BEHAVIOR, SOCIO-BIOLOGY, AND REPRODUCTIVE LIFE HISTORY OF THE FLORIDA KEY DEER, *ODOCOILEUS VIRGINIANUS CLAVIUM*

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James William Hardin

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I hereby recommend that the dissertation prepared under my supervision by

James W. Hardin

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W D Klimstra
In Charge of Dissertation

William M. Lewis
Head of Department

Recommendation concurred in

Howard J. Stains
Eugene W. Foote
George H. Waring
William G. Dyer

Committee
for the
Final Examination

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INTRODUCTION

The Florida Key deer, Odocoileus virginianus clavium Barbour and Allen, is the smallest of the eastern races of North American white-tailed deer and occurs only on the lower Florida Keys, which are islands located to the southwest off the southern tip of Florida (Barbour and Allen 1922). Although the origin of these deer is unknown and the history is based on information from early visitors to the Keys, local residents and hunters, it appears that the deer population fluctuated with very low numbers occurring in some years (Dickson 1955, Barbour and Allen 1922, U. S. Fish and Wildlife Service Narrative Reports 1939-1967).

Life history information on the Florida Key deer also has been based mainly on reports by local residents and on chance sightings of deer in the early 1950's when the population was low. Dickson (1955), observing aspects of the life history, noted that males polished their antlers in September and shed them in March and April. Others cited observations of deer in velvet every month of the year (U. S. Fish and Wildlife Service Narrative Reports 1939-1967). Barbour and Allen (1922), citing hunters, noted no special breeding season for Key deer. Dickson (1955), however, reported that rutting occurred in February with spotted fawns being observed during August through June. He also noted that does were most often seen with single fawns, although twins were occasionally observed. There have been no previous organized behavioral studies conducted on the Key deer.

In 1968 a 5-year study was initiated to investigate those factors influencing the Key deer population size, rate of increment, and

relationships to the insular environment (Klimstra 1974). A study on behavior, social organization and life history, which represented a portion of the comprehensive 5-year investigation, was conducted to ascertain their effects on the population dynamics of the herd, and to contribute to developing a more feasible management program for the Key deer.

Study Area

The Florida Keys are composed of two types of Pleistocene-aged limestone: the elevated coral reef rock known as Key Largo Limestone, which forms the upper keys, underlies the oolitic facies of the Miami Limestone that forms the lower Keys (Hoffmeister and Multer 1968:1489). That the two meet off the southeast point of Big Pine Key may explain the diversity of plant life in this region. The native flora of the Lower Keys is largely West Indian in origin and much of the fauna, including all of the mammals, is North American (dePourtales 1877).

Six basic types of habitat described for Big Pine Key include pinewoods, hammock, open-mixed hardwoods, buttonwood park, open scrub, and mangrove thicket (Yaw 1966:8). Pinelands, which make up about 38 percent of the island (Dickson 1955:27), occur in elevated areas free from salt water intrusion. Red mangroves form a natural fringe around the island and also occur in depressions containing brackish water. Black and white mangroves also occur in these fringe areas where the elevation increases from sea level. Buttonwood-scrub mangrove prairies exist as open savannahs where scattered, often dense clumps of buttonwood and hardwood intermingle on high ground and where red mangrove grows in lower areas having salt water. Hardwood and hammock

habitats range from dense stands of hardwood species to more mature hammocks that have an open understory, heavy canopy, and a thick layer of leaves and other debris. These occur on higher areas of the islands replacing pinelands if they are undisturbed by fire over long periods (Alexander and Dickson 1973, Stern and Brizicky 1957).

Artificial open areas representing another habitat type have been cleared by man to provide roads, housing developments, and locations for businesses. Such clearings are characteristic of those islands on which the overseas highway and connecting roads provide easy access. In some cases mangrove areas have been filled with marl to provide elevated "new land", and other natural habitat types have been replaced by residential developments. In these housing subdivisions dredged waterways have been developed to facilitate access to the channels by boat (Figure 1). These serve as barriers to normal deer movements on some Keys, and allow for intrusion of salt water into certain areas of the Key.

Additional strips of vegetation were cleared through all habitat types along the mosquito ditches, which were dug by the Monroe County Mosquito Control District in 1964-1965. The ditches, which drain 4,976 acres of Big Pine Key (about 6,000 acres in size), serve to drain or flush potential mosquito breeding sites as the tides fluctuate (Figure 1)(Alexander and Dickson 1973:91). Big Pine, No Name, Big Torch, and Cudjoe Keys have numerous artificial clearings, as well as the six habitat types described by Yaw (1966); other islands have varying amounts of some or all of these habitats with only high islands having pines, and most outer Keys lacking the extensive artificial openings created and maintained by man.

Figure 1. Aerial photograph of a portion of Big Pine Key showing dredged canals in a new housing development (left of center) and a network of mosquito ditches in an adjacent section of hardwoods (broken lines, upper right part of picture).

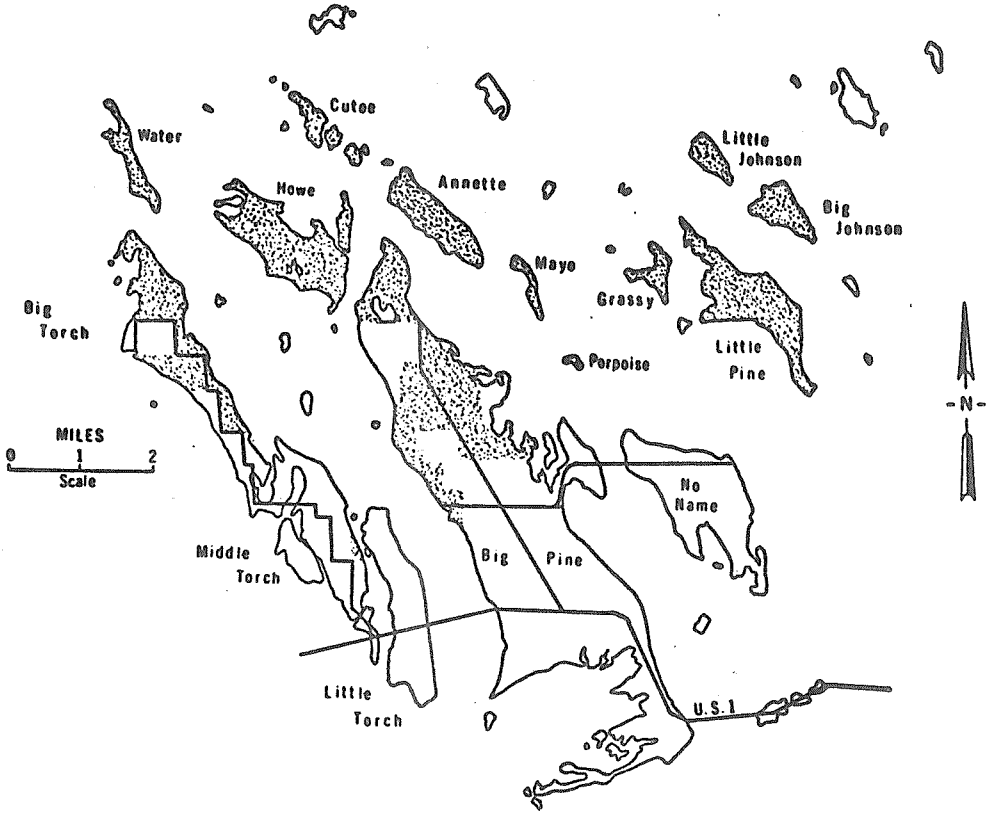
Information during this study was gathered mainly from deer on Big Pine Key, as techniques were not available for capturing and monitoring deer on adjacent islands. Big Pine Key, the largest of the lower Florida Keys, has an approximate area of 6,000 acres and is 8.3 miles long and 2.0 miles wide at the widest point (Dickson 1955:20). During the study the population was estimated at around 200-250 deer on Big Pine Key (Klimstra 1974). The distance between Big Pine Key and adjacent islands ranges from 0.06 miles in the case of Munson Island, to 0.81 miles in the case of Porpoise and Mayo Keys (Figure 2).

Dates Of Study

The 5-year ecological study of the Key deer was begun in January 1968 and ended in September 1973 (Klimstra 1974). Except for periods during January 1972 to 15 March 1972, and 16 June 1972 to 15 March 1973, staff of the Cooperative Wildlife Research Laboratory at Southern Illinois University (CWRL) were in residence on the islands collecting field data. In addition employees of CWRL collected census data and roadkill information during 15 January 1972 through 15 March 1972. Brief periods were also spent in the field during September and December of 1972.

Field work by this author included periods from September 1969 through August 1971, April 1972 through 15 June 1972, 2 weeks in December 1972, and 10 April 1973 through 8 May 1973. During January 1968 through September 1963 along with their own studies, other CWRL staff recorded incidental information on life history and behavior which contributed to this paper.

Figure 2. Map of Big Pine Key and adjacent islands; stippled areas represent refuge lands.


Water
Cutoe
Howe
Annette
Little Johnson
Big Johnson
Mayo
Grassy
Big Torch
Porpoise
Little Pine
MILES
0 1 2
Scale
N
No Name
Middle Torch
Big Pine
Little Torch
U.S. 1

MATERIALS AND METHODS

Capture And Marking Techniques

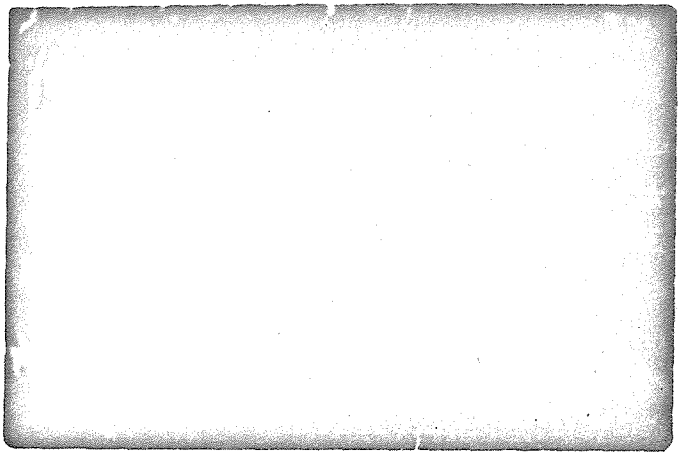
All data on captured and marked deer, some of which were recorded before I initiated the field work, contributed to the present study, since many of the animals handled were used for subsequent behavior observations. Techniques for capturing Key deer prior to and during this study included use of trail traps, immobilizing drugs, portable nets, and capture by hand. Most of the 233 deer (32 adult males, 61 adult females, 19 yearling males, 22 yearling females, 70 fawn males, 29 fawn females) which were captured and marked throughout the 5-year study, served during 1969-1973 to provide behavioral and life history information.

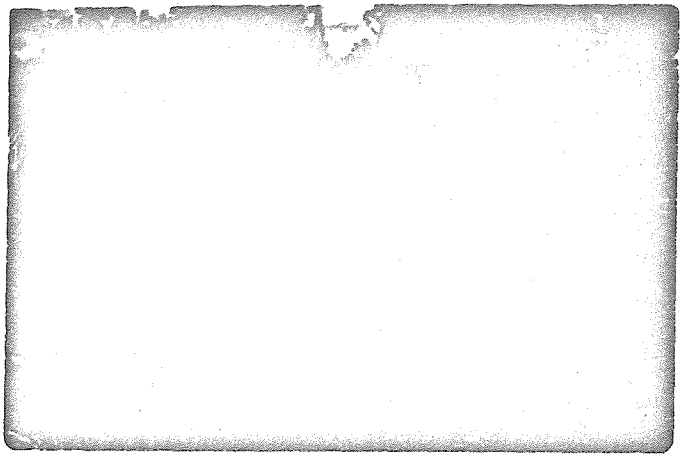
Various marking techniques which were used included experimental collars, bells, radio-transmitters, numbered ear tags, streamers, and ear tattoos (Figure 3). Descriptions and evaluations of all capture and marking techniques, which were used throughout the 5-year study, were presented by Klimstra (1974). The following discussion is limited only to those methods which directly contributed to collecting data on socio-behavior and life history of Key deer.

Collecting data on social organization and behavior necessitated the ability to recognize individual free-ranging deer whenever they were seen. Collars made from 3x16-inch strips of 0.125-inch guage boltaron, a thermal plastic premolded to conform to the shape of the deer's neck, served to facilitate recognition of individuals at a distance. Yearling and adult does received permanent collars, which

Figure 3. Yearling Key deer female marked with a numbered plastic ear tag and streamer, bell, and radio-transmitter mounted on a collar bearing a symbol made from reflective tape.

Figure 4. A model 23 Hy-gain, three-element, 4-foot directional hand-held yagi antenna used when "walking-in" on deer.





were rivetted in a closed position around their necks. For yearling and adult males, whose necks increased in size during the rut, and for fawns, collars were held in place by strips of elastic that allowed for neck expansion and growth. Collars were individually marked using numbers, letters, and symbols cut from four different colors of scotch-lite reflective tape, which was visible and distinctive at a distance in daylight and under artificial light at night.

Thirty-three fawns, aged up to 4 months, were fitted with collars made from 1x2-inch squares of boltaron, covered with reflective tape; they were attached snuggly around the neck by means of a 1-inch wide elastic strap held in place by a rivet. The elastic stretched as the fawns grew, and some collars were worn for 2 years without adverse effects before they were lost or removed.

To facilitate detailed studies, radio-transmitters, made by W. H. Cochran (A.V.M. Electronics Corp., Champaign, Illinois) and Jim Buitt, research assistant at CWRL, were mounted on collars for deer of all sex-age classes. During the study, 187 radios were placed on 119 deer (20 adult males, 38 adult females, 7 yearling males, 6 yearling females 31 fawn males and 17 fawn females). For adults, radios were two-stage or three-stage, long-range 148 MHz pulsing transmitters, powered by four or six Mallory 1.4-volt batteries. The weight was around 450 g, and the transmitters had an expected life of 9 to 24 months. Each radio for newborn fawns was a one-stage 148 MHz pulsing transmitter powered by one 1.4-volt hearing aid battery. These had an expected life of around 30 days and weighed about 17 g. Older fawns were able to carry two 1.4-volt batteries that powered the radios for about 60 days.

Attempts were made to recapture fawns and other deer carrying transmitters to replace the batteries just before the theoretical life of the radio was reached. Using radio signals, fawns up to 1 month of age with functional radios could often be located and captured at night after they had bedded. Fawns which had previously been captured by this method and those which were older than 1 month left their bed sites to run from the lights before they were located and captured. Deer with non-functional radios were recaptured as opportunity permitted.

Radio-locating Deer

To locate radio-marked deer an A.V.M. Model 12 receiver with 12 channels and fine tuning allowed several deer to be radioed simultaneously in the same area. A maximum of 43 deer carried functional radio transmitters during May 1971. Directions of individual signals were determined using two Model 23 Hy-Gain, three-element, 4-foot directional yagi antennas, one of which was mounted on a vehicle (Silvy 1974); the other was hand-carried while "walking-in" on deer (Figure 4).

Radio signals were initially detected by using the vehicle-mounted antenna. By driving roads and firetrails in areas occupied by specific radioed deer, it was generally possible to detect the radio signal and determine the direction of the deer by noting the direction from which the strongest signal was received. By taking two or three "fixes" on the signal from various points along the road, it was possible to accurately determine the location of the deer. The vehicle was then driven to a point downwind of and as close as possible to the

deer without disturbing it. Visual observations were possible by using the hand antenna to "walk-in" on the deer, moving in the direction of the strongest radio signal until visual contact was made.

Care was taken while "walking-in" on deer to observe but not disturb them. In some cases deer were visible from the road and they were kept under observation as long as possible. Occasionally up to 90 minutes or more was required to make contact; in some instances deer were not seen due to thick vegetation and/or their behavior.

Deer were approached from downwind so that they could not detect the observer through olfactory cues. Approach from upwind generally resulted in the deer's leaving the area before being sighted. Days of moderate wind (5-15 mph) were best for "walking-in", since the rustling of vegetation helped cover most noises. The least desirable conditions for "walking-in" were on days with no wind or with variable winds. On days with very strong winds (30 mph or more) deer were cautious and stayed in heavy cover. Days of light rain or heavy dew were good for "walking-in" on deer since little noise was made by stepping on damp vegetation; however, very wet weather interfered with operation of the A.V.M. receivers and thus made following radio signals more difficult.

The best habitat type for "walking-in" on and observing deer was the open pinewoods, which provided enough cover (generally palms) to conceal the observer, yet was open enough to allow for observance of, and movement with a deer at a distance. Least desirable were young hardwood-hammock areas in which dense growth made noiseless movement with antenna and other equipment nearly impossible, and resulted in few observations of undisturbed radioed deer.

It was possible to maneuver quietly in old mature hammocks with more open understory and some areas of open fringe mangroves. Areas of dry leaf litter and debris and extensive proproots in young mangrove stands, however hampered silent movement.

Data Collection

To facilitate observing adult radio-marked deer, 1x1¼-inch colored vinyl ear streamers were attached to 1¾-inch aluminum ear tags. Streamers facilitated locating deer in thick cover. Bells were placed on five deer to make locating and following them easier; however, the activities of some of the instrumented animals in housing subdivisions at night resulted in complaints from residents; also some dogs learned to follow the sound of the bells. Use of bells was thus discontinued and bells which were previously attached were removed. Specific deer were followed as long as possible by sight, radio signal, and in some instances by listening for the bells.

An effort was made to radio-mark a number of deer from each sex-age class to facilitate detailed studies of their behavior without causing disturbance to them. At various times observations on deer of specific sex-age classes were emphasized to clarify specific aspects of their life history. During the 1969-70 and 1970-71 breeding seasons an attempt was made to mark and observe activities of adult males. During the first season, few animals were available to be marked, and bucks either lost or damaged their radios while fighting. Most observations of reproductive behavior resulted from chance encounters of free-ranging deer and observations of tame penned deer. Prior to and during the

second season adult males were radioed and some carried functional radios at all times.

During February and March each year, emphasis was on capturing and radioing adult females that occupied more open pinewoods areas. This was to note behavior prior to, during, and after parturition, to observe aspects of life history and productivity, and to capture, mark and gather information on newborn fawns. Does were observed two to three times a day as they approached term. Their new fawns were marked at as early an age as possible and monitored to note behavior and survivorship. Yearlings were monitored to note dispersal tendencies during the breeding and fawning seasons.

To observe behavior during parturition, one semi-tame, free-ranging adult female was observed more closely, since she could be approached by the observer without causing her to noticeably change her behavior. During 1970-1972, the observer began monitoring her about 5 weeks before parturition, spending several minutes to several hours each day moving in the open and upwind of her. After such conditioning she was relatively undisturbed by the observer's presence only 20 yards away during and after birth of the fawn.

Life history data were gathered on captured deer, roadkilled animals, penned deer and all deer seen in the field. Attempts were made to observe deer at all hours of the day and night; however, the problem of disturbing deer at night, the sporadic use of open areas at night where observations were made, and the necessity to spend extended periods of time with select deer in specific habitats, precluded using random schedules of observation or of limiting observations to standard time intervals.

During all daylight hours I worked in the field observing marked and unmarked deer and radio-tracking specific animals. At night, observations on behavior were recorded two or three times a week throughout the study at varying hours in association with capture attempts. During 1969-70 a simultaneous study on movements, ranges, and habitat utilization was conducted on the Key deer, during which times data on social behavior of the deer were collected while locating them at random hours of the day and night (Silvy 1974). I assisted in night tracking in order to trap deer and collect behavior data at the same time. Observations of marked deer were also noted by other staff of the CWRL that worked in the Keys during the 5-year period. Observations were made whenever possible and for maximum lengths of time without disturbing the deer in order to get the maximum amount of accurate information.

On some days deer which moved into thick vegetation were never actually seen, despite hours spent moving with them. Reproductive activities were difficult to monitor as they often occurred in thick vegetation that obscured visual contact. During pre-copulatory activities, which involved chases over several acres, much of the behavior was observed during brief intervals as these deer passed close by the observer or when the observer made visual contact after radio-locating them as they paused between chases. Does were wary when running with the males and close observation was more difficult. Also males often followed females at a distance and kept them in sight. This occasionally resulted in disturbance to one of the breeding pair while "walking-in" on the other (see Figure 33).

In instances when deer could not be sighted, their behavior was recorded as "unknown"; when deer behavior was influenced by the observer, they were recorded as being disturbed. The number of recorded observations varied between different hours of the day and night, since at some hours deer were more easily disturbed and harder to observe than at other hours. Thus comparisons between data collected during the various time periods should be handled with caution.

Use of 7x35 binoculars facilitated identification of deer and observation of behavior. Observations were made in open areas at every opportunity. Night observations were limited to roadsides or other open areas, since all night observations necessitated use of spotlights from vehicles and use of lights away from open areas or away from areas that could be driven was impossible. In some instances deer did not terminate their behavior when lighted; however, often such observations disrupted the normal behavior and deer fled, especially in areas where deer captures occurred frequently. The only night "walking-in" occurred in connection with checking on or capturing very young radioed fawns.

For all animals captured, any distinctive physical features, antler development and reproductive status were recorded, and they were then weighed, sexed, and aged using tooth replacement and wear criteria (Severinghaus 1949). April 1 was arbitrarily designated as the birth date of Key deer since this date was near to the peak fawning time. Thus all deer were considered to become one year older on 1 April.

Unmarked deer observed in the field were identified as fawns, yearlings, or adults based on physical features. It was especially difficult at certain times of the year to determine the sex of yearlings,

distinguish 6-12-month fawns from yearlings, and yearlings from adult females. Most accurate was the identification of adult males during mid-July to March when they had full-developed antlers. Fetal sex ratios were determined from roadkilled pregnant does when possible.

All observations of marked and unmarked deer, their behavior, the date, time, location, weather conditions and associations with other animals were recorded during this study. Most observations were made on the north 3,000 acres of Big Pine Key on lands owned and/or managed by the government or on privately-owned or developed areas where marked deer were more concentrated. Observations of all deer seen in other areas of Big Pine Key as well as on other islands were also recorded.

Three observation towers constructed early in the study were designed for observing deer in adjacent open areas. Due to only sporadic utilization of these open areas and the regrowth of a thick area of bracken ferns in the vicinity of one of the towers, such observation from a fixed point was less productive than following marked deer or moving through areas until deer were sighted. Except for a period of limited use during the breeding season, towers were seldom utilized for observing behavior.

Tame penned deer were observed to note basic behavior patterns. The sequence of antler development and behavioral characteristics during various times of the year were observed in the adult male. Basic postures during solitary and mutual grooming, nose-trailing, and other reproductive behavior, including copulation, were observed in these penned animals. An adult female which was apparently unable to conceive, was periodically "tested" by allowing her and a mature tame

male to use the same pen. From these encounters the period between female estrus cycles was determined and male-female pre-copulatory, copulatory, and post-copulatory behaviors were observed.

Basic patterns of aggression were observed in penned deer since the tame male's responses to the observers were similar to the responses of free-ranging males toward other adult males during the breeding season. Postures and sequences of behavior were noted.

Meteorological factors were recorded to determine their effects on behavior patterns. Wind speed (categorized as none, 0-5 mph, 5-15 mph, or 15-30 mph) and wind direction were noted for each observation period. Cloud cover was also categorized as being absent, light (up to around 30 percent), moderate (30 to around 75 percent), or heavy (over about 75 percent). When the moon was visible, its phase was indicated; any precipitation was noted. Maximum and minimum temperatures for Big Pine Key were obtained from Mr. Ralph Higgs, who maintained a weather station on the north half of Big Pine Key. Temperatures at the times of deer observations were based on readings from Mr. Higgs and on notes recorded in the field.

Factors affecting survival of Key deer were examined. During April-June each year mosquito ditches were examined to find fawns which might have fallen in and drowned. Due to the extensive ditching on Big Pine, only a small portion of the total number could be adequately checked, thus those areas in which large concentrations of marked deer overlapped with areas of extensive ditching were walked every 2 to 3 days; other were covered as time permitted. In addition during 1971, to prevent any carcasses from floating into the channels with the outgoing

tides, major ditches were blocked using traps constructed from two 3-foot 2x2-inch poles with fine-mesh wire stretched between them. No fawns were found in traps; however, one carcass was found in a ditch near one of the traps. Radio-transmittered fawns which drowned were easily located in the ditches using their radio signals. Unmarked fawns were found only by chance.

Data Analysis

From data based on field observations of marked and unmarked deer, the percent of time marked deer were seen alone and with other deer, the seasonal changes in social groups, and seasonal group sizes were determined. To compare the Key deer to northern populations, frequencies of association were determined between related marked deer. Using (1) the number of times two deer, A and B, were seen together; (2) the number of times deer A was seen alone, and (3) the number of times deer B was seen alone, the frequency of association was determined as follows:

$$F.\ A. = \frac{(1)}{(1) + (2) + (3)}$$ (Hawkins and Klimstra 1970b).

Social organization and behavior of individual deer were compared throughout the year to determine how, when, and why any changes occurred.

Behavior was noted to determine times of activity and inactivity, and use of open areas was compared over daily and yearly periods to facilitate development of a census technique and other management techniques. Sex-age class differences were noted. During periods of

activity, the proportion of time deer performed various types of behavior was determined.

Reproductive behavior and performance were analyzed, based on field observations of reproductive activity, monitoring pregnant does, examining newborn fawns, and examining captive animals, and deer killed on the highway. From these techniques it was possible to determine at what age deer began to breed, which deer participated in breeding, the number and sex-ratios of fawns produced and successfully reared, the dates of breeding, and other aspects of life history and breeding biology. Special emphasis was made to determine the effects of behavior on reproductive performance.

Statistical analyses were performed whenever any comparisons were made between groups of data. Frequency of association values were tested using Student's t-test. Other data which were compared as ratios or percentages were analyzed using the chi-square contingency test unless otherwise indicated. All statistical tests and tables were from Sokal and Rohlf (1969) and Rohlf and Sokal (1969). The level of significance selected and employed throughout the analyses in all of the tests of significance was 0.05. All tests, unless otherwise indicated were performed on an Olivetti Underwood programma 101- desk-top computer, programmed by John Roseberry of the CWRL.

RESULTS AND DISCUSSION

Social Organization

Social organization of the white-tailed deer has been characterized as being limited to the family group comprised of an older doe with her fawns and offspring from previous years (Severinghaus and Cheatum 1956, Townsend and Smith 1933, Queal 1962, and Tibbs 1967). Although generally small, group size was occasionally as large as six (Chapman 1939) or seven individuals (Queal 1962). Hawkins and Klimstra (1970b: 409) characterized the "family group" as:

> "any group involving does and fawns that are spatially and socially related (frequency of association between all members of 50 percent or more) over a substantial period of time (usually several months)."

The earliest doe-fawn associations, termed "primary associations" (Hawkins and Klimstra 1970b:409), were generally maintained until the following fawning season when groups broke up; these deer formed "secondary associations" when new fawns were able to move with their does. This was also found for New York and Pennsylvania deer (Severinghaus and Cheatum 1956, Tibbs 1967).

In New York and Ohio, bucks often formed groups of two or three when feeding after breeding season and in summer, and they seldom associated with does (Townsend and Smith 1933:305, Chapman 1939:260); such groups were not considered family groups (Hawkins and Klimstra 1970b:409). DeVos et al. (1967:392) suggested that family units were characteristic of all deer in the genus Odocoileus but noted that of all Odocoileus, white-tailed deer were the least gregarious (p. 413).

Size and composition of Texas white-tailed deer social groups varied during the year (Michael 1970). They formed larger groups when feeding than when bedded, and group size in summer and winter was smaller than average due to rutting activities and the abundance of single does and does with fawns. Thomas (1966) recorded that groups of Illinois deer increased in size from February to mid-April and decreased during late April and early May. In summer, groups were composed of adult and yearling does, fawns, and yearling males; but no males aged 2½ years or older were represented until rutting season. Males formed small feeding groups during summer but in September male group size declined; this was also recorded by Crawford (1962) in the same herd. Similar trends were seen in Pennsylvania deer with more females being seen alone in June than any other month (Tibbs 1967).

The social organization of white-tailed deer was attributed to "the presence of a definite dominance hierarchy based on frequent aggressive-submissive interactions of all individuals" (Collias 1950: 98). In a penned enclosure adult males dominated all other deer, whereas does and yearlings with few exceptions dominated fawns. Severinghaus and Cheatum (1956:118) noted that "in the majority of cases an adult doe would drive an equally large or even larger adult buck away from the feed rack".

Robinson (1962) observed that heavy animals were dominant over lighter ones, and Tibbs (1967) noted group dominance by the larger deer. Ozoga (1972) found that in white-tails, yearling males rarely challenged larger deer and were subordinate to older males and aggressive females. The exception was a very old male that had similar status as yearling

males. In penned mule deer Browman and Hudson (1957:250) noted that a "kick order" was maintained and three adult females were dominant over all deer except adult males to which they gave way.

The social structure of Key deer was basically similar to that reported for the other white-tailed deer; however, the social bonds appeared more flexible in the Key deer. Of 13,743 observations of marked and unmarked deer, 9,853 observations (71.7 percent) were of single animals, whereas 3,890 observations (28.3 percent) were of two or more deer in a group (Table 1). Many of these observations were of deer feeding together or associating during the breeding season and did not represent strong social bonds. The maximum number of deer in a group was observed in August when nine animals (three does, three fawns and three adult males) all fed in an area while the males harassed the females. This group was not permanent, but rather a feeding assemblage and represented a "random association" of deer such as that described by Dasmann and Taber (1956:149). The same holds for the sightings of six and seven deer in groups (Table 1); most of these were temporary feeding or reproductive groups formed when several males harassed females accompanied by yearlings and fawns.

Deer were seen in groups most often in October through February and were more solitary during March through September (Table 1). The fewest groups were noted during May when 79.1 percent of the observations were of single deer; at this time young fawns did not move with does into open areas; yearling females had not yet reassociated with their does after being chased away during the fawning period; and males that had lost antlers were not moving together in open areas.

Table 1. Sightings of marked and unmarked deer as singles and in groups of 2 or more.

Month	Observations of deer in groups of									Total
	1	2	3	4	5	6	7	8	9	
April	929(76.6)[a]	234(19.3)	38(3.1)	7(0.6)	4(0.3)	0	0	0	0	1,212
May	1,080(79.1)	243(17.8)	34(2.5)	3(0.2)	3(0.2)	2(0.1)	0	0	0	1,365
June	1,197(74.9)	332(20.8)	54(3.4)	13(0.8)	1(0.1)	2(0.1)	0	0	0	1,598
July	992(73.6)	279(20.7)	65(4.8)	9(0.7)	0	1(0.1)	1(0.1)	0	0	1,347
August	799(72.2)	245(22.2)	51(4.6)	6(0.5)	3(0.3)	0	0	1(0.1)	1(0.1)	1,106
September	592(76.6)	144(18.6)	29(3.8)	2(0.2)	4(0.5)	1(0.1)	0	0	0	772
October	611(67.6)	235(26.0)	44(4.9)	11(1.2)	2(0.2)	1(0.1)	0	0	0	904
November	702(68.0)	284(27.5)	45(4.4)	2(0.2)	0	0	0	0	0	1,033
December	911(66.7)	387(28.3)	57(4.2)	9(0.6)	0	1(0.0)	1(0.0)	0	0	1,366
January	663(67.2)	269(27.2)	51(5.2)	3(0.3)	1(0.1)	0	0	0	0	987
February	628(64.5)	272(27.9)	58(6.0)	8(0.8)	7(0.7)	0	1(0.1)	0	0	974
March	749(69.4)	267(24.7)	53(4.9)	8(0.7)	1(0.1)	1(0.1)	0	0	0	1,079
Total	9,853(71.7)	3,191(23.2)	579(4.2)	81(0.6)	26(0.2)	8(0.1)	3(0.0)	1(0.0)	1(0.0)	13,743

[a]Numbers in parentheses represent percentages of the total number of deer seen during the month.

The frequency of association between deer belonging to matriarchal groups and for deer frequently seen together, changed throughout the year and varied depending upon the sex and age of animals involved. The frequencies of association were determined for 27 deer belonging to 10 family groups monitored over a period of from 3 to 24 months (Tables 2 and 3). Doe-doe fawns had an average frequency of association of 33.4 percent during the year while doe-buck fawns averaged 26.6 percent. The frequency of association between doe-doe yearlings averaged 23.9 percent while doe-buck yearlings averaged 13.7 percent; doe-doe associations between adult females averaged 18.4 percent. These values varied seasonally depending upon sex and age of the animals. For example, the frequency of association between doe-doe fawns varied from a low of 17.2 percent in May to 61.2 percent in August, while doe-buck fawns varied from a frequency of association of 12.5 percent in April to 71.2 percent in December. Yearlings also varied from a frequency of association of 37.0 percent between doe-doe yearlings in February to 0.0 percent for doe-buck yearlings during October, November and January.

During November through March after fawns were 7 months of age or older, the frequency of association between doe-doe fawns averaged 37.0 percent, while that for doe-buck fawns averaged 40.4 percent; doe-doe yearlings averaged 27.8 percent and doe-buck yearlings averaged 6.0 percent during the same period. Hawkins and Klimstra (1970b) found that for Illinois white-tailed deer, the frequency of association during a comparable period when fawns were between 4 and 8 months of age, were 72 percent for doe-doe fawns, and 75 percent for doe-buck fawns. The frequency of association for doe-doe yearlings during this period was

Table 2. Frequencies of association between marked does and their fawns

Month	Adult doe-fawn doe N	$\bar{X}_{F.A.}$	Range	Adult doe-fawn buck N	$\bar{X}_{F.A.}$	Range
April	3	24.4	7.8-35.0	3	12.5	3.4-25.7
May	4	17.2	7.1-25.0	8	14.6	4.5-23.1
June	4	22.8	0.0-36.4	6	29.0	14.3-59.3
July	2	48.2	40.8-55.6	4	30.7	20.0-44.4
August	2	61.2	52.3-70.0	4	29.4	20.0-47.6
September	2	21.8	0.0-43.5	3	14.5	0.0-26.7
October	2	39.9	30.9-48.9	3	25.2	16.7-38.9
November	2	37.1	35.0-39.1	2	31.7	11.1-52.2
December	3	42.1	16.7-60.5	2	71.2	66.7-75.6
January	3	26.9	0.0-44.4	2	41.9	13.3-70.4
February	4	43.1	25.0-60.0	2	34.7	14.3-55.0
March	4	34.8	17.0-49.0	2	22.8	20.0-25.6
Mean	35	33.4	0.0-70.0	41	26.6	0.0-75.6

Table 3. Frequencies of association between marked does and their yearlings.

Month	Adult doe-yearling doe N	$\bar{X}_{F.A.}$	Range	Adult doe-yearling buck N	$\bar{X}_{F.A.}$	Range
April	8	27.3	0.0-50.0	5	22.1	0.0-50.0
May	8	24.8	0.0-66.7	5	15.9	10.0-24.1
June	8	15.0	0.0-50.0	5	21.8	0.0-34.0
July	5	9.9	0.0-20.0	3	9.2	0.0-20.0
August	5	33.9	0.0-75.0	3	14.8	0.0-44.4
September	4	16.6	0.0-42.9	3	1.7	0.0- 5.0
October	3	32.9	24.6-42.9	3	0.0	0.0- 0.0
November	3	13.0	0.0-21.7	3	0.0	0.0- 0.0
December	3	30.3	20.7-42.9	4	15.0	0.0-60.0
January	3	37.0	10.0-71.4	1	0.0	0.0- 0.0
February	3	26.1	14.0-50.0	0	--	--
March	3	22.7	8.7-40.0	0	--	--
Mean	56	23.9	0.0-75.0	35	12.7	0.0-60.0

64 percent. They found that the frequency of association between doe-buck yearlings was 3 percent in summer and doe-doe yearlings averaged 5 percent during summer. Key deer, following the break-up between the doe and her old fawns (now yearlings), averaged 18.5 percent with doe-yearlings and 17.2 percent with buck yearlings during April through July. During and after August the frequency of association for doe-doe yearlings remained relatively high except during September and November when it dropped, possibly due to breeding activities. Does and yearling males associated very little after October; one exceptional doe-buck yearling association that was unusually strong lasted until the male was 2 years of age.

That the social organization of Key deer fluctuated seasonally was reflected in the amount of time deer spent alone. Records, maintained for 10 (5 male and 5 female) radioed fawns to determine the amount of time spent alone and with their does, revealed that the first day fawns spent nearly 100 percent of the time with their does. If does were disturbed they left the fawn, moved up to 100 yards away and then rejoined it after the disturbance ceased. As fawns increased in age up to around 5 weeks, progressively more time was spent alone (Table 4). During the second, third and fourth weeks, fawns were found to be alone 68 percent, 71 percent, and 69 percent of the time, respectively. During the first 3 months of life, males were found alone more than females except during weeks sex, seven, and ten; however, differences were not statistically significant.

During the first 3 months males averaged 68.8 percent of their time alone while females averaged 54.9 percent alone. After about 3

Table 4. Observations in which young fawns of known age were seen alone and with related deer.

Age (Weeks)	Males Seen			Females Seen		
	Alone	With Mother or Sibling	Total Observations	Alone	With Mother or Sibling	Total Observations
0- 1	20(62.5)[a]	12(37.5)	32	10(47.6)	11(53.4)	21
1- 2	22(75.9)	7(24.1)	29	4(44.4)	5(55.6)	9
2- 3	13(72.2)	5(27.8)	18	7(70.0)	3(30.0)	10
3- 4	14(73.9)	5(26.1)	19	8(61.5)	5(38.5)	13
4- 5	16(94.1)	1(5.9)	17	8(72.7)	3(27.3)	11
5- 6	8(53.3)	7(46.7)	15	7(53.8)	6(46.2)	13
6- 7	10(66.7)	5(33.3)	15	7(70.0)	3(30.0)	10
7- 8	9(69.2)	4(30.8)	13	9(64.3)	5(35.7)	14
8- 9	6(46.2)	7(53.8)	13	6(35.3)	11(64.7)	17
9-10	12(66.7)	6(33.3)	18	7(70.0)	3(30.0)	10
10-11	10(58.8)	7(41.2)	17	4(40.0)	6(60.0)	10
11-12	12(80.0)	3(20.0)	15	7(46.7)	8(53.3)	15
0-12	142(68.8)	69(31.2)	221	84(54.9)	69(45.1)	153

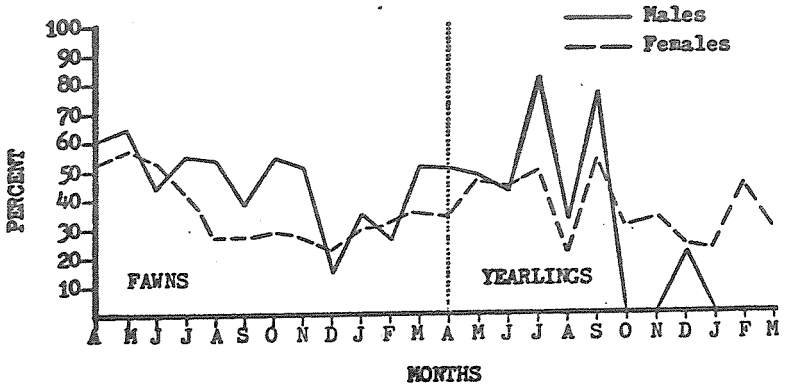
[a]Numbers in parentheses represent the percent of the total observations of fawns in each sex-age category.

months of age the amount of time females were alone decreased, whereas males stayed alone slightly over half of the time until September and after November, when they decreased the amount of time spent alone (Figure 5). Males spent significantly more time alone than females during August, October, November, and March. Both males and females showed an increase in time spent alone in March, just before their mothers gave birth to new fawns; this was a reflection of the disassociation of family units. While time spent alone decreased after fawns reached 5 months of age, the amount of time spent with their does increased (Figure 5). Females during June, July, and August, and males after November, spent relatively more time moving with their does. The only significant difference occurred in August when female fawns spent more time with their does than did male fawns.

The amount of time that marked yearling females were seen with doe known to be their mothers, varied from 29 percent in September to 68 percent in January (Figure 6, Table 5). The amount of time that all marked yearling females were observed with adult does, either known or suspected to be their mothers, varied from 20 percent in November to 55 percent in April. The sightings of yearling females with dams decreased during June and July, increased slightly in August, then was lower in September, October, and November. In December, after the breeding season, yearling females and their does reassociated and were seen together up to 68 percent in January. Prior to the parturition of new fawns, the amount of time yearling females were with does decreased in February and March to just under 50 percent.

Figure 5. Observations in which marked male and female fawns and yearlings were found alone. Only those deer for which the dam was known were included. Percentages were based on the number of deer in each of the sex-age classes.

Figure 6. Observations in which marked male and female fawns and yearlings were found with their own dams. Only those deer for which the mother was known were included. Percentages were based on the number of deer in each of the sex-age classes seen per month.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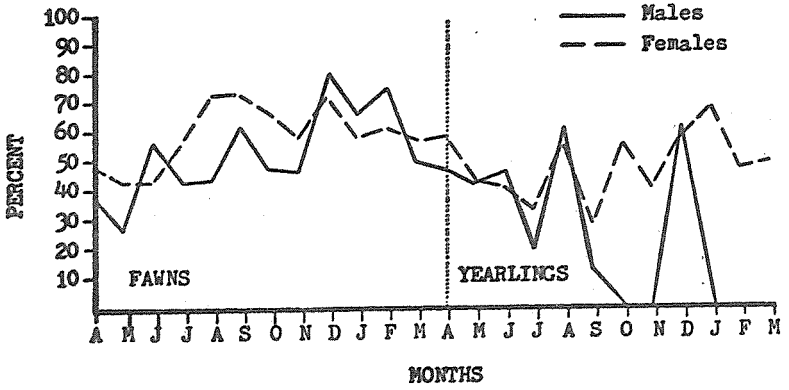
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Table 5. Observations in which marked yearling females belonging to known does were seen alone and with other deer.

Month	Alone	Seen With: Their Own Mothers	Seen With: Other Adult and Yearling Females	Seen With: Adult and Yearling Males	Seen With: Fawns	Total Number Seen
April	29(33.0)[a]	52(59.1)	15(17.0)	1 (1.1)	1 (1.1)	88
May	36(51.4)	31(44.3)	7(10.0)	0	2 (2.9)	70
June	29(43.3)	27(40.3)	10(14.9)	1 (1.5)	5 (7.5)	67
July	20(48.8)	14(34.1)	8(19.5)	1 (2.4)	4 (9.8)	41
August	7(20.6)	19(55.9)	14(41.2)	3 (8.8)	4(11.8)	34
September	16(51.6)	9(29.0)	6(19.4)	0	1 (3.2)	31
October	12(29.3)	23(56.1)	3 (7.3)	4 (9.8)	12(29.3)	41
November	10(32.2)	13(41.9)	3 (9.7)	2 (6.4)	5(16.1)	31
December	14(24.6)	33(57.9)	4 (7.0)	9(15.8)	15(26.3)	57
January	8(20.5)	27(69.2)	3 (7.7)	0	11(28.2)	39
February	15(42.8)	17(48.6)	2 (5.7)	0	6(17.1)	35
March	7(29.2)	12(50.0)	2 (8.3)	0	11(45.8)	24
Total	203(36.4)	277(49.6)	77(13.8)	21 (3.8)	77(13.8)	558

[a]Numbers in parentheses represent percentages of the total number seen per month; percentages do not always equal 100%, since several deer were often together at once.

At this time yearling females showed signs of dispersal, possibly being driven out by their mothers or by other does with new fawns. Thomas (1966) reported that during May and June, white-tailed does chased and drove yearlings away and Tibbs (1967) reported that during the period when fawns were young, does were hostile toward other group members.

While in a new area any Key deer giving birth probably remained in these new areas with their fawns. That the bonds between doe and fawn were strong enough to cause a doe to remain in the vicinity of a newborn fawn was indicated by data on does using areas having no fresh water where their young fawns were located (see Doe-fawn bonds).

Data on associations involving yearling males were limited because many yearling males did not maintain associations with family groups, were not seen after breaking away from the groups, or were known to have died during or following summer. Marked males spent from 0 percent in October, November and January through March to 62 percent in August with their does (Figure 7, Table 6). With exception of one yearling male, the amount of time spent with the adult female decreased from April through September and after October no yearling males were seen with their does. The one exceptional 2-year old animal was still with his mother when she gave birth to fawns during both subsequent years after his birth. Based upon observations of all marked yearling males, it appeared that after April over 50 percent of their time was spent alone (Figure 7).

During May adult females were alone around 66 percent of the time; they spent little time with their new fawns and yet spent little time

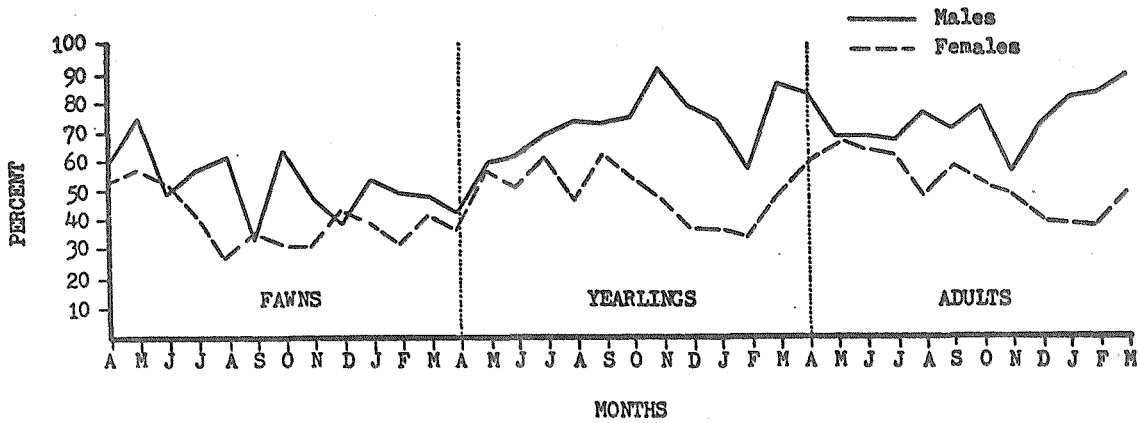


Figure 7. Observations in which marked deer of each sex-age class were seen alone. Percentages were based on the number of deer in each sex-age class which were seen per month.

Table 6. Observations in which marked yearling males belonging to known does were seen alone and with other deer.

Month	Alone	Seen With: Their Own Mothers	Seen With: Other Adult and Yearling Females	Seen With: Adult and Yearling Males	Seen With: Fawns	Total Number Seen
April	32(49.2)[a]	30(46.2)	0	3(4.6)	2 (3.1)	65
May	19(45.2)	18(42.8)	3 (7.1)	2(4.8)	4 (9.5)	42
June	18(41.9)	20(46.5)	6(14.0)	0	4 (9.3)	43
July	4(80.0)	1(20.0)	0	0	0	5
August	4(30.8)	8(61.5)	1 (7.7)	1(7.7)	1 (7.7)	13
September	6(75.0)	1(12.5)	0	0	1(12.5)	8
October	0	0	0	0	0	0
November	0	0	0	0	0	0
December	1(20.0)	3(60.0)	1(20.0)	0	0	5
January	0	0	0	0	0	0
February	0	0	0	0	0	0
March	0	0	0	0	0	0
Total	84(46.4)	81(44.8)	11 (6.1)	6(3.3)	12 (6.6)	181

[a]Numbers in parentheses represent percentages of the total number seen per month; percentages do not always equal 100%, since several deer were often together at once.

with other group members (Figure 7, Table 7). As fawns matured and moved more with their does, the does also spent more time with yearlings as secondary associations were established and does spent progressively less time alone during June through August. Adult females were found alone around 58 percent of the time in September, then they decreased the time spent alone until January and February when they were alone less than 40 percent of the time. In March they were alone around 50 percent of the time; time spent alone increased in April and May as they gave birth to new fawns. This sequence of time spent alone corresponded to the cycle of birth of new fawns in April and May, establishment of social groups from June to September, disruption of these groups by the breeding activities in September, strengthened social bonds during December through February, then disruption of the groups in March and April as does began to give birth again to new fawns.

Adult males spent significantly more time alone than adult females in all months except May and November (Figure 7, Table 8). In May males were alone around 68 percent of the time as they were regrowing new antlers, were relatively non-aggressive, and were associating with other males only during periods of feeding or bedding in open areas. They spent around 33 percent of their time with other deer during May, June and July; however, in August there was less association between males, and the amount of time alone increased to 76 percent. As they shed velvet in September no compatible buck associations were witnessed; however, males were seen together in association with females that were being harassed or serviced during the breeding season; by March males spent up to 90 percent of their time alone.

Table 7. Observations in which marked adult females were seen alone and with other deer.

Month	Alone	Seen With				Total Number Seen
		Yearlings	Fawns	Adult Females	Adult Males	
April	551(59.5)[a]	193(20.8)	64 (6.9)	144(15.6)	7(0.8)	926
May	520(66.3)	128(16.3)	76 (9.7)	89(11.4)	12(1.5)	784
June	451(58.5)	144(18.7)	143(18.5)	89(11.5)	14(1.8)	771
July	309(56.0)	66(12.0)	135(24.5)	99(17.9)	15(2.7)	552
August	213(48.7)	87(19.9)	131(30.0)	77(17.6)	14(3.2)	437
September	142(58.0)	30(12.2)	56(22.9)	31(12.6)	8(3.3)	245
October	164(52.1)	45(14.3)	98(31.1)	23 (7.3)	16(5.1)	315
November	132(48.7)	34(12.5)	82(30.2)	18 (6.6)	25(9.2)	271
December	160(40.0)	79(19.8)	166(41.5)	43(10.8)	11(2.8)	400
January	116(39.6)	51(17.4)	104(35.5)	49(16.7)	1(0.3)	293
February	129(38.0)	68(20.0)	156(46.0)	56(16.5)	5(1.5)	339
March	227(49.4)	47(10.2)	182(39.6)	86(18.7)	4(0.9)	459
Total	3,114(54.4)	972(17.0)	1,393(24.3)	304(14.0)	132(2.3)	5,792

[a]Numbers in parentheses represent percentages of the total number seen per month; percentages do not always equal 100%, since several deer were often together at once.

Table 8. Observations in which marked adult males were seen alone and with other deer.

Month	Alone	Seen With: Adult and Yearling Males	Seen With: Adult and Yearling Females	Seen With: Fawns	Totals
April	113(83.1)[a]	13 (9.6)	7 (5.1)	2(1.5)	136
May	101(67.8)	36(24.2)	21(14.1)	1(0.7)	149
June	126(68.1)	50(27.0)	15 (8.1)	0	185
July	128(67.0)	49(25.6)	22(11.5)	4(2.1)	191
August	106(76.2)	25(18.0)	13 (9.4)	4(2.9)	139
September	64(71.1)	13(14.4)	15(16.7)	2(2.2)	90
October	75(58.9)	12(12.6)	13(13.7)	1(1.0)	95
November	56(56.0)	11(11.0)	31(31.0)	6(6.0)	100
December	71(71.7)	13(13.1)	18(18.2)	2(2.0)	99
January	51(81.0)	7(11.1)	6 (9.5)	2(3.2)	63
February	42(84.0)	6(12.0)	1 (2.0)	1(2.0)	50
March	44(89.8)	3 (6.1)	2 (4.1)	1(2.0)	49
Total	977(72.6)	238(17.7)	164(12.2)	26(1.9)	1,346

[a]Numbers in parentheses represent percentages of the total number seen per month; percentages do not always equal 100%, since several deer were often together at once.

Between mid-September and mid-December adult males were not seen to associate with one another unless there was overt aggression between them or unless they were tending or otherwise harassing a female. The first non-aggressive association between adult males after the breeding season was on 8 December as two males were seen moving together; the first sightings of males feeding together were not until 23 December. The percent of time that adult males were seen associated with one another ranged from 27 percent in June to a low of 6 percent in March (Table 8). During March, when antlers were being shed, males without antlers were suddenly almost defenseless and became solitary; adult males with antlers and adult females were more aggressive. In South Dakota, Progulske and Duerre (1964) found that few bucks frequented open meadows when antlers were growing; they attributed this to secretive behavior resulting from physiological changes accompanying antler growth. They noted that summer feeding associations were established between adult males, and yearlings and adult males were seen with other deer more often.

The social structure of the Key deer was not fixed, but rather was a flexible, dynamic system, which changed during the annual cycle. During the breeding season, adult males were dominant over all other animals. Whether yearling males and adult females dominated one another varied, depending upon the situation at the time. While both were subdominant to adult males, they were dominant over yearling females and fawns. Yearling females were dominant to fawns. This hierarchy was maintained through aggression communicated by postures, displays, or actual physical force.

Within each sex-age class there existed a hierarchy among individuals. The 3- to 6-year-old males were dominant over 2-year olds and over very old males; all of these in turn were dominant over yearling males. In general older does were dominant over younger does.

Physical characteristics were important in determining the status of an individual. Males with broken antlers or with one antler were sub-dominant to bucks of equal size that had full racks. One adult male (AM032) which lost one antler each year just after loss of velvet, was challenged by 2-year-old males, which normally avoided combat with older adults with full racks. During the breeding season in encounters between a yearling male and an adult female, the yearling male was dominant unless the female was accompanied by her fawn or unless the female was feeding and the male was interrupting the feeding; then the adult female was dominant and the yearling was sub-dominant.

Following the breeding season the hierarchy shifted. In December adult males began reassociating with one another without aggression and adult females, yearling females and fawns formed matriarchal groups. Yearling males were often seen harassing other deer, nose-trailing and occasionally breeding receptive females. During this time, older adult females were the dominant animals in the groups, even over yearling males. Whereas encounters in December through February between adult males and females resulted in the female's backing away or running at the buck's approach, after males shed antlers in March and continuing through June, adult females were the dominant animals.

Adult females often forcefully drove unrelated deer as well as their older fawns (now yearlings) out of their ranges. One adult

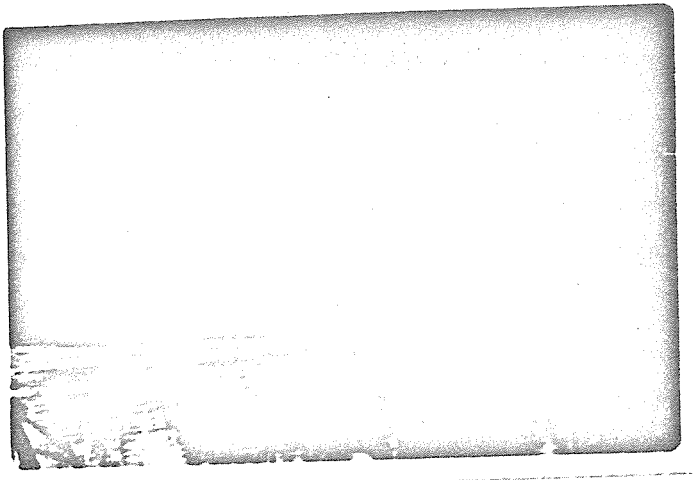
maternal doe was observed driving a smaller pregnant doe out of her feeding area by rushing and striking with the front feet. Then as the pregnant deer retreated, the maternal doe slowly followed at a distance of 30 to 50 yards until the pregnant doe was out of the normal range of the maternal doe. In another year the maternal doe pushed her 2-year-old male offspring away from her repeatedly, using her head to "butt" him gently in the side and pushing him until he retreated from the area where she had her new fawn. Adult females with fawns were dominant over the antlerless males, which they drove out of areas where they had fawns.

Until mid-July bucks in velvet were subordinate to females; however, after mid-July bucks with well-developed racks in velvet began to reassert themselves. During this time, the female's aggression toward all deer subsided somewhat as fawns were moving with them and family groups had reformed. It was at this time in mid-summer that the most prolonged bouts of aggression were seen between males and females. Males challenging females used the forelegs to strike or flail at females that did not retreat at their advances; however, the challenge was often met with a flail by the adult female when her fawns were present (Figure 8). On 4 July 1970, an adult male and female flailed one another three times over a period of 5 minutes at up to 5 to 30 seconds each time. Another male and a yearling fed nearby; but they did not participate in the activities other than to move out of the way of the two dominant deer.

In the summer the frequency of such encounters increased and by September adult males were again dominant over adult females. Such a

Figure 8. Flailing behavior between adult male and female deer. Such behavior was an intense type of aggression between deer of nearly equal status in the social hierarchy.

Figure 9. An alarmed deer demonstrating typical "curiosity" behavior. The raised tail and erect caudal hair indicated a high level of excitement as the deer circled the object of interest until the scent was detected or the object was otherwise identified.



system of shifting hierarchies and the activities of adult males and adult females during times of breeding and fawning led to the shift in composition of the social units. Adult males were essentially solitary, with exception of forming transitory associations with adult females during the breeding season, and with other adult males when feeding and bedding during the summer. The matriarchal units changed in their composition as fawns increasingly spent more time with their does, and older female offspring associated with them during June through September. This primary association was disrupted only slightly during the breeding season; some male fawns did not reassociate with their family groups after this disruption. The second disruption occurred in March and April when new fawns were born, and old fawns (now yearlings) were driven out of the range of their does and were harassed by other does that had fawns in the area. The result was a breaking-apart of the family units.

While these units did not reform until late May and June, members of the units were often seen to feed together in the same areas; the bonds between them did not appear as strong. Few yearling males reassociated with their family units. Those yearlings remaining in the same area as their does were harassed during the breeding season by adult males and they began chasing females themselves; after the breeding season they did not appear with their does again.

While the Key deer shows the same basic social structure of other groups of white-tailed deer that have been studied, the social groups of Key deer appear much weaker, the deer having lower frequencies of association and many fawns never being seen with their own does. Often

fawns were seen attempting to follow any other deer that they encountered and on occasion showed care-seeking behavior toward unrelated deer and attempted to nurse.

The looser social organization of Key deer, no doubt, reflects their history in the insular environment, where absence of predators and the tendency for most females to occupy the same range for life, result in different selective pressures from those on the mainland. White-tailed deer exposed to predation tend to have greater chances for survival when young are more dependent on family members, rather than being independent at an early age. It was found by White et al. (1973), that Texas fawns which were more independent, active, and inquisitive were more susceptible to predation and accidents. Such selection against independent young would not exist in the Keys to the extent that it is found on the mainland.

In northern populations deer typically leave their spring and summer ranges to spend the winter in large groups in deer yards (Severinghaus and Cheatum 1956). Bonds between family units may become weakened after high frequency of contact with large numbers of animals, and as they return to their spring and summer ranges, members of family units reassociate with much mutual grooming and interaction (Miller 1971b). Such interaction was suggested by Miller (1971b) as being a social bonding mechanism, reducing aggression among those animals (see Grooming). It would seem that strong bonds between family members would facilitate these annual reassociations, and allow for female members of the family units to reoccupy overlapping ranges with minimal antagonism between them. Since, with few exceptions, female Key deer

tend to occupy the ranges which overlap with that of their mothers most of their lives (Silvy 1974), the need for strong bonds to facilitate a periodic reassociation after interacting with a number of unrelated deer seems less important.

One possible advantage of the looser social organization may be a greater capability for dispersal by younger animals at times of relatively high population levels. If the deer population were periodically reduced at the edge of its range, such as on outlying islands (see Mortality), a flexible social organization could result in greater dispersal from Big Pine and other Keys having high populations. Weaker social bonds between fawns or yearlings and their family groups would not serve to tie the young to one area; they would thus seem more likely to leave their home area than deer closely associated with the matriarchal group.

In at least two instances during the study, marked Key deer females appeared to establish ranges in new areas (Silvy 1974). One 2-year-old doe (AF061) left her old range that her other family members occupied and in which she was raised. Another doe (AF847) was found on No Name Key after being captured and tracked for 7 months on Big Pine Key. The former shifted her range after the fawning season when maternal does often drive deer out of areas where they have fawns. Also the "displaced" doe may have had a fawn in the new area and may then have become reestablished in a new range (see Doe-fawn bonds).

Antler Development

It was apparent that the status of a male in the social hierarchy was greatly influenced by the extent of development of the antlers as well as the size and physical condition of the animal. To appreciate the changing social structure of deer it is helpful to know the seasonal sequence of antler development of males.

Adult and yearling males began to regrow new antlers immediately after the loss of old antlers in March and April. By May most males had 2- or 3-inch stubs and by 30 June adult males had three or four points per beam; growth of racks was nearly complete. Velvet antlers were completely formed by July. The earliest observation of a polished rack occurred on 7 September 1971 when a yearling was seen with strips of velvet hanging from his spikes. Most polishing occurred during the second and third week of September. In 1971 all deer seen after 23 September were polished except for fawns which had velvet-covered buttons through December.

During the breeding season bucks were occasionally seen with broken and missing antlers due to combat injuries. One adult male lost his left beam prematurely during the 3 years, dropping it the first year by 18 February, the second year by 8 December, and the third year in September, shortly after shedding the velvet. Most normal antler loss occurred in mid-March, the latest sightings of a wild deer with an antler was on 26 April. The penned male lost buttons as a fawn on 30 May, and dropped antlers on 7 May and 30 May in subsequent years.

Regrowth of antlers was almost immediate. The development of racks with three and four points occurred later in the life of Key deer

than in northern white-tails (Klimstra 1974). This fact along with the agonistic behavior between males, resulted in deer aged 2½ years or less less, aged 6½ years or more, and deer with broken racks playing subdominant roles to 3- to 5-year old animals having large six- and eight-point racks.

Descriptive Behavior

In North American deer the types of activity and times when these activities are observed vary with weather conditions (Linsdale and Tomich 1953, Michael 1970, Palmer 1951, Hawkins and Klimstra 1970a, Ozoga and Gysel 1972), hour of the day or night in relation to sunrise and sunset (Michael 1967, Thomas 1966, Browman and Hudson 1957, Marshall and Whittington 1968, Jeter and Marchinton 1964, Halloran 1943, Ozoga and Verme 1970), age and physiological condition of the animal associated with fawning and antler development (Progulske and Duerre 1964, Jackson et al. 1972, Tibbs 1967), human activities (Montgomery 1963, Townsend and Smith 1933, Autry 1967), sex (Jackson et al. 1972), moon phase (Progulske and Duerre 1964, Thomas 1966), and whether deer were previously active or inactive (Tibbs 1967, Ruff 1938).

During this study behavior was classified into the four basic types: standing, moving, feeding, and bedding. These were characteristic postures basic to other more specialized types of behavior. Reproductive activities incorporated other types of behavior into unique patterns which were seen only during the breeding season. Other behavior patterns incorporating the four basic patterns were seen throughout the year. Deer were considered inactive when they bedded

and were active when standing, moving, or feeding. A brief description of the common behavior patterns seen in Key deer, the conditions under which they were performed, and their frequency of occurrence are discussed in the following sections.

Standing

Deer stood when they were disturbed, when they paused between bouts of feeding, when resting in the shade, at times when they groomed themselves, or when engaged in some type of mutual interaction with other deer, such as grooming or displaying. Of all observations of standing behavior 96.9 percent occurred when deer were disturbed by some distant intruder or by some unidentified noise. This included disturbance from humans, vehicles, or other mechanical equipment, other animals that were heard but not identified, and animals that came into view or approached from a distance. Key deer were seen to stop other types of behavior to stand when distant objects alerted them and they often stood when a beam of light was directed at them at night.

Standing behavior has been described by Townsend and Smith (1933), who found that deer in New York stared intently until a noise or movement was identified as another deer. Tibbs (1967) noted that Pennsylvania white-tails stood when disturbed, and Linsdale and Tomich (1953) noted that mule deer stood and stared at distant intruders.

Postures of the body while standing varied with the degree of excitement. The lowest levels of excitement were evident in Key deer that observed other animals at a distance and in deer that were grooming themselves or chewing cud. Excitement levels increased as a source of

disturbance approached, was more suddenly presented to them, was in an area where capture attempts and night-lighting attempts were frequent, or when the deer smelled, heard, or saw dogs or men at close range. As a rule, the closer the disturbance, the greater the excitement level (see Flight distance).

When standing, deer usually had all feet on the ground with the head erect and in line with the body, turned in the direction of a disturbance, or positioned so as to see around obstacles. They occasionally lifted and shook their legs, ears, or head, and flipped the tail to dislodge flies and mosquitoes, especially when these pests were numerous.

When observing other deer at a distance, there was generally no alarm or aggression and interest in them usually lasted up to around 30 seconds, after which other activities were resumed. Strange deer moving into the open at a distance often received closer scrutiny. As the excitement level increased the tail was partially or completely raised, pilo-erection increased as did nervous stomping, shifting the position of the body, snorting, and movements of the head and neck up and down a few inches while staring in the direction of the intruder. Slowly-moving objects visible at a distance or distant noises or scents from a partially concealed intruder elicited stalking or curiosity behavior. This stance was one of standing with all feet placed firmly on the ground, with the body at a 180° angle to the intruder, and with the head toward the object of interest. The deer walked forward a few paces at a time to within 50 to 100 yards of the object, stretching the neck in the direction of the disturbance with ears and eyes alert to the front;

it occasionally turned to the side or to the rear as if to retreat; however, if the intruder remained concealed, they resumed the stalking (Figure 9).

Head-bobbing was often performed by adult and yearling does and fawns but rarely by older males. Such head-bobbing was described by Tibbs (1967:41) for Pennsylvania white-tails, which when ". . . trying to detect scent or visually appraise the observer (the deer) lowered their nose to the ground, then lifted it as high as they could and also moved their head from side to side." Then they moved short distances and repeated this. Linsdale and Tomich (1953:123) described "head-bobbing" in mule deer as ". . . a quick lowering of the head from an alert position high above shoulder level, to one near shoulder level and a rapid return." The greater the excitement the farther it lowered its head.

When disturbed, Key deer usually raised the tail and tarsal tufts to some degree and adjacent deer often closely watched the performing deer and were alert in all directions rather than assuming the same orientation as the curious deer. A typical behavior associated with this was a stomping of one or alternate front feet. This was performed by raising one leg, bending it at the joints and holding it positioned above the ground for several seconds. Then with a shift of the body weight forward at the same time as the leg was straightened, the foot was forcefully thrust to the ground. The result was a slight noise, not audible to the observer at 20 yards; however, it alerted other deer nearby.

Often curiosity and stomping were combined with snorting, which served to intimidate the intruder or caused him to reveal his position

(see Communication). Often the deer moved in a large circle around the object of interest until getting downwind and picking up olfactory cues to identify it. Linsdale and Tomich (1953:163) noted that mule deer showed curiosity toward strange objects which they could not "identify satisfactorily" and Severinghaus and Cheatum (1956:129) referring to northern white-tailed deer noted that the "inability to locate the origin and creator of a sound often arouses its curiosity", and

> "Often when a deer has spotted an object it does not immediately identify, it blows and snorts, stomps its front feet, and then slowly moves to a position downwind to the object of its curiosity."

Fawns became cautious and alert when their does stomped, remained nearly motionless except for movement of the ears to detect any sound, and then bounded for cover if the does snorted or made any rapid movements. When the intruder moved, advanced, or was very close when discovered, the deer became alarmed and escape behavior followed.

Moving

Observations of movement involved disturbed deer 67.5 percent of the time as they left an open area for cover when disturbed by the observers, vehicles, dogs, or other aggressive deer. Speeds of movement increased and patterns of movement changed as excitement levels increased. Deer observed to be moving while feeding were not classified as moving as long as they spent most of their time browsing or grazing.

Movement patterns of Key deer were similar to the basic quadrupedal patterns of moving diagonal limbs in sequence (Zug 1972, Linsdale and Tomich 1955, Severinghaus and Cheatum 1956). Movement of the right front leg was followed by left rear, then left front by right rear; the

sequence was then repeated. There were four gaits observed in deer: walking, trotting, galloping, bounding. Deer of all sex-age classes were seen to use these four types of locomotion and often two or more types were utilized in changing positions.

Walking was observed in undisturbed deer moving from one site to another or when moving while feeding. Three feet were generally on the ground at one time, while only one was off the ground and moving at any given time. The same sequence of limb movement was followed as indicated above. As the pace increased to a fast walk, two or three feet were on the ground at one time with one or two being moved at a time; however, if two were moving simultaneously they did not touch down at the same time. Fawns walked more cautiously by slowly moving each limb and not raising one limb until the other three were on the ground.

When trotting diagonal feet touched the ground simultaneously, and only two feet were on the ground at once. This occurred when deer were chased by other deer or when otherwise disturbed, and was often performed with ears oriented toward the source of disturbance and with tail either lowered or raised depending on the excitement level. It resulted in a rapid movement from place to place. Deer often trotted after tossing the head while playing.

The gallop or run was seen as deer changed from one gait to another and was characterized by a disruption of the normal movement of diagonal limbs. It served as a transitional gait between trotting and bounding. Although diagonal feet moved together they did not touch down at the same times. Deer were most often seen to gallop as they retreated from some threatening situation and often used two or more

gaits. Those deer retreating from open areas at night most often ran unless being actively pursued, in which case they bounded.

The greatest speed was attained using the bound, in which back legs thrusting together, propelled the animal forward while the front legs, moving together, served to support the weight of the deer between bounds. Hind feet landed ahead of the front feet and forelegs extended forward during the long strides. The tail was raised and ears were erect and directed backward toward the threat. Deer bounding from an area tended to cause other deer to follow by bounding or galloping. This gait most often occurred when deer retreated from man or some immediate danger. The greatest measured distance covered in one stride by a bounding deer was 30 feet; this occurred when an adult female escaped from an area during an attempt to recapture her with the net.

Swimming

An additional form of locomotion displayed by Key deer was swimming. Although this was not frequently observed, deer proved to be capable swimmers. Palmer (1951:276) reported that when the deer "Billy" was first brought into Tomhegan Camp he jumped off the dock and swam so rapidly that two men paddling a canoe had trouble overtaking him. Behrend (1966:59) reported that his results "clearly show that deer will freely enter the water to wade and swim, in order to avail themselves of desirable food", and Severinghaus and Cheatum (1956:162) reported that "deer will take to water to escape dogs, other predators, and man."

During this study two deer were captured as they swam between islands: one was swimming between Big Torch and Water Key, a distance of 0.35 miles and the other swam between Big Pine and Porpoise Key, a distance of 0.81 miles (Figures 2 and 10). One other deer was observed swimming in Bogie Channel between No Name and Big Pine Key, a distance of 0.45 miles. These latter two females swam to fawns on No Name and Porpoise Key and returned periodically to Big Pine.

During 23 capture attempts when deer jumped into canals, 15 escaped by out-swimming or out-maneuvering the trappers. Although not a common means of locomotion, swimming deer were occasionally reported by professional fishing guides and local residents. While deer swam between islands, this appeared to be associated more with temporary dispersal to islands over very short distances and probably occurred in response to aggressive behavior by dominant males or females that displaced younger or subdominant deer, due to changes in habitat causing shifts in areas of deer use, or due to unusual circumstances such as giving birth in an area where lack of food or suitable water made frequent trips to islands with food and water necessary.

Feeding

Feeding behavior occurred as deer stood or walked slowly. Tails were limp and twitched at 10- to 60-second intervals from side to side, especially during the rainy seasons when insect pests were bad. Ears were generally directed in varying directions but very seldom were the openings in the same direction at once unless the deer became attentive to some disturbance. Ears were frequently flipped when insects were

Figure 10. An adult doe swimming the 0.8-mile channel between Big Pine Key and Porpoise Key, where she gave birth to a fawn.

Figure 11. An adult doe balanced on her hind legs while feeding on thatch palm fruits. Front legs were hanging limp in front of her.

numerous. The head was raised one to five times a minute as deer fed, but if undisturbed these periods of looking around were only for a few seconds duration. Deer were selective as to what was eaten and often passed up many plants to select specific plant parts to browse. When feeding on flowering stalks, or fruits of palms or other tall growth forms, normally not of their reach while standing on four feet, they often stood balanced on their back legs with forelegs bent and used to maintain balance; the tail was at a 90° angle away from the body (Figure 11). Generally the back legs were moved while maintaining their balance. Bouts of feeding ranged from brief periods of 5 to 10 minutes up to 1½ hours. At night and in mid-morning feeding was often interspersed with periods of bedding and grooming.

When mildly disturbed deer often appeared to show displacement behavior by turning to feeding rather than fleeing or resuming previous behavior. At such times deer bit off some vegetation and quickly raised the head to watch the source of disturbance while chewing, then very quickly took another bite. Michael (1970) noted that deer spent more time feeding than in any other activity, and Ozoga and Verme (1970) found that deer were most active when seeking food and rested and chewed their cud at other times.

Deer ruminated either while standing or bedding. Deer chewed on a cud 17 to 28 times before swallowing, then after a 3- to 5-second delay the next cud was regurgitated and masticated. McLean (1940) noted that Odocoileus hemionus averaged 33 chews per cud while Browman and Hudson (1957) observed an average of 54 chews per cud. Types of food eaten probably influenced this. Some does chewed cuds while fawns nursed and

most often chewed immediately after bedding and grooming. Bedded deer often became inattentive and closed their eyes while chewing the cud; they generally maintained the ears alert.

When nursing, fawns approached the doe from the front, side or rear (Figure 12). If the doe was bedded, fawns dropped to their wrists to nurse but if the doe stood, small fawns stood to reach the teats. As fawns increased in size they bent their front legs slightly, lowering their shoulders and extending the neck while moving the chin outward from the body so that the head was almost vertically positioned directly beneath the udder. Fawns of all ages shoved against the udder while nursing and older fawns shoved with sufficient force to cause the doe to shift her footing.

Older fawns dropped to their wrists to assume nursing positions beneath the doe. Approaching from the sides or rear, they merely bent the front legs slightly to accommodate getting beneath the doe. The most common nursing posture was with the fawn directly beneath the doe with its head oriented toward the doe's rear end. When in this position the fawn presented its perianal region, which was frequently sniffed and cleaned by the doe. Her behavior may have been stimulated or directed to the perianal region by the fawn's rapid wagging of the erect tail from side to side when nursing. Such tail wagging began as soon as the fawn saw its doe and rapidly ran to her. Fawns were generally weaned by the age of 4 months; however, this varied with individuals; one male still attempted to nurse his mother when he was 2 years old.

Figure 12. A fawn briefly nursed its mother as she moved along feeding. Fawns nursed while positioned beneath, alongside, or behind the doe.

Figure 13. A fawn sniffs of its mother's mouth and muzzle as she chews on vegetation. Such behavior may enable the fawn to learn which plants are used by adults. That the doe was very alert, was indicated by a partially raised tail and intense stare.

As very young fawns began to move with the doe and browsed vegetation, they frequently sniffed or licked the mouths of their does or other related deer as they chewed vegetation (Figure 13). Bits of vegetation protruding from the doe's mouth were occasionally sampled. This may have served as learning or cultural transmission of what plants were palatable. Fawns may associate the odors or tastes of plants on the ground with those protruding from their doe's mouth.

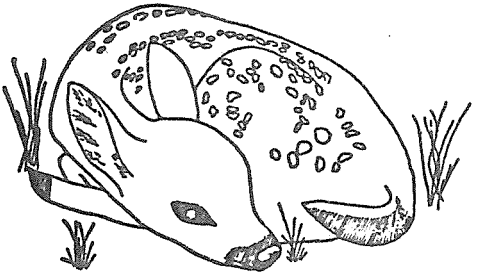
Fawns aged 3 months old, when not with their does, often attempted to nurse any deer that they encountered; some fawns even approached bucks and attempted to nurse. Deer quickly retreated from strange fawns or struck at strange fawns after sniffing them, refusing to let them nurse.

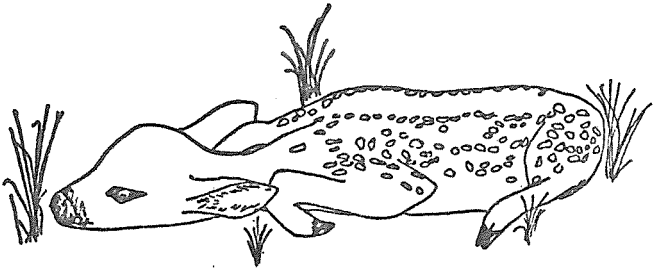
Bedding

When bedded, the legs were generally concealed beneath the body as the deer rested on its brisket. After being bedded for a period of 1 to 2 hours, deer often shifted to lie on one side with the legs exposed and extended laterally; often front legs were extended anteriorly. Fawns generally bedded slightly on one side with two or more legs exposed and to the side; legs were bent with forefeet directed rearward and hind feet pointing anteriorly or slightly outward away from the body (Figure 14). Very young fawns bedded with their chin on the back legs and had ears either up and alert or pressed backward against the neck. Eyes were often partially or completely shut. When disturbed the only movement that could be detected was that of the nose. Older deer often bedded in similar positions but if disturbed they ran instead of "freezing".

Figure 14. Characteristic bedding posture of a young undisturbed fawn. If disturbed while bedded, young fawns maintain this position. Adult deer occasionally assume this posture when bedded.

Figure 15. Typical "freeze" posture of a disturbed young fawn after dropping to the ground from a standing position. The legs, bent at the joints, were positioned alongside, rather than beneath the body, the neck was outstretched, with the chin resting on the ground.





During mid-day when deer became somewhat inactive, bedding occurred in thick cover where dense vegetation provided shade and cooler mid-day temperatures. These sites were often in dense palmetto depressions in pinewoods, under dead thatch palm fronds, which formed a tent-like shelter, in dense hardwood or hammock vegetation, or in large clumps of red mangroves that grew in low-lying areas. At times, use of low-lying areas occurred during high tides when beds were wet and deer were bedded partially in water. During twilight and in darkness, bed sites were in more open areas, where tall grass or clumps of low vegetation grew at the edge of or in mowed fields. Bedding in mowed areas within housing subdivisions at night was not unusual. Kjos and Montgomery (1969) noted that fawns bedded in sites that averaged 3° cooler than in open areas.

When suddenly disturbed, young fawns, which were standing or moving, characteristically dropped to the ground, with legs bent at the joints and folded beneath them; the neck was outstretched on the ground between the forelegs; the chin rested on the ground to the front. When in this posture, ears were pressed alongside the neck, eyes were wide open, and tail was tightly pressed against the rump (Figure 15). This posture was often held for several minutes even when the observer stood over the animal; when the disturbance ceased and the doe called to the fawn, it then stood and moved away. Similar "freeze" postures were described for white-tailed deer fawns (Queal 1962).

Some adult deer were seen to bed in similar fashion when disturbed by night-lighting. Both adult males and females that had previously been captured and marked moved to tall grass or bedded on the spot where they were standing when the beam of light was directed at them. Legs

were bent at the joints as the body was slowly lowered to the ground; the neck was outstretched to the front in line with the body as the head rested on the ground. If approached they stood and retreated. Only certain individuals used this method of concealment, and it certainly was not characteristic of older deer.

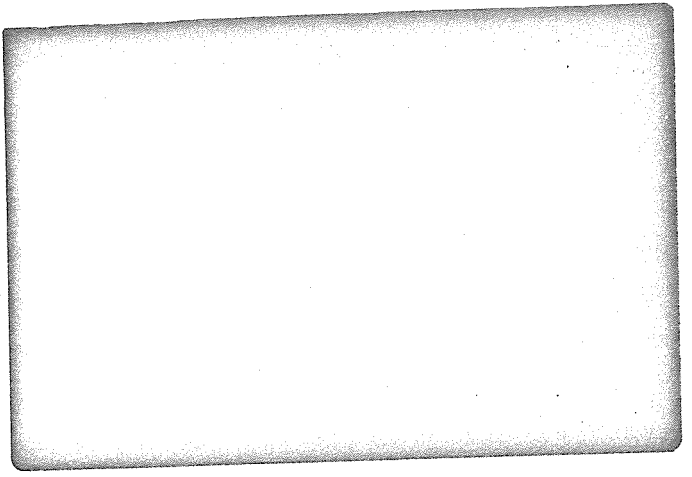
When "hit" with a light at night in areas where the one escape route was completely or nearly blocked by the researchers, some adult males lowered the head, bent the leg joints slightly, lowering the body, and slowly moved toward the exit, using tall grasses for concealment. This was similar to the quiet retreat from open areas of other deer when danger was seemingly detected before the source of danger was seen.

Response to insects

Exceptional bedding activity occurred during the rainy season in June 1970 and to lesser extent in June 1971 when deer moved into open areas to bed in late morning and late afternoon, presumably to escape insect pests. Since insects (mosquitoes and deer flies) were more numerous in the heavy vegetation, deer moved to open areas and bedded in a way that reduced areas vulnerable to insect attack. In these instances the legs were concealed beneath them while the head was turned and pressed closely to the side of the body. By rubbing the head against its sides, the deer reduced the number of insects around the eyes and muzzle (Figure 16). By covering part of the face and concealing the legs, two major sites of insect attack were protected. The ears were constantly twitching, which dislodged some insects. During

Figure 16. Mosquitoes feeding around the eyes of an adult male Key deer. Note the "blood" spots along the neck and face where mosquitoes have fed.

Figure 17. Cattle egret feeding on insects, which were picked from the deer, or which were disturbed as the deer moved through vegetation. Such a relationship mutually benefited the deer by reducing the number of insect pests, and the bird by providing relatively abundant food.



this time deer generally moved only to avoid humans, dominant deer or other objects that disturbed them; they then promptly bedded again in the open when they had escaped the disturbance.

Cattle egrets often stayed with these deer in open areas, feeding on mosquitoes and flies picked off of them and consuming those insects disturbed as deer moved through the vegetation (Figure 17). At times when deer were in tall grass or buttonwood and hardwood areas where they were concealed from the observers, their locations could be determined by the presence of several egrets nearby. Although birds did follow deer into heavy vegetation they did not move with them into the very dense stands of hardwood.

Patterns of Activity

Patterns of deer activity have been well defined and discussed for many populations of white-tailed deer and mule deer. Linsdale and Tomich (1953:366) reported that in mule deer a day consisted of "alternating intervals of rest, including rumination, and periods of activity, mainly foraging, with occasional travel from one site to another." Jackson et al. (1972) recorded similar alternating periods of activity and rest in Texas white-tailed deer. They found three to six periods of rest and rumination each lasting from $\frac{1}{2}$ to 2 hours during the day; one to three of these occurred at night. In Texas, feeding and travel dominated activity periods, which occurred in two peaks, one just after dawn, and the other in late afternoon. Lesser activity peaks occurred in mid-day and midnight. Marshall and Whittington (1968) found that maximum movement occurred in mid-morning followed by a movement to

daytime rest areas by Georgia white-tails in the spring. Halloran (1943), Michael (1967, 1970), Montgomery (1963) and Tibbs (1967) studying white-tailed deer from Texas and Pennsylvania, and Browman and Hudson (1957) studying penned mule deer in Montana, all reported that there were two major peaks in activity corresponding to sunrise and sunset with lulls occurring in mid-day and after sunset. Ozoga and Verme (1970) found five peaks of activity in Michigan deer, spaced at 4 to 6 hours in winter, most heavily at sunrise, mid-day, sunset, and twice during the night. All deer showed a major evening peak which usually occurred during the 2 hours before sunset and ended abruptly after sunset. They were most active when seeking food. Thomas (1966), studying white-tailed deer in Illinois, noted three periods of activity at night.

Seasonal differences have been noted in deer activity patterns. Linsdale and Tomich (1953) found mule deer were more active at night in spring and summer but were often active throughout the day in fall. Trends in seasonal movement were affected by character and availability of food and cycle of weather throughout the year. Pennsylvania deer were found active in all seasons 1 to 2 hours before sunset until around 1 hour after sunset (Montgomery 1959, 1963). In summer peak bedding occurred 7 to 8 hours after sunset and nearly all were active at dawn; this shifted in winter so that most were active 4 hours after sunset and were bedded 6 hours after sunset.

Halloran (1943) noted that during July and August, Texas white-tailed deer fed commonly at all hours of the night; however, by 0700 hours they were feeding or bedded in brush. In mid-afternoon they moved

to open areas and increased activity until sunset. Ozoga and Gysel (1972) found Michigan deer were inactive shortly after sunset and showed a decrease in nocturnal activity in late winter. High mid-day movement was common in February and April and a low in night-time traffic was seen during April.

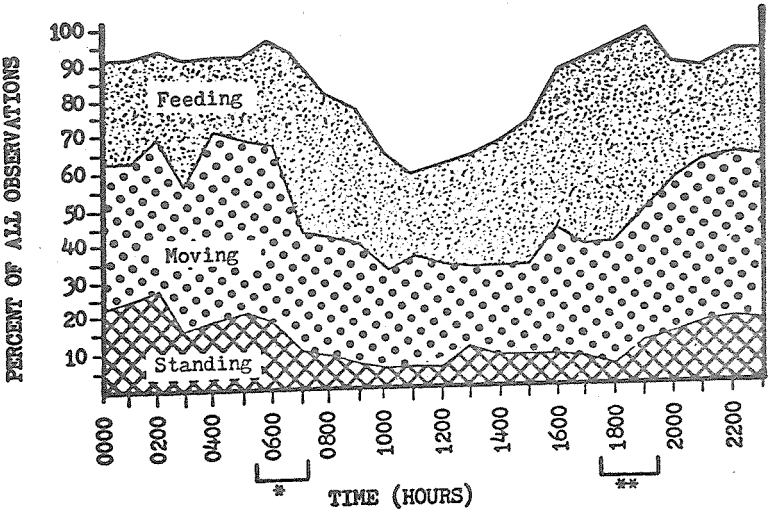
Daily patterns

In Key deer the four basic types of behavior were seen at all hours of the day and night and behavior patterns were similar to those described in other North American deer. Of the total observations of marked Key deer, 14.5 percent involved deer which were standing, 38.1 percent involved moving deer, 33.9 percent involved feeding deer, and in 13.4 percent of the observations the deer were bedded. Standing and moving behavior were influenced by the fact that these often resulted from some disturbance. Included in such disturbance was that caused by humans or other animals during the day, and by automobiles and spot-lighting at night. Thus these two values were somewhat high at the expense of other types of behavior. Deer ceased feeding or bedding to stand or escape from an area when disturbed.

Behavior patterns varied with the time of day (Figures 18 and 19). Deer were observed to stand and move more during hours of darkness, reflecting the response to disturbance by spot-lighting activities. Deer using open areas in housing subdivisions often became conditioned to escape at the approach of the research vehicles, especially those deer in areas where repeated captures occurred frequently. During the day when deer were monitored they often were observed without being

Figure 18. Daily patterns of Key deer activity during September 1969 - August 1971. Hours of sunrise (*) and sunset (**) are indicated.

Figure 19. Daily pattern of Key deer inactivity (=bedding) during September 1969 - August 1971. Hours of sunrise (*) and sunset (**) are indicated.


PERCENT OF ALL OBSERVATIONS
100
90
80
70
60
50
40
30
20
10
Feeding
Moving
Standing
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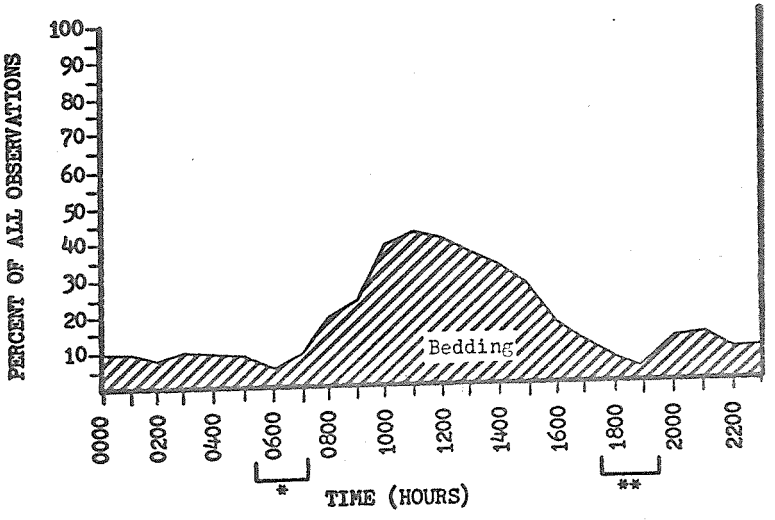
0400
0600
0800
1000
1200
1400
1600
1800
2000
2200
*
**
TIME (HOURS)


PERCENT OF ALL OBSERVATIONS
100
90
80
70
60
50
40
30
20
10
Bedding
0000
0200
0400
0600
0800
1000
1200
1400
1600
1800
2000
2200
*
**
TIME (HOURS)

disturbed. When in more remote areas away from human activity or in thicker vegetation their alarm threshold was not as low; and, they were therefore not as easily disturbed. Thus variation in daily patterns of standing and moving reflected in part the conditions under which observations were made.

Movement increased in the afternoon and during the night to a peak around 0400-0600 hours, then decreased rapidly after sunrise (Figure 18). Standing activities began to increase after 1800, reaching a peak around 0200 the next morning. In general deer were more wary in early morning hours when approached or "hit" with a beam of light. It was therefore more difficult to study deer behavior in hours just before sunrise than at other times.

Feeding behavior occurred in two peaks, generally corresponding to sunrise and sunset; lows between peaks occurred at 1100 and 0400 hours (Figure 18). Feeding increased about 1 hour before sunrise, reached a peak at or just after sunrise, then tapered gradually until 1100 hours. Deer increased feeding activities from noon until 1600-1700 hours, and then decreased quickly after sunset to a low around 2100. While feeding occurred sporadically throughout the night as deer alternately fed and bedded in the open, the fewest deer were seen feeding at 0400 hours.

Bedding activity (periods of inactivity = rest) occurred in two main peaks. One occurred during the mid-morning hours, extended through noon, and decreased between 1400 hours through 1900 hours (Figure 19). Another slight peak occurred around 2000 through 2100 hours and around 0300 hours. The large peak in mid-day corresponded to the peak of human

activity, which caused deer to cease use of open areas where they could be observed, and more importantly, coincided with the hotter parts of the day. Deer bedded at this time in palmetto-filled depressions, under thick accumulations of thatch palm fronds, or in hardwood hammock areas affording dense canopy. Such areas were cooler than open areas where little protection from the sun was provided. Similar activities were recorded in Pennsylvania deer (Montgomery 1959).

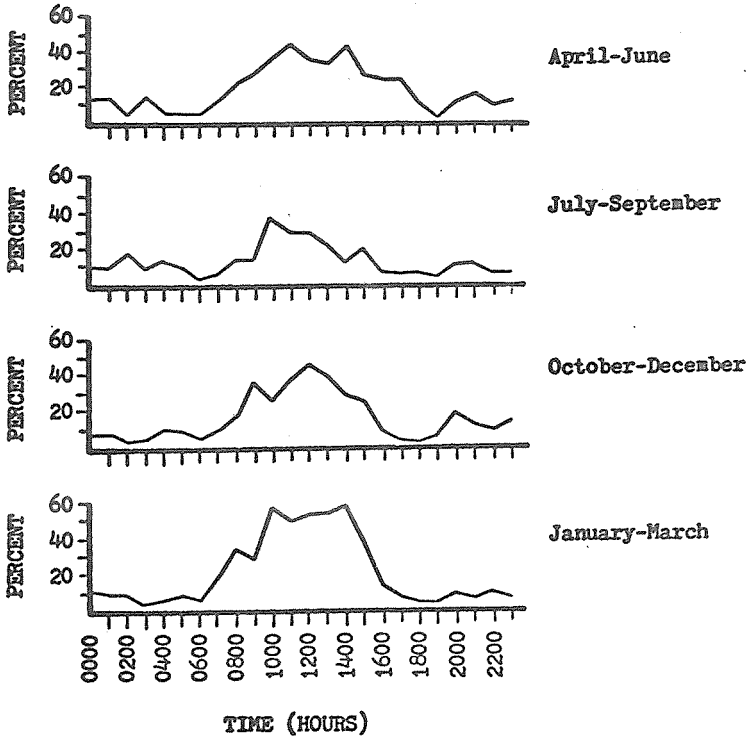
Seasonal patterns

Seasonal shifts in daily activity patterns occurred. In general proportionately less time was spent bedded in mid-day during July through September than during other months; however, the basic pattern persisted (Figure 20). While deer fed at all times during the day there was a tendency for deer to feed more in mid-day during July through September than during other months and usually spent more time feeding at night in summer months (Figure 21).

Deer stood more in early morning during October through December than during other months (Figure 22). They moved more in early morning during January through September but movement remained relatively consistent during the day from October through December (Figure 23). These shifts in activity patterns appeared to be affected by breeding activities, fawning behavior, meteorological factors and human activities.

As the breeding season began, more time was spent moving as part of the reproductive chases in October and December and less time was spent feeding and standing during the day. Deer bedded more in mid-day during January and March as the breeding activities decreased.

Figure 20. Seasonal patterns of Key deer bedding behavior computed over 3-month intervals. Percentages were based on the total number of deer observed at each hour during the designated 3-month interval.


PERCENT
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April-June
July-September
October-December
January-March
0000
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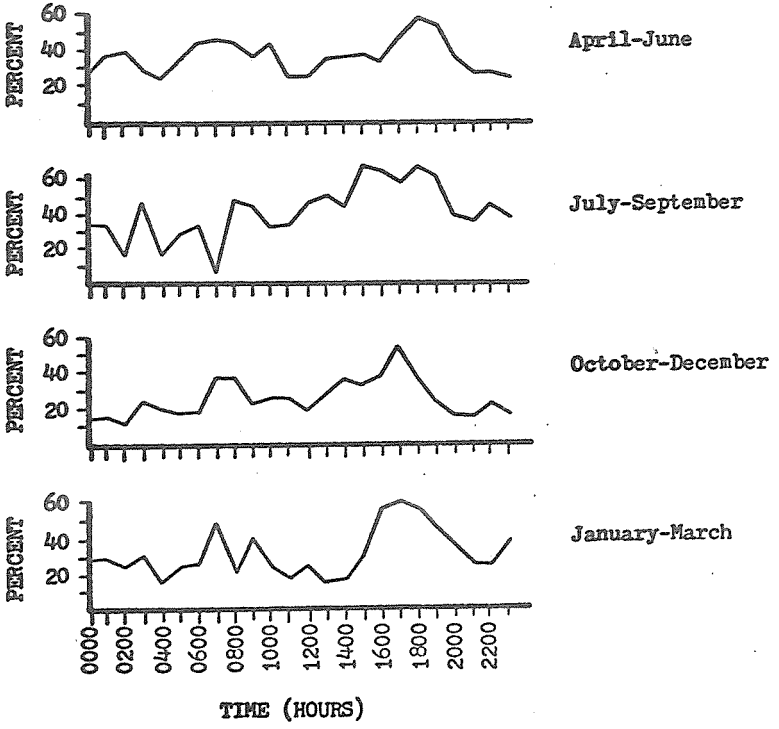
0400
0600
0800
1000
1200
1400
1600
1800
2000
2200
TIME (HOURS)

Figure 21. Seasonal patterns of Key deer feeding behavior computed over 3-month intervals. Percentages were based on the total number of deer observed at each hour during the designated 3-month interval.


PERCENT
60
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20
April-June
July-September
October-December
January-March
0000
0200
0400
0600
0800
1000
1200
1400
1600
1800
2000
2200
TIME (HOURS)

Figure 22. Seasonal patterns of Key deer standing behavior computed over 3-month intervals. Percentages were based on the total number of deer observed at each hour during the designated 3-month interval.

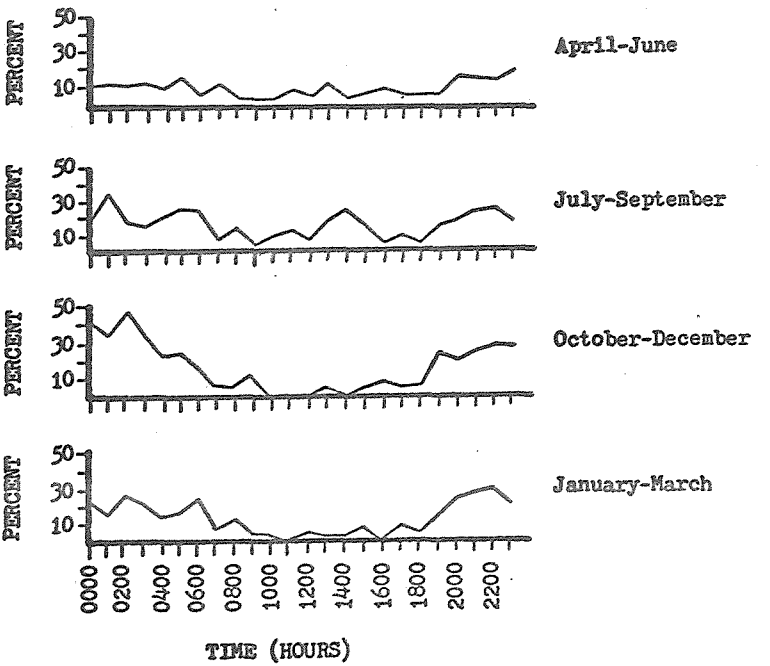
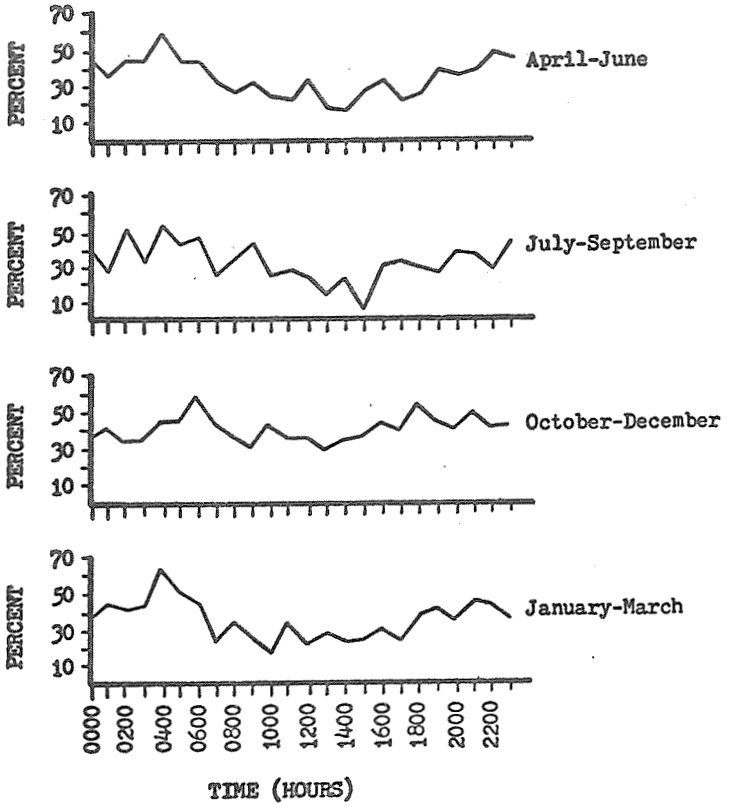

PERCENT
50
30
10
April-June
July-September
October-December
January-March
0000
0200
0400
0600
0800
1000
1200
1400
1600
1800
2000
2200
TIME (HOURS)

Figure 23. Seasonal patterns of Key deer moving behavior computed over 3-month intervals. Percentages were based on the total number of deer observed at each hour during the designated 3-month interval.


PERCENT
70
50
30
10
April-June
July-September
October-December
January-March
0000
0200
0400
0600
0800
1000
1200
1400
1600
1800
2000
2200
TIME (HOURS)

Sex-age differences

Fawn activity patterns - Variations in activity patterns were noted between deer of different sex and age classes and between individuals. During their first week of life, fawns remained bedded when alone, and when with their does they were observed to be bedded 52 percent of the time, feeding 35 percent of the time and moving 13 percent of the time (Tables 9 and 10). Young fawns did not move when disturbed but as they aged and became more agile, they moved about more on their own and ran when approached.

The youngest fawn which abandoned its bedding site to run when disturbed was 4 weeks of age. At this age, fawns changed positions at the bedding site by shifting only a few inches or turning, often moving into or out of the shade. Four-week-old fawns moved from open bedding sites in late afternoon to sites affording heavy cover where they remained for the night; these moves usually occurred after the doe had left them and involved distances up to 20 yards, but usually less. At 4 weeks of age fawns were first seen feeding alone, sniffing and nibbling a few plants. Verme (1963) noted that Michigan white-tails ate solid food at 2 weeks. Key deer males were recorded moving 2 weeks earlier than females. This varied with the individual and with the circumstances.

Two-month-old fawns moved more and bedded less than during the first month (Tables 9 and 10). During this time females as well as males moved alone and fed, ran when disturbed, moved long distances with their mothers, and associated freely but briefly during the day with other members of their family units. Movement was restricted to

Table 9. Behavior of known-aged young fawns at times when they were alone.

Age (Weeks)	Males Seen					Females Seen				
	Standing	Moving	Feeding	Bedded	Total	Standing	Moving	Feeding	Bedded	Total
0- 1	0	0	0	20(100)[a]	20	0	0	0	10(100)	10
1- 2	1 (4.5)	0	0	21(95.5)	22	0	0	0	4(100)	4
2- 3	1 (7.7)	1 (7.7)	0	11(84.6)	13	0	0	0	7(100)	7
3- 4	0	2(14.3)	2(14.3)	10(71.4)	14	0	2(25.0)	0	6(75.0)	8
4- 5	0	5(31.2)	2(12.5)	9(56.2)	16	0	0	1(12.5)	7(87.5)	8
5- 6	1(12.5)	0	1(12.5)	6(75.0)	8	0	2(28.6)	1(14.3)	4(57.1)	7
6- 7	0	0	1(10.0)	9(90.0)	10	0	1(14.3)	0	6(85.7)	7
7- 8	0	3(33.3)	2(22.2)	4(44.4)	9	0	3(33.3)	1(11.1)	5(55.6)	9
8- 9	0	2(33.3)	1(16.7)	3(50.0)	6	1(16.7)	3(50.0)	0	2(33.3)	6
9-10	0	3(25.0)	5(41.7)	4(33.3)	12	0	1(14.3)	1(14.3)	5(71.4)	7
10-11	1(10.0)	1(10.0)	5(50.0)	3(30.0)	10	2(50.0)	1(25.0)	0	1(25.0)	4
11-12	0	1 (8.3)	6(50.0)	5(41.7)	12	0	0	0	7(100)	7

[a]Numbers in parentheses represent percentages of the total number of fawns seen in each sex-age category.

Table 10. Behavior of known-aged young fawns at times when they were with their does or siblings.

	Males Seen					Females Seen				
(Weeks)	Standing	Moving	Feeding	Bedded	Total	Standing	Moving	Feeding	Bedded	Total
0- 1	0	2(16.7)[a]	5(41.7)	5(51.7)	12	0	1 (9.1)	3(27.3)	7(63.6)	11
1- 2	0	0	7(100)	0	7	0	0	5(100)	0	5
2- 3	0	1(20.0)	4(80.0)	0	5	0	0	3(100)	0	3
3- 4	0	3(60.0)	2(40.0)	0	5	0	4(80.0)	1(20.0)	0	5
4- 5	0	1(100)	0	0	1	0	1(33.3)	2(66.7)	0	3
5- 6	1(14.3)	4(57.1)	2(28.6)	0	7	0	0	5(83.3)	1(16.7)	6
6- 7	0	2(40.0)	3(60.0)	0	5	1(33.3)	0	1(33.3)	1(33.3)	3
7- 8	0	4(100)	0	0	4	0	2(40.0)	2(40.0)	1(20.0)	5
8- 9	1(14.3)	3(42.8)	2(28.6)	1(14.3)	7	0	3(27.3)	5(45.4)	3(27.3)	11
9-10	0	3(50.0)	3(50.0)	0	6	0	2(66.7)	1(33.3)	0	3
10-11	1(14.3)	2(28.6)	4(57.1)	0	7	0	2(33.3)	2(33.3)	2(33.3)	6
11-12	0	2(66.7)	1(33.3)	0	3	0	2(25.0)	3(37.5)	3(37.5)	8

[a]Numbers in parentheses represent the percentages of the total number of fawns seen in each sex-age category.

familiar areas within the doe's range; as the fawns aged familiar areas increased.

During the third month of life, fawns were observed bedded with the doe and other related deer 7.8 percent of the time, feeding 18.3 percent, and moving 16.5 percent; when alone they bedded less and spent more time feeding. These activities corresponded to an increase of vegetation in their diet and less dependency on milk.

During the first 6 to 8 months, fawns gradually decreased the amount of time they were inactive (Figure 24) as measured by the proportion of time they spent bedded. From September and November through March, the amount of time bedded remained relatively stable at between 10 and 20 percent. Except for May, during which males bedded significantly more than females, doe fawns bedded more than males. This was significant during July, December, January and February. Feeding activities increased as fawns matured (Figure 25). Except for December when females fed more than males, there was no significant difference in the amount of time each spent feeding. During October all fawns appeared to feed less as reproductive activities disrupted the feeding behavior of family groups in open areas during the summer months. During December as female fawns increased time spent feeding, males continued to decrease this activity until January when they increased feeding.

Fawns increased the amount of time they spent moving as they matured; however, there was a decrease in the amount of moving in September as feeding activities proportionately increased. Following this, an increase in moving corresponded to increased reproductive

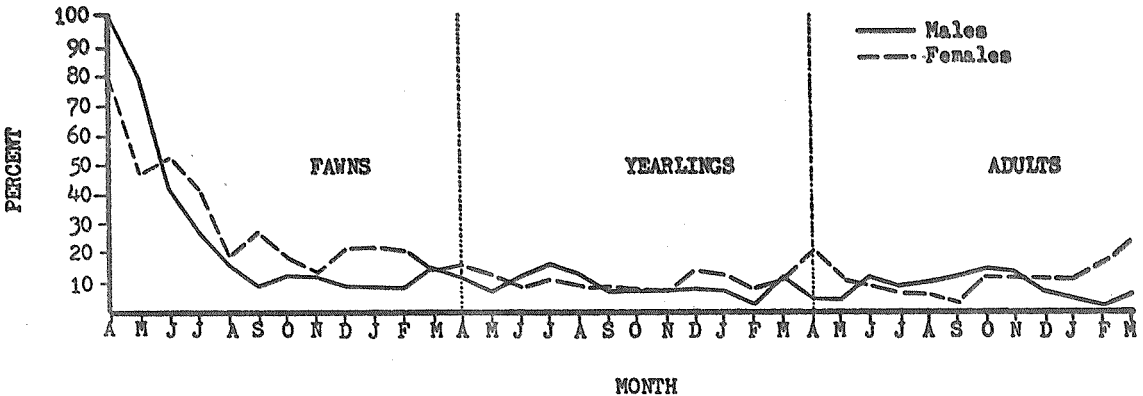
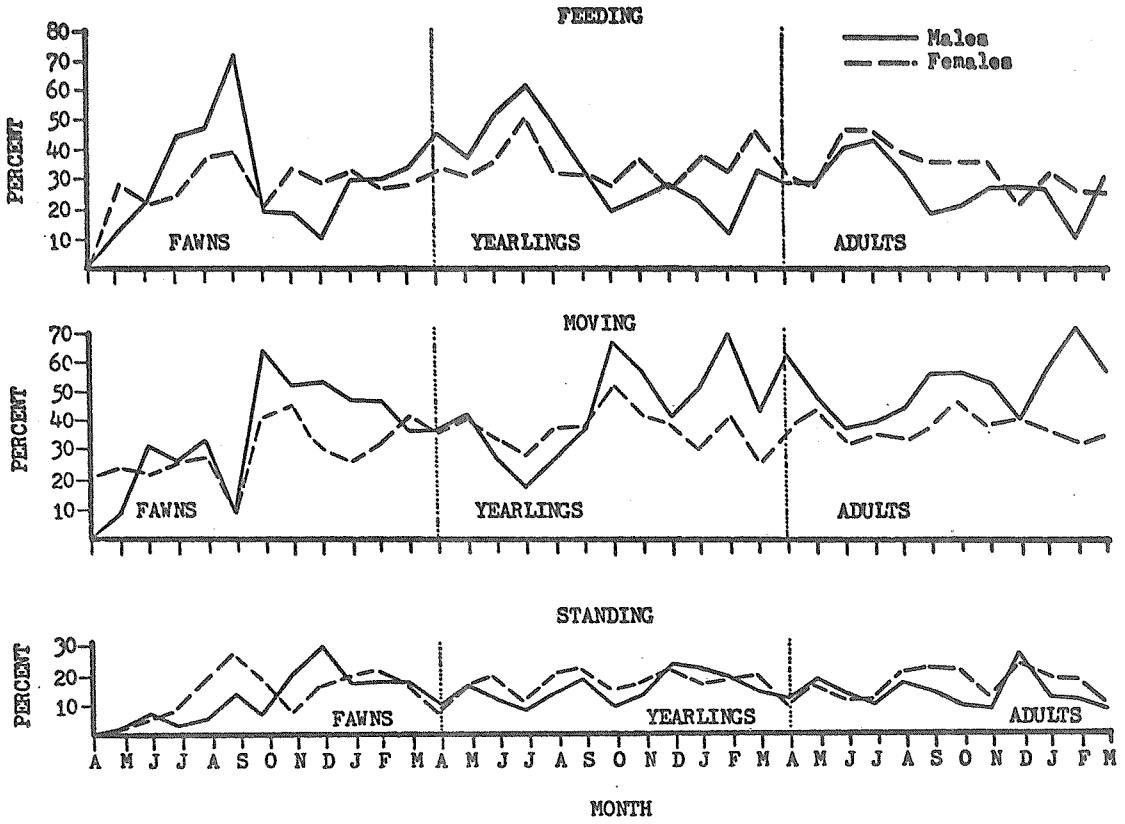


Figure 24. Seasonal patterns of inactivity (bedding behavior) of marked Key deer. The percent of time each month that deer of different sex and age were observed bedding are indicated. Percentages are based on the number of observations each month of deer in a sex-age class.

Figure 25. Seasonal activity patterns of marked Key deer. The percent of time each month that deer of different sex and age were observed performing each of the three basic types of activity are indicated. Percentages are based on the number of observations each month of deer in a sex-age class.


FEEDING
Males
Females
PERCENT
80
70
60
50
40
30
20
10
FAWNS
YEARLINGS
ADULTS
MOVING
PERCENT
70
60
50
40
30
20
10
FAWNS
YEARLINGS
ADULTS
STANDING
PERCENT
30
20
10
FAWNS
YEARLINGS
ADULTS
A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M
MONTH

activities and harassment by older animals. While female fawns moved significantly more during March, males moved more in October, December, January and February. Such movement in these months corresponded to harassment of fawns during the breeding season and reflected a looser association between male fawns and the other members of their family units.

Standing activities increased to peaks in September for female fawns and a peak in December for males (Figure 25). Males stood more during the breeding months. These differences were significant with females standing more in August and males more in November and December.

Using motion sensitive transmitters Jackson et al. (1972) also found that daytime activity increased as fawns aged and that males were more active than females. Most activity in the first few days of life involved nursing and grooming. They found that 2-week-old fawns were equally likely to run as to "freeze" when disturbed. The first week fawns were active 0.8 percent of the time, 10-15 percent active at 2 to 4 weeks, and at 8 weeks they were active 20 percent of the time. The estimate for Key deer was higher than that for Texas deer, possibly an over-estimate since fawns were more easily seen when active than when bedded. It may be, however, that Key deer are more active than Texas fawns as there would be a tendency for active Texas fawns to fall to predation more frequently than active Key deer fawns, and thus be selected against.

<u>Yearling activity patterns</u> - Yearlings spent up to 15 percent and as little as 4 percent of their time inactive in any one month (Figure 24). Despite slight fluctuations in the amount of time these deer were

inactive, the differences were not significant. During April through September, females were observed to stand and move more than males, while males fed more; during September through March, females fed more, while males engaged more in standing and moving activities. During June and July, females stood and moved significantly more than males, while males fed significantly more in June and August. This trend was reversed in January and February when males moved more and females fed more. During all months of the year there was a tendency for males to spend more time alone than females. The differences were significant in August and all months from October through March.

Yearlings of both sexes showed peaks in feeding during July which tapered off during August and September (Figure 25). The proportionately lower feeding activities after September corresponded to the breeding season when there was an increase in the amount of moving, especially by the males. The amount of time that deer were inactive during the year was relatively stable, with bucks being slightly less inactive after December and females becoming slightly more inactive in December and January.

That bucks were more active from October through March, the season when more traffic was concentrated on major highways in the Keys, accounted for the greater proportion of males being killed on the highways. During 1968 through September 1973, yearlings were roadkilled at a rate of 3.13 males for each yearling female (Table 11). Yearling males tended to move greater distances when dispersing than yearling females (Silvy 1974). Taber and Dasmann (1954) concluded that because yearling black-tailed deer males strayed farther from their does than females,

Table 11. Sex and age ratios of highway mortalities of Key deer during January 1968 through June 1973.

Year[a]	Adult Buck	Adult Doe	Yearling Buck	Yearling Doe	Fawn Buck	Fawn Doe	Ratio Buck:Doe:Fawn	Ratio Yg. Buck:Yg. Doe	Ratio Fawn Buck:Fawn Doe	Ratio Doe:Yearling
-1968	1	2	1	0	2	0	0.50:1:1.00	-- :1	-- :1	1:0.50
1968-69	8	6	6	1	5	2	1.33:1:1.17	6.00:1	2.50:1	1:1.17
1969-70	15	5	13	3	8	6	3.00:1:2.80	4.33:1	1.33:1	1:3.20
1970-71	7	9	6	3	7	4	0.78:1:1.22	2.00:1	1.75:1	1:1.00
1971-72	14	14	12	4	6	5	1.00:1:0.78	3.00:1	1.20:1	1:1.14
1972-73	16	5	7	4	2	3	3.20:1:1.00	1.75:1	0.67:1	1:2.20
1973[b]	8	7	2	0	0	1	1.14:1:0.14	-- :1	-- :1	1:1.28
Totals	69	48	47	15	30	21	1.44:1:1.06	3.13:1	1.43:1	1:1.29

[a]Data are grouped into yearly periods beginning on 1 April to enable evaluation of the impact of the fawn and yearling age classes each year.

[b]Only includes data collected during April through 15 June.

this resulted in the trapping of 10 males for each female. Of all yearling males seen, 16 percent were with adult does while 47 percent of the yearling Key deer females were seen with adult does.

Adult activity patterns - In adult animals periods of inactivity, measured by the proportion of time they were observed bedded, were similar during June through August, October and November, with slight differences occurring in April, May, September, and December through March (Figure 24). During April, February and March, females bedded significantly more than males, while in September, just prior to breeding activities, males bedded significantly more than females. Differences in behavior during periods of activity were mainly in the amounts of time deer spent moving and feeding (Figure 25). Feeding activities were relatively high (greater than 40 percent of the time in June and July) during early to mid-summer, but tapered off in August through September. The amount of time spent feeding fluctuated around 30 percent from November through March. Except for December, when males fed slightly more than females, does exceeded bucks in the relative amount of time spent feeding. They fed significantly more than males in September and February.

Males, on the other hand, moved more than females in all months except December when they both moved about 40 percent of the time (Figure 25). Peaks in moving for males were noted in September, October and February. Throughout the year females moved consistently about 40 percent of the time; males moved significantly more than females in April, August, September, November, and January through March. Much of the movement from September through November was associated with the

rut when bucks were chasing females over a large part of the island; and, the peak in February corresponded to times of antler loss when adults, harassing one another, caused movement whenever more than one male was in an area. Fewer bucks were seen during this period and seldom were males seen in open areas except when moving.

Sightings of adult deer which were standing varied from 9 percent of the observations in April to around 25 percent in December. The only significant difference in standing occurred in October when males stood more than females.

For all deer of all age classes, the seasonal activity and the interactions between deer appeared to follow the same general cycles. In March, April, and May deer were relatively solitary and, except for fawns which were largely inactive, most deer spent more time moving. Summer months were characterized by males associating with other deer, females associating with fawns and reassociating with their yearling females. The activities were largely involved with moving rather than feeding. These relationships and behaviors largely reflected the activities associated with breeding and fawning.

Use of open areas

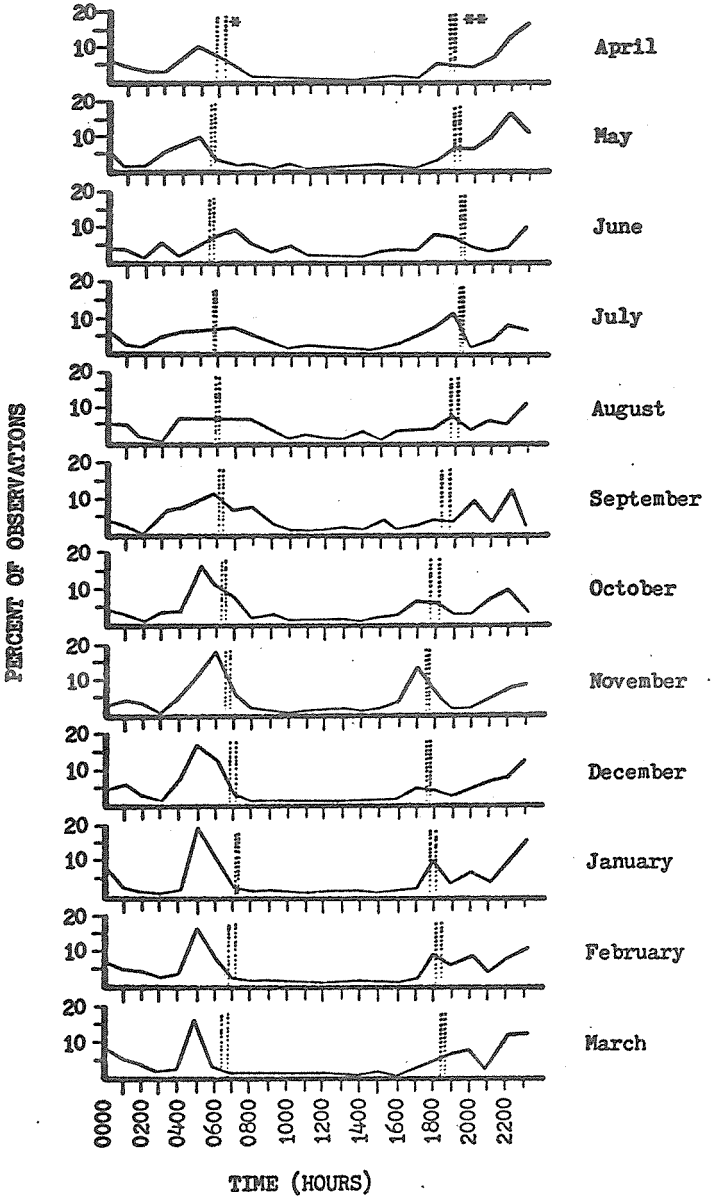
Records were maintained on all deer seen during September 1969 through September 1971 to determine when they used open areas in housing subdivisions and along roads. Based on 11,694 observations of deer it appeared that deer used open areas more in December (19.8 percent), July (10.6 percent), and June (10.3 percent) than during other months. The fewest deer were recorded for September (5.7 percent); however,

heavy rains in September 1971 made observations difficult and during a 2-week period in September 1970 only one observer was in the field.

Deer were seen to use open areas along roadways, in housing subdivisions where few houses had been constructed, and man-made openings along firetrails during all hours of the day and night. There was a tendency for the deer to spend more time in these areas, where human activities occurred on a regular basis, during those hours of less human activity. Such times included hours of early evening throughout the night, and ended in early or mid-morning (Figure 26). Similarly, Progulske and Duerre (1964) observed that deer moved to meadows at night to bed and loaf. That human activity may have been responsible for keeping deer out of open areas during the day, was suggested by the fact that deer continued to use openings in more remote areas away from the human influence until later in the morning, and began use of them earlier in the evening.

There appeared to be two activity patterns in open areas during a 24-hour period (Figure 26). One pattern was seen during September through May, the other during June through August. During September through May, there were two major peaks in activity in the open and several smaller peaks associated with them. One major peak came around 2 hours before sunrise and tapered off to very low levels of activity just after sunrise. Few deer were seen during the day until about 1½ hours before sunset when deer became active again, around 1600 hours. This peak was more pronounced in November through February. This activity subsided after a low that occurred about 1 hour after sunset. Then after 2 to 4 hours deer began using open areas again with

Figure 26. Observations of marked and unmarked deer in open areas in housing subdivisions and along roads. Percentages were based on the total number of deer seen each month during September 1969 through August 1971. Times of sunrise (*) and sunset (**) are indicated.


PERCENT OF OBSERVATIONS
20
10
April
May
June
July
August
September
October
November
December
January
February
March
0000
0200
0400
0600
0800
1000
1200
1400
1600
1800
2000
2200
TIME (HOURS)

activity peaking around 3 to 4 hours after sunset, usually around 2000-2200 hours. This activity usually was evident until around 0200-0300 hours; however, this led to an increase in activity again, $1\frac{1}{2}$ to 2 hours before sunrise. These patterns closely approximated peaks of feeding activity.

A second activity pattern, which was seen during June through August, was one in which more activity was seen at all hours of the day instead of occurring in such well-defined peaks that were characteristic during the rest of the year. Deer used open areas later in the morning after sunrise, sometimes until 1000 hours; they then began using open areas about 3 hours before sunset, around 1600 hours (Figure 26). At times, some deer could be found in open areas at any hour of the day or night. Such use of open areas may have been due to their reaction to insect pests as discussed above. During 1970, following late May-early June rains when mosquitoes and deer flies became numerous, deer increased use of all open areas, being seen performing all four basic types of behavior in the open where slight breezes kept the number of insects to a minimum.

During June, peak activity occurred 1 hour after sunrise, gradually subsided during the morning so that by 1200 little activity was evident. Around 1500 hours deer began moving and activity peaked $1\frac{1}{2}$ hours before sunset around 1800 hours. Activity then decreased slightly but was followed by a peak around 2300 hours. Deer then alternated periods of activity and inactivity, increasing their activity through sunrise.

Use of open areas by deer was apparently affected by human activities in these areas. During the day, traffic to and from housing

subdivisions within the refuge and activities in open areas within the subdivisions were certainly responsible for some deer staying out of these areas, moving into them only when human activities were low between around 2300 hours at night and 0630 in the morning. Observations of deer in remote areas of the refuge tended to confirm this conclusion; however, it was found that deer in these remote areas followed the same basic activity patterns during the day. Peaks of activity were not so pronounced in these remote open areas as in areas of human occupancy. Human activities appeared to accentuate the peaks of activity and inactivity of deer in open areas rather than alter them.

Repeated disturbance to deer in an area resulted in discontinued use of the area for a period of time. Such was the case when intense deer capture was attempted. Deer either terminated use of the area or shifted the times of use of the areas. Similarly, Montgomery (1963) found that people working on the area may have caused deer to bed in the woods rather than in the fields during the day. Autry (1967:37-38) reported that during the hunting season, Illinois deer became more wary and inactivity increased (i.e., diurnal activity decreased). After hunting they became "conditioned to hiding during the day. . ." Townsend and Smith (1933) reported that if deer were frightened during regular feeding hours, they came out at some other hours.

Effects of weather

That weather affects deer activity patterns has been noted by several authors. Michael (1970) noted that decreased feeding occurred

with increased temperature and that moderate precipitation in summer caused Texas deer to terminate bedding to feed. Wind and moon phase had no statistically significant effects on them in summer, but in winter, high wind, precipitation and low temperature with blowing sleet altered feeding activities. Palmer (1951) noted that deer were nervous and restless on windy days; Montgomery (1963) found daytime activity of various cervids was greater on cool, cloudy days than on sunny days.

Tibbs (1967) found that Pennsylvania white-tails increased their activity as temperatures increased during June to August. With high relative humidity deer activity was lower and they appeared earlier in the day and later in the evening. Light rain did not seem to greatly affect activity; however, deer activity was retarded during periods of moderate to heavy precipitation. No relationships between deer behavior and barometric pressure, cloud cover, or wind were noted. In winter, activity of Michigan deer increased as temperature dropped, probably as they moved to sheltered areas (Ozoga and Gysel 1972). Hawkins and Klimstra (1970a) found that temperature altered trap success by altering feeding preferences; they also noted that high relative humidity and rainfall appeared to restrict deer movements. Relatively low temperature and humidity and relatively high barometric pressure improved trap success. They also reported that Barick (1952) had better trap success trapping before low pressure storms, and Hahn (1949) found that deer were most active during cloudless days of low relative humidity; as relative humidity increased, deer movements decreased. Rain hampered trap success.

Progulske and Duerre (1964) found that deer remained active in rain and fog; 85.28 percent of variation of deer counts was caused by the interaction of five weather factors: cloud cover, temperature, precipitation, dew and relative humidity. Deer were less wary on dark nights and did not flee as readily as on bright, moonlit nights. As night temperatures increased or decreased from one night to the next, deer counts generally followed the same pattern.

Thomas (1966:12) reported that feeding activity of Illinois white-tailed deer was higher when the barometric pressure was 29.80-30.29 than at the extremes; more fed when the barometric pressure was steady than when rising or falling. A minimum temperature of 40° F was associated with highest deer activity; above 40° F feeding was stable and at lower temperatures feeding decreased.

Townsend and Smith (1933) concluded that deer activity in the Adirondacks largely depended on local factors. Such conclusions were also drawn from observing the Key deer behavior patterns. Significant differences, which were observed in Key deer activities under the various weather conditions are discussed below. All differences were tested using chi square tests for equality with the level of significance at 0.05.

Cloud cover - Deer bedded significantly more when cloud cover was heavy than when it was only moderate (Table 12). Thus they were less active when there was heavy cloud cover and more active under moderate clouds. They fed more when there were light or heavy clouds than when clouds were moderate, and fed less when it was clear than when clouds were present. Deer moved less under heavy cloud cover and stood less

Table 12. Observations of Key deer behavior performed under different amounts of cloud cover.

	Amount of Cloud Cover			
Behavior	None	Light (0-30 %)	Moderate (30.75 %)	Heavy (75-100 %)
Standing	511(17.0)[a]	258(12.0)	671(15.9)	80(14.9)
Moving	1,144(38.0)	789(36.7)	1,595(37.8)	165(30.7)
Feeding	950(31.6)	825(38.4)	1,441(34.1)	211(39.2)
Bedded	402(13.4)	279(13.0)	515(12.2)	82(15.2)
Total	3,007	2,151	4,222	538

[a]Numbers in parentheses represent percentage of the total number of deer observed under the specified type of cloud cover.

Table 13. Observations of Key deer behavior performed under different wind speeds.

	Wind Speed			
Behavior	None	Light (0-5 mph)	Moderate (5-15 mph)	Heavy (15-30 mph)
Standing	126(13.8)[a]	731(16.2)	521(12.9)	46(17.0)
Moving	423(46.2)	1,766(39.2)	1,409(34.9)	98(36.3)
Feeding	316(34.5)	1,541(34.2)	1,429(35.4)	66(24.4)
Bedded	50 (5.5)	469(10.4)	679(16.8)	60(22.2)
Total	915	4,507	4,038	270

[a]Numbers in parentheses represent percentage of the total number of deer observed under the specified wind speed.

as cloud cover decreased from moderate to light; movement was less under light cloud cover than under clear skies.

Wind speed - Deer were more active when there was no wind than when there was wind; they became significantly less active as wind velocities increased (Table 13). Deer fed significantly less at times when wind speed was 15-30 mph than at times of less wind. Movement decreased as wind speeds increased; the greatest movement occurred when there was no wind and more movement occurred with winds of 0-5 mph than with winds of 5-15 mph. Deer stood less when winds were 5-15 mph than when 0-5 mph. Due to the types of behavior performed by deer at different wind speeds, they were more easily observed at times of little or no wind.

Wind direction - Activities of deer varied as wind direction varied (Table 14). Deer bedded more when wind was from the northeast than when from the north, southwest, or west, and bedded less when wind was from the west than when from the southeast, south and northwest.

Feeding occurred more often when wind was absent or from any direction other than north. They progressively fed less as winds were from the west, south, southeast, east, and southwest. Movement progressively decreased as wind blew from the southwest, north, south, east, northeast, and west. Deer moved most when there was no wind. Standing occurred most frequently when wind was from the north; standing progressively decreased as winds were from the northeast, southeast, east, south, and northwest.

Table 14. Observations of Key deer behavior performed at times when wind was from different directions.

Behavior	No Wind	Wind Direction							
		N	NE	E	SE	S	SW	W	NW
Standing	126(13.8)[a]	171(19.9)	286(15.7)	263(13.3)	379(15.5)	115(12.8)	42(12.1)	19(12.8)	27(10.0)
Moving	423(46.2)	367(42.6)	696(38.1)	763(38.5)	842(34.4)	295(32.9)	151(43.5)	47(31.8)	108(40.0)
Feeding	316(34.5)	220(25.6)	568(31.1)	692(34.9)	873(35.7)	364(40.6)	116(33.4)	70(47.3)	95(35.2)
Bedded	50 (5.5)	103(12.0)	275(15.1)	263(13.3)	353(14.4)	123(13.7)	38(11.0)	12 (8.1)	40(14.8)
Total	915	861	1,825	1,931	2,447	897	347	148	270

[a]Numbers in parentheses represent percentages of the total number of deer observed under the specified wind direction.

Precipitation - Deer fed and bedded more when there was no rain than when rainfall occurred (Table 15). They moved more under light and moderate rainfall than when there was no rain. No significant difference in standing was seen.

Temperature - In general deer became less active as temperatures increased; however, no significant differences in bedding occurred at temperatures of 40°, 50°, or 60° F (Table 16). As temperatures increased above 50° F up to over 90° F, deer became less active. This corresponded to daily temperature patterns, with high mid-day temperatures corresponding to peak bedding behavior and lower night-time temperatures occurring when deer were more active. As temperatures increased above 50° F, deer fed more and stood and moved less.

Moon phase - Activity of deer from 1 hour after sunset to around 1 hour before sunrise varied depending on moon phase. Although deer tended to be less inactive on bright moonlight nights, the only significant difference in bedding was between nights of no moon when deer tended to bed more and full moon when they bedded less (Table 17). Significant differences were noted in moving and standing activities, deer standing more when there was no moon, and less when the moon was in the 1/4 phase than when there was more moon visible. Deer moved more when the moon was at 1/4, 3/4, and full phase than when it was absent. No significant difference occurred in feeding activities at various moon phases.

Deer were generally more spooky or wary when there were moonlight conditions than when there was no moon, and thus were much more

Table 15. Observations of Key deer behavior performed under different amounts of precipitation.

Behavior	Amount of Precipitation			
	None	Light	Moderate	Heavy
Standing	1,289(14.9)[a]	45(17.8)	5(10.6)	2(14.3)
Moving	2,991(34.5)	115(45.4)	27(57.4)	8(57.1)
Feeding	3,192(36.8)	69(27.3)	10(21.3)	3(21.4)
Bedded	1,192(13.8)	24 (9.5)	5(10.6)	1 (7.1)
Total	8,664	253	47	14

[a]Numbers in parentheses represent percentages of the total number of deer observed under the specified type of precipitation.

Table 16. Observations of Key deer behavior performed under different temperatures.

Behavior	Temperature (Degrees Fahrenheit)					
	40	50	60	70	80	90
Standing	23(23.7)[a]	176(23.6)	362(16.6)	668(13.9)	155 (9.1)	25(13.2)
Moving	35(36.1)	336(45.0)	953(43.7)	1,817(37.7)	506(29.6)	41(21.7)
Feeding	31(32.0)	179(24.0)	637(29.2)	1,710(35.5)	728(42.6)	74(39.1)
Bedded	8 (8.2)	56 (7.5)	227(10.4)	623(12.9)	319(18.7)	49(25.9)
Total	97	747	2,179	4,818	1,708	189

[a]Numbers in parentheses represent percentages of the total number of deer observed under the specified temperature.

Table 17. Observations of Key deer behavior performed under different amounts of moonlight.[a]

Behavior	Moon Phase				
	None	1/4	1/2	3/4	Full
Standing	603(24.6)[b]	36(11.8)	115(20.4)	74(20.3)	141(20.6)
Moving	973(39.7)	148(48.4)	237(42.1)	165(45.3)	303(44.3)
Feeding	637(26.0)	91(29.7)	156(27.7)	100(27.5)	191(27.9)
Bedded	239 (9.7)	31(10.1)	55 (9.8)	25 (6.9)	49 (7.2)
Total	2,452	306	563	364	684

[a]Observations included only those between one hour after sunset to one hour before sunrise.

[b]Numbers in parentheses represent percentages of the total number of deer observed under the specified moon phase.

difficult to see, as they ran before they could be approached. Progulske and Duerre (1964) noted similar behavior in South Dakota deer.

As a result of meteorological conditions the best times for seeing deer were times of light to moderate cloud cover, times when wind was absent or very light from the north, when there was no or very light rain, or at times when temperatures were in the 70's or less. Conditions when the fewest deer were seen were on bright moonlight nights, in periods of heavy rains and at times of strong winds.

Grooming

Grooming activities have been described in groups of white-tailed deer and black-tailed. Townsend and Smith (1933) noted the use of the hind foot to scratch the nose, and use of the tongue in grooming the sides and back. Similarly, Linsdale and Tomich (1953) noted use of the tongue to lick with firm upward strokes in grooming the back. Use of the hind foot to scratch the head region and use of velvet antlers to groom the perineum by scratching the inside of the upper part of the raised hind leg were also noted. Biting at the front legs, shaking of the coat, and rubbing against objects were also described as part of the mule deer's grooming behavior.

Espmark (1971a) observed that all antlered reindeer scratch their back with the tips of their antlers by raising the head to an almost vertical position and then slowly swinging it from side to side. Marchinton and Moore (1971) noted that licking of the genitalia resulted in masturbation by males.

Mutual grooming or grooming involving more than one deer has been described and its possible significance has been discussed. Palmer (1951:276) noted that for several weeks after birth of fawns, the does licked their fawns, especially the anal region "In June when the deer start to shed their winter coat the does lick the hair off the fawns and the latter reciprocate with the mother and/or litter mates or those of the previous litter."

Miller (1971b) noted that all age classes and both sexes were observed in simultaneous mutual groomings, dominant animals always initiating the activity. Licking and nudging the neonate may serve to facilitate development, stimulate eliminative activity, and stimulate it to get to its feet (Altmann 1963, Hersher et al. 1963).

Since the first mutual communication between mother and young is the licking by the maternal doe and reciprocal licking by the newborn young, it may have bonding value, which may serve to fortify their ties in later life (Miller 1971b). Mutual grooming alleviates irritation of inaccessible parts of the body, "but serves also a social purpose" (p. 300). He based this conclusion on the facts that mutual grooming extends to parts of the body accessible to the deer being groomed, and he noted it in February and March when small "family" groups reformed. It may therefore serve to re-establish strong bonds between certain deer that had been weakened by the high frequency of contact with a relatively large number of deer during the gregarious winter period.

Miller (1971b:300) also indicated that mutual grooming was "probably a behavioural response with ontogenetic origin expressed through two sources: the mother-young bond and consort activity."

The act of mutual grooming reinforces the social bonds between members of a closed group by promoting the psychological well-being of the subordinate animals within the group, thereby strengthening the unity of the group.

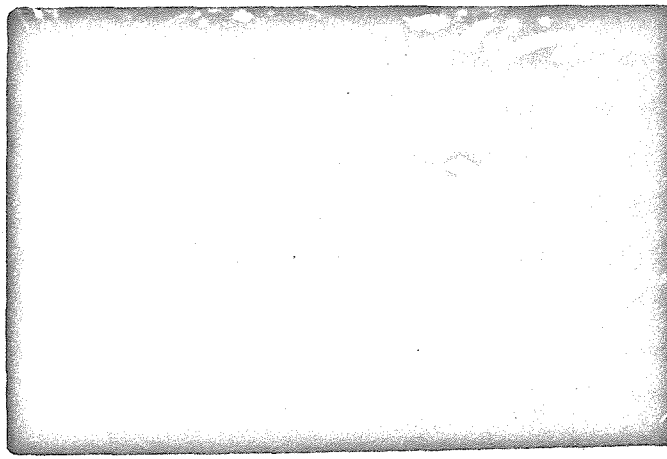
That deer can be stimulated to groom others was demonstrated by Muller-Schwarze and Muller-Schwarze (1969:24): "Touching the cheek of a fawn released licking of the area it can reach with its tongue . . ." Such grooming serves as an appeasement gesture, even with adult bucks in rut. In the wild a doe also stimulates elimination in the fawn by licking the anal region of the latter. Ozoga (1972) used grooming (care-giving = epimeletic) behavior, bleating (care-soliciting = et-epimeletic) behavior, and lack of aggression between deer in identifying doe-fawn groups.

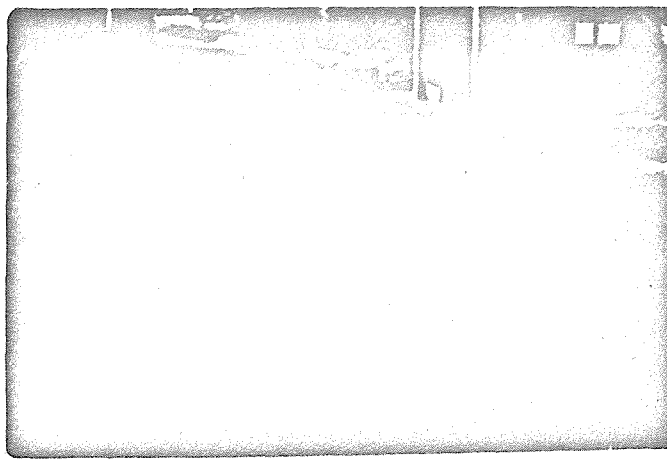
Grooming was most often seen in Key deer during those times when deer leisurely fed or loafed during the day. Captive deer were seen occasionally grooming at night; however, this was seldom observed in wild deer which were disturbed by the lights. It is probable that grooming occurred during these times however. Grooming was accomplished by use of the tongue, hooves, and in rare instances antlers.

The most common grooming behavior involved a single deer grooming itself using the tongue to lick the back, rump, rear, or legs (Figure 27). It occurred most often after feeding; deer moved to sheltered or shaded areas, such as beneath trees, and groomed immediately before bedding. Other deer bedded and then groomed before ruminating. After urinating, deer often licked their hocks, especially when they had urinated on them. At times when insect pests were severe, deer often

Figure 27. A marked 4-month old Key deer male groomed himself after using the hind foot to scratch about his head and ears; he licked the hoof and lower leg. Note the expansible collar on this animal, which has nearly lost his fawn pelage.

Figure 28. Typical "hock-urination" posture, in which the deer rubbed his hind legs together while urinating on the metatarsal glands. Deer of all sex-age classes were observed to perform such behavior at various times of the year.





licked their fore- and hind-legs where flies and mosquitoes had bitten them. Standing deer often twisted so as to enable them to lick the perianal region or rear legs, which were straightened and extended forward. A bedded or standing deer typically twisted the neck so the head was alongside the body, then with an upward motion of the head while the tongue was extended, they proceeded to lick the sides and back.

Hind feet were used to scratch the neck, behind the ears, on the head and the muzzle. After scratching with the hind feet the hoof was licked before replacing it to the ground. When deer sneezed, they usually scratched at the nose with the hind foot, presumably to relieve some type of irritation to the nasal passages.

The captive adult male was observed to use the antlers to scratch the back and rump, and performed auto-erotic behavior after using the velvet-covered and polished antlers to rub under the raised hind leg and genitalia. During this behavior the neck was turned so that the head was at a 90° angle or greater to the body axis, the neck was twisted and turned so that one antler was beneath him in the region of the penis. Then by awkwardly twisting his head the antler was thrust against the lower leg and sheathed penis. After five or six of these thrusts the male gave slight pelvic thrusting motions and then licked the penile area. Masturbation has been reported in other white-tailed deer; however, the related use of antlers in this manner was not noted (Marchinton and Moore 1971). Linsdale and Tomich (1953) noted grooming of the perineal region by similar use of antlers but did not note masturbation.

Mutual grooming appeared to play an important role in the social organization of the Key deer. Fawns and yearlings were groomed by their does whenever they came into contact after a period of separation. Such grooming appeared ceremonial at times when one deer began licking the other's neck and the second reciprocated by moving its head to alongside the neck of the first and began to lick its neck in the same manner. The intensity of this mutual licking increased with time, occurred in bouts of 30 to 60 seconds or more with brief pauses between bouts as one or both deer looked around. Licking by one undisturbed deer initiated licking by the other.

The penned doe was stimulated to perform such a behavior by placing the arm by her head and neck and gently stroking her neck with the hand. She immediately began to lick the arm rapidly from the side, just as deer licked the necks of other deer which were in similar positions at the time. Such mutual grooming was never observed between a doe and her older yearlings when she had very young fawns present; however, as fawns matured, grooming was seen to occur between the doe and both her fawns and yearlings. Mutual grooming was never observed between adult males and females and was only observed between does and fawns or yearlings that were known or suspected to be of a family unit.

Grooming began early in the life of a deer and probably was important in the initial formation of the bond between mother and offspring (Miller 1971b). Immediately after the birth of a fawn, the adult doe extensively cleaned it by licking fluids from it and continually licked and sniffed the drying fawn. If identification of a fawn by its doe depended on olfactory cues, it is probable that this postnatal

activity was an integral part of establishing the association between the doe and her fawn. Does licked the perianal region of fawns up through 2 months of age as they nursed. The fawn wiggled its tail rapidly during this behavior. Haugen and Speake (1957) describing similar behavior for white-tailed deer suggested such licking may stimulate bowel movement.

Key deer does, which were nursing strange fawns, rejected the fawn after sniffing of the perianal region, and no grooming occurred. Thus mutual grooming, which served the role of cleaning, may additionally serve as a social bonding mechanism (Miller 1971b) and it has been interpreted as being an appeasement behavior (Muller-Schwarze and Muller-Schwarze 1969).

A specialized type of grooming occurred with the loss of velvet from antlers in the fall. Linsdale and Tomich (1953) reported that mule deer shed velvet by thrashing vegetation. Although some wild deer and the tame buck occasionally lost velvet by rubbing against posts and trees, the main technique of velvet loss was by kicking at the antlers and scratching the loose tissue away using the hind feet. The tame deer and one wild deer were observed to kick the antlers with the hind hoof, turning the head to the side and back so as to present the antlers at the proper angle for contact with the foot. Periodically the deer stopped and licked the hoof, then returned to kicking. Deer were seen to kick for a period on one side with a hind foot, then, turning the head to the other side and standing on three feet, it would use the fourth to kick the velvet from the other side. During the two years that the tame deer was observed, he used this technique to remove velvet,

even though trees and posts were available on which he later scraped the polished antlers.

Play

Play was defined by Michael (1968b:535, after Bourliere 1964) to include those "activities without evident (immediate) object that seemed to affort pleasure to those taking part in them." In a discussion of play, Marler and Hamilton (1968:194-195) characterized it as a type of behavior consisting of sequences of various types of "non-play" behavior rearranged into new and unusual patterns. The pattern of behavior is less dependent on the normal stimulus-response relationship and occurs when animals: "have nothing else to do". In addition some behavior patterns occur only when playing.

Play behavior has been reported in several groups of ungulates, and has mainly involved young animals. Fawns as young as one week of age have been observed playing (White et al. 1972); Dasmann and Taber (1956: 161) noted that "it is most frequently observed during the early months of a fawn's life, at which times yearlings and sometimes adult does may join in fawn play." They suggested that play "probably indicates an excess of energy" (p. 162). Tibbs (1967) observed fawns playing with adult does as they ran in a large circle.

Townsend and Smith (1933:307) described play by single fawns as taking the form of "more or less running about, dodging bushes and frisking this way and that, apparently overflowing with energy", and play has been described as appearing similar to a game of "tag" (Michael 1968b:535, Tibbs 1967:39). Michael (1968b:535) found that "mock fights"

appeared to occur more commonly among older fawns. Muller-Schwarze (1968) described play activities in black-tailed deer including head-jerking, butting, rushing, mounting, leaping, running, kicking, neck-craning, neck-twisting, and head shaking.

Among Key deer, although young animals were most often involved in apparent "play" activities, older deer occasionally participated in such behavior. Fawns at 6 weeks of age and older performed mock escape behavior, running in small circles, jumping to the side, tossing the head upward and back, kicking the heels, and sprinting for short distances in the vicinity of their does. This behavior followed nursing periods while their does were still close by. Such behavior involved only the fawn, with the older deer watching but feeding and moving along slowly.

In one instance, the adult deer joined the fawn in a chase. In an open field at twilight a 2-month-old fawn, its doe, and an older doe all fed while the fawn ran short distances, looked around alertly, tossed the head, then jumped in the air to run and quickly bound from side to side. Once the fawn ran directly at the doe, then turned to the side as it approached her. This elicited a head-toss by the doe during which she shifted her weight to the rear, lifted the front legs slightly off the ground, twisted the body and came down on the front legs to the side, lifted the hind legs while in the air, and performed a twisting motion in mid-air, similar to "bucking" behavior seen in horses or cattle. She then began chasing the fawn in a circle. The older doe joined the chase; however, the fawn's doe then began running in another circle on her own; the fawn joined in chasing her as did the older doe. This play behavior

lasted a period of about 4 minutes and the participants ran into the woods where they were out of sight.

Yearling deer were observed to "buck" in the same manner by jumping and twisting, then running at top speed for a short distance. This occurred when two or more deer, moving together through a field, were approached by another deer. In response the deer initiating the behavior kicked the heels, tossed the head, and gave the bucking motion which seemed to stimulate the other deer to respond in similar manners.

Fawns often went through part or all of the sequence of aggressive behavior patterns while playing. These patterns were not incorporated into complete sequences which were performed by older deer, and often the most aggressive patterns were performed without preliminary threat postures. Fawns playing together often struck at other fawns which were a short distance away. On two occasions one fawn flailed at another fawn which did not return the challenge. In all cases these fawns did not have ears back nor did they execute the sequence of preliminary displays characteristic of agonistic behavior in yearlings and adults.

Older fawns (9 months of age or older) incorporated these patterns into complete sequences. During the play behavior, larger fawns tended to dominate smaller fawns, and fawns in the vicinity of their does were dominant over other fawns and often over yearlings. Play may serve the function of muscle development, development of social interactions functional in herd organization, and the development of motor patterns useful in escape and communication.

Flight Distance

In a discussion of flight distance, a concept formulated by Hediger (1934) in North American cervids, Altmann (1958:207) described it as "the distance to which a person can approach a wild animal without causing it to flee." Behrend and Lubecek (1968) expanded this definition to include the response to vehicles as well as humans in his study of flight distance of white-tailed deer.

Altmann (1958) found that the flight distance of wapiti and moose varied due to a "seasonally changing threshold of sensitivity due to reproductive and nutritional status; variations due to type of habitat; and variations due to the specific experience of the individual or the group." Behrend (1966) also noted that in northern white-tailed deer, the flight distance showed seasonal variation and varied with the circumstances.

Although precise flight distances were not measured in this study several generalizations regarding the distance to which a deer could be approached by man, vehicle, or other species of animal appear valid. Flight distance varied with time of year, time of day, and the specific circumstances.

Deer were more wary in the early morning hours than at night (see Patterns of Activity). The number of deer moving in early morning hours was proportionately higher than late at night as a result of this increased flight distance. After repeated attempts at capturing deer, flight distance increased and deer were more wary when they were in areas where capture attempts were frequent. After being captured deer showed greater flight distances than at other times.

Behrend and Lubecek (1968) noted that hunted deer had greater flight distances than unhunted deer; and, Autry (1967) noted that flushing distance of bedded deer changed after hunting as deer remained concealed more often. In remote open parts of the Key deer range, deer often stood when approached at a distance until within 50 yards. During fawning season, deer were more spooky and left when approached to within 200 yards.

When the scent of an intruder was detected, deer had greater flight distances than if visual cues alone alerted them. One doe quietly ran from an open area with tail between legs and without any noise when she apparently detected the scent of a dog, which appeared at the edge of the opening only 90 seconds later from a direction upwind of the doe.

Does with fawns had a greater flight distance and were extremely spooky when with their fawns. Michael (1967) also noted that white-tailed does with fawns were more wary than other deer. Flight distance was variable between individuals. Some deer that were more accustomed to humans through interaction in housing subdivisions had very small flight distances. Some deer, especially males, could be approached to within 6 to 12 feet without becoming alarmed, while others, notably does, were more wary and fled when approached from over 100 yards. One free-ranging doe (AF034), however, became so tame that she did not become alarmed or cease activities even when the observer remained only 10 yards from her.

Communication

For communication deer rely first on scent, second on hearing, and last on sight (Severinghaus and Cheatum 1956). Detailed examination of glandular tissues of deer (Quay 1959, Quay and Muller-Schwarze 1970) and analysis of pheromones and their effects on deer behavior (Muller-Schwarze 1971) have provided insight into the importance of odors in communication among these animals.

Use of scent for recognition of offspring by a doe, and for locating hidden fawns, has been demonstrated in white-tailed deer (Jackson et al. 1972, White et al. 1972). Muller-Schwarze (1971) found that black-tailed deer marked their home ranges using forehead scent, left interdigital scent on the ground when alarmed, and used urine and metatarsal scent in conveying messages over moderately large distances. Deer appeared to be identified as to sex, age, and individual at close range by means of tarsal odor. Rubbing the forehead against twigs and leaving odor may serve as a means of agonistic interaction between deer (Muller-Schwarze 1972).

Key deer employed types of communication which best enabled them to relay information at a distance throughout wooded areas where visual interaction was limited. Such communication included primarily scent and sound, which carried in wooded areas over greater distances than visual signals that required open areas. Visual communication occurred more in open areas or where deer were in close contact with one another.

Olfactory communication

In Key deer, olfaction served as a basic means of communication. The bond between doe and fawn appeared to be established when the doe was cleaning away membranes and fluids, and extensively sniffing the newborn fawn. As fawns matured and does encountered them in the wild, the doe sniffed the fawn's perianal region and hocks as they were presented to the doe with rapid wagging of the tail. Does rejected fawns other than their own only after sniffing them.

Adults and yearlings seemed to recognize one another by odor; each deer sniffed another's hocks when they met and agonistic displays were often maintained between deer until they were identified by odor. When disturbed, deer standing together in an area approached one another and frequently sniffed the hocks of other deer while maintaining alert watches in all directions.

Young fawns (1 to 2 months old) relied on scent to identify their mothers, and approached other deer cautiously until they detected the scent of the deer. If the deer was identified as their doe, they then trotted to her to nurse. Older fawns attempted to nurse on any larger deer they encountered. That fawns can follow scents was observed when an apparently abandoned fawn followed an irregular path through the pinewoods, while following a man who had passed near its bed site. The human had moved out of sight before the fawn got to its feet, vocalized, and slowly followed with its nose to the ground.

Alarm reactions appeared to be conveyed by odor. Deer, feeding or bedded downwind from an alarmed deer, were seen to become very alert,

usually moving to near the alarmed deer, staring at it, and remaining very alert in all directions. Such behavior, which apparently was triggered by some olfactory cue, may have been the result of the raising of the tarsal tufts and tail (Figure 9, p. 41). This has been noted in black-tailed deer when they became alarmed (Muller-Schwarze 1971). Raising of the tuft and tail may release large amounts of pheromones which, when detected by other deer nearby, serve to alert them to danger. The sight of raised tufts and tail may also cause deer nearby to become alert.

At certain times of the year, the observer detected "musky" odors from adult does, which were standing or moving at very close range. This usually was during times when does nursed fawns, and may have resulted from increased pheromones, which served to help the fawn maintain or gain contact with the doe. They also may have resulted when does, which were more alert during these times, became disturbed by the observer and released the odor when the hair tufts and caudal hairs were elevated.

Deer, apparently detecting scents of humans and dogs at distances of up to 200 yards, were observed to quietly trot to heavy cover off to the side or directly downwind of the intruding animal. This was done without flagging, snorting, stomping, or any other obvious alarm response. Such deer generally avoided detection by the intruder.

Sign-posting behavior

Sign-posting behavior has been described for black-tailed deer, in which use of odor and scraping of vegetation serves for keeping family

members together in the same area and serves to intimidate intruders (Graf 1956). Immediately after polishing the antlers, and throughout the breeding season, Key deer bucks scraped and mutilated small plants and limbs of trees by rubbing with their antlers and forehead. This often took the form of sham battles as males directed antlers forward, gradually made contact, then thrashed the flexible objects by twisting and turning the head while pushing. At other times, the buck stood calmly and twisted its antlers in overhanging branches. Often broken branches were sniffed and licked. Deer were observed antlering vegetation while alone, when with does, and between bouts of combat with other bucks. No rubbing of preorbital glands or the forehead at the base of the antlers was witnessed; however, it could not be determined that such behavior did not occur.

In one instance a buck moved through the woods sniffing vegetation until he came to a section of low plants, which had been previously mutilated, as evidenced by twisted branches bearing dried leaves. He then rethrashed these branches, sniffing and licking the broken twigs. After 3 to 4 minutes of antlering these shrubs, he moved off through the woods. This, and other antlering of vegetation above the head, resembled the "head rubbing" behavior described in mule deer (Muller-Schwarze 1971, Muller-Schwarze 1972). This behavior also resembled descriptions of territorial "sign-posting" behavior (Graf 1956, Linsdale and Tomich 1953); however, neither hock urination, pawing the ground, nor scent marking of any type were observed at these times. It seems to have little or no significance as far as denoting territories of males, since several males used the same area and each male moved extensively during the breeding season.

While it may not have territorial significance for these insular animals, rubbing of antlers against trees and shrubs could serve to attract animals into the area. During the reproductive season, this could increase the chances that breeding animals made contact with one another, and would be especially advantageous at low population levels. In 1969-1970, numerous marked adult animals moved into Watson Hammock for periods of 1 to 2 days to several weeks, in the case of adult males. The cause of this movement was not evident; however, it may have resulted in large numbers of deer using a small area during the breeding activities, and may have functioned in bringing animals into close contact. Adult does were not seen to make such moves during the 1970-1971 season; however, males from the north end of Big Pine Key were seen to frequent the hammock area. Males may have been chased out of other areas by larger males; however, this seemed unlikely, since the males that entered the hammock were prime-aged animals, and it appeared that there were higher concentrations of males in the hammock than outside of the area.

Some scent marking was evidenced during this study; it was performed by both males and females, and occurred during all times of the year. Both males and females hock-urinated. This was accomplished while urinating; the rear end was lowered, the hind legs were slightly bent at the ankle, positioned so that they met at the mid-line and were beneath the stream of urine (Figure 28). The hocks were moved so that tarsal glands were rubbed together as the urine was passing over them. Similar behavior was observed and described for adult deer by Browman and Hudson (1957); Severinghaus and Cheatum (1956) noted that 10-day-old

fawns attempted to urinate on their hind legs. Rub-urinating, which was observed in Key deer of all sex-age classes, has been interpreted in other deer as a behavior which serves to mark territories, to deposit urine with pheromones that indicate physiological estrus, to mark and identify home areas used by fawns, and to mark fawn bedding sites (Muller-Schwarze 1971, DeVos et al. 1967). A captive adult deer, sniffing areas where he or other deer had urinated, gave the "flehmen" response (see Reproductive patterns). Often he licked these areas and then urinated on the spot. Key deer were observed to urinate without hock-rubbing at all times of the year as well. The stimulus to hock-rub was not clear.

Auditory communication

Kiley (1972) noted that in artiodactyls, calls were not situation specific, but that the call depended on the stimulus interest of the situation and the level of excitement of the animals. As this increased, the calls became louder, longer, and of higher pitch. He hypothesized that a frustration type of situation evoked a vocalization; however, the type of vocalization given depended on the level of excitement of the animal, rather than the specific situation. Thus, they did not convey specific messages, but rather conveyed information on the emotional state of the animal.

Linsdale and Tomich (1953) noted that the most frequent sounds produced by mule deer were those of snorting, sneezing, vocalization or locomotion. These varied in their manner of expression, and in their effect on other animals; each conveyed a variety of meanings. They

found snorting to be closely associated with wariness in deer. Deer have also been observed to use sounds as contact calls between does and their offspring (DeVos et al. 1967, White et al. 1972, Townsend and Smith 1933), and between males and females during the breeding season (Linsdale and Tomich 1953). Some cervids appear to distinguish each other by voice (Espmark 1971b); however, this has not been documented in North American deer. Use of snorting and non-vocal sounds, such as stomping the feet, serve to intimidate or arouse an intruder (Linsdale and Tomich 1953, Waring 1969).

Key deer used a wide range of auditory communication; most did not carry over great distances, and they served mainly as contact calls. Deer of all ages and both sexes emitted contact calls. During the breeding season, adult and yearling males, while nose-trailing or pursuing other deer, emitted a low muffled grunt every 2 to 3 seconds. Solitary males, as well as those with females, emitted these grunts, which were audible (to the observer) at 30 yards or more on a calm day.

Adult does began maternal contact calling immediately after giving birth to a fawn; when the fawn began crawling or moving out of reach or out of sight of the doe, she began to call (see Fawn activity). On three occasions, two does, which were observed giving birth, called within 7 minutes of parturition (Tables 24 and 25). Two inexperienced 2-year-old does did not call to their fawns, even when the fawns moved out of their sight and cried. Contact calls may serve to reinforce the dam-fawn bond between the two animals. Does, when moving in areas where fawns were last bedded, uttered low contact calls while searching for them.

Yearlings occasionally uttered contact calls while following their does at a distance, or when seeking contact with them. Occurrence of such behavior decreased when family groups split. Yearling males generally ceased this behavior; however, yearling and adult does occasionally uttered contact calls when following other members of their family units. One male, which had remained with his doe for over 2 years, cried when following or making contact with her, and uttered distress calls when she was out of sight. This behavior, although not characteristic of all males, was observed in yearling males prior to their separation from the family units.

Distress calls were uttered by deer that had become "lost" from their family units. When captured, deer often bleated loudly at first; however, they then became mute, even when subjected to the continued stressful conditions of marking. Under conditions of stress, fawns gave a distress call, which was audible at over 100 yards, and no doubt served to rejoin them with their does. Does responded to distress calls by rapidly moving to retrieve the fawns. When one fawn fell into a mosquito ditch and cried loudly, its doe ran to stand by the ditch, despite the presence of the observer only 40 yards away in full view.

Vocalizations were used as expressions of alarm by disturbed deer. When suddenly disturbed by an object at close range, deer often snorted by suddenly forcing air through the constricted nares. While adults, yearlings, and older fawns responded in this manner when startled, it was more characteristic of adult females than other deer. Often such snorting was continued when they touched down with their

front feet as they bounded away. Often deer, which stalked a foreign object or some intruder, snorted and stomped the forefeet. It may serve to alert other deer nearby to potential hazard, and also to startle or intimidate an intruder, as observed in pronghorns (Waring 1969). Ozoga (1972) found that bucks and does used a snort when confronting other deer; however, this was observed in Key deer only between males during the breeding season.

While displaying to other bucks, males emitted a series of very rapid, loud snorts, caused by constriction of nasal passages and forcing air in very rapid bursts through the nose in a series of four to eight snorts during 2 to 3 seconds. At this time, the body was tensed, neck muscles appeared strained, and the deer generally positioned himself at an angle of about 30° from the object toward which he displayed. These were usually accompanied by "ears-back" and "hard-look", and were often followed by a "sidle" (see Agonistic postures and aggression).

This rapid snorting was an intense type of agonistic display, heard only during the breeding season when intruding males were challenged. It was often performed with enough force to take on a quality of a whistle. Such loud alarm, warning, or intimidation calls had the advantage of being heard over a large distance, and served to alert other deer within a 100- to 200-yard area.

One other sound, which served as an alerting agent, was a foot stomp, which could be heard by the observer up to 20 yards away when performed on bare ground. Deer, alarmed by some unidentified source, often snorted, pranced, advanced cautiously, and stomped one or alternate front feet. Stomping served to alert other nearby deer of possible

danger. Fawns became very alert when the doe stomped her feet, ready to spring for cover at any further disturbance. Fawns responded to snorts and stomping by quickly retreating to cover at top speed, or in the case of young fawns, dropping in place and "freezing" (Queal 1962) until the danger passed. Other noises made by deer included sneezing, apparently caused by some irritation to the nasal lining.

Visual communication

Visual communication between deer of the genus Odocoileus is facilitated by antlers and arrector pilorum smooth muscles, associated with areas of contrasting color patterns (Henshaw 1971, Guthrie 1971). Postures, that optimize body size and antler size, are utilized to communicate agonistic behavior between deer (Cowan and Geist 1961, Michael 1968a), but all these visual displays are useful only in open areas, or only to a limited extent in dense vegetation.

Key deer used postures to express alarm and various stages of excitement. When disturbed, deer raised their tail and erected hair that surrounded the perianal region (Figure 9, p. 41); raised tails served to alert other deer standing within sight of them; however, other means of communicating alarm were more effective in the hammocks and pinewoods areas, where vision was restricted by dense vegetation. Deer running from apparent danger, carried the tail up; as the degree of excitement increased, the amount of tail "flagging" increased. When "sneaking-out" of an area, the tail was down, closely pressed against the rear end; these deer were much more difficult to see. Various postures, discussed elsewhere, involved tail position.

Agonistic postures and aggression - Use of postures as expressions of aggression and submission was commonly observed in Key deer. Since agonistic postures and aggression were very closely associated, they should be considered concurrently. Throughout the year deer of all sex-age classes were seen to assume aggressive or submissive postures and participate in aggression to varying degrees. This reached a peak in intensity for males during the breeding season, and for females during and following the fawning season.

Thomas et al. (1965:319-320) described five distinct postures, which in white-tailed deer, conveyed aggressive intent. With the less intense "hard-look", the neck and head were extended, ears were along the neck, and the deer stared "intently at his adversary for a period of 3 to 10 seconds". With the "sidle", the buck "turned his head and body 30° from his antagonist". With head erect and chin tucked in, he took several steps toward his adversary; the arrector pili effect of elevated shoulder hairs was pronounced. Cowan and Geist (1961:523) noted the "crouch" and "circling" in mule deer to be a similar behavior. The fourth threat noted by Thomas et al. (1965:321) was the "antler threat" in which "the head was lowered so that the tines of the antlers pointed directly toward the rival." The final action, the "rush", which was also described by Cowan and Geist (1961), occurred when antlers made contact and vigorous pushing ensued. The "rush" was seen only twice by Thomas et al. (1965) in white-tailed deer. In addition, Ozoga (1972) noted snorting, "striking", and "flailing" in Michigan white-tailed deer in winter.

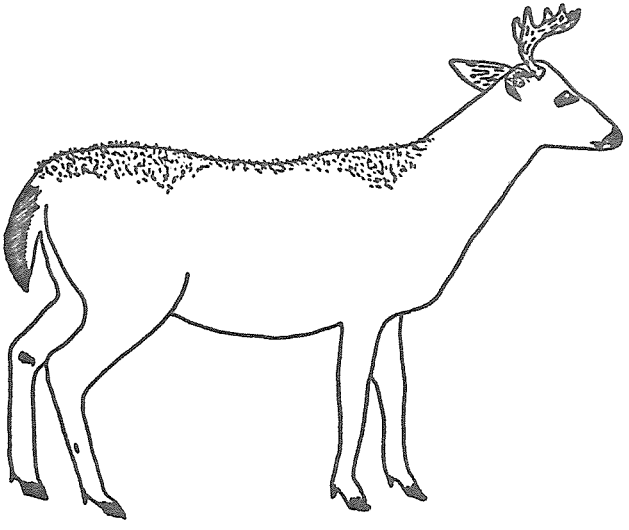
Similar postures and displays as those described above were frequently observed in Key deer conveying aggression or dominance-submissive relationships. Displays were often seen when two deer came into contact while feeding or moving, prior to identifying one another. Smaller deer generally assumed submissive postures when larger or more aggressive deer advanced toward them. Until deer recognized others as familiar deer or family members, some aspects of posturing were evident. Postures ranged from mild threat displays to extreme aggression with "flailing" or use of antlers. These displays, in order of increasing aggression, are discussed below.

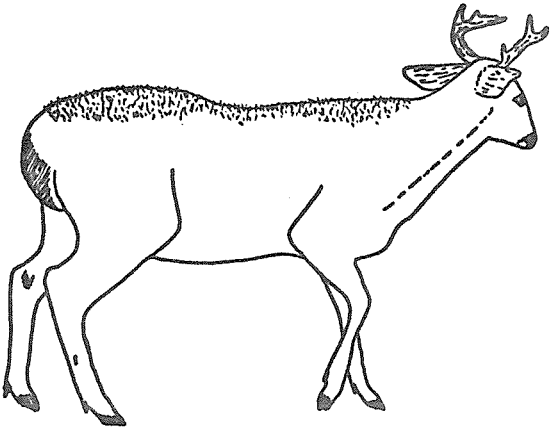
The "ears-back" posture was assumed by an aggressive animal or by one animal which was being approached by another; often both animals assumed the posture. Ears were firmly pressed back and alongside the neck, the openings directed backward and away from the neck (Figure 29). Often the neck was stretched and the head was elevated with the chin pulled in toward the body. The animal either looked away or to the side of the other animals.

Performing a "stare", the deer faced in the direction of the opponent and stared at him. The head was in line with the body, the ears laid alongside the neck, and often the head was lowered to just below shoulder level, while erecting the hair on the neck and shoulders gave the body a larger, hunched effect. If the opponent was nearby, this generally lead to a "head-up" threat, in which the deer raised the head, chin extending upward at an angle, while the ears were against the neck, and the displaying deer kept the opponent in sight. This appeared to be an intention movement, just prior to rearing up for a

Figure 29. Typical "ears-back" posture, used as a mild threat display. Note the erect head and pilo-erection along the shoulders, back, and rump.

Figure 30. Typical "sidle" posture, a threat display used when males encountered one another during the breeding season. The enlarged neck was presented as the male slowly advanced toward or around the intruder. Note the ears-back and pilo-erection.





"strike". Generally smaller animals or clearly sub-dominant animals retreated from the "head-up" threat. Deer meeting a challenge by staring at one another, moving stiff-legged in a tight circle, and presenting the side of the body to the opponent performed the "sidle" (Figure 30).

Those animals remaining in the face of this threat or those that retreated slowly usually evoked the "strike". With the head elevated, chin tucked in, and with ears back and hair erect, the aggressive deer shifted its weight toward the rear, and, using one front leg, kicked out sharply toward the object of its aggression. Usually the leg was directed toward the side or rear of another deer; however, deer were seen to "strike" head-on on occasion when another deer fed too close and ignored other displays. Generally the "strike" resulted in a retreat away from the aggressor.

A more intense form of aggression occurred when the "strike" was combined with a "rush", in which the aggressive deer "struck" out at another deer while chasing it. This was often seen when yearlings harassed one another, and when adult does chased other does and yearlings out of areas where they had young fawns. Ozoga (1972:864) noted that does used "the rush or snort or both to dominate bucks in half of their victories"; however, Key deer did not use snorting in their aggressive encounters with other deer, but often used the rush.

In some instances, where the object of the aggression did not retreat, but rather challenged the aggressor by returning the stare and "head up" posture, the result was a "flail" display, in which both deer shifted weight to the rear, stood upright on their back legs, and kicked out toward the other deer with the front legs. Such "flailing"

generally lasted for a period of 5 to 10 seconds and resulted in one of the two deer turning to the side and backing away from the "flailing" opponent. The dominant deer often "rushed" and "struck" out at the retreating deer for a very short distance. The "flail" occurred between well-matched deer, both of which were highly motivated and nearly equal in dominance. It was observed in those periods when a shift occurred in the hierarchy, that is, when adult male dominance shifted to adult doe dominance or vice versa. Such shifting in the social hierarchy occurred between breeding and fawning seasons.

On 4 July 1970 at 0800 hours, while two adult males in velvet and an adult female with a yearling male were feeding in an area together, one adult male and the female "flailed" at each other three times during a period of 5 minutes (Figure 8, p. 41). The other adult male always moved away from the aggressive pair, and the fawn fed nearby without being disturbed. During this period males were reasserting themselves over adult females, which had been dominant during the fawning season.

Females used the "strike" and "flail" more often than males, and deer of all ages were observed engaged in these activities. Bucks were seen to "strike" or "flail" only during those times when they did not carry polished antlers. Bucks with polished antlers always used the antlers in their aggressive activities. Those bucks in velvet or without antlers, with only one exception, were never observed to use antlers in aggression, rather they used the front legs. Michael (1968a) noted that antlerless or velvet males used the "flail" and "strike" in aggressive encounters. Use of antlers in velvet could prove dangerous, since the delicate skin covering the developing antlers was easily injured.

On 28 June 1971, a 4-year-old male approached a 1-year-old male from the right rear and by turning his head to the side and downward so that the antlers were toward and slightly lower than the yearling buck, strongly thrust his head laterally toward the deer, and at the same time raised and rotated his head to a normal position. His antlers struck the younger deer sharply in the side. Such action with polished antlers would have probably caused severe wounds; however, the velvet-covered antlers appeared to cause no external injury. The action resulted only in the younger deer trotting away for 30 yards, then slowly walking ahead of the adult male, which followed him into thick vegetation.

Aggressive behavior was generally restricted to very brief bouts of actual combat, except in those pushing bouts between equal-sized adult males during the breeding season. Most aggressive behavior rarely proceeded beyond the "stare" or "head-up" threat. Generally, deer faced with a larger or dominant animal that assumed the "stare" or "head-up" threat, lowered its head, looked away, kept the tail tightly against the body and between the legs, turned the head and shoulders to the side, and began to move off in the direction in which he was facing. When backed down, deer moved to a position downwind, or extended the head and sniffed at an aggressor (Figure 31). A submissive deer rarely resumed a challenge once it had backed down. The aggressor often maintained a "stare" in the direction of the submissive animal; and, in cases where a male was defending a female, or in which a female was chasing other deer from the area of her fawn, these aggressors chased or followed the retreating deer for a distance, occasionally trotting to catch up and resume the "strike" and "rush".

Adult does became aggressive toward their yearlings during and after giving birth to new fawns, and also showed some aggression toward their own fawns when weaning them. The form of aggression varied, however, depending upon whether or not the deer were related. While does "struck" and "flailed" deer which were not part of their family units, they were much more gentle in repelling their own offspring. Does trying to get away from a nursing fawn, first tried to back away, straddling the suckling with the front legs and moving awkwardly in reverse. When the fawn simply moved forward and continued to nurse, the doe then moved to the side, stepped over the fawn with her back leg, leaving the fawn nursing from behind. She then moved away faster and the fawn usually stood licking his muzzle or trotted after her crying. Fawns trying to nurse unrelated does were "struck" across the back, just before they could get in position to nurse. Often the doe moved away from the strange fawn; then "struck" at it, driving it away.

Does driving their fawns or yearlings from an area used the "ears-back", "stare" and "rush" to drive them away; however, at least one doe pushed gently with her head to drive her 2-year-old buck ahead of her. By placing her head beneath his rib cage from the side, then lifting her head, she partially lifted him off the ground. Repeated attempts usually resulted in a gentle shoving from the side rather than lifting him off his feet. Such aggression was a gentle manner of driving the deer from the area. Following this behavior, this male and his sibling female yearling began using areas where they had never before been seen, and seldom spent time with their doe. Apparently the doe had chased them from the area where she kept her newborn fawn.

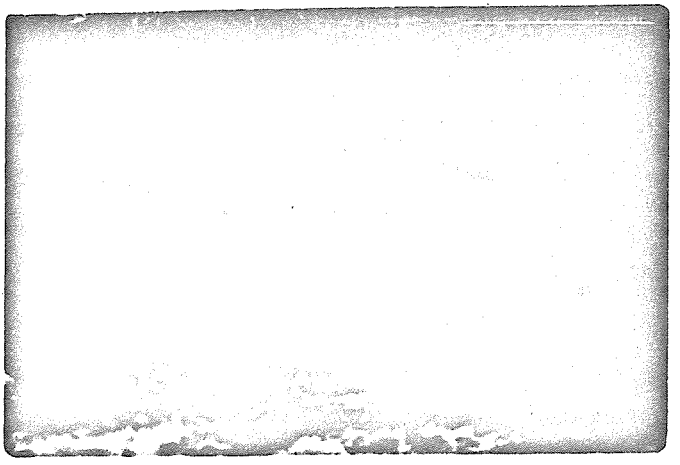
Male combat - Rutting activities of most species are largely ritualized, antlers serving the function of displaying more than jousting weapons (Henshaw 1971). While encounters between Key deer males occurred frequently during the breeding season, actual combat was rarely seen. Smaller bucks backed away immediately from a larger male, as was reported by Marchinton and Moore (1971) for Georgia white-tails, or else the two deer performed a series of aggressive behaviors that varied in intensity.

Most often one deer approached another cautiously with ears pressed against the neck or presenting the antlers and performing a "sidle". Deer of equal size often continued displaying and moving in small circles; this occasionally led to actual combat.

When combat followed displays, males gradually approached one another, "sidling" with ears back and staring hard at the opponent. They then lowered their heads until noses nearly touched the ground, presenting their antlers close to the other deer. They gradually moved forward until their antlers touched, after which they vigorously twisted their heads from side to side while pushing with their bodies, pivoting in a circle with the antlers being the central point around which they moved (Figure 31). Brief pushing bouts were interrupted by 15 to 90 seconds of resting and quick glances around them. Each quickly responded by presenting his antlers and bracing himself for combat when the opponent lowered his head or presented his antlers.

When two well-matched deer fought, the contest often became vigorous enough to potentially result in injury to the participants. During a battle between two 2-year-old males, when one of the contestants was thrown off his feet by the other deer, the second deer backed

Figure 31. Two yearling males fighting during the breeding season. Combat between equal-sized males occasionally resulted in injury to one or both individuals.



slightly, resuming the bout only after the former regained his footing. Similarly, Michael (1968a) noted that in two different fights, downed males were not attacked by their opponents while they were down.

When fighting, both deer tended to place the forefeet forward, bending the legs slightly, lowering the neck and head between the forelegs, hunching the shoulders, and using the hind legs to push forward and to move from side to side. Once a deer was thrown off balance one or two times, or was pushed backward several yards, it terminated the fight by moving 20 to 30 yards away to feed or bed. Combat seldom was resumed at a later time. Other deer feeding nearby generally ignored the fighting, moving out of the way only when the bucks moved near them while vigorously trying to push their opponent off balance.

That such combat may occasionally lead to serious injury or death was indicated by the appearance of several deer, during and after the breeding season, that had large scars on the head, neck, and shoulders, leg injuries, broken antlers, and, in two instances, bone exposed between the antlers with sections of the frontals chipped and loose. Remains of six adult bucks were found with holes between the frontal bones along the suture line, apparently caused by antlers of another deer. Another deer, found with a hole in his side during the breeding season, was suspected to have succumbed to combat. Adult and yearling males lost collars and radio-transmitters durirg the breeding season as a result of the vigorous activities engaged in during fights with other males.

Deer of all sex and age classes were harassed by males during the breeding season; but, normally all deer fled from the advances except

receptive does or bucks that stood to meet their challenge. Adult males emitted a series of rapid staccato snorts when challenging other males (see Auditory communication). This was observed twice in the field, once by an adult male that, while with a receptive female, responded to another male that appeared and stood at the edge of a wooded area 150 yards away. The second male snorted while staring toward a vehicle that blocked a road along which he was nose-trailing. A tame penned adult male repeatedly snorted when I stood by the pen. When one of the does was in estrus, the buck often responded to the researchers in a manner similar to wild bucks responding to other males. Cowan and Geist (1961) noted similar behavior in mule deer as they circled in the crouch position; however, Thomas et al. (1965) never noted this behavior in white-tails.

On 7 October 1970 a 2½-year-old male appeared to engage in a type of displacement activity by antlering shrubs between bouts of fighting with a 6½-year-old male, who had broken one antler and prematurely lost the other. The smaller buck moved about 30 yards away from the dominant animal and thrashed a low-hanging limb. After the dominant male had been bedded for 5 minutes, the 2½-year-old deer initiated another pushing bout. Both deer then moved into the thick vegetation together. Other deer fed briefly when backed down by a larger male; this appeared to be a type of displacement behavior.

Reproductive Patterns

To appreciate the impact of Key deer behavior on the life history data collected from deer observed in the field, it was necessary to investigate their reproductive performance and mortality, in addition to their behavior. However, the fact that behavior of the deer influenced their productivity and mortality, made delineating the impact of each of these more difficult. Various aspects of the deer's reproductive behavior and performance and their effects on the observed population dynamics and herd structure (sex-age ratios) are discussed below.

Reproductive behavior

Fraser (1968:80) reported that there were "certain major activities springing from the sex drive", which were linked and "virtually common to ungulate subjects." These included threatening and displaying, challenging and contesting, sign-posting and marking, searching for and breeding females, and prompting and tending. All of these activities, related to sexual behavior, were observed to some degrees in the Key deer.

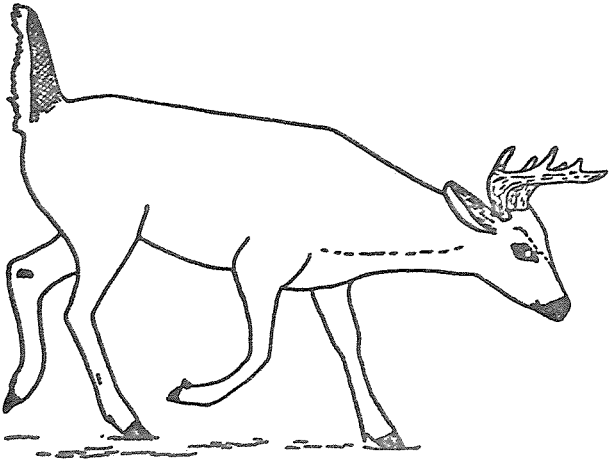
Reproductive behavior incorporated other types of behavior discussed previously into characteristic sequences or patterns, which were associated only with the breeding activities. The behavior that was most commonly seen during the breeding season was harassment of all other deer by adult and yearling males; this occurred while testing unreceptive females, and while tending and prompting receptive females as described by Fraser (1968).

Male white-tailed deer and mule deer approach females at a rapid trotting pace and chase them, sometimes for up to several minutes (Severinghaus 1955, Linsdale and Tomich 1953, Browman and Hudson 1957, Crawford 1962, Golley 1957). Males may begin chasing females 2 to 3 days before the doe becomes receptive (Severinghaus and Cheatum 1956), but unreceptive females run a short distance and avoid the males (Crawford 1962). Chases end when receptive females stand while the males breed them. Browman and Hudson (1957) noted that the first attempts to mount a receptive doe were unsuccessful, and Golley (1957) noted that during the courtship and precoital stages of deer breeding behavior, first attempts were never successful.

In Key deer typical harassment involved an adult male chasing or trailing other deer; this behavior was termed nose-trailing, when directed toward females in estrus. The pursuing male characteristically had the neck outstretched to the front, the head lowered to a level of shoulder height or below, the nose extended either forward toward the doe or just off the ground when trailing at a distance (Figure 32). The erect tail wagged from side to side as the buck trotted just behind the doe, and he emitted a low grunt at 5- to 10-second intervals during the chase. Similar behavior was described by Browman and Hudson (1957) in penned mule deer, Odocoileus hemionus.

Males were attentive toward receptive females, which they followed, disregarding other deer and often even the observers, vehicles, or other objects that normally elicited alarm reactions. Males bedded when females bedded, and usually stayed downwind of them, often as close as 10 yards away or within sight. When does became active after periods

Figure 32. Typical nose-trailing posture of an adult male during the breeding season. The neck was outstretched with the nose near the ground or at the level of a female's hocks or vagina, when she was just in front of him. The erect tail indicated a high level of excitement; the gait was most often a trot or fast walk.



of bedding, males resumed the chase, harassing them as if to test their receptiveness (Figure 33). Fraser (1968) suggested that this may be a form of bio-stimulation, which could be a necessary prelude to prompting and tending.

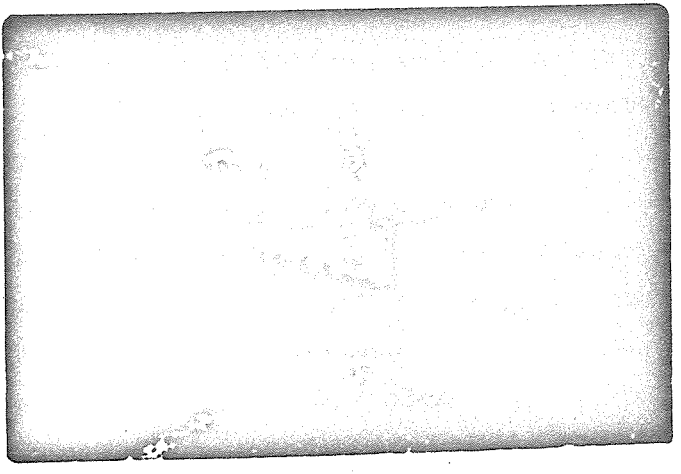
When does moved about feeding, males maintained sight of them and generally followed at a distance, occasionally rushing them briefly. Unreceptive females moved to the side and stayed away from males; after brief chases males abandoned them. Does coming into heat generally ran or trotted about 6 to 20 feet ahead of the buck. Ears were directed backwards toward him and the tail was erect; no arrector pili effect was noted.

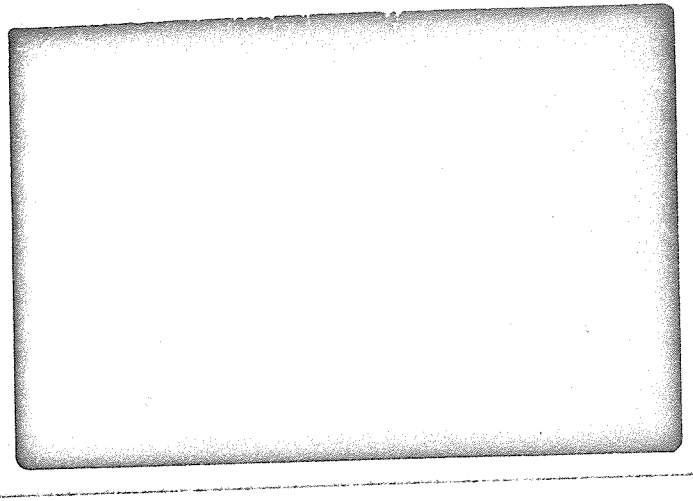
Generally, the only way to determine which does were receptive was to note their behavior toward males; however, one adult female being harassed by males was captured and examination revealed a swollen vulva. Bucks appeared to determine which females were becoming receptive, largely by olfactory cues; however, the female signalled readiness to breed by standing and allowing the male to mount. Unreceptive females ran at a buck's approach.

On 24 August 1971, two adult males in velvet chased an adult and yearling female while feeding. Chases occurred whenever the males approached to within 6 to 8 feet of the females; however, these bouts lasted for only 5 to 10 seconds, and then deer resumed feeding after the females avoided the males. After males had lost the velvet from their antlers, chases and harassment became more intense; males harassed all other deer that they encountered.

Figure 33. Adult male and adult female disturbed during a reproductive chase. That males follow adult does so closely at this time made monitoring these animals difficult. Note the mosquito ditch in front of these deer.

Figure 34. An adult male sniffs the hocks of an adult female during the breeding season. While this behavior was frequently observed during the breeding season, deer were often seen to sniff hocks of other deer when they encountered one another, joined a group of deer, or became alarmed.





Males sniffed female perianal regions and hocks, and were seen to test their urine during all times of the year (Figure 34). When sniffing urine of another deer, bucks gave the typical lip curl (Geist 1963), also termed a "flehmen" response (Schneider 1930, as in Fraser 1968) or "artiodactyl grimace" (Cowan 1956), which has been observed in most ungulates (Estes 1969, Walther 1960, as in Fraser 1968). The upper lip was raised, the nose was wrinkled, and the head and muzzle were usually elevated as the deer inhaled. This was interpreted as a means of analyzing the urine (Shank 1972, Ewer 1968, Fraser 1968, Browman and Hudson 1957). Bucks, approaching a receptive female, typically sniffed the hocks or urine, gave a lip curl response (Figure 35), then rested the chin on the female's rump or side. One penned deer gently nudged the female with his antlers, similar to the head rubbing or butting noted in goats and bulls (Fraser 1968). This was never seen in free-ranging deer; however, occasionally the captive male, as well as free-ranging males, used their antlers in harassing the unreceptive females.

If the female stood as the male nudged her, he then moved forward while shifting his center of balance backwards, lifting his front end off the ground, walking with the hind feet, and supporting his front end on the female's rump. While positioning himself above the female, his forelegs were held stiff and came to be positioned just in front of the female's hind legs. The body of the buck was hunched over her back and his head was positioned alongside of her shoulders (Figure 36).

The penis was brought in close to the perineal region of the female as erection occurred and intromission was achieved. After 5 to 10

Figure 35. "Lip-curl" or "flehmen response" performed by an adult male after sniffing the urine of another deer. Such behavior has been interpreted as a means of "analyzing" urine.

Figure 36. Typical breeding posture of adult male and female Key deer.

seconds, the buck performed 5 to 10 pelvic thrusts, followed by one strong thrust, which pushed the female forward, and resulted in the male sliding off her back. This was followed by both deer grooming themselves and one another; and, then was followed by a period of 2 to 5 hours of bedding behavior. While the post-coitus behavior, in which northern deer showed no interest in one another after copulation (Golley 1957), was not similar to Key deer, that reported by Verme (1965), in which males repeatedly serviced females and showed interest after breeding (Severinghaus 1955), was similar.

If intromission was not achieved at the first attempt, which was commonly the case, the mounting behavior was repeated almost immediately. The male followed the receptive female, feeding briefly and watching her closely, even when she was motionless. Does becoming receptive generally ran with the male for 2 to 3 days before holding for him, but some does remained with bucks from 1 to 5 days. Periods of receptivity lasted for only about 24 hours, similar to the 24 to 36 hours reported for northern deer (Cheatum 1949, Erickson et al. 1961, Behrend 1966, Verme 1965). Severinghaus (1955:239) reported that in northern deer, "does may cause vigorous sexual stimulation in bucks for at least 3 days prior to receptiveness and for at least 2 days after mating." One doe may attract a buck's "continuous and ardent attention" for 5 or 6 days.

More than one male per female was seen on several occasions. Of 148 observations of breeding or nose-trailing, 126 (85.1 percent) involved only a single male and female, 19 (15.1 percent) involved two males, and 3 (2.4 percent) involved three males. Despite this activity

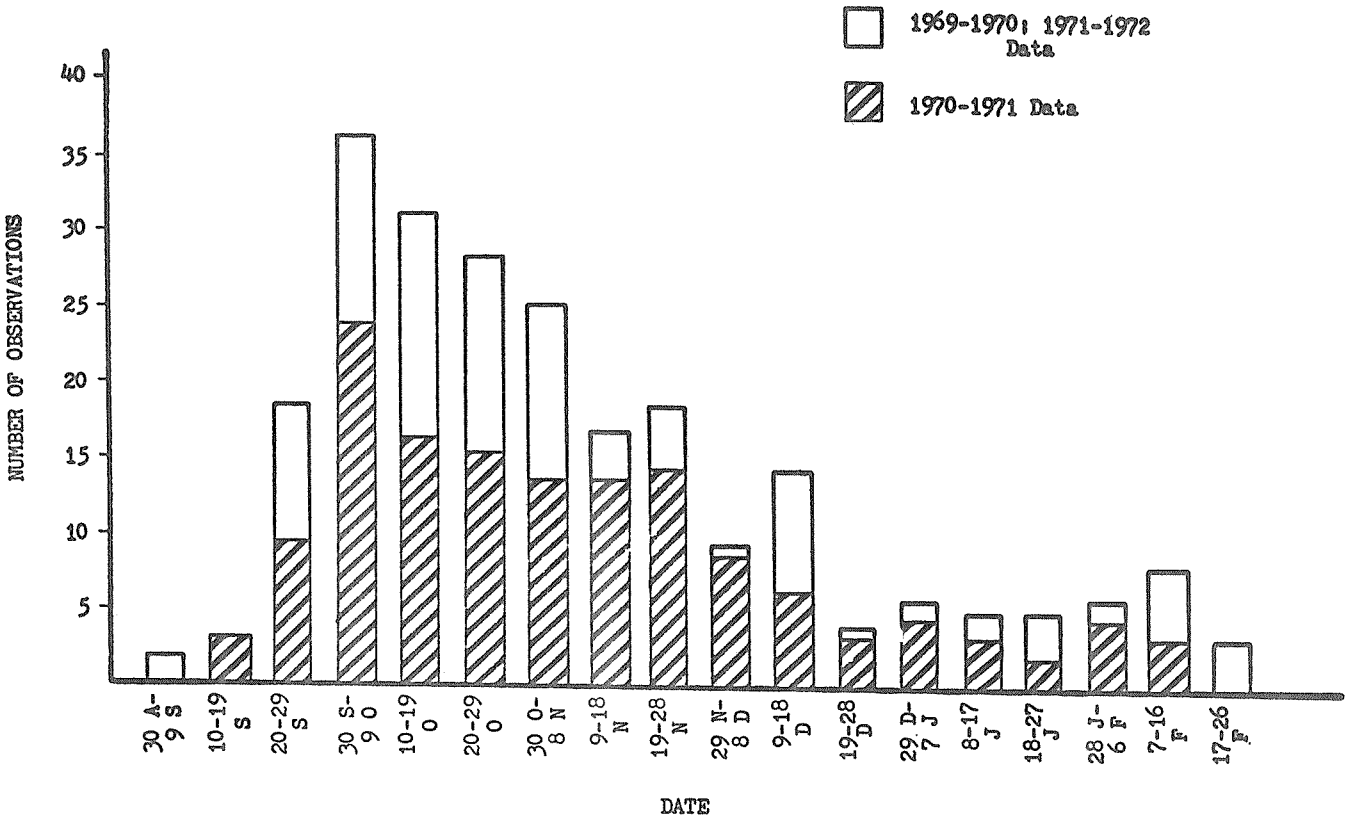
it is believed that no more than one male bred these females, since the surplus males were generally smaller and remained away from the pair or else the males fought with one backing down. This was also noted in northern populations in which the largest male of the group was dominant (Skinner 1929, as in Severinghaus and Cheatum 1956, Severinghaus 1955, Crawford 1962). Occurrence of large numbers of females being bred simultaneously by a number of males, as described by Shank (1972) for goats, did not occur in Key deer; although a frantic chase involving three males and an adult doe caused four yearlings and fawns to become excited and join in the chase behind the males.

Breeding dates

Various reports suggest that breeding of Key deer is non-seasonal (Barbour and Allen 1922, Severinghaus and Cheatum 1956). However, data from this study indicate that breeding peaked in October, then declined through December; a few breedings occurred as late as February. On 24 August 1971 the earliest pre-breeding activity was observed among a group of two adult males in velvet, an adult doe and her yearling female. These activities only involved brief chases as males harassed the females; but, behavior leading up to breeding did not occur. No males in velvet or males without antlers were observed to participate in breeding; however, adult males appeared capable of breeding as soon as velvet was lost from their antlers.

Intense breeding behavior involving bucks with polished antlers was first seen on 6 September and increased in intensity through late September, reaching a peak in early October (Figure 37). There was then

Figure 37. Observations of breeding activities. Each column represents the number of breeding observations recorded during that time period. Shaded area represents 1970-71 breeding season, during which observations were made throughout the reproductive season. Data for 1969-70 and 1971-72 were not for the entire period.


1969-1970; 1971-1972 Data
1970-1971 Data
NUMBER OF OBSERVATIONS
40
35
30
25
20
15
10
5
30 A-9 S
10-19 S
20-29 S
30 S-9 O
10-19 O
20-29 O
30 O-8 N
9-18 N
19-28 N
29 N-8 D
9-18 D
19-28 D
29 D-7 J
8-17 J
18-27 J
28 J-6 F
7-16 F
17-26 F
DATE

a gradual decrease through November and December; and, occasional sightings of bucks trailing or harassing females occurred into February before subsiding. During 1970-1971, when observations of breeding were made throughout the season, 74 percent of the observations of breeding were recorded between 20 September and 15 November. Ninety percent of the breeding observations were recorded by 22 December. Numerous mangled shrubs evidenced male activities during the breeding season after they shed their velvet in September; these activities, as well as chasing deer of other sex-age classes, occurred into February.

When considering the general pattern of breeding activities of North American white-tailed deer, deer in southern latitudes seem to have earlier breeding seasons than those to the north. Nixon (1971) noted that Ohio deer began breeding in late October and peaked in early November; Georgia deer in an enclosure completed the rut by mid-November (Downing 1965). New York deer had peak rutting between 10 November and 14 December (Cheatum and Morton 1946, as in White 1973), and on the Aransas Wildlife Refuge, 72 percent of the deer bred between 16 October and 7 November (White 1973). Loveless (1959) reported that breeding activity in Everglades white-tails occurred throughout the year, was most pronounced during September, and most breeding had subsided by the end of October. Although from these studies it appeared that in southern latitudes deer tend to have earlier breeding seasons, Severinghaus and Cheatum (1956), basing their information on various isolated studies of deer herds at different latitudes, indicated that deer of southern latitudes bred later. Our study suggests that the Key deer basically fit the north-south pattern, in which southern deer breed

earlier. The Key deer, in addition, demonstrated a prolonged breeding season, with breeding occasionally occurring as late as February.

One apparent exception to the north-south reproductive pattern was that of the Everglades deer herd, which demonstrated peak breeding activities in March (Loveless 1959), nearly 1 month earlier than Key deer. These populations were separated by only 100 to 200 miles. The explanation of these differences may be in the adaptation of the populations to local conditions.

The onset of breeding activity has been attributed to response to shortened day length (Turner 1966); however, deer herds may be adapted to local conditions that tend to modify, somewhat, the onset of breeding. White (1963) found that deer on the Aransas Wildlife Refuge in Texas had a different reproductive pattern than deer in the surrounding areas. These differences he attributed to adaptation to the local plant phenology in the moist coastal refuge lands. Differences between Key deer and Everglades deer may be due to similar local adaptations. Based on the descriptions of conditions in the Everglades (Loveless 1959), an early fawning season might increase the potential survivorship of Everglades fawns, since the May-September rainy season, which limits available food and space for bedding, would have a greater adverse effect on newborn fawns. During this same period in the Keys, rainfall did not have the same effects, since water levels on the surface did not increase because of drainage. That adaptations to local conditions in the various deer herds in North America could cause local differences in breeding seasons, no doubt has contributed to the problems of determining patterns of breeding in deer at various latitudes, and in determining what mechanism(s) triggers the onset of breeding.

Gestation period

Based on marked does, for which breeding and parturition dates were known, the gestation period of Key deer was around 204 days. This was similar to gestation periods reported for deer in Northern states. Severinghaus and Cheatum (1956) noted a 201-day gestation period for northern deer, while Cheatum (1949) indicated that in general, deer of northern latitudes carried fawns 6½ months (196 days) before giving birth. In Michigan deer, Erickson et al. (1961) reported a gestation period of 200 to 210 days, while Verme (1965) recorded a 204-day period (range, 196-211 days) in penned white-tailed deer. The greatest range was reported for upper Michigan white-tails as 197 to 222 days (Haugen and Davenport 1950). Seemingly the gestation period is relatively uniform for all Odocoileus, as indicated by gestation periods of 203 days (range, 199 to 207) in black-tailed deer (Golley 1957), and 202-209 days in mule deer (Robinette et al. 1955, Robinette and Gashwiler 1950, Dixon 1934).

Fawning dates

Birth of most Key deer fawns occurred in late April and early May. Late breeding deer produced fawns throughout the summer, as was evidenced by pregnant does killed on the highway in June and July with small fetuses; occasionally, small spotted fawns were seen in August and September. A female fawn, which bred in February, gave birth in September, nearly 6 months later than most other does.

For fawns, which were captured as newborns (1 day of age or less), by backdating 204 days from the date of birth, it was determined that

the earliest were conceived around 12 September, and the latest around 27 October. This did not support earlier reports that there was no special season for fawning by Key deer (Barbour and Allen 1922).

The fawning season basically fits the pattern for North American cervids, with southern forms giving birth earlier than northern forms. In Alabama, peak fawning occurred in mid-June and early July (Adams 1960). On the Ocala National Forest in central Florida, it occurred in April (Strode 1954, as in Loveless 1959), and in the Everglades in March and early April (Loveless 1959). Key deer fawning peaked about 1 month later than those in the Everglades, and was, no doubt, a result of local adaptations (see Breeding dates).

The fawning season appeared relatively stable during the 5-year study. However, in some herds, variations in fawning occur and show strong correlations with rainfall of the previous summer, temperatures preceding the rut, and cloud cover in months immediately preceding the rut (McGinnes and Downing 1972).

Times of breeding

Observations of breeding behavior were made at all hours except during 2000-2059 hours, during which there was a tendency for deer to become less active and bed more (see Patterns of activity). The greatest breeding activity occurred at around 0700-0800 hours and at 1500 hours (15.5 percent of all observations were made at 0700, while 12.7 percent of all breeding occurred at 1700 hours). This corresponds to times when deer normally moved about just after sunrise and just after mid-day bedding periods, respectively. At such times, bucks resumed the chases.

Most copulations probably occurred at night or in twilight, resulting in few being observed. One adult male mounted a female (AF099) at 1920 hours on 4 October 1971, a yearling male (YM051) bred a fawn doe at 1245 on 11 February 1970, and on 21 January 1971, at 0800, an unmarked adult male mounted a yearling female, but intromission was not achieved before they moved into thick cover. A captive adult male repeatedly mounted an adult female at intervals throughout the day and night, but the artificial conditions may not typify actual events in the wild; also, they were separated until the female appeared to be receptive.

Participants in breeding

The earliest breeding activity involved adult animals, followed later by yearlings, and then by some fawn females. No fawn males participated in breeding females (Figures 38-42). The first bucks that participated in active pursuit of females were in the 2- to 7-year age class, with 2-year olds being excluded by 3- and 4-year-old deer whenever there was such an encounter around a receptive female. Yearling males participated in early chases and later breedings, but did not actually breed during the peak breeding season. As 3- and 4-year-old males participated in fewer breeding activities, they were replaced by animals aged 5 years and older and by yearlings. In several instances two or three yearlings remained off to the side pushing against one another while an adult male remained with an adult female. Yearlings occasionally participated in chases, but seldom bred does. Similar breeding sequences of various-aged deer were reported for

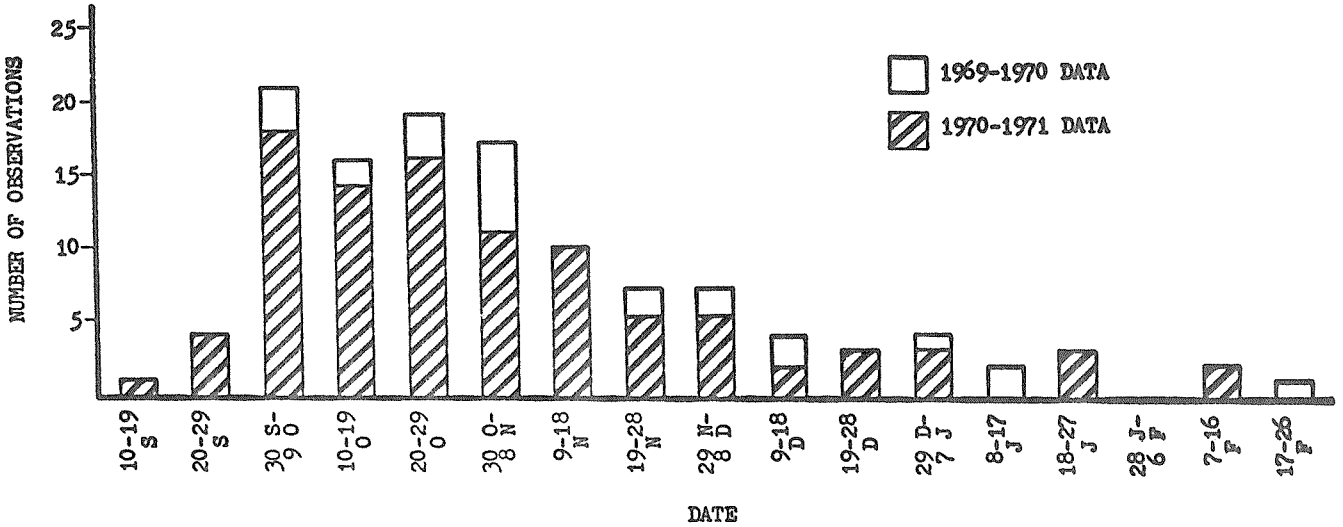


Figure 38. Observations of adult male breeding activities during September 1969 through 26 February 1971.

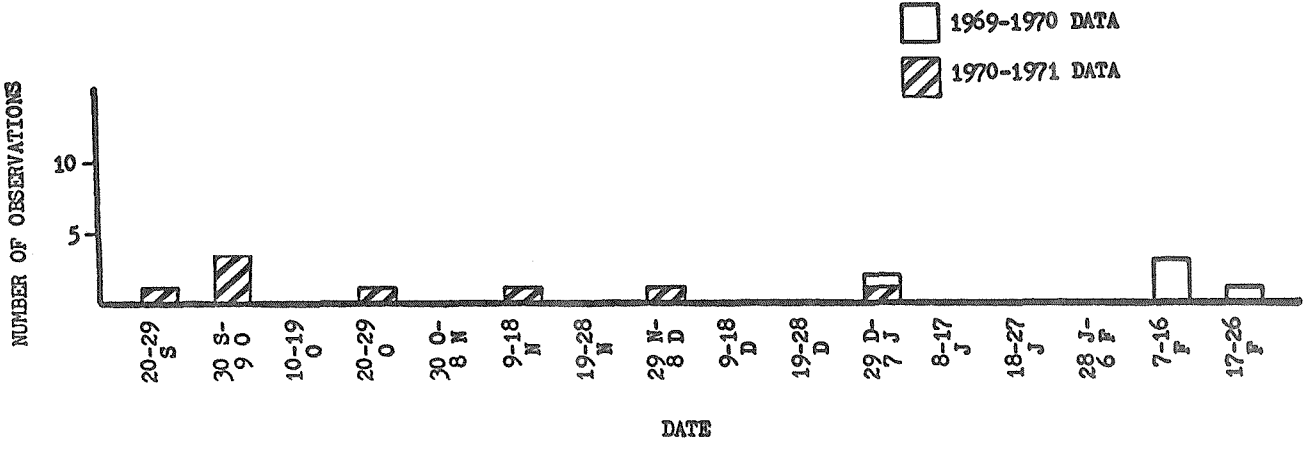


Figure 39. Observations of yearling male breeding activities during September 1969 through 26 February 1971.

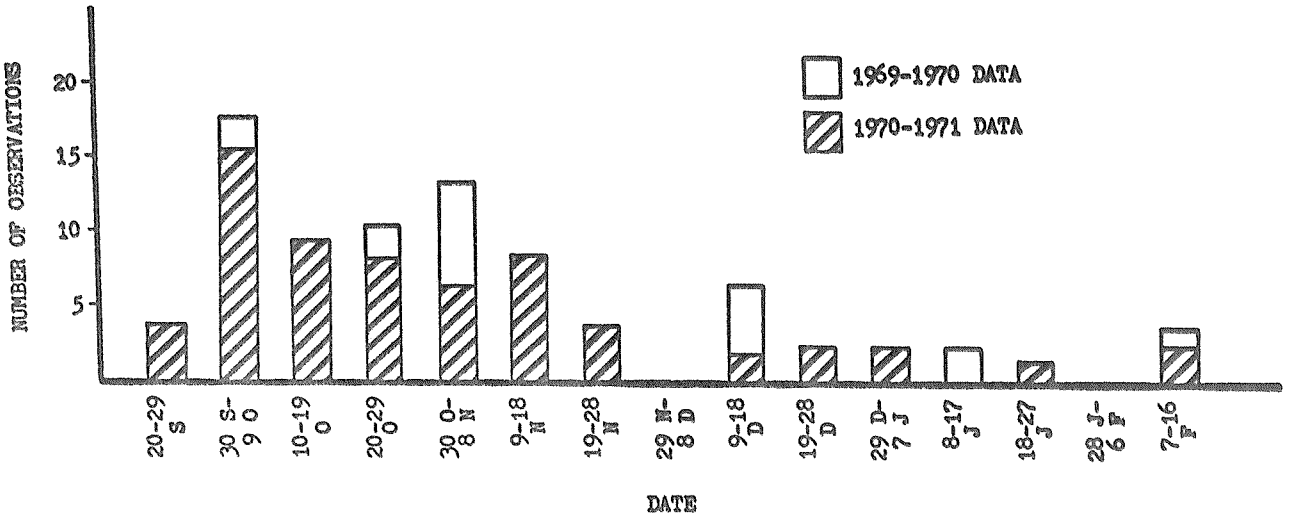


Figure 40. Observations of adult female breeding activities during September 1969 through 26 February 1971.

northern deer, with younger males and females breeding only later in the season (White 1973, Robinette and Gashwiler 1950, Roseberry and Klimstra 1970, Crawford 1962).

Whenever an adult female was present alone with a yearling male, the male often nose-trailed her, either for a short distance, or actively chased her over longer periods of time if she was near estrus. On 8 October 1970, a yearling male attempted to mount an unreceptive female, even after she turned and "struck" at him, driving him a short distance away. He repeatedly attempted to mount her until she trotted to thick cover as he nose-trailed behind her. One yearling male mounted his own mother less than 24 hours after she had given birth to another fawn. This aberrant behavior was seen only on this occasion, and did not involve the typical precopulatory activity of chasing or nose-trailing; intromission was not achieved.

During times of peak breeding, yearling males were seen to participate in only 3.9 percent of the activities, whereas in early September, November, January and February, they participated in 13.3 percent, 11.4 percent, 25.0 percent and 47.1 percent of the activities, respectively (Figure 39). Similarly, yearling females showed an increase in activity, participating in 7.7 percent of the activities in September, 14.5 percent in October, 17.1 percent in November, 30.0 percent in December, and 37.5 percent in January (Figure 41).

Most early observations of yearlings breeding involved short chases, which ended with the males being distracted by other deer, or by the pair stopping to feed. Only in November and into January were yearling females seen to engage in intense breeding chases, indicating

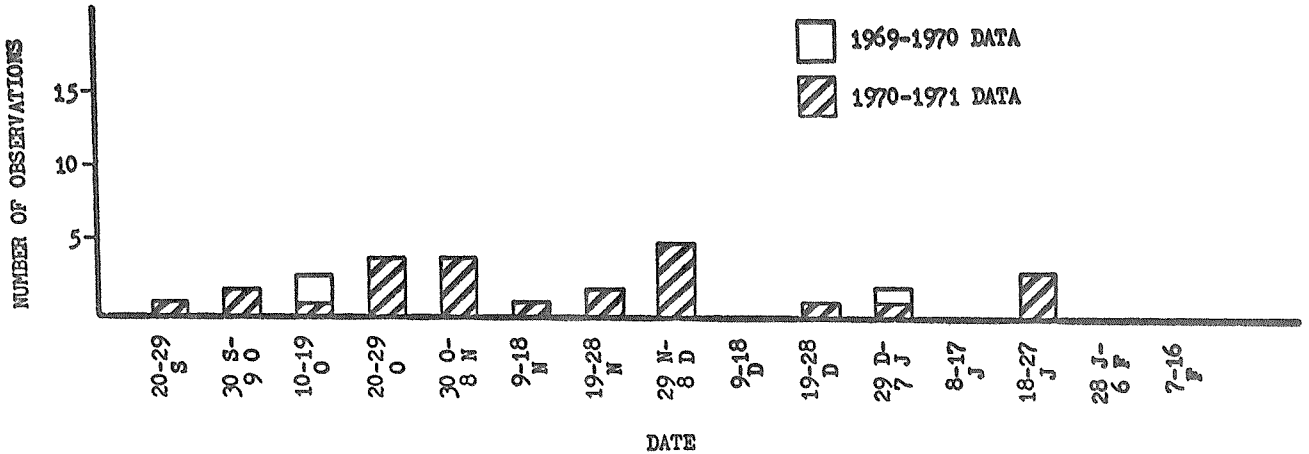


Figure 41. Observations of yearling female breeding activities during September 1969 through 26 February 1971.

that they were coming in season. Both adult males and females participated in breeding most often in October and November, tapering off through December and January. Chases involving yearling males were seen sporadically through the season, although those chases seen late in the season were much more intense. Those sightings in September and October usually involved adult males. Yearling females participated most often in October and November, just after the peak of adult female participation.

On 12 occasions female fawns participated in chases, usually late in the season (Figure 42). Some fawn females participated in reproductive chases when they were in the vicinity of their doe or sister when chases began, and thus became involved in the activity. Later in the season, however, they were more frequently chased by adult and yearling males. On 12 February a fawn female, which had been running with a radioed yearling male for 2 days, held while the male mounted her and achieved intromission. The results of these observations indicate that adult females first came into heat; yearlings tended to become receptive somewhat later in November or January and February, and a limited number of fawns were bred as late as February.

The percent of fawn participation in reproductive activities appears to have decreased during the study (Figure 42). In 1969-1970, fawns were seen running with males in November, December, and February, and participated in breeding activities up to 80 percent of the time in February. This, in part, may be due to bias of the researcher toward mis-classifying yearlings as fawns; however, this is not believed to have been the major cause of this larger figure for fawn breeding.

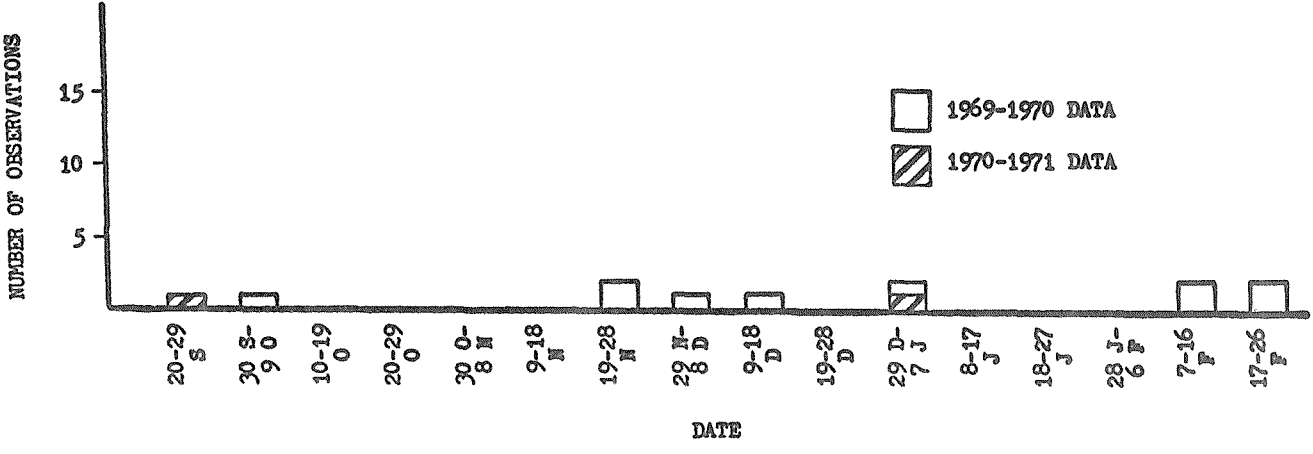


Figure 42. Observations of fawn female breeding activities during September 1969 through 26 February 1971.

During 1970-1971, only two fawns participated in what appeared to be breeding activity, and during 1971-1972, only one fawn was involved in a chase. It appears that there was a decrease in the reproductive activity of female fawns during this study. The one fawn, known to have bred, was seen in the 1969-1970 season; one yearling female was believed to have bred as a fawn during the 1968-1969 season, and was consistently seen with the fawn during the fall and winter of 1969-1970. There was no evidence during 1971-1972 of fawns having bred. In some white-tailed deer populations, male fawns have been found fertile; however, the contributions to the breeding activities are considered negligible (Follmann and Klimstra 1969). In Key deer, male fawns did not participate in breeding activities.

The exclusive behavior of 3- and 4-year-old males in breeding receptive females could potentially limit the number of females which were serviced when they came into estrus. Lambiase et al. (1972) suggested that deer may produce enough sperm for one or two daily fertile matings over a prolonged period of time; however, if they mate several times daily, they probably deplete their sperm reserve and suffer a decline in fertility. That this potentially could reduce the reproductive output of the Key deer population was countered by the fact that those adult does, which did not conceive in first breedings, recycled in 25 to 27 days. One penned doe, which had a hip injury that apparently hindered her ability to conceive, was observed to enter estrus at least four times in one season. These periods were spaced at 24- to 27-day intervals. Other researchers of white-tailed deer have noted that the ovarian cycle is 28 to 29 days in New York and Minnesota (Behrend 1966, Severinghaus and Cheatum 1956, Erickson et al. 1961).

Late breeding adult females were probably deer which had not been serviced earlier, or which had not successfully conceived during previous estrus periods. The result of this was that all estrus females could be potentially serviced, regardless of the male's behavior. The result was that the prime-aged males serviced a large number of females during the peak breeding period; however, those does not serviced were later bred by less "fit" older or younger males. This may have influenced the sex ratio of fawns produced, since more males breeding may result in more buck fawns (see Fetal sex ratios); it also spread the breeding season over a longer period of time, and resulted in a number of fawns which varied in size being seen at any time of the year.

Productivity

Based on observations of deer in the field, it appeared that there was a low reproductive success and a high proportion of male fawns produced (see Sex-age Ratios). It was therefore necessary to ascertain whether this apparent low productivity was a function of the behavior of the deer, or represented actual productivity of the herd. The age of first breeding, the percent of deer in each age class which bred, and the number of fawns produced per age class all affect the rate of population increment. To determine whether females were reproductively active, all females captured were examined to determine the extent of udder development, to determine whether they were lactating, or to determine whether they were pregnant. As Key deer were stocky (proportionately shorter legs compared to northern deer) they normally appeared heavy. Field determination of pregnancy was, therefore, difficult except during the late stages, just before parturition, when

pregnant does appeared very heavy, and udders were obvious. Since Key deer fawns were weaned at around 4 months of age, maternal does normally lactated throughout the summer. During the breeding season, it was often impossible to determine whether a doe had bred; however, some does still had slightly enlarged but dry udders when captured, and were therefore assumed to have bred during the previous season and produced a fawn. It was impossible to determine from external examination that a deer was not pregnant, due to the variation in times of dropping fawns by individual deer.

The reproductive status of captured deer was determined when possible (Table 18). No fawns were found to be reproductively active (i.e., pregnant or lactating), and 3 (13 percent) of the 23 yearlings were pregnant or lactating when captured. Two (67.0 percent) of these had bred as fawns. Of the 35 2-year olds captured, 23 (65.7 percent) were reproductively active; 20 (87.0 percent) of these 23 deer had bred as yearlings. For the 127 does aged 2½ years and older, 106 (83.5 percent) were reproductively active, while 21 (16.5 percent) were in an unknown condition.

Examination of roadkilled does provided more detailed information on the reproductive status of females. No fawns or yearlings were found to be pregnant. Twenty-six (44.1 percent) of 59 does were pregnant, while 10 (16.9 percent) were lactating (Table 19). The number of fetuses per adult doe was 0.80, and the number of fetuses per pregnant doe was 1.19. Assuming each lactating female produced at least one fawn, the minimum fawn count per female examined and aged at 2 years or older was 1.05.

Table 18. Reproductive data gathered on female Key deer captured during January 1968 through June 1973.

Age of Doe (Years)	Number of Does Examined	Reproductively Active When Captured	Number Pregnant	Number Lactating	Udder Present But Not Lactating	Number of Does Breeding at Each Age[a]
½-1	17	0	0	0	0	2
1-2	23	3 (13)[b]	2	1	0	21
2-3	35	23 (65)	10	5	8	27
3-4	38	34 (89)	22	9	3	25
4-5	22	19 (86)	10	7	2	18
5-6	19	18 (94)	11	4	3	10
6-7	9	8 (88)	3	4	1	4
7-8	2	2(100)	1	1	0	2
8-9	2	2(100)	0	2	0	0
Total	167	109 (65)	59	33	17	109
≥ 2 Total	127	106 (84)	57	32	17	86

[a]Ages adjusted to the ages when they last bred; does examined after 1 April spent the breeding season aged 1 year less than when examined.

[b]Numbers in parentheses represent the percent which were reproductively active.

Table 19. Reproductive data gathered from female Key deer roadkilled during January 1968 through June 1973.

Age of Doe (Years)	Total Number of Does Examined	Number Pregnant	Number Lactating	Single Fetuses			Twin Fetuses			Total Fetuses	Fetal Sex Ratio M:F	Fetuses Per Doe	Fawns Produced Per Doe
				M	F	UK	M	F	UK[a]				
½-1	5	0	0	0	0	0	0	0	0	0	--	0.00	0.00
1-2	13	0	0	0	0	0	0	0	0	0	--	0.00	0.00
2-3	12	7	2	4	0	2	0	2	0	8	4:2	0.67	0.83
3-4	9	7	2	2	2	2	0	2	0	8	2:4	0.89	1.11
4-5	4	2	2	1	0	0	2	0	0	3	3:0	0.75	1.25
5-6	5	3	2	1	2	0	0	0	0	3	1:2	0.60	1.00
6-7	1	0	1	0	0	0	0	0	0	0	--	0.00	1.00
7-8	1	0	1	0	0	0	0	0	0	0	--	0.00	1.00
Adults (age unknown)	9	7	0	3	0	0	3	3	2	11	6:3	1.22	1.22
Totals	59	26	10	11	4	4	5	7	2	33	16:11	0.56	0.73
≥ 2	41	26	10	11	4	4	5	7	2	33	16:11	0.80	1.05

[a]M = male; F = female; UK = sex unknown.

These females were collected at all times of the year and those killed in April, May, and June were aged as 1 year older than their age during the breeding season, since 1 April was considered the birth date of Key deer. Thus if the age of each roadkilled deer was adjusted to the age during the current or previous breeding season (in the case of those killed out of the breeding season) the contribution of various age classes could be better appreciated.

No fawns were found to be reproductively active; however, three (37.5 percent) of eight yearlings examined had bred to produce a minimum fawn count of 0.38 per doe (Table 20). Eleven (91.7 percent) of the 2-year olds had bred, producing a minimum fawn count of 1.08 per doe, and of all deer 2½ or older, 33 (92 percent) had bred to produce 1.11 fawns per doe. Since during November through June, does that were pregnant or successfully suckling fawns should be distinguishable when examined, examination of these animals may provide a more accurate picture of the actual reproductive output of the Key deer.

Roadkill data in the months of November through June during 1968 through 1973, supported the field observations that few fawns and yearlings were bred (Table 21). Of six fawn females examined, none were reproductively active; eight yearlings were not reproductively active. Of 35 does, 2 years or older, 26 (74 percent) were pregnant, 5 (14.3 percent) were lactating, giving a number of 31 (88.6 percent) reproductively active does during November through June.

Using data in which ages were adjusted to breeding ages, of the six yearlings, three (50 percent) were reproductively active (Table 22). Of 11 2½-year-old deer, 10 (90.9 percent) had bred. Of the 19 deer aged

Table 20. Reproductive status of roadkilled female Key deer. Ages represent the ages of these animals during the breeding season.

Age of Doe (Years)	Total Number of Does Examined	Number Pregnant	Number Lactating	Single Fetuses			Twin Fetuses			Total Fetuses	Fetal Sex Ratio M:F	Fetuses Per Doe	Fawns Produced Per Doe
				M	F	UK	M	F	UK[a]				
½	15	0	0	0	0	0	0	0	0	0	--	0.00	0.00
1½	8	2	1	1	0	1	0	0	0	2	1:0	0.25	0.38
2½	12	8	3	4	0	2	0	4	0	10	4:4	0.83	1.08
3½	7	5	2	2	2	1	0	0	0	5	2:2	0.71	1.00
4½	5	3	2	1	1	0	2	0	0	4	3:1	0.80	1.20
5½	2	1	1	0	1	0	0	0	0	1	0:1	0.50	1.00
6½	1	0	1	0	0	0	0	0	0	0	--	0.00	1.00
7½	0	0	0	0	0	0	0	0	0	0	--	--	--
Adults (Age unknown)	9	7	0	3	0	0	3	3	2	11	6:3	1.22	1.22
Totals	59	26	10	11	4	4	5	7	2	33	16:11	0.56	0.73
≥ 2½	36	24	9	10	4	3	5	7	2	31	15:11	0.86	1.11

[a]M = male; F = female; UK = sex unknown.

Table 21. Reproductive data gathered from female Key deer during November through June of each year, beginning January 1968 through June 1973.

Age of Doe (Years)	Total Number of Does Examined	Number Pregnant	Number Lactating	Single Fetuses			Twin Fetuses			Total Fetuses	Fetal Sex Ratio M:F	Fetuses Per Doe	Fawns Produced Per Doe
				M	F	UK	M	F	UK[a]				
½-1	6	0	0	0	0	0	0	0	0	0	--	0.00	0.00
1-2	8	0	0	0	0	0	0	0	0	0	--	0.00	0.00
2-3	11	7	1	4	0	2	0	2	0	8	4:2	0.73	0.82
3-4	8	7	1	2	2	2	0	2	0	8	2:4	1.00	1.12
4-5	4	3	1	2	0	0	2	0	0	4	4:0	1.00	1.25
5-6	4	3	1	1	2	0	0	0	0	3	1:2	0.75	1.00
6-7	0	0	0	0	0	0	0	0	0	0	--	--	--
7-8	1	0	1	0	0	0	0	0	0	0	--	0.00	0.00
Adults (age unknown)	7	6	0	2	0	0	3	3	2	10	5:3	1.43	1.43
Total	49	26	5	11	4	4	5	7	2	33	16:11	0.67	0.78

[a]M = male; F = female; UK = sex unknown.

Table 22. Reproductive data gathered on roadkilled female Key deer examined during November through June of each year. Deer are categorized by their age during the breeding season.

Age of Doe (Years)	Total Number of Does Examined	Number Pregnant	Number Lactating	Single Fetuses			Twin Fetuses			Total Fetuses	Fetal Sex Ratio M:F	Fetuses Per Doe	Fawns Produced Per Doe
				M	F	UK	M	F	UK[a]				
< 1	13	0	0	0	0	0	0	0	0	0	--	0.00	0.00
1½	6	2	1	1	0	1	0	0	0	2	1:0	0.33	0.50
2½	11	9	1	4	0	3	0	4	0	11	4:4	1.00	1.09
3½	6	5	1	3	2	0	0	0	0	5	3:2	0.83	1.00
4½	3	2	1	0	1	0	2	0	0	3	2:1	1.00	1.33
5½	2	2	0	1	1	0	0	0	0	2	1:1	1.00	1.00
6½	1	0	1	0	0	0	0	0	0	0	--	0.00	1.00
Adults (age unknown)	7	6	0	2	0	0	3	3	2	10	5:3	1.43	1.43
Total	49	26	5	11	4	4	5	7	2	33	16:11	0.67	0.78
≥2½	30	24	4	10	4	3	5	7	2	31	15:11	1.03	1.17

[a]M = male; F = female; UK = sex unknown.

as $3\frac{1}{2}$ years or older, or as adults of undetermined age, 18 (95.0 percent) had bred. The one $2\frac{1}{2}$-year-old deer that had not bred, was killed in November, and might have bred later had she not been killed.

Number of fawns produced

Birth of single fawns was usual, while birth of twins was exceptional. Only one set of newborn twins was found; these were born to an adult doe that had lost her fawn during the previous year, when it drowned at about 12 hours of age. One of these twins died from an unknown cause at 1 day of age, while the other survived. The one may have been too weak to survive. Occasional sightings of does with what appeared to be twins, suggests that twins do occur; however, this seems exceptional.

Of those roadkilled deer that were reproductively active, yearlings all carried singles, six (75.0 percent) of eight $2\frac{1}{2}$-year olds had singles, while two (25.0 percent) had twins; the 16 pregnancies of adults and those aged $3\frac{1}{2}$ years and older, resulted in 11 (68.8 percent) singles and 6 (31.2 percent) sets of twins. Of all females examined, the number of fawns carried by females, which bred as yearlings, was 0.25 per female, whereas those which bred at the age of $2\frac{1}{2}$ years and over carried 0.86 per doe (Table 20).

The Key deer reproductive output was strikingly similar to that of other south Florida deer herds, as reported by Harlow and Jones (1965: 118), in which 80 percent of the adult deer bred, producing 1.00 embryos per doe at a rate of 75 percent singles and 25 percent twins. These reproductive rates were generally lower than other Florida herds (Harlow

and Jones 1965) and other northern deer herds. Verme (1965) found well-fed deer in Michigan had 1.74 young per doe, with 88 percent of all litters being twins, while those on poor diets produced 0.95 young per doe and 10 percent twins. Nixon (1971) reported Ohio fawns carried 1.29 fetuses each, yearlings had 1.87 fetuses per doe, and older does carried 2.04 fetuses per doe. In New York, fawns carried 1.00 embryo per doe, yearlings carried 1.76 per doe, and adults produced 1.93 per doe (Cheatum and Morton 1946). Roseberry and Klimstra (1970) reported that 56 percent of Illinois deer bred as fawns. Texas deer produced 0.15 fetuses per fawn doe, 1.4 fetuses per yearling doe, and 1.59 fetuses per adult doe (White 1973).

Robinette et al. (1955) reported 2.6 percent of the fawns in black-tailed deer of Utah bred, and 2-year-old does had the greatest pregnancy rate of 1.76 fawns per doe. Ninety-four percent of the prime-aged does (3 to 7 years) were pregnant, yielding 1.70 fetuses per doe; does aged 8 years or older produced 1.64 fetuses per doe. Behrend (1966) noted that in a New York herd, does bred first as yearlings. Adams (1960) noted that fawns on the Choccolocco range in Alabama rarely bred; first births were of singles and twins were produced thereafter.

Verme (1969:883) observed that in a Michigan herd, "a physically mature doe bearing just a single young was in sub-par condition during the rut, since healthy animals, as a rule conceive twins or triplets." That the stress of caring for young fawns in one season may affect the doe's productivity in the next season was suggested by Verme (1962:23), who noted that "does relieved of lactation stress normally come into the fall breeding season in good physical condition. As a result, these

animals exhibit early estrus and exhibit greater than expected fecundity." That the physical condition of females may be responsible for the low number of twins produced by Key deer was suggested when a 4-year-old female in good condition, after losing her 12-hour old fawn the previous year, produced twin fawns. In all previous and subsequent years, she was monitored and found to produce single fawns. It is possible that, due to the nutritional plane or possibly due to a lack of certain soil minerals, the Key deer doe does not sufficiently recover from the physiological stress of suckling a fawn to produce multiple births in the subsequent years. Too few Key deer does, which had lost fawns, could be recaptured and monitored during subsequent years to substantiate this hypothesis in the Key deer herd.

Another possibility to be considered was that social stress upon these deer may have affected reproductive output. Christian et al. (1960) concluded that social stress, resulting from high population density, on an island population of Sika deer, Cervus nippon, caused physiological derangements and was accompanied by massive dieoff of females and young. Snyder (1961) indicated that in Rattus, Cleithrionomys, Microtus, Ondatra, Sigmodon, and Lepus, an inverse relationship existed between density and reproductive function. Christian (1961) suggested a behavioral-endocrine mechanism that resulted in reproductive decline in mice at high population densities. That such social stress could be functional in reducing the reproductive performance of Key deer merits investigation.

It has been postulated that plane of nutrition and lack of soil elements may be responsible for the similarly low reproductive output of

other deer herds. Smith et al. (1963) reported that inadequate levels of the soil mineral cobalt resulted in vitamin B deficiencies in North Carolina deer, that resulted in reduced productivity. Harlow (1972) suggested that the periodic low reproductive performance of central Florida deer, which produced 0.98 fetuses per doe, was due to a combination of lack of some mineral element in the soil and low acorn and palmetto mast production (as cited by Harlow and Tyson 1959). The role of soil elements or nutritional plane of Key deer has not been sufficiently investigated to determine its possible role in affecting productivity.

Fetal sex ratio

The sex ratio of Key deer fetuses taken from roadkilled does was unequal (Table 19). Of 33 fetuses examined, the 27 (82 percent) that could be sexed occurred at a ratio of 1.45 males to 1 female. Although there appeared to be more males than females in this sample of the population, these did not prove to be significantly different from a 50:50 ratio, using a chi square test of equality at a level of significance of 0.05. This is due, no doubt, to small sample size and a number of unsexed fetuses. There appeared to be a greater proportion of male fawns produced, since more male than female fawns were captured, more were observed in the field, and more were killed on highways; however, behavior seems to account for some of this difference (see Patterns of Activity).

Unbalanced sex ratios have been reported for fawns born in other populations of white-tailed deer, and these vary among various deer

herds. In studies of North American deer, male to female fetal sex ratios were 1:3 for five south Florida does examined (Harlow and Jones 1965), 1.03:1 on the Aransas Wildlife Refuge of Texas (White 1973), 0.82:1 in New York (Cheatum and Morton 1946), and 4:1 in a Georgia enclosed herd (Downing 1965). McDowell (1959) cited the following male:female fetal ratios: 117.6:100 in Massachusetts (Shaw and Mclaughlin 1951), 135.7:100 in Texas (Illige 1951), 94:100 in West Virginia (Chiavetta 1952), 150.7:100 in Wisconsin (Dahlberg and Guttinger 1956), and Severinghaus and Cheatum (1956) reported a male: female ratio of 117.2:100 for several northeastern states.

Sex ratio varied between groups of does on different planes of nutrition and varied depending upon the age of the mother. Verme (1965) found sex ratios of from 0.55:1 in deer on good diets to 2.17:1 in undernourished deer herds. Fawns and yearlings were found to carry more male fetuses in Ohio (Nixon 1971), and Harlow and Jones (1965) noted yearling does carried fawns at a ratio of 7 males per female. Robinette et al. (1957) found that the male:female fetal sex ratio in does having their first young was 1.22:1, while for "experienced" does, the ratio was 1.06:1. This trend was not evident in Key deer, due to small sample size, a number of unsexed fetuses, and a number of does categorized as "adult", since their condition when examined, made precise aging unreliable (Table 19).

In explaining a male:female fawn sex ratio of 4:1 in a Georgia enclosure, Downing (1965) postulated that due to limited movement, causing more uniform contact among all individuals, few males bred more than once, and the result was a high number of male fawns produced.

This was based on a theory by Dahlberg and Guttenger (1956, as in Downing 1965), that the first service of a buck each year produced predominately female offspring.

Whatever the causes for unbalanced sex ratios, the effects on the population dynamics of a polygamous species, such as the Key deer, can be important. Verme (1969:884) indicated this when he noted that:

> ". . . the variations in fawn sex ratios probably constitute a natural phenomenon which contributes to the self-regulation of a population. As deer are polygamous, limited fawn production coupled with a disproportionate number of male births would markedly depress the herd's annual increment when the range carrying capacity is seriously deteriorating."

In other words, this was postulated as an intrinsic mechanism for reducing the rate of herd increment. A similar phenomenon was cited by Andersen (1961), who noted that in certain lepidopterans and parasitic hymenoptera, sex ratio varied with density; the ratio of females decreased at higher densities, serving as a negative feedback mechanism to regulate density.

Compared to other deer herds, it is evident that deer of south Florida, including the Key deer, have low rates of reproduction when compared to other populations of deer. The facts that most females do not become reproductively active until $1\frac{1}{2}$ years of age, do not commonly produce twins, carry only about 1.05 fetuses per mature doe each year, and produce fawns at a ratio of 1.45 males per female, result in a population having a relatively low level of recruitment.

Since in a polygamous species, potential productivity is measured by the proportion of the herd which is made up of reproducing females, an excess of males over the minimum number required for breeding does not substantially increase productivity. Thus, in Key deer, not only is

the productivity of each female relatively low, but the potential productivity of each fawn age class is reduced by the high proportion of males. With such low productivity, and consequently with a low increment, mortality has a greater impact, since any loss is accounted for more slowly under such conditions.

Parturition behavior

There appeared to be no one particular time that does gave birth to fawns during the day. Two newborn fawns were found that had been dropped between 0800 and 0900, three were born between 1130-1200, five were born between 1200 and 1600, and one was born around 1700 hours (Table 23). Golley (1957) noted that in penned deer, birth occurred in the morning, at noon, and in early evening. Queal (1962) reported peak birth to occur between 0600-0900 and 1600-1900; the fewest births occurred at night. He noted that night births would probably be disadvantageous, due to cooler temperatures than during the day, and due to higher numbers of nocturnal predators.

There were no records of Key deer fawns being dropped at night or in twilight hours; however, this may partially be a result of when observations were made on deer, rather than on actual behavior. Deer were not adequately monitored at night, since use of lights disturbed them. No does giving birth were found by chance without use of transmitters to locate them. Eight does were located that had just dropped fawns. These fawns were still wet or just freshly licked dry when found. Two does were observed giving birth to fawns.

Table 23. Times when marked does gave birth to fawns.

Date	Reference Number of Doe	Age of Doe (Years)	Hour of Parturition
14 Apr 70	043	5	0800-0930
30 Apr 70	034	3	1200-1600
8 Apr 71	037	5	0300-0900
23 Apr 71	010	6	1420
24 Apr 71	034	4	1130-1200
1 Apr 72	034	5	1152
5 Apr 72	090	2	1200-1730
11 Apr 72	160	2	1700-1730
13 Apr 72	114	4	1200-1600
4 May 73	099	5	1200-1400

White et al. (1972) reported that birth in deer was casual, occurring largely within the regular activities of the dam and with few obvious changes in routine or special preparations, except for isolation from other deer. Downing and McGinnes (1969) found that some does isolated themselves 1 or 2 days before parturition, while others waited until new fawns were born before driving off their yearlings.

Characteristic behavior was performed before and during parturition and was modified very little by individual deer. The adult female became somewhat solitary 2 or 3 days before "dropping" the fawn, feeding alone, and in some instances, becoming aggressive toward her older fawns or yearlings. The does remained within their normal ranges (Silvy 1974).

Three does, for which breeding dates were known, were observed closely prior to parturition. They each began walking slowly over a large part of their daily home range 3 to 6 hours before moving to the area where they gave birth. They were constantly on the move, scarcely feeding and paying little attention to anything along their paths of travel. This behavior appeared similar to the "uncomfortable" behavior described in reindeer cows prior to giving birth (Espmark 1971a). Golley (1957) also noted a nervousness and pacing in two penned does before parturition; however, other deer did not demonstrate this.

Pre-partum Key deer females drove other deer away forcefully or by using aggressive displays. One doe moved to the same area each of 3 years before dropping her fawn. In 2 years, when disturbed she moved 100 yards to a low, small buttonwood clump where she gave birth; however, during the third year, she was in labor when discovered, and when

disturbed she moved only a short distance before rebedding and giving birth to the fawn.

During labor, does selected remote areas away from human disturbance to drop their fawns. These sites provided dense canopies with good cover and yet had relatively open understories where they could stand and maneuver with little difficulty. Selected parturition sites included hardwood hammock clumps located in the pinewoods, large mature palmetto depressions in pinewoods, dry elevated areas within mangrove clumps, or dense buttonwood clumps at the edge of openings. One exception to this was a doe that gave birth in the open pines where canopy was sparse and ground cover consisted of scattered thatch palms, that partially concealed her from surrounding areas.

Labor was characterized by alternate periods of standing and bedding (Tables 24 and 25). When bedded the does shifted to their sides with legs extended slightly out to the sides, or with folded front legs pointing backward and rear legs directed forward. Does alternately stood, turned around, sniffed the ground and vegetation in the immediate vicinity, then rebedded. Such standing lasted less than 2 minutes, and often was just long enough to turn in place. When bedded, the doe visibly strained abdominal, neck and leg muscles when contractions occurred, thrusting the head forward and extending the legs. In one instance the doe placed her muzzle firmly against the abdomen, appearing to push on the abdomen with her nose. At times she extended the legs away from the body and with outstretched neck, rested the head and chin on the ground in line with the body.

Table 24. Selected field notes recorded when adult female 010 gave birth to a male fawn on 23 April 1971. Observations were made from a distance of about 30 feet.

Time	Observations
1345	- AF010 bedded alone in open pinewoods of Audubon I on Big Pine Key.
1347	- AF010 stood and had a thin watery membrane hanging from her vagina. She bedded immediately on the same spot.
1350	- AF010 stood and turned in place; had trouble moving back legs; watery membrane still hanging. She licked something on the ground, then bedded facing east.
1400	- She stood and moved 5 feet, then bedded in the open pines. She pushed against her abdomen with her muzzle.
1404	- She extended her neck in line with the body, placing her chin on the ground to the front, then stood but had trouble getting up. She turned and bedded again on the left side.
1420	- AF010 heaved and kicked by extending the front and hind legs, then stood, turned around, lay down and began licking a fawn which was on the ground behind her.
1424	- She licked the fawn thoroughly as it nuzzled her and licked under her chin.
1427	- Fawn tried to stand but rolled over and fell away from AF010; AF010 stood and moved to the fawn, then bedded down and continued cleaning it. AF010 grunted softly when moving to the fawn.
1430	- Fawn moved along AF010's side by using its wrists and hind legs.
1442	- Fawn nuzzled AF010 and got to her udder, but the doe stood, turned and bedded in a position to lick the fawn. Fawn may have nursed briefly.
1445	- Fawn stood briefly but fell when AF010 licked her rear.
1500	- Fawn uttered a weak "mew" as AF010 licked it; it wobbled about nuzzling AF010.
1520	- Fawn and doe bedded quietly in sun, AF010 licked it when it stood. AF010 licked the fawn's rear as it stood on its wrists and hind legs with the rear elevated and the tail wagging rapidly.
1535	- Fawn moved about sniffing everything around it.
1545	- Fawn up and moving; got head under AF010's rear leg and AF010 cleaned its rear; fawn may have nursed for about 15 seconds.

Table 24. (Continued)

Time	Observations
1613 -	AF010 stood and dropped embryonic membranes. Turned then bedded and began eating the membranes; fawn nosed the membranes and licked AF010.
1640 -	AF010 finished eating the membranes; groomed herself, licked the ground, and grunted every 2 to 3 minutes while staring at the fawn.
1655 -	AF010 stood looking toward the observer; fawn stood and nursed for 20 to 30 seconds, then licked lips and nose.
1700 -	AF010 saw the observer and moved away slowly; fawn followed slowly. When AF010 suddenly ran, fawn fell to the ground, assuming a "freeze" position. AF010 moved 60 yards out of sight and stood. When handled the male fawn cried once and struggled.

Table 25. Selected field notes recorded when adult female 034 gave birth to a female fawn on 1 April 1972. Observations were made from a distance of about 15 feet.

Time	Observations
1125 -	AF034 moving alone in dense mangrove thicket on a dry area. The muzzle of a fawn protruded from the vagina as she moved in an area of about 15-foot diameter.
1139 -	AF034 bedded on her side; heaved her body twice, each lasting about 5 to 10 seconds. Her head was extended in line with the body, legs were partially extended and muscles were strained.
1140 -	AF034 chewed her cud and bedded quietly.
1146 -	She stood and turned; front legs of a fawn protruded with the head. AF034 bedded again on the same spot.
1150 -	AF034 heaved as the head and front legs of the fawn came out, followed by the shoulders. As AF034 stood and turned, the fawn slid out of the birth canal and fell to the ground.
1151 -	AF034 stood over the fawn licking it, starting at the head; the fawn occasionally vigorously shook its head from side to side.
1200 -	AF034 grunted as the fawn crawled about sniffing and nuzzling anything it encountered.
1205 -	Fawn cried; AF034 answered with a low grunt.
1210 -	Audible sucking sounds were made by the fawn; it was not near the udder but nuzzled AF034 on the side.
1216 -	Fawn stood on all four feet for first time; very wobbly before it fell.
1325 -	AF034 stood, pulled a long string of membrane from her vagina, ate it, then licked her perineum. She grunted periodically and looked toward the fawn.
1335 -	While AF034 stood, the fawn sniffed her, close to the teats; AF034 cleaned the fawn's rear. Fawn may have nursed for 5 or 10 seconds.
1341 -	AF034 passed more membranes and ate them. Sounded as if she ate some hard substances.
1405 -	AF034 sniffed around the area and licked anything that had fluid or membranes on it.
1500 -	AF034 stood and slowly moved north calling softly; the fawn followed her slowly.

Recorded accounts of parturition involving penned deer were similar: females were observed to stand and lie down as contractions increased (Miller 1965, Severinghaus and Cheatum 1956, Haugen and Speake 1957). Similar behavior was recorded in reindeer cows (Espmark 1971a).

One doe, observed during parturition, was bedded when the front feet of the fawn first extended from the birth canal. Another doe was moving about when the muzzle and front feet were first seen extruding from the birth canal. Michael (1964) also noted a doe walking about with a portion of the fawn protruding. Key deer females generally were bedded when contractions occurred and remained bedded while the body of the fawn was pushed from the canal; however, one doe stood as the fawn dropped to the ground.

Licking the fawn began immediately after birth and the doe cleaned it for 10 to 20 minutes while alternately standing and bedding. The doe moved over a small area following the fawn as it clumsily moved about. Once the fawn was cleaned, the doe directed her attention to cleaning herself and licking the ground where fetal membranes and fluids had fallen. She kept the fawn in sight and called to it as it moved about her. Passage of the membranes occurred up to 1 hour after birth and they were promptly eaten by all adult females observed (Tables 24 and 25). Adult does licked their perianal region and vulva, and often strained to pull at partially extruded membranes. The area was completely examined for membranes that had fallen on the ground, caught on vegetation, or remained on her body. Cleaning of the area required up to 2½ hours after the actual birth.

Haugen and Speake (1957) observed passage of afterbirth 29 minutes after the birth of a second of two fawns; but, no mention was made of whether it was eaten. When autopsying a dead doe, Knowlton and Michael (1965) found a portion of the placenta that she had eaten. Severinghaus and Cheatum (1956) observed a doe to pull the membranes from the vagina and swallow them. Miller (1965) noted a black-tailed doe licking and eating something off the ground where she had just given birth to a fawn. One doe gave birth to twin fawns in less than 1 hour, and there was no indication that birth was prolonged, such as that reported by Hesselton and VanDyke (1969), in which twins were born two days apart.

Inexperienced does were not as efficient at cleaning up the area as were older adult deer. One 2-year-old doe, giving birth to her first fawn, did not consume the afterbirth, and left it on the ground beside the fawn. She only partially licked the fawn clean, allowing much of the fluid to become dried on the fawn's coat; and, unlike older does, she failed to perform any vocal communication with the new fawn. She did allow the fawn to nurse, and stayed with it until it fell into a ditch and drowned.

Fawn characteristics and development

The mean weight of 13 fawns captured as newborns was 3.4 lb, with a range of 2.2 to 4.5 lb. There was no significant difference between the weights of male and female fawns that were captured and weighed (Table 26). The 2.2-lb fawn was found dead on the second day after birth; however, the cause was undetermined; it may be that it was too small to survive, or it may have been deserted by the doe after it was marked.

Table 26. Weights of newborn Key deer fawns captured during April and May 1970-1973.

Sex	Reference Number	Estimated Age (Hours)	Weight (Pounds)
Males	000	$\frac{1}{2}$	2.2
	161	6	4.5
	705	1	3.0
	730	24	4.0
	731	$< \frac{1}{4}$	3.0
	732	4	3.2
	742	1	3.0
Mean		< 5	3.3
Females	160	24	3.2
	702	1	3.5
	711	24	3.8
	728	3	3.5
	729	4	3.5
	737	6	3.5
Mean		10	3.5

At birth the fawn was marked with white spots on a dark reddish-brown coat. Spots began to fade on the fawn's shoulders when it was around 2 months of age. By 4 months light spots were visible only on the back and hips, and by 5 months, most had completely lost their fawn pelage. One yearling male was observed with light spots on his back in late summer; however, this is believed to be due to molting patches of hair; the old grizzled hairs interspersed in the new darker hairs resulted in a spotted appearance.

Since fawns were born from mid-March to, occasionally, as late as August or September, sightings of spotted fawns could occur from mid-March through December. This fact may be responsible for impressions that the breeding season of Key deer occurred year-round (Barbour and Allen 1922).

Fawn activity

Fawns were active immediately after birth, shaking the head from side to side at 5- to 10-second intervals; this seemed to be stimulated by the licking activities of the doe (Tables 24 and 25). It no doubt served to help remove any membranes clinging to the head that could potentially serve to suffocate the fawn. Also, the doe began licking that area that was moving the most, which was the animal's head. Fawns attempted standing as soon as they were born; however, a fawn was able to successfully stand only after 45 minutes. Most movement after 10 minutes was performed by shifting from one side to the other. Often the fawn was thrown off balance by the force of the doe's licking and cleaning efforts. The back legs were sufficiently sturdy to support

the weight of the rear end. The forelegs, however, were less sturdy, and much of the movement during the early minutes after birth were performed by the fawn "standing" on its wrists and hind feet. Since the hind legs were longer, the fawn usually toppled over with each strong thrust with the back legs.

Fawns moved around their does or up to 4 to 6 feet away from them. At first the doe got to her feet, moved to the fawn, bedded, and resumed the cleaning however, after the fawn became dry, the doe remained bedded or cleaned up the afterbirth and called to the fawn. After 14 minutes from birth, the fawn answered with a very low "mew", similar to the low cry of a kitten. After an hour, the fawn bedded a few feet away from the doe in the open, usually in the sunshine. It rested its head on the hind legs in a characteristic bedding posture, with its body forming a semicircle. At 5- to 15-minute intervals, the fawn got to its feet and either moved to the doe or shifted its position, bedding in a new spot. All the fawn's activities were centered around the doe.

After 2 hours, the doe moved the fawn to a new site, usually only 10 to 30 feet from the birth site. If disturbed, the doe moved the fawn farther. Fawns followed any slow-moving object and responded to the doe's low call by crying and moving unsteadily in her direction. Any sudden movement or loud noise resulted in the fawn "freezing" as described above.

White (1972) noted that Texas white-tailed fawns also followed slow-moving objects, but dropped in their tracks to assume the cervid "freeze" position (McCullough 1969) when startled. McGinnes and Downing (1969) noted that when a doe leaves an area by high bounds with tail

raised, the fawn drops; whereas, walking slowly and frequently looking back results in the fawn following her.

Nursing activities began almost immediately after birth. The fawn nuzzled any part of the doe it encountered, paying more attention to any moving part. Contact with the udder appeared to be by chance, and the doe made no effort in directing the fawn's probing; in fact, one doe moved each time the fawn made contact with the teats until after 1½ hours. Sucking sounds made by a fawn were audible after 19 minutes, and a fawn first nursed one and three-quarters hours after birth. Nursing may have occurred earlier when the doe was oriented so that the fawn was concealed from the observer.

Young fawns made little or no noise when moving. Each foot was slowly raised, while the other three were firmly on the ground. Each foot was firmly on the ground before the next one was raised. Bedded fawns were concealed from most directions, since they crawled into very thick vegetation after the morning feeding. They remained hidden during the day. Three-week-old fawns changed positions at the bedding site when they were alone, turning or shifting a few inches into or out of the shade. They emerged only to feed in late afternoon and then bedded in more open areas during the evening hours. After being left by the doe, 4-week-old fawns moved up to 20 yards or less to more concealed sites to bed during twilight, where they remained for the night. Bedding sites were generally areas that provided thick cover near the ground, such as limbs and vegetation from an uprooted tree, dry depressions filled with palmettos, or low palms that had dead fronds forming a "tent" around the base of the plant. During the first 4

weeks, fawns generally remained bedded at the sites where they were last left by the doe until the doe returned at the next feeding period.

White et al. (1972) described fawn-seeking behavior, which they indicated was elicited by discomfort from a distended udder. When moving over distances greater then 0.2 mile to the fawn, the doe walked steadily, but when within 200 yards of it, displacement activities were included while she remained alert and wandered in circles, uttering "soft plaintive mews" (p. 898). Similar behavior occurred in Key deer. All encounters between the doe and fawn were initiated by the doe. At feeding time, the doe moved to the area where she had last left her fawn, calling in a low grunt at 15- to 30-second intervals while moving and feeding. Calling became more frequent and louder in intensity as she continued to search, and feeding behavior became replaced by more intent searching for the fawn. Ears were maintained alert forward, and movement was in segments of short distances.

As does moved through the woods and uttered contact calls, older fawns uttered bleats in response. In addition, as fawns began to move on their own, they often uttered contact calls. At first they called very weakly however, if contact with the doe was not achieved, the cries progressively increased in intensity until they could be heard up to over 100 yards away. Young fawns uttered cries after feeding as they wandered away from their does, crying until they reached sheltered areas and bedded down. This may have helped identify the spot for the does when they later searched for fawns at feeding time. Both does and fawns increased their calls in intensity when they did not make contact. One doe, which had called for nearly 1 hour while feeding in an open area, was bellowing loudly at 30-second intervals.

At first young fawns responded to the doe's call; however, at 4 to 6 weeks of age, they often responded to the doe only after detecting the scent. On three occasions the doe passed by the bedded fawn, moving up to 50 yards away before the fawn left its bedding site to join the mother to nurse. On other occasions fawn-searching behavior appeared fruitless; the cause may have been that the hidden fawn detected the observer and remained concealed in the brush. The ability of a fawn to follow a trail using olfactory cues seems certain (see *Olfactory communication*), and could function to aid the doe and fawn in making contact, especially when the fawn began to wander on its own.

During the first 4 weeks, nursing periods were brief, and occurred during the day around 0900 and 1100 and between 1600 and 1800. Few young fawns were observed to nurse before 1600 or after 1800 hours. During nursing the fawn wagged its tail vigorously, while the doe groomed it, particularly around the perianal region. As older fawns nursed, does usually began feeding after initially grooming the fawn.

Does either stood in one spot for young fawns to nurse, or in some cases, bedded as fawns nursed; however, they terminated nursing bouts by moving ahead, often stepping over the fawn as they returned to feeding. Young fawns nursed intermittently for 15- to 30-second intervals over a period of 2 to 5 minutes. After nursing, the doe either moved the fawn to a new location by very slowly moving and calling, or she terminated the encounter by either moving away quickly or by stopping to feed or bed down in the area. The fawn then moved on its own to a bed nearby. The fawn chose its own bedding site; no doe was observed to force a fawn to choose a site or encourage by any motion, bedding in a particular spot.

Visits to the fawn by does may have occurred during the night; however, these were believed to have been brief encounters only, and involved little interaction or movement from one site to another by the fawn. One 3-week-old fawn doe was observed nursing its doe at 0300 hours along a highway; however, this was the only encounter witnessed at night between a doe and her young fawn. That fawns usually were bedded in the morning where they had previously been found the night before suggested that the doe and fawn had not been together. Also, fawns examined early in the morning did not appear to have nursed, since recently-fed fawns with full stomachs often had the paunch distended.

If the doe was disturbed while with the fawn, she generally moved it to a new area. This move often occurred at night or at times when human activity was at a minimum. Such moves of very young fawns posed a hazard to them due to the extensive mosquito ditching in some areas on Big Pine Key, and due to hazards from automobiles, humans, and dogs.

Movement of young fawns by the doe always occurred just after the fawn nursed. As fawns aged, the doe moved them more throughout her range, gradually familiarizing the fawn with a greater part of her range. When fawns began moving on their own they restricted movement to these familiar areas, thus adult does and their fawns had overlapping ranges (Silvy 1974).

Since the doe returned to the site where she and the fawn had last been together; and, since a fawn increasingly moved over more of its familiar range as it aged, encounters between them became less frequent. At first does spent more time searching for fawns at nursing time; however, as encounters took longer the searching behavior waned. Three-

month-old fawns occasionally did not encounter their does for 2 or 3 days at a time.

From the time that fawns began to nose and nibble on solid food at 2 to 3 weeks up to the time that they were weaned at around 4 months, the amount of solid food eaten increased gradually. Three- or four-month-old fawns often moved with their does in the evening after nursing for 5 to 15 seconds, feeding on vegetation. During this time, fawns periodically approached their does, sniffed the muzzle and nibbled bits of vegetation that protruded from the doe's mouth. Such behavior may have served to help the fawn learn what plants were palatable.

Doe-fawn bonds

That the bond between a doe and young fawn was strong, was evidenced during this study by behavior of does that lost fawns (see Loss of fawns), and by behavior of does toward their surviving fawns. One adult female, which gave birth to a fawn on Porpoise Key, a small island lacking permanent fresh water, swam the 0.8-mile channel between Porpoise and Big Pine Key prior to late June, when rainfall provided drinking water on Porpoise Key. She made this trip every other day during June and July except when rainfall provided fresh water. While on Big Pine, she was observed feeding and apparently drank before returning to Porpoise Key.

Another doe, resident to east Big Pine Key, swam to No Name Key every day where she was seen suckling a fawn. While the cause for dropping their fawns in areas other than their normal ranges was not

clear, their behavior of repeatedly swimming to the islands demonstrated a strong attachment to nursing fawns. As fawns aged, these bonds weakened considerably, even to the point that at 6 months of age, some fawns commonly followed does other than their own; some 6-month-old fawns were never seen with does.

Udder development

No udder development was observed in does captured 20 days before parturition. Those examined 10 to 15 days before birth showed small udder development, and those examined 5 to 6 days before giving birth had udders that were approximately 75 percent of full size. Full-sized udders were evident in does by the third day before parturition; no does were found lactating before parturition.

Does aged $2\frac{1}{2}$ years or older when captured were found lactating during April through October. None were lactating during November through March, although deer with large or moderate udders in November and December evidenced prior suckling activities. Of 28 does handled in April, 4 (14 percent) were lactating, 13 (59 percent) of 22 does were lactating in May, 6 (75 percent) of 8 were lactating in June, 3 (100 percent) were lactating in July, 6 (60 percent) of 10 were lactating in August, 2 (67 percent) of 3 were lactating in September, and 3 (100 percent) were lactating in October. This corresponded to parturition beginning in March, and the end of lactation of these late breeding does that gave birth in July and August. One fawn killed in November had curdled milk in its stomach when examined.

Some does, that were roadkilled, and some live-captured does had moderate-sized udders when examined in November and December, but did not appear to be lactating, since no milk could be expressed from the teats. Does, which lost newborn fawns, did not have large udders when examined 3 weeks later, and had little or no bag after 5 to 6 weeks when captured and examined.

Loss of fawns

During 1969 through September 1971, of 16 marked adult does, whose newborn fawns were captured, 9 lost their fawns. Six (66.7 percent) fawns drowned after falling into mosquito ditches, while two (22.2 percent) were found dead of unknown causes at the age of two days; one (11.1 percent) may have been abandoned after marking. In all cases the does remained in the areas up to 14 to 20 days after the fawn had died. These does responded to any disturbances by becoming very alert and uttering contact calls. If the source of disturbance remained unidentified, she then moved to downwind of it. All does gave positive responses to imitation of fawn calls during this period.

Does spent prolonged periods of time moving through areas where fawns had been bedded prior to death, calling loudly with calls increasing in intensity as time passed. This behavior became less intense after a week and lessened steadily until it was absent. This corresponded to a diminution of the udder size and drying. Miller (1971a) noted that three black-tailed does, which lost fawns, showed fawn-seeking behavior in the vicinity of the fawn's last bed site, the behavior probably being reinforced by continued milk production. This behavior was discontinued as drying occurred.

Although there was no evidence of any doe adopting another fawn after loss of its own, evidence suggested that a young fawn belonging to a radio-marked 2-year-old doe was following an older, presumably unrelated, doe for up to 2 days before it fell into a ditch and drowned. McGinnes and Downing (1969) noted that some adoption of abandoned fawns occurred in Virginia white-tails.

During September 1969 through December 1972, 94 (67.1 percent) of 140 marked does were seen with fawns (Table 27). During 1969, observations began in September; therefore, earlier months, when fewer fawns were normally seen with does, were not included, and the result was a higher percentage of does seen with fawns than during the full years of 1970 and 1971. During 1972, the only observations made were in April, May, June, and December, thus reducing the ratio of fawns seen per doe.

During 1970 and 1971, of 101 does observed, only 70 (69.3 percent) were observed with fawns. At least seven does that were seen with young fawns during 1970-1972 were known to have lost their fawns, and one doe lost one of a set of twins. Such losses of fawns belonging to other does may account for part or all of those sightings of 30.7 percent without fawns. The eight known losses occurred in April and May and involved very young fawns. Since this was a period of time when fawns normally were not seen with does, it may be that more undetected losses occurred, and thus 30 percent of the does may not either produce fawns or successfully raise them. It may also be that these does never brought fawns into areas during the year where they could be observed; however, this seems somewhat unlikely.

Table 27. Estimated productivity of adult Key deer based on observations of marked adult females with fawns during April of each year through March of the next year.[a]

Year	Total Number of Does Observed	Number of Maternal Does With Fawns	Number of Fawns Observed	Ratio Fawns Per Maternal Doe	Number of Fawns Known Lost	Ratio of Surviving Fawns Per Doe Observed
1969-70	13	11(84.6)[b]	12	1.09:1	0	0.92:1
1970-71	42	32(76.2)	33	1.03:1	2	0.74:1
1971-72	59	38(64.4)	39	1.03:1	5	0.58:1
1972-	26	13(50.0)	13	1.00:1	1	0.46:1
Total	140	94(67.1)	97	1.03:1	8	0.71:1
1970-71; 1971-72 Totals	101	70(69.3)	72	1.03:1	7	0.64

[a]1969-70 included only the months of September 1969 through March 1970; 1972- included only April through December 1972.

[b]Numbers in parentheses represent the percent of marked does which were seen with fawns.

Survivorship

The structure of a population is determined by the age-specific birth rate, the sex ratio at birth, and the mortality for each specific sex and age class. A total of 110 Key deer (55 males; 55 females), which were marked for varying periods of time, were either known to be alive at the end of the study or died at a known age. Using the age of these animals when captured, and the age at which they died, a survivorship table was developed based on the percent of animals in each age class that were known to have survived into the next age class (Table 28). April 1 was considered the birth day for each animal.

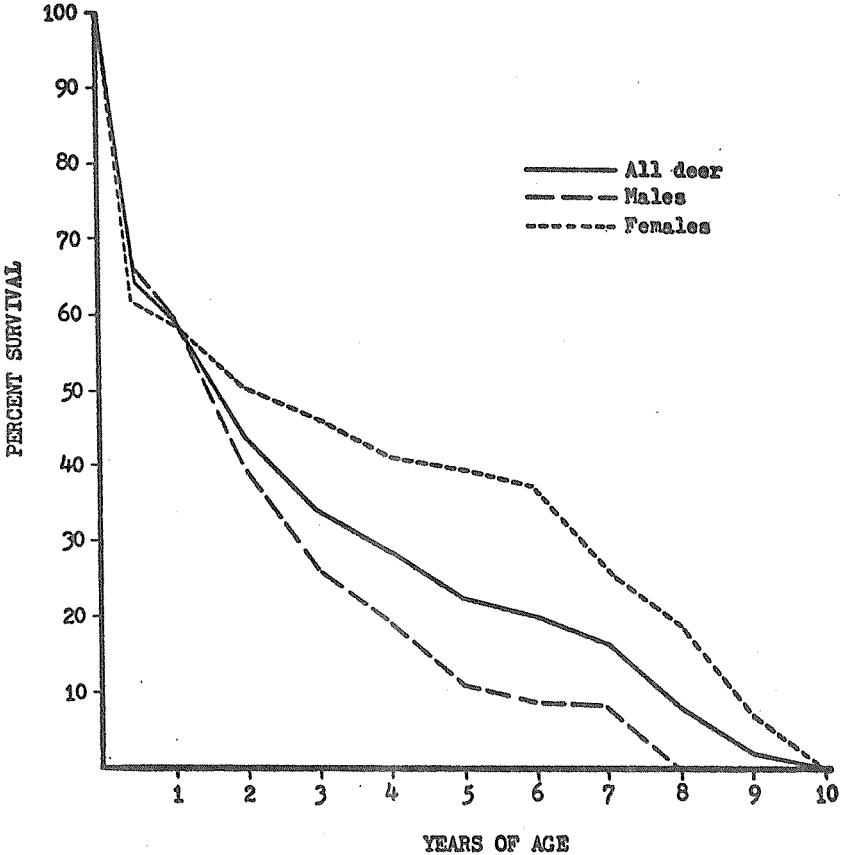
Both males and females showed a high mortality rate during the first 6 months of life; most mortality occurred during the first few days after birth, chiefly through drowning in ditches (Figure 43). Females had a slightly lower survival than males up to 6 months; but, thereafter, they showed an improved survival rate. Such differential mortality was, no doubt, the result of subtle behavior differences, such as amount of movement by fawns of different sex, and not-so-subtle differences in activities of yearlings and adults of different sexes (see Patterns of Activity). No males were known to live beyond 8 years of age, and no females were known to live beyond 9 years. Fifty percent of the males survived to $1\frac{1}{2}$ years, while females showed a 50 percent survival to around $2\frac{1}{2}$ years.

One weakness in this model was the inaccurate aging of deer over 2 years of age. The use of tooth wear and replacement criteria

Table 28. Survival of Key deer from one age class to the next based on 110 marked animals of known fate.

Age Class (Years)	Sex	N	% Dying in This Age Class	% Survival to Next Age Class
0-½	Male	17	35.3%	64.7%
	Female	8	37.5%	62.5%
	Total	25	36.0%	64.0%
½-1	Male	32	9.4%	90.6%
	Female	14	7.2%	92.8%
	Total	46	8.7%	91.3%
1	Male	31	32.3%	67.7%
	Female	22	13.6%	86.4%
	Total	53	24.5%	75.5%
2	Male	23	34.8%	65.2%
	Female	24	8.3%	91.7%
	Total	47	21.3%	78.7%
3	Male	12	25.0%	75.0%
	Female	28	10.7%	89.3%
	Total	40	15.0%	85.0%
4	Male	7	42.9%	57.1%
	Female	20	5.0%	95.0%
	Total	27	14.8%	85.2%
5	Male	4	25.0%	75.0%
	Female	17	5.9%	94.1%
	Total	21	9.5%	90.5%
6	Male	2	0.0%	100.0%
	Female	13	30.8%	69.2%
	Total	15	26.7%	73.3%
7	Male	3	100.0%	0.0%
	Female	7	28.6%	71.4%
	Total	10	50.0%	50.0%
8	Male	0	--	--
	Female	3	66.7%	33.3%
	Total	3	66.7%	33.3%
9	Male	0	--	--
	Female	0	--	--
	Total	0	--	--

Figure 43. Survivorship curve for the Key deer population, based on the percent of marked deer in each age class that survived to the next age class. Determinations were based on deer marked during January 1968 through June 1973.


100
90
80
70
60
50
40
30
20
10
PERCENT SURVIVAL
All deer
Males
Females
1
2
3
4
5
6
7
8
9
10
YEARS OF AGE

(Severinghaus 1949) was not believed especially accurate for Key deer; however, those captured as fawns and yearlings were accurately aged. There was also the possibility that survival of marked animals was different from that of unmarked animals. Any adult deer, known or suspected to have been a capture mortality, or known to have died due to marking devices, was eliminated. Too, it was possible that some very young fawns died due to being moved or abandoned by the doe because of disturbance caused by the observers; however, this was not believed to be greatly different than for unmarked deer in the same areas, or in other areas where the human population was high.

Mortality

Mortality of Key deer was monitored to note the causes and to determine the effects of behavior on the number of deer lost. During January 1968 through June 1973, 304 mortalities were recorded for Key deer on 10 different islands. Sixty-five (21.4 percent) involved marked or captured animals. The main known cause (76.0 percent) of mortality was collision with automobiles (Table 29). Most of these occurred on Big Pine Key. Thirty-four (14.7 percent) of the roadkills involved marked animals.

Such highway mortalities occurred every month of the year, with most occurring in November, April, and May (Figure 44). Peaks tended to correspond to times of breeding, when deer increased their activity, and fawning, when animals were moving more due to pressures from adult does. Roadkills also varied with the time of day, although deer were killed at all hours. Peak mortality occurred around 0600 to 1200 hours

Table 29. Recorded Key deer mortality, January 1968 through June 1973.

Sex and Age	Highway Mortality	Drowning Mortality	Capture & Marking Mortality	Combat Mortality	Miscellaneous	Unknown	Total
Adult Male	69	1	7	7	1	6	91(29.9%)[a]
Adult Female	48	1	2	0	0	8	59(19.4%)
Yearling Male	47	0	3	0	2	1	53(17.4%)
Yearling Female	15	0	3	0	1	2	21 (6.9%)
Fawn Male	30	6	3	0	3	3	45(14.8%)
Fawn Female	21	4	0	0	1	2	28 (9.2%)
Fawn (Unknown)	0	2	0	0	0	1	3 (1.3%)
Unknown	1	0	0	0	0	3	4 (0.3%)
Total	231	14	18	7	8	26	304(100%)

[a]Numbers in parentheses represent percent of the total number killed.

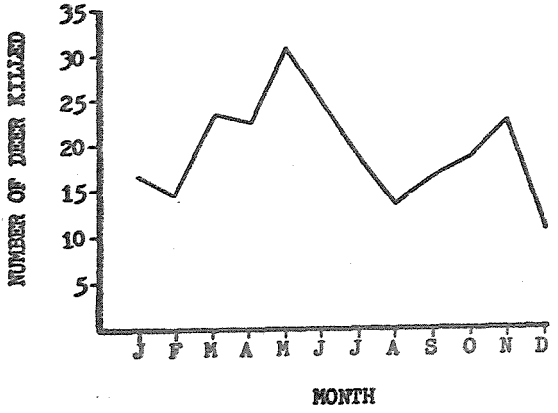


Figure 44. Monthly distribution of 238 Key deer roadkills during January 1968 through June 1971.

(Figure 45). Although this did not correspond to a normal feeding peak or to the peak activity in open areas, it did represent an overlap between a time of moderate deer activity and moderate to heavy automobile traffic. The least number of deer were killed around 0300-0500 hours, when deer activities were slack, and human activity was at a low, and again in mid-afternoon, when deer generally remained in cover, away from human activities. A slight increase in mortalities occurred in early evening, corresponding to the evening feeding periods in open areas.

There was an obvious differential sex mortality with males being roadkilled more frequently than females (ratio of 1.74 males to 1 female) (Table 11). This resulted from a greater number of young males in the population and a difference in behavior between males and females. As discussed earlier, males tended to be more independent of family groups and moved about more in open areas after 2 to 3 months of age. These activities occurred especially in April, May, September, and October (the fawning and breeding seasons), when younger deer, especially males, were moving more due to harassment by older animals. Adult males were much less cautious during the breeding season, and they frequented areas where they were more likely to be injured or killed. Sparrowe and Springer (1970) noted that rutting activities made northern deer more vulnerable to rifle hunters, and White et al. (1973) found young males to be more independent, active, and inquisitive and thus were more vulnerable to predation and accidents.

Accounting for 4.6 percent of the mortalities were deer that drowned, chiefly newborn fawns. Many fawns were born in areas

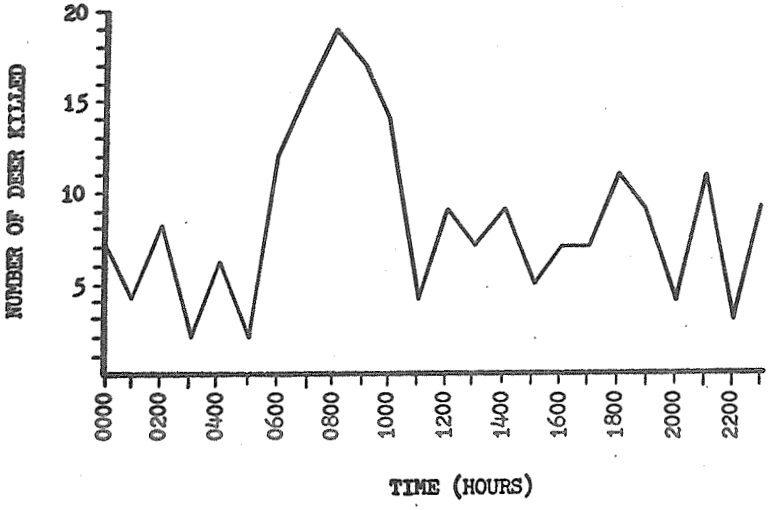


Figure 45. Times when 202 Key deer were roadkilled. Mortality of 36 other deer occurred at unknown hours.

completely surrounded by mosquito ditches (Figure 1). These drainage ditches were designed to connect water holes, which served as potential mosquito breeding sites, to the salt water channels, allowing fish to get into these holes and allowing for some flushing action with the tides. Many of these ditches were of sufficient depth that a deer, which fell into them, could not escape. While a 2- to 3-week-old fawn could jump across these ditches, a very young fawn attempting to cross, often fell in (Figure 46). Of 33 marked newborn fawns, 6 (18.2 percent) drowned in ditches. In addition, remains of five unmarked fawns were found in these ditches, and four fawns were rescued from ditches that were isolated and nearly dry, or that had little water during low tide. Three of these fawns fell in on two different occasions, one drowned the second time.

Although traps set on four ditches during 1973 failed to collect any fawn carcasses, evidence suggested that dead fawns may often be flushed out of the ditches into the channel with outgoing tides, and thus never be found. Other fawns in blocked ditches, or on side ditches no doubt quickly deteriorate in the warm stagnant water; and, were also devoured by fish, crabs, and alligators. Two fawns, that had fallen into ditches, had portions of their flesh eaten away by crabs in less than 12 and 18 hours, and partial remains of three other fawns were found in stagnant side ditches.

Although deer generally did not move young fawns great distances, in certain areas of extensive ditching, any movement jeopardized fawns. No doubt, some does moved their fawns after being disturbed, and the 18.2 percent mortality recorded may have been a slight exaggeration;

Figure 46. Young fawn which had drowned in a mosquito ditch. Fawns less than 1 week of age often drowned after falling into these ditches. Carcasses either were carried into the channels with outgoing tides, or remained in stagnant side ditches to quickly deteriorate and be eaten by fish, crabs, and probably, alligators.

however, it was not believed to be greatly different from actual mortality of unmarked deer in the same areas, or in other areas of high human activity. Fawn mortality, due to drowning in mosquito ditches, appeared to be rather frequent in ditched areas of Big Pine Key.

Remains of seven (2.3 percent) adult males with holes in the skull between antlers and with injury to the neck and thoracic cavity suggested that combat with other males was probably involved in their deaths. That severe injury could result from combat was evidenced by males with broken antlers and wounds of various degrees of severity during the breeding season. Two adult males examined had fragments of the frontal bones broken loose and held in place only by connective tissue.

Various unknown causes accounted for 8.6 percent of the losses (Table 29). These included remains of four adult does, one adult buck, one fawn, and a deer of unknown sex and age, which were found in or near dried water holes on Howe, Big Johnson, Little Pine, and Big Munson Keys. Six of these deer were found just after the drought in 1970 and 1971; all may have succumbed to the harsh conditions on these outlying islands during the drought.

An additional 2.6 percent of the mortalities were attributed to miscellaneous factors, including two yearling males and one yearling female that were injured while attempting to escape from fenced areas, and three fawns, that were possibly abandoned or lost, two of which were moving alone through the woods when found. A 6-month-old fawn was found dead in a dry solution hole. Capture mortalities, discussed above accounted for 5.9 percent of the deaths.

Insect pests may also have posed a hazard to deer, especially fawns. In 1971 and in April, 1972 and 1973, the relatively dry conditions resulted in only mild infestations of mosquitoes; however, in 1969-1970 after heavy rains, insect pests were such that deer regularly moved to along the roadways and open areas to bed in a breeze and escape mosquitoes that remained in thicker cover. It was not uncommon to see deer of all ages moving to open areas, the head and legs covered with mosquitoes and even blood spots around the eyes and on the face (Figure 16). In such years it was not inconceivable that mosquitoes could have caused enough loss of blood in small fawns to result in illness and death. Evidence from mortalities to substantiate this, however, would be difficult to determine, even if such animals could be found.

Sex-age Ratios

Sex and age ratios within the Key deer population, determined from mortalities, live-captures, and field observations during October 1969 through 15 June 1972, varied depending upon the method used to determine them, as well as the time of year when data were collected. Based on 18,212 recorded field observations of deer during March 1968 through December 1971, and during April through 15 June 1972, 13.1 percent were adult males, 42.9 percent adult females, 10.1 percent yearling males, 12.5 percent yearling females, and 21.3 percent fawns (Table 30). The composition of the herd varied from one year to the next, and varied from month to month (Table 31). Monthly variations primarily reflected the seasonal changes in behavior of the different sex and age classes (see Patterns of Activity).

Table 30. Sex and age ratios of deer observed during March 1968 through 15 June 1972.

Date[a]	Adult Buck	Adult Doe	Yearling Buck	Yearling Doe	Fawn	Ratio Buck:Doe:Fawn	Ratio Yearling:Yearling Buck	Ratio Yearling:Yearling Doe	Ratio Doe:Yearling
March 1968	9	30	5	6	1	0.30:1:0.03	0.83:1		1:0.37
Apr 68-Mar 69	292	563	48	152	421	0.51:1:0.75	0.32:1		1:0.36
Apr 69-Mar 70	331	1,067	249	404	858	0.31:1:0.80	0.62:1		1:0.61
Apr 70-Mar 71	1,029	3,462	824	1,032	1,808	0.30:1:0.52	0.80:1		1:0.54
Apr 71-Dec 71[b]	668	2,356	606	606	753	0.28:1:0.31	1.00:1		1:0.51
Apr 72-Jun 72[c]	65	341	106	77	43	0.19:1:0.13	1.38:1		1:0.54
Total	2,394	7,819	1,838	2,277	3,884	0.31:1:0.50	0.81:1		1:0.53

[a]Data are grouped into years beginning on 1 April to enable evaluation of the impact of the fawn and yearling age classes each year.
[b]There were no observations during January-March 1972.
[c]Observations were discontinued on 15 June 1972.

Table 31. Observations of Key deer recorded each month, March 1968 through 15 June 1972.[a]

Month	Adult Buck	Adult Doe	Yearling Buck	Yearling Doe	Fawn	Ratio Buck:Doe:Fawn	Ratio Yearling:Yearling Buck Doe	Ratio Doe:Yearling
April	175	843	225	227	7	0.21:1:0.01	0.99:1	1:0.54
May	212	864	262	209	89	0.24:1:0.10	1.25:1	1:0.54
June	292	938	254	313	220	0.31:1:0.23	0.81:1	1:0.60
July	281	788	239	282	257	0.36:1:0.33	0.85:1	1:0.66
August	226	622	200	216	285	0.36:1:0.45	0.93:1	1:0.67
September	158	429	117	124	228	0.37:1:0.53	0.94:1	1:0.56
October	281	648	123	156	406	0.43:1:0.63	0.79:1	1:0.43
November	172	529	108	129	421	0.33:1:0.80	0.84:1	1:0.45
December	235	721	120	226	575	0.32:1:0.80	0.53:1	1:0.48
January	136	452	81	139	428	0.30:1:0.95	0.53:1	1:0.49
February	106	395	58	121	460	0.27:1:1.16	0.48:1	1:0.45
March	120	590	51	135	508	0.20:1:0.86	0.38:1	1:0.32
Total	2,394	7,819	1,838	2,277	3,884	0.31:1:0.50	0.81:1	1:0.53

[a]Observations were not made during January-March 1972 or after 15 June 1972.

The proportion of adult males observed increased to a peak in October, then decreased to lows in March and April. This increase was associated with activities just before and during the rut, and the lows occurred at times of antler loss and reproductive quiescence. It appeared that there was roughly one-third the number of adult bucks as adult does in this population.

The ratio of fawns to other age classes observed showed an increase during the year, especially when older fawns increased their movements into open areas. Observations of fawns in open areas alone or with does, generally did not occur until June or July; however, this varied with weather and number of insect pests. A drop in the ratio of fawns to does in March reflected the disassociation of fawns and adults preceding and during parturition of new fawns. Harassment from older deer may have tended to keep older fawns out of open feeding areas and thus out of sight of the observers.

A decrease in the ratio of yearlings to adults in September and October reflected behavior changes during breeding seasons, especially of yearling bucks, which often left ranges, which they previously had occupied (Silvy 1974). Both bucks and does decreased use of open areas somewhat. A secondary drop occurred in March, when does drove yearlings from their ranges as they gave birth to fawns. The ratio of yearlings gradually decreased throughout the year, as they left their home areas, at which times they were often not seen again; many were killed on roadways.

The ratio of deer observed, therefore, does not reflect the actual herd composition, since different behavior of deer in each sex-age

class results in their being seen at different rates. Over many years trends or changes in herd composition should become evident in deer observed. The observed ratio of adult males to females and fawns to females decreased during the later years of the study (Table 30). Care in interpreting these data is necessary, however; for example, data excluding some months cannot be compared to data incorporating those months, due to differences in behavior. Since the 1972 data does not include a complete year, sex ratio values are not comparable to the other years.

There was an apparent increase in the percent composition of the adult age class with a decrease in the fawn category during the 5-year study (Table 30). Such a condition may result in a population having a low rate of annual increment or showing signs of stability.

The sex ratio of deer captured was biased in the older age classes, as most deer in open areas, where captures occurred, were marked early in the study, and thus were not selected for in later years (Table 32). With the exception of occasional captures of new adults, most new captures involved fawns and yearlings. Thus the age structure and sex ratios taken from capture tables are not accurately depicted, with the possible exception of the sex ratio of young fawns.

During the year, fawns were captured at a rate of 2.41 males per female, while fawns aged 1 day or less were captured at a rate of two males per female. Fawns were captured during April and May at a rate of 1.75 males per female, and during the remainder of the year at a rate of 2.72 males per female. Severinghaus and Tanck (1964) recorded that in New York, the sex ratios of fawns aged 5 to 7 months was 106.2 males per 100 females.

Table 32. Sex and age ratios of deer captured during January 1968 through June 1973.

Year[a]	Adult Buck	Adult Doe	Yearling Buck	Yearling Doe	Fawn Buck	Fawn Doe	Ratio Buck:Doe:Fawn	Ratio Yg. Buck:Yg. Doe	Ratio Fawn Buck:Fawn Doe	Ratio Doe:Yearling
-1968	0	1	0	0	1	0	0.00:1:1.00	--	--	--
1968-69	10	9	1	4	13	3	1.11:1:1.78	0.25:1	4.33:1	1:0.56
1969-70	3	14	4	3	11	4	0.21:1:1.07	1.67:1	2.75:1	1:0.50
1970-71	12	20	5	7	18	6	0.60:1:1.20	0.71:1	3.00:1	1:0.60
1971-72	5	12	3	5	15	8	0.42:1:1.92	0.60:1	1.88:1	1:0.67
1972-73	1	1	4	1	10	5	1.00:1:15.0	4.00:1	2.00:1	1:5.00
1973-74	1	3	1	2	2	3	0.33:1:1.67	0.50:1	0.67:1	1:1.67
Total	32	61	18	22	70	29	0.52:1:1.62	0.82:1	2.41:1	1:0.66

[a]Data are grouped into yearly periods beginning on 1 April to enable evaluation of the impact of the fawn and yearling age classes each year.

Despite the small sample size, there appeared to be a trend of increased male fawns in the Key deer herd, either due to higher mortality of newborn doe fawns, or due to behavioral differences, resulting in bucks being seen and captured more frequently. Since males and females had slightly different amounts of activity at different ages (see Patterns of Activity), this probably accounted for the differential trapping, thus exaggerating actual differences that existed in fawn sex ratios.

Behavior of deer greatly influenced sex and age data available from roadkills (Table 11). In addition to more male fawns, which may really exist, the ratio of adult males and yearling males to females was a reflection of greater male activity and movement in areas of heavy traffic, especially during breeding seasons. As bucks were selected out at a greater rate, this resulted in a large proportion of females in the older age classes remaining in the herd.

Population Dynamics

The Key deer, which apparently evolved without predators, appears to possess an inherent mechanism, which slows the rate of population increment. This mechanism, a low reproductive output, is probably responsible for the gradual recovery of the Key deer population from a low in the 1940-1950's. Currently another mechanism slowing the population increment is the relatively high mortality suffered on the highways and in mosquito ditches.

On outlying islands away from Big Pine Key, the rate of increment is probably reduced periodically by an absence of fresh water, resulting

in either high mortality or dispersal to other islands having fresh water. In the past, such loss of fresh water may have resulted from drought or from storms that contaminated lowlying water sources with salt. That such a potential mortality factor exists was suggested by the occurrence of mortalities on outer islands following a drought, and by the disappearance of a fawn on Porpoise Key, where there was no fresh water, except just after rainfall. The mother of this fawn moved back to Big Pine Key, but the fawn was never seen with her; it possibly died on Porpoise Key or drowned while attempting to swim the 0.8-mile, swift-current channel.

The intrinsic mechanism that slows population increment appears to be more physiological than behavioral; however, a behavioral-endocrine mechanism that reduced productivity, such as that described by Christian et al. (1960), cannot be ruled out. Behavior of prime-aged bucks reduces the number of males participating in peak breeding activities, and potentially reduces reproductive output; however, the female's recycling tends to counter its effects, and ultimately a large number of males may participate in breeding does which recycle. While this activity extends the breeding season over several weeks, it also may influence the sex ratio of fetuses produced, assuming that the number of males participating in breeding affects the sex ratio of offspring, as was suggested by Verme (1969). The greater number of does recycling may result in more individual males breeding, and, consequently, a higher proportion of male offspring produced. This would affect the potential productivity of the deer herd (see Fetal sex ratio).

While the actual mechanism of population control is unclear, delayed age at first breeding until $1\frac{1}{2}$ years, a low reproductive output of 1.05 fawns per female, and the production of fetuses at a rate of 1.45 males per female results in low annual increment. Coupled with a mortality factor, which, at present, nearly matches the apparent yearly recruitment (Klimstra 1974), the result appears to be a nearly stable population.

Reflections on Evolution of Key Deer

As indicated in previous sections, the Key deer appears to be somewhat different behaviorally from northern white-tails. Most striking were differences in social organization, with Key deer forming looser family units. This may reflect evolution without a predatory influence, and consequently, evolution which did not select against solitary independent young animals. In most northern populations, such animals would likely be selected against, since such independent animals are more susceptible to predation (White 1973).

The Key deer demonstrates variability in many aspects of its behavior and social organization; for example, some animals are highly social while others are extremely solitary. Such variability, which limits the generalizations that can be made, may in itself be an important reflection of the Key deer's history. It appears that the population has passed through several periods of low numbers (Dickson 1955, U. S. Fish and Wildlife Service Narrative Reports 1939-1967), a situation, which, in a population having no isolation between members, would tend to limit variability. The variability in socio-biology

and other features of the Key deer (Klimstra 1974, Silvy 1974) suggests that some isolating mechanisms may have resulted in semi-isolated breeding groups of deer.

Groups of islands, forming separate island complexes, separated by swift-flowing currents, may have had little interchange of deer between them; this may have resulted in semi-isolation. Interchange between islands may have occurred only in those years of relatively large deer populations. The variability evident in deer on Big Pine Key may be due to occasional immigration from outer island complexes over the years.

At times of very low population numbers, the role of behavior may have been to bring breeding animals together. Such behavior as the thrashing of vegetation with antlers, hock urination by both males and females, and movement into the same areas by animals of both sexes could have served this function. At high population densities, the effects of some of this behavior were less evident. The role of adult male breeding activity, in which non-prime-aged males were excluded, resulted in prolonging breeding activities over an extended period of time and may have influenced fawn sex ratio (see Population Dynamics, Fetal sex ratios). It also resulted in a longer fawning season than to the north, where adverse fall and winter weather would tend to select against fawns born late in the year.

That the reproductive performance of Key deer may be the result of evolution of an intrinsic mechanism, which tends to retard overpopulation of the environment (see Population Dynamics), should be investigated. Such a mechanism, resulting in a low reproductive output,

if it persists, may result in an inability of the Key deer to compensate for the relatively high level of man-related mortality. Unless the deer can adapt to accommodate for this unnatural loss, it could be unable to maintain itself.

Management Implications

A management program for the Key deer should provide for monitoring the status of the deer herd, whether by using trend data based on casual observations of deer, regular censuses, physical condition of animals, or some other index to the population status. In monitoring the population it is necessary to consider behavioral characteristics of the deer since these influence the results of monitoring techniques. Deer activity varies with time of day, season, and sex and age; thus data from field observations should be interpreted with this in mind.

Data on deer observed is useful for noting trends or changes in the sex-age composition, rather than depicting actual herd structure. Differential behavior of deer results in seasonal changes in sex-age ratios of deer observed. The most accurate observations of the sex-age structure probably occur in July and August, after fawns have begun to associate with the family groups. Does are less aggressive toward their yearlings and non-related deer at such times, and bucks in velvet have not become aggressive toward one another. They all use open areas for feeding. At other times deer of various sex-age classes remain out of open areas, do not associate with other deer, or in the case of adult males, show increased movements during the breeding season which result in a disproportionate representation of them in the sex-age categories.

Use of roadkill data to determine the herd structure is impractical due to differential susceptibility to mortality of the various sex-age classes, males being more highly represented than females. Such is obviously a result of differential behavior.

Determining productivity of a given female from field observation is often misleading, due to the loose social organization of the Key deer. While northern deer form tightly bound family groups (Hawkins and Klimstra 1970), the Key deer is less strongly sociable; therefore, fawns often are seen feeding in the vicinity of non-related deer, and often even try to nurse bucks or foreign does. This is usually unsuccessful. Basing productivity on field observations of does with fawns during the year gives an overestimate of the number of fawns successfully raised by a doe. Most reliable information on productivity of Key deer is available from examination of reproductive tracts of pre-partum females.

Based on patterns of deer activity and use of open areas, the best time for monitoring deer is in the late evening or early morning between 2200 and 0200 hours. This is a time when deer generally are active, are using open areas, and are not as wary as at other times. Before 2200 hours, fewer deer use open areas and many bed after the early evening feeding activities. Early morning hours, from 0400 hours until after sunrise, is a period when deer are active in open areas; however, their behavior is not conducive to censusing or observing them, because their flight distance is much greater than during 2200-0200 hours.

The best conditions for observing deer are on dark nights when there is no full moon and when there is not heavy rain or wind. Nights

when human activities are high, as on weekends, generally tend to be less ideal for seeing deer, since they stay out of housing subdivisions more than on quiet nights.

Management practices for the Key deer should take into account their reproductive life history. Fawns are born in mid-March through the summer months, with peak birth occurring in April and May; thus any habitat manipulation, which could serve as a hazard to very young fawns, should be avoided. Burning should occur either prior to or after the fawning season; however, during April, May, and June, fire could severely reduce the year's fawn population.

SUMMARY

A study of the social behavior, life history, and reproductive performance of the Florida Key deer was conducted during September 1969 through August 1971, and during periods of 2 weeks in 1972 and 2½ months during 1973. This study, which was a portion of a 5-year ecological study of the Florida Key deer, was conducted on Big Pine Key and adjacent islands in Monroe County, Florida. Most of the 233 deer, which were captured and marked, provided behavioral and life history information.

Animals were marked for individual identification by using bells, plastic collars, numbered ear tags, streamers, and tattoos. Radio-transmitters, placed on 119 deer, were used in locating these animals. Deer of specific sex-age classes were monitored at various times of the year for as long as possible to gather behavioral and life history information. Data, which were recorded for all deer observed, included notes on their behavior, their location, other animals with them, and weather conditions. Reproductive data were gathered from roadkilled and captured deer. Penned deer were observed to note specific behavior patterns.

Key deer formed small matriarchal groups, consisting of the adult doe, her female yearling, and fawns. Family groups broke up when does gave birth to new fawns and during breeding activities, but re-formed at other times. Bonds between group members appeared weaker than those between related deer on the mainland. Adult and yearling males were generally solitary.

A dominance hierarchy, which was maintained through aggressive interactions and posturing, shifted during the year, with adult males being dominant during the breeding season, and adult females dominating other deer at times when fawns were young. Physical characteristics were important in determining the social status of animals. Males with polished antlers were dominant to males without antlers and those with velvet-covered antlers.

Activity patterns appeared similar to those described for other populations of white-tailed deer; there were daily and seasonal variations. Deer were generally less active in mid-day, and were more active around sunrise and sunset. Feeding was more frequent from 1 hour before sunrise to just after sunrise, and from after noon until 1600-1700 hours. They bedded less during mid-day in July through September than in other months. During October through December, deer moved more and fed less during the day; this appeared associated with breeding activities. From birth up to 7 months of age, fawns increased their amounts of activity.

Activity in open areas, which varied throughout the year and during the 24-hour period, reflected the presence of humans in these areas. After heavy rains in May and June, deer spent more time in the open where insect pests were less numerous. Cattle egrets appeared to play important roles by feeding on insects which were external parasites on the deer.

Deer were more active and easier to see at times of light to moderate cloud cover, little or no wind, light or no rain, and when the temperature was 70° F or less. Fewer deer were seen on bright

moonlit nights when they were more wary, and in periods of heavy rains or strong winds when they bedded more.

Deer groomed themselves using the tongue, feet, and in some instances, antlers. Mutual grooming occurred between related deer whenever they encountered one another. Mutual grooming began immediately after the birth of a new fawn. Such grooming may enhance the ability of the doe and fawn to recognize one another through scent.

Play activities, alarm reactions, curiosity, and aggression appeared similar to that described for other white-tailed and black-tailed deer. While behavior similar to that described as "sign-posting" behavior and territorial behavior in other deer was observed, no territorial significance could be determined for these activities in the Keys. Deer appeared to rely mainly on scent for recognition of individuals, location of other deer, and conveying alarm. They combined auditory communication with visual communication in some instances to convey alarm, aggression, care-soliciting, care-giving, and distress behavior.

Breeding activities began in September, peaked in October, and declined through December; occasional breedings occurred as late as February. Adults bred earlier than yearlings, which bred earlier than female fawns. Males aged 3 to 5 years generally excluded younger and older males during peak breeding activities, but other males played increasingly important roles later in the breeding season. This did not limit the number of females bred, however, since does recycled in 24 to 27 days if they did not conceive in earlier periods of estrus. This tended to extend the breeding season, and may have influenced the sex ratio of fawns produced. No fawn males were observed to breed.

The gestation period of Key deer was around 204 days, and peak parturition occurred in April and early May. Some fawns were born as late as August and September. Examination of roadkilled deer revealed no fawn females to be pregnant; 37.5 percent of the yearlings had bred, producing 0.38 fetuses per doe, and 29 percent of all deer aged 2½ years or older had bred, producing 1.11 fetuses per doe. All pregnant yearlings carried single fawns; 75 percent of the 2½-year olds had singles, while 25 percent carried twins. Of the 16 pregnant roadkilled deer aged 2½ years and older, 68.8 percent carried singles, while 31.2 percent had twins. The sex ratio of Key deer fetuses was 1.45 males per female. While more males were born, the behavior of fawns accentuated these differences. Males were captured at a greater rate than females, more were observed in the field, and more male fawns were roadkilled, largely a result of males being slightly more active.

Does gave birth to fawns within their normal ranges, generally in areas providing heavy cover with open understory, which allowed freedom of movement. The bond between a doe and her fawn was strong during the first 2 to 3 months. After loss of fawns, does spent much of their time wandering through areas where the fawns had been bedded, calling and investigating any slight noises. Fawn-seeking behavior waned after one week. Although no does were seen to adopt fawns, one doe was suspected to have been caring for a fawn before it fell into a ditch and drowned.

Mortality appeared to be influenced by deer behavior. Fawns, which moved at early ages, often drowned in mosquito ditches, especially in areas of extensive ditching. That more males than females were killed

on highways reflected greater activity and mobility of the males. The differential mortality was reflected in survivorship of marked deer; 50 percent of the males survived to just over $1\frac{1}{2}$ years, while 50 percent of the females survived to over 2 years. Peaks in highway mortality occurred during the breeding season and the fawning season, when dominant animals tended to harass other deer and cause them to disperse.

The independence of young Key deer and their loose social organization possibly resulted from their evolution in the island environment, in which there were no predators to select against these traits. Variability in Key deer behavior probably resulted from semi-isolation between breeding groups of deer, possibly a result of the various island complexes, separated by channels having swift-flowing currents.

The low reproductive output and high ratio of males born in the population tends to slow the rate of population increment. Due to the low reproductive output and high mortality, the deer population currently appears to be increasing very slowly if at all.

Due to the differential behavior of deer in the various sex-age classes, observations of deer should be used only to note population trends, rather than determine actual herd composition from them. Management practices, which accommodate the breeding and fawning seasons, were recommended, and some techniques of censusing and monitoring the population in order to take advantage of the behavior were recommended.

LITERATURE CITED

Adams, W. H., Jr. 1960. Population ecology of white-tailed deer in northeastern Alabama. Ecology 41:785-790.

Alexander, T. R., and J. D. Dickson, III. 1973. Vegetational changes in the National Key Deer Refuge - II. Q. J. Florida Acad. Sci. 35(2):85-96.

Altmann, M. 1958. The flight distance in free-ranging big game. J. Wildl. Manage. 22:207-209.

Altmann, M. 1963. Naturalistic studies of maternal care in moose and elk. Pages 233-253 in Rheingold, ed. Maternal behavior in mammals. John Wiley and Sons, Inc., New York. 349pp.

Andersen, F. S. 1961. Effect of density on animal sex ratio. Oikos 12(1):1-16.

Autry, D. C. 1967. Movements of white-tailed deer in response to hunting on Crab Orchard National Wildlife Refuge. M.S. Thesis. Southern Illinois Univ. Carbondale. 44pp.

Barbour, T., and G. M. Allen. 1922. The white-tailed deer of eastern United States. J. Mammal. 3(2):65-78.

Barick, F. B. 1952. Deer trapping coordinated with weather. Wildl. in North Carolina 16(10):10-11, 20.

Behrend, D. F. 1966. Behavior of white-tailed deer in an Adirondack forest. Ph.D. Dissertation. State Univ. College of Forestry at Syracuse Univ. 200pp.

Behrend, D. F., and R. A. Lubeck. 1968. Summer flight behavior of white-tailed deer in two Adirondack forests. J. Wildl. Manage. 32(3):615-618.

Bourliere, F. 1964. The natural history of mammals. Knopf, New York. 387pp.

Browman, L. G., and P. Hudson. 1957. Observations on the behavior of penned mule deer. J. Mammal. 38(2):247-253.

Chapman, F. B. 1939. The whitetail deer and its management in southeastern Ohio. Trans. N. Amer. Wildl. Conf. 4:257-267.

Cheatum, E. L. 1949. The use of corpora lutea for determining ovulation incidence and variations in the fertility of white-tailed deer. The Cornell Vet. 39(3):282-291.

Cheatum, E. L., and G. H. Morton. 1942. Techniques used in determining the period of rut among white-tailed deer of New York State. Trans. N. Amer. Wildl. Conf. 7:334-342.

Cheatum, E. L., and G. H. Morton. 1946. Breeding season of white-tailed deer in New York. J. Wildl. Manage. 10(3):249-263.

Chiavetta, K. J. 1952. P. R. Job Completion Rept. W. Va., Project 25-R-3, Work Plan II, Job C. 20pp. mimeo.

Christian, J. J. 1961. Phenomena associated with population density. Proc. Natl. Acad. Sci. 47:428-449.

Christian, J. J., V. Flyger, and D. E. Davis. 1960. Factors in the mass mortality of sika deer, Cervus nippon. Chesapeake Sci. 1(2):79-95.

Collias, N. E. 1950. Some variations in grouping and dominance patterns among birds and mammals. Zoologica 35(2):97-119.

Cowan, I. M. 1956. The life and times of the Coast black-tailed deer. Pages 523-619 in W. P. Taylor, ed. The deer of North America. Stackpole Co., Harrisburg, Pa. 668pp.

Cowan, I. M., and V. Geist. 1961. Aggressive behavior in deer of the genus Odocoileus. J. Mammal. 42(4):522-526.

Crawford, G. J. 1962. A preliminary investigation of the white-tailed deer on Crab Orchard National Wildlife Refuge. M.A. Thesis. Southern Illinois Univ., Carbondale. 42pp.

Dahlberg, B. L., and R. C. Guettinger. 1956. The white-tailed deer in Wisconsin. Wisconsin Conserv. Dept. Tech. Wildl. Bull. 14. 282pp.

Dasmann, R. F., and R. D. Taber. 1956. Behavior of Columbian black-tailed deer with reference to population ecology. J. Mammal. 37(2):143-164.

dePourtales, L. F. 1877. Hints on the origin of the flora and fauna of the Florida Keys. Amer. Nat. 11(1):137-144.

deVos, A., P. Brokx, and V. Geist. 1967. A review of social behavior of the North American cervids during the reproductive period. Amer. Midl. Nat. 77:390-417.

Dickson, J. D., III. 1955. An ecological study of the Key deer. Florida Game and Fresh Water Fish Comm. Tech. Bull. 3. 104pp.

Dixon, J. S. 1934. A study of the life history and food habits of mule deer in California. California Fish and Game J. 20(3): 181-282; 315-354.

Downing, R. L. 1965. An unusual sex ratio in white-tailed deer. J. Wildl. Manage. 29(4):884-885.

Downing, R. L., and B. S. McGinnes. 1969. Capturing and marking white-tailed deer fawns. J. Wildl. Manage. 33(3):711-714.

Erickson, A. B., V. E. Gunvalson, M. H. Stenlund, D. W. Burcalow, and L. H. Blankenship. 1961. The white-tailed deer of Minnesota. Minnesota Dept. Conserv. Tech. Bull. 5. 64pp.

Espmark, Y. 1971a. Mother-young relationships and ontogeny of behaviour in reindeer (Rangifer tarandus L.). Z. Tierpsychol. 29:42-81.

Espmark, Y. 1971b. Individual recognition by voice in reindeer mother-young relationship. Field observations and playback experiments. Behaviour 40(3-4):295-301.

Estes, R. D. 1969. Territorial behavior of the wildebeest (Connochaetes taurinus Burchell, 1823). Z. Tierpsychol. 26: 284-370.

Ewer, R. F. 1968. Ethology of mammals. Plenum Press, New York. 418pp.

Follmann, E. H., and W. D. Klimstra. 1969. Fertility in male white-tailed deer fawns. J. Wildl. Manage. 33(3):708-711.

Fraser, A. F. 1968. Reproductive behavior in ungulates. Academic Press, London and New York. 202pp.

Geist, V. 1963. On the behavior of the North American moose in British Columbia (Alces alces andersoni petersen 1950). Behaviour 20:377-416.

Golley, F. B. 1957. Gestation period, breeding and fawning behavior of Columbian black-tailed deer. J. Mammal. 38(1):116-120.

Graf, W. 1956. Territorialism in deer. J. Mammal. 37:165-170.

Guthrie, R. D. 1971. A new theory of mammalian rump patch evolution. Behaviour 38(1-2):132-145.

Hahn, H. D., Jr. 1949. A method of censusing deer and its application in the Edwards Plateau of Texas. Texas Game, Fish and Oyster Comm. Job Compl. Rept. P-R Proj. Rept. 25R. 24pp.

Halloran, A. F. 1943. Management of deer and cattle on the Aransas National Wildlife Refuge, Texas. J. Wildl. Manage. 7(2):203-216.

Harlow, R. F. 1972(1974). Reproductive rates in white-tailed deer of Florida. Q. J. Florida Acad. Sci. 35(4):165-170.

Harlow, R. F., and F. K. Jones, Jr. 1965. The white-tailed deer in Florida. Florida Game and Fresh Water Fish Comm. Tech. Bull. 9. 240pp.

Harlow, R. F., and E. L. Tyson. 1959. A preliminary report on the effect of mast abundance on the weight and reproduction of deer in central Florida. Proc. Ann. Conf. Southeast. Assn. Game and Fish Comm. 13:62-69.

Haugen, A. O., and L. A. Davenport. 1950. Breeding records of white-tailed deer in the upper Peninsula of Michigan. J. Wildl. Manage. 14(3):290-295.

Haugen, A. O., and D. W. Speake. 1957. Parturition and early reactions of white-tailed deer fawns. J. Mammal. 57:420-421.

Hawkins, R. E., and W. D. Klimstra. 1970a. Deer trapping correlated with weather factors. Trans. Illinois State Acad. Sci. 63(2): 198-201.

Hawkins, R. E., and W. D. Klimstra. 1970b. Social organization of white-tailed deer. J. Wildl. Manage. 34(2):407-419.

Hediger, H. 1934. Zur Biologie und Psychologie der Flucht bei Tieren. Biol. Zbl. 54:1-2.

Henshaw, J. 1971. Antlers -- the unbrittle bones of contention. Nature 231(5303):469.

Hersher, L., J. B. Richmond, and A. U. Moore. 1963. Maternal behavior in sheep and goats. Pages 203-232 in Rheingold, ed. Maternal behavior in mammals. John Wiley and Sons, Inc., New York. 349pp.

Hesselton, W. T., and E. VanDyke. 1969. Twin fawns born two days apart. New York Fish Game J. 16(2):261.

Hoffmeister, J. E., and H. G. Multer. 1968. Geology and origin of the Florida Keys. Geological Soc. of America Bull. 79:1487-1502.

Illige, D. 1951. An analysis of the reproductive pattern of white-tailed deer in south Texas. J. Mammal. 32:411-421.

Jackson, R. M., M. White, and F. F. Knowlton. 1972. Activity patterns of young white-tailed deer fawns in south Texas. Ecology 53(2): 262-270.

Jeter, L. K., and R. L. Marchinton. 1964. Preliminary report of telemetric study of deer movements and behavior on the Eglin Field Reservation in northwestern Florida. Proc. Southeast Assn. Game and Fish Comm. 18:140-152.

Kiley, M. 1972. The vocalizations of ungulates, their causation and function. Z. Tierpsychol. 31:171-222.

Kjos, C. G., and G. G. Montgomery. 1969. Daytime locations and bedsites of white-tailed deer fawns. Trans. Illinois State Acad. Sci. 62(2):117-119.

Klimstra, W. D. 1974. Key deer investigations final report. Period of study: December 1967 - June 1973. 184pp.

Knowlton, F. F., and E. D. Michael. 1965. Placental ingestion and possible parturient mortality in wild white-tailed deer. J. Mammal. 46(1):107.

Lambiase, J. T., Jr., R. P. Amann, and J. S. Lindzey. 1972. Aspects of reproductive physiology of male white-tailed deer. J. Wildl. Manage. 36(3):868-875.

Linsdale, J. M., and P. Q. Tomich. 1953. A herd of mule deer. Univ. California Press, Berkeley. 567pp.

Loveless, C. M. 1959. The Everglades deer herd life history and management. Florida Game and Fresh Water Fish Comm. Tech. Bull. 6. 104pp.

Marchinton, R. L., and W. G. Moore. 1971. Auto-erotic behavior in male white-tailed deer. J. Mammal. 52(3):616-617.

Marler, P., and W. J. Hamilton, III. 1968. Mechanisms of animal behavior. John Wiley and Sons, Inc. New York. 771pp.

Marshall, A. D., and R. W. Whittington. 1968. A telemetric study of deer home ranges and behavior of deer during managed hunts. Proc. SE Assn. Game and Fish Comm. 22:30-46.

McCullough, D. R. 1969. The tule elk: its history, behavior, and ecology. Univ. California Publ. Zool. 88. 209pp.

McDowell, R. D. 1959. Relationship of maternal age to prenatal sex ratios in white-tailed deer. Proc. NE Section of the Wildl. Soc. Mimeo. 5pp.

McGinnes, B. S., and R. L. Downing. 1969. Fawn mortality in a confined Virginia deer herd. Proc. SE Assn. Game and Fish Comm. 23:188-191.

McGinnes, B. S., and R. L. Downing. 1972. Variation in peaks of fawning in Virginia. Mimeo. 10pp.

McLean, D. D. 1940. The deer of California, with particular reference to the Rocky Mountain mule deer. California Fish and Game J. 26:139-166.

Michael, E. D. 1964. Birth of white-tailed deer fawns. J. Wildl. Manage. 28(1):171-173.

Michael, E. D. 1967. Drinking habits of white-tailed deer in south Texas. Proc. SE Assn. Game and Fish Comm. 21:51-57.

Michael, E. D. 1968a. Aggressive behavior of white-tailed deer. SW Nat. 13(4):411-420.

Michael, E. D. 1968b. Playing by white-tailed deer in south Texas. Amer. Midl. Nat. 80(2):535-537.

Michael, E. D. 1970. Activity patterns of white-tailed deer in south Texas. Texas J. Sci. 21(4):417-428.

Miller, F. L. 1965. Behavior associated with parturition in black-tailed deer. J. Wildl. Manage. 29(3):629-631.

Miller, F. L. 1971a. Behavior of maternal black-tailed deer (Odocoileus hemionus columbianus). Z. Tierpsychol. 28(5):527-533.

Miller, F. L. 1971b. Mutual grooming by black-tailed deer in northwestern Oregon. Canadian Field-Nat. 85(4):295-301.

Montgomery, G. G. 1959. Social behavior in a refuge population of white-tailed deer (Odocoileus virginianus) studied with specially developed marking techniques. M.S. Thesis. Pennsylvania State Univ., State College. 70pp.

Montgomery, G. G. 1963. Nocturnal movements and activity rhythms of white-tailed deer. J. Wildl. Manage. 27(3):422-427.

Muller-Schwarze, D. 1968. Play deprivation in deer. Behaviour 31: 144-162.

Muller-Schwarze, D. 1971. Pheromones in black-tailed deer (Odocoileus hemionus columbianus). Anim. Behav. 19:141-152.

Muller-Schwarze, D. 1972. Social significance of forehead rubbing in black-tailed deer (Odocoileus hemionus columbianus). Anim. Behav. 20:788-797.

Muller-Schwarze, D., and C. Muller-Schwarze. 1969. A herd of blacktail deer. Pacific Discovery 22(4):22-26.

Nixon, C. M. 1971. Productivity of white-tailed deer in Ohio. Ohio J. Sci. 71(4):217-225.

Ozoga, J. J. 1972. Aggressive behavior of white-tailed deer at winter cuttings. J. Wildl. Manage. 36(3):861-868.

Ozoga, J. J., and L. W. Gysel. 1972. Response of white-tailed deer to winter weather. J. Wildl. Manage. 36(3):892-896.

Ozoga, J. J., and L. J. Verme. 1970. Winter feeding patterns of penned white-tailed deer. J. Wildl. Manage. 34(2):431-439.

Palmer, R. W. 1951. The white-tailed deer of Tomhegan Camps, Maine, with added notes on fecundity. J. Mammal. 32(3):267-280.

Progulske, D. R., and D. C. Duerre. 1964. Factors influencing spot-lighting counts of deer. J. Wildl. Manage. 28(1):27-34.

Quay, W. B. 1959. Microscopic structure and variation in the cutaneous glands of the deer, Odocoileus virginianus. J. Mammal. 40(1):114-128.

Quay, W. B., and D. Muller-Schwarze. 1970. Functional histology of integumentary glandular regions in black-tailed deer (Odocoileus hemionus columbianus). J. Mammal. 51(4):675-694.

Queal, L. M. 1962. Behavior of white-tailed deer and factors affecting social organization of the species. M. Wildl. Manage. Thesis. Univ. Michigan, Ann Arbor. 140pp.

Robinette, W. L., and J. S. Gashwiler. 1950. Breeding season, productivity, and fawning period of the mule deer in Utah. J. Wildl. Manage. 14(4):457-469.

Robinette, W. L., J. S. Gashwiler, D. A. Jones, and H. S. Crane. 1955. Fertility of mule deer in Utah. J. Wildl. Manage. 19(1):115-136.

Robinette, W. L., J. S. Gashwiler, J. B. Low, and D. A. Jones. 1957. Differential mortality by sex and age among mule deer. J. Wildl. Manage. 21(1):1-16.

Robinson, W. L. 1962. Social dominance and physical condition among penned white-tailed deer fawns. J. Mammal. 43(4):462-469.

Rohfl, F. J., and R. R. Sokal. 1969. Statistical tables. W. H. Freeman and Co., San Francisco. 253pp.

Roseberry, J. L., and W. D. Klimstra. 1970. Productivity of white-tailed deer on Crab Orchard National Wildlife Refuge. J. Wildl. Manage. 34(1):23-38.

Ruff, F. J. 1938. The white-tailed deer on the Pisgah National Game Preserve, North Carolina. USDA Forest Service Publ. 249pp.

Schneider, K. M. 1930. Das Flehmen. Zool. Garten 3:183-198.

Severinghaus, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. J. Wildl. Manage. 13(2):195-216.

Severinghaus, C. W. 1955. Some observations on the breeding behavior of deer. New York Fish Game J. 2(2):239-241.

Severinghaus, C. W., and E. L. Cheatum. 1956. Life and times of the white-tailed deer. Pages 57-186 in W. P. Taylor, ed. The deer of North America. Stackpole Co., Harrisburg, Pa. 668pp.

Severinghaus, C. W., and J. E. Tanck. 1964. Productivity and growth of white-tailed deer from the Adirondack region of New York. New York Game and Fish J. 11(1):13-27.

Shank, C. C. 1972. Some aspects of social behavior in a population of feral goats (Capra hircus L.). Z. Tierpsychol. 30:488-528.

Shaw, S. P., and C. L. McLaughlin. 1951. The management of white-tailed deer in Massachusetts. Massachusetts Div. Fish Game Res. Bull. 13. 59pp.

Silvy, N. J. 1974. Population dynamics, movements, and habitat utilization of radio-tagged Key deer, Odocoileus virginianus clavium. Ph.D. Dissertation, Southern Illinois Univ. Carbondale. (In preparation)

Skinner, M. P. 1929. White-tailed deer formerly in the Yellowstone Park. J. Mammal. 10(2):101-115.

Smith, S. E., R. W. Gardner, and G. A. Swanson. 1963. A study of the adequacy of cobalt nutrition in New York deer. New York Fish Game J. 10(2):225-227.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W. H. Freeman and Co., San Francisco. 776pp.

Snyder, R. L. 1961. Evolution and integration of mechanisms that regulate population growth. Proc. Natl. Acad. Sci. 47:449-455.

Sparrowe, R. D., and P. F. Springer. 1970. Seasonal activity patterns of white-tailed deer in eastern South Dakota. J. Wildl. Manage. 34(2):420-431.

Stern, W. L., and G. K. Brizicky. 1957. The woods and flora of the Florida Keys. Tropical Woods 107.36-65.

Strode, D. D. 1954. The Ocala deer herd. Florida Game and Fresh Water Fish Comm. Game Bull. 1. 42pp.

Taber, R. D., and R. F. Dasmann. 1954. A sex difference in mortality in young columbian black-tailed deer. J. Wildl. Manage. 18(3): 309-315.

Taylor, W. P., ed. 1956. The deer of North America. Stackpole Company, Harrisburg, Pa. 668pp.

Thomas, J. W., R. M. Robinson, and R. G. Marburger. 1965. Social behavior in a white-tailed deer herd containing hypogonadal males. J. Mammal. 56(2):314-327.

Thomas, K. P. 1966. Nocturnal activities of the white-tailed deer on Crab Orchard National Wildlife Refuge. M.S. Thesis. Southern Illinois Univ., Carbondale. 37pp.

Tibbs, A. L. 1967. Summer behavior of white-tailed deer and the effects of weather. M.S. Thesis. Pennsylvania State Univ., University Park. 93pp.

Townsend, M. T., and M. W. Smith. 1933. The white-tailed deer of the Adirondacks. Roosevelt Wild Life Bull. 6(2):161-325.

Turner, C. D. 1966. General endocrinology. 4th ed. W. B. Saunders Company, Philadelphia, Pa. 579pp.

U. S. Fish and Wildlife Service Narrative Reports. 1939-1967. Key deer information. Bureau of Sport Fisheries and Wildlife, Atlanta, Ga.

Verme, L. J. 1962. Mortality of white-tailed deer fawns in relation to nutrition. Proc. Natl. White-tailed Deer Dis. Symp. Univ. Georgia, Athens. 1:15-28.

Verme, L. J. 1963. Effects of nutrition on growth of white-tailed deer fawns. Trans. N. Amer. Wildl. and Nat. Resour. Conf. 28:431-443.

Verme, L. J. 1965. Reproduction studies on penned white-tailed deer. J. Wildl. Manage. 29(1):74-79.

Verme, L. J. 1969. Reproductive patterns of white-tailed deer related to nutritional plane. J. Wildl. Manage. 33(4):881-887.

Walther, F. 1960. Antilopenhafte-Verhaltensweisen im Paarungsyeremoniell des Okapi (Okapi jonstoni Scalter 1901). Z. Tierpsychol. 17:188-210.

Waring, G. H. 1969. The blow sound of pronghorns (Antilocapra americana). J. Mammal. 50(3):647-648.

White, M. 1973. The whitetail deer of the Aransas National Wildlife Refuge. Texas J. Sci. 24(4):457-489.

White, M., F. F. Knowlton, and W. C. Glazener. 1972. Effects of dam-newborn fawn behavior on capture and mortality. J. Wildl. Manage. 36(3):897-906.

Yaw, E. 1966. Key Deer Investigations Progress Report. Key Deer National Wildlife Refuge. 1965-1966. U. S. Bureau Sport Fisheries and Wildl. 12pp.

Zug, G. R. 1972. A critique of the walk pattern analysis of symmetrical gaits. Anim. Behav. 20:436-438.

VITA SHEET

NAME: James William Hardin DATE OF BIRTH: July 16, 1943

LOCAL ADDRESS: Box 262, Rt. 1, Makanda, Illinois 62958

HOME ADDRESS: Middlefork Road, Inez, Kentucky 41224

UNIVERSITIES ATTENDED:

University of Kentucky, Lexington, 1961-1965, B.S., Zoology

University of Kentucky, Lexington, 1965-1967, M.S., Zoology

POSITIONS:

Teaching Assistant, University of Kentucky, Lexington, 1966-1967
Research Assistant, University of Kentucky, Lexington, 1967
Instructor, Memphis State University, Memphis, Tennessee, 1967-1969
Research Assistant, Southern Illinois University, Carbondale, 1969-1971, 1972-1973
Teaching Assistant, Southern Illinois University, Carbondale, 1971-1973
Researcher, Cooperative Wildlife Research Laboratory, Southern Illinois University, Carbondale, 1974

HONORS:

Sigma Xi, Phi Kappa Phi

PROFESSIONAL SOCIETIES:

American Society of Mammalogists
The Wildlife Society
Illinois Chapter of The Wildlife Society

DISSERTATION OR THESIS TITLE:

Thesis - Waking periods and movement of Myotis sodalis during the hibernation season

Dissertation - Behavior, socio-biology, and reproductive life history of the Florida Key deer, Odocoileus virginianus clavium

PUBLICATIONS:

1967. Homing in Lasionycteris noctivagans. J. Mammal. 48:323. (With W. H. Davis)

1969. Flight speeds of five species of vespertilionid bats. J. Mammal. 50:152-153. (With A. P. Patterson)

1969. Home range, movements, and activity of the eastern worm snake, Carphophis amoenus amoenus. Ecology 50:470-476. (With R. W. Barbour and M. J. Harvey)

1969. Observations on the activity of a seal salamander, Desmognathus monticola. Herpetol. 25:150-151. (With R. W. Barbour and J. P. Schafer)

1969. Home range, movements, and activity of the dusky salamander, Desmognathus fuscus. Copeia 1969:293-297. (With R. W. Barbour, M. J. Harvey, and J. P. Schafer)

1970. Observations on the home range of a yellow-nosed cotton rat, Sigmodon ochrognathus. Southwestern Nat. 14:353-355. (With W. H. Davis and R. W. Barbour)

1970. Observations on waking periods and movements of Myotis sodalis during hibernation. J. Mammal. 51:829-831. (With M. D. Hassell)

1973. Circadian rhythm in the golden mouse, Ochrotomys nuttalli. J. Tennessee Acad. Sci. 48:77-79. (With M. J. Harvey and M. L. Kennedy)

1974. A new record of Pipistrellus subflavus from Florida. Q. J. Florida Acad. Sci. 37(1): In press.

1974. Population ecology of Key deer (Odocoileus virginianus clavium). Natl. Geogr. Soc. Res. Repts. (Submitted with W. D. Klimstra and N. J. Silvy)

1974. Report on endangered species in Florida - the Key deer. Florida Acad. Sci. Endangered Species Comm. (Submitted with W. D. Klimstra and N. J. Silvy)