SOCIAL BEHAVIOR OF THE NEW ENGLAND COTTONTAIL,
SYLVILAGUS TRANSITIONALIS (BANGS) WITH A REVIEW
OF SOCIAL BEHAVIOR IN NEW WORLD RABBITS
(MAMMALIA: LEPORIDAE)

Brian C. TEFFT* and Joseph A. CHAPMAN**

The New England cottontail Sylvilagus transitionalis is primarily an inhabitant of dense woodlands and boreal habitats of the Appalachian mountains of the United States. The rabbit has been described as secretive, one which rarely ventures out into the open (Chapman, 1975 a).

The New England cottontail occurs from southeastern New England, south along the Appalachian mountains as far as Alabama. The range of the animal is severely restricted in parts due to numerous factors, including competition from Eastern cottontails S. floridanus and destruction of habitat (Chapman and Morgan, 1973). Chapman and Stauffer (1981) believe that S. transitionalis has restricted habitat requirements and is most commonly associated with dense cover and conifers. They also believe that the present distribution of the rabbit appears similar in nature to other species which are called « refugio­nal relics » by Udvardy (1969). This species is found from sea level in New England, to above 1 300 meters along the southern Appalachians.

Several attempts have apparently been made to introduce the species into mainland Europe (especially into the mountains of Italy) as an alternate game species for Oryctolagus and Lepus in the region (see Sasse, 1983 ; or Chapuis et al., 1985 a, 1985 b ; Arthur and Chapuis, 1982). Since the source of the introductions has been largely New York State it is likely that both S. floridanus and S. transitionalis have been released into Europe.

There were two major objectives of this study : (1) to record and describe the basic behavioral repertoire of the New England cottontail, and (2) to evaluate and compare the social organization of New England cottontails with that of other rabbits ; including : S. floridanus, S. aquaticus, S. nuttallii, S. auduboni, S. palustris, S. bachmani, S. idahoensis, S. brasiliensis, Romerolagus diazi and Oryctolagus cuniculus.

I. — MATERIALS AND METHODS

The enclosure for New England cottontails was constructed in Garret County, Maryland, near the town of Finzel on Big Savage Mountain. The

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Rev. Ecol. (Terre Vie), vol. 42, 1987
enclosure was 30.48 m × 15.24 m. Natural conditions were simulated as closely as possible (Fig. 1); trees and ground cover were left in place wherever possible.

The pen walls were built with 3 m wooden posts and 2.6 cm by 4.37 cm mesh chicken wire, and extended 2.13 m above the ground. Hardware cloth 0.6 m wide was laid flat on the ground with half placed on each side of the upright wall. This mesh was then woven to the wall with galvanized steel wire. Each side was then covered with heavy rocks and soil to prevent escape by digging. No rabbits escaped from the enclosure during the study. The enclosure was covered with nylon Toprite netting to exclude avian predators and ground predators which might attempt to climb over the fence.

A semi-enclosed observation tower at the uphill side of the enclosure allowed full view of the entire pen. Night observations were made possible with five 150 watt, battery powered floodlights. Hand held spotlights were employed to facilitate identification of individuals more clearly. Since the New England cottontail is a crepuscular animal, the greatest part of its activity occurred well before dusk or just after dark. As a result, natural light was used to the fullest extent in observations whenever possible.

Vegetation consisted of a variety of ferns, herbs, and woody sprouts arising from the stumps of cleared hardwoods. Seven different species of overstory trees and 15 different species of grasses and herbs were common in the enclosure (Table I). Three brush piles were constructed in the pen to provide additional cover for the rabbits. Wooden box traps, closed at one end, were placed two to each pile to provide protection from the heavy rains and snows common to the area.

The diet of the animals was supplemented with commercially prepared rabbit pellets and clipped oats. These were placed in two covered poultry feeders near the center of the enclosure. No free water was provided in the pen.

The cottontails were live trapped in the Savage River State Forest in the vicinity of Elk Lick Run, Garrett County, Maryland, U.S.A. Standard sized wooden box traps were used for capture. Three animals were introduced to the enclosure (1 female, 2 males). Each cottontail was marked with a flexible eartag, similar to that described by Labisky and Lord (1959), and then released into the enclosure.
TABLE I

Overstory and ground vegetation in the New England cottontail enclosure.

<table>
<thead>
<tr>
<th>Overstory Trees</th>
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<tbody>
<tr>
<td>Sugar Maple</td>
<td>Acer saccharum</td>
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<tr>
<td>Black Cherry</td>
<td>Prunus serotina</td>
</tr>
<tr>
<td>White Oak</td>
<td>Quercus alba</td>
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<tr>
<td>Red Oak</td>
<td>Quercus rubra</td>
</tr>
<tr>
<td>American Beech</td>
<td>Fagus grandifolia</td>
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<tr>
<td>Eastern Hemlock</td>
<td>Tsuga canadensis</td>
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<tr>
<th>Ground Layer</th>
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<tbody>
<tr>
<td>Wild lily of the valley*</td>
<td>Maianthemum canadense</td>
</tr>
<tr>
<td>Wood squirrel</td>
<td>Oxalis stricta</td>
</tr>
<tr>
<td>Painted trillium</td>
<td>Trillium undulatum</td>
</tr>
<tr>
<td>Red trillium</td>
<td>Trillium erectum</td>
</tr>
<tr>
<td>May apple</td>
<td>Podophyllum peltatum</td>
</tr>
<tr>
<td>False solomons seal*</td>
<td>Smilacina palustris</td>
</tr>
<tr>
<td>True solomons seal*</td>
<td>Polygonatum biflorum</td>
</tr>
<tr>
<td>Shining club moss</td>
<td>Lycopodium lucidulum</td>
</tr>
<tr>
<td>Common blue violet</td>
<td>Viola papilionaceae</td>
</tr>
<tr>
<td>Round leaf yellow violet*</td>
<td>Viola rotundifolia</td>
</tr>
<tr>
<td>Northern white violet</td>
<td>Viola pallens</td>
</tr>
<tr>
<td>Sumac*</td>
<td>Rhus sp.</td>
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<tr>
<th>Stump sproutings:</th>
<th></th>
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<tbody>
<tr>
<td>Witch hazel*</td>
<td>Hammenalis virginiana</td>
</tr>
<tr>
<td>Black locust*</td>
<td>Robinia pseudacacia</td>
</tr>
<tr>
<td>Sugar maple*</td>
<td>Acer saccharum</td>
</tr>
<tr>
<td>Grasses*</td>
<td>Gramineae</td>
</tr>
<tr>
<td>Ferns*</td>
<td>Poly podiaceae</td>
</tr>
</tbody>
</table>

*Food plants taken frequently by S. transitionalis in the enclosure.

Social activity was recorded in a similar manner to a method used by Marsden and Conaway (1963) and Marsden and Holler (1964). In this method the entire enclosure was scanned with the naked eye until animal activity was observed. The activity was then watched through 7 by 50 mm binoculars for its duration. At the conclusion of the behavior, the scanning process was resumed until another interaction developed. A grid system was employed to note exact locations of cottontails during the observation. Each observation was recorded individually with a portable cassette tape recorder. Data recorded for each interaction included time, location in the pen, rabbits involved, and a complete description of the behaviors elicited by the animals. Cassette tapes were later replayed and the data summarized on prepared data sheets.

Observations were made at times of day when peak activity was expected, usually late afternoon or early evening. Each observation period was at least one hour in duration and most were at least two hours in length. Observations of longer length were undertaken when particularly interesting social behavior was observed. Calculation of the number of social interactions per hour of observation was a good indicator of the intensity of activity for any particular period.

The rabbits were observed from January to September 1980. During that time, a total of 67 observation periods were held for a total of 107.25 hours of field observation. Observations
were usually held in the evening between 17:30 and 21:00 hours. As the breeding season progressed, it became obvious that an observation each night was not necessary. In light of this, observations were made at least every other night, and during periods of peak activity each night.

A method was devised to determine a rabbit's area of concentrated activity in the pen. Areas of concentrated activity were regions where an individual spent a majority of the time in such activities as feeding, exploring, patrolling, or resting. The area of activity was calculated from the percent of total time an individual spent in certain regions of the enclosure during a routine 2-hour observation period. Five randomly chosen observation periods per month were selected to calculate the activity areas for each rabbit. The results were presented graphically and are helpful for describing associations between members of the population.

New behaviors described in this paper for *S. transitionalis*, not previously described for the species or any other member of the genus *Sylvilagus*, will be denoted as a new behavior in the descriptions.

The nesting and nestling stage behavior of *S. transitionalis* is described including location, structure, and construction materials used for each nest. Vegetative cover type, orientation, and nest dimensions were also recorded for each nest found.

### II. DESCRIPTION OF THE BEHAVIORS OF *SYLVILAGUS TRANSITIONALIS*

The behaviors observed in *S. transitionalis* during this study are in Table II. Each of these behaviors is discussed in detail below.

#### A. NON-SOCIAL BEHAVIOR

1) *Feeding Behavior*

New England cottontails began their evening activity period by feeding in an area near the daytime form. Rabbits preferred to feed in the protective cover offered by clumps of dense vegetation and only rarely ventured out into the open to feed. After leaving their daytime resting spot, rabbits would sit motionless for extended periods at the edge of dense cover apparently watching for signs of danger. New England cottontails move very cautiously in a slow, secretive manner, always alert to noises which often caused rapid retreat to dense cover.

Brush rabbits (*S. bachmani*) utilized dense cover prior to and while feeding similar to New England cottontails. Brush rabbits apparently remain just inside dense brushy cover watching for signs of danger before leaving cover (Orr, 1940). Mainland populations of brush rabbits studied by Orr rarely fed in open areas and preferred to feed in sheltered areas close to protection offered by dense brush. The Mountain cottontail (*S. nuttallii*) shares this secretive habit and reportedly prefers to feed in the shelter of brush or in small clearings a few meters from dense cover (Chapman, 1975b). However, Zoloth (1969) discovered that island populations of brush rabbits in California preferred to feed in open areas and not in dense brush. This may have been due to the fact that there were no mammalian predators of rabbits and predation by raptors was rare.

New England cottontails forage by moving randomly among clumps of vegetation choosing food items. Ferns (*Polypodiaceae*) were very abundant in
TABLE II
Non-social and social behaviors of the New England cottontail.

<table>
<thead>
<tr>
<th>Non-social behavior</th>
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<tbody>
<tr>
<td>Feeding</td>
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<tr>
<td>Grooming</td>
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<tr>
<td>Escape</td>
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<tr>
<td>Loaﬁng</td>
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<tr>
<td>Exploration</td>
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<tr>
<th>Social behavior</th>
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<tbody>
<tr>
<td>Postures</td>
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<tr>
<td>Alert</td>
</tr>
<tr>
<td>*Roosting</td>
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<tr>
<td>Submissive</td>
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<tr>
<td>Approach</td>
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<tr>
<td>Female Behaviors</td>
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<tr>
<td>Female aggressive threat</td>
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<tr>
<td>Female charge</td>
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<tr>
<td>Female jump</td>
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<tr>
<td>Male Behaviors</td>
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<tr>
<td>Scent marking</td>
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<tr>
<td>Rush</td>
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<tr>
<td>Dash</td>
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<tr>
<td>Attempted mounting</td>
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<tr>
<td>Vocalizations</td>
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<tr>
<td>Tick-squeal</td>
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<tr>
<td>Squeak</td>
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<tr>
<td>Distress cry</td>
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<tr>
<td>Male-Female Interactions</td>
</tr>
<tr>
<td>Face off</td>
</tr>
<tr>
<td>Reproductive dislodgement</td>
</tr>
<tr>
<td>*Jump/Circle</td>
</tr>
<tr>
<td>Reproductive chase</td>
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<tr>
<td>Following</td>
</tr>
<tr>
<td>Copulation</td>
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<tr>
<td>Female chase</td>
</tr>
<tr>
<td>Consort</td>
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<tr>
<td>Dominant Subordinate Interactions</td>
</tr>
<tr>
<td>Aggressive chase</td>
</tr>
<tr>
<td>Dislodgement</td>
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<tr>
<td>Avoidance</td>
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</tbody>
</table>

*New behavior for S. transitionalis

the enclosure and were an important source for S. transitionalis. Fern is also a common and frequent part of known habitat for S. transitionalis in western Maryland (Chapman and Stauffer, 1981). In a food preference study, ferns were determined to be a non-favored food of S. transitionalis in Massachusetts (Pringle, 1960). When feeding on ferns rabbits move into dense clumps, snip the fern at the base of the stalk, and consume the entire frond. A variety of succulent growth from herbaceous plants and woody plants were utilized by S. transitionalis (Table I).

Clipped oats and commercial rabbit pellets were provided for the rabbits in addition to natural foods. New England cottontails preferred native vegetation to commercial foodstuffs.
Cottontails were not observed drinking and no free water was provided in the pen. Water present in the stems of herbaceous plants probably served as the main source. On a few occasions, rabbits were observed licking patches of snow and ice. There was very little succulent plant material available during winter as a water supply.

Male and female *S. transitionalis* were often observed feeding together during early evening foraging periods. During feeding sessions a mutual tolerance was shown by both individuals with no aggression apparent. The dominant male and female often comprised a feeding pair. Rabbits would feed together at preferred food clumps at 0.5 to 1 m apart. This feeding pair was most often observed during consort between dominant male and female (see Male/Female Interactions). Marsden and Holler (1964) noted that both the Swamp rabbit (*S. aquaticus*) and the Eastern cottontail often exhibited gregariousness in their feeding habits. Zoloth (1969) reported groups of brush rabbits feeding together with «individual distance» (Wynne-Edwards, 1962: 133-134) maintaining spacing between rabbits.

Grubbing and digging is a type of feeding behavior exhibited by both male and female *S. transitionalis*. Rabbits would move over an area where the soil had been exposed and nuzzle with the mouth into the upper organic horizon of the soil. Small bits of decayed leaves, roots, and bark were eaten by the rabbits. The rabbits would also paw at the earth with the front feet (digging) to expose tender roots which would then be extracted with the incisors and eaten. Movement was very slow and meticulous as the individual was always intent on this feeding activity.

2) *Grooming*

Grooming behavior was frequent throughout the evening's activity period. This was sterotyped and occurred in much the same pattern each time it was observed (Fig. 2). Stereotyped grooming was noted by Marsden and Holler 1964: 9) in both swamp rabbits and eastern cottontails. In that study, grooming occurred throughout the activity period and next to feeding was the second most common behavior. Brush rabbits are reported to return to resting forms to groom following feeding activity (Zoloth, 1969). In brush rabbits, the grooming pattern was: (1) licking forefeet to clean face and head; then body, (2) cleaning hind feet, (3) cleaning front legs and feet. Cervantes and Lopez-Forment (1981) reported that volcano rabbits licked their genital region following copulation.

In *S. transitionalis*, a pattern similar to that described for other rabbits was observed. Cleaning and licking the legs, feet, and hindquarters was the initial grooming activity, followed by grooming of the face and ears. In this case, the forepaws are licked several times, then rubbed over the face and ears in a motion, ear to nose. Grooming of the hindquarters, breast, and abdomen completed the grooming session. A combination of licking and biting movements were involved in cleaning these regions of the body (Fig. 2). The amount of time spent grooming varied from three to seven minutes per session.

3) *Escape*

Rapid, zig-zag dashes with individuals running at maximum speed for dense cover typified *S. transitionalis* escape movements. When startled, rabbits would sit up alertly and freeze as if trying to determine the source and
direction of the disturbance. When escape to cover was necessary, rabbits would leap from the freeze position and dash for a brush pile. In many instances escape was a direct line escape for cover without zig-zag movements. When a rabbit was startled by the observer (inside the pen) zig-zag escape was obvious. This may be some type of predator confusing behavior causing a less agile predator to become lost in a futile chase. Escape maneuvers of this type have been described for the Eastern cottontail, the Swamp rabbit, and the Audubons' cottontail, *S. audubonii* (Marsden and Holler, 1964: 9; Orr, 1940).

Concealment in escape cover followed escape. In a concealment posture, the rabbit assumed a compact shape, with its legs and the neck withdrawn close to the body. Once in the concealment position, New England cottontails were difficult to see against the background of dense escape cover (Fig. 3).
4) **Loafing**

Loafing behavior may aid cooling in *S. transitionalis*. When loafing, rabbits assumed a stretched-out position with the belly resting directly on the ground and the hind legs fully extended behind. *S. floridanus* and *S. aquaticus* assume a loafing posture on their side with the legs stretched out in front (Marsden and Holler, 1964: 9). New England cottontails were never observed in that position; their legs were consistently stretched out front and back (Fig. 4).

Loafing was often observed during warm, humid days of June, July, and August. The underparts of the rabbit’s body in contact with the cool earth, which is exposed at the bottom of forms, may be an aid to temperature regulation. At times, individuals panted rapidly with the eyes completely closed.

![Figure 4. — Loafing posture of *Sylvilagus transitionalis*.](image-url)
5) Dusting

Dusting or dog-like rolling in dusty areas was reported for *S. floridanus* (Marsden and Holler, 1964: 9). This behavior was not observed in *S. transitionalis*. Marsden and Holler (1964) also reported that the behavior was not observed in the Swamp rabbit, and the literature does not report its occurrence in other *Sylvilagus*. 

6) Exploration

Exploration of the enclosure involved active investigation by the rabbits. This behavior occurred at the beginning of or early in the activity period. Once the rabbit had left its daytime form, exploration began as the animal searched for food.

When exploring the pen, the rabbits moved about in alert posture (see Social Behavior). The dominant male (MR1) was the most frequent explorer during the activity period. This individual also had the greatest range of area within the pen. The subordinate male rabbit (MP2) had a lesser range and did not use the alert-aggressive posture of the dominant rabbit. The female rabbit (FG1) often explored the enclosure in the alert stance in much the same fashion as the dominant male. Exploratory behavior was often a prelude to other forms of social activity.

During periods of high reproductive activity, exploratory behavior allowed the males to locate the estrus female. The search often began in familiar territory then extended into other areas of the enclosure. Exploration during estrous often led to aggressive encounters between males (see Social Behavior). The importance of exploratory behavior is that it allows rabbits to gain information about the social condition of the population and its members, in addition to locating food and nest sites.

7) Patrolling

Patrolling of the perimeter of the enclosure by rabbits is another form of exploratory behavior. In the patrol, the individual would move along the edge of the enclosure sniffing the ground or stopping to perch on a stump or rock to groom. Patrolling, in the strict sense, involved active movement along the fence row in some type of information gathering search. The senses of hearing and smelling seemed to be used a great deal during patrol. Rabbits sniffed the air and ground often and held the ears stiffly alert, remaining very attentive to any extraneous noise. Large deposits of droppings ringed the pen along the patrol path, with well-worn travelways easily visible.

Along the patrol pathway, low perches such as rocks, logs or old stumps were scattered, on which rabbits would stop to rest. Droppings were concentrated around these perching sites. The use of perches by other rabbits is well noted in the literature. The use of low prominences such as logs or stumps has been observed in the Audubons' cottontail (Orr, 1940). Heavy concentrations of droppings were deposited around these perches and they were believed to function as lookout posts used by the rabbits after dark. The use of elevated defecation sites is reported for swamp rabbits (Terrel, 1972) and marsh rabbits, *S. palustris* (Blair, 1936).

With the approach of estrus, the female *S. transitionalis* was often observed patrolling in an unusual manner. The rabbit would run along the patrol pathway back and forth, stopping only to perch at selected sites to peer
outside the pen. She appeared very nervous and interested in the area just outside the pen. This behavior occurred on nights just prior to estrus when female aggression toward males had increased dramatically. This nervous patrol by the female was a reliable indicator that the onset of estrous activity was imminent.

B. — SOCIAL BEHAVIOR

1) Alert Posture

An alert posture was exhibited by both male and female *Sylvilagus transitionalis*. This posture was similar to the posture described for *S. aquaticus* and *S. floridanus* by Marsden and Holler (1964). In the alert stance, the animal moved with the weight shifted slightly forward and the rump slightly higher than the head. When the animal stopped, the ears were held stiffly alert and the animal stood up on the hind legs (Fig. 5 a). Marsden and Holler (1964 : 10) describe the behavior as a male stance which was used when confronting a female or subordinate male rabbit. In *S. transitionalis* the alert posture was exhibited by both sexes in a variety of behavioral contexts.

Female alert stance was noted most often when the rabbit moved about the pen exploring and searching for food. The female would assume an alert posture at other times when interacting with male rabbits just prior to estrus and parturition. During this period, males would attempt to maintain close contact with the female by moving with her and remaining within one to two meters at all times. A female response to the male’s persistence involved the use of an alert postured approach by the female followed immediately by reproductive dislodgement of the persistent male.

![Figure 5. — Basic postures of *Sylvilagus transitionalis*. A, Alert or alert aggressive posture; B, Roosting posture; and C, submissive posture.](image-url)
In male rabbits, the alert posture was used in other social contexts. Dominant males assumed the posture when approaching a subordinate male or receptive female. The alert-aggressive approach by a male appeared jerky, with quick movements. This behavior was observed most often just prior to reproductive interactions or dominant-subordinate interactions. Another form of the alert posture was exhibited by males as they searched the pen for food.

2) Roosting Posture

During inactive periods rabbits often adopted a rest and concealment stance identified here as a roosting posture. This was the posture most commonly observed during daylight hours while resting in forms. Characteristically, the body was hunched with the limbs, neck, and tail withdrawn and the ears laid back against the base of the neck (Fig. 5 b). This posture is undoubtedly an essential aid to concealment during daylight hours as individuals blended easily with the surrounding backdrop. This compact shape may also aid in thermoregulation during extremely cold inactive periods where movement otherwise would use up energy.

The roosting posture was often attained during evening observation periods. It was observed during periods of low social activity where solitary rabbits would move to a dense clump of fern and roost for periods of up to 45 minutes without the slightest movement.

3) Submissive Posture

In a submissive posture, New England cottontails would hunch the body with the neck, tail, and feet withdrawn and the ears laid against the back of the neck (Fig. 5 c). The posture was similar to that described for swamp rabbits and eastern cottontails by Marsden and Holler (1964: 10). In the submissive posture rabbits were ready to spring away and retreat from a dominant-subordinate confrontation. From the posture, submissive rabbits could move slowly away into cover from the confrontation. The roosting posture assumed by _S. transitionalis_ during periods of rest and concealment appeared identical in form to this posture.

4) Approach

The approach occurred in both sexes in a variety of social contexts. The approach was always slow and cautious, with the approaching rabbit constantly watching the other rabbit. The alert posture was assumed by the approaching rabbit.

The approach was a prelude to interactions between males or between male and female rabbits. The approach was utilized by a dominant male when challenging a subordinate. The approaching male would assume an alert posture and approach the subordinate rabbit. During the initial stages of estrus, when female aggression was predominant, a female would use the approach to confront a male in an aggressive stance prior to reproductive dislodgement. This sequence of female approach leading to male dislodgement was observed several times and appeared stereotyped in _S. transitionalis_.

Marsden and Holler (1964: 10) describe an approach as primarily a male behavior. In swamp rabbits they found that displacement behaviors, such as nibbling of vegetation, often accompanied an approach. Other dominant behaviors such as paw-raking were observed when a dominant approached a subordinate. This form of male approach was not observed in _S. transitionalis_.

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C. — FEMALE BEHAVIORS

1) Female Aggressive Threat

An aggressive posture was often attained by a female when confronting a male rabbit. Female aggression was at its peak during the period prior to receptivity in post-partum estrus. The aggressive threat was similar to the behavior observed in *S. floridanus* and *S. aquaticus* by Marsden and Holler (1964: 11). The female would crouch with the chin tilted upward and the ears laid back (Fig. 6). From this position the female was ready to spring at an approaching male in an aggressive manner.

In the sequence where the female assumed an aggressive posture while approaching a male rabbit, the stance was characterized by the weight being distributed equally on all four feet, with the tail withdrawn and the ears held alert. After a face-off was reached between rabbits, the threat posture was maintained for a brief time followed immediately by the female charge at the male. The «tick-squeal» vocalization (see Vocalizations) was often emitted by the female during an aggressive-threat posture.

2) Charge

A charge was a rapid dash by a female rabbit directly at a male rabbit. The charge was an important part of the reproductive dislodgement sequence (see Social Behavior), after a face-off had been reached. In the sequence, a male and female would face-off, at which time the female would present the aggressive threat posture. From this posture she would rush directly at the male, often butting him with her head (example is shown in Fig. 13c). Following the charge and male retreat, the female usually pursued the male a short distance. The charge was one of the few behaviors where male and female rabbits made physical contact.

In the Swamp rabbit and the Eastern cottontail, a charge often involves the female biting and striking the male rabbit. This occurred when a male's retreat from the charge was not immediate (Marsden and Holler, 1964: 11). In *S. transitionalis*, biting and striking of the male rabbit by a charging female was not observed. The only physical contact which occurred was the occasional butt of the male, with the head, by the female rabbit.

![Figure 6. — Female aggressive threat of *Sylvilagus transitionalis.*](image-url)
3) Jump Behavior

Jump behavior was exhibited by a female *S. transitionalis* during an aggressive interaction with a male rabbit. The jump appeared as an extension of the aggressive threat posture and charge which occurred during reproductive dislodgement. In this case the excited female would leap directly over the male following a face-off and charge. The energy of the jump carried the female over the male without further contact. Urination by the female at the height of the jump, which was observed in swamp rabbits and eastern cottontails, did not occur in *S. transitionalis*. A sequence including jump behavior might be: male/female face-off, female aggressive threat, female charge, female jump, male retreat (Fig. 7). This sequence may be repeated again almost immediately.

4) Boxing

Boxing is an aggressive behavior exhibited by female swamp rabbits and eastern cottontails in response to a male's advance (Marsden and Holler, 1964: 11). In the contact, the female would rise up on the hind feet from the threat position and strike the approaching male with the forefeet. This aggressive display by female rabbits was not observed in *S. transitionalis*.

D. — MALE BEHAVIORS

1) Scent Marking

Contrary to other Lagomorphs, *S. transitionalis* did not use glandular odors in territorial marking. Use of infraorbital glands or submandibular glands was not observed during this study. At no time was the dominant male rabbit observed marking when in the presence of female, subordinates, or while alone. Resting forms within the cover of brush piles were heavily laden with droppings and may function as watching stations as described for *S.*

Figure 7. — Jump behavior sequence of *Sylvilagus transitionalis*. Female leaps from threat posture over the male which has assumed the submissive posture.

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*bachmani* (Orr, 1940). Dung hills appeared at selected, rocks along the perimeter of the enclosure on the patrol pathway. The coating of fecal pellets in dung hills with secretions from anal glands in *S. transitionalis* may convey scent messages to conspecifics. New England cottontails were often observed sitting at these posts, which apparently serve as a territory marker or lookout in this species.

Absence of the use of glandular marking behaviors in *S. transitionalis* seem to suggest a lesser degree of social organization than either *S. aquaticus* or *S. floridanus*. Both of the latter species make use of glandular odors, and *S. aquaticus* has developed a system of breeding territories which are maintained by chinning and aggressive defense by dominant males. Other members of *Sylvilagus*, the Brush rabbit, Mountain cottontail *S. nuttallii*, Audubon's cottontail and Marsh rabbit show a lesser and generally poorer use of glandular scent marks (Chapman, 1974, 1975a, 1975b; Chapman and Feldhamer, 1981; Chapman et al., 1980, 1982; Chapman and Willner, 1978, 1981).

2) *Rush*

The rush of a male directly at the female was the prelude to some form of reproductive interaction. After a face-off had been reached, a male rabbit would continue his approach toward a female and rush at her at a distance of less than 30 cm. The rush occurred just prior to a jump/circle sequence in a reproductive contact between a male and female (see male-female Interactions). The male attained an alert-aggressive stance throughout the contact.

3) *Dash*

The dash sequence has been described for both swamp rabbits and eastern cottontails by Marsden and Holler (1964: 10). The dash is a precopulatory behavior which occurs during the initial stages of estrus when male excitement is increasing. The behavior involves the male rushing rapidly past a female at close range, while displaying the white underside of the tail when enurinating on the female as described for *Oryctolagus* by Mykytowycz (1972: 339). New England cottontails did not display this form of the dash sequence. There was no display with the tail and enurination of the female did not occur.

A reproductive behavior, similar to a dash sequence, did occur in *S. transitionalis* just prior to the jump-circle sequence (see male-female Interactions). This behavior appeared as a pre-copulatory behavior which closely coincided with the jump-circle sequence. In the behavioral sequence, a male rabbit would dash past a female, then turn, and the two rabbits would continue to dash past each other in a circle up to ten times. The dash sequence in *S. transitionalis* did not appear as a separate behavior as in swamp rabbits or eastern cottontails but appeared as preliminary courtship behavior in combination with the jump-circle sequence.

At no time during the precopulatory behavior of *S. transitionalis* was enurination of the female observed. This behavior, together with the white undertail display, were the distinguishing components of the dash in swamp rabbits and eastern cottontails described by Marsden and Holler (1964). In *O. cuniculus*, enurination by males is a vital part of precopulatory behavior (Myers and Poole, 1961). Presumably, enurination is one way for males and their sexual partners to present signals to their conspecifics concerning their relative spheres of influence (Mykytowycz, 1972). This is another means for dominant male rabbits to express dominance by claiming a larger social space.
The undertail display is a significant part of this social interaction. Erection of the tail, exposing the anal and inguinal glands, can distribute odor. In wild rabbits, prominent display of the tail is a dominant gesture for dissemination of odor by dominant males. Erection and display of tail undersides by swamp rabbits and eastern cottontails undoubtedly serves to spread odor from similar glands in these species.

It is apparent that *S. transitionalis* does not utilize scent communication to the extent of other Leporids thus far studied. The absence of enurination and the undertail display in *S. transitionalis* further support this fact.

4) Attempted Mounting

An attempted mounting occurred when an excited male rabbit tried to copulate with the female prior to the receptive period. The behavior appeared as part of the reproductive chase where the male would climb up onto the females back, on the run, and attempt to copulate with her. In *S. transitionalis* this behavior occurred just prior to successful copulation. Marsden and Holler (1964) describe the behavior as mounting without trusting of a female by a male.

5) Scratching and Pawraking

Scratching and pawraking is an expression of dominance in both swamp rabbits and eastern cottontails (Marsden and Holler, 1964: 35). This behavior may have developed to prevent fighting between dominant males of different breeding groups and as a mechanism for maintaining territories in the swamp rabbit. Behavioral mechanisms for maintaining territories appear to be more developed in swamp rabbits than eastern cottontails which protect only small areas around breeding females. In both species, however, the behavior functions to secure adequate social space around a female or the female in a breeding group. A behavioral expression of dominance like this did not appear in *S. transitionalis*.

A scratching gesture was recorded on two separate occasions for a female *S. transitionalis*. In these instances, the female was seen to straighten her back and draw her front paws across the ground several times in a drumming manner. During this sequence, the back was held vertical and the ears were alertly perked up. On both occasions when this behavior was observed, a male rabbit was present at a distance of 4 to 4.5 meters. The behavior seemed to be directed towards the male and was observed just prior to littering and post partum estrus. This is probably another form of female aggression directed at the male during the period of unreceptivity.

III. — VOCALIZATIONS

Three different vocalizations were recorded for New England cottontails. These calls were used in many social contexts and were included in nearly all social encounters.

A. — TICK-SQUEAL

A chattering noise was emitted by both male and female rabbits. This vocalization was highly variable in *S. transitionalis* and can be described as a
chirping, clicking, or chattering. Pringle (1960) noted a call which was emitted by *S. transitionalis* when rabbits were released from traps which he termed «tick-squeal». This is undoubtedly the same chirp-chatter vocalization.

The tick-squeal was made under a variety of social conditions. An aggravated ticking sound was made by unreceptive females when being followed by advancing males. In this instance, a loud tick was sounded with a frequency of 2 or 3 ticks per 10-second period. During dislodgement, the female first emitted the sound when the male was at a distance of 1 to 2 meters; males did not vocalize at this time.

A rapid staccato version of the tick-squeal, we termed the chatter-click was heard from both sexes during reproductive interactions. Chatter was mixed with squeaks during jump-circle sequences. Chatter-click was emitted by males during a dominant-subordinate interaction. In this case, the dominant male would vocalize at a greater than usual volume and frequency, and the chatter would continue as the subordinate retreated. In another form of this vocalization, a low pitched, occasional chirp was heard when rabbits were disturbed from their daytime forms by the observer.

**B. — SQUEAK**

A squeak was heard when an excited male rabbit was interacting with a receptive female. Both males and females squeaked during jump-circle sequences with this sounding as high-pitched intermittent squeaks. The sound was observed during reproductive interactions with one exception. In that case, an alarmed male rabbit squeaked at the approach of a feral cat from outside the pen. This call from the male cottontail startled the other rabbits in the pen and caused them to run for cover. The squeak may function similar to the alert call of swamp rabbits in response to a variety of predators (Marsden and Holler, 1964: 12).

**C. — DISTRESS CRY**

The distress cry was made by both adults and kittens. The cry was a loud, high-pitched scream emitted when danger threatened. From adults the scream was heard when they were handled or removed from box traps. In young kittens, handling during measuring periods often resulted in screams from the tiny rabbits. Kittens at 7 to 10 days old were capable of a scream nearly as loud as the adults.

The scream is high-pitched, loud and startling and may have developed in these rabbits as some type of warning signal. The call may serve two purposes in this rabbit. First it may serve as a warning in the event of predator disturbance. Second, the cry could startle a predator which has attacked a rabbit, causing the predator to release its grip on the rabbit for an instant, enough for the rabbit to escape. Distress cries in swamp rabbits and eastern cottontails serve to alert members of those populations to danger (Marsden and Holler, 1964: 12).

**D. — VOCALIZATIONS OF OTHER LEPORIDS**

Other *Sylvilagus* use vocalizations to various degrees. Swamp rabbits are very vocal animals in which five distinct calls have been recorded (Marsden and Holler, 1964: 11). A highly developed use of vocal communication in the
species helps to support a well-organized social structure. Other members of this genus are much less vocal. Many authors report the use of some form of distress cry when rabbits are handled after trapping. For instance, marsh rabbits squeal or cry when they are handled or penned (Blair, 1936). Ingles (1941) reports squealing from Audubon's cottontails when they are removed from traps or handled. Eastern cottontails are not nearly as vocal as swamp rabbits and only a squeal and distress cry have been noted in this species (Marsden and Holler, 1964 : 12). Brush rabbits are reported to make use of squeals and distress cries (Chapman, 1974). The Mountain cottontail is the only member of the Sylvilagus for which there are no reports in the literature of vocalizations (Chapman, 1975b). Romerolagus emits a distress-type cry when attacked by predators and during copulation (Cervantes and Lopez-Forment 1981). According to Lockley (1974 : 23) Oryctolagus has only two rare calls, a low nasal grunt and a vocal squeal.

The results of this study indicate that New England cottontails are highly vocal, especially during breeding periods. They have three primary calls; however, the tick-squeal (and variations of this), appears to be the most important to social communication in reproduction and dominance relationships.

IV. — MALE/FEMALE INTERACTIONS

A. — FACE-OFF

The face-off occurred between male and female rabbits as a prelude to most reproductive interactions. One rabbit would approach another in an alert stance and the other would turn to face-off, often nose to nose (Fig. 8). Both male and female approaches resulted in face-offs between interacting rabbits.

The face-off was described as a reproductive interaction in swamp rabbits and eastern cottontails (Marsden and Holler 1964 : 12). Their description of

Figure 8. — Face-off between male and female Sylvilagus transitionalis. There are several possible female sequences elicited from the males approach. A common face-off posture of the female is similar to the roosting posture; however, the body is more elongated and the ears are held alert. In the male the ears are forward and the rabbit sits on all fours in a crouched position. The two rabbits may remain motionless in the face-off position for several seconds before the next behavior begins.
the behavior included a male approach followed by a female face-off from the threat posture. The description did not mention a female approach resulting in a face-off, which was occasionally observed in *S. transitionalis*.

When a male rabbit approached a female, the female might respond in a number of ways. Reproductive dislodgements occurred at times of high female aggression towards males. At times of receptivity to a male’s advances, a face-off between male and female might prelude a male dash and jump-circle sequence.

B. — REPRODUCTIVE DISLODGETMENT

Female aggressiveness toward males was at a peak just before the receptivity period and estrus. During this time the dominant male tried to maintain close contact with the female in spite of her aggression. A reproductive dislodgement occurred when a male and female had achieved a face-off and the female presented the aggressive-threat posture. Following the threat, the female would charge at the nearby male and he would retreat into cover. The sequence was most common as estrus approached with the appearance of the first dislodgements signaling the onset of breeding and post-partum estrus. Female *S. transitionalis* always dislodged males in this sequence.

Physical contact was very rare in reproductive dislodgements for *S. aquaticus* and *S. floridanus* (Marsden and Haller, 1964: 12). In *S. transitionalis*, however, the charge of the female rabbit often resulted in contact (a butt with the head) between male and female when the male did not retreat from the charge quickly enough.

C. — JUMP-CIRCLE SEQUENCE

A jump-circle sequence by *S. transitionalis* indicated that breeding was very close at hand. The behavior was variable in form and the intensity of the interaction indicated how close breeding was to occurrence. The sequence of behaviors in a jump-circle sequence is: male-female face off; male rush at female with the two individuals exchanging places. In most cases the male would go over the top and the female underneath (Fig. 9). The sequence was repeated rapidly several times for a period up to 10 seconds.

Very little jumping actually takes place in this behavior and when it did occur it was a low jump. The rabbits more accurately exchanged places several times in a circling fashion rather than a jumping fashion and the behavior is more accurately termed a jump circle. Mutual or alternate jumping from a face off which occurs in *S. floridanus* (Marsden and Holler, 1964: 11), did not occur in *S. transitionalis*. During the sequence, a variation of the tick-squeal (chatter-click) vocalization was often heard. Once the full sequence had been completed, the partners would either face off and begin another sequence or move off to another area of the enclosure and begin some other behavior.

The jump-circle behavior in *S. transitionalis* is apparently similar to the jump behavior which is described for swamp rabbits and eastern cottontails (Marsden and Holler, 1964: 14). There are, however, primary differences between the behaviors in these species. In *S. transitionalis*, jump-circle behavior was exhibited at times of peak male excitement, just prior to estrus and breeding. The behavior was not observed during other periods of the cycle, only during estrus. In swamp rabbits and eastern cottontails, jump behavior

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was found not to be a component of true estrus and was displayed when an excited male interacted with a female during peaks of sexual receptivity other than true estrus (Marsden and Holler, 1964: 14).

D. — REPRODUCTIVE CHASES

During a reproductive chase, the female in estrus was pursued vigorously by either one or both male rabbits. Two- and three-way chases between rabbits were commonplace at this time. Chatter-click vocalizations were emitted by rabbits and chases lasted from five to ten seconds in length. A chase could be interrupted when a female ran to dense cover and the males lost the trail, however, once located, another chase began.

E. — FOLLOWING

Following behavior was observed when an excited male followed at the heels of an estrus female. After a face-off and reproductive interactions had been completed, the pair would separate, moving to other areas of the enclosure. As the female moved off, the male would follow close behind. This behavior occurred in the period of post-partum estrus when the dominant male was attempting to isolate the female in reproductive behavior. Very often following was broken up by the aggressive chasing of the other male.

F. — COPULATION

The description of copulation provided by Marsden and Holler, (1964) agrees with what was observed in *S. transitionalis*. In the copulatory sequence,
the male *S. transitionalis* made a rapid rush at the receptive female from the side or rear. In mounting the female, the male grasped her sides with his front legs and produced four or five quick thrusts. This was followed by the break away of the partners as they each moved off and began some other behavior. The act of copulation was very brief in itself; however, the sequence of events leading to the act provided a reliable indication of its occurrence. This is contrary to the copulatory behavior reported for *Romerolagus* in which a series of pelvic thrusts lasting 80 seconds followed mounting by the male (Cervantes and Lopez-Forment, 1981).

The most reliable indicator that a successful copulation had occurred was the abrupt change in social atmosphere which followed. Following copulation, both partners would move off to another area of the pen and begin to feed or groom. The endless pursuit of the female by the dominant male, which had occurred prior to copulation, subsided drastically. A sequence which included copulation was: male-female reproductive chase; approach by male; male rush and mount of female; copulation; breakaway and retreat by partners. Copulation was observed only once per estrus period in *S. transitionalis*.

G. — *FEMALE CHASE*

A female chase occurred when an aggressive female successfully dislodged a male who was attempting to form a consort with her. The chase was preceeded by a female charge resulting in a short chase of not more than two to three meters.

H. — *CONSORT*

At certain times during the reproductive cycle, the dominant male and female would maintain close contact with one another without any conflict between the two partners occurring. This passive interaction or partnership was called a consort, after a similar behavior described by Marsden and Holler (1964: 15). In the consort, two individuals foraged and explored the same vicinity of the pen, often at distances of no more than one to two meters. The subordinate male rabbit was never observed to approach a consort pair and was never included in this type of social activity.

A consort between male and female has been described for swamp rabbits and eastern cottontails (Marsden and Holler, 1964: 15). This behavior was not classified as an interaction because the female's role was passive and the male maintained close proximity without approach or following. These observations are consistent with the behavior of *S. transitionalis* during consort.

A consort between dominant male MR1 and female FG1 was formed on several occasions during the course of the study. Male MR1 would maintain close contact with FG1 and the rabbits would never venture very far apart. They, in fact, appeared inseparable in their movements. Subordinate male MP2 was generally far removed from the consort pair, and both MR1 and FG1 were highly aggressive towards this subordinate individual.

Zoloth (1969) observed groups of brush rabbits feeding together in the same area. A minimum distance between rabbits was maintained by minimum individual distance (Hediger, 1955). The minimum average distance for brush
rabbits was 30 cm with lower limits for young animals. When the individual distance is violated by another rabbit, individuals either move away or exhibit some form of aggressive behavior, usually a chase.

Individual distance appeared to affect *S. transitionalis* behavior during consort. During consort rabbits maintained an average approximate distance of 60 cm and this distance was not violated by either rabbit.

V. — DOMINANT-SUBORDINATE INTERACTIONS

Dominant-subordinate behaviors functioned to maintain the dominance order between dominant male MR1 and subordinate male MP2. The two males in this study formed a clearcut dominance hierarchy with one male dominant throughout the study. No reversal of rank was recorded. Swamp rabbits and eastern cottontails display linear dominance hierarchies (Marsden and Holler, 1964:26; McKinney, 1970; Brenner and Flemming, 1979). The social structure of other species of *Sylvilagus* has not been studied in enough detail to determine if hierarchies exist.

A. — AGGRESSIVE CHASE

Aggressiveness by the dominant male was the primary means of maintaining the social hierarchy. In *S. transitionalis*, the dominant male would approach the subordinate in an alert aggressive posture, constantly vocalizing. At some distance, depending upon the motivation of the aggressor, the dominant would rush at the subordinate. This rush results in submission and retreat by the subordinate into another quadrant.

The intensity of the chase depended on the motivational drive of the rabbit (see Alcock, 1975:189). When reproduction and estrus were very near, the dominant male would stare at the subordinate from distances of up to four meters. During periods of peak aggression, a rush might occur from this distance as the dominant rabbit would chase the subordinate around the pen several times in a chase lasting up to ten seconds. During periods of lower social excitement, brief chases were common with short rushes and pursuits by the dominant rabbit common.

Eyesight and olfaction seemed to be important in aggressive interactions between male *S. transitionalis*. Often the dominant male would raise up on the hind feet and look directly at the subordinate from across the enclosure. The subordinate male was, conversely, observed on the hind feet visually inspecting the pen for the whereabouts of the dominant rabbit. Olfactory senses seemed also to be employed by males in gaining information about rival males. Both males were observed sniffing the air and ground during periods of peak aggression in an apparent effort to locate the rival male.

B. — DISLODGEMENT

A dislodgement sequence between males was similar to that which occurred between a male and female in reproductive dislodgement. In this case, the dominant male would approach a subordinate in an alert posture and charge at the subordinate male. Following the charge, the subordinate would retreat, but would not be followed, by the dominant rabbit. The aggressor
would instead occupy the subordinates spot and begin sniffing the vacated area. Dislodgement commonly occurred at times when a lower intensity of activity prevailed between males.

C. — AVOIDANCE

The subordinate male avoided contact with the dominant rabbit. Avoidance is accomplished by the subordinate male slinking into vegetative cover to avoid a contact with the dominant.

D. — FIGHTING

Actual fighting was not observed in New England cottontails. Fighting is not considered a normal part of cottontail social behavior (Marsden and Holler, 1964: 15; McKinney, 1970). In one study (Marsden and Holler, 1964), fighting between eastern cottontails occurred when a strange male was introduced into the enclosure. These fights were of short duration and no physical harm was done. Fighting behavior was often observed in cottontails that were placed in small pens (Brenner and Flemming, 1979).

There are limited reports of fighting in other Sylvilagus. Blair (1936) reports that penned marsh rabbits may bite and slap opponents to defend themselves, and that both sexes fight one another. Ingles (1941) reports that fighting may occur in Audubon’s cottontails but it was not observed. Chapman and Verts (1969) reported on an aggressive encounter between a Brush rabbit and an Eastern cottontail in an enclosure which resulted in the death of the Brush rabbit.

Violent, aggressive, and long-lasting fights have been documented in the European wild rabbit. Mykytowycz (1958) observed one fight between two males which lasted 20 minutes and which occurred upon the introduction of a strange male into an enclosure.

VI. — SOCIAL STRUCTURE OF THE PEN POPULATION

A. — CONFINEMENT AND SHELTERING IN FORMS

New England cottontails hide or rest in small, body-sized cleared spots on the ground called forms. Forms are a shallow depression in the snow or ground surface, contoured to body shape. During periods of inclement weather, daylight hours, and periods of low social activity, rabbits were content to remain confined to their well-established forms. The forms of New England cottontails were all located within the cover of dense brush piles. When snow cover predominated, forms were simple bodyshaped melt spots. Each cottontail established a series of personal forms as resting spots used by that individual alone. Forms and their immediate surroundings were heavily laden with droppings.

The use of resting forms is well documented for most Leporid species. In the Sylvilagus the use of forms is reported for Audubon’s cottontails (Orr, 1940: 128), brush rabbits (Orr, 1940: 173), mountain cottontails (Orr, 1940: 105), swamp rabbits (Lowe, 1958), eastern cottontails (Dalke, 1942) and Tapeti, S. brasiliensis (Durant, 1981). In all species, the form acts as a hiding and resting place, frequently under the cover of dense brush and thicket.
The type of habitat cover present in a rabbit’s home range may influence the use of forms and or burrows in rabbits (Orr, 1940). Rabbits inhabiting areas of dense vegetative cover are likely to spend most of their hours above ground in forms under protection offered by the dense cover. Rabbits may resort to burrows or rock crevices in areas of low cover during periods of rest.

The use of burrows and the ability to dig these burrows is based on limited reports in the literature for Sylvilagus. Burrows inhabited by Audubon’s cottontails were often located away from brushy cover at the base of small trees. The building of burrows is generally attributed to animals other than the rabbit; however, Orr (1940 : 129) provides evidence of Audubon’s cottontail constructed burrow. The use of a burrow system by both young and adult mountain cottontails is reported by Orr (1940 : 106). The Pygmy rabbit (S. idahoensis) reportedly constructs its own burrow (Walker, et al., 1964).

Marsh rabbits reportedly use their long toe nails for digging holes, although they do not live in burrows (Tomkins, 1935). Eastern cottontails do not construct burrows, although they possess the ability to dig slanting nest chambers for young rabbits. Likewise, the New England cottontail, based on results from this study, do not construct burrows in which to live. The evidence, however, of two slanting nest chambers dug in the enclosure by S. transitionalis, indicates that the species does possess the ability to dig holes. In spite of the fact that neither S. floridanus nor S. transitionalis construct burrow systems of their own to live in, both species will make use of burrows as shelters when they are available.

Throughout the study, forms positioned in each of the three brush piles were favorite resting areas for New England cottontails. Several box shelters, which were provided for the animals, were not popular as resting spots. Each day, prior to observation, the daily resting form chosen by each rabbit was recorded. During the study period, each rabbit selected a particular form and was usually found there before watches. Following the 25 May 1980 removal of male MP2 the selection of a resting spot by the rabbits changed.

Rabbits resting in forms were not easily disturbed. When approached by an observer, rabbits remained very still and flushed only after considerable disturbance by an observer. Once flushed, rabbits would escape in a rapid zig-zag manner to another brush pile. Rarely did two males ever occupy the same brush clump simultaneously (Fig. 10).

B. — MALE SOCIAL RELATIONSHIPS

During this study, MR1 was dominant over male MP2. The individual’s rank was determined on the basis of the outcome of numerous aggressive interactions between the two. The relationship between male MR1 and male MP2 was clear, as male MR1 displayed 21 acts of dominance and none of subordinance during the initial phase from March 20 to May 25. Male MR1, alone, accounted for 100% of the dominant behavior between the two males and no reversals of rank were recorded. Marsden and Holler (1964 : 17) determined that the greatest challenge to a male’s social status, for both swamp rabbits and cottontails, was presented by the male immediately below him. This appeared to hold true for S. transitionalis as well.

Dominance hierarchies have been studied in other species of leporids. Marsden and Holler (1964) reported the existence of well-established dominance orders in both swamp rabbits and eastern cottontails. They
suggested that the male hierarchy was essential for prevention of reproductive fighting, especially during estrus periods. Their results are supported by later studies conducted with eastern cottontails (McKinney, 1970; Brenner and Flemming, 1979).

McKinney (1970) reported that social position was distinct among the two top-ranking males, but rather unclear among the remaining subordinate individuals. Brenner and Flemming (1979) support the findings of Marsden and Holler (1964) in respect to the function of social hierarchies in rabbits. Agonistic behavior by dominant rabbits serves to reinforce the dominance structure in the population, and also serves to reduce reproductive fighting and agonistic behavior in other members of the population.

The European wild rabbit also exhibits a dominance hierarchy in the male social organization (Mykytowycz, 1958). Within the hierarchy, all rabbits were found to chase their subordinates frequently, without provocation.
Experimental manipulations, with the social hierarchy of *Oryctolagus*, indicated that individuals of equal rank did not exist. The function of the hierarchy in *Oryctolagus* is undoubtedly similar to *Sylvilagus* in that it reduces reproductive fighting in the population through agonistic displays by dominant rabbits.

In this study, the dominant male MR1 would chase the subordinate male MP2 whenever the two individuals came into close contact in the enclosure. These displays of aggression by the dominant individual were usually brief chases with the dominant male rushing at the subordinate who had assumed a submissive posture. Following the rush of the dominant male, the subordinate male would retreat, followed by a short pursuit by the dominant male.

As estrus approached, chases among males became more frequent and of greater intensity. During this period, the dominant male MR1 would rush at male MP2 from distances of up to 4.5 m and begin the chase. At times, male MR1 appeared to watch for the subordinate male MP2 and attack him whenever the two came into visual contact. The subordinate moved cautiously during these periods and always retreated to either the A or B quadrant (Fig. 1). Aggressive chases between male swamp rabbits and eastern cottontails are reported in the literature and are similar to those recorded in New-England cottontails. Marsden and Holler (1964) found that on the night of parturition, aggressive chases between males became constant and continued until the termination of estrus. On some occasions, subordinate male MP2 was observed standing on the hindfeet and visually inspecting the enclosure as if he were looking for the dominant male MR1. This was done during periods of highly aggressive male chases.

Vocalizations were commonly used by the dominant male as he approached the subordinate individual. The dominant MR1 would approach in an alert-aggressive stance and emit the chatter-click in an easily audible tone. As the dominant approached closer, the vocalizing increased in volume as the subordinate was dislodged and chased away. Following this type of interaction, the aggressor would move off emitting a barely audible chatter vocalization.

C. — TERRITORIAL BEHAVIOR

New England cottontails did not display territorial defensive behavior. Male *S. transitionalis*, however, did exhibit a preference for certain areas (see Activity and Social Spacing) where most of their feeding, exploring, patrolling, and nesting took place. These areas were not defended territories and aggressive chases between males occurred irregardless of position in the enclosure. Behavioral modifications designed to aid in territorial defense, such as aggressive displays and scent marking, were not observed in *S. transitionalis*.

Aggressive behaviors developed for territorial defense (scratching and paw-raking) have been described for swamp rabbits and eastern cottontails (Marsden and Holler, 1964: 35). These aggressive behaviors were absent in the New England cottontail. Scent marking, which is another important means of territory marking in *O. cuniculus, S. aquaticus, and S. floridamus*, is poorly developed in *S. transitionalis*.

Territorial defense by the Swamp rabbit is limited to protection of an area surrounding a small breeding group of females (Marsden and Holler,
Aggression by dominant male swamp rabbits, directed toward subordinate individuals, occurred primarily in the area of the breeding group of females. Any subordinate male violating this area around the females was chased away; however, the same area in the absence of the breeding group would not be protected by the dominant male. The territory was a moving area of protection by the dominant male rabbit preventing individuals of lower social status from gaining access to females. Actual territorial defense of a breeding area was not observed in \textit{S. floridanus}; however, female cottontails on two occasions defended nest sites (Marsden and Holler, 1964). Dominant male cottontails in that study defended areas around females irregardless of their position in the enclosure.

Male \textit{O. cuniculus} display a variety of territorial behaviors and scent markings to establish and maintain territories. Aggressive behavior and scent marks are used extensively by dominant male European wild rabbits to exclude subordinates from certain areas. According to Mykytowycz (1958), dominant males acted as if they «controlled» areas and features of the warren and either tolerated or excluded subordinates from these areas.

D. — \textit{MOVEMENTS OF NEW ENGLAND COTTONTAILS}

The New England cottontail was very discreet and cautious with its movements about the enclosure. The cautious nature and secretive manner of this rabbit have been reported previously (Chapman, 1975a). In the enclosure, the rabbit utilized patches of dense cover most frequently. During the evening observation periods, both males and females moved about very discreetly; rarely venturing far from some dense form of vegetative cover. Dense clumps of ferns (Polypodiaceae) occurred throughout the enclosure and were utilized extensively by the rabbits. Cottontail would move from clump to clump as the evening activity period progressed.

Extended periods of stillness often occurred during the evening observations as an individual assumed a roosting posture among ferns. This posture offered excellent concealment for the cottontails. On occasions when clear, cool weather conditions offered seemingly ideal conditions for foraging and exploration, \textit{S. transitionalis} preferred to remain concealed in forms, moving only very little in a shy manner, always close to cover.

Path usage is an important aspect in the spacing and social behavior of animals (Mykytowycz, 1972). In home ranges and territories, pathways establish recognizable, standard patterns of movement which can be rapidly negotiated by animals when danger threatens. The patrol pathway in the New England cottontail pen was well-trodden with lookout and dung posts, upon which rabbits would sit for extended periods of time to survey the pen. Additional paths between brush piles were used extensively by the rabbits in fleeing to escape cover. We observed rabbits fleeing danger by running along the edge of obstacles, brush, or vegetation until they reached an opening or pathway and darted away along it.

\textit{O. cuniculus} evidently places great confidence in pathways throughout the home range (Mykytowycz, 1972). European wild rabbits apparently choose a pathway and follow it blindly, irrespective of any obstacles placed in the path. Taking advantage of this fact, Mykytowycz (1972) was able to capture rabbits escaping toward burrows with long handled nets placed across the pathways.
VII. — USE OF THE SENSES

New England cottontails were often observed using the senses of hearing and smelling to guide them in their movements. During explorations, both sexes were especially attentive to auditory and olfactory cues from the surrounding environment. On several occasions, during exploration, *S. transitionalis* was observed with its nose in the air sniffing in a 180°-360° degree circle. Hearing was also used as rabbits would stop during exploration to rotate the ears alertly, being extremely attentive to other noises.

A. — ACTIVITY AND SOCIAL SPACING

New England cottontails showed an affinity for particular areas in the enclosure. These regions, which we denoted as areas of concentrated activity, were those areas where an individual rabbit spent the majority of time feeding, exploring, patrolling, and resting. These areas of concentrated activity should not be confused with territories, as they were not protected areas. The division of space, evidenced by these areas, was vital for the maintenance of the social organization which was controlled by the dominant pair, male MR1 and female FG1.

In calculating a male's activity area, patterns of concentrated activity became evident. There was considerable range overlap between the two males, in spite of their distinct preference for particular areas. During the initial phase of the study (March 20 to May 25), male MR1 spent a majority of his time (76.8%) in quadrants C and D, while spending only a minor portion (24.2%) in quadrants A and B. In the same period, male MP2 spent a majority of the time (82.1%) in quadrants A and B, and a minor portion (18.1%) in quadrants C and D (Fig. 11).

Both males spent their time feeding, grooming, resting, or exploring their respective areas in addition to social contacts with the female rabbit. During periods of high reproductive activity, the range restrictions of males were less evident as they pursued the estrus female.

Female FG1 displayed an area of concentration which appeared to shift during the initial phase of the study (March 20 to May 25). During March and April, FG1 concentrated 72.1% and 63.6%, respectively, of her activity in quadrants A and B. During May, however, her activity concentration area shifted into quadrants C and D where she spent a total of 64.1% of her time. This shift was evident from changes in daytime resting locations, grazing spots, grooming locations, explorations, and patrols. In May, the range of the female correlated with that of the dominant male MR1, while earlier her range was more closely correlated with the subordinate male MP2. During May several consorts were recorded between the dominant male MR1 and the female FG1 in the C and D quadrants (Fig. 11).

Other studies have shown how the range of the dominant male and female seem to be correlated (Marsden and Holler, 1964: 18). In swamp rabbits, a male's social status was closely tied with a female's activity area, as subordinate males were usually excluded from areas used by females.

The number of contacts and interactions between individual cottontails is useful for evaluating social relationships between individuals in a population (Marsden and Holler, 1964: 19). A contact is described here as the number of times a male cottontail encounters a female in the enclosure while each specific
behavioral act following the contact constitutes a single interaction. This provides a means for evaluating both the number of contacts and the intensity of the contact between a male and female. The intensity can be expressed as the number of interactions per contact.

For eastern cottontails and swamp rabbits, Marsden and Holler, (1964: 33) suggested that a relationship exists between male social status and the amount of contact with females. In their study, the dominant male was usually able to maintain contact with an estrus female by chasing away or dislodging subordinates. They also believed that the number-two male was frequently as effective in contacting and interacting with estrus females at the time of peak synchronous reproduction. Together the dominant and the number two male accounted for the majority of male-female contacts and interactions. In spite of this fact, the dominant males accounted for most of the copulations.

In New England cottontails, the relationship between the female and two males is much like that described for swamp rabbits and eastern cottontails.
The dominant male succeeded in maintaining contact during estrus by chasing and dislodging his subordinate. On several occasions, however, the subordinate male succeeded in making contacts with the female, although few were tolerated by the dominant male during peak estrus periods. During periods of high female receptivity, it was the dominant rabbit that made most of the contacts and interactions, while the subordinate male was chased and excluded from these activities.

During the months of March and April, female FG1 was closely associated with the range of male MP2. In that period, male MP2 enjoyed slightly more of the contacts and interactions with female FG1 (Tables III and IV). In March, male MP2 accounted for 70% of the contacts and 75.6% of the interactions compared to 30% of the contacts and 24.3% of the interactions for male MR1 during the same period. In April, the number of contacts and interactions between the two males were equal with each male accounting for 50% of the contacts and interactions with the female.

**TABLE III**

*Summary of male contacts and interactions with female FG1 during the 1980 breeding season.*

<table>
<thead>
<tr>
<th>Month</th>
<th>Number contacts</th>
<th>% Total</th>
<th>Number interactions</th>
<th>% Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>MR1</td>
<td>MP2</td>
<td>MR1</td>
<td>MP2</td>
</tr>
<tr>
<td>February</td>
<td>0</td>
<td>1</td>
<td>—</td>
<td>100</td>
</tr>
<tr>
<td>March</td>
<td>6</td>
<td>14</td>
<td>30</td>
<td>70</td>
</tr>
<tr>
<td>April</td>
<td>6</td>
<td>6</td>
<td>50</td>
<td>50</td>
</tr>
<tr>
<td>May</td>
<td>14</td>
<td>6</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>June</td>
<td>9</td>
<td>*</td>
<td>100</td>
<td>—</td>
</tr>
<tr>
<td>July</td>
<td>4</td>
<td>—</td>
<td>100</td>
<td>—</td>
</tr>
<tr>
<td>August</td>
<td>5</td>
<td>—</td>
<td>100</td>
<td>—</td>
</tr>
<tr>
<td>Totals</td>
<td>44</td>
<td>27</td>
<td>18</td>
<td>54</td>
</tr>
</tbody>
</table>
* MP2 found dead, removed from pen.

**TABLE IV**

*Pattern of male contacts and interactions with female FG1 during the period February 16 to May 25, 1980.*

<table>
<thead>
<tr>
<th>Male</th>
<th>Number contacts</th>
<th>% Total</th>
<th>Number interactions</th>
<th>% Total</th>
<th>Number copulations observed</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>MR1</td>
<td>26</td>
<td>49</td>
<td>50</td>
<td>48</td>
</tr>
<tr>
<td></td>
<td>MP2</td>
<td>27</td>
<td>51</td>
<td>54</td>
<td>52</td>
</tr>
<tr>
<td>Totals</td>
<td>53</td>
<td>100</td>
<td>104</td>
<td>100</td>
<td>3</td>
</tr>
</tbody>
</table>
* Early March.
During May a reverse trend became evident where male MR1 accounted for 70% of the contacts and 70% of the interactions with the female. In this same period, the area of concentration of FG1 shifted into quadrants C and D where she spent 64.1% of her time (Fig. 11). The activity of the female during this latter phase was closely allied with male MR1 who also spent the majority of his active time in quadrants C and D.

The two consortees displayed a mutual tolerance for one another but neither showed any tolerance for subordinate male MP2 who was constantly chased away by one of the consort members. The subordinate male was usually far removed from the consort pair and spent the majority of his periods in quadrants A and B, feeding and exploring.

Male MP2 died and the corpse was removed on May 25. The removal of this individual prompted both male MR1 and female FG1 to undergo another range shift. In June, male MR1 spent most of his active time in quadrants A and B (77.7%) (Fig. 11). These quadrants had previously been used extensively by male MP2. Daytime resting areas, grazing areas, and exploration all seemed to confirm this shift of movement by male MR1. Female FG1 also shifted her active range into the A and B quadrants following the removal of male MP2, where she spent 83% of her active time (Fig. 11).

Consorts between male MR1 and female FG1 were a commonplace occurrence throughout the remainder of the study. Consorts were most common during periods of low socio-reproductive activity, between estrus peaks; consorts became less frequent and finally disappeared when estrus approached very near. A dramatic increase in the female’s intolerance toward the male’s presence in her immediate area became quite obvious at this time.

B. — **DAILY ACTIVITY, SOCIAL ACTIVITY RHYTHMS, AND THE ONSET OF ESTRUS**

The number of interactions which occurred between individuals of the population varied greatly from night to night throughout the study. Some observation periods, held when very little reproductive behavior was expected, showed a low intensity of activity between the population members. The number and intensity of social interactions increased dramatically with the onset of estrus in March, and with the approach of each successive post-partum period throughout the 1980 breeding season. The number of male/female interactions occurring per hour of observation from 16 February to 1 September 1980 is illustrated in Fig. 12.

The onset of estrus occurred 20 March, during an observation period where ten interactions per hour were recorded. During this period of sexual awakening, the intensity of the reproductive behavior observed was the greatest recorded during the entire study. Reproductive chases, jumps, and copulations together with extensive testing of the male’s dominance structure, predominated during the period. Social and reproductive behavior remained high during the next six days in spite of the pregnancy of female FG1. On 26 March, female FG1 became highly aggressive towards the approaches of male rabbits and most of the encounters at this time were aggressive in nature. Social activity remained very low during the next two weeks until 9 April when the first reproductive dislodgements were recorded. The first litter was born on 11 April, and the first post-partum estrus period, with successful copulation, occurred following parturition.
Figure 12. — Social activity and reproductive rhythms for *Sylvilagus transitionalis* during the 1980 season based on the number of male/female interactions per hour of observation. A, onset of estrus; B, first post-partum estrus; C, second post-partum estrus; D, third post-partum estrus; E, reproductive behavior associated with no post-partum estrus. (Based on 67 observation periods totalling 107.25 hours).

VIII. — REPRODUCTION

During the course of the study female FG1 produced 3 litters. Litters of 4, 6, and 5 were produced (Table V). No litters were produced after the third litter on 6 June 1980. Following the estrus period on 6 June, warm, humid weather persisted at the study site throughout June and into July which may have had some effect on the breeding individuals. Definite periods of estrus activity were recorded following 6 June at regular 28-30 day intervals, although no successful copulations occurred.

**Table V**

*Productivity of female FG1 during the 1980 breeding season.*

<table>
<thead>
<tr>
<th>Litter</th>
<th>Date of birth</th>
<th>Litter size</th>
<th>Sex ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>04/11/80</td>
<td>4</td>
<td>3 males, 1 female</td>
</tr>
<tr>
<td>2</td>
<td>05/09/80</td>
<td>6</td>
<td>3 males, 3 females</td>
</tr>
<tr>
<td>3</td>
<td>06/06/80</td>
<td>5</td>
<td>3 males, 2 females</td>
</tr>
</tbody>
</table>

Total production 1980 season 15 9 males, 6 females

\( \bar{x} = 5 \)
A. — THE ESTRUS CYCLE, PARTURITION, AND POST-PARTUM BREEDING

Reproductive behavior, indicating the onset of estrus, appears two to three days prior to parturition and post-partum estrus. This period is characterized by an increase in male interest in the female, and other visible changes in female behavior. A recognizable sequence of events leading to post-partum estrus was observed for the female S. transitionalis in this study. This was a regular pattern of behaviors which were used to identify reproduction in this rabbit that occurred at regular intervals throughout the breeding season.

Many investigators have observed nest construction in the eastern cottontail. Casteel (1966) indicated that nest construction was completed just prior to parturition while Dalke (1942) and Beule (1940) indicated that nests were constructed and lined three days prior to parturition. Marsden and Holler (1964:16) indicate that females began to show nest building behavior two or three days prior to estrus.

Nest construction in New England cottontails began 24 to 48 hours prior to parturition. That is to say, the nest chamber was constructed during this time and some scanty lining added. Full lining of the nest with fur occurs minutes before the parturition sequence.


B. — GESTATION

During the breeding season, two periods of gestation were monitored from the point of conception until parturition occurred. These periods were both 28 days in length. Three other periods of exceptionally high reproductive activity, when copulation was unsuccessful, occurred at regular 28 to 30 days periods throughout the season (Table VI).

Thus, the gestation period of S. transitionalis is 28 days and confirms the work of Dalke (1942) who observed a litter of four born 28 days after conception. The gestation period in New World rabbits varies from 27 days in S. floridanus to 42 days in S. brasiliensis (Chapman, 1984).

TABLE VI
Breeding chronology for female FG1 during the 1980 breeding season.

<table>
<thead>
<tr>
<th>Period</th>
<th>Date</th>
<th>Event</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>03/18 to 03/20/80</td>
<td>First estrus</td>
</tr>
<tr>
<td>2</td>
<td>04/11/80</td>
<td>First litter produced, first post-partum estrus</td>
</tr>
<tr>
<td>3</td>
<td>05/09/80</td>
<td>Second litter, second post-partum estrus</td>
</tr>
<tr>
<td>4</td>
<td>06/06/80</td>
<td>Third litter, third post-partum estrus unsuccessful</td>
</tr>
<tr>
<td>5</td>
<td>07/09/80</td>
<td>Estrus behavior evident, no litter, or copulation</td>
</tr>
<tr>
<td>6</td>
<td>08/06/80</td>
<td>Estrus behavior evident, no litter, or copulation</td>
</tr>
</tbody>
</table>
C. — Estrus Sequence

The onset of estrus and first conception, and two subsequent post-partum estrus periods were observed and recorded for *S. transitionalis*. In addition, three other periods of high reproductive behavior were observed in which certain phases leading to estrus were identifiable. The following account is the composite description of these individual observations.

The male's interest in the female increases noticeably two to three days prior to estrus. During this first phase of the estrus cycle, the male rabbit began to accompany the female. Most often, the dominant male would attempt to maintain close contact with the female, commonly forming a consort with this rabbit. This behavioral change in male rabbits (towards interest in the female) that follows a period of male disinterest in females is quite an abrupt change.

The dominant male (MR1) was often observed close by or just outside the female's form before she began her activity period. A male was often observed following the female at this time as she moved about feeding and exploring. Males, however, did not attempt to approach the female since such an attempt was met with a great deal of female aggression. The most common behavioral interaction between the dominant male and female at this time was following. Female *S. transitionalis* were highly aggressive towards males during this phase of the cycle. Reproductive dislodgement was common as the aggressive female dislodged a male who was attempting to form a consort with her. Reproductive dislodgement during this phase occurred as: male approach; male/female face off; female threat posture; male submissive posture; female charge; male retreat. The female often pursued the male only a short distance and then gave up the chase (Fig. 13). Butting the head of the male by the female occurred on occasion. In spite of female aggression, males were persistent in attempts to form a consort with the female. Dislodgements were frequent during this period, occurring at a frequency of one to three per hour, or whenever the male and female come into contact. The persistence of the dominant male rabbit during this phase was obvious.

Vocalizing by the female was common during this phase. Persistent males nearby caused the female to emit continuous loud chatter-click sounds. There was a minimum distance (2 to 3 meters) at which the female would begin to vocalize continuously until the male had either moved off or been dislodged by the female. This occurred when the female's minimum individual distance (Hediger, 1955) was violated by male rabbits and caused aggression by the female. Zoloth (1969) reported a minimum distance for brush rabbits when feeding of 30 cm. New England cottontails in consort display an individual distance of 60 cm; any closer an aggressive behavior results. During initial phases of reproduction, the female maintains an even greater personal individual distance resisting male advances with aggression at two to three meters. This type of behavior may serve to heighten male excitement and interest in females at this time.

The female *S. transitionalis* moved with quick jerky motions during this initial phase of estrus, often exhibiting unusual patrolling behavior. Prior to the first reproductive dislodgements, this nervous activity was the first sign that the female was nearing estrus. Unusually intensive patrols were often recorded as the female ran nervously along the entire perimeter of the enclosure peering outside the pen.
A second phase in the estrus sequence involved nest lining, parturition, and first feeding of the kittens. When parturition was imminent, the female would move to her previously constructed nest, while pulling fur from the back and sides. In the Eastern cottontail, Casteel (1966) determined that hair was pulled from the shoulders, flanks, back, legs, and feet, but never from the abdomen. Fur was then mixed with bits of leaf litter. The nest was then ready to receive the litter of kittens.

Following the nest lining phase, parturition was imminent. For eastern cottontails, the hair pulling phase of nest construction is reported to be abrupt and usually indicated that parturition was very near (Casteel, 1966). During parturition, the female S. transitionalis lowered her body onto the nest opening and was barely visible at this time. During the sequence, the mother frequently looked down to examine herself or the newborn kittens. The mother appeared alert to happenings in the surrounding environment as she kept watch from the nest burrow.

Following parturition, an initial feeding of the kittens occurred. Here again, the mother kept constantly checking the kittens during the feeding period.

After feeding was completed, the kittens were licked individually by the mother and placed into the nest chamber with her nose. A thick inner cap of fur was stuffed into the opening first. This apparently provides insulation for the newborn rabbits (Fig. 14).

Finally, the nest chamber is covered by the mother with an external cap of dead leaves and twigs which she designs with her front feet. The surrounding leaf matter was scratched over the nest first and later tramped down by the female. Very little fur was mixed with this outer cap. Camouflage of the nest chamber is extremely efficient. The total time recorded to complete parturition, first feeding, and nest covering was 15 minutes.

Male S. transitionalis do not interfere with the birth process. Their excitement reaches a peak when the female leaves the nest and the post-partum estrus period begins.

After leaving the nest, the female was chased by the excited males. Two- and three-way reproductive chases were common at this time. A reproductive chase occurred any time a male rabbit discovered the estrus female. When the dominant male could isolate the female, several intensive reproductive interactions usually followed.

Males often attempted to mount the estrus female on the move as she retreated following a reproductive interaction. These were unsuccessful attempts occurring just prior to successful copulation. Following the copulation, both partners moved off to familiar areas of the pen to either feed

Figure 13. — Reproductive dislodgement sequence in Sylvilagus transitionalis. A. Male approaches female in alert posture — the female feeding responds with a face-off. B. Following the face-off the female assumes a threat posture — male responds with submissive posture. From this position, the female makes her charge and « butt » of the male « dislodging » him from his submissive posture. In the charge the female moves directly at the male. C. Female charges at male from threat posture, sometimes she butts the male when he does not retreat quickly enough. Following the charge and butt the female stops to sniff the vacated spot and does not chase the male further (occasionally a short chase of less than 1 meter occurs). D. Once the male rabbit has been dislodged, the female sniffs the space formerly occupied by the male and the sequence ends.

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or groom themselves. The males seemed to rapidly lose interest in the female at this time. Also, the frequency of male/male interactions dropped off very quickly, within one-half to one hour of the copulation.

Estrus ends as the female moves off into one of her identified feeding areas unpursued by males. At this time she feeds, grooms, or explores. It is interesting to note that the ranges of the male cottontails, which appear fairly rigid prior to estrus activity, seem to be forgotten in the estrus excitement. During this time both males ranged over the entire enclosure, both equally in pursuit of the female.

The female’s rapid return to aggressive behavior occurred within 24 hours of the termination of estrus. Displays of reproductive dislodgement occurred whenever a male and female came into contact. This was the best indication that estrus had ended. Males, at this time, avoid the female and her aggressive nature and also return to their normal areas of concentrated activity in the enclosure. The intensity of social behavior dropped off dramatically during these periods following estrus with very few or no male/female interactions recorded during evening observations. Male/male interactions also were reduced dramatically. Most activity during this period included feeding, grooming, or exploring of the enclosure.
As the gestation of the female proceeded she became less aggressive toward the dominant buck. Consorts between male MR1 and female FG1 were common. At the same time, female FG1 showed very little tolerance for the subordinate male MP2. At all times, except for peak estrus excitement, when a male and female New England cottontail came into contact, the female was dominant and the male gave way.

D. — FEEDING THE KITTENS

The female New England cottontail was observed at the nest feeding the kittens only once per day. This usually occurred just prior to dusk or just after dark. The mother would approach the nest very slowly and cautiously. The area was first inspected visually and any male cottontails in the vicinity of the nest were chased away. Feeding of the kittens was not observed during the morning watches.

The lactation sequence, observed a number of times, took approximately 12 minutes to complete. The mother would approach the nest in an alert posture being very attentive to the nest site. The nest cap was first removed with the forefeet and the nestlings were removed from the chamber and arranged with the mouth. The mother then squatted over the kittens in a form which had been created in front of the nest burrow.

At the conclusion of the period, the mother began grooming the abdomen and mammae. Kittens are replaced into the chamber with the mouth. The nest cap is finally replaced with the front paws and the mother moves off. Male cottontails showed very little interest in the female during this time and did not bother the mother while feeding the kittens at the nest.

E. — NESTS

Two nests were constructed by the female *S. transitionalis*. The first and second litters were produced in the same nest and the third litter was produced in a new nest. Both nests were located in fairly open cover, against a stump, suggesting a preference by *S. transitionalis* for that situation. Beule and Studholme (1942) reported that most *S. floridanus* nests in orchards or wooded areas were located at the base of a tree or stump.

The nest chamber, constructed and used for litters 1 and 2, was a burrow-like chamber excavated by the mother. The dimensions of the cavity were 13 cm wide, 15 cm long, and 11 cm deep. Other investigators have described nest cavities for *S. floridanus* which are hollow depressions in the ground surface (Dalke, 1942; Beule, 1940; Casteel, 1966). Casteel (1966) measured 21 *S. floridanus* nests in Illinois and determined that the average measurements for the nests were 10 cm deep, 12 cm wide, and 15 cm long. Other investigators have reported similar measurements for the eastern cottontail nests (Linder and Hendrickson, 1956). No previous records for nest size dimensions of *S. transitionalis* have been reported. The nest containing the third litter was not a chamber but a surface depression constructed up against a black locust stump. The measurements of this nest were 17 cm wide, 11 cm long, and 9 cm deep. The construction of the burrow-type nest indicates at least limited digging by this species.

Casteel (1966) reported that no apparent relationship existed between the size of the excavation and the size of the litter for 12 nests he tested; in this
study, litters of 4, 5, and 6 were produced in nests with very similar measurements.

Orientation was recorded for the *S. transitionalis* nests in the study. Litters 1 and 2 were born in a nest with a northern facing direction (352°). Litter 3 was born in a nest opened at a southerly direction (184°). Both nests were built up against old stumps. The soft soil and humus underneath the stump allowed easy digging. The inside of the chamber was adequate in size for tiny kittens (1-7 days old), but older kittens rapidly outgrew the chamber.

The location of the nest was very well hidden by the mother. We located the nests by observing parturition or by observing suckling. The nest cap was made up primarily of leaves with twigs and a tiny amount of fur mixed in. Very little fur was obvious from the surface (Fig. 14 A). Upon removing the cap, the opening of the chamber was stuffed with one-half to one inch of grey fur providing both insulation and protection for the kittens (Fig. 14 B).

The nests of other *Sylvilagus* vary considerably. For example, the nests of *S. brasiliensis* are elaborate surface structures consisting of covered birth chambers and a series of runways. The nest chambers are lined with grass and often placed between two clumps of vegetation (Chapman and Willner, 1982). Other *Sylvilagus* such as the Pigmy rabbit *S. idahoensis* use excavations for their nesting structures (Chapman *et al.*, 1982).

**F. — NESTLINGS**

Young cottontails appeared to be very secretive in their movements about the enclosure in much the same manner as the adults. Movement of kittens was very limited and individuals confined their movements primarily to their daytime resting forms and a small area around these. It was common for two or three kittens from the same litter to remain together for three or four weeks. Throughout this period young rabbits never ventured very far from secure escape cover; in this case, brush piles. Young eastern cottontail kittens, in a similar study, are reported to have noticeably different behavior patterns (Bruch and Chapman, 1983), frequently playing and feeding boldly out in open areas of the pen a good distance from escape cover.

Playing behavior was often recorded for young *S. floridanus* by Marsden and Holler (1964). Playing behavior was never recorded in young New England cottontails. The reclusive, secretive nature of young *S. transitionalis* cannot be over-emphasized. The movements and behaviors of these young rabbits were often difficult to observe as they remained confined for a majority of the evening observation periods.

Young kittens, when handled, often emitted loud distress cries. This vocalization by the young usually caused the mother to frantically exit her daytime form to investigate. The adult female, on more than one occasion, charged at the observers at the sound of a kitten’s distress cry.

This behavior indicates some communication between parent and offspring, with a degree of parental care by female *S. transitionalis* suggested. The distress sound did not affect male New England cottontails. During one inspection of a nest, several 11-12 day-old kittens escaped from a holding bag and began to run throughout the pen, some squealing. This excitement brought the mother to an attempted rescue as she tried to corral and carry the young rabbits off in her mouth. The awkward size of the kittens prevented the rescue attempt, in spite of the mother’s persistence. Rongstad (1966) reported that
kittens 16 days of age or older responded to the distress cries of litter mates by crawling out of the nest and scattering in all directions. This was also observed in young *S. transitionalis*. The distress cry of one individual often caused others still in the nest to become restless and begin to scatter throughout the pen. This may increase the survival of ten-day-old litters which might escape an intruding predator. Beule (1940) also reported that squealing by young eastern cottontails induced some adult females to approach as if to protect them. This also suggests a degree of parental care.

On one other occasion, distress cries from kittens brought the mother charging out of her form. After retreating to a form near the dominant male (MR1), she began to chase this male. An extremely aggressive chase of ten-second duration resulted with the mother seemingly redirecting her aggression towards this male. Both individuals eventually retreated to their daytime resting forms.

Kittens and adult rabbits seldom interacted. After leaving the nest, the mother and kittens were not observed together. In one instance a 12-day-old rabbit, which had just left the nest, was confronted by the subordinate male (MP2). The adult seemed to be following after and pushing the young kitten from behind. The mother was not seen at this time. Once the kittens had left the nest, distress cries seemed to have little effect on the mother rabbit. Young rabbits, who were often captured for measuring after they had left the nest, emitted distress cries which had no apparent effect upon the mother. For a discussion of the growth and development of nestlings see Tefft and Chapman (1983).

SUMMARY

The social and reproductive behavior of the New England cottontail, *Sylvilagus transitionalis* (Bangs) was studied between January 1980 and September 1980. The behavioral repertoire of the rabbit is divided into non-social and social behavior. Non-social behavior is commonly observed behavior of lone rabbits. Social behavior includes basic postures, vocalizations, movements, reproductive interactions and dominant-subordinate interactions of adult males and females. The basic behavioral patterns of *S. transitionalis* are stereotyped and ritualized, much like behavioral patterns reported for some other Leporids. Many of the behavior sequences and postures are illustrated.

The development and maintenance of a social organization in a population of three adult New England cottontails (two males, one female) is presented in detail. The onset of estrus occurred between 12 and 18 March for the 1980 breeding season. Access to the female, and reproduction, was regulated by the formation of a dominance order in the males. Estrus activity was observed at five periods throughout the breeding season. Intervals between estrus periods were characterized by little social interaction.

The reproductive, nesting, and nestling behavior of *S. transitionalis* is described. Reproductive behavior signaling the onset of estrus appears two to three days prior to parturition and post-partum breeding. A regular, recognizable sequence of events precedes post-partum breeding in this rabbit. Three successful litters of *S. transitionalis* were produced in the enclosure during the breeding season. Methods of nest construction and behavior of the young are described.
The behavior of adult and juvenile *S. transitionalis* is contrasted with published available data on behavioral patterns and postures of other rabbits, including: *S. floridanus, S. aquaticus, S. nuttallii, S. aubudonii, S. palustris, S. bachmani, S. idahoensis, S. brasiliensis, Oryctolagus cuniculus, and Romerolagus diazi*.

RÉSUMÉ

Le comportement social et reproducteur du Lapin de Nouvelle Angleterre (*Sylvilagus transitionalis*) a été étudié en conditions semi-naturelles, de Janvier à Septembre 1980, dans le Maryland.

Le répertoire comportemental de l’espèce est décrit en détail, et comparé à celui de neuf autres lapins du Nouveau Monde appartenant aux genres *Sylvilagus* et *Romerolagus*.

ACKNOWLEDGEMENTS

The authors are grateful to George A. Feldhamer, Kent B. Fuller, James Howard and Gale R. Willner for reviewing the manuscript and making many helpful suggestions. The field assistance of David Bruch and Janet Tefft is also gratefully acknowledged. Marcia Faulhaber and Lynne Howard typed the manuscript and Dr. Dan M. Harman prepared the illustrations. This publication is based in part on a thesis submitted to Frostburg State College by B. C. Tefft in partial fulfillment for the Master of Science degree in Wildlife Management. The initial draft of this paper was prepared while Joseph A. Chapman was at the Appalachian Environmental Laboratory, University of Maryland. The final drafts of this paper were prepared while Joseph A. Chapman was a visiting professor in the Departamento de Biologia, Universidade de Los Andes, Merida, Venezuela, and Professor and Head of the Department of Fisheries and Wildlife, Utah State University, Logan, Utah 84322-5210, U.S.A. The Ecology Center, Utah State University provided funds to cover the costs of publication.

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