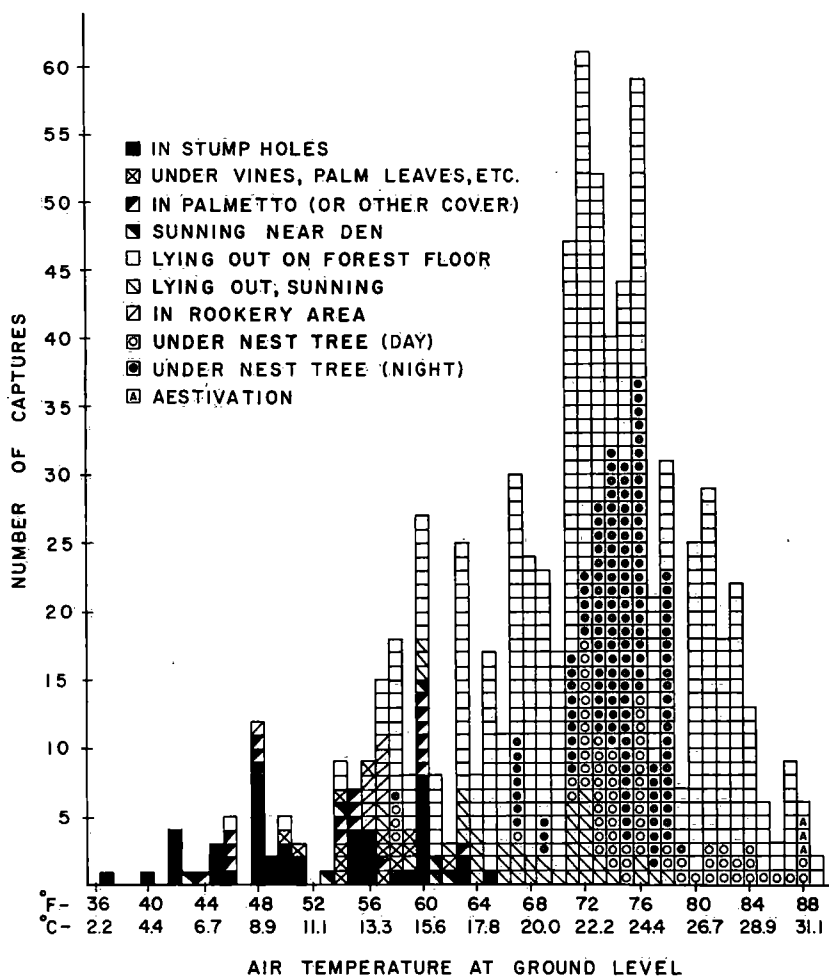
FIGURE 9. Cottonmouth captures at specific air temperatures, indicating behavior or body position.

The warm-up of a dark, basking cottonmouth is relatively rapid. On 10 March 1957 I placed a large, completely docile female on dried grass background of a neutral color on the open beach. The sun was at an approximate angle of 40°. The sand under the grass at a depth of 25 mm had a temperature of 15.4°C, the humidity was 78 per cent, and the snake was uniformly dark. The thermometer was gently inserted about 36 mm into the cloaca and held in a central position. Seven readings taken from 09:13 to 09:40 showed the snake's tempera-

ture rose from an initial 8.8°C (air 11.3°C) to 21.5°C, a rise of 12.7 degrees. During the first 6 minutes the temperature rose 0.9°C per minute, and thence roughly 0.4°C per minute for the remaining 21 minutes.

This snake was so docile, neither swelling nor moving during the entire test, that I gently moved it to a shady area beneath the mangroves and recorded the rapidity of heat loss. The air temperature remained at 12.0°C and the shaded sand covered by dead leaves also registered 12.0°C. I took 11 cloacal readings at 5-minute intervals while the snake's temperature dropped to 14.8°C, a loss of 6.7°C in 60 minutes. For the first 15 minutes the heat loss was approximately 0.2°C per minute, thereafter for 7 readings, 0.1°C per minute. Some physiological control over rate of change, as Bartholomew and Tucker (1963) note for a lizard, is possible.

During this test the importance of central cloacal temperature was demonstrated. Turned so that it rested against the body wall on the shaded side of the snake the thermometer showed a drop of 0.3°C; but held against the side of the snake in the sun it registered 4.6°C higher than central cloacal temperature.

During the winter Sea Horse Key snakes often remain in one position for considerable periods of time. I saw five individuals that had remained coiled in one spot on the ground for at least 24 hours. Two
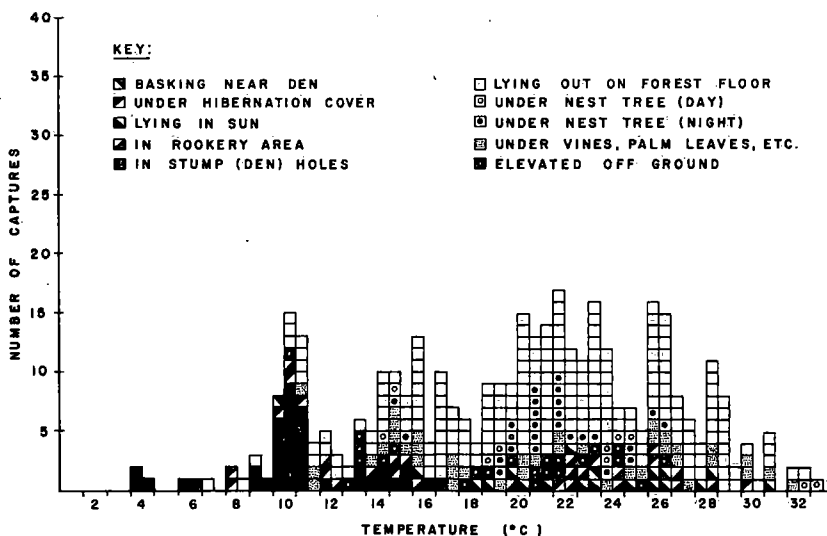

FIGURE 10. Observations on 387 cottonmouths captured at specific cloacal temperatures, indicating behavior or body position.

remained in one spot 72 hours without moving. Others seemingly moved only 5 m or less in 72 hours.

Demeanor on approach was noted on 50 per cent of the cottonmouths. Such information renders at best only a crude picture of the behavior of the snakes, as one does not always approach at the same speed. Some snakes are approached more cautiously because of ready refuge near. Others appear to be asleep. Reactions were classed in five categories: violently aggressive, aggressive, warning, passive, and escape. The first two involve striking; warning signifies opening the mouth (gaping); escape means any attempt to crawl away. Between 4.4°C and 15.6°C 36 per cent of the snakes captured showed aggressive behavior. This contrasts with approximately 4.1 per cent between 15.6 and 32.2°C. No escape reactions were noted between 4.4 and 10.0°C. Between 10.0 and 5.6°C 6.8 per cent tried to escape, and 4.6 per cent between 15.6 and 21.1°C. However, at higher temperatures (to 32.2°C) 17.5 per cent of snakes tried to escape. Lueth (1941), working with young water snakes of the genus *Natrix*, noted a tendency to escape at temperatures above 27°C.

Body Fat and Survival

Volsoe (1944), St. Girons (1957), Tinkle (1957, 1962) and Wharton (1966) have discussed the relation of body fat to reproduction in snakes. Body fat also forms an important energy reserve for snakes. Benedict (1932) shows that during fasting, the respiratory quotient quickly becomes that of pure fat (0.72).

Cottonmouths carry body fat in two long bundles ventral to the reproductive and excretory organs. Though it clings tightly in the vicinity of the spleen and gall bladder, it may be stripped out almost as a discrete unit. Figures 11 and 12 show weights of fat bodies dissected from snakes collected on Snake and Sea Horse Keys. Large fat bodies are white or yellowish. When depleted they appear as two coiled orange bands; these were classed as negative fat, and symbols representing them appear in the graphs along the abscissa. Far more Sea Horse Key snakes had negative fat bodies than did those from Snake Key. This supports my earlier statement (1966) that 50 per cent of the Sea Horse Key cottonmouths gained no weight during the study.

Benedict (1932) demonstrates a direct relationship between metabolic rate and higher temperature in reptiles, and notes that the heat production of all cold-blooded animals is extraordinarily uniform. A snake's surface area (S) may be computed by the formula $S=$

Table 6. Fat Weight Island Cottonmouths Need from March through September and Its Caloric Equivalent in Available Fish

Snake length (mm)	Snake weight (g)	Calculated fat weight (g)	No. of 46-g fish yielding caloric equivalent
457	53	13.6	2.1
800	475	59.5	9.1
940	907	91.4	13.9
1168	1404	122.2	18.6
1422	2608	185.8	28.3

$K \times \frac{2}{3}W$, where K is a constant (12.5) times $\frac{2}{3}$ weight in grams. Using values from Benedict's rattlesnake curve, I computed the grams of fat needed by five cottonmouths of varying sizes (Table 6). As the weight-length data show that Benedict's rattlers were well-fed, heavy specimens, I selected five fat cottonmouths. While the body surface
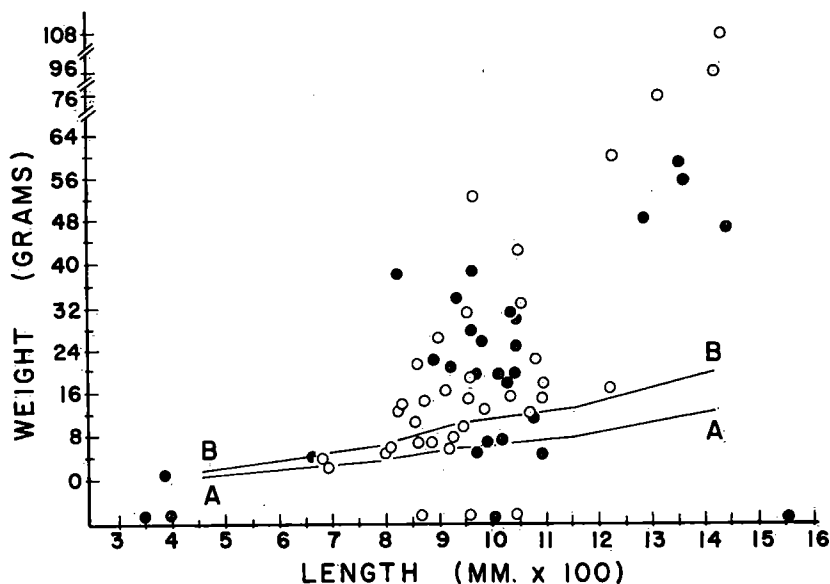

FIGURE 11. Fat-body weight in grams versus length of Snake Key cottonmouths. Curves indicate weights of fat bodies for winter survival. Captures below zero grams indicate negligible fat bodies. A, cold winter (1954-55); B, warm winter (1956-57); solid symbols, nonfeeding period (1 Oct.-28 Feb.); open symbols, feeding period (1 Mar.-30 Sept.)

80
72
64
56
48
40
32
24
16
8
0

WEIGHT (GRAMS)

B

A

B

A

3   4   5   6   7   8   9   10   11   12   13   14   15   16
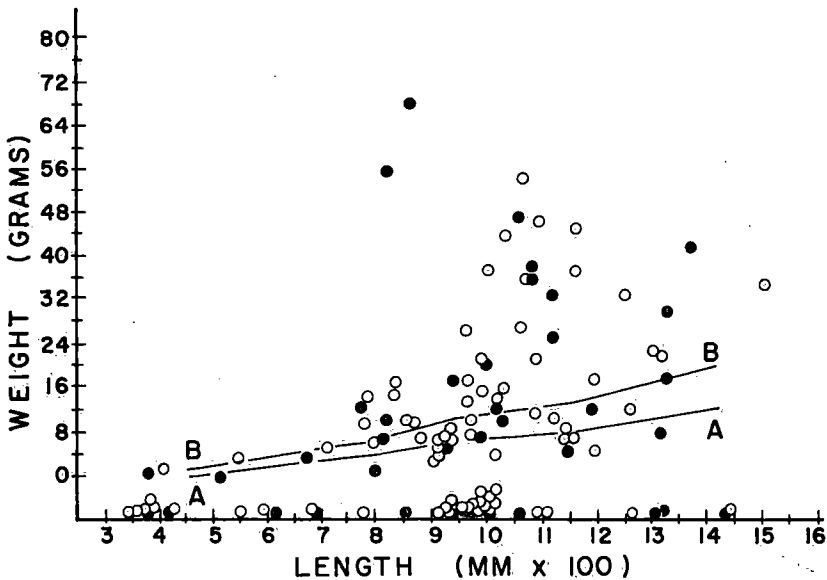
LENGTH   (MM X 100)

FIGURE 12. Fat-body weights in grams versus length of Sea Horse Key cotton-mouths. Curves indicate weights of fat bodies for winter survival. Captures below zero grams indicate negligible fat bodies. A, cold winter (1954-55); B, warm winter (1956-57); solid symbols, non-feeding period (1 Oct.-28 Feb.); open symbols, feeding period (1 Mar.-30 Sept.).

of an emaciated snake almost equals that of a fat one, Benedict's constant requires snakes of reasonable similar condition.

The formula gives a figure which, divided by 10,000, yields the approximate calories needed by a cottonmouth of these surface areas per 24 hours. This figure was multiplied by the number of days in the seasons considered. Curves were drawn to connect points plotted for each of the five snakes mentioned above for both warm and cold winters at Sea Horse and Snake Keys (Fig. 11, 12). Curve A, figure 11, shows that 6 of 30 winter captures (20%) on Snake Key had less fat than needed to survive a winter as cold as the 1954-55 season (monthly mean, 16.3°C), curve B that 11 of 30 winter captures (36%) had inadequate fat reserves for a winter as warm as 1956-57, (monthly mean 18.7°C). In addition, a winter as warm as the latter would endanger 13 of 38 summer captures (34%) unless their fat reserves were increased.

These figures may be contrasted with those of the Sea Horse Key population (Fig. 12) where, in the colder of the two winters 17 of 31

(55%) had inadequate fat reserve, while 24 of 31 (77%) had insuffi-cient fat reserves to survive a 5-month winter period similar to that of the 1956-57 season. On Sea Horse Key 52 of 79 summer captures (66%) had inadequate reserves to meet a warm winter.

Lueth (1941) found that the rate at which snakes utilize their energy reserves during starvation varies directly with air temperature. Volsoe (1944) concluded that the European viper evinces no observ-able reduction of fat bodies during hibernation, but that these bodies become reduced after long starvation or during pregnancy.

The cottonmouths showed no marked difference in their fat-body weights in summer and winter (Fig. 11, 12).

While undoubtedly useful for both males and females in reproduc-tion, evidently the major function of fat bodies is to provide energy during warm weather when food is scarce and, although they are not markedly reduced in normal winters, they serve to offset the effects of unseasonal warmth during the cooler parts of the year when little food is available or digestion impossible.

Figures 11 and 12 show that the fat body weights needed for average winter survival are not high, but a prolonged winter warm spell subjects cottonmouths to emergency demands on stored fat, particularly as they do not go into deep dens where the temperature remains uniform throughout the winter. Winter warm spells occur frequently in Florida—the extreme warm period in December of 1956 and the mild period that persisted into February over much of northern Florida in 1957 are examples. Volsoe (1944) suggests that cold winters are more favorable to hibernating vipers than mild ones. To the island cottonmouths the winter warm spells may be critical; following the warm spell in January and February of 1957, I picked up eight dead snakes. Evidently fat reserves are more important for snakes in the variable climate of the southeastern United States than for either northern or tropical forms that live in uniformly cold or warm temperatures.

The statistical relationship of fat weight to snake length was in-vestigated in snakes from both Sea Horse and Snake Keys. The sexes were treated separately and subjected to four F-tests. Only with the males of Sea Horse Key did the fat weight increase exponentially with increasing length. For females from Sea Horse Key and males from Snake Key, a linear equation best expresses the relationship between fat and total length. Neither curve appeared to fit the data for females from Snake Key. No relationship between fat weight and total length was apparent.

Energy demands are larger in small snakes because of their proportionately larger surface area. During warm seasons food needs rise to high levels, and unless it eats promptly, a snake with negligible body fat must begin converting its own protein into energy. Negative fat bodies in Sea Horse Key snakes occur most consistently in spring and summer. Figures 11 and 12 have no curves for the fat requirements of the five snakes during the warmer months. Their energy requirements (in fat) from March through September, were computed by using the mean (25.3°C) of the three 7-month feeding seasons (Table 6). The number of fish needed to supply these amounts of energy for the warm months was calculated. Mattice (1950) gives the average caloric yield of protein and fat from 6 common marine fish as about 300 calories per 277 g of fish. The average length of pinfish eaten by cormorants is about 115 mm; toadfish, about 127 mm. Fish of these measurements weigh about 46 g. Table 6 lists the approximate number of fish of this size necessary to maintain cottonmouths at 25.3°C for the warm period from March through September, providing growth demands are ignored.

Sea Horse Key snakes have various ways of offseting rapid heat loss. Undoubtedly tight coiling reduces the exposed surface area. The snakes also take refuge in holes or under thick cover at high environmental temperatures. On very hot days it is often difficult to find snakes at all. On one occasion, when snakes were avoiding the open rookery area (33.3°C, rel. hum. 54%), I found them 50 m away beneath dense canopy (31.7°C, rel. hum. 62%). I noted 3 snakes seeking den holes in excessively hot weather.

The frequency of negative fat bodies and the randomness of the fat body weights in reference to the length of the snakes (Figure 12) suggest that many Sea Horse Key snakes lead a precarious borderline existence, with competition and chance operating to produce a haphazard food intake. The Snake Key population is better fed.

A factor difficult to assess is water supply. Klauber (1956) records rattlesnakes drinking water from their own skin and from the surface of rocks and outlines the reasons why snakes require little water. While I have seen young cottonmouths suck up water from leaves or the backs of other snakes after being sprinkled, I have not observed this behavior in adults. Adult cottonmouths should be able to drink limited amounts of rain water caught in curled leaves. Possibly dehydration, as well as food shortage, is an important factor in snake survival on these islands.

MORTALITY AND PREDATION

The remains of 20 snakes found dead were measured in the field and compared with the closest matching sizes of prepared skeletal material; only one of the dead snakes would have had a total length less than 1000 mm. The mean length of the 20 snakes was calculated to be 1291 mm, their mean weight 1634 grams.

The chief cause of death is probably starvation, though dehydration may also be important. Most dead snakes appeared thin and emaciated. I have found a number of individuals in a moribund condition with scarcely enough vitality to crawl.

Death may sometimes be due to other causes. I once found a large male that appeared to have been in good condition before death. The posterior end of a linguatulid worm completely blocked the glottis.

Adult cottonmouths apparently have few enemies on Sea Horse Key. Rats do not seem to disturb live cottonmouths, nor do they molest dead snakes. Possible predators of young cottonmouths are the red-shouldered hawk and various species of herons. Walter Auffenberg (pers. comm.) once saw American egrets feeding on young cottonmouths in roadside ditches between Daytona Beach and Deland, Volusia County, Florida. Allen and Swindell (1948) state that herons and cranes eat young moccasins, and mention a Great Blue Heron choked to death on a cottonmouth it had stabbed through the head.

Barbour (1956) found a cottonmouth half devoured by a raccoon. A few snakes are possibly eaten when raccoons are present on Sea Horse Key.

Eyes are apparently not important to the survival of island cottonmouths. Two healthy male snakes were captured that were uniformly and bilaterally blind, suggesting a genetic cause. There was no macroscopic vestige of pupil—the supraocular scales nearly touched the upper labials. Number 131 (total length 1200 mm), in good condition, was captured 4 times between January 1955 and April 1956. Once, it was struggling for possession of a fish with another snake. Number 153 was actually fat (total length 1245 mm, weight 1517 g) and was captured 3 times between June 1955 and November 1956. Both snakes were in as good or better condition than the average island snake. If this blindness is genetic it suggests the intriguing possibility that eyelessness might compete successfully with the eyed condition on this island, as food is apparently detected best by olfaction.

DISCUSSION

The cottonmouth is believed to have descended from an Asiatic viperid that crossed the Bering land bridge in late Miocene (Neill, 1964) to become an element of the Arcto-Tertiary forest fauna. It has been present in Florida since the Pleistocene (Brattstrom, 1953; Auffenberg, 1963) where it has evidently preserved an endogenous biennial sexual cycle inherited from viviparous ancestral forms (Wharton, 1966). This adaptation to cold climates serves the snake well in the food-scarce environment of the Cedar Keys.

Various authors (Hamilton and Pollack, 1955; Dundee and Burger, 1948; Allen and Swindell, 1948) have found mainland cottonmouths in dry habitats, often far from water. The migration of mainland progenitors from one drying pond to another has probably equipped this snake to cope with different habitats and to seek food actively on dry uplands. Such vagility, coupled with the development of excellent olfaction, enables the island snakes to find and exploit both the rookeries and the indigenous vertebrates. The swamp-dwelling specialization has resulted in an ability to feed on both warm and cold-blooded prey, including dead fish, which fits it perfectly as a rookery scavenger. Its wide temperature tolerance and the absence of notable behavioral thermoregulation is probably an adaption to a cool, amphibious swamp life, allowing it to survive in a canopied forest where feeding at low temperatures is often necessary.

Cottonmouths have been reported not to feed in zoos in winter (Conant, 1929). This trait may vary between populations. The Cedar Keys cottonmouths feed in winter and at that season augment their warm-season scavenging diet with litter-feeding mammals and birds. The ability to forage both by active pursuit and by ambush serves them well on a year-round basis on the island. At the same time its odor and venom exempt it from predation by most mammals.

The young retain a primitive color pattern, shared with the copperhead, that affords protective coloration in upland deciduous forest leaf litter. Young cottonmouths are cryptozoic in habits, feeding largely on lizards and frogs lured by worm-imitating tail tips (Wharton, 1960), a characteristic shared with other members of the genus. The adult cottonmouth usually loses its primitive, juvenile pattern by darkening and thus blends well with the normal swamp substrate. Increased size, more venom, secretiveness, and nocturnality enable the adult to offset its lack of protective coloration in upland habitats.

The cottonmouth is able to move into deciduous forests in the

winter and seek underground safety in a wide variety of refuges, in habitats entirely different from its summer haunts. This ability has not only led to ease of ecesis on the Florida coastal islands, but has encouraged the development of a homing ability and, perhaps, a persistant site-memory.

The Snake Key population survives well entirely by scavenging, as competing and potentially-edible rodents are absent. Both Snake and Sea Horse populations exist in high numbers partly because of the legal protection afforded the rookeries; reciprocally the presence of so many venomous snakes must deter human molestation at crucial periods in the birds' life cycle.

The cottonmouth thus appears almost ideally preadapted to exploit the unique habitat offered by the outer islands of the Cedar Keys. The niche might be termed that of a terrestrial carnivore-scavenger.

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