Systematics and Biology of the Woodland Jumping Mouse, *Napaeozapus insignis*

ROBERT E. WRIGLEY

ILLINOIS BIOLOGICAL MONOGRAPHS

Volumes 1 through 24 contained four issues each and were available through subscription. Beginning with number 25 (issued in 1957), each publication is numbered consecutively. No subscriptions are available, but standing orders are accepted for forthcoming numbers. Prices of previous issues still in print are listed below, and these may be purchased from the University of Illinois Press, Urbana, Illinois 61801. Microfilm and photo-offset copies of out-of-print titles in the Illinois Biological Monographs are available from University Microfilms, Inc., 300 North Zeeb Road, Ann Arbor, Michigan 48106, and the Johnson Reprint Corporation, 111 Fifth Avenue, New York, New York 10003.

Balduf, W. V. (1959): Obligatory and Facultative Insects in Rose Hips. 12 pls. No. 26. $3.50.

Brandon, Ronald A. (1966): Systematics of the Salamander Genus *Gryinophilus*. 23 figs. No. 35. $4.50.

Campbell, John M. (1966): A Revision of the Genus *Lobopoda* (Coleoptera: Alleculidae) in North America and the West Indies. 174 figs. No. 37. $5.75.

Jones, George Neville (1968): Taxonomy of American Species of Linden (Tilia). 6 pls. 52 halftones. No. 39. $5.95.

Langebartel, David A. (1968): The Hyoid and Its Associated Muscles in Snakes. 19 figs. No. 38. $4.95.

Levine, Norman D., and Virginia Ivens (1965): The Coccidian Parasites (Protozoa, Sporozoa) of Rodents. 2 figs. 48 pls. No. 33. $7.50.

Levine, Norman D., and Virginia Ivens (1970): The Coccidian Parasites (Protozoa, Sporozoa) of Ruminants. 61 pls. No. 44. $8.50.

List, James Carl (1966): Comparative Osteology of the Snake Families Typhlopidae and Leptotyphlopidae. 22 pls. No. 36. $13.75.

Morgan, Jeanne (1959): The Morphology and Anatomy of American Species of the Genus Psaronius. 82 figs. No. 27. $3.00.

Northcutt, R. Glenn (1970): The Telencephalon of the Western Painted Turtle. 19 figs. No. 43. $5.95.

Pinto, John D., and Richard B. Selander (1970): The Bionomics of Blister Beetles of the Genus *Meloe* and a Classification of the New World Species. 198 figs. No. 42. $10.00.

Ray, James Davis, Jr. (1956): The Genus Lysimachia in the New World. 20 pls. 11 maps. Vol. 24, Nos. 3-4. $2.50.

Rominger, James M. (1962): Taxonomy of *Setaria* (Gramineae) in North America. 6 pls. 15 maps. No. 29. $4.50.

Ross, Herbert H., and William E. Ricker (1971): The Classification, Evolution, and Dispersal of the Winter Stonefly Genus *Allocapnia*. 111 figs. No. 45. $8.95.

Sawyer, Roy T. (1972): North American Freshwater Leeches, Exclusive of the Piscicolidae, with a Key to All Species. 37 figs. No. 46. $8.50.

Selander, Richard B. (1960): Bionomics, Systematics, and Phylogeny of *Lytta*, a Genus of Blister Beetles (Coleoptera, Meloidae). 350 figs. No. 28. $4.50.

Selander, Richard B., and Juan M. Mathieu (1969): Ecology, Behavior, and Adult Anatomy of the Albida Group of the Genus *Epicauta* (Coleoptera, Meloidae). 60 figs. No. 41. $5.95.

Stannard, Lewis J., Jr. (1957): The Phylogeny and Classification of the North American Genera of the Suborder Tubulifera (Thysanoptera). 14 pls. No. 25. $2.50.

Unzicker, John D. (1968): The Comparative Morphology and Evolution of the Internal Female Reproductive System of Trichoptera. 14 pls. No. 40. $3.95.

Systematics and Biology of the
Woodland Jumping Mouse,
Napaeozapus insignis

Systematics and Biology of the Woodland Jumping Mouse, *Napaeozapus insignis*

ROBERT E. WRIGLEY

ACKNOWLEDGMENTS

CONTENTS

I. INTRODUCTION

The woodland jumping mouse, *Napaeozapus insignis* (Family Zapodidae), is a brightly colored rodent with a long white-tipped tail and elongate hind limbs, occurring in eastern Canada and northeastern United States. The species was last revised in 1899 by Preble, who recognized three geographic races based on 135 specimens. Four additional subspecies have subsequently been described, with a rather inadequate knowledge of populational variation since few specimens were available. The objectives of the present systematic study were to investigate age, individual, and secondary sexual variation within populations, and to analyze clinal and nonclinal geographic variation exhibited by the species. These data formed the basis for a systematic revision of the genus *Napaeozapus*. Morphological data, including original work, were reviewed in a comparative study of *Napaeozapus* with related genera.

The preferred habitats of *Napaeozapus* are streambanks and forest-edge sites, within spruce-fir and hemlock-hardwood forests. The species is relatively rare, highly localized in distribution, and a profound hibernator; hence habitat relationships and life history are relatively little known. The ecological study attempted to define the factors limiting local and geographic distribution and to summarize information presently known on life history, including personal observations and the literature.

1

II. METHODS AND MATERIALS

The systematic study was based on 2,529 conventional museum specimens. Total length, tail length, and hind foot length were recorded from specimen labels, and cranial measurements were taken with dial calipers to one-tenth of a millimeter. The methods used in measuring the skull were similar to those used by Krutzsch (1954:352-353) on *Zapus,* with the following exceptions:

Condylobasal length. — Distance from the anterior surface of the incisors where they meet the premaxillary plate to the posterior border of the occipital condyles.

Nasal length. — Distance from the anterior projection of the nasals to the posteriormost projection of the nasofrontal suture.

Rostral breadth. — Distance across the rostrum at the anterior border of the premaxillary-maxillary suture, viewed dorsally.

Bony palate length. — Distance from the posterior border of the incisive foramen to the anterior point of the postpalatal notch.

Maxillary toothrow length. — Distance between the anterior and posterior margins of the alveoli of the first and third upper molars, respectively.

The hyoid apparatus, phallus, and baculum were studied in specimens preserved both in alcohol and in the dry state. These structures

were cleared in 4% KOH, stained with Alizarin Red, and stored in glycerin. The technique used for processing bone marrow for chromosomes was that of Lee (1969).

Geographic variation in morphology was studied by preparing iso-phene maps for each of the three external and twelve cranial characters. To obtain larger-sized groups as samples, the specimens from numerous localities were combined into 114 grouped localities. This method revealed clinal and nonclinal variation and regions of rapid change in characters. Subspecific units were determined on the basis of areas of character discontinuities obtained by superimposing the 15 isophene maps, and by analyzing color variation in the specimens.

Ecological data on *Napaeozapus* were collected during field studies over a period of five years. Though much of the work was centered in southern Quebec, field trips were made to Laurentides Park and the Gaspé Peninsula in Quebec, Prince Edward Island, Nova Scotia, New York, Kentucky, Virginia, Tennessee, and North Carolina. Areas in Ontario, Manitoba, Pennsylvania and Connecticut were studied briefly. Other sources which yielded information on ecology were museum specimen labels, field notebooks, and correspondence with others involved in field and physiological studies of *Napaeozapus*.

Specimens recorded in this study are in the following collections. The names of persons in charge of the collections, or others who offered assistance, are included.

AMNH	American Museum of Natural History (R. G. Van Gelder, H. M. Van Deusen, G. G. Musser)
ANS	Academy of Natural Sciences, Philadelphia
BMNH	British Museum (Natural History) (A. W. Gentry)
CMNH	Cleveland Museum of Natural History (L. G. Isard)
CMP	Carnegie Museum (J. K. Doutt, C. A. Heppenstall)
CUM	Cornell University, Museum of Natural History (W. J. Hamilton, Jr.)
DCM	Dartmouth College Museum (R. G. Chaffee)
FM	Chicago Natural History Museum (J. C. Moore)
JJC	Collection of J. J. Christian
JOW	Collection of J. O. Whitaker, Jr.
KU	University of Kansas, Museum of Natural History (J. K. Jones, Jr., E. R. Hall)
MCZ	Museum of Comparative Zoology (Barbara Lawrence)
MMNH	Minnesota Museum of Natural History (O. T. Kalin)
MSU	Michigan State University (R. H. Baker)
MVZ	Museum of Vertebrate Zoology (W. Z. Lidicker, Jr.)

NBM   New Brunswick Museum of Natural History (D. S. Christie)
NCSC   North Carolina State College (F. S. Barkalow, Jr.)
NCSM   North Carolina State Museum (W. M. Palmer)
NMC   National Museum of Canada (P. M. Youngman)
NYSM   New York State Museum (R. S. Palmer, P. F. Connor)
PM   Peabody Museum of Natural History (C. G. Sibley)
QWS   Quebec Wildlife Service, Quebec City
RM   Redpath Museum, McGill University (A. W. Cameron, H. Ouellet)
ROM   Royal Ontario Museum (R. L. Peterson)
SUCO   State University College, Oneonta, New York (J. G. New)
UAMZ   University of Alberta, Museum of Zoology (N. Panter)
UCM   University of Connecticut Museum (R. E. Dubos)
UG   University of Georgia Museum
UI   University of Illinois, Museum of Natural History (D. F. Hoffmeister)
UK   University of Kentucky, Lexington (C. L. Rippy, W. H. Davis)
UMA   University of Massachusetts (D. J. Klingener)
UMd   University of Maryland
UMMZ   University of Michigan, Museum of Zoology (D. M. Lay, E. T. Hooper)
USNM   United States National Museum, Fish and Wildlife Service (R. H. Manville, R. M. Wetzel)
WVMS   West Virginia Museum of Science, Marshall University (W. G. Frum)

III. PHYLOGENY

Napaeozapus (Zapodidae) is known from mid-Pleistocene deposits in Maryland (Gidley and Gazin, 1938), and four late-Pleistocene sites in Pennsylvania, Virginia, and Tennessee (see Past Distribution and Subspeciation, p. 59). The family extends back to the upper Oligocene of Eurasia (*Plesiosminthus*), excluding *Simimys* of the upper Eocene of North America. The following genera have been described:

SUBFAMILY SICISTINAE

Plesiosminthus	Upper Oligocene of Europe and Asia
(including *Parasminthus* and *Schaubeumys*)	Lower Miocene to Mio-Pliocene of North America
Heterosminthus	Lower Pliocene of Asia
Macrognathomys	Lower Pliocene of North America
Sicista	Upper Pliocene to Recent of Europe and Asia

SUBFAMILY ZAPODINAE

Megasminthus	Mio-Pliocene of North America
Sminthozapus	Lower Pliocene to Lower Pleistocene of Europe
Pliozapus	Upper Pliocene of North America
Eozapus	Recent of Asia
Zapus	Upper Pliocene to Recent of North America
Napacozapus	Middle Pleistocene to Recent of North America

The sicistines are the least specialized of the superfamily Dipodoidea, with brachyodont, tuberculate dentition, and unspecialized hind limbs in *Sicista*. The zapodines have a subhypsodont, flat-crowned dentition, and hind limbs elongated for saltation in Recent forms.

In discussing the status of *Eozapus*, *Zapus* and *Napaeozapus*, Krutzsch (1954) pointed out differences in the dentition (tooth number and occlusal pattern), bacula, and ear ossicles. In addition, the os clitoris, phallus, hyoid apparatus, and possibly chromosomes serve to separate the genera where these characters have been described. In most other features, however, the forms are similar and were initially described as subgenera of *Zapus* (Preble, 1899). Generic status was given to *Napaeozapus* by Miller (1899) and to *Eozapus* by Ellerman, Hayman, and Holt (1940).

Zapus and *Napaeozapus* resemble each other more closely than either resembles *Eozapus* of China, which shows greater affinity to the extinct *Pliozapus* of North America. *Pliozapus* appears at a structural level ancestral to the series of *Eozapus*, *Zapus*, and *Napaeozapus*. However it is unlikely that *Pliozapus* gave rise directly to *Eozapus* since the former is too specialized in some characters (Wilson, 1937). Stehlin and Schaub (1951:313) placed *Pliozapus* and *Eozapus* in the Sicistinae, but Wilson (1936:32), Krutzsch (1954:357) and Klingener (1963:259), on the basis of additional morphological features and specimens, referred the two genera to the Zapodinae.

Krutzsch visualized the evolution of the Zapodinae in two stages: a dispersal of primitive pre-*Eozapus* stock to Asia, with the extinction of the less progressive *Macrognathomys* and *Pliozapus* lines; the specialization of the primitive zapodine stock into *Zapus* by the late Pliocene, and *Napaeozapus* by mid-Pleistocene.

Klingener (1966) suggested that *Sminthozapus*, *Pliozapus*, and *Eozapus* formed a zapodine subgroup centered mainly in Asia, which has persisted since early Pliocene. *Eozapus* may well have had no closer relationship to North American zapodids than that of having arisen from a common *Plesiosminthus* stock.

Megasminthus is structurally intermediate in most dental and palatal characters between sicistine and zapodine rodents, and may have given rise directly to *Zapus*. The primitive sicistine *Plesiosminthus* possesses the dentition expected in a form ancestral to zapodines, including *Megasminthus* — dentition tuberculate, low-crowned, anteroconid small but present on all three molars (Klingener, 1966). The sicistines may well have been ancestral to both the zapodines and the dipodids (Wilson: 1949b:128).

The jumping mice (Zapodinae), birch mice (Sicistinae) and jerboas were originally united in the family Dipodidae. Lyon (1901) placed *Zapus* and *Sicista* in a new family Zapodidae on the basis of their less progressive skeletal structures (metatarsals unfused and unreduced in number, cervical vertebrae unfused, auditory bullae not inflated, and other differences). Further study of several rare jerboas revealed intermediate conditions, including the metatarsal characteristics and lack of fusion of cervical vertebrae. Consequently, Vinogradov (1937), Klingener (1964a), and Ellerman, Hayman and Holt (1940) reunited the two groups in the family Dipodidae. The latter pointed out, however, that the differences between the generalized *Sicista* and specialized *Jaculus* were greater than differences displayed within other rodent families. Most American mammalogists still retain the two families in a superfamily Dipodoidea.

Klingener (1964a) reviewed the three main hypotheses concerning the relationships of the Dipodoidea — with hystricomorphs, another group of forms of uncertain position, and muroids. The dipodoids and muroids were thought to have the greatest affinity by most authorities, though there was a difference of opinion whether there existed any special relationship other than sharing a recent common ancestry along with several other lines. Wilson (1949b) and Klingener (1964a), the latter on the basis of a myological study, indicated a common ancestor more recent than that of the dipodoids, muroids, and other Myomorpha.

Wilson (1949a) viewed the genus *Simimys* (Upper Eocene of North America) as a survivor of the stock which gave rise to both cricetids and dipodoids, though he included it in the muroids on the basis of skull and dental features. Stehlin and Schaub (1951:312) and Klingener (1963) regarded *Simimys* as a dipodoid, but in a later paper Klingener (1964a) did not include it.

The fossil record of the dipodoid line leading to *Napaeozapus* suggests the emergence of the dipodoid stock in the late Eocene, attainment of the primitive sicistine level of *Plesiosminthus* by Upper Oligocene, the primitive zapodine stage of *Megasminthus* by Upper Miocene, the appearance of *Zapus* in Upper Pliocene, and the emergence of the progressive *Napaeozapus* by Middle Pleistocene. *Zapus* has apparently occupied much of North America, and the phyletic relationships of various species and subspecies are relatively well known (Klingener, 1963:258). *Napaeozapus* appears to have originated from early *Zapus* stock and has evolved in northeastern North America.

IV. MORPHOLOGY

External Characters

Napaeozapus is muriform in appearance and of medium size —
total length 204 to 256 mm, tail length 115 to 160 mm, body length 80
to 100 mm, hind foot length 28 to 34 mm, ear length 15 to 18 mm,
weight 17 to 26 g (without embryos or fat). The tail is long (59-63%
of total length), attenuate and annulate. The hind feet are elongate,
extending out at a 45 degree angle when sitting. The front limbs are
small. Five digits are present on the front and hind limbs, though the
pollex is greatly reduced in size. The eyes and ears are of medium size.
There are four pairs of teats — one pectoral, two abdominal and one
inguinal pair. Internal cheek pouches are absent (Klingener, 1971),
though they have often been reported in this species. The coarse pelage
has a tricolor pattern — brown to black on the dorsal stripe, orange
with a yellow or red tint and scattered dark guard hairs on the sides,
and white underparts. Hairs on the dorsum of the feet are white. The
tail is distinctly bicolored, grayish brown above, white below, virtually
always with a white tip (0 to 42 mm). The ears are dark (blending
with the dorsal stripe), often with a light margin.

Guard hairs have a discontinuous medulla and coronal cuticular
scales with dentate edges in the proximal half of the hair, and serrate
edges distally. The underfur hairs have coronal scales with serrate
edges (Adorjan and Kolenosky, 1969).

The coloration of *Napaeozapus* simulates dead vegetation, which

Fig. 1. *Napaeozapus insignis* from South Bolton, Brome County, Quebec.

enables the animal to avoid detection by predators. Individuals often remain motionless for many minutes, partially hidden by grass or leaves. The dark dorsum, medium sides, and light underparts greatly reduce body shadows caused by an overhead light source, and presumably moonlight under natural conditions. The dorsolateral margin (between the dark dorsum and orange sides), passing in the vicinity of the eyes and ears, and the ventrolateral margin (between the orange sides and white ventrum), passing along the lower jaw, limbs and tail, would also tend to obscure the animal's outlines (Fig. 1).

Saunders (1921) believed that the colors of *Napaeozapus* faded rapidly after death, though no difference between live individuals and museum specimens was noted in the present study, taking into account the flattened hairs of the latter. Cameron (1953) remarked that museum specimens collected in water traps exhibited a peculiar orange coloration on the sides, and suspected that this alteration may have led Anderson (1942) to recognize the subspecies *N. i. gaspensis*. The change due to wear is marked, often accounting for much of the color variation seen within populations. In the worn pelage, the sleek appearance is lost, the dorsal stripe darkens and the sides become yellowish, showing patches of gray. In this condition the animal more closely resembles *Zapus*. No abnormally colored individuals (melanistic, albinistic, yellowish, white-spotted) were noted in examination of more than 2,500 specimens.

The white tip on the tail of *Napaeozapus* (absent in *Zapus*) has drawn comment from several sources. Rhoads (1903:113) speculated, "Owing to its variable amount . . . it seems to show a condition of change, not improbably toward a future atrophy of the terminal vertebrae and shortening of a member which some change in environment has shown to be uselessly or dangerously long." Clarke (1935) believed that the white tip was sexually dimorphic (longer in males); however, Preble (1938), Foster (1947), and I found no significant differences. Preble (1899) reported that the white tip averaged shorter in *N. i. roanensis* than in *N. i. insignis,* and I agree. The character, however, is too variable to be of much taxonomic value, as the following measurements show: 16 specimens from North Carolina averaged 10 mm (1-30); 6 from Wisconsin, 7 mm (3-9); 50 from Pennsylvania, 13 mm (0.1-36); 24 from Quebec, 19 mm (8-35); 16 from Nova Scotia, 19 mm (3-35); 27 from Ontario, 30 mm (6-36). Foster (1947) and Preble (1938) reported a range from 0 to 42 mm in specimens from Ohio and the New England area. Bole and Moulthrop (1942) noted one specimen, and Connor (1966) three specimens, with no white tip. I noted a dozen others without white tips in museum collections.

The pelage of *Napaeozapus* consists of underfur and guard hairs of two types — coarse, and fine (overhairs). Vibrissae are present on the cheeks, rostrum, carpus, and around the eyes. A tuft of short stiff hairs covers the area above the nose, and the tail ends in a pencil of white hairs. The coarse guard hairs are long (sample lengths on the dorsum, 10.0-10.6 mm; sides, 9.7-10.4 mm; ventrum, 9.3-9.6 mm), stiff with a weak base, elliptical in cross section, and tapered at both ends. The dorsal guard hairs have a gray base and black shaft, while those on the sides have, in addition, orange tips. Most ventral guard hairs are white, some having a fine black stripe near the tip. Orange guard hairs with a white tip predominate in the ventrolateral line, but a few are scattered through the belly fur.

Overhairs are also elliptical, but shorter and narrower than coarse guard hairs (sample lengths on the dorsum, 5.2-8.2 mm; sides, 5.1-9.6 mm; ventrum, 4.6-6.8 mm). The dorsal overhairs are gray at the base with a black shaft, some tipped with orange. Laterally, most overhairs are orange with a gray base, but a few have a black medial segment. Most ventral overhairs are entirely white, some have a fine black stripe distally, while a few others are pale orange with a white tip.

The underfur is fine, wavy and short (sample lengths on the dorsum, 2.8-4.4 mm; sides, 3.9-5.3 mm; ventrum, 2.1-3.8 mm). The numerous fine hairs are gray on the dorsal stripe, gray with orange tips on the sides, and white on the underparts.

The tricolor pattern is also characteristic of the other recent zapodines. A number of subspecies of *Zapus hudsonius, Z. princeps* and *Z. trinotatus* exhibit dorsal and lateral coloration well within the range of that found in *Napaeozapus*. The white tail tip present in *Napaeozapus* is occasionally found in *Zapus* (noted in three specimens among about 400 examined). The few available specimens of the Chinese jumping mouse (*Eozapus*) are indistinguishable from *Napaeozapus* in the color of the sides and back, even including a white tip on the tail. A dark ventral stripe is present in some specimens and absent in others.

Cranial Characters

The skull of *Napaeozapus* is murine in appearance, delicate, convex, and without strong angularity. The braincase, mastoids and auditory bullae are not inflated. The zygoma is simple and narrow, with the jugal plate extending dorsally along the maxillary ramus and articulating with the lacrymal. The large infraorbital foramen is obliquely oval and transmits the masseter muscle and nerve. The nasals project considerably anterior to the incisors. A large premaxillary plate is present between the upper incisors. The palate is short and concave posteriorly, extending only to M_3. The mandible is delicate. The angular process extends medially, and the coronoid process is weak.

Ear Ossicles

Krutzsch (1954:363-365) described the ear ossicles of *Napaeozapus, Eozapus* and *Zapus*. Distinctive features of the malleus and incus were considered supporting evidence for the recognition of generic status for the three taxa, since variation in the auditory bones is usually slight even at the family level. The ear ossicles of *Napaeozapus* and *Zapus* showed a greater resemblance to each other than to *Eozapus*. The head and neck of the malleus were less robust in *Napaeozapus*. The body was rounded dorsally and directed anteriorly, and the lateral surface was nearly flat rather than curved as in the other genera. The long limb of the incus was angular and long, while the short limb was broad at the base, compared to *Zapus*. The limbs and neck of the stapes were more slender than in *Zapus*.

Hyoid Apparatus

The hyoid apparatus of zapodids has not been studied previously. Examination of the structure in adult specimens — five *Napaeozapus* and one *Zapus hudsonius* (preserved dry or in alcohol) — showed the sutures between the basihyal, hypohyal, and thyrohyal to be no longer discernible. In *Napaeozapus* (Fig. 2, p. 12) the basihyal was
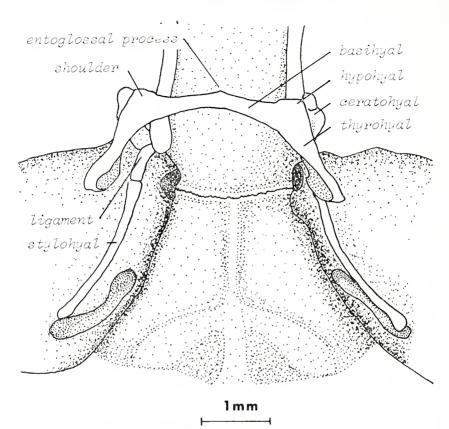
FIG. 2. Hyoid apparatus of *Napaeozapus* (ventrolateral view).

bar-shaped and flattened, with pronounced "shoulders" anterior to the thyrohyals, and a slight, median entoglossal process. The ceratohyal was short and straight, and the thyrohyals were relatively short, with a terminal lateral deflection. The stylohyals extended posteriorly to the carotid canal and stapedial foramen. No marked variation was observed in the structure of the hyoid in the five *Napaeozapus*. The hyoid of *Zapus* was relatively smaller, with a long, thin ceratohyal and a scapular-shaped thyrohyal. The hyoid apparatus of the Zapodinae is similar to that found in the dipodid *Dipus* (Tullberg, 1899) and many Cricetinae (Sprague, 1941).

Dentition and Dental Anomalies

The dental formula of *Napaeozapus* is 1/1, 0/0, 0/0, 3/3 = 16. The incisors are colored orange or yellow. The upper incisors are short and

A   **B**   **C**
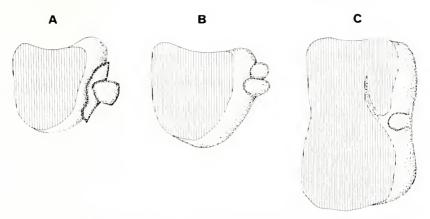
Fig. 3. Dental anomalies on the lingual side of the upper right molars in *Napaeozapus*. View A = M_3 (suco 66-306), B = M_3 (ucm 8518), C = M_1 (rom 11976).

grooved. The lower incisors are long and slender. Premolars are absent. Molars are rooted, semihypsodont, not quadritubercular. The occlusal surface is noncuspidate and flat-crowned, with numerous isolated islands and re-entrant folds (for changes in occlusal pattern due to attrition, see Fig. 11, p. 24).

The cheek teeth of the Zapodidae were studied in detail by Krutzsch (1954:360-362). *Eozapus*, *Zapus* and *Napaeozapus* were arranged in a progressive series according to increased complexity of the enamel and dentine flexures, tuberculate to flat-crowned occlusal surface, the presence and size of the anteroconid, plus other minor distinctions. The decrease in size of P_4 from *Eozapus* to *Zapus*, and its absence in *Napaeozapus* also indicated that the latter was the most progressive zapodid.

I did not attempt a study of variation of the complicated occlusal pattern of the molars, though I did observe that the position and shape of cusps and folds varied in many specimens (for example, ummz 53572, 84450, 86078; cmp 35773; rom 35-8-16-28). In an examination of about 2,520 skulls, one specimen showed a small upper left P_4 (ummz 84450, previously reported by Klingener, 1964b), and one individual from Quebec (ui 38893) revealed an extra small tooth posterior to upper M_3 on both sides of the jaw. Fifteen individuals had one or more cusplike structures on the lingual side of the upper molars, seldom reaching the occlusal surface (Fig. 3). Two showed a single cusp on the right M_1 (rom 15053 from Ontario, 11976 from Quebec). Two had a single cusp on the right M_2 (rom 36-1-2-272 and 35-7-31-8 from

Ontario), one had two cusps on the right M_2 (ROM 35-7-31-10 from Ontario), and another had one cusp on the left and right M_2 (UMMZ 86073 from West Virginia). A single cusp was present on the right M_3 of six individuals (UCM 4324, 8515 from Vermont; CUM 7411 and SUCO 66-306 from New York; UI 9690 and UMMZ 101030 from Maine), two others had single cusps on both M_3 (UMMZ 88394 from New Hampshire; NBM 373 from New Brunswick), while one individual showed two cusps on both M_3 (UCM 8518 from Vermont). Lastly, a specimen from Ontario (MVZ 57133) had both upper M_3 partly covered by an overlapping shelf from the second molars.

Postcranial Characters

The vertebral column consists of 7 unfused cervical vertebrae; 12 thoracics of medium size; 7 large lumbars, with the posterior four having pronounced neural and transverse processes; 4 sacrals with transverse processes joined, the two anterior sacrals connected with the ilia; 39 caudals (Krutzsch, 1954:384, reported 7 sacrals and 36 caudals in *Zapus*, while Hatt, 1932:720, with only 3 specimens of *Zapus*, reported 4 sacrals and only 33 to 35 caudals), with "H-shaped" chevron bones on the ventral surface of the larger caudal vertebrae. The tail has become elongated by an increase in both length and number of vertebrae. The five metatarsals are enlarged (first and fifth subequal) but not fused. The tibia and fibula are fused proximally, with the fibula reduced in size distally.

Os Penis

The os penis of *Zapus* was described by Tullberg (1899) as small, with a slightly bowed and expanded tip. Vinogradov (1925), in a study of *Sicista, Eozapus* and *Zapus,* found the structure bow-shaped in the subfamily Sicistinae and slightly bowed in the reverse direction in the Zapodinae. Krutzsch (1954:361 and 363) compared the os penis of *Eozapus, Napaeozapus,* and the three species of *Zapus,* and reported differences in the size and shape useful in distinguishing the five species. The baculum of *Napaeozapus* was characterized by a narrow base, lanceolate tip, and a slender, curved shaft in lateral view. However, the base is narrow only in comparison with *Eozapus,* and is as wide or wider than in *Zapus.* Eighteen specimens from eastern Canada failed to reveal as great a curve in the central shaft as the specimen shown by Krutzsch (1954:Fig. 31). Burt (1960:69) reported that the bone differed from *Zapus* in having a round, but spatulate, distal end and a less pronounced longitudinal groove on the dorsal surface of the

distal
glans

baculum

A

urethra   corpora
cavernosa

1mm

B

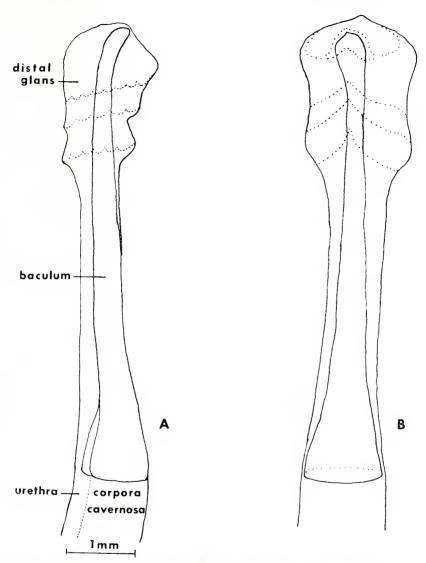Fig. 4. Phallus of *Napaeozapus* (A = lateral view, B = dorsal view).

expanded base. Since this groove contains the urethra, which lies ventral to the baculum and corpora cavernosa, the groove should be described as lying on the ventral surface. Burt's figure (1960:Plate 1, c) has the ventral side facing dorsally. The orientation of the baculum within the phallus has not been illustrated previously and is shown in Fig. 4.

Burt (1960) gave measurements of the bacula from nine specimens from Maryland, West Virginia, North Carolina and Michigan as: length, 5.8 mm (5.2-6.3); width of base, 0.7 mm (0.5-0.9); height of base, 0.47 mm (0.4-0.7). These dimensions are considerably smaller than those from nine specimens from Prince Edward Island, Nova Scotia, and southern Quebec: length, 6.3 mm (5.9-6.6); width of base, 1.0 mm (0.9-1.2); height of base, 0.9 mm (0.9-1.0). Apparently, the baculum has greater dimensions in the larger animals of northern populations.

Os Clitoris

Whitaker (1966) reported on the os clitoris in *Napaeozapus* and *Zapus*. The shape of the bone varied greatly in the former species, from gently bowed to "U" shaped. Each of the four bones of *Napaeozapus* was larger than a single one of *Zapus:* length, 2.1-2.4 mm; greatest width, 0.17-0.24 mm; least width, 0.10-0.17 mm; and 1.7 mm, 0.20 mm, 0.08 mm respectively.

Phallus

The phallus serves to differentiate the members of the family Zapodidae (Fig. 5). Vinogradov (1925) described the peculiarities of the phallus of *Sicista* and *Eozapus,* and Tullberg (1899) reported the presence of spines in *Zapus*. In the present study, *Napaeozapus* and *Zapus* were found to resemble each other more closely in phallic structure than either resembled the Asian genera. The distal portion of the glans penis of the North American zapodids was covered with numerous rows of epidermal spines, enlarged proximally as large scales tipped with spines. The arrangement of spines was similar in both genera but the structure was larger and rectangular, not tapered, in *Napaeozapus*.

Male Accessory Reproductive Glands

Tullberg (1899:188) gave a brief description of the genital glands in *Zapus,* noting vesicular, bulbo-urethral and lobed prostate glands. In the present investigation the genital glands of six *Napaeozapus* and one *Zapus hudsonius* were studied, including both fresh and preserved material (Fig. 6). No differences in gross morphology were observed between the two species. Bulbo-urethral, vesicular, and three pairs of prostate glands were present, but ampullary and preputial glands were not located. Arata (1964) studied the glands of 24 muroid genera and found that among the forms with a complex type of phallus (formed
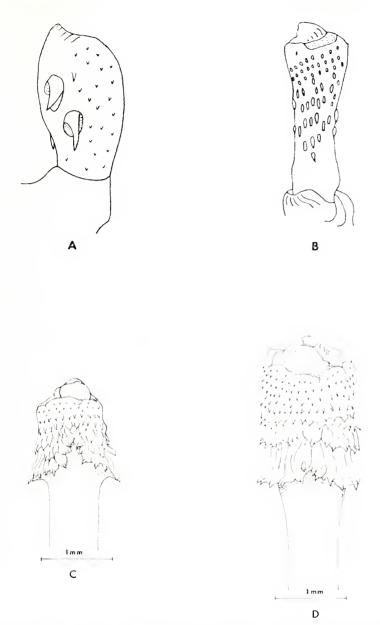
FIG. 5. Phallic structure. Lateral view: *Sicista napaea* (A) and *Eozapus setchuanus* (B) (scale unknown; after Vinogradov, 1925). Dorsal view: *Zapus hudsonius* (C) and *Napaeozapus insignis* (D).
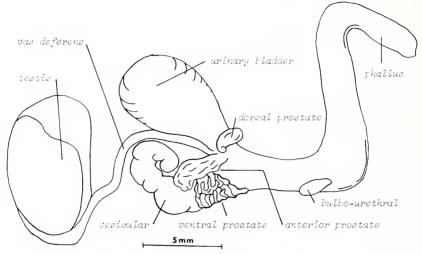
FIG. 6. Male urogenital tract of *Napaeozapus* (lateral view).

around a baculum with three distal digits), a complete or almost complete set of accessory glands was present. Variation in the form and number of glands was greater in the forms with a simple type of phallus, as possessed by zapodids. Ampullary glands were absent only in *Ochrotomys* and *Onychomys*, and preputial glands were not found in several genera including *Peromyscus*. However, no genera lacked both sets of glands as in the Zapodinae. A complex phallus and complete set of accessory glands may be the generalized or primitive condition for muroid rodents and possibly for all Myomorpha (Arata, 1964:28). Further study of the Zapodidae may show the family to exhibit a highly modified condition.

Myology

Klingener (1964a) examined the musculature of *Napaeozapus* in a comparative study with *Zapus, Sicista,* and *Jaculus*. He noted no constant differences between the two jumping mice, but cautioned that his standard for considering a muscle as different in two forms may vary from the criteria of other anatomists, and that this should be taken into account if myological similarity is used as evidence in considering the two mice congeneric.

Karyology

The dipodoids exhibit a widely variable number of chromosomes. The dipodids *Allactaga williamsi* and *Jaculus jaculus* have a diploid

Fig. 7. Karyogram of *Napaeozapus insignis* from South Bolton, Brome County, Quebec (ui 40894, male). ×1150.

number of 48 chromosomes, the sicistines *Sicista betulina* and *S. subtilis* possess 32, and *Zapus princeps*, *Z. hudsonius* and *Napaeozapus insignis* have 72 (Meylan, 1968). With material from one specimen of *Napaeozapus*, Meylan could not determine whether there were 70 or 72 chromosomes. Also, a single large X chromosome and a diploid number of 71 was found in two females of *Z. princeps*, which led Meylan to suspect that females of this species possessed an XO/XY sex-determining mechanism.

In the present study, the chromosomes of 7 specimens of *Napaeozapus* and 16 specimens of *Zapus princeps* were examined. The high diploid number and small size of many chromosomes necessitated the photographing of all metaphase spreads that were to be counted — *Napaeozapus* (3 males, 4 females), 41 spreads; *Zapus princeps* (6 males, 10 females), 213 spreads. A diploid number of 72 was confirmed in males (Fig. 7) and females (Fig. 8) of both species. Several females (*Napaeozapus* — 1, *Zapus* — 6) revealed only one large X chromosome (Fig. 9), while the other females possessed the usual two large X chromosomes. The XO constitution is known in females of six other mammalian species, but in these instances the diploid number is always reduced by one and all females are XO. In *Napaeozapus* and *Zapus*, the diploid number of all females remains normal (i.e., 72). Thus, *Napaeozapus* and *Zapus* are distinct in two ways: (1) Both XO and

FIG. 8. Karyogram of *Napaeozapus insignis* from South Bolton, Brome County, Quebec (UI 41439, XX female). ×1250.

FIG. 9. Karyogram of *Napaeozapus insignis* from South Bolton, Brome County, Quebec (UI 40895, Xx female. × 1300.
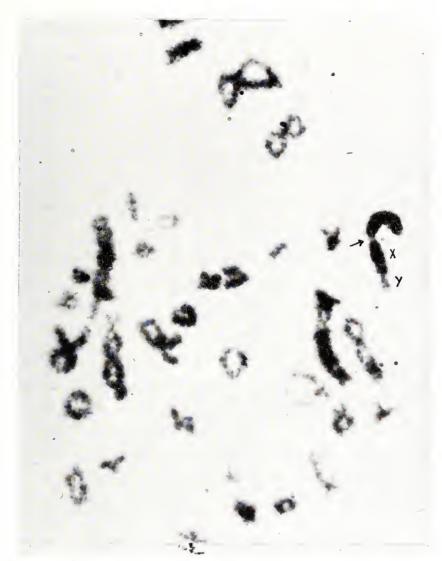
FIG. 10. Meiotic spread of *Napaeozapus insignis* from South Bolton, Brome County, Quebec (UI 40896, male). Note X and Y chromosomes and centrally located secondary constriction (marked by arrow). ×1050.

XX females occur in about equal numbers within the same population; (2) XO females have a normal diploid complement.

The full complement of 72 chromosomes in the diploid set of XO females is not readily explainable. Possibly a large portion of one X has been deleted. The remaining fragment would not be recognizable with the present technique. This interpretation was also proposed by Bianchi and Contreras (1967) in a study of the field mouse *Akodon azarae*, and Matthey (1967) in studies of *Mus triton* and *M. minutoides musculoides*. In these latter studies, females of Xx constitution revealed a complete 2N complement, but one X chromosome was greatly deleted. Since in zapodines the full diploid set of 72 chromosomes is present in females with only one X, it seems preferable to designate these individuals as Xx.

The presence of fertile Xx females in high proportions in the same population with normal XX females would seemingly result in an unequal sex ratio in favor of females, since Xx females would lose 50% of the male zygotes (xY males have not been found). But such unequal sex ratios do not appear in natural populations. The selective advantage or disadvantage of this mechanism is unknown.

The X chromosome in both genera is considerably larger than the autosomes. In most placental mammals, this chromosome constitutes approximately 5% of the haploid set (Ohno, 1967:50-51). In *Napaeozapus* and *Zapus*, both length measurements and weight of cut-out chromosomes gave a value of the X chromosome of 12 to 13% of the haploid set. This may be due to a replication of genetically inactive sex chromatin, as found in a few other rodents.

Examination of meiotic spreads of the two genera showed a small Y chromosome synapsed to the X chromosome (Fig. 10, p. 21). The Y chromosome could not be distinguished in mitotic spreads from the numerous small autosomes (Fig. 7, p. 19). Apparent were at least 15 pairs of bi-armed and about 40 acrocentric autosomes, ranging in size from medium to minute. The fundamental number was approximately 100. The great number of very small chromosomes did not permit identification of particular elements, hence differences between the mitotic chromosomes of *Napaeozapus* and *Zapus* were not apparent. In meiotic spreads, there appeared to be a greater number of chiasmata in *Napaeozapus*. A secondary constriction, present in the X chromosome during meiosis in both genera, was more pronounced and centrally located in *Napaeozapus*.

V. VARIATION IN *NAPAEOZAPUS*

Age Variation

BASES FOR DETERMINING AGE GROUPS

Age variation was surveyed to determine which individuals could be regarded as adults and to study the effect of age on the taxonomic characters. Body size, weight, and cranial measurements, relative to known adults in the same population, were taken into account in deciding adult status, but dentition provided the most significant basis. Six arbitrary age classes were established, based on the degree of wear on the upper molars (Fig. 11). Since dental attrition is a continuous variable, many intermediate stages were recognized. The molars erupt in order from M_1 to M_3, but the third molar usually wears at a faster rate than the preceding teeth. The one age level of taxonomic importance was that which differentiated between subadult and adult (age-groups 2 and 3). since only groups 3 to 6 were included in the systematic study.

Age-group 1 consists of juveniles in which M_1 and M_2 have not reached full height and M_3 has just erupted through the alveolus. Age-group 2 is composed of subadults in which M_1 and M_2 are full size and of equal height, and show slight wear. The third molar has reached the occlusal surface but little wear is apparent. Age-group 3
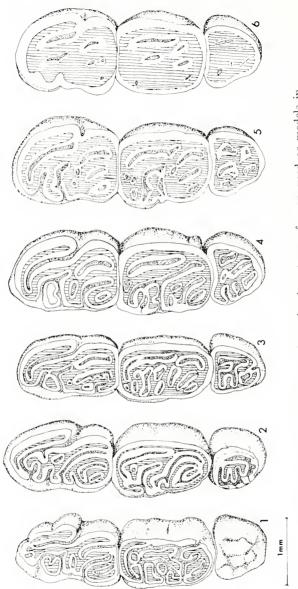
Fig. 11. Right maxillary molars, showing stages of wear, used as models in establishing age-groups 1 to 6 for *Napaeozapus*. Group 1 consists of juveniles; group 2, subadults; groups 3 to 6, adults.

individuals are considered adults and all three molars show signs of wear and slight reduction in height. Age-group 4 animals still exhibit a well-defined occlusal pattern, but the crown of M_3 has been reduced to less than two-thirds its original height. Age-group 5 animals have lost most of the occlusal pattern, but a few of the main cusps and re-entrant folds are still present. The third molar has been reduced to about one-third the original crown height. Age-group 6 individuals show molars which have been worn down to or near the cingulum. All occlusal surfaces are ground smooth except for an occasional groove or pit — the remains of deep folds between the cusps. A number of specimens showed only the roots of all three molars, the crowns having worn completely away.

DEVELOPMENT OF EXTERNAL AND CRANIAL CHARACTERS

The relation of age to anatomic development was studied in 77 specimens from Pancake Bay, Ontario (Table 1), collected in late August and early September, which accounts for the abundance of subadults. The anatomic dimensions in age-group 3 may be somewhat smaller than expected, since many individuals were included which had just reached the adult level. In most structures growth is rapid through groups 1 and 2, and considerably slower after stage 3 is reached. The hind foot appears almost full length in group 1, and the interorbital breadth seems to decrease slightly. Groups 4 and 5 show little change from group 3 in external or cranial development, but group 6 exhibits greater size of several characters. The body length appears to increase throughout life while the tail reaches full length in age-group 2. Continued elongation of the skull with age is indicated by greatest skull length, condylobasal length, zygomatic length, nasal length and length of the incisive foramina, although the increase in any one feature is not marked. The braincase increases in breadth slightly, but the other breadth measurements are relatively unchanged.

Age-groups 3 to 6 were also compared in a population from South Bolton, Quebec, because of the small sample size of several age classes in the Ontario sample. Age-groups 3, 4, 5, and 6 were represented by 10, 32, 25 and 6 specimens respectively. Most measurements were found to increase slightly through each age class, group 6 specimens being about four per cent larger than group 3, particularly in body and various cranial lengths — greatest skull length: group 3, 23.00 mm (22.6-23.7); group 4, 23.60 mm (22.5-24.6); group 5, 23.92 mm (23.1-24.8); group 6, 24.12 mm (23.4-24.7). Apparently, growth in a number of characters may continue throughout the life-span in *Napaeozapus*. Individuals of

TABLE 1

AVERAGE MEASUREMENTS OF SIX AGE GROUPS IN *NAPAEOZAPUS* FROM PANCAKE BAY, ONTARIO

Age Groups[a]	1	2	3	4	5	6	% Incr.: Age-Groups 3 to 6
Number Examined	5	35	13	11	8	5	
Total Length	217.0	229.9	239.5	241.6	237.3	241.8	1.0
Tail L.	139.4	145.4	150.2	148.2	145.8	146.6	—
Body L.	77.6	84.5	89.3	93.4	91.5	95.2	6.6
Hind Foot L.	31.2	31.5	31.6	31.8	31.1	31.6	—
Greatest Skull L.	21.75	23.15	24.29	24.26	24.25	24.68	1.6
Condylobasal L.	18.25	19.74	20.65	21.02	20.93	21.38	3.5
Zygomatic L.	9.07	9.70	10.14	10.13	10.01	10.34	1.9
Zygomatic Breadth	11.15	11.71	12.27	12.40	11.88	12.38	0.8
Mastoid B.	10.40	10.37	10.77	10.55	10.74	10.75	—
Braincase B.	10.65	10.70	10.88	11.11	10.96	11.10	2.0
Nasal L.	8.80	9.64	10.21	10.16	9.90	10.36	1.4
Rostral B.	4.20	4.56	4.76	4.52	4.58	4.72	—
Interorbital B.	4.50	4.30	4.38	4.30	4.39	4.42	0.9
Bony Palate L.	3.00	3.20	3.25	3.20	3.23	3.28	1.0
Incisive Foramina L.	4.10	4.40	4.64	4.65	4.66	4.86	4.7
Maxillary Toothrow L.	3.65	3.75	3.83	3.79	3.68	3.70	—

[a] Sexes combined in calculating means (in millimeters).

age-groups 5 and 6 usually average slightly larger than groups 3 and 4, but their measurements generally fall within the range of the latter groups. Continued growth in adults was not detected in *Zapus* by Krutzsch (1954:378), but Dice (1936) reported significant increases in external and cranial measurements in captive *Peromyscus maniculatus* more than two years of age.

Individual Variation

Individual variation within populations of *Napaeozapus* was studied in two samples (sexes and age-groups 3 to 6 combined) — 39 specimens from Pancake Bay, Ontario, and 55 specimens from Cascapedia River, Quebec (Table 2). A number of collectors measured external structures, and I measured the skulls. The coefficients of variation in the external characters were surprisingly low considering the difficulty in accurately measuring soft parts of the anatomy. The differing coefficients between the two populations probably reflect the varying techniques of measurement by the many collectors. Among the cranial measurements, lengths of the nasals, bony palate, incisive foramen, maxillary tooth-row, and breadths of the rostrum and interorbital region showed higher coefficients of variation. The method of measuring nasal length and rostral breadth depended on the position of sutures, which varied to a certain degree. The other characters with high coefficients were small and difficult to measure accurately with calipers, resulting in relatively high variability. They were probably no more variable than most other cranial parts. Cranial coefficients which were relatively high in one population were also high in the other. All anatomic features examined showed normal variability and none had coefficients too high to be of taxonomic use. This suggested that the sexes and age-groups 3 to 6 could be combined in the study of geographic variation.

Secondary Sexual Variation

Three widespread populations were studied for comparative measurements of male and female *Napaeozapus*. The largest sample (37 ♂ and 40 ♀, total 77) was collected by the author from several localities in the vicinity of South Bolton, Quebec. The hind foot and rostral breadth averaged somewhat larger in males, whereas in all other characters females were slightly larger (Table 3). Most measurements differed less than 1%, although total length and condylobasal length differed significantly at the 0.05% level (t = 2.197 and 2.157 respectively).

<div align="center">

TABLE 2

INDIVIDUAL VARIATION IN POPULATIONS[a] OF *NAPAEOZAPUS*
FROM ONTARIO AND QUEBEC

</div>

CHARACTER	PANCAKE BAY, ONT.			CASCAPEDIA R., QUE.		
Total Length	239.30^{39} 6.9023	$\pm$	1.1052 (2.88)	233.90^{51} 7.9495	$\pm$	1.1131 (3.40)
Tail L.	148.10^{39} 2.2396	$\pm$	0.3586 (1.51)	145.25^{55} 5.9835	$\pm$	0.8068 (4.12)
Hind Foot L.	31.60^{39} 0.6529	$\pm$	0.1045 (2.06)	31.30^{55} 1.1098	$\pm$	0.1497 (3.55)
Greatest Skull L.	24.29^{30} 0.5208	$\pm$	0.0950 (2.14)	24.36^{46} 0.4817	$\pm$	0.0710 (1.98)
Condylobasal L.	20.94^{31} 0.4690	$\pm$	0.0842 (2.24)	20.87^{45} 0.5027	$\pm$	0.0749 (2.41)
Zygomatic L.	10.15^{35} 0.2867	$\pm$	0.0484 (2.83)	9.91^{53} 0.3167	$\pm$	0.0435 (3.20)
Zygomatic Breadth	12.26^{32} 0.4662	$\pm$	0.0824 (3.80)	12.40^{43} 0.3497	$\pm$	0.0533 (2.82)
Mastoid B.	10.71^{21} 0.2985	$\pm$	0.0660 (2.79)	10.89^{38} 0.2410	$\pm$	0.0391 (2.21)
Braincase B.	11.00^{31} 0.3225	$\pm$	0.0579 (2.93)	11.07^{47} 0.2161	$\pm$	0.0315 (1.95)
Nasal L.	10.14^{31} 0.3677	$\pm$	0.0660 (3.63)	9.80^{54} 0.3736	$\pm$	0.0508 (3.81)
Rostral B.	4.63^{35} 0.1977	$\pm$	0.0334 (4.27)	4.54^{54} 0.2064	$\pm$	0.0281 (4.55)
Interorbital B.	4.34^{36} 0.1738	$\pm$	0.0289 (4.00)	4.74 0.1439	$\pm$	0.0196 (3.03)
Bony Palate L.	3.23^{35} 0.1237	$\pm$	0.2090 (3.83)	3.06^{54} 0.1758	$\pm$	0.0239 (5.75)
Incisive Foramina L.	4.68^{36} 0.2154	$\pm$	0.0359 (4.61)	4.67^{54} 0.1631	$\pm$	0.0222 (3.50)
Maxillary Toothrow L.	3.77^{35} 0.1212	$\pm$	0.0205 (3.22)	3.53^{54} 0.1371	$\pm$	0.0186 (3.89)

[a] Sexes and age-groups 3 to 6 combined. Mean (in millimeters) with sample size as superscript, followed by standard error. Standard deviation below, followed by coefficient of variation in parentheses.

TABLE 3

COMPARATIVE MEASUREMENTS[a] OF MALE AND FEMALE
NAPAEOZAPUS FROM QUEBEC

CHARACTER	MALES[a]	FEMALES[a]	PER CENT LARGER
Total Length	227.6[33]	231.9[40]	1.9♀
	(8.8772)	(7.9318)	Significant (0.05)
Tail L.	138.8[33]	139.8[40]	0.7♀
	(6.4634)	(5.6427)	
Hind Foot L.	30.6[36]	30.5[40]	0.4♂
	(0.9970)	(0.8149)	
Greatest Skull L.	23.59[34]	23.76[35]	0.7♀
	(0.5267)	(0.6287)	
Condylobasal L.	20.28[36]	20.56[38]	1.4♀
	(0.5524)	(0.5630)	Significant (0.05)
Zygomatic L.	9.74[37]	9.81[39]	0.7♀
	(0.3308)	(0.3418)	
Zygomatic Breadth	12.13[36]	12.30[38]	1.4♀
	(0.4014)	(0.3441)	
Mastoid B.	10.69[36]	10.75[37]	0.6♀
	(0.2699)	(0.3152)	
Braincase B.	10.76[36]	10.83[39]	0.7♀
	(0.2746)	(0.2897)	
Nasal L.	9.46[35]	9.51[35]	0.6♀
	(0.3515)	(0.4173)	
Rostral B.	4.54[37]	4.50[39]	0.8♂
	(0.2186)	(0.2481)	
Interorbital B.	4.66[37]	4.72[39]	1.3♀
	(0.1584)	(0.1679)	
Bony Palate L.	3.10[37]	3.14[39]	1.5♀
	(0.1507)	(0.1729)	
Incisive Foramina L.	4.65[37]	4.69[39]	0.7♀
	(0.1764)	(0.1723)	
Maxillary Toothrow L.	3.53[37]	3.56[39]	0.8♀
	(0.1443)	(0.1478)	

[a] Age-groups 3 to 6 combined in calculating means (in millimeters). Sample sizes indicated as superscript numbers. Standard deviations in parentheses below means.

In a population sample of woodland jumping mice from Pancake Bay, Ontario (21 ♂ and 18 ♀, total 39), females had a significantly greater total length and braincase breadth, while males had a greater rostral breadth. Specimens from Cascapedia River, Quebec (31 ♂ and 24 ♀, total 55), revealed no significant differences. Since sexual variation appeared minimal compared to geographic variation, and sample sizes from most localities were small, the sexes were combined in the systematic study.

Krutzsch (1954:381) detected no important secondary sexual variation in a sample of 32 *Zapus hudsonius* from Michigan. However, Whitaker (1963a:219-220), in 106 *Zapus* from New York, found males larger only in hind foot and tail length while females averaged larger in many other characters — significantly larger in body length, diastema length, condylobasal length and mastoid breadth. It appears that in both species of jumping mice, females average slightly larger than males in most external and cranial characters.

Geographic Variation

MORPHOLOGY

Much of the geographic variation in morphology of *Napaeozapus* is clinal, with the largest animals from northern areas and the smallest along the southwest periphery of the range (Table 4). External and cranial characters with clinal variation average 12% (7-17) larger in northern populations. In some characters the gradient shows a fairly even transition from south to north, as seen in the isophene lines for breadth of braincase (Fig. 12). In this general pattern of continuously varying populations are regions of character discontinuity, often associated with partial isolation (Fig. 13). The Great Lakes and St. Lawrence River presently bisect the range of the species and interrupt gene flow between populations on either side of the water barrier (Table 5, p. 34; Fig. 14, p. 38). A high degree of concordance in clinal breaks exists between Ontario and the states of Minnesota, Wisconsin, and Michigan (across lakes Superior and Huron). Smaller discontinuities are present between the Lower Peninsula of Michigan, and the Upper Peninsula of Michigan and Wisconsin (across Lake Michigan), and between Wisconsin and Minnesota. Populations from Michigan are quite different from those of Ohio and Pennsylvania in almost every character (populations separated by gap of 230 miles of unsuitable land habitat and Lake Erie). Clinal breaks are apparent in the mountainous regions of West Virginia and the hills of western Pennsylvania.

TABLE 4

CLINAL VARIATION IN TWO SERIES OF GROUPED POPULATIONS
OF *NAPAEOZAPUS*

SERIES I. MAINLY N-S, EAST-CENTRAL QUEBEC TO N. CAROLINA

CHARACTERS (measurements in millimeters)	QUE. (EC)	QUE. (Gaspé)	QUE. (S)	N.Y. (SE)	PA. (C)	W.VA. (EC)	N.C. (WC)
Total Length	246	235	230	227	225	226	224
Tail L.	153	148	141	139	138	138	136
Great. Skull L.	25.0	24.4	23.8	23.7	23.4	23.2	23.0
Braincase Breadth	11.3	11.0	10.9	10.8	10.7	10.6	10.5
Zygomatic L.	10.5	9.9	9.9	9.8	9.6	9.4	9.3
Zygomatic B.	12.8	12.4	12.3	12.2	12.0	11.9	11.7
Nasal L.	10.7	9.8	9.5	9.5	9.4	9.4	9.2
Incisive F. L.	4.8	4.7	4.7	4.5	4.5	4.4	4.3

SERIES II. MAINLY N-S, WESTERN ONTARIO TO KENTUCKY

CHARACTERS (measurements in millimeters)	ONT. (W)	MINN. (NE)	MICH. (NW)	MICH. (NE)	OHIO (NE)	W.VA. (NC)	KY. (SE)
Total Length	249	236	234	235	218	217	214
Tail L.	153	144	143	145	132	130	131
Great. Skull L.	24.9	24.7	23.8	24.3	23.0	22.9	22.1
Braincase Breadth	11.4	11.1	10.9	11.0	10.6	10.6	10.4
Zygomatic L.	10.4	10.5	10.1	10.2	9.3	9.4	9.3
Zygomatic B.	12.8	12.5	12.2	12.3	11.9	11.8	11.8
Nasal L.	10.4	10.2	9.5	9.9	9.1	9.0	8.9
Incisive F. L.	4.7	4.8	4.5	4.7	4.6	4.4	4.4

Populations occurring southwest of this zone of intergradation repre-
sent the minimal extremes of clinal variation for most characters.
Populations north and east of this area show a relatively consistent
cline of increasing size, reaching a maximum within the same race in
extreme southern Ontario and Quebec, the Gaspé Peninsula and Mari-
time Provinces. Jumping mice on either side of the upper St. Lawrence
(from Lake Ontario to the Saguenay River) are not notably different,
the region of abrupt change occurring considerably farther north. In
the region where the St. Lawrence widens (between the Gaspé Penin-
sula and the North Shore), disruption in clinal trends is extensive.
There are few specimens from central Ontario and Quebec, and without
a knowledge of variation in these populations, conclusions cannot be
drawn with much assurance. Jumping mice east of the Saguenay River
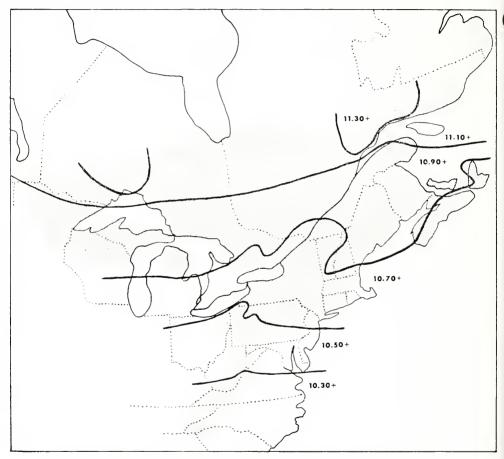
FIG. 12. Geographic variation in breadth of braincase of *Napaeozapus* (isophene interval, 0.2 mm).
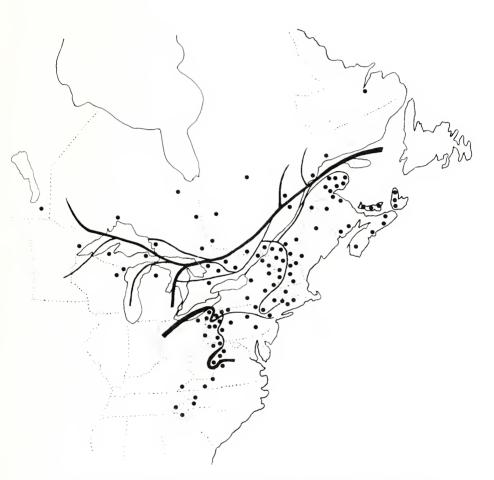
Fig. 13. Demarcation lines in the geographic range showing character shifts in *Napaeozapus*. Width of lines indicates the degree of concordance and magnitude of change in characters. Dots represent grouped localities.

TABLE 5

RANGE OF AVERAGES OF MEASUREMENTS IN POPULATIONS OF FIVE SUBSPECIES OF *NAPAEOZAPUS*

(in millimeters)

CHARACTERS	SAGUENAYENSIS	ABIETORUM	FRUTECTANUS	INSIGNIS	ROANENSIS
Total Length	245.50–247.00	232.00–244.80	227.70–235.60	221.30–241.70	214.30–225.10
Tail L.	148.00–153.20	146.40–153.50	140.00–145.50	136.70–150.40	130.70–140.20
Body L.	93.30–94.00	86.10–91.60	88.90–92.10	83.90–93.70	83.60–89.90
Hind Foot L.	33.00–33.30	31.20–33.00	30.70–31.10	30.10–32.40	28.90–30.70
Great. Skull L.	24.40–25.05	23.95–25.03	23.80–24.74	23.20–24.38	22.10–23.29
Condylobasal L.	20.65–21.80	20.70–21.63	20.13–21.10	19.83–20.98	19.00–19.93
Zygomatic L.	10.46–10.80	10.09–10.47	9.80–10.46	9.36–10.13	9.04–9.60
Zygomatic Breadth	12.80–13.05	12.18–12.97	12.00–12.45	11.89–12.62	11.23–12.00
Mastoid B.	10.90–11.20	10.66–11.02	10.67–10.84	10.42–10.96	10.27–10.57
Braincase B.	11.20–11.40	10.93–11.38	10.83–11.08	10.54–11.08	10.30–10.69
Nasal L.	10.30–11.10	10.00–10.67	9.49–10.22	9.28–9.82	8.90–9.58
Rostral B.	4.57–4.72	4.63–4.83	4.17–4.31	4.33–4.82	4.23–4.49
Interorbital B.	4.35–4.60	4.30–4.45	4.23–4.43	4.51–4.85	4.43–4.76
Bony Palate L.	3.10–3.40	3.23–3.53	3.28–3.63	2.97–3.48	2.90–3.08
Incis. Fora. L.	4.63–4.90	4.50–4.80	4.47–4.79	4.41–4.80	4.30–4.68
Max. Tooth. L.	3.50–3.78	3.70–3.90	3.60–3.73	3.42–3.71	3.35–3.60

and Lake St. John appear to be slightly larger in most characters, and are marked by a difference in the color of the pelage.

Breadths of the interorbital and rostral regions exhibit nonclinal variation. Populations from the Upper Peninsula of Michigan have a very narrow interorbital region (breadth 4.00-4.28 mm). North of the Great Lakes and the St. Lawrence River, population means average around 4.4 mm (4.30-4.63), and to the south in the eastern half of the range, 4.7 mm (4.43-4.85). Rostral breadth in specimens from Minnesota, Wisconsin, and Michigan averages 4.20 mm (4.17-4.31), while specimens on the opposite side of Lake Superior in Ontario average 4.70 mm (4.66-4.83). Populations in the New England States and southeastern Canada reveal a rostral breadth less than 4.60 mm (most about 4.5). Samples from three populations from Prince Edward Island (n = 18) average 4.81 mm (4.80-4.82).

COLOR

Napaeozapus exhibits both clinal and nonclinal variation in color. Individuals occurring south of West Virginia are characterized by a reddish tint, apparent in the dorsal stripe as well as on the sides. North to Pennsylvania is a zone of intergradation in which the lateral coloration becomes progressively yellower, with various populations showing intermediate shades and both extremes. From Ohio and Pennsylvania to the extreme southern parts of Ontario and Quebec, the Gaspé, Maritime Provinces, and New England States, specimens are yellowish orange on the sides and dark brown to blackish on the dorsum. Along the north shore of the St. Lawrence, from the Lake St. John region to Hamilton Inlet, Labrador, individuals are yellow on the sides and have black ears. Westward across central Quebec and Ontario, woodland jumping mice show a greater number of black hairs on the yellowish-orange sides and usually have a white border on the edge of the ears. Pale sides, dark dorsum and white ear-edging distinguish the animals from Minnesota, Wisconsin, and Michigan. These color descriptions are representative of the majority of individuals in each subspecies. Examination of a large series of specimens from one region often shows specimens that are within the range of color variation of other subspecies, except for the white ear margins of the northwestern populations.

VI. ACCOUNTS OF SUBSPECIES

GENUS *NAPAEOZAPUS* PREBLE — Woodland Jumping Mouse.

Napaeozapus Preble (as a subgenus of *Zapus*), 1899:33. Type *Zapus insignis* Miller.

Napaeozapus, Miller (regarded as genus), 1899:330.

Zapus insignis Miller (1891:742). Type from Restigouche, New Brunswick (BMNH).

Napaeozapus insignis abietorum (Preble)

Zapus (Napaeozapus) insignis abietorum Preble (1899:36).

Napaeozapus insignis abietorum, Miller (1900:114).

Type. Adult male, No. 4268, collection of G. S. Miller, Jr., now deposited in the British Museum (Natural History). Collected by G. S. Miller, Jr., on September 27, 1896, at Peninsula Harbor, north shore of Lake Superior, Thunder Bay District, Ontario. Type not examined.

Range. From north shore of Lake Superior and Lake Nipigon region of Ontario, north to lower James Bay, east to lakes Albanel and Mistassini, Quebec, then southwest to Laniel, Quebec, west to Lake Nipissing, Ontario, and along the north shore of lakes Huron and Superior.

Diagnosis. Size very large, with rostral breadth and maxillary tooth-row averaging greater than in any other subspecies; interorbital region

small. Color of sides yellowish orange with numerous dark guard hairs resulting in an undefined dorsal stripe; ears often with white edging.

Mean and range (in millimeters) of external and cranial characters in 17 specimens from Thunder Bay District are: Total L., 244.8 (232-263); Tail L., 153.2 (142-161); Hind Foot, 31.9 (31-34); Great. Skull L., 24.85 (24.4-25.5); Condylobasal L., 21.35 (20.8-21.9); Zygomatic L., 10.41 (10.1-10.7); Zygomatic B., 12.78 (12.2-13.3); Mastoid B., 11.02 (10.4-11.5); Braincase B., 11.38 (11.1-11.8); Nasal L., 10.37 (10.0-10.6); Rostral B., 4.66 (4.4-5.0); Interorbital B., 4.39 (4.1-4.6); Bony Palate L., 3.49 (3.2-3.8); Incisive Foramina L., 4.72 (4.4-5.0); Maxillary Toothrow, 3.74 (3.6-3.9).

Comparisons. N. i. abietorum differs from *N. i. insignis* (northern populations composed of large individuals) in: slightly longer tail and hind foot; slightly larger in many cranial characters, particularly greatest length of skull and condylobasal and zygomatic lengths, zygomatic breadth and maxillary toothrow; larger (0.18 mm) in nasal length; interorbital breadth much smaller, with no overlap in population means (4.30-4.45 mm in *abietorum*, 4.51-4.85 mm in *insignis*). Color of sides usually darker due to greater density of black hairs; ears often with a white border.

Compared to *N. i. frutectanus, N. i. abietorum* is considerably larger in tail and hind foot lengths, condylobasal and nasal lengths, breadths of zygoma, braincase and rostrum; other characters equal to or slightly larger than *frutectanus; abietorum* lacks pale colors, sharply defined dorsal stripe and blackish face of *frutectanus*.

For comparison with *N. i. saguenayensis* and *N. i. roanensis*, see accounts of those subspecies (pp. 56 and 52).

Remarks. Along with *N. i. saguenayensis, N. i. abietorum* consists of the largest animals of the species. Individuals from Thunder Bay District are greater in size than other populations of the subspecies. Morphologically, the race is readily distinguishable from *insignis* and *frutectanus.* The high degree of color variation in *abietorum* reduces the value of this character. Many individuals, particularly along the southern boundary of the subspecies, are identical in coloration to *insignis* while others come within the range of *frutectanus*.

The range of *abietorum* in central Ontario and Quebec is poorly known. The few specimens available from these regions do not permit an adequate study of variation in color or morphology.

Specimens examined. Total number, 213, from: ONTARIO. THUN-DER BAY DIST.: 90 mi. N Port Arthur, 1 (UI); Rossport, Tp. 86, 9 (ROM), 1 (MVZ); Silver Islet, Sibley Tp., 1 (NMC); Peninsula, Pie Tp.,
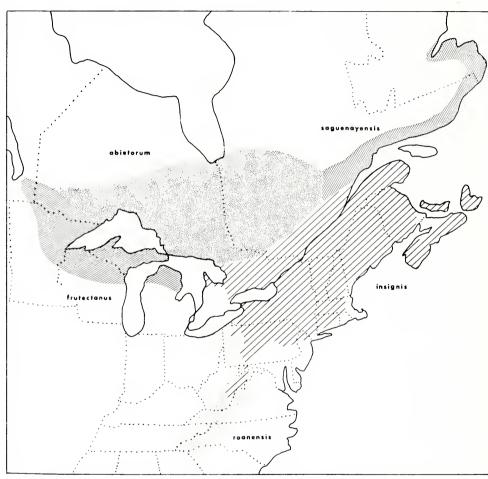
FIG. 14. Geographic distribution of the subspecies *abietorum, saguenayensis, frutectanus, insignis,* and *roanensis* of *Napaeozapus insignis*.

Fig. 15. Distribution of *Napaeozapus*. Each dot represents one specimen or more from a single location or several neighboring localities. Included are records of specimens examined, and additional records. The stars represent sites of Pleistocene deposits which have yielded remains of *Napaeozapus*.

1 (ROM); Macdiarmid, Lake Nipigon, 3 (ROM); Sturgeon River, S Lake Nipigon, 2 (ROM); Murillo, Oliver Tp., 1 (ROM); Schreiber, 1 (ROM); Terrace Bay, 4 mi. E Schreiber, 2 (ROM); Nakina, 1 (ROM); COCHRANE DIST.: Albany River, 20 mi. E Kenogami River, 1 (ROM); Coral Rapids, Hamlet Tp., 1 (ROM); Onakawana, Dyer Tp., 7 (ROM); Fraserdale, Pinard Tp., 12 (ROM); Smoky Falls, Harmone Tp., 50 mi. NNE Kapuskasing, 2 (ROM); Ghost River, Rand Tp., Lake Abitibi, 1 (ROM); Low Bush, Purvis Tp., Lake Abitibi, 1 (ROM); Moosonee, 1 (ROM); ALGOMA DIST.: Swampy Ground Portage, Missinaibi River, Coderre Tp., 2 (CMP); 1.1 mi. ESE Aubrey Falls, Mississagi River, 1 (KU); Carp Lake, Fisher Tp., 18 (NMC); Pancake Bay, Lake Superior, 46°57′N, 84°41′W, 68 (NMC); MacLennan, Tarbutt Adl. Tp., 1 (ROM); TIMISKAMING DIST.: 7 mi. W King Kirkland, Label Tp., 1 (ROM); 1 mi. W King Kirkland, 4 (ROM); Hough Lake, Savard Tp., 2 (ROM); SUDBURY DIST.: Wakimika Lake, Shelburne Tp., 1 (NMC); West Bay, Wanapitei Lake, Norman Tp., 1 (ROM); Bigwood, Bigwood Tp., 1 (ROM); Sadler Tp., 2 (ROM); PARRY SOUND DIST.: French River, S of Sudbury, 1 (ROM); Frank Bay, Lake Nipissing, 9 (ROM); NIPISSING DIST.: Timagami, 13 (ROM); Portage Bay, Timagami, 3 (ROM); Mc-Clean Peninsula, Timagami, 4 (ROM); Cross Bay, Lake Timagami, 4 (ROM); Island Bay, Lake Timagami, 2 (ROM); Balsam Creek, 25 mi. NE North Bay, 2 (ROM); Jocko Lake, Osborne Tp., 1 (ROM); Aileen Stream, Vogt Tp., 2 (ROM); Gull Lake, Torrent, Scholes Tp., 4 (ROM); Pike Lake, Bastedo Tp., 1 (ROM); Trout Lake, East Ferris Tp., 1 (ROM); Obabika Lake, Belfast Tp., 1 (NMC).

QUEBEC. ABITIBI Co.: Lake Albanel, 2 (NMC); 1 mi. N Mistassini Post, 2 (NMC); WEST ABITIBI Co.: 5 mi. E Duparquet, 3 (ROM); EAST ABITIBI Co.: Obalski, 2 (RM); 15 mi. N Senneterre, 1 (ROM); TEMISCAMING Co.: 10 mi. W Arntfield, Hert Lake, 1 (ROM); 3 mi. S Laniel, 2 (ROM); 6 mi. S Laniel, 1 (ROM).

Additional Records. ONTARIO. THUNDER BAY DIST.: Peninsula Harbor, 1 (BMNH) — Type specimen; NIPISSING DIST.: North Bay, 6 (BMNH).

Napaeozapus insignis frutectanus Jackson

Napaeozapus insignis frutectanus Jackson (1919:9).

Type. Adult male, No. 227349 United States National Museum. Collected by H. H. T. Jackson on September 6, 1917, original number 896, from Crescent Lake, Oneida County, Wisconsin. Type examined.

Range. Extreme southeastern Manitoba to Rainy River District of Ontario, northeastern Minnesota, the northern half of Wisconsin, the

entire Upper Peninsula of Michigan, and the upper third of the Lower Peninsula of Michigan.

Diagnosis. Size medium, about the size of large northern *N. i. insignis* in external and cranial characters; length of bony palate large; breadths of rostrum and interorbital area small. Sides dull yellow or clay color, with numerous black hairs; dorsal stripe dark and sharply defined; face and rostrum dark; borders of ears white; white terminus of tail relatively short.

Mean and range (in millimeters) of external and cranial characters in 16 specimens from the Lower Peninsula of Michigan are: Total L., 234.7 (205-250); Tail L., 145.5 (119-155); Hind Foot, 30.7 (29-33); Great. Skull L., 24.34 (22.9-25.3); Condylobasal L., 20.86 (20.5-21.8); Zygomatic L., 10.16 (9.4-10.7); Zygomatic B., 12.35 (11.4-12.7); Mastoid B., 10.84 (10.5-11.2); Braincase B., 10.99 (10.6-11.3); Nasal L., 9.87 (9.2-10.6); Rostral B., 4.31 (3.9-4.5); Interorbital B., 4.45 (4.2-4.8); Bony Palate L., 3.33 (3.1-3.6); Incisive Foramina L., 4.73 (4.3-5.0); Maxillary Toothrow 3.70 (3.4-3.9).

Comparisons. N. i. frutectanus differs from *N. i. saguenayensis* in: smaller size in every character except bony palate and maxillary toothrow lengths. There is no overlap in the ranges of population means of the two races in the following characters: total, tail, and hind foot lengths, breadths of zygoma, mastoid, braincase, rostrum, and nasal length. The other characters average considerably smaller in *frutectanus. N. i. saguenayensis* lacks the pale lateral color, dark, sharply defined dorsal stripe, black face and white edging on the ears characteristic of *frutectanus.*

Compared to *N. i. roanensis, N. i. frutectanus* averages smaller in rostral and interorbital breadths, but larger in all other characters. The following characters are considerably larger, so that the ranges of population means of the two races do not overlap: greatest skull length, condylobasal length, lengths of zygoma, bony palate, and breadths of the mastoids, braincase and zygoma. The pale lateral pelage, dark face, and white ear borders of *frutectanus* contrast with the dark reddish orange of southern *roanensis* and the yellowish orange of northern *roanensis,* which have less dark coloration on the face and dark orangish-brown ear edging.

For comparison with *N. i. abietorum* and *N. i. insignis,* see accounts of those subspecies (pp. 36 and 43).

Remarks. The races *N. i. frutectanus, saguenayensis,* and *roanensis* occupy the three distant corners of the triangular range of the species. Separated by water and ecological barriers or intervening populations,

their isolation is reflected in the degree of divergence in morphology and color.

Specimens of *frutectanus* from the Lower Peninsula of Michigan are slightly larger in body size and have a more robust skull than specimens from the Upper Peninsula and three individuals from adjacent Wisconsin (Woods Creek, Crescent Lake, and Kelly Lake). Fourteen specimens from Minnesota and extreme northwestern Wisconsin average slightly larger than the sample from the Lower Peninsula of Michigan in length of hind foot, and in the various dimensions of skull length.

A record of *Napaeozapus* from Turkey Run, Parke Co., Indiana (UMMZ 65310) is not considered valid in this study. The locality is over 300 miles from the known range of the species in Wisconsin, Michigan, and Ohio. Subsequent trapping in the supposed area of capture has failed to produce further specimens (Mumford, 1969). The specimen is a subadult, and may be referred to *N. i. frutectanus* on the basis of small interorbital and rostral breadths.

Specimens examined. Total number, 93, from: MANITOBA. Cedar Lake, 2 mi. N Vivian, 1 (UAMZ); Caddy Lake, Whiteshell Forest Reserve, 1 (UAMZ).

ONTARIO. RAINY RIVER DIST.: Rainy River, 1 (ROM).

MINNESOTA. CLEARWATER Co.: Itasca State Park, 1 (MMNH); ST. LOUIS Co.: Pelican Lake, 1 (MMNH); COOKE Co.: Sawbill Lake, 9 (MMNH); CARLTON Co.: Cloquet, 1 (USNM); Cloquet Forest, 2 (MMNH); CROW WING Co.: Upper Long Lake, 1 (MMNH).

WISCONSIN. BAYFIELD Co.: Herbster, 1 (USNM); Basswood Lake, 10 mi. SE Iron River, 1 (USNM); BURNETT Co.: Danbury, 1 (USNM); ONEIDA Co.: Crescent Lake, 1 (USNM); FLORENCE Co.: Woods Creek, 1 (UMMZ); OCONTO Co.: Kelly Lake, 2 (USNM); Lakewood, 3 (USNM); CLARK Co.: Withee, 1 (USNM); Worden Tp., 1 (AMNH).

MICHIGAN. GOGEBIC Co.: Fish Hawk Lake, 5 (UMMZ), 1 (MCZ); ONTONAGON Co.: 3 (UMMZ); MARQUETTE Co.: Huron Mt., 1 (UMMZ); LUCE Co.: Two Hearted River, 18 mi. N Newberry, 1 (UMMZ); CHIPPEWA Co.: Sugar Island, 1 (UMMZ); MENOMINEE Co.: 8 mi. N Hermansville, 1 (UMMZ); 5 mi. E Daggett, 2 (UMMZ); 6 mi. NW Banat, 3 (UMMZ); 8 mi. SW Banat, 2 (UMMZ); 13 mi. WSW Stephenson, 3 (UMMZ); 7 mi. E Stephenson, 3 (UMMZ); 5 mi. SW Cedar, Hayward Bay, 2 (UMMZ); 5 mi. N Menominee, 19 (UMMZ); EMMET Co.: Game Refuge, Big Stone Bay, 1 (CUM); CHEBOYGAN Co.: Burt Lake, Carp Creek, 1 (CUM); Douglas Lake, 2 (UMMZ), 1 (ROM); PRESQUE ISLE Co.: Barnhardt Lake, 4 (UMMZ); CHARLEVOIX Co.: Boyne Falls, 6 (UMMZ);

Montmorency Co.: Valentine Lake, 2 (mvz); Oscoda Co.: S Branch of Au Sable River, 1 (ummz).

Additional Records. MINNESOTA. Pine Co.: Cloverdale, 1 (Beer, 1953); Lake Co.: (Beer, 1953).

WISCONSIN. Price Co.: 2 (Jackson, 1961, p. 269); Sawyer Co.: Teal Lake, 1 (Jackson, 1961, p. 269); Portage Co.: Jordan Pond Cedar Swamp, 1.5 mi. E Jordan Pond, 1 (Long, 1970).

MICHIGAN. Crawford, Alcona Cos.: (Burt, 1946); Marquette Co.: 4 mi. W Marquette, 1 (msu); Huron Mountain, 1, in alcohol (ummz); Alger Co.: Cusino State Game Area (Blair, 1941); Charlevoix Co.: Pigeon River Trout Res. Sta., 4 (msu); Kalkaska Co.: 7 mi. E Kalkaska, 2 (msu); Gogebic Co.: Lindsley Lake, 1, in alcohol (ummz).

Napaeozapus insignis insignis (Miller)

Zapus insignis Miller (1891:742).

Napaeozapus insignis, Miller (1899:330).

Napaeozapus insignis algonquinensis Prince (1941:1). Type from Smoke Lake, Algonquin Park, Ontario (No. 14730 Royal Ontario Museum). Type examined.

Napaeozapus insignis gaspensis Anderson (1942:39). Type from Federal Zinc and Lead Mine, about 1,500 feet elevation, on upper waters Berry Mountain Brook, a tributary of Grand Cascapedia River, Shickshock Mountains, about halfway between Gulf of St. Lawrence and Baie de Chaleur, Gaspé Co., Quebec (No. 4786 National Museum of Canada). Type examined (see Remarks).

Type. Adult male. No. 464/387 collection of G. S. Miller, Jr., now in British Museum (Natural History). From Restigouche River, Restigouche Co., New Brunswick, collected by E. A. Bangs on September 10, 1880. Topotype examined but not type specimen.

Range. Southern Ontario south of Lake Nipissing, to Lake Edward, Quebec Co., Quebec, the Gaspé Peninsula, New Brunswick, Prince Edward Island, Nova Scotia, south to northern New Jersey, northeastern and central Pennsylvania, and eastern West Virginia.

Diagnosis. External and cranial features of medium size for the species; rostral and interorbital breadths relatively great. Lateral pelage bright yellowish orange; dorsal stripe dark brown, occasionally blackish; edging of ears brownish orange.

Mean and range (in millimeters) of external and cranial characters in 89 specimens from the vicinity of South Bolton, Brome Co., Quebec,

are: Total L., 229.3 (212-252); Tail L., 139.2 (128-158); Hind Foot L.,
30.5 (28-32); Great. Skull L., 23.73 (22.5-24.8); Condylobasal L., 20.45
(19.4-21.6); Zygomatic L., 9.80 (9.1-10.4); Zygomatic B., 12.25 (11.5-
13.0); Mastoid B., 10.73 (10.0-11.3); Braincase B., 10.81 (10.2-11.4);
Nasal L., 9.53 (8.8-10.2); Rostral B., 4.52 (4.1-5.0); Interorbital B.,
4.69 (4.4-5.1); Bony Palate L., 3.12 (2.8-3.7); Incisive Foramina L.,
4.66 (4.4-5.2); Maxillary Toothrow, 3.54 (3.3-3.9).

Comparisons. *N. i. insignis* differs from *N. i. frutectanus* in: consid-
erably larger rostral and interorbital breadths (no overlap in the
ranges of population means); much smaller in greatest length of skull,
zygomatic length, and bony palate length; in most other characters the
range of variation of *insignis* includes that of *frutectanus*. In colora-
tion, *insignis* lacks the pale yellowish tint on the sides, white edging on
the ears, and blackish face of *frutectanus*.

Compared to *N. i. saguenayensis*, *N. i. insignis* has a larger inter-
orbital breadth, is slightly smaller in total length (shorter tail and
body), hind foot, incisive foramen and maxillary toothrow, and is
much smaller in all other characters. There is no overlap in the range
of population means of the two subspecies in greatest skull length and
lengths of the zygoma and nasals, breadths of the zygoma and brain-
case. Color of *insignis* seldom is as yellow on the sides and black on
the ears as in *saguenayensis;* the dorsal stripe usually is more sharply
defined in *insignis*.

For comparison with *N. i. abietorum* and *N. i. roanensis*, see accounts
of those subspecies (pp. 36 and 52).

Remarks. *N. i insignis,* as here recognized, excludes the small-sized
populations of Ohio, western sections of Pennsylvania, New York, and
Maryland, while including populations in eastern West Virginia. Rea-
sons for these changes are discussed in the account of *N. i. roanensis*.

The subspecies *N. i. gaspensis* from the Gaspé and *N. i. algonquin-
ensis* from southern Quebec, north of the St. Lawrence, and southern
Ontario, were segregated from *insignis* mainly on the basis of color dif-
ferences which I fail to detect, considering the variation found in *in-
signis*. Specimens from the extreme southern part of the range in On-
tario are almost identical in size and color to specimens from extreme
southern Quebec and adjacent New York, and much of New England.
Slightly farther north, a comparison of populations from (1) the Gaspé,
(2) Lake Edward, Quebec Co., Quebec, and (3) Algonquin Park, Nipis-
sing Dist., Ontario, shows identical means in total length (233 mm) and
tail length (145 mm). Cranial characters are also very similar, with
some minor differences — specimens from the Gaspé average larger in

interorbital breadth (about 0.2 mm), and specimens from Ontario are smaller in greatest skull length, nasal length, and breadths of braincase and zygoma.

Most individuals of *N. i. gaspensis* and *N. i. algonquinensis* are relatively large compared to typical *insignis*. But in the absence of any appreciable gap in clines of increasing size northward, it seems preferable to reunite *gaspensis* and *algonquinensis* within the nominate race. This results in a subspecies *insignis* with a greater range of size in external and cranial characters than the other races.

An area of rapid change in many characters exists between *N. i. insignis* from southern Ontario and *N. i. abietorum* in the vicinity of Lake Nipissing. There are so few specimens from similar latitudes in Quebec that the range of the two races and degree of intergradation are unknown. In the east, a large sample of *insignis* from Lake Edward appears to be well differentiated morphologically from *saguenayensis;* however, this may be due partly to the lack of knowledge of variation in *saguenayensis* since less than 25 specimens have been collected.

In the eastern part of the range, there is present a cline of increasing size from eastern Pennsylvania and New Jersey to the Gaspé and the Maritime Provinces. Populations at opposite ends of the cline are considerably different, though isophene lines drawn for all 15 characters show no consistent areas of character discontinuity.

The type specimen of *N. i. gaspensis* (NMC 4786) has the following measurements on the label: total length, 248 mm; tail length, 155 mm; hind foot, 31 mm. Anderson (1942:40) reported different lengths in the original description (240-150-30). The latter measurements are identical to the specimen 4798 NMC (skull missing) from Ste. Anne River, Gaspé, collected several weeks later.

Specimens examined. Total number, 1,953, from: ONTARIO. PARRY SOUND DIST.: Ardbeg, 1 (AMNH); E Shore Pickerel Lake, 7 mi. NE Burk's Falls, 8 (CMNH), 7 (ROM); Katrine Sta., Armour Tp., 1 (ROM); Noganosh Lake, Brown Tp., 5 (ROM); Sundridge, Bernard Lake, 1 (ROM); Gordon Bay, 8 (ROM); Arnstein, Mills Tp., 1 (ROM); South Bay, Lake Nipissing, 1 (ROM); NIPISSING DISTRICT: Little Nipissing River, 1 (ROM); Lake Canisbay, Canisbay Tp., 1 (USNM); Lake Sasajewan, Canisbay Tp., 1 (USNM), 48 (ROM); Source Lake, Canisbay Tp., 2 (ROM); Cache Lake, Canisbay Tp., 31 (ROM); Lake of Two Rivers, Canisbay Tp., 5 (ROM); Algonquin Park, Canisbay Tp., 1 (NMC), 3 (ROM); Smoke Lake, Peck Tp., 16 (ROM); Canoe Lake, Peck Tp., 10 (ROM); Joe Lake, Peck Tp., 1 (ROM); Brewer Lake, Sproule Tp., 1 (ROM); Opeongo Lake, Bower Tp., 4 (ROM); Brule Lake, Hunter

Tp., 3 (ROM); Long Lake, Bigger Tp., 6 (ROM); Butt Lake, Butt Tp., 2 (ROM); Lister Tp., 1 (ROM); BRUCE Co.: Red Bay, 2 (ROM); Southhampton, 1 (ROM); GREY Co.: Eugenia, 1 (ROM); Bentinck Tp., 1 (ROM); MUSKOKA DISTRICT: Lake of Bays, Franklin Tp., 1 (ROM), 1 (USNM); Lake Solitaire, Huntsville, 16 (ROM); Redwood, Medora Tp., 1 (ROM); Dorset, 2 (ROM); Port Sydney, Stephenson Tp., 3 (ROM); HALIBURTON Co.: Mountain Lake, Cardiff Tp., 3 (ROM); Haliburton, Dysart Tp., 11 (ROM); Minden, Minden Tp., 2 (ROM); Haliburton Lake, Harburn Tp., 1 (ROM); Boshkung Lake, Stanhope Tp., 1 (ROM); RENFREW Co.: Combermere, 2 (NMC); Golden Lake, N Algona Tp., 2 (ROM); Bark Lake, Jones Tp., 1 (ROM); DUFFERIN Co.: 1 mi. W Glen Cross, 1 (ROM); WENTWORTH Co.: 3 mi. W Freelton, 1 (ROM); PEEL Co.: Credit Forks, Caledon Tp., 20 (ROM); YORK Co.: Nancy Lake, 2 (ROM); Aurora, 2 (ROM); ONTARIO Co.: Glen Major, Brock Tp., 6 (ROM); HASTINGS Co.: Bird Creek, Herschel Tp., 1 (ROM); 2 mi. E Fuller, Huntingdon Tp., 2 (ROM); ADDINGTON Co.: Buckshot Lake, Abinger Tp., 1 (ROM); FRONTENAC Co.: Arden, Kennebec Tp., 1 (CUM); Plevna, 10 (ROM); CARLETON Co.: Ottawa, 1 (NMC).

QUEBEC. QUEBEC Co.: Lake Edward, 1 (MCZ), 46 (ROM); CHAR-LEVOIX Co.: Camp de la Roche, Laurentides Park, 47°41'N, 70°50'W, 1 (QWS); GATINEAU Co.: Whitefish Lake, 2 (ROM), Lac Ste. Marie, 2 (ROM); Lac Philip, Gatineau Park, 2 (NMC); St. Charles Lake, Far-rellton Park, 2 (NMC); Gatineau River, 10 mi. below Gatineau Forks, 2 (NMC); Meach Lake, 6 mi. N Ottawa, 3 (NMC); Kazabazua, 6 (ROM); 7 mi. E Lepine Depot, 1 (ROM); 15 mi. W Mt. Laurier, 2 (ROM); LABELLE Co.: Lac des Sables, 1 (ANS); MONTCALM Co.: Lac Tremblant, 1 (RM); Mont Tremblant Lodge, 1 (JJC); 8 mi. S St. Donat, 1 (ROM); 1 mi. W Rawdon, 6 (ROM); 1 mi. E Rawdon, 1 (ROM); ARGENTEUIL Co.: 1 mi. NE St. Adolphe de Howard, 2 (ROM); VAUDREUIL Co.: 2 mi. S Rigaud, 1 (ROM); MATANE Co.: 10 mi. E Matane, 3 (CUM); WEST GASPÉ Co.: Gaspesian Provincial Park, Stream 2.5 mi. E of Hotel, 3 (KU); Mt. Albert, 4 (AMNH), 3 (NMC), 3 (RM), 2 (ROM); Ste. Anne des Monts, 3 (AMNH); Ste. Anne River, 2 (NMC); Lac Ste. Anne, 3 (RM); Cap Chat, 1 (NMC); 2 mi. W Cap de la Madeleine, 1 (NMC); Berry Mt. Brook, Cascapedia River, 2 (NMC); EAST GASPÉ Co.: 2 mi. W Coin de Banc, 1 (USNM); Percé, 3 (CUM), 1 (NMC); Cortoreal, 2 (NMC); St. Helier, 5 (NMC); MATAPEDIA Co.: 1 mi. E Causapscal, 1 (UI); BONAVENTURE Co.: Cascapedia, 7 (NMC); 1 mi. N Carleton, 2 (CUM); Red Camp, 8 mi. up Cascapedia River, 21 (AMNH), 2 (RM); Middle Camp, 12 mi. up Cascapedia River, 12 (AMNH); New Derreen, 20 mi. up Cascapedia River, 11 (AMNH); 12 mi. N Grand Cascapedia, 1 (NMC); 15 mi. N Grand Cascapedia, 1 (NMC);

Port Daniel Provincial Park, 2 (RM); TEMISCOUATA Co.: Ste. Rose, 5 (USNM); CHAMBLY Co.: Mt. Bruno, 1 (RM); ROUVILLE Co.: Mt. St. Hilaire, 6 (RM), 3 (CUM), 1 (NMC); Mt. Yamaska, 9 (RM), 1 (UI); SHEFFORD Co.: Mt. Shefford, 2 (RM); STANSTEAD Co.: Mt. Orford, 2 (NMC); BROME Co.: South Bolton, 36 (NMC), 33 (UI); Glen Mountain, 1 (NMC); Glen Sutton, 6 (NMC); Mt. Echo, 2 (NMC); 3 mi. E Sutton, 14 (ROM); COMPTON Co.: Megantic Mountain, 9 (NMC); RICHMOND Co.: 2 mi. SSW Upper Melbourne, 2 (ROM); Not Located: Danford Lake, 2 (NMC); Kingsmere, 1 (NMC).

NEW BRUNSWICK. MADAWASKA Co.: Baker Lake, 2 (NMC); 6 mi. N St. Leonard, 2 (NMC); GLOUCESTER Co.: 15 mi. SE Bathurst (Miramichi road), 12 (NMC); VICTORIA Co.: Fork of the Tobique River, 3 (AMNH) · W side St. John River, 1.5 mi. S Andover, 2 (UI); Tobique, 1 (NBM); YORK Co.: Scotch Lake, 1 (NMC); McAdam, 2 (MVZ); Little Digdequash, 1 (NBM); Fredericton, 3 (NBM); KINGS Co.: Lakeside, 1 (AMNH); Browns Flats, 3 (NBM); CHARLOTTE Co.: St. Andrews, 2 (NMC); ALBERT Co.: Fundy National Park, 4 (SUCO); ST. JOHN Co.: St. John, 6 (NBM); RESTIGOUCHE Co.: Restigouche River, 1 (MCZ); Upsalquitch, 2 (NBM); 2 mi. SW Jacquet River, 1 (ROM); NORTHUMBERLAND Co.: Dungarvon Bridge, 4 (NBM); Greystone, 1 (NBM); KENT Co.: Rexton, 1 (NBM).

PRINCE EDWARD ISLAND. PRINCE Co.: 1 mi. NE Alma, 3 (UI); QUEENS Co.: 5 mi. S Hunter River, 13 (UI); KINGS Co.: Fortune, 2 (NMC).

NOVA SCOTIA. INVERNESS Co.: West Mabou, 6 (NMC); Frizzleton, 1 (NMC); 1 mi. N Frizzleton, 3 (UI); West Bay, Cemetery Brook, 6 (RM); VICTORIA Co.: 2 mi. W Cape North, 3 (UI); Cape North, 1 (NMC); Boularderie, 1 (PM); ANTIGONISH Co.: James River, 3 (USNM), 4 (MCZ); ANNAPOLIS Co.: 2 mi. S South Milford, 2 (AMNH); 1 mi. W Maitland Bridge, 1 (UI); Lake Kejimkujik, 8 (USNM), 8 (MCZ), 16 (UMMZ); QUEENS Co.: New Grafton, 3 (UI); HALIFAX Co.: Bicentennial Drive, 1 (RM); Halifax, 3 (MCZ), 1 (UMMZ); Moser River, 4 (ROM); SHELBURNE Co.: Barrington Passage, 2 (NMC).

NEW YORK. ST. LAWRENCE Co.: 4.5 mi. SE Norfolk, 5 (NYSM); 2 mi. N Brasher, 1 (NYSM); 2 mi. SE Winthrop, 1 (NYSM); 5 mi. SW Hopkinton, 1 (NYSM); Wilson Hill G.M.A., 1 (NYSM); 2 mi. NW Louisville, 1 (NYSM); 2 mi. N Stark, 2 (NYSM); FRANKLIN Co.: Axton, 1 (CUM), 1 (UMMZ); 2 mi. W Saranac Lake, 2 (CUM); Saranac Inn, 1 (CUM); Moose Pond, Saranac Lake, 5 (AMNH); Tupper Lake, 10 (MVZ), 1 (CMP); Spectacle Pond, Brighton Tp., 6 (AMNH); ESSEX Co.: Elizabethtown, 1 (USNM); Keene Heights, 72 (MCZ); Beebe Brook, Keene, 1 (CUM), 1 (AMNH); Moose Pond, Newcomb, 3 (CUM); Panther

Gorge, 4 (CUM); Whiteface Mt., 6 (CUM); Franklin Falls, Whiteface
Mt., 2 (CUM); Adirondack Lodge, Road at Ausable River, 5 (AMNH);
Adirondack Lodge, Mt. Jo, 7 (NYSM); Heart Lake, 5 (NYSM); S Mea-
dowbrook, 7 mi. SE Lake Placid, 2 (CMP); Elk Lake, 8 (AMNH); New
Russia, 1 (AMNH), 3 (MVZ); St. Huberts, 7 (CMNH); 5 mi. WNW Wil-
mington, 1 (CUM); JEFFERSON Co.: 10 mi. N Carthage, 2 (CUM); LEWIS
Co.: 4 mi. NW West Leyden, 2 (NYSM); 6 mi. W West Leyden, 3
(NYSM); 5 mi. N Osceola, 2 (NYSM); 10 mi. W Houseville, 10 (NYSM);
2.5 mi. W Houseville, 6 (NYSM); 0.75 mi. N Rector, 2 (NYSM); Lyons
Falls, 1 (USNM); 3.5 mi. SW Martinsburg, 7 (NYSM); 4 mi. SW Low-
ville, 1 (NYSM); 6 mi. SW Lowville, 4 (NYSM); HERKIMER Co.: Old
Forge, 1 (CUM); HAMILTON Co.: Indian Lake, 10 (NYSM), 2 (CUM);
Raquette Lake, 1 (AMNH); 4 mi. W Blue Mountain Lake, 1 (UI); Lake
Eaton, 3 (KU); Blue Mountain Lake, 1 (MVZ); Piseco, 5 (USNM);
WARREN Co.: Lake George, 1 (USNM); GENESEE Co.: Bergen Swamp,
1 (CUM); CAYUGA Co.: 2.5 mi. SW Victory, 1 (NYSM); MADISON Co.:
Hamilton, 2 (UI); Peterboro, 2 (MCZ), 3 (SUCO); SCHENECTADY Co.:
Glenville, 1 (USNM); WASHINGTON Co.: Erebus Mt., 3 (CUM);

TOMPKINS Co.: Ithaca, 62 (JOW), 6 (CUM), 1 (SUCO); Ithaca, Bald
Hill, 25 (CUM); Ithaca, Connecticut Hill, 3 (CUM); Enfield Gorge,
Ithaca, 1 (CUM); 5 mi. Rt. 13, vic. Ithaca, 1 (CUM); Ringwood,
Ithaca, 8 (CUM), 1 (PM); Smiley's Woods, 1 mi. E Varna, 5 (CUM);
Cayuga Inlet, 1 (JOW); Caroline Centre, 2 (AMNH); W Airport, 2
mi. N Dillwoods, 1 (CUM); McLean Preserve, 2 (CUM), 1 (NYSM),
1 (JOW); Dryden, 2 (CUM); Ellis Hollow, 1 (PM); OTSEGO Co.: Coop-
erstown, 1 (SUCO); 4 mi. N Cooperstown, 1 (NYSM); Gilbert Lake
State Park, 5 (NYSM); 1 mi. S Milford, 1 (NYSM); Burlington, 2
(NYSM); Oneonta, 3 (SUCO), 1 (JOW); 3 mi. N Oneonta, 2 (SUCO);
SCHOHARIE Co.: 3 mi. SE Cobleskill, 4 (NYSM); 2 mi. W, 1 mi. N
North Blenheim, 4 (NYSM); 1 mi. W, 0.5 mi. N Summit, 4 (NYSM);
5 mi. E, 1.75 mi. N Jefferson, 2 (NYSM); ALBANY Co.: Rensselaerville,
5 (CUM), 2 (UI); Thacher Park Res., 1 (NYSM); RENSSELAER Co.:
Berlin, 26 (AMNH); Berlin Mt., 6 (NYSM); Babcock Lake, vic. Peters-
burg, 5 (NYSM); East Poestenkill, 1 (NYSM); Grafton, 1 (NYSM);
Petersburg, 1 (NYSM); 0.5 mi. SW Dutch Church, 4 (NYSM); 2.5 mi.
NNE West Stephentown, 2 (NYSM); 1.75 mi. ESE West Stephentown,
1 (NYSM); 0.75 mi. N Hoag Corners, 1 (NYSM); GREEN Co.: Kaater-
skill Jct., 1 (USNM); Devils Tombstone, Hunter, 2 (NYSM); Hunter,
3 (CUM); Stony Clove, 4 (SUCO), 2 (CUM); Edgewood, 2 (NYSM);
Notch Lake, 3.5 mi. SSE Hunter, 16 (NYSM); Catskill, 1 (USNM);
ULSTER Co.: 3 mi. NW Lackawack, 3 (NYSM); 3 mi. SW Phoenicia,
7 (MVZ); W Branch Leanto, 3 (SUCO); Slide Mt., 23 (SUCO); SULLIVAN

Co.: Debruce, 2 (PM), 1 (CUM); Mongaup Creek, vic. Debruce, 8 (SUCO); PUTNAM Co.: 5.5 mi. E Cold Spring, 3 (NYSM); ORANGE Co.: Tuxedo, 1 (AMNH); Tamarack Swamp, 1 (USNM); Not Located: Chapel Pond, Brookside, Adirondacks, 1 (AMNH); Taylor Hollow, Hunter Mt., 1 (UI); Cascadeville, 4 (Preble, 1899, p. 35).

VERMONT. LAMOILLE Co.: Mount Mansfield, 9 (USNM); Smuggler's Notch, Mount Mansfield, 5 (USNM); Howe Brook, 2 mi. SE Smuggler's Notch, 2 (RM); ESSEX Co.: Brighton, 5 (UCM); 2 mi. NE Victory, 4 (UCM); CALEDONIA Co.: Lyndon, 4 (UMMZ); 8 mi. SW Lyndon, 2 (UCM); Lyndon Center, 18 (UCM); 8 mi. W Lyndon Center, 9 (UCM); Burke Mt., 1 (UMMZ); Hardwick, 8 (UCM); WASHINGTON Co.: Plainfield, 1 (UCM); Maple Hill, 1 (UCM); Woodbury, 29 (UCM); Greenwood Lake, 3 (UCM); 2 mi. SW Hardwick, 7 (UCM); ORANGE Co.: Ainsworth, 1 (UCM); Williamstown, 1 (UCM); Ely, 4 (ANS); RUTLAND Co.: Chittenden, 13 (AMNH); Mendon, 1 (CMP), 1 (AMNH), 22 (UCM); Mount Mendon, 4 mi. S Rutland, 11 (UCM); Sherburne Center, Mount Killington, 4 (CMP), 1 (USNM); Sherburne Center, 7 (UCM); Gully Brook, 3.1 mi. 131° from Castleton, 3 (CMP); 2.1 mi. 202° from Castleton, 2 (CMP); Herrick Mt., 3.2 mi. NW Ira, 3 (CMP); WINDSOR Co.: Woodstock, 1 (USNM); Pomfret, 1 (AMNH); WINDHAM Co.: Londonderry, 14 (UCM); Not Located: Bingham Falls, 3 (DCM).

NEW HAMPSHIRE. Coos Co.: Pittsburg, 2 (CMNH); Nathan Pond, 2 (UMMZ); 0.25 mi. W Randolph, Mt. Crescent, 1 (ANS); Mt. Washington, 17 (CUM); Base Station, Mt. Washington, 2 (USNM), 3 (MVZ); 3 mi. W Base Station, Mt. Washington, 8 (KU); Upper Hermit Lake, Mt. Washington, 4 (AMNH); Hermit Lake, Tuckerman Ravine, 5 (AMNH); Pinkham Notch, 2 (KU), 6 (AMNH), 4 (USNM); Fabyan, 3 (USNM); Dartmouth Brook, Bretton Woods, 1 (UMMZ); Crawford Notch, 2 (CUM); Jefferson Notch, 6 (ROM); GRAFTON Co.: Profile Lake, Franconia Notch, 6 (AMNH), 5 (UMMZ), 3 (MCZ), 6 (CUM); Franconia, 1 (MCZ); Mt. Moosilauke, 1 (CMNH); Gail River, near Bethlehem, 1 (MCZ); 3 mi. SW Lebanon, 4 (UMMZ); CARROLL Co.: Jackson, 11 (CMNH); Intervale, 1 (USNM), 1 (UMMZ); 2 mi. S Ossipee Center, 1 (USNM); Upweekis Chocoma Mt. (Chocorua Mt., ?), 3 (AMNH); CHESHIRE Co.: Jaffrey, 1 (CMNH); Dublin, 3 (MCZ); HILLSBOROUGH Co.: Antrim, 1 (MCZ).

MAINE. PISCATAQUIS Co.: Chimney Pond, Mt. Katahdin, 4 (USNM); Roaring Brook Camp, Mt. Katahdin, 6 (CUM), 15 (UMMZ), 2 (PM); Mt. Katahdin, 6 (AMNH), 3 (FM); King and Bartlett Lake, 9 (ANS); OXFORD Co.: Wilsons Mills, 8 (UI); Fryeburg, 1 (AMNH); Grafton, 1 (ROM); Not Located: Frost Pond, 1 (NMC).

PENNSYLVANIA. Erie Co.: Burgess Gulf, 4 mi. SW North East, 4 (CMP); Warren Co.: Benson Swamp, 5 mi. E Columbus, 3 (CMP); 1 mi. SE Garland, 1 (CMP); 1.5 mi. N Pittsfield, 1 (CMP); 10 mi. SE Warren, 1 (USNM); McKean Co.: Sugar Run, 10 mi. SW Bradford, 7 (CMP); 4 mi. N Clermont, 1 (CMP); Red Mill Brook, 4 mi. NE Clermont, 1 (CMP); Port Allegany, 1 (CUM); Bradford Co.: 6 mi. SSW Wyalusing, 1 (CMP); Susquehanna Co.: 9 mi. NW Montrose, 1 (CMP); Laurel Lake, 9 mi. NNW Montrose, 1 (CMP); 5.25 mi. N Montrose, 6 (CMP); Wayne Co.: Starlight, 8 (JJC); Balls Creek, 6.5 mi. NE Starrucca, 3 (CMP); Balls Creek, 5.5 mi. NE Starrucca, 1 (CMP); Pocono Peak, Lake Preserve, 3 mi. NE Gouldsboro, 1 (CMP); Lake Como, 1 (CMP); Island Lake, 2 (CMP); Mercer Co : 2 mi. N Clarks Mills, 2 (CMP); Venango Co.: McCrea Run, 9 mi. E Oil City, 7 (CMP); 1 mi. SW President, 1 (CMP); Jefferson Co.: 5.5 mi. NE Sigel, 12 (CMP); Lycoming Co.: Slacks Run, 1 mi. E Bodines, 2 (CMP); Sullivan Co.: Ogdonia Creek, 4.25 mi. SSE Hillsgrove, 13 (CMP); Ganoga Lake, 1 (CMP); Laporte, 1 (MVZ); Eagles Mere, 2 (ANS); Luzerne Co.: 8 mi. WNW Sweet Valley, 5 (CMP); Monroe Co.: Tributary of Brodhead Creek, 1 (ANS); Buck Hill Falls, 2 (CMP); 2.5 mi. NE Kresgeville, 3 (CMP); Mt. Pocono, 1 (ANS); 2 mi. NW Pocono Lake, 3 (CMP); Pocono Lake, 4 (CMP); Swiftwater, 6 (USNM); Pike Co.: 5 mi. SE Greentown, 4 (CMP); Indiana Co : 2.5 mi. SSE Indiana, 1 (CMP); 9 mi. SSE Indiana, 2 (CMP); Centre Co.: Gum Stump, 3.5 mi. NNW Wingate, 1 (CMP); 2.3 mi. SE Woodward, 2 (CMP); Coburn, 1 (MVZ); Union Co.: Penns Creek Mt., 1 mi. S Glen Iron, 3 (CMP); Schuylkill Co.: 0.75 mi. NE Port Clinton, 2 (CMP); Cambria Co.: Cresson, 1 (CMP); 5 mi. NNE Ebensburg, 3 (CMP); 1.75 mi. SW Patton, 4 (CMP); 2.5 mi. S Patton, 1 (CMP); Blair Co.: 3.25 mi. SE Tyrone, 1 (CMP); 4.5 mi. SE Tyrone, 1 (CMP); Huntingdon Co.: 1.5 mi. SSW Pennsylvania Furnace, 3 (CMP); 5.5 mi. NE McAlevys Fort, 4 (CMP); Mifflin Co.: 3 mi. WSW Milroy, 4 (CMP); 3.5 mi. WNW Milroy, 1 (CMP); Bedford Co.: 1.5 mi. W Imler, 1 (CMP); 7 mi. NW Imler, 3 (CMP); 1 mi. NE Osterburg, 3 (CMP); Berks Co.: 2.5 mi. NNW Shartlesville, 1 (CMP).

MASSACHUSETTS. Berkshire Co.: North Park Field Farm, 5 mi. S Williamstown, 1 (MVZ); Mount Washington, 6 (AMNH); Mt. Greylock, 1 (MCZ); Franklin Co.: Roaring Brook, 6.5 mi. NE Amherst, 2 (KU).

CONNECTICUT. Litchfield Co.: Sage Ravine, Bear Mt., 3 (AMNH); Mt. Riga, 2 (UCM); Sharon, 5 (AMNH); Macedonia Park, 4 (AMNH); Norfolk, 6 (UCM); Lime Rock, 1 (UCM); Catlin's Woods, White Memorial Forest, 2 (UCM); Kent, 7 (CUM); Colebrook, 2

(MCZ); TOLLAND Co.: Cedar Swamp, 2 mi. N Storrs, 1 (UCM); Pink Ravine, Storrs, 1 (UCM); 2 mi. NW Storrs, 1 (UCM); Storrs, 1 (UCM); 1 mi. E Storrs, 7 (UCM); Hemlock Ravine, Bigelow Hollow State Park, 3 mi. E Union, 3 (UCM); Bigelow Hollow Brook, 1 (UCM); Maple Road, 1 mi. from S Eagleville Road, 5 (UCM); Charter Marsh, Tolland, 2 (UCM); WINDHAM Co.: Pomfret, 1 (KU); South Woodstock, 3 (AMNH); Ashford, 1 (UCM); Brooklyn, 2 (UCM); Plainfield, 1 (PM); FAIRFIELD Co.: New Fairfield, 1 (UCM); MIDDLESEX Co.: Meshomasic State Forest, 4 (UCM); Portland, 2 (UCM).

NEW JERSEY. SUSSEX Co.: Stokes State Forest (Campsite 15), 2 (AMNH), 2 (CUM); Haneys Mill, 1 (AMNH); MORRIS Co.: Chester (Blackwater River), 1 (CUM); Lake Hopatcong, 3 (ANS); HUNTERDON Co.: Fairmount, 1 (AMNH).

WEST VIRGINIA. TUCKER Co.: Davis, 2 (WVMS); 1 mi. SSW Davis, 7 (WVMS); 5 mi. SSE Davis, 3 (WVMS); RANDOLPH Co.: 4.5 mi. NE Glady, 4 (WVMS); Cheat Bridge, 1 (USNM), 2 (PM); 8.9 mi. NNW Durbin, 1 (WVMS); 5 mi. NNW Durbin, 3 (WVMS); Blister Run, 4 mi. NNW Durbin, 5 (UMMZ); Base of Gaudineer Knob, 1 (PM); Red Run, near Shavers Fork, 2 (PM); PENDLETON Co.: Spruce Knob, 2 (USNM); 3.1 mi. NW Circleville, 4 (WVMS); POCAHONTAS Co.: Blue Knob, Gauley Mt., 1 (CMP); Cranberry Glades, 3,300 ft., 1 (USNM); 5 mi. N Durbin, Gaudineer Knob, 1 (UMMZ); S slope Cranberry Mt., 9 mi. WSW Marlinton, 4 (UMMZ); NICHOLAS Co.: 2 mi. N Richwood, 1 (WVMS); GREENBRIER Co.: 1.2 mi. N Kieffer, 1 (WVMS).

Additional Records. ONTARIO. RENFREW Co.: Petawawa, 33 (Prince, 1941:2).

QUEBEC. RIVIÈRE-DU-LOUP Co.: Trois Pistoles (Cameron, 1953, p. 185); PONTIAC Co.: La Vérendrye Park (Pirlot, 1962); TERREBONNE Co.: Lac Carre (Pirlot, 1962); MONTCALM Co.: Mont Tremblant Park (Pirlot, 1962).

NEW BRUNSWICK. RESTIGOUCHE Co.: Restigouche River, 2 (BMNH), Type specimen.

NOVA SCOTIA. ANNAPOLIS Co.: 16 mi. S Annapolis Royal, 2 (Rand, 1933).

NEW YORK. ESSEX Co.: New Russia, 1 (DCM); Elizabethtown, 9 (BMNH), 1 (DCM); Adirondack Lodge, 7 (BMNH); MADISON Co.: Peterboro, 28 (BMNH).

VERMONT. ESSEX Co.: Brighton, 7 (DCM); Maidstone, 11 (DCM); LAMOILLE Co.: Mt. Mansfield State Forest, 9 (DCM); Cambridge, 5 (DCM); Eden, 4 (DCM); WINDSOR Co.: Norwich, 4 (DCM); Woodstock, 1 (DCM); RUTLAND Co.: Mendon, 2 (DCM); Sherburne Center, 2 (DCM);

Mount Killington, 1 (DCM); Wallingford, 7 (DCM); 10 mi. E Danby, 1 (UMA); 1 mi. S, 1 mi. E Danby, 2 (UMA).

NEW HAMPSHIRE. GRAFTON Co.: Franconia Notch, 8 (DCM); Mt. Moosilauke, 7 (DCM); Lyme, 1 (DCM); Hanover, 3 (DCM); Profile Lake, ? (BMNH); CARROLL Co.: Chocorua, 8 (Preble, 1899, p. 35); Jackson, 113 (UCM, D. A. Lovejoy); Bartlett, 28 (UCM, D. A. Lovejoy); Harts Location, 39 (UCM, D. A. Lovejoy); Albany, 22 (UCM, D. A. Lovejoy); Coos Co.: Milan Hill State Park, 3 (DCM); Gorham, 3 (DCM); Randolph, 10 (DCM); Hermit Lake, Mt. Washington, 13 (DCM); Shelburne, 1 (DCM); Mt. Washington, 3 (NCSC).

MAINE. CUMBERLAND Co.: Brunswick (Pope, 1922; The Maine Naturalist, Vol. 2); HANCOCK Co.: East of Champlain Mtn., Mount Desert Island, 1 (Branin, 1936), 2 in alcohol (USNM); 0.5 mi. S Tarn, Acadia National Park (Stupka, 1934); Sieur de Monts Spring, 1 (Manville, 1942); PISCATAQUIS Co.: Mt. Katahdin, 20 (DCM).

PENNSYLVANIA. POTTER Co.: Cherry Springs, 1 (Preble, 1899, p. 35); ELK Co.: Howard Station (Rhoads, 1903).

MASSACHUSETTS. HAMPSHIRE Co.: vic. Amherst, 12 (UMA); vic. Pelham, 2 (UMA); WORCESTER Co.: Quabbin Reservoir, 1 (UMA); 1.2 mi. S, 5 mi. E Holden, 1 (UMA); BERKSHIRE Co.: 2 mi. E, 1.2 mi. N Savoy, 9 (UMA); Pittsfield State Forest, 1 (UMA); 7 mi. SSE Great Barrington, 1 (UMA); 4 mi. N Monterey, 8 (UMA); FRANKLIN Co.: 2.5 mi. NE North Amherst, 1 (UMA); Shutesbury, 2 (UMA); 3 mi. W Shutesbury, 1 (UMA); 2 mi. SW Orange, 1 (UMA); Quabbin Reservoir, 3 (UMA); Sunderland, 1 (UMA); Mt. Toby, 1 (UMA).

CONNECTICUT. LITCHFIELD Co.: Norfolk, Doolittle Lake, 1 (UMA).

RHODE ISLAND. PROVIDENCE Co.: Pascoag (Hamilton, 1935, p. 188).

WEST VIRGINIA. GREENBRIER Co.: White Sulphur Springs, 1 (Kellogg, 1937); RANDOLPH Co.: Turkeybone Mountain, 2 mi. SSE Pickens (Brooks, 1911); UPSHUR Co.: French Creek (Brooks, 1911).

Napaeozapus insignis roanensis (Preble)

Zapus (*Napaeozapus*) *insignis roanensis* Preble (1899:35).
Napaeozapus insignis roanensis, Miller (1900:114).

Type. Adult male, No. 66283 United States National Museum, from Magnetic City, foot of Roan Mountain, Mitchell County, North Carolina. Collected by A. G. Wetherby on May 22, 1894. Type examined.

Range. Ohio to extreme southwestern New York, sections of western Pennsylvania, northern West Virginia, western Virginia, western

Maryland, western North Carolina, extreme northern South Carolina and Georgia, eastern Tennessee, southeastern Kentucky and western West Virginia.

Diagnosis. Size very small, with external and cranial measurements (except interorbital breadth) averaging smaller than in any other subspecies. Color characterized by reddish tint, apparent on dorsal stripe as well as sides; white tip on tail relatively short.

Mean and range (in millimeters) of external and cranial characters in 15 specimens from the type locality (Roan Mountain, N.C.) are: Total L., 223.5 (208-236); Tail L., 132.4 (122-142); Hind Foot, 30.7 (30-31); Great. Skull L., 22.86 (21.8-23.9); Condylobasal L., 19.93 (18.3-20.5); Zygomatic L., 9.33 (8.7-9.9); Zygomatic B., 11.52 (10.9-12.1); Mastoid B., 10.28 (10.0-10.5); Braincase B., 10.46 (10.2-10.7); Nasal L., 9.19 (8.3-9.8); Rostral B., 4.44 (4.0-4.6); Interorbital B., 4.58 (4.4-4.8); Bony Palate L., 3.07 (2.8-3.4); Incisive Foramina L., 4.36 (4.1-4.8); Maxillary Toothrow, 3.52 (3.3-3.8).

Comparisons. N. i. roanensis differs from *N. i. insignis* in: smaller average size in every character, though there is some overlap in character means, particularly in the zone of intergradation; dorsal and lateral pelage distinctly redder.

N. i. roanensis differs from *N. i. abietorum* in being of much smaller size in all characters except interorbital breadth, which averages about 0.2 mm larger. There is slight overlap in population averages only in body length and incisive foramina length; dorsal and lateral pelage is distinctly redder; ears lack white edging usually present in *abietorum.*

For comparison with *N. i. frutectanus* and *N. i. saguenayensis*, see accounts of those subspecies (pp. 40 and 56).

Remarks. N. i. roanensis consists of populations at the end of a cline of decreasing size, which accounts for the nonoverlap in character means when compared to the large northern races. The smallest animals occur in populations in the southwest — eastern Kentucky, northern West Virginia and Ohio. Although the zone of intergradation with *insignis* was previously recognized in central West Virginia (Hall and Kelson, 1959:779, see distribution records), specimens from Ohio, extreme southwestern New York, sections of western Pennsylvania, and Maryland do not differ greatly in external and cranial characters from typical *roanensis.* Specimens from east-central West Virginia, formerly designated *roanensis,* are comparable in size and color to *insignis* from eastern Pennsylvania.

Color is also variable over a broad zone. The dark reddish tint of *roanensis* is evident in specimens from those parts of the range south of

Kentucky and extreme southern Virginia. Individuals resembling *insignis* in color are found at Burkes Garden and Laurel Fork, Virginia, and most of east-central West Virginia. Intermediate specimens are found in Giles County, Virginia, 9 mi. WSW Marlinton, Cransville, Terra Alta, and Oglebay Park in West Virginia, and Maryland. It is evident that the reddish color decreases in intensity and frequency in populations north of southern Virginia.

Specimens from Ohio, western Pennsylvania, southwestern New York, and most individuals from Maryland have coloration typical of *insignis*, but are relatively small in size. These populations could be left within the race *insignis* (separated from other populations by character breaks), possibly be described as a new subspecies of small size and *insignis*-like coloration, or placed with *roanensis* on the basis of numerous morphological similarities but atypical color. Considering the clinal variation in size and color, and the convergence and concordance of isophene lines in this area of intergradation, these populations are here referred to *N. i. roanensis*. Those populations in West Virginia are considered closer to *N. i. insignis*.

Specimens examined. Total number, 254, from: NEW YORK. Erie Co.: 2 mi. N Springville, 1 (KU); CATTARAUGUS Co.: Quaker Run, Allegany Indian Res., 1 (NYSM); Buffalo Camp, Allegany Park, 1 (NYSM); Red House, Allegany Park, 1 (CMP).

OHIO. CUYAHOGA Co.: North Chagrin Metropolitan Park, 2 (CMNH); Gates Mills, 1 (CMNH); LAKE Co.: Willoughby, 1 (CMNH); Mentor, 1 (CMNH); Kirtland Hills, 1 (CMNH); Holden Arboretum, 8 (CMNH), 2 (KU); GEAUGA Co.: Chesterland Caves, 3 (CMNH); Little Mountain, 3 (CMNH); Carvers Pond, 3 (CMNH); Shady Lake, 9 (CMNH); Lake Punderson, 1 (CMNH); BELMONT Co.: Cat Run, Powhatan Pt., 1 (CMNH).

PENNSYLVANIA. POTTER Co.: Costello, 1 (CMP); Carter Camp, 2 (CMP); Buckseller Run, 6.5 mi. S Ulysses (Lewisville), 12 (CMP); Rapplee Hollow, 5.5 mi. SW Ulysses, 3 (CMP); Woodcock Run, 7.5 mi. WSW Ulysses, 1 (CMP); CAMERON Co.: 3 Mile Run, 8 mi. NNW Emporium, 14 (CMP); CLINTON Co.: Tamarack, 9 mi. NNW Renovo, 4 (CMP); BEAVER Co.: 0.5 mi. W Bieler Run, 4 (CMP); BUTLER Co.: Harbison, 1 (CMP); Thorn Creek, 2 mi. W Saxonburg, 12 (CMP); 2 mi. E Middle Lancaster, 1 (CMP); CLEARFIELD Co.: McGees Mills, 12 (CMP); WESTMORELAND Co.: 1.5 mi. SE New Florence, 1 (CMP); 1.5 mi. ESE Laughlintown, 1 (CMP); 5 mi. SSE Rector, 1 (CMP); FAYETTE Co.: 0.25 mi. S Ohiopyle, 1 (CMP); 2 mi. NW Markleysburg, 1 (CMP); SOMERSET Co.: 1 mi. S Somerset, 6 (CMP); 2 mi. SSE Somer-

set, 1 (cmp); 5 mi. SW Somerset, 3 (cmp); 0.5 mi. NW Bakersville, 6 (cmp); 0.5 mi. W Bakersville, 1 (cmp); 5 mi. SW Bakersville, 2 (cmp); New Lexington, 1 (axs).

WEST VIRGINIA. Hancock Co.: 5 mi. SSW Chester, 3 (wvms); Ohio Co.: Oglebay Park, 6 (uk); Monongalia Co.: 8 mi. S Morgantown, 1 (wvms); Preston Co.: 4.5 mi. E Bruceton Mills, 6 (wvms); 0.5 mi. NW Pisgah, 1 (wvms); 1 mi. E Terra Alta, 2 (cmp), 2 (uk); 1 mi. SSE Cransville, 1 (ummz); Wayne Co.: Cabwaylingo State Forest, Arkansas Branch of Twelvepole Creek, 1 (wvms); Mercer Co.: 1.5 mi. NE Cooper Rock, 1 (wvms).

MARYLAND. Garrett Co.: Camp Algawa, near Bittinger, 1 (cmp); Finzel, 1 (usnm); 5 mi. SE Grantsville (Savage River State Forest), 8 (ummz).

VIRGINIA. Highland Co.: Laurel Fork, 9 mi. NNW Monterey, 12 (ummz), 1 (usnm); Giles Co.: Castle Rock, Big Mt. N of Mountain Lake, 1 (ummz); 1 mi. S Mountain Lake, 2 (ummz); Eggleston, 1 (ummz); Little Meadows, 1 (ummz); Wise Co.: 6 mi. N Wise, 1 (ummz); 4 mi. NW Appalachia, 2 (ui); Smyth Co.: Whitetop Mt., 3 (ummz); Grayson Co.: Mt. Rogers, 1 (ummz).

KENTUCKY. Harlan Co.: Black Mountain, 4 (cum), 5 (ku); Black Mountain, 2 mi. E Lynch, 1 (ui).

TENNESSEE. Carter Co.: NE slope Roan Mountain, 6.5 mi. SW Town of Roan Mountain, 1 (cmp); Cocke Co.: 4.5 mi. SE Cosby, Great Smoky Mountains, 1 (usnm); Sevier Co.: Indian Gap, 1 (ui), 2 (usnm); Greenbrier Cove, 1 (fm); Hemlock, between Trilium Gap and Greenbrier Cove, El. 4,000 ft., 2 (ui).

NORTH CAROLINA. Mitchell Co.: Magnetic City, Roan Mountain, 22 (usnm); Yancey Co.: Mt. Mitchell, 2 (usnm), 1 (cum); Toe River Gap, Mt. Mitchell, 1 (usnm); Bald Knob 5,000 ft., 3.5 mi. S summit of Mt. Mitchell, 11 (ummz); Buncombe Co.: Bent Creek, Pisgah National Forest, near Ashville, 4 (usnm); Swaine Co.: Great Smoky Mountains, 1 (ui); Macon Co.: Cove Creek, Highlands, 1 (usnm).

SOUTH CAROLINA. Oconoe Co.: 15 mi. N Walhalla, 1 (usnm).

Additional Records. OHIO. Ashtabula Co.: Mechanicsville, 1 (cmnh).

PENNSYLVANIA. Westmoreland Co.: Kingston (near Latrobe), 1 (Preble, 1899, p. 35); Crawford Co.: 4.5 mi. SE Spartansburg, 2 (uma).

WEST VIRGINIA. Cabell Co.: Huntington, 1 (wvms, comm. W. G. Frum).

MARYLAND. ALLEGANY Co.: Dans Mountain, 2 (Paradiso, 1969); GARRETT Co.: Muddy Creek Falls, 3 (UMd); Swallow Falls State Forest (Muddy Creek), 1 (Paradiso, 1969).

VIRGINIA. Shenandoah National Park, 1 (USNM); HIGHLAND Co.: Laurel Fork, 2 (USNM); TAZEWELL Co.: Burkes Garden, 9 (USNM); RUSSELL Co.: Laurel Bed, Clinch Mt., 6 mi. NNW Saltville, 21 (USNM); Mudders Gap, Clinch Mt., 3 (USNM).

TENNESSEE. SEVIER Co.: Eagle Rocks Creek, 7 (Komarek and Komarek, 1938:160); MACON Co.: Town of Highlands about 4.000 ft., 2 (UG).

NORTH CAROLINA. YANCEY Co.: 5.4 mi. SW Busick, 1 (NCSM); 4.7 mi. SW Busick, 1 (NCSM).

SOUTH CAROLINA. GREENVILLE Co.: Caesars Head, 3,000 ft., 2 (Coleman, 1940).

GEORGIA. RABUN Co.: Near North Carolina line, 3,075 ft., 1 (UG); UNION and FANNIN Cos.: (Golley, 1962).

Napaeozapus insignis saguenayensis Anderson

Napaeozapus insignis saguenayensis Anderson (1942:40).

Type. Adult male, No. 9318 National Museum of Canada, from Trout Lake, near Moisie Bay, North Shore of Gulf of St. Lawrence, Saguenay County, Quebec. Collected by C. G. Harrold on June 12, 1928, original Number 83. Type examined.

Range. From Lake St. John area northeast along north shore of the St. Lawrence River to the Strait of Belle Isle, then north to Hamilton Inlet, Labrador. Its range inland from the coast is unknown.

Diagnosis. Size large, with body and hind foot lengths averaging larger than in any other race. Skull averages larger than in other races, except for interorbital breadth, bony palate length, maxillary toothrow length and braincase breadth. Color of sides yellowish; dorsal stripe not contrasting sharply with sides; ears almost black, with dull inconspicuous ochraceous edge.

Mean and range (in millimeters) of external and cranial characters in a total of six specimens from the type locality (4) and nearby St. Margaret River (2) are: Total L., 246.8 (241-252); Tail L., 153.2 (143-156); Hind Foot L., 33.3 (32-34); Great. Skull L., 25.05 (24.6-25.5); Condylobasal L., 21.40 (20.6-22.2); Zygomatic L., 10.46 (10.1-11.0); Zygomatic B., 12.80 (12.6-13.1); Mastoid B., 11.0 (11.0); Braincase B., 11.30 (11.1-11.5); Nasal L., 10.66 (10.4-11.0); Rostral B., 4.72 (4.4-5.4); Interorbital B., 4.38 (4.3-4.5); Bony Palate L., 3.36

(3.3-3.4); Incisive Foramina L., 4.84 (4.7-5.0); Maxillary Toothrow, 3.78 (3.7-3.8).

Comparisons. N. i. saguenayensis differs from *N. i. abietorum* as follows: slightly larger in most external and cranial characters, particularly the hind foot, zygomatic length and nasal length; slightly shorter bony palate, maxillary toothrow; smaller rostral breadth; sides more yellowish, ears darker, without white edging.

From specimens of *N. i. roanensis, N. i. saguenayensis* averages considerably larger in every character other than interorbital breadth, which is slightly smaller. There is no overlap in character-means except in lengths of incisive foramina and maxillary toothrow.

For comparison with *N. i. insignis* and *N. i. frutectanus,* see accounts of those subspecies (pp. 43 and 40).

Remarks. Anderson (1942) described this race mainly on the basis of four specimens from the type locality and emphasized the large hind foot (32 to 34 mm), short braincase, spreading zygoma and pelage characters. Since only 16 specimens were available in the present study (several with skulls damaged), the variation in cranial dimensions remains poorly known. Six specimens from the Lake St. John region were included in this race, being fairly well differentiated by large size in external and cranial characters from *N. i. insignis* from Lake Edward directly south (previously *N. i. algonquinensis*). Comparison of specimens of *saguenayensis* with *insignis* from opposite sides of the St. Lawrence shows major differences in many characters — particularly larger in hind foot, nasal length, bony palate, zygomatic length and mastoid breadth, but smaller interorbital breadth. The widening of the river has served to isolate the two races in the east, but farther upstream, specimens on both shores as far east as Lake Edward are referrable to *insignis.*

A larger series of *saguenayensis* would probably reveal further overlap in morphological characters with *abietorum.* Both races are at the large end of clines of increasing size apparent throughout the range of the species. The hind foot and pelage differences seem to be consistent since very few individuals of *abietorum* have a hind foot length over 32 mm, though four specimens nearest the range of *saguenayensis* (lakes Albanel and Mistassini) vary from 32 to 34 mm.

Specimens examined. Total number, 16, from: QUEBEC. Lake St. John-WEST Co.: St. Félicien, 1 (NMC); Val Jalbert, 4 (NMC); Lake St. John-EAST Co.: Bell River, 1 (CMP); SAGUENAY Co.: Godbout, 2 (USNM); Third Portage, St. Margaret River, 2 (CMP); Trout Lake, N of Moisie Bay, 4 (NMC).

NEWFOUNDLAND (LABRADOR). Hamilton River, Muskrat Falls, 1 (USNM); Labrador, 1 (MCZ).

Additional records. QUEBEC. CHICOUTIMI Co.: Lake Chitigama, (Pirlot, 1962); SAGUENAY Co.: Godbout, 4, in alcohol (USNM).

LABRADOR. Hamilton River, 1 (Bangs, 1898:493); Hamilton Inlet (Anderson, 1946:172).

VII. ENVIRONMENT AND DISTRIBUTION

Past Distribution and Subspeciation

The past distribution of *Napaeozapus* can only be surmised on the basis of a few fossil records and information on the displacement of associated communities during the Pleistocene. The earliest record of *Napaeozapus* is from the mid-Pleistocene deposits at Cumberland Cave, Maryland, situated at the periphery of the present range. The lower jaw, molars and incisors are similar in size to the Recent species (Gidley and Gazin, 1938). During the maximum advance of the Wisconsin ice sheets, about 22,000 years ago, the present range of *Napaeozapus* was glaciated except for regions south of northern Pennsylvania. In the postglacial period, habitat suitable for *Napaeozapus* (spruce-fir forest, or a mixture of boreal and deciduous forest) occurred from Ohio and West Virginia to Connecticut (Dillon, 1956), and southward throughout most of Kentucky and the Carolinas (Martin, 1958), Tennessee and Pennsylvania (Guilday, Martin, and McCrady, 1964), and Georgia (Golley, 1962). The species has been found at four late-Pleistocene sites, two of which are on the southeastern periphery of the range — New Paris No. 4, Bedford Co., Pennsylvania (Guilday, Martin, and McCrady, 1964); Natural Chimneys, Augusta Co., Virginia (Guilday, 1962); and two localities considerably outside the present distribution — Bootlegger Sink, York Co., Pennsylvania (Guil-

day, Hamilton, and McCrady, 1966), and Robinson Cave in north-
central Tennessee (McCrady and Schmidt, 1963). Specimens from
New Paris No. 4 and Natural Chimneys average 10% larger than
Recent individuals occurring in the same areas. Recent boreal popu-
lations (*N. i. abietorum* and *saguenayensis*) consist of individuals
which also average about 10% larger than central Appalachian stock
(Figs. 14 and 15, pp. 38 and 39).

The earliest late-glacial flora from Saskatchewan to Michigan con-
sisted of a mixture of plants of boreal and temperate affinities. There-
after the coniferous forest in Manitoba disappeared almost entirely,
succeeded by a relatively rapid expansion of grassland from the south-
west. In Minnesota and southern Ontario, mixed deciduous forest re-
placed the coniferous forest (Ritchie, 1966). Grassland, deciduous
forest, and glacial Lake Agassiz may have been influential in prevent-
ing *Napaeozapus* from extending farther west than eastern Manitoba
and Minnesota.

Late-glacial deposits (about 15,500 BP) in Iowa and Kansas con-
tain pollen and wood of hemlock, spruce and fir (Guilday, 1964:182),
indicating a possible habitat for *Napaeozapus*. Subsequent expansion
of the prairie community to the north and east during the xerothermic
period (3,000-5,000 BP) would have driven the woodland jumping
mouse from these regions. The meadow jumping mouse, *Zapus hud-
sonius*, would not be so restricted, and is currently distributed across
northern North America.

During the Pleistocene, *Napaeozapus* was doubtlessly subjected to
major geographical shifts in range as a result of a number of glacial
advances. The establishment of morphological variation during these
periods as a result of the formation and disappearance of isolates,
restricted gene flow, and adaptation of widely separated populations
to local conditions may be speculated upon, using the few Pleistocene
records and the present distribution and variation of the species.
Populations inhabiting the boreal forest in the central Appalachians
10,000 to 15,000 years ago appear to have consisted of large individuals
comparable to those occurring within the boreal forest in Ontario and
Quebec at the present time. With the retreat of the Wisconsin glaciers
northward, these populations may have followed the advancing boreal
flora into the central regions of Ontario and Quebec. Populations oc-
curring north of the Gulf of St. Lawrence (*N. i. saguenayensis*) became
differentiated from those farther west (*N. i. abietorum*), the latter
dispersing north of the Great Lakes drainage into western Ontario.

A medium-sized race (*N. i. frutectanus*) inhabiting the region south-
west of the Great Lakes drainage may have been isolated from popu-

lations in the east by the Ohio-Mississippi glacial drainage, and later by the disappearance during the xerothermic period, of suitable habitat (hemlock–northern hardwood forest) between northern Michigan and northeastern Ohio.

The small race, *N. i. roanensis,* probably occupied areas south and west of the Appalachians, partially isolated by the Appalachian highlands from a medium-sized race (*N. i. insignis*) in the northeast. With progressive amelioration of conditions in the north, the latter race expanded from eastern Pennsylvania and adjacent regions, through New York and the St. Lawrence lowlands, reaching southern Ontario and Quebec. *Napaeozapus* either crossed the eastern outlet of the Great Lakes or took advantage of some land corridor or change in drainage pattern in the region from the present Lake Erie to the upper St. Lawrence. This waterway does not exclusively separate subspecies on opposite shores in any mammalian species (one or more subspecies always occur on both sides of the waterway). Where the St. Lawrence widens into the Gulf, populations of *Napaeozapus* on opposite shores (North Shore and Gaspé Peninsula) are quite distinct.

Cameron (1958) presents strong evidence that land connections were available to mammals in reaching Prince Edward Island and Cape Breton Island, and the same is probably true in the case of Mount Desert Island, Maine. Populations of woodland jumping mice inhabiting these islands are not subspecifically distinct from mainland *N. i. insignis.*

The relatively regular clinal variation apparent in *Napaeozapus* is doubtless due to the effects of environmental gradients and gene flow between local populations. It is noteworthy that three of the five subspecies (*N. i. frutectanus, saguenayensis,* and *roanensis*) are peripheral to populations in the central part of the range, and contact other races only in relatively narrow areas as a result of various water barriers or unsuitable habitat. Restriction or absence of gene exchange between populations in these areas would account for the major breaks in phenotypic variation as revealed in this study.

Habitat Relationships

VEGETATION

Napaeozapus inhabits the spruce-fir and hemlock-hardwood forests in the eastern half of North America. As illustrated (Fig. 16), its distribution coincides well with the combined ranges of balsam fir, *Abies balsamea* (L.) Mill., and eastern hemlock, *Tsuga canadensis*

Fig. 16. Distribution of *Napaeozapus* relative to various environmental factors. Hatched area represents the range of *Napaeozapus*. Stippled area represents the combined ranges of eastern hemlock and balsam fir. A = approximate southern limit of discontinuous permafrost. B = mean annual air isotherm of $-1°C$. C = mean annual growing season of less than 140 days. D = mean air isotherm of $21°C$ during July and August.

(L.) Carr. Plant associations containing hemlock are typical habitat in the southern half of the range, while the spruce-fir association is characteristic in the north (except in the forest-tundra ecotone of the boreal forest), and at higher elevations in the Appalachians. Balsam fir is relatively unimportant west of Lake Winnipeg — the western limit of *Napaeozapus*. Both associations form mixed stands in many areas (Figs. 17 and 18).

Hemlock–northern hardwood forest is composed mainly of hemlock, white pine, beech, sugar maple, yellow birch, basswood, and red,

FIG. 17. Spruce-fir stand at South Bolton, Quebec. Species collected here in addition to *Napaeozapus insignis* were: *Sorex cinereus, S. fumeus, S. palustris, Blarina brevicauda, Condylura cristata, Lepus americanus, Tamiasciurus hudsonicus, Tamias striatus, Peromyscus maniculatus, Clethrionomys gapperi, Erethizon dorsatum,* and *Mephitis mephitis.*

striped, and mountain maple, with spruce and balsam fir occasionally present in moist situations. This forest extends from Minnesota across southern Canada to the Maritime Provinces, then southward along the Appalachian highlands to northern Georgia and South Carolina at intermediate elevations and in cool, moist coves on northern slopes. South of Pennsylvania many species of the mixed mesophytic forest are represented — white basswood, yellow buckeye, tuliptree, cucumbertree, sweet birch, rhododendron, mountain laurel and others.

The spruce-fir forest, composed predominantly of white spruce and balsam fir, extends across Canada north of the hemlock-northern hardwood forest, and occupies the higher elevations in the Appalachians as far south as northern Georgia. In the north, black spruce, tamarack, paper birch, balsam poplar, and quaking aspen are important constituents, particularly in subclimax stages. From New Brunswick to Georgia in the east, red spruce tends increasingly to replace white spruce, while Fraser fir and yellow birch take the place of balsam fir and white birch in the south.

Data on the habitat of *Napaeozapus* are available from every prov-

FIG. 18. Hemlock-hardwood forest downstream from site in Fig. 17. Two specimens of *Zapus hudsonius* were found here with many *Napaeozapus*.

ince and state in which the species occurs, although many accounts are brief notes based on few specimens. Habitat information from the literature and personal observations are summarized in the Appendix (pp. 106-108).

From the St. Lawrence River south to Georgia and South Carolina, *Napaeozapus* and associated fauna and flora occupy increasing elevations in the Appalachians — from sea level in the north to from 3,000 to 6,600 feet (915 to 2,013 meters) in the south. Many populations are isolated on mountain peaks and cool moist coves (Roan and Smoky mountains of Tennessee and North Carolina, Mount Mitchell, N.C., and others) or in relict stands of forest (Chagrin River area of northeastern Ohio, western West Virginia). *Napaeozapus* is absent from the mixed mesophytic forest in areas where hemlock is scarce, as well as oak associations on the Piedmont and Cumberland plateaus which surround the Appalachian highlands as far north as eastern Massachusetts and Ohio. Along the western periphery of the range from the southern regions of Michigan, Wisconsin, Minnesota, and southeastern Manitoba, *Napaeozapus* is exceedingly rare. Hemlock and balsam fir associations are replaced by deciduous forests of beech-maple, maple-basswood, oak-hickory and aspen parkland as tall grass prairie is approached.

In northern regions of the spruce-fir forest *Napaeozapus* becomes increasingly restricted to optimum sites of spruce-fir growth and to watercourses lined with alder, willow, and sedge. Black spruce–tamarack bogs as well as drier areas supporting heaths, lichens, and open spruce woods appear to be unsuitable habitat. Possibly the species has not spread westward across Canada in the boreal forest because of the large lake systems in Manitoba, the oak-aspen community to the south, and the bog and forest-tundra associations which predominate to the north.

The coincident ranges of *Napaeozapus* and hemlock–balsam fir indicate a preference for similar environmental conditions — abundant moisture and cool temperatures. However the overall distributional pattern does not appear to be restricted by low moisture or temperature extremes. Perhaps these factors are more important indirectly, through an effect on the availability of the preferred flora.

COVER

Snyder (1924), Whitaker (1963b), Brower and Cade (1966) and others stressed the importance of dense herbaceous growth as cover for these mice. Brower and Cade found 8.4 mice per 100 trap nights (79

individuals) in dense cover, 2.2 (28) in intermediate cover, and 1.7 (31) in sparse cover. No association with particular species of herb or shrub was detected. In the present investigation it was apparent that logs and moss-covered piles of rocks also afforded jumping mice suitable cover, since they were trapped under this debris on many occasions. In tracts of forest where the canopy was dense, permitting but a scant growth of herbs, the mice were either absent or very rare.

Napaeozapus rarely leaves the forests for any great distance to enter grass or sedge cover, though the converse is not true for *Zapus*. In those cases where individuals have been taken in herbaceous cover outside of woods (Townsend, 1935; Barbour, 1951a; Cameron and Morris, 1951; Pirlot, 1962; Connor, 1960 and 1966; Brower and Cade, 1966; personal observations), the sites were usually forest-edge habitats, since alder, willow, and other bushes were present. Whitaker (1963b) found one individual in a field 40 meters from the forest edge, but judging from the mouse's stomach contents he believed it must have come directly from the woods. Since woodland jumping mice are often attracted to areas with grassy cover, probably for seeds and insects, it is not clear why they restrict their activities to forest and forest-edge situations.

MOISTURE

The majority of studies have associated *Napaeozapus* with moist habitats — edges of streams, lakes and ponds, swamps, bogs, and springs. Connor (1960), Whitaker (1963b), and Brower and Cade (1966) suggested that vegetative ground cover, often more abundant near water, was attracting the mice rather than moisture. Connor noted that about one-third of 119 individuals collected in New York were taken far from permanent water, including 18 found on a summit of a hill over one-half mile from the nearest stream. Brower and Cade also found no special association with habitats near watercourses, obtaining 3.6 mice per 100 trap nights (43 individuals) adjacent to water — within 200 feet (61 meters), 3 6 (30) close to water — 200 to 600 feet (61-183 meters), and 3.2 (65) far from water — more than 600 feet.

Trapping results obtained in the present study also indicated that surface water was not an essential component of the habitat. Apparently dew, moisture in the food, and metabolic water were sufficient for the species' moderate water requirements (see Physiology: Water Balance, p. 72). However, *Napaeozapus* was always taken in moist or mesic habitats, while xeric situations, even with suitable cover, were consistently avoided. Thibault (1969) detected increased activity in previously unoccupied dry areas after rainfall. The absence of watercourses

in areas where jumping mice are common does not necessarily show that surface water or soil moisture are without effect on local distribution. A variety of other factors may override an attraction to moist sites at different periods of the season. For example, the seasonal availability of a food source may draw individuals from their usual range. Also, late in the season jumping mice may depart from low, moist areas in search of well-drained sites for hibernation. Considering that the species usually avoids moist areas with poor cover as well as dry situations with good cover, it appears that both moisture and cover combine to form the optimum habitat.

Woodland jumping mice inhabit regions where the annual precipitation may range from 20 to 60 inches. Local factors such as seasonal precipitation, vegetative cover, soil type, drainage and evaporative rate modify the amount of moisture available to animals, hence the relation between annual precipitation and the distribution of *Napaeozapus* is obscure. The species is generally most abundant in regions which are moist throughout the active season.

TEMPERATURE

In the south, the species does not occur in areas where the mean air temperature during the warmest months of the year (July and August) exceeds 21°C (Fig. 16, p. 62). It is unlikely that jumping mice are ever exposed to the critical temperature of 37°C (see Physiology: Thermoregulation and Metabolism, p. 72), since they remain in cool underground burrows in the forest during the day. A relatively low tolerance to high temperature would not appear to be a major limiting factor.

The range of *Napaeozapus* does not extend north of the mean annual air isotherm of −1°C, or into areas where the growing season is less than 140 days. The species fails to reach the region of discontinuous permafrost, hence the location of suitable hibernacula, where soil temperatures would remain above freezing, would not present a serious problem. The zone of permanent permafrost, considerably farther north, apparently limits the distribution of *Zapus*. Since *Zapus* is able to reproduce and prepare for prolonged hibernation during the short summer within the region of discontinuous permafrost, probably *Napaeozapus* is precluded from the area by factors other than low temperature and short growing season.

Food Habits

Whitaker (1963b) examined the stomach contents of 103 *Napaeozapus* taken in New York from April to October. By volume, food items

were: subterranean fungi (*Endogone* and *Hymenogaster*), 37%; various seeds (*Impatiens, Anthoxanthum odoratum*), 24%; fleshy fruits (*Rubus, Fragaria virginiana, Vaccinium*), 12%; lepidopterous insect larvae, 10%; coleopterous insects, 8%; miscellaneous vegetation, 8%; unidentified animal material, 1%. *Endogone* was the most important food source, present in 68.9% of the stomachs and comprising 33.3% by volume. Traces of spiders, diptera, and mites were also detected. In an earlier paper, Whitaker (1962) reported finding large quantities of *Endogone* in food analyses of *Napaeozapus* from Tennessee, North Carolina, and New Hampshire. It was also noted that the fungus was eaten by *Zapus* and *Clethrionomys*, although *Peromyscus leucopus* seldom ate it.

Hamilton (1935, 1941) found the following food items during stomach analyses: considerable quantities of lepidopterous and dipterous insect larvae, various small invertebrates including crane flies, caterpillars, spiders, centipedes and worms, green leaves and rootstocks, *Asplenium* fern fronds, *Mitella diphylla* seeds, *Podophyllum peltatum* fruits, berries, seeds, and small nuts. Sheldon (1938) added butterflies, moths, grasshoppers, and dragonflies, though no mammalian flesh except when females ate their young in captivity. Connor (1966) determined that plant and insect material composed 77.4% and 22.2% of the total food volume, respectively. Goodwin (1935) caught a jumping mouse feeding on the inflorescence of a skunk cabbage, and Sheldon (1934) reported that alder cones and new needles of spruce were also consumed. Sheldon (1934) and Hamilton (1941) found that *Napaeozapus* practiced little or no food storage in captivity or under natural conditions, although Schwentker (1957) noted that the mice sometimes stored grain in captivity.

Colonialism

The distribution of *Napaeozapus* is notably local, and often the species inhabits a relatively small area in the vicinity of a watercourse, a moist glade, or the forest edge, apparently avoiding adjacent areas which seem identical. Sheldon (1934, 1938) interpreted these disjunct populations as colonies, inferring that individuals were attracted to areas partly by the presence of others. Three separate colonies were reported along a lake shore in Nova Scotia, each occupying 100 to 200 yards of shoreline. In Vermont, a large colony was found to move several hundred yards each season for four years. In contrast, Preble (1956) observed that when conditions were favorable over wide areas, no colonialism was apparent. Local aggregations were thought to be the result of isolation of suitable habitats.

In the present investigation, *Napaeozapus* was found to be abundant in only two areas, in southern Quebec and Prince Edward Island. In both situations the mice inhabited 60 to 100 yards of wooded stream-bank, and were absent from similar habitat up- and downstream. Whether the mice were attracted to each other or to some source of food or cover was not clear. Though jumping mice are amiable toward each other in captivity, there is no evidence that this is true under natural conditions. When population numbers are high, individuals appear in marginal and unusual habitats (dry wooded hillside and dry forest edges at South Bolton, Quebec), which suggests competition may force some animals to seek new locations. Temporary food sources, such as the ripening of berries at the forest edge, often attract large numbers of jumping mice. Also, the fact that colonies may move from year to year (Sheldon, 1938) indicates that the mice are drawn to new areas as ecological conditions change. They may remain in the same locale for many seasons (four years at South Bolton, Quebec) or disappear entirely. Near Ithaca, New York, where Hamilton (1935) had collected a total of 108 *Napaeozapus* in 1932 and 1933, the species appeared to be absent when I studied the area briefly in 1969. The habitat seemed unchanged from its original description, though the ground cover along the streambank was sparse. In consideration of these data, I interpret apparent colonialism in *Napaeozapus* as the result of attraction to environmental factors in a species which has relatively specific habitat requirements.

Interspecific Relationships

Napaeozapus often occurs in association with *Sorex cinereus, S. fumeus, Blarina brevicauda, Condylura cristata, Parascalops breweri, Tamias striatus, Peromyscus maniculatus, P. leucopus, Microtus pinetorum, Synaptomys cooperi, Clethrionomys gapperi,* and *Zapus hudsonius.* The habitat requirements of the woodland jumping mouse and several other species overlap considerably. Whether possible competition as well as behavioral confrontations are important in the local distribution of *Napaeozapus* is difficult to determine, although some evidence is available from field studies.

Meadow and woodland jumping mice are fairly well segregated ecologically, generally occupying different stages in the successional sequence of plant communities. It is only in the intermediate stages that these two species are commonly found together, particularly in shrub or forest-edge stages. In New York, Miller (1899) and Connor (1960) reported both species in situations which combined the habitat characteristics of both forms — grassy, thinly wooded borders of

streams, marshy borders of woodland ponds, and small clearings in woods. Sheldon (1934) in Nova Scotia and Soper (1923) in central Ontario caught both species of jumping mice in the grass and shrubbery along the shore of lakes in deep forest. Hamilton (1935) and Preble (1956) found *Zapus* invading *Napaeozapus* habitats, but not the reverse. Whitaker (1963b) caught one *Napaeozapus* in a grassy field, one in a brushy field, two in brush, and three in open wet woods, along with many *Zapus*. Since the absence of one species was not followed by an invasion into the vacant habitat by the other, it was concluded that the two species had little or no direct effect on the distribution of each other. Brower and Cade (1966) concurred, except in forest-edge situations where they found *Zapus* invading when *Napaeozapus* was removed.

During the present study the two species were taken together on nine occasions in southern Quebec and Prince Edward Island — under growth of speckled alder at the edge of a lake in spruce-fir forest, in a bog overgrown with young northern white-cedar, in balsam fir-hemlock–northern hardwood forest, four occasions along streams at the forest edge, and two other occasions at moist forest edges. Each time only one *Zapus* was present with several *Napaeozapus*. The latter was not found in fields more than a few feet from the woods. This evidence agrees with the supposition of Brower and Cade that the two species of jumping mice meet frequently only in forest-edge situations and that the abundance here of one species may adversely affect the other. Both *Napaeozapus* (Townsend, 1935; Brower and Cade, 1966) and *Zapus hudsonius* (Quimby, 1951; Whitaker, 1963a) may attain large populations in this type of habitat.

Brower and Cade (1966:54) reported a complementary pattern in local distribution between *Napaeozapus* and *Clethrionomys gapperi*, with jumping mice abundant in six areas where voles were scarce. The species were partly segregated within the forest, the jumping mice preferring dense undergrowth, the voles, sparse ground cover under conifers; near the forest edge, however, there was no apparent difference in habitat utilization. A disruptive interaction was proposed rather than competition for limited resources. It was suspected that the timid and nervous jumping mice vacated areas having many voles, since the voles are aggressive and intolerant. The authors called attention to other field studies which indicated similar examples of interference (Hamilton, 1935; Townsend, 1935; Blair, 1941; and Jameson, 1949), though the principle had not been advanced. Observations during this study support Brower and Cade's hypothesis — though the two species are often found together when numbers are low, they are never abun-

dant in the same area. On numerous occasions in Quebec and the Maritime Provinces, when *Clethrionomys* was abundant, jumping mice were absent. At Hunter River, Prince Edward Island, where jumping mice were abundant, no voles were found. At South Bolton, Quebec, four years of trapping in the area where *Napaeozapus* was common, produced only an occasional red-backed vole.

Considering food habits, cover and habitat selection, the species most likely to compete with *Napaeozapus* is *Peromyscus maniculatus.* Yet there is no evidence that either species adversely affects the local distribution or abundance of the other. In fact, Hamilton (1935) and Blair (1941) both reported instances of catching the two species together in live traps, with no indication of fighting. Brower and Cade (1966:55) suggested the two may exist in the same area without much contact since jumping mice seemed more active on cold nights, while deer mice showed greater activity on warmer, cloudy nights. Thibault (1969) also found evidence for complementary activity patterns. There is, however, no doubt that the requirements of two species overlap greatly and that confrontations are numerous. I found no evidence for exclusion or consistent differences in habitat utilization. In the two instances where jumping mice were abundant, deer mice were also common. At Mont Yamaska in southern Quebec where deer mice were very numerous (24 individuals in about 200 trap nights), jumping mice and red-backed voles were also taken (9 individuals of each species).

I observed a captive *Napaeozapus* attacking a deer mouse which had approached the former's nest area. Perhaps the timid woodland jumping mouse displays this aggressive behavior toward the deer mouse under natural conditions in the vicinity of the burrow. Deer mice may not be able to force jumping mice out of an area as the more aggressive red-backed voles appear to do. The two species probably tolerate each other by mutual avoidance.

VIII. PHYSIOLOGIC ASPECTS OF LIFE HISTORY

Physiology

WATER BALANCE

Brower and Cade (1966) found that the *ad libitum* water consumption of *Napaeozapus* did not differ significantly from a predicted weight-relative value. Ten individuals averaged 0.16 cc $H_2O/g/day$ (0.09 to 0.24 cc), which was almost twice that of *Peromyscus maniculatus* and *P. leucopus*. *Clethrionomys* had a higher water requirement than predicted, and consumed 2.4 times as much as *Napaeozapus*. Minimal water requirements were not determined.

Evaporative water loss in the jumping mouse was less than in the other species (3.2 mg $H_2O/g/hr$ at 29°C), and it was suggested that this might be an adaptation to reduce dessication during hibernation. *Napaeozapus* did not spread saliva over the fur for additional cooling at high ambient temperatures as did *Peromyscus*.

THERMOREGULATION AND METABOLISM

Brower and Cade (1966) reported that *Napaeozapus* did not show a labile body temperature during day-night activity cycles or during exposure to ambient temperatures of 5° to 33.5°C, as had been found in the birch mouse, *Sicista betulina* (Johansen and Krog, 1959) and in *Zapus hudsonius* (Morrison and Ryser, 1962). Brower and Cade, and Klein (1957) noted that a number of woodland jumping mice were

torpid in live traps during cold summer nights. Klein exposed 11 *Napaeozapus* which were not prepared for hibernation (collected in June) to a temperature of 7°C for periods of one to four days. If food was supplied the mice remained active, whereas without food they became torpid within 12 hours. Five mice died while in the torpid state, three died after reviving, and another succumbed during the experiment even though supplied with food and water. The cause of death was not determined.

Normal body temperatures were 37.3°C for *Zapus* (Morrison and Ryser) and 37°C for *Napacozapus*. Above Ta 33.5°C *Napacozapus* became hyperthermic. Brower and Cade suggested that the long, sparsely haired tail may aid in heat loss. At the upper critical temperature of 37°C, heat loss by evaporation was 39% compared with 72% in *Peromyscus* as a result of spreading saliva on the fur. Partly by this means *Peromyscus* was able to survive at 39°C. Thermal conductance of *Napaeozapus* was calculated to be 1.3 kcal/g hr °C, slightly higher than *P. maniculatus* (1.1). Morrison and Ryser estimated a value of 1.0 kcal/g hr °C for *Zapus*.

The average basal metabolic rate of 11 *Napacozapus* was 8.6 kcal/g hr (Brower and Cade). Pearson (1947) reported values of 11.5 kcal/g hr for a fat *Napacozapus* and 14.9 for two lean *Zapus* tested late in the fall. Morrison and Ryser determined rates ranging from 22 kcal/g hr in fat *Zapus* to 12.4 in lean individuals.

Above and below the narrow zone of thermoneutrality (31° to 33.5°C) in *Napacozapus*, the metabolic rate increased. At 20°, *Napacozapus* averaged 21.1 kcal/g hr (Brower and Cade), *Sicista betulina* ranged from 16.8 to 27.4 (Johansen and Krog) and three fat *Zapus* had values of 16.8 to 19.2 kcal/g hr (Morrison and Ryser). *Zapus* showed an increase in metabolic rate with decreasing ambient temperatures from 17° to 3°C, while *Napacozapus* and *Sicista* revealed a lower rate below 10°C.

Brower and Cade characterized the physiology of the two jumping mice as having deep seasonal hibernation, precise thermoregulation during the active season, high lower critical temperature and poor tolerance to high ambient temperature. This physiological pattern was thought to have evolved as a result of adaptation to a cold climate.

Hibernation

PREPARATION

Woodland jumping mice prepare for hibernation by accumulating large amounts of fat, often comprising one-third of the body weight. An

adult weighing 20 g in the spring may exceed 30 g by fall. Fat is deposited in the mesenteries and under the skin, particularly in the inguinal and dorsolumbar regions. The time at which individuals begin to store fat reserves varies with age and possibly sex. Also, latitudinal differences probably exist, but this remains to be shown since there are few specimens with pertinent data from northern and southern populations. There is evidence that photoperiod is involved, since Neuman and Cade (1964) found that jumping mice exposed to short days (8 hours light, 16 hours dark) became fat in a two-week period prior to hibernation, while others on long days (16 hours light, 8 hours dark) did not.

Juveniles and subadults usually lack fat until very late in the season — late September and October (Preble, 1956; Connor, 1960). Some adults show fat deposition by late August (Goodwin, 1924), most do by mid-September (Blair, 1941), and many are hibernating by the end of the month. Additional data on the presence of fat were recorded from museum specimens. Perhaps it is difficult for the young to find sufficient nutrients to form energy reserves while still growing rapidly, though several juveniles with fat were noted in museum collections. Females that have recently produced a litter or are still lactating might be expected to fatten later in the season, but no evidence is available.

ENTRANCE

As shown in Fig. 21 (p. 89), the number of adults older than one year (age-groups 4, 5 and 6) declines rapidly in late September, and presumably most have begun hibernation. In early October about 86% of the nonhibernating population is comprised of animals from spring and summer litters, and in the latter part of the month they are the only ones still active, with juveniles, subadults and spring-born adults representing 13, 37 and 50%, respectively. It appears that the great majority of woodland jumping mice more than one year old enter hibernation in the latter half of September, followed in several weeks by young of the year.

Of 175 museum specimens taken from September 16 to October 29, a total of 58% were males and 42% were females. This closely approaches the sex ratio during the summer (55:45 respectively), and considering that males have a more extensive home range and are more likely to be trapped, there does not appear to be a marked difference between the sexes in the time of entrance into hibernation.

Napaeozapus was common in an area near South Bolton, Quebec, on September 7 but absent when the area was revisited on October 9. The population had either vacated the area in search of hibernacula

on better-drained sites, or had already entered hibernation (Wrigley, 1969). The latest record in the fall in Canada was a specimen from New Brunswick collected on October 9 (AMNH). Other late season records were reported by Connor (1960) from New York on October 24, and Grimm and Roberts (1950) from Pennsylvania on October 29. Though the species may be active later into the fall in the southern part of the range, there are too few specimens available to determine this. In New York, Hamilton (1935) and Layne and Hamilton (1954) found that a number of captive jumping mice in outdoor enclosures did not hibernate until middle and late November, though other individuals were torpid in mid-October. Since there are no records of woodland jumping mice having been collected in November, activity at this late date would seem to be highly unusual under natural conditions.

Neuman and Cade (1964) found that jumping mice which had not accumulated fat reserves under a reversed photoperiod of 16 hours of light per day were unable to hibernate successfully. Periods of torpor averaging only 3.3 days were followed by active periods lasting 2.9 days. Mice on a more natural photoperiod of 8 hours of light per day put on weight and hibernated for an average of 9.4 days with 1.5-day periods of activity. At 2° to 5°C the mice without fat reserves steadily lost weight and eventually starved, though food and water were available. The mice with fat stores (weight 30 g) lost weight rapidly during the first few days of hibernation but then leveled off, decreasing slowly until the end of the hibernating season. Morrison and Ryser (1962) found that Zapus, physiologically prepared for hibernation, would also starve to death when maintained at 25°C, since they refused food and did not lower their body temperature or metabolic rate. Food in the digestive tract results in death (Sheldon, 1934; Hamilton, 1935), which may explain why fat and fat-free jumping mice usually refuse food prior to hibernation or during periods of arousal, even if death ensues by starvation. Food is not stored in the hibernaculum. Consequently, mice without sufficient fat reserves to last for at least six months would perish.

Sheldon (1934) noted that during periods of arousal, the mice drank much water, particularly if the relative humidity was low. The ears and tail became dry and subject to scab if the air was not saturated.

During hibernation the animal buries its snout in the belly fur, which probably reduces evaporative water loss through breathing. The forelegs are held to the chest and the hind limbs are drawn up along the face. The tail is coiled under or alongside the animal (Hamilton, 1935:194).

During the present investigation, 12 Napaeozapus increased their

weight rapidly during the latter two weeks of September. In October adults weighed 26 to 34 grams and became torpid for periods of several days, even at a room temperature of 20° to 25°C. Sheldon (1934) reported that temperatures below 10° to 13°C were necessary for extended hibernation. Torpid individuals lowered the respiration rate to 12 per minute, while sleeping mice in the same nest had a rate over 200 per minute. The sleeping mice aroused quickly when disturbed, but those in torpor required three to five minutes to become active. When torpid animals were first handled their eyes opened only halfway, muscle coordination was poor, and they lost their balance if probed gently. The body was noticeably flattened from the lack of muscle tone and heavy fat deposits. The mice stretched when arousing from sleep or torpor by extending the body forward on the front limbs, arching the back and dragging the large hind legs. In January and February the captive mice no longer became torpid and appeared to have lost most of the body fat.

EMERGENCE

The earliest record of emergence was a young adult captured on April 16 at Mont St. Hilaire in southern Quebec (Wrigley, 1969). The specimen was fat and its stomach contained pieces of beech nuts and insects. The site was near a stream in a forest of hemlock, beech, and maple, where a substantial snow cover remained, though adjacent higher ground was bare. There are only 14 other records in April, from Pennsylvania (Roslund, 1951), New York, Wisconsin, and North Carolina.

To determine the time of emergence at South Bolton, Quebec, where this species was known to be abundant, snap and pitfall traps were set along a stream on April 19 and checked daily. Not until the snow had melted and the soil had thawed did *Napaeozapus* appear. On May 6, five males and one female were taken. Whether they had just emerged or moved in from higher ground could not be determined. In New York, Hamilton (1935) found that the species had not emerged by the first week of April, when temperatures had risen to 18°C. By May 3, a number of individuals were abroad.

There is no indication, as shown in Fig. 21 (p. 89), that any particular age group emerged early. A difference in the time of emergence between the sexes is evident. Among 100 museum specimens collected prior to May 15, males totaled 87%, females only 13%. The majority of males were abroad in early May while most females did not appear until the latter half of May. Roslund (1951), in Pennsylvania, reported 13 males between April 27 and May 5, with the first females (two individuals containing small embryos) taken on May 9. Preble (1956),

in New Hampshire, collected 15 males and no females from May 29 to 31 in 1952, and in 1955 found 11 males and no females from May 13 to 15, and an almost equal sex ratio among 21 specimens from May 27 to 29.

SURVIVAL

The hibernation period apparently extends from early October to early May for the majority of woodland jumping mice. Sufficient fat reserves must be accumulated to supply energy for at least six months of hibernation, since the mice do not store food for emergency use. Late season activity of young mice observed under natural and experimental conditions (Sheldon, 1934; Hamilton, 1935; Neuman and Cade, 1964) reflects a reluctance or inability of the mice to enter prolonged torpor without being physiologically prepared (including an adequate energy supply). Hamilton found that only 3 of 11 *Napaeozapus* survived the winter while in outdoor enclosures, the survivors losing 30 to 35% of the body weight. One male weighed 27.5 g on November 24, and 25.9 g four days after becoming torpid, but only 17.8 g in the spring. Most jumping mice die or arouse often during experiments in hibernation. Though this may be the result of unnatural conditions of humidity, temperature and prior physiological conditioning, it also suggests that in the wild state the rigors of hibernation, plus accidents such as spring flooding of the hibernacula or exposure to subzero temperatures, may decrease population size considerably. Young from late summer litters might be expected to fare less well than adults that have had a longer period to prepare.

Data on survival in hibernation under natural conditions are meager. A comparison of age groups between fall and spring (Fig. 21, p. 89) is difficult to interpret, since each age group continually decreases as its members advance to an older category. Growth and tooth wear would theoretically have continued during the periods from time of capture to entrance into hibernation, and from emergence to time of capture. Therefore, the presence of juveniles in the fall and their absence in the spring does not show that all juveniles have perished during hibernation, though their great reduction suggests that some do not survive.

Reproduction

Meager data are available on reproduction because of relative scarcity of the woodland jumping mouse, low number of litters per year, and difficulty in breeding the species in captivity. The most in-

Locality	Date	Breeding Sign[a]
Southern Quebec	June 4	6–8 mmE
	10	4–15 mmE, 5PS, 4PS
	11	4–2 mmE
	12	6–4 mmE, 5–19 mmE, 3–3 mmE
	13	5–1 mmE, 4–10 mmE
	14	5–6 mmE, 4PS, –PS
	18	5–4 mmE, 4–10 mmE
	19	4–14 mmE, Estrus
	20	5–10 mmE, 5–2 mmE
	July 1	2PS
	31	Old PS
	August 6	4–16 mmE, 3–15 mmE, 5PS
	8	3–10 mmE
	11	6–1 mmE
	16	5PS
	18	5PS, Old PS
	19	Old PS
Prince Edward Island	June 22	5PS, Estrus
	24	Estrus
Nova Scotia	June 27	5–5 mmE
	28	Estrus
	30	5–18 mmE, –PS
	July 1	5–10 mmE

[a] E = embryos, PS = placental scars.
6–8 mmE = 6 embryos each 8 mm long

formative studies are those of Connor (1960, 1966), Hamilton (1935) and Townsend (1935) in New York, Preble (1956) in New Hampshire, Richmond and Roslund (1949) in Pennsylvania, and Sheldon (1934, 1938) in Nova Scotia and Vermont. Personal data from southern Quebec, Prince Edward Island and Nova Scotia are shown in Table 6. Reproductive data from all sources were combined (literature, personal field work, and information from museum specimen tags), to ensure coverage throughout the reproductive season. Data were collected from approximately 200 females, utilizing evidence of estrus, embryos, placental scars, and lactation. The size of the gonads was recorded in more than 100 males.

To minimize possible effects of latitude on the breeding season, the range of *Napaeozapus* was divided into three arbitrary groups and analyzed separately. The northern group, north of latitude 47°, con-

sisted of populations in central Ontario and Quebec, including the Gaspé Peninsula. The central group, from Michigan, southern Ontario and Quebec, and the Maritime Provinces south to Pennsylvania, supplied the most information since the species has received more attention in this area. Unless otherwise stated, data on reproduction refer to the central group. The southern group was recognized from south of about 40°, near the southern boundary of Pennsylvania.

BREEDING SEASON AND NUMBER OF LITTERS PER YEAR

Data on reproduction compiled from 170 females from the central part of the range are recorded in Fig. 19. The earliest breeding records are May 8 and 9, with four females from Pennsylvania carrying embryos only 1 to 2 mm in length. These early dates suggest that females are able to bear young soon after emergence from hibernation. No doubt the paucity of pregnant females in early May is attributable partly to the lack of sufficient collecting at this time. It is probable, also, that only a small proportion become pregnant this early. June is the main breeding season for the species, since more females are pregnant or show signs of having recently produced a litter during this time than at any other period. Not all females reproduce in May or June, and a majority of those that do not are apparently individuals born late in the previous year (age-groups 2 and 3). Quimby (1951) found that 30% of the females of *Zapus hudsonius* did not breed in June, but produced young the following month.

Reproduction continues at a low rate through July. Most females breeding at this time did not have young in June, since the mammae show no sign of having nursed recently. Connor (1960) reported that two specimens from New York were pregnant and also lactating on July 12 and 14, evidence that second litters may be produced early in the season. A second breeding peak is apparent in August. Three pregnant females I collected in early August from southern Quebec were carrying at least their second litter. Three specimens from Vermont and another from New York showed the same evidence — embryos and recent lactation. It is certain then that some females reproduce twice annually. Since the two main breeding peaks occur in June and August and the majority of females pregnant in July are carrying their first litter, a third litter is probably unusual under natural conditions. Schwentker (1957) obtained more than two litters a year in captive *Napaeozapus*, but these animals were probably active over a longer part of the year than wild individuals. Quimby (1951) claimed a third litter for several *Zapus hudsonius* in Minnesota.

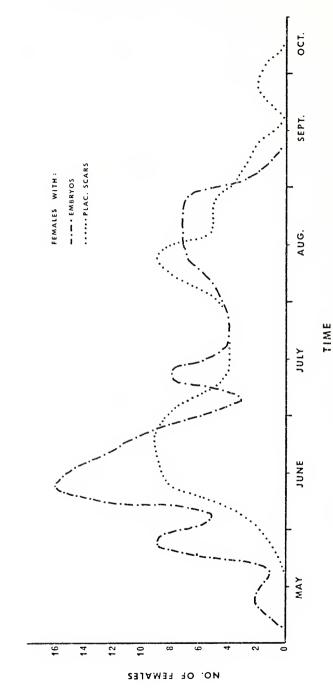FEMALES WITH:
–·–·EMBRYOS
······PLAC. SCARS

Fig. 19. Reproduction data on females from central populations of *Napaeozapus*.

The latest pregnancies of the season were reported on September 1 and 2 by Connor (1960) from New York. A few animals with placental scars were noted throughout September, the last from a Pennsylvania specimen dated October 4. June and August seem to be the main breeding periods of the woodland jumping mouse and also *Zapus hudsonius* in New York (Whitaker, 1963a:243).

Only two subadults (age-group 2) were found bearing embryos, which suggests that young of the year do not breed until the following year. The two specimens from New York were pregnant on May 14 and July 21 and were believed to have been from late litters of the previous year. Quimby (1951), using weight and body size as age criteria of live *Zapus*, claimed that females born in the spring were able to reproduce successfully at the age of two months. With the additional evidence of age from tooth wear, it is apparent that only females which have overwintered are sexually mature in *Napaeozapus*.

TESTIS LENGTH

The testis length of more than 100 males was recorded throughout the active season. Testes measuring 7 to 11 mm were enlarged and considered functional (J. J. Christian, personal communication, concurred on the basis of an histological study). The reproductive tract apparently becomes active within days after emergence from hibernation, since the testis length of all males taken in early spring was more than 7 mm. The first spring adult was collected on April 16 (individual of age-group 3 from southern Quebec) and had 8 x 4 mm testes. Hock (1960) indicated that arctic ground squirrels were able to reproduce almost immediately after emergence because partial gametogenesis occurs in both sexes during the hibernation period (probably during the periodic arousals), and the same may be true for jumping mice.

No significant decrease in size of the gonads was noticed until the latter part of August, and by the first week of September testes were less than 6 mm long. Blair (1941) also found that males collected during late August and early September in Michigan had small testes.

Thirteen males from spring litters, collected during the last three weeks of August and early in the following month, had testes measuring only 4.5 to 6 mm, suggesting that males do not become sexually active the first season.

LITTER SIZE

Eighty litters averaged 4.6 ± 0.11 (2-7) embryos, and 45 counts of placental scars averaged 4.3 (2-7). There is some evidence that second

litters have a reduced number of embryos, since eight females carrying second litters during July and August averaged only 3.8 embryos.

GESTATION PERIOD AND ESTRUS

Schwentker (1957) reported that there was no postpartum estrus in *Napaeozapus*, though it appeared possible to induce estrus by weaning the young. As long as lactation continued, estrus did not occur. Sheldon (1938:451) placed a female, which had been nursing young for 16 days, with a male, and 23 days later the female produced another litter. This is the only study which gives evidence for the length of the gestation period. Quimby (1951) found that *Zapus* could mate successfully soon after parturition while nursing continued. The gestation period was 18 days, prolonged 2 to 3 days if the animal was lactating when mated.

AGE DISTRIBUTION OF REPRODUCING FEMALES

The percentages of each age group in the total population and in the female breeding population are shown in Table 7. Pregnant females of age-groups 2 and 3, either in spring or summer, are believed to be from late summer litters of the previous year. Only two subadults (age-group 2) were found with embryos, so they do not appear to contribute significantly to the breeding stock at this age. Since group 3 adults exhibit a low reproductive rate compared to their total number in the population, it seems that many postpone reproduction in the spring. Animals from spring litters do not have young in late summer as they become age-group 3. Age-group 4 and 5 females, thought to be in their second and possibly third year, comprise almost 75% of the breeding stock. Far from being senile, females of age-group 6 form about 18%

TABLE 7

PERCENTAGES OF EACH AGE GROUP IN TOTAL POPULATION
AND IN FEMALE BREEDING POPULATION OF *NAPAEOZAPUS*
(data from Figs. 19 and 21)

	LATE MAY AND JUNE		JULY AND AUGUST	
AGE-GROUP	% Tot. Pop.	% Breed. Pop.	% Tot. Pop.	% Breed. Pop.
	n = 310	n = 40	n = 920	n = 46
2	5–6	3	4–23	2
3	14–24	10	10–31	7
4	33–48	42	20–41	39
5	18–30	27	12–25	35
6	9–14	18	5–14	17

of the breeding population throughout the season, some producing at least two litters annually.

REPRODUCTION IN NORTHERN AND SOUTHERN POPULATIONS

Though 364 specimens were examined from northern populations (north of 47°), only 11 pregnant females were found. They were noted from June 2 to July 30, and averaged 3.9 (3-6) embryos. It would be interesting to know if this low litter size is representative of northern populations or just a sampling error. Lord (1960) reported that hibernating prey species did not show increased litter size at higher latitudes. It was suggested that hibernation so reduced the mortality sustained by the overwintering population that a relatively large breeding stock was present in the spring. This increased survival may have reduced the selection for larger litters in the north. Probably the active season is shorter in the northern extremes of the range, which would decrease the number of females having two or three annual litters. The absence of juveniles in September (Fig. 22, p. 91) would support this conclusion. Of 13 females showing reproductive signs, a specimen from Temagami, Ontario, on July 10, and another from Carp Lake, Ontario, on July 30, appeared to be carrying second litters.

Breeding information was present for 10 of 150 females from southern populations (south of 40°). Five litters averaged 4.2 (3-5) embryos. Breeding records extended from May 22 (lactating female from North Carolina) to August 28 (specimen from Kentucky, carrying second litter). Although these data do not show a prolongation of the breeding season in the south, the large proportion of juveniles present in September (Fig. 22) suggests that such may be the case.

Development of Young

There have been few studies on the postnatal development of *Napaeozapus* since captive females usually destroy the young soon after birth. Litters have been born to females which were pregnant when captured (Hamilton, 1935) and to females bred in captivity (Sheldon, 1938). Layne and Hamilton (1954) presented the most complete account of developmental changes, in a litter of three (Table 8, p. 84). Newborn young were hairless except for vibrissae (thought to be absent at birth by Hamilton, 1935). The four pairs of mammae were visible in both sexes. With the exception of the thumbs, blunt claws were present on the digits of both front and hind feet. At 10 days, pigmentation appeared on the dorsum, and the pinnae of the ears unfolded, though the external auditory meatus was still closed. The vibrissae were prominent, the

longest mystacial measuring 3 to 4 mm. At 12 days fine hair appeared
on the dorsum of the head, body and limbs, the mystacial vibrissae
measured 6 mm, and the young could stand on four feet and take a
few steps. White hair appeared on the venter at 14 days. At 19 days
the dorsal pelage was luxuriant with a golden sheen, though the dorsal
stripe was not yet evident. The lower incisors protruded 0.2 to 0.3 mm
and the claws were well formed. At 21 days individuals were able to
stretch, yawn, and sit up. They attempted short hops of one inch but
usually fell. The lower incisors were longer than 0.5 mm and the upper
incisors appeared. At 24 days the dorsal stripe was pronounced and
the female began to nurse on her side instead of hunching over the
young. The eyes and external auditory meatus opened at 26 days and
the young became active, progressing by short hops. The large hind
feet spread out at a 45° angle when sitting. By 28 days the lower in-
cisors were 2 mm long, the upper 1 mm; hops exceeded one foot; tail
drumming was observed. By 34 days the color of the sides was yel-
lowish brown, not orange as in the adult, and weaning commenced.
Copulation was attempted by a male at 38 days of age, but was pre-
mature, since even males 64 days old had inactive testes measuring
5 by 3 mm. Molt into adult pelage was believed to occur when the ani-
mals were between 63 and 80 days of age.

Postnatal development of *Napaeozapus* parallels that of *Zapus*
(Quimby, 1951) but is somewhat slower, which may be expected since
the woodland jumping mouse averages slightly larger. Both zapodids
have a considerably slower developmental rate than various cricetids.
For example, pinnae unfolding, eruption of the lower incisors, opening
of the eyes, and weaning occur at averages of 2.8, 5.7, 13 and 19 days
in *Peromyscus leucopus noveboracensis* (Layne, 1968:178 and 186);
7, 13, 23.5 and 25 days in *Zapus hudsonius* (Quimby, 1951); 10, 19, 26,
and 34 days in *Napaeozapus* (Layne and Hamilton, 1954). The pro-

TABLE 8

DEVELOPMENT OF *NAPAEOZAPUS*[a]

Day	Total Length (mm)	Tail Length (mm)	Hind Foot (mm)	Weight (g)
0	35.2	11.0	5.0	0.87
6	48	16	6.5	1.6
14	73	25	12	3.9
26	123	70	23	8.5
64	199	120	28	14.1

[a] Based on a litter of 3, and condensed from Tables 1 and 2 of Layne and Hamilton, 1954.

longed period of development of zapodids is probably correlated with a number of intrinsic factors such as growth and coordination of the highly specialized limbs. Zapodids are also born at a relatively early stage in development, with a gestation period of 18 to about 23 days, while most species of *Peromyscus* require at least 23 days (Layne, 1968:155).

Molt

Information on molt was recorded from more than 250 museum specimens and 20 fresh animals. Sharp molt lines between the new and old pelage were usually not apparent, but molt patterns were readily detected by lifting the hair with a probe and noting the presence of pigmented spots in the skin or new patches of yellowish-orange hair in the gray underfur. A single annual molt occurs in *Napaeozapus* and is generally complete before entrance into hibernation. Individuals with worn pelage were most prevalent in early August. Juvenile and adult molts were noted. The transition from juvenile to subadult (age-group 1 to 2) was not marked by a change in pelage; subadults did not reveal signs of molting until they were almost two months old, when they were regarded as adults (age-group 3). Hence, there does not appear to be a subadult molt as found in many cricetids. At a number of localities, molting individuals were noted from early June to mid-October, evidently the result of various age groups molting at different periods and of individual variation in molting times. The pelage of animals from spring litters showed signs of wear by late July, and replacement of the hair began in late August and extended into late September. Some animals from summer litters completed the molt in late September and October while others postponed the pelage change until the following spring (mostly in June, but a few in early July). A majority of the adults older than one year (age-groups 4, 5, and 6) molted earlier than adults of the year, some showing new patches of hair in mid-June, most in August, and a few in early September. Gender apparently was not a factor in the differences in onset of molt.

The usual molt sequence of *Napaeozapus* is illustrated in Fig. 20. The first sign of molt in a fresh or museum specimen is a darkened area in the skin and presence of numerous pigmented spots. The next stage is the appearance of stiff yellowish-orange hairs, while the completed molt is characterized by an extremely dense growth of relatively long hair. New growth generally appears first on the cheeks and sides of the neck, then spreads to the rostrum, eyes, shoulders, and forelimbs. The molt progresses rapidly along the sides, extending slowly to the dorsal
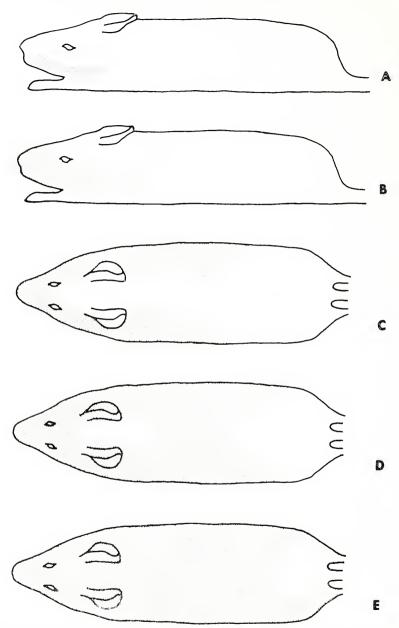
FIG. 20. Progress of molt (A to E) in adult *Napaeozapus*. Darkened areas represent new growth of hair.

medial line and underparts. Often a patch of old hair remains from the forehead to the interscapular region, as the molt passes posteriorly. In the final stage, new hair appears on the hind limbs and rump. Variations of this sequence are numerous, as particular waves of new hair spread more quickly in some areas than others. The direction of the molt is consistent, however.

The molt sequence of *Napaeozapus* differs from *Zapus*, as described by Krutzsch (1954:374-375), mainly in the primary area from which new growth of hair spreads. In *Napaeozapus* the center is located on the check and neck region, while in *Zapus*, the center appears between the shoulders and also on the rostrum.

IX. POPULATIONS AND EXTERNAL FACTORS IN SURVIVAL

Population Structure

AGE

A total of 2,100 museum specimens of *Napaeozapus* from all parts of the range were incorporated into six arbitrary age groups, utilizing evidence of tooth wear, weight, and measurements (see Bases for Determining Age Groups, p. 23). To detect differences in age composition in populations at various latitudes, groups of populations from northern, central, and southern sections of the range were studied separately (for delineation of the three sections see Reproduction, p. 77). The following discussion is based on the central group, for which more complete data were available (1,586 specimens), and concludes with a comparison of northern (364 specimens) and southern (150 specimens) populations.

The age composition of the central populations of *Napaeozapus* is illustrated in Fig. 21. Members of age-group 1 are classified as juveniles and are thought to be less than seven weeks old. Weaning occurs at four to five weeks and juveniles rarely emerge from the burrow until after this period. Juveniles first appear above ground in late June and reach a peak of 17% of the population in early August. Juveniles decrease in number in mid-August as they become subadults (group 2). A
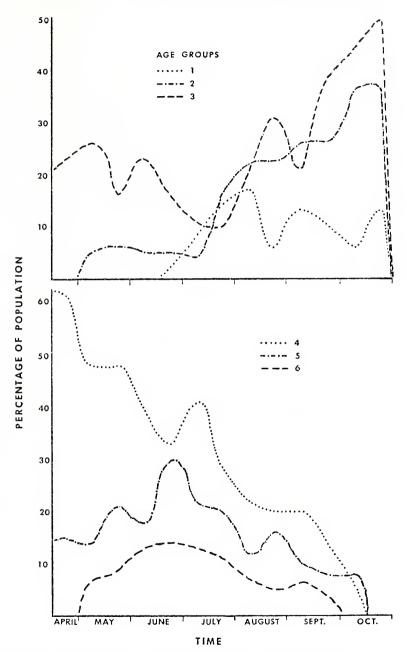
FIG. 21. Age composition of central populations of *Napaeozapus*.

second but lower peak of juveniles in early September results from the offspring of summer litters, which reach the group-2 stage during September and October. The third increase in percentage in late October is due to the adults having entered hibernation so that they are no longer trappable.

Age-group 2 individuals are subadults and believed to be seven to ten weeks old. Overwintering subadults would be an additional six months older. They form about 5% of the population emerging from hibernation and their numbers do not increase until the second week of July, as a result of recruitment from spring litters. Subadults form one-quarter of the population during August and September, the high level being maintained from summer litters. The increase to 36% in October results from late-season litters as well as late entrance into hibernation. The abundance of subadults in the fall and scarcity in the spring might suggest that animals from summer litters suffer high mortality during winter torpor. But since the group-2 state is estimated to represent only three or four weeks, many individuals classed as subadults in the fall would probably have been designated adults of age-group 3 in the spring, following some period of activity and growth prior to and after hibernation.

Members of age-group 3 are regarded as adults and comprise about 25% of the spring population. These individuals are from litters of the previous year and hence would be about nine or ten months old. Numbers decline to a low in July as they enter age-group 4. In late August, group 3 increases from recruitment of individuals born in the spring, which are estimated to be at least ten weeks old. The high proportion of group-3 adults in October derives partly from their late entrance into hibernation. In September, before the older adults become dormant, animals born that season (age-groups 1, 2, and 3) comprise almost 70% of the population.

Age-group 4 adults are in their second season and thought to be more than ten months old. Their great abundance in the spring is accounted for by assimilation of group-3 individuals which were predominant in the previous fall. Their numbers exhibit a steady decline due to decreasing recruitment from group 3 as the season progresses, loss to age-group 5, and mortality.

Adults of age-group 5 are estimated to be in their second and possibly third season while those of age-group 6 may be in their third or fourth year; there is no method of determining the age of these animals with any assurance. Attrition of the molars down to the cingulum, in a species which uses the dentition for only five or six months of the year,
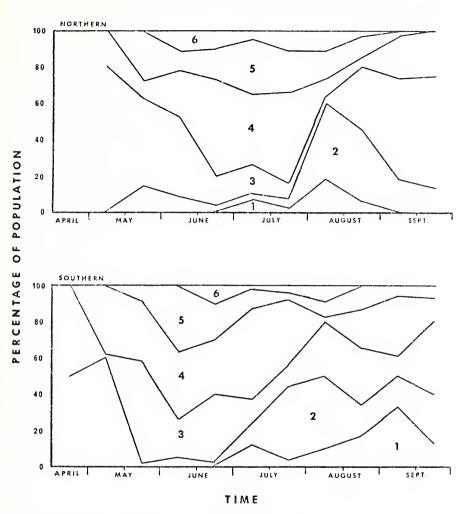
FIG. 22. Age composition (age-groups 1 to 6) of northern and southern populations of *Napaeozapus*.

also suggests that group-6 individuals might well be three or four years old. Though this life-span is seldom attained among other small North American rodents, it is apparently not unusual in the zapodids. *Zapus princeps* may survive at least 4 years (Brown, 1970), and *Sicista betulina*, 3.3 years (Walker, 1964), both under natural conditions. The majority of individuals in age-groups 5 and 6 emerge from hibernation in May and enter dormancy relatively early (by the end of September). They reach their greatest proportion of the population in late

June (30 and 14%, respectively) before the young appear. The older age groups also contribute significantly to the breeding population.

Fewer specimens are available in northern and southern groups of populations (no October records and only a few from April in the north). There are indications of shorter breeding and active seasons in the north (Fig. 22, p. 91). Juveniles reach a peak in early August and are absent in September in the north, while in the south, a peak is not attained until September, indicating a greater percentage of summer litters. Subadults from spring litters appear several weeks later in the north, and group-3 adults are slower to change into group 4 during the spring, since they appear to have been born later in the previous season and may also have been dormant longer.

SEX

The sex ratio among 2,351 museum specimens of *Napaeozapus* was 57% males, 43% females. Data prior to May 15 should not be included since males emerged from hibernation several weeks earlier than females, resulting in a spring sex ratio of 87% males and 13% females (n = 100). Subsequent to September 16, males were also more abundant, 58% (n = 175); however, the hibernation period had begun and may have prejudiced the results. Considering the data from May 15 to September 15, the sex ratio among 2,076 specimens was 55% males, 45% females. This difference indicates a probable sampling error involving several factors. Females, pregnant or caring for the young, would likely reduce activity above ground and remain closer to the burrow. In addition, females generally have a smaller home range than males. Both factors would result in fewer females being collected in the sample.

The sex ratio in a single population of *Napaeozapus* at South Bolton, Quebec, was 33 males to 32 females. Ratios reported for *Zapus hudsonius* by Quimby (1951) were 48% males, 52% females (n = 325), and by Whitaker (1963a), 53% males to 47% females (n = 890).

Population Density and Home Range

The few estimates of population density and home range of *Napaeozapus* have varied greatly as a result of differing methods of trapping and calculation. Population studies have generally been conducted in areas where numbers were exceptionally high, though the species is local in distribution and usually present in small numbers or entirely absent in other suitable habitats. Evaluation of the home range is diffi-

cult since the mice often move to new areas and individual mice are seldom caught a sufficient number of times for an accurate assessment.

In central New York, Townsend (1935:93) calculated 24 woodland jumping mice per acre in moist woods (apparently hemlock–northern hardwoods), representing 21% of the small mammal community. In dry woods (apparently beech-maple) there were 6 to 11 per acre representing 8 to 11%, and in moist meadows (apparently forest edge), 6 per acre, comprising 10%. Snap traps in stationary and moving quadrates were utilized, and the resulting census figures are undoubtedly too high. The percentages of *Napaeozapus* of the small mammal community are probably more realistic than the population estimates.

Brower and Cade (1966:54-55), using mark and release methods, trapped 56 *Napaeozapus* on a 1.5-acre plot in New York during one month. Twelve individuals were taken three or more times but only eight were considered resident; 5.2 residents per acre from August 10 to September 13 were thus calculated. The study area was situated on an abandoned ski slope and was surrounded on three sides by rather unsuitable habitat. This fact, along with the abundance on the plot of raspberries, blackberries, alder fruit, and birch seeds, constituted an unusual situation and may have concentrated the mice. The large number of transients would seem to support this conclusion.

High densities of *Napaeozapus* have also been reported by Hamilton (1935) and Connor (1960) in New York, Blair (1941) in Michigan, and Preble (1956) in New Hampshire. In the present study these mice were found to outnumber other small mammals at two localities. Fourteen specimens were taken in two nights along 60 yards of streambank at Hunter River, Prince Edward Island. Short trapping sessions in four years yielded 65 individuals from the vicinity of a stream at South Bolton, Quebec.

Burt (1946) reported a home range of one or two acres, with fall populations of three per acre. Blair (1941) found 52 *Napaeozapus* living on an 18.18-acre plot in Michigan from August 25 to September 22. The home range was relatively large and varied greatly in different individuals. Females ranged from 1.0 to 6.5 acres and males, 1.0 to 9.0 acres. Thirty-two animals were taken 5 or more times and one female was caught 22 times. Males tended to wander more widely and the home ranges of both sexes overlapped.

In Vermont, Sheldon (1938) observed that the mice were reluctant to enter live traps more than once and that individuals did not reside in a particular area for long. One male traveled 117 yards in 24 hours, and only one male was taken again the second year. Numbers fluctu-

ated annually, and a low during one year was thought to have been caused by a January flood drowning the hibernating mice.

Mortality

There are few records of predation on *Napaeozapus*. Hamilton (1935:191) found two individuals in the stomach of a skunk caught in November, which supposedly had penetrated the burrow and found the mice hibernating. Blair (1941) reported that a *Mustela* sp. forced open the door of a live trap and ate the brains of a captive *Napaeozapus*. Platt (1968) gave an account of a mink killing and eating (except for tail and haunches) at least nine jumping mice captured in live traps, during six days. *Napaeozapus* was the most abundant species on the area (26 individuals). However, 22 animals of four other species (*Blarina, Tamias, Peromyscus leucopus,* and *Clethrionomys*) were not touched. No reason for this selective predation could be found. Greenfield (1938) noted that the first specimen of *Napaeozapus* recorded in Virginia was found in the stomach of a rattlesnake (*Crotalus horridus*) in 1937. Another was subsequently discovered in a copperhead (*Agkistrodon contortrix*). The University of Connecticut Museum has two specimens (UCM 4169, 9589), a juvenile and subadult, which were caught by house cats.

Parasites

Jumping mice appear to be less subject to infestation by external parasites than other rodents (Hamilton, 1935:191). Hamilton reported several fleas (*Ctenopthalmus pseudagyrtes* Baker) on one *Napaeozapus*. Red mites (*Trombicula harperi*), affecting the ear and occasionally the nostrils and forelegs, have been found on *Napaeozapus* from Michigan by Manville (1949:69-70), from New York by Harper (1929), and also on six other specimens from New York (NYSM). Botfly larvae (*Cuterebra fontinella* Clark) embedded in the fascia of the inguinal region, dorsolumbar area, scrotum, and front and hind legs, have been reported by Blair (1941) in Michigan, Sheldon (1934, 1938) in Nova Scotia and Vermont, and in single specimens from the Gaspé, Quebec (USNM), New York (AMNH), Pennsylvania (CMP), and West Virginia (WVMS). Blair recorded the highest frequency of infestation, with botfly larvae present in 5 of 25 males and 7 of 27 females taken from August 25 to September 22.

The most complete study on parasites of *Napaeozapus* is that by Whitaker (1963b) in New York. Three animals each had one flea

(*Orchopeas leucopus* Baker) and the following mites were recorded on many other individuals: *Androlaelaps fahrenholzi* (Berlese) (= *Haemolaelaps glasgowi* Ewing), *Eulaelaps stabularis* Koch, *Haemogamasus ambulans* (Thorell) (= *H. alaskensis* Ewing), *Protomyobia brevisetosa* Jameson, *Radfordia ewingi* (Fox), *Pergamasus* sp., *Labidophorus* (= *Dermacarus*) later identified as *Dermacarus hypudaei* (Koch) by Rupes and Whitaker (1968). A protozoan (*Hexamita*) was noted in cecal smears of two mice, six harbored cestodes including *Hymenolepis,* two had the nematode *Rictularia,* and many harbored the nematode *Citellinoides zapodis* Ditmans.

X. ACTIVITY AND BEHAVIOR

Runways and Burrows

Napaeozapus appears to be less restricted to definite runways than are many other small mammals. Natural openings are often traversed (Cameron, 1958:29) and the species does not hesitate to use the runways of other rodents, as well as the trails of beaver, moose, and deer (Sheldon, 1934). Many specimens have been collected along the banks of watercourses, often on the sand or mud shore, and along the forest edge (Hamilton, 1935; Townsend, 1935; Sheldon, 1938; personal observations). The presence of water does not seem to deter the species from its pathways and Jameson (1949) found a runway that was flooded most of the time.

Woodland jumping mice are able to dig their own burrows, though they often use those of other small mammals. Peterson (1966) noted their propensity for exploring cavities in the ground and a consequent susceptibility to pitfall traps. The opening of the burrow leading to the nest is carefully concealed and consequently nests have rarely been found. The author excavated several tunnels where pregnant or lactating females had been trapped, but none led to a nest chamber. Stupka (1934) reported a nest on Mount Desert Island, Maine, which contained a female and young. The globular structure, made of leaves and dry grass, was situated in a brush pile. Snyder (1924) located a nest

with young in central Ontario. The ball of leaves (6 by 5 by 4.5 inches) was placed five inches underground, in the middle of a 3.5-foot blind tunnel. The female carried nest material in her mouth and carefully covered the entrance during the day.

Locomotion

PROGRESSION ON LAND

The locomotion of *Napaeozapus* was observed in the field and laboratory. Several gaits were recognized, each characterizing a particular rate of locomotion. A quadrupedal walk was used when moving slowly, as when searching for food, creeping around obstacles, or entering the nest cavity. The forelimbs were placed one after the other, as were the hind limbs. A more rapid walk was achieved by planting the forefeet either together or alternately, and then bringing forward the two hind limbs together. The gait most often used when moving directly to another location was the quadrupedal hop. The body rocked forward and backward as the weight was shifted from the front limbs to the back. Both front feet were planted at the same time, as were the hind feet an instant later. The body became airborne for a short distance from the thrust of the hind limbs. When startled the animal was capable of leaping more than four feet (1.2 m), attaining a height of two feet (0.6 m). It was difficult to observe the leaping and landing movements during this rapid and erratic mode of progression. Usually the forelimbs preceded the hind limbs on landing, though on occasion, all four limbs were planted almost simultaneously, approaching a bipedal hop. During the leap the forelimbs were folded on the chest, while the long tail trailed behind, assisting in balance. Miller (1899) commented on the resultant loss of balance during leaps when part of the tail was missing.

Early reports of distances attained by the quadrupedal hop of jumping mice were probably excessive. Seton (1909) stated that a *Zapus* covered 10 to 12 feet (3.1-3.7 m) in one leap, and Snyder (1924) observed a *Napaeozapus* clearing 7 feet (2.1 m) in a normal jump, and 10 to 12 feet when disturbed. In subsequent accounts, estimates were more conservative and 6 feet (1.8 m) would appear to be about maximum. Hamilton (1935:190) reported that woodland jumping mice did not jump more than 4 to 6 feet, and usually covered only half this distance. Sheldon (1934) observed a *Napaeozapus* leap 5 to 6 feet after escaping from a trap, and another startled mouse jumped 3 to 4 feet (0.9-1.2 m) along a dry streambed, clearing the ground from 1 to 2 feet (0.3-0.6 m) (Sheldon, 1938). Quimby (1951) and Whitaker

(1963a) doubted whether *Zapus hudsonius* could jump more than about 3 feet, and Whitaker suggested that many records of long leaps ascribed to *Zapus* may have resulted from confusion with the slightly larger *Napaeozapus*.

In the field I have not seen *Napaeozapus* jump farther than 4 feet, and individuals usually progressed by successive hops of only 2 to 3 feet. In captivity, jumping mice were able to jump 2 feet to the top of the cage, and could well have leaped higher. When pursued in a closed room *Napaeozapus* appeared to tire quickly and could easily be caught by hand. Individuals which had become obese prior to hibernation were less agile.

CLIMBING

Hamilton (1935:190) found that the scansorial ability of *Napaeozapus* was well developed. Individuals climbed easily over brush and limbs in outdoor enclosures. He suggested that in the wild they ascend *Rubus* bushes to obtain the berries. Sheldon (1934) commented on their agility in bushes, noting the mice were able to reach alder cones and new needles of spruce which served as food. Saunders (1921) also suspected they would climb alders for the fruit. In the present study, mice were often observed climbing along the sides and top of wire cages. There are no records of the mice having been collected in trees, even though many mammalogists, in their general collecting, regularly set some traps in trees. Woodland jumping mice apparently restrict their climbing to bushes, in contrast to the more arboreal deer mice and white-footed mice, which have been caught in tree traps.

SWIMMING

Napaeozapus and *Zapus* are often associated with watercourses, and, to judge from published accounts of swimming jumping mice, they do not hesitate to enter the water when escaping danger. Many have been trapped on stones and small islands in the middle of streams, which implies that crossings are a regular occurrence in wandering over the home range. Hamilton (1935:190) stated that jumping mice swam well (4 to 5 minutes or longer), with the head held high and the tail arched near the middle. Only the hind feet were used in swimming. Priddy (1949) observed a jumping mouse, believed to be *Napaeozapus*, swimming a few inches below the surface with fair speed and ease and utilizing the hind feet only. Quimby (1951) released several *Zapus* from a boat and described the swimming motions as rapid lunges at first, using only the hind limbs together, followed by a steady, slow gait employing all four limbs at once. When approached closely they

submerged and swam several feet before resurfacing. Whitaker (1963a: 236) reported that a *Zapus* swimming on the surface used both front and hind limbs, whereas only the hind limbs were used when submerged.

In the present study a *Napaeozapus* was forced to swim in a large aquarium in order to examine the movements of the limbs and body. Its performance was compared to several other species of woodland and grassland rodents. When placed in the water the woodland jumping mouse swam with a rocking motion of the body, utilizing all four limbs. The forefeet were employed simultaneously, while the hind feet were being drawn to the body. The hind limbs were then extended together, propelling the body forward. The movements gave the impression that the animal was attempting to hop on the surface. Apparently the forelimbs are used only when swimming on the surface, as they serve to maintain the head above water. Due to the strenuous action of the limbs and body, the mouse tired quickly and was removed after three minutes.

In sharp contrast to *Napaeozapus*, *Peromyscus leucopus* and *P. maniculatus* were able to swim for more than 30 minutes. Air trapped in the fur of *Peromyscus* appeared to assist in keeping the head and back above water, and there were short periods when the animals floated, thereby resting the limbs. The hind feet, working alternately and rapidly, provided the propulsion. There was no bending of the back, and the forefeet were only occasionally used, especially during turning movements.

Clethrionomys gapperi, *Microtus pennsylvanicus*, and *M. ochrogaster* also used the hind feet in "dog paddle" fashion, utilizing the forelimbs only as a last resort to maintain the head above water. The voles were able to remain afloat for 5 to 15 minutes.

It was not possible to measure the rate of swimming in the aquarium, but the jumping mouse seemed to attain the greatest speed. It would be preferable to test a number of individuals of each species in a lake, where one could obtain a better estimate of speed, endurance, as well as orientation. However, the present experiments indicated that the relatively poor performance of *Napaeozapus* when compared to *Peromyscus* and *Microtus* resulted from its more strenuous movements. The body and both front and hind limbs were employed in a sequence resembling the quadrupedal hop on land. The cricetids used only the hind limbs in short alternating strokes with little effort (as long as buoyancy was maintained by the fur). The limited data suggest that *Napaeozapus* would have no difficulty in traversing small streams, but its apparent lack of endurance might preclude extended swims across lakes and rivers.

Behavior

ACTIVE PERIODS

Woodland jumping mice are mainly nocturnal, but are occasionally active in late morning and evening (Sheldon, 1934), particularly if the weather is rainy or cloudy (Bider, 1968). Goodwin (1924) reported seeing two individuals abroad during the day. Hamilton (1935), Bider (1968), and Thibault (1969) found increased activity during cloudy, rainy nights. Brower and Cade (1966) noted no effect, while Sheldon (1934) reported an inverse relationship. No difference in the number of captures (about 150 specimens) was noticed on rainy or clear nights, in the present study. Even on clear nights the habitats of *Napaeozapus* were often very wet as a result of air moisture and dew, and relatively dark because of dense vegetation.

Brower and Cade (1966) and Thibault (1969) reported more activity during cold than warm nights, and Hamilton (1935) found individuals active in June at temperatures of about 4°C. Bider (1968) noted that woodland and meadow jumping mice exhibited a period of high activity from August 1 to September 14 (possibly correlated with the search for additional food in preparation for hibernation), followed by decreased activity toward the end of September.

ESCAPE

The escape behavior of *Napaeozapus* has been described briefly by Sheldon (1934, 1938) and Hamilton (1935), and is similar to that of *Zapus* (Quimby, 1951; Whitaker, 1963a). After taking several moderate to long leaps, the startled animal stops abruptly under the nearest cover and remains motionless unless pursued. The dark dorsal stripe and orange sides blend well with shadows and dead leaves and grass. The series of rapid, erratic jumps usually carry the mouse away from view, and the camouflage afforded by its pelage, together with its ability to remain motionless, make the individual difficult to find. Whitaker suggested that their relative lack of odor and their "freezing" behavior may aid the mice in avoiding detection by predators. In the present investigation several individuals of both species were captured by hand after a slow approach. Many more escaped, however, appearing only as a quick flash in the vegetation.

EXCITABILITY

When first captured, woodland jumping mice are extremely nervous, leaping frantically at the slightest noise or motion, even of another

individual. Ricocheting at great speeds, the mice often collide in mid-air and may receive fatal head injuries from hitting the cage roof if they are not supplied with some material like sphagnum moss in which to hide. Tail drumming is another sign of nervousness. Townsend (1935:94) remarked on their excited leaping and quivering, and questioned whether they were ever at ease in captivity. During the present investigation individuals became docile within a month and could be hand-fed and handled without apparent anxiety.

SOCIABILITY

Sheldon (1934) noted that during the breeding season captive females would attack males, injuring the tail and ears. At other times, however, the species was not belligerent. In the present study, captive individuals were very tolerant of their own kind and no aggressive acts were observed. Three groups of four animals, including both sexes, were maintained in large cages and additional individuals were accepted without disturbance. They preferred to sleep together in the same nest box, often lying one on top of another. The following observation illustrates their tolerance. A captive jumping mouse seized a grasshopper after an excited chase, held it down with the front feet, and proceeded to eat the insect. Another mouse succeeded in pilfering the remains and retreated several inches. Then followed several exchanges and "tugs-of-war" with the insect parts during which time there was no antagonism except for gentle nudging on the rump, side, and cheek. When one mouse approached the feeding individual, the intruder extended the body, with ears depressed and eyes half-closed, nudging the other with its snout until the insect was snatched away. Neither food items nor areas of the cage were defended. Possibly this same intraspecific tolerance ensues under natural conditions and may be involved in the apparent colonialism of the species.

VOCALIZATION

Sheldon (1934, 1938) reported that the young were vociferous soon after birth. The voice of adults was not harsh or shrill, but a soft clucking sound. When sleepy or entering hibernation the mice squealed continuously if disturbed. In the present study, a dozen individuals were maintained in captivity; and prior to and after the onset of torpor, the adults made no audible sounds.

XI. SUMMARY

The woodland jumping mouse inhabits cool, moist areas within the spruce-fir and hemlock-hardwood forests of eastern Canada and northeastern United States. Its range appears to be controlled by the distribution of the preferred flora, rather than by the direct effects of temperature and moisture. The diet includes insects, fungi (particularly *Endogone*), seeds, berries, rootstocks, and some green plant material. Average population density in good habitat is about three per acre. The abundance of *Napaeozapus* is negatively affected by *Clethrionomys gapperi* within the forest, and by *Zapus hudsonius* in forest-edge habitats. Several weeks prior to hibernation jumping mice build up fat reserves totaling about one-third of the body weight. Overwintering adults enter hibernation in late September, while young of the year become torpid from late September to late October. Some individuals emerge in late April but most do not appear until May. Males appear about two weeks before females. The breeding season commences in early May and ends in early September, with peaks in June and August. Some females produce two litters per year, but many apparently have only one litter. Males remain sexually active from near the time of emergence to late August. Males and females are not sexually mature until the second season. The gestation period is about 23 days and the average number of embryos per litter

is 4.61 ± 0.11 (2-7). Young of the year comprise about 70% of the fall population. A large percentage of individuals live two years and many attain an age of three years or more.

Skunks, mink, weasels, snakes, and house cats are known to prey on jumping mice. The species is relatively free of parasites although fleas, mites, botfly larvae, protozoans, cestodes, and nematodes have been found.

Napaeozapus does not often make well-beaten pathways, but utilizes natural openings such as sandy shores and streambanks. Nests are situated in shallow underground burrows or in brush piles and are lined with grass and leaves.

The mice progress by a quadrupedal walk and quadrupedal hop (up to six feet). Escape behavior consists of a number of erratic leaps, followed by "freezing" lasting many minutes. The species climbs well in bushes and swims rapidly for short distances.

The fossil record of the dipodoid line leading to *Napaeozapus* suggests the emergence of the dipodoid stock in the late Eocene, attainment of the primitive sicistine level of *Plesiosminthus* by late Oligocene, the primitive zapodine stage of *Megasminthus* by late Miocene, the appearance of *Zapus* in the late Pliocene, and *Napaeozapus* in the Middle Pleistocene. The closest living relatives of *Napaeozapus* are three species of *Zapus* occurring in northern and central North America, and *Eozapus*, a rare and poorly known jumping mouse from a restricted area of China. Included in the same family as the jumping mice are a number of species of birch mice, *Sicista*, from Eurasia. *Sicista* is the most generalized member of the family while *Napaeozapus* is the most specialized in dental characters and in modification of metatarsal length.

The body and skull of *Napaeozapus* are murine in appearance, the tail is long (60% of total length), and the hind limbs are elongated for saltation. The molars are semihypsodont and flat-crowned, with a complicated series of re-entrant folds in the enamel and dentine. Premolars are lacking. Ear ossicles, hyoid apparatus, dentition, os penis, os clitoris, phallus, and possibly chromosomes serve to differentiate the Recent zapodids where these characters have been studied. Both *Napaeozapus* and *Zapus* reveal an unusual feature in the sex chromosomes — XX and Xx females in the same population.

The pelage is notable for its tricolor pattern which probably affords camouflage protection from predators. There are juvenile and adult molts, but no subadult molt. Animals born in the spring undergo molt before entering hibernation, whereas some individuals from late litters

do not change into adult pelage until the following spring. Adults more than one year of age may molt during any period from mid-June to late September. New hair generally appears first on the cheeks and neck, and spreads dorsally, ventrally, and posteriorly to the rump.

Growth, as revealed by external and cranial characters, is rapid through the juvenile and subadult stages and considerably slower after adulthood has been reached (more than two months old). The hind foot length and interorbital breadth attain full size in the juvenile stage, tail length reaches a maximum in subadults, while body and skull lengths continue to increase slightly throughout life.

The 15 taxonomic characters used in the systematic study show normal variability, with coefficients of variation ranging from 1.51 to 5.75. Females average slightly larger than males in most external and cranial characters. Much of the geographic variation in morphology of *Napaeozapus* is clinal, and individuals from northern populations average 12% (7-17) larger in most characters than individuals from the south. Breadths of the interorbital and rostral regions exhibit nonclinal variation.

Five subspecies are recognized; three of these have only limited contact with other races because adjacent water barriers and unsuitable land habitat leave only a narrow zone of access. Two subspecies, *N. i. algonquinensis* and *N. i. gaspensis*, are placed in synonomy, since they appear to be populations at the end of a cline of increasing size, and few character discontinuities are displayed. The five races have characteristic color differences although intergradation over a wide range is present between several subspecies.

The Great Lakes and Gulf of St. Lawrence have acted as major barriers to gene flow. Populations on either side of the upper St. Lawrence and Lake Ontario waterway are not noticeably different, however, and have probably been separated for only a relatively short time. The Appalachians may have partially restricted gene flow between *N. i. roanensis* and *N. i. insignis* during the late Pleistocene. The other three subspecies, *N. i. frutectanus, abietorum,* and *saguenayensis*, which are now situated in northwest, north-central, and northeast regions, were likely isolated for periods by various drainage systems. Individuals inhabiting the boreal forests which were present in Pennsylvania and Virginia during the Wisconsin glaciation are comparable in size to the large individuals which now inhabit the boreal forest in Canada (*N. i. abietorum* and *saguenayensis*).

Napaeozapus remains have been found at a mid-Pleistocene deposit in Maryland, and four late-Pleistocene sites in Pennsylvania (two de-

posits), Virginia, and Tennessee. One site from Pennsylvania and the Tennessee record are considerably outside the present range of the species. These records and the distribution of spruce-fir and hemlock-hardwood forests during the period of maximum glaciation of the Wisconsin advance suggest that *Napaeozapus* occurred farther from the Appalachian highlands, possibly throughout most of Kentucky, Tennessee, Georgia, and the Carolinas.

APPENDIX

Habitat Data on *Napaeozapus*

Habitat data on the woodland jumping mouse were compiled from the literature, which contained information in varying amounts, and from personal observations. A systematic geographical analysis, by province and state, revealed that vegetational conditions preferred by *Napaeozapus* could be classified into six main types of habitat. These, together with their abbreviated reference forms, are listed below, followed by the geographical analysis arranged from north to south. When adequate habitat information was not presented in the literature, the descriptions were assigned to the category that seemed most appropriate, considering the fauna and flora associated with the jumping mice. Hyphenated reference abbreviations in the geographical descriptions denote a combination of types.

HABITAT TYPES

HH   Hemlock-hardwood forest.

HHE   Forest-edge between hemlock-hardwood forest and clearings. Included are a number of forest-edge situations; open mature forest with ground cover of grasses or sedges; open second-growth woods; deciduous shrubs in clearings; zone of shrubs,

sedges and grasses where forests abut on lakes; speckled alder–willow growth along streams in open areas; edges of swamps.

SF   Spruce-fir forest.

SFE   Forest-edge between spruce-fir forest and openings. Also included are high-shrub stage of bogs and watercourses consisting of speckled alder, willows, grasses and sedges; subclimax bog forest of black spruce and tamarack, or northern white-cedar.

M   Meadows of grasses and sedges with few shrubs. Usually *Napaeozapus* caught here are within a short distance from woody cover. Wet meadows within deciduous and coniferous forests often attract the mice.

B   Bogs. Treeless areas with a ground cover of mosses, heaths, sedges, grasses, horsetails, cattails, and numerous small shrubs such as Labrador tea.

GEOGRAPHICAL HABITAT ANALYSIS

MANITOBA. SFE, Soper (1937, 1938).

ONTARIO. SFE, Saunders (1921); SFE, Soper (1923); SFE, Snyder (1924); SFE, SF, HHE, HH, M, B, data from ROM specimens.

QUEBEC. SF, SFE, Goodwin (1924, 1929); M, B, SFE, Cameron and Morris (1951); SF, HH, M, Pirlot (1962); HH–SF, HHE, SFE, B, Wrigley (1969).

NEWFOUNDLAND (LABRADOR). SF, Bangs (1898).

NEW BRUNSWICK. SFE, B, Morris (1948).

PRINCE EDWARD ISLAND. SFE, Cameron (1958); HH–SF, SFE, personal field work.

NOVA SCOTIA. SF, HH, Rand (1933); HHE, B, Sheldon (1934); HH, SF, Smith (1940); SFE, Cameron (1958); HH–SF, HHE, SFE, personal field work.

MINNESOTA. Not examined, Surber (1923); SF, Beer (1953); SF–HH, O. Kalin (personal communication).

WISCONSIN. SFE, SF, Jackson (1961); SFE, Long (1970).

MICHIGAN. HH, Blair (1941); HH, Burt (1946); HHE, Manville (1949); HH, Dalby (1968).

MAINE. HHE, Branin (1936).

NEW YORK. HH–SF, Harper (1929); HH–SF, Hamilton (1935); HHE, M, Townsend (1935); HH, Jameson (1949); HH, SF, HHE, M, Connor (1960, 1966); HHE, HH, M, Whitaker (1963b); HHE, HH–SF, SF, M, Brower and Cade (1966).

VERMONT. HH–SF, Sheldon (1938); SF, Osgood (1938).

NEW HAMPSHIRE. HHE, SF, M, Preble (1956).

MASSACHUSETTS. HH, Platt (1968).

CONNECTICUT. HH, Goodwin (1935).

RHODE ISLAND. HHE, Hamilton (1935).

OHIO. HH, B, Bole (1935) ; HH, Bole and Moulthrop (1942).

PENNSYLVANIA. HH, HHE, Richmond and Roslund (1949) ; HH, Grimm and Roberts (1950) ; HH, HHE, M, Gifford and White-bread (1951) ; HH, B, Doutt (1966).

NEW JERSEY. HHE, Rhoads (1903).

KENTUCKY. HHE, M, Barbour (1951a) ; M, personal field work with W. and L. Goodpaster.

WEST VIRGINIA. Not examined, Brooks (1911) ; HH–SF, Kellogg (1937).

MARYLAND. HH, Paradiso (1969).

VIRGINIA. M, HH, Handley and Patton (1947) ; HH, personal field work with W. and L. Goodpaster.

TENNESSEE. HH, SF, Komarek and Komarek (1938) ; HH, SF, personal field work.

NORTH CAROLINA. HH, Odum (1949) ; HH, SF, personal field work.

GEORGIA. HH, Autrey and Odum (1949) ; HH, Golley (1962).

SOUTH CAROLINA. HHE, Coleman (1940).

LITERATURE CITED

Adorjan, A. S., and G. B. Kolenosky. 1969. A manual for the identification of hairs of selected Ontario mammals. Research Report (Wildlife), Ontario Dept. Lands and Forests, 90:23.

Anderson, R. M. 1942. Six additions to the list of Quebec mammals with descriptions of four new forms. Annual Report for 1941, Provancher Soc. Nat. Hist. of Canada, pp. 31-43.

————. 1946. Catalogue of Canadian Recent mammals. Bull. Natl. Museum Canada 102:1-238.

Arata, A. A. 1964. The anatomy and taxonomic significance of the male accessory reproductive glands of muroid rodents. Bull. Florida State Museum 9:1-42.

Autrey, H. V., and E. P. Odum. 1949. Woodland jumping mouse (*Napaeozapus*) in Georgia. J. Mammal. 30:200.

Bangs, O. 1898. A list of the mammals of Labrador. Am. Naturalist 32:489-507.

Barbour, R. W. 1951a. The mammals of Big Black Mountain, Harlan County, Kentucky. J. Mammal. 32:100-110.

————. 1951b. Notes on mammals from West Virginia. J. Mammal. 32:368-371.

Beer, J. R. 1953. Two new locality records for mammals in Minnesota. J. Mammal. 34:384-385.

Bianchi, N. D., and J. R. Contreras. 1967. The chromosomes of the field mouse *Akodon azarae* (Cricetidae, Rodentia) with special reference to sex chromosome anomalies. Cytogenetics 6:306-313.

Bider, J. R. 1968. Animal activity in uncontrolled terrestrial communities as determined by a sand transect technique. Ecol. Monographs 38:269-308.

Blair, W. F. 1941. Some data on the home ranges and general life history of the short-tailed shrew, red-backed vole, and woodland jumping mouse in northern Michigan. Am. Midland Naturalist 25:681-685.

Bole, B. P., Jr. 1935. *Napaeozapus insignis insignis* in Ohio. J. Mammal. 16: 153-154.

———, and P. N. Moulthrop. 1942. The Ohio Recent mammal collection in the Cleveland Museum of Natural History. Sci. Publ. Cleveland Museum Nat. Hist. 5:83-182.

Branin, M. L. 1936. *Napaeozapus* on Mount Desert Island. J. Mammal. 17: 174.

Brooks, F. E. 1911. The mammals of West Virginia. Rpt. West Virginia State Board Agr. 20:9-30.

Brower, J. E., and T. J. Cade. 1966. Ecology and physiology of *Napaeozapus insignis* (Miller) and other woodland mice. Ecology 47:46-63.

Brown, L. N. 1970. Population dynamics of the western jumping mouse (*Zapus princeps*) during a four-year study. J. Mammal. 51:651-658.

Burt, W. H. 1946. The mammals of Michigan. Univ. Michigan Press, Ann Arbor. 288 pp.

———. 1960. Bacula of North American mammals. Misc. Publ. Museum Zool., Univ. Michigan 113:1-76.

Cameron, A. W. 1953. The mammals of the Trois Pistoles area and the Gaspé Peninsula. Bull. Natl. Museum Canada 128:168-188.

———. 1958. Mammals of the Islands in the Gulf of St. Lawrence. Bull. Natl. Museum Canada 154:1-165.

———, and W. A. Morris. 1951. The mammals of the Lake Mistassini and Lake Albanel regions, Quebec. Bull. Natl. Museum Canada 123:120-130.

Clarke, C. H. D. 1935. White tips of *Napaeozapus* tails. Canadian Field-Naturalist 49:139.

Coleman, R. H. 1940. *Napaeozapus insignis roanensis* in South Carolina. J. Mammal. 21:95.

Connor, P. F. 1960. The small mammals of Otsego and Schoharie counties, New York. Bull. New York State Museum and Sci. Serv. 382:1-84.

———. 1966. The mammals of the Tug Hill Plateau, New York. Bull. New York State Museum and Sci. Serv. 406:1-82.

Dalby, P. L. 1968. Kalkaska County record for woodland jumping mouse. Jack-Pine Warbler 46:95.

Dice, L. E. 1936. Age variation in *Peromyscus maniculatus gracilis*. J. Mammal. 17:55-57.

Dillon, L. S. 1956. Wisconsin climate and life zones in North America. Science 123:167-176.

Doutt, J. K. 1966. Mammals of Pennsylvania. The Pennsylvania Game Comm., Harrisburg. 273 pp.

Ellerman, J. R., R. W. Hayman, and G. W. C. Holt. 1940. The families and genera of living rodents, with a list of named forms. British Museum Nat. Hist., London, 1:1-689.

Foster, C. A. 1947. On tail color in *Napaeozapus*. J. Mammal. 28:62.

Gidley, J. W., and C. L. Gazin. 1938. The Pleistocene vertebrate fauna from Cumberland Cave, Maryland. Bull. U.S. Natl. Museum 171:1-99.

Gifford, C. L., and R. Whitebread. 1951. Mammal survey of south-central Pennsylvania. Final Report P-R Project 38-R. Pennsylvania Game Comm., Harrisburg. 75 pp.

Golley, F. B. 1962. Mammals of Georgia. Univ. Georgia Press, Athens. 218 pp.

Goodwin, G. G. 1924. Mammals of the Gaspé Peninsula, Quebec. J. Mammal. 5:246-257.

———. 1929. Mammals of the Cascapedia Valley, Quebec. J. Mammal. 10: 239-246.

———. 1935. The mammals of Connecticut. Bull. State Geol. and Nat. Hist. Survey 53:1-221.

Greenfield, R. 1938. *Napaeozapus insignis* in Virginia. J. Mammal. 19:254.

Grimm, W. C., and H. A. Roberts. 1950. Mammal survey of southwestern Pennsylvania. Final Report P-R Project 24-R. Pennsylvania Game Comm., Harrisburg. 99 pp.

Guilday, J. E. 1962. The Pleistocene local fauna of the Natural Chimneys, Augusta County, Virginia. Ann. Carnegie Museum 36:87-122.

———, P. S. Martin, and A. D. McCrady. 1964. New Paris No. 4: A Pleistocene cave deposit in Bedford County, Pennsylvania. Natl. Speleological Soc. 26:121-194.

———, H. W. Hamilton, and A. D. McCrady. 1966. The bone breccia of Bootlegger Sink, York County, Pennsylvania. Ann. Carnegie Museum 38: 145-163.

Hall, E. R., and K. R. Kelson. 1959. The mammals of North America. Ronald Press Co., N.Y. 2 vols., 1083 pp.

Hamilton, W. J., Jr. 1935. Habits of jumping mice. Am. Midland Naturalist 16:187-200.

———. 1941. The food of small forest mammals in eastern United States. J. Mammal. 22:250-263.

Handley, C. O., Jr., and C. P. Patton. 1947. Wild mammals of Virginia. Publ. Commonwealth of Virginia, Comm. of Game and Inland Fisheries, Richmond. 220 pp.

Harper, F. 1929. Notes on mammals of the Adirondacks. New York State Museum Handbook 8:51-118.

Hatt, R. T. 1932. The vertebral columns of ricochetal rodents. Bull. Am. Museum Nat. Hist. 63:599-738.

Hock, R. J. 1960. Seasonal variations in physiologic functions of arctic ground squirrels and black bears. *In* Mammalian hibernation. Edited by C. P. Lyman, and A. R. Dawe. Bull. Museum Comp. Zool., Harvard, 124:155-169.

Jackson, H. H. T. 1919. The Wisconsin *Napaeozapus*. Proc. Biol. Soc. Wash. 32:9-10.

———. 1961. Mammals of Wisconsin. Univ. Wis. Press, Madison. 504 pp.

Jameson, E. W., Jr. 1949. Some factors influencing the local distribution and abundance of woodland small mammals in central New York. J. Mammal. 30:221-235.

Johansen, K., and J. Krog. 1959. Diurnal body temperature variations and hibernation in the birch mouse, *Sicista betulina*. Am. J. Physiol. 196:1200-1204.

Kellogg, R. 1937. Annotated list of West Virginia mammals. Proc. U.S. Natl. Museum 84:443-479.

Klein, H. G. 1957. Inducement of torpidity in the woodland jumping mouse. J. Mammal. 38:272-274.

Klingener, D. 1963. Dental evolution of *Zapus*. J. Mammal. 44:248-260.

———. 1964a. The comparative myology of four dipodoid rodents (Genera *Zapus*, *Napaeozapus*, *Sicista*, and *Jaculus*). Misc. Publ. Museum Zool., Univ. Michigan, 124:1-100.

———. 1964b. Notes on the range of *Napaeozapus* in Michigan and Indiana. J. Mammal. 45:644-645.

———. 1966. Dipodoid rodents from the Valentine Formation of Nebraska. Occas. Papers Museum Zool., Univ. Michigan, 644:1-9.

———. 1971. The question of cheek pouches in *Zapus*. J. Mammal. 52:463-464.

Komarek, E. V., and R. Komarek. 1938. Mammals of the Great Smoky Mountains. Bull. Chicago Acad. Sci. 5:137-162.

Krutzsch, P. H. 1954. North American jumping mice (Genus *Zapus*). Univ. Kansas Publ., Museum Nat. Hist. 7:349-472.

Layne, J. N. 1968. Ontogeny. *In* Biology of Peromyscus (Rodentia). Edited by J. A. King. Spec. Publ. Am. Soc. Mammal. 2:148-253.

———, and W. J. Hamilton, Jr. 1954. The young of the woodland jumping mouse, *Napaeozapus insignis insignis* (Miller). Am. Midland Naturalist 52:242-247.

Lee, M. R. 1969. A widely applicable technic for direct processing of bone marrow for chromosomes of vertebrates. Stain Technology 44:155-158.

Long, C. A. 1970. Mammals of central Wisconsin. Wisconsin State Univ., Museum Nat. Hist., Faunal and Floral Rep. Wisconsin, 3:1-59.

Lord, R. D., Jr. 1960. Litter size and latitude in North American mammals. Am. Midland Naturalist 64:488-499.

Lyon, M. W., Jr. 1901. A comparison of the osteology of the jerboas and jumping mice. Proc. U.S. Natl. Museum 23:659-668.

Manville, R. H. 1942. Notes on the mammals of Mount Desert Island, Maine. J. Mammal. 23:391-398.

———. 1949. A study of small mammal populations in northern Michigan. Misc. Publ. Museum Zool., Univ. Michigan, 73:1-83.

Martin, P. S. 1958. Pleistocene ecology and biogeography of North America. *In* Zoogeography. Edited by C. L. Hubbs, Am. Assoc. Adv. Sci. Pp. 375-420.

Matthey, R. 1967. Etude de deux femmelles hétérozygotes pour une délétion partielle portant sur un bras du chromosome X chez *Mus* (*Leggada*) *minutoides musculoides* Temm. Cytogenetics 6:168-177.

McCrady, A. D., and V. Schmidt. 1963. Second Interim Report — Late Pleistocene fossils from Robinson Cave, Tennessee. The Netherworld News, Pittsburg Grotto, Natl. Speleological Soc. 11:19-27.

Meylan, A. 1968. Formules chromosomiques de quelques petits mammifères nord-americains. Rev. Suisse de Zool. 75:691-696.

Miller, G. S., Jr. 1891. Description of a new jumping mouse from Nova Scotia and New Brunswick. Am. Naturalist 25:742-743.

———. 1899. Preliminary list of the mammals of New York. Bull. New York State Museum 6:271-390.

———. 1900. Key to the land mammals of northeastern North America. Bull. New York State Museum 8:59-160.

Morris, R. F. 1948. The land mammals of New Brunswick. J. Mammal. 29:165-176.

Morrison, P., and F. A. Ryser. 1962. Metabolism and body temperature in a small hibernator, the meadow jumping mouse, *Zapus hudsonius*. J. Cell. and Comp. Physiol. 60:169-180.

Mumford, R. E. 1969. Distribution of the mammals of Indiana. Indiana Acad. Sci. Indianapolis. 114 pp.

Neumann, R. L., and T. J. Cade. 1964. Photoperiodic influence on the hibernation of jumping mice. Ecology 45:382-384.

Odum, E. P. 1949. Small mammals of the Highlands (North Carolina) Plateau. J. Mammal. 30:179-192.

Ohno, S. 1967. Sex chromosomes and sex-linked genes. Springer-Verlag, New York. 192 pp.

Osgood, F. L., Jr. 1938. The mammals of Vermont. J. Mammal. 19:435-441.

Paradiso, J. L. 1969. Mammals of Maryland. N. Am. Fauna 66:1-193.

Pearson, O. P. 1947. The rate of metabolism of some small mammals. Ecology 28:127-145.

Peterson, R. L. 1966. The mammals of eastern Canada. Oxford Univ. Press, Toronto. 465 pp.

Pirlot, P. 1962. Mammifères de la Province de Québec. Nat. Canadien 89:129-147.

Platt, A. P. 1968. Selective predation by mink on woodland jumping mice confined in live traps. Am. Midland Naturalist 79:539-540.

Preble, E. A. 1899. Revision of the jumping mice of the genus *Zapus*. N. Am. Fauna 15:1-42.

Preble, N. A. 1938. Sexual dimorphism in *Napaeozapus*. J. Mammal. 19:254.

———. 1956. Notes on the life history of *Napaeozapus*. J. Mammal. 37:196-200.

Priddy, R. B. 1949. Jumping mouse, underwater swimmer. J. Mammal. 30:74.

Prince, L. A. 1941. A new race of *Napaeozapus insignis* from Ontario. Occas. Papers Royal Ontario Museum Zool. 7:1-3.

Quimby, D. C. 1951. The life history and ecology of the jumping mouse, *Zapus hudsonius*. Ecol. Monographs 21:61-95.

Rand, A. L. 1933. Notes on the mammals of the interior of western Nova Scotia. Canadian Field-Naturalist 47:41-50.

Rhoads, S. N. 1903. The mammals of Pennsylvania and New Jersey. Publ. Samuel N. Rhoads, Philadelphia. 266 pp.

Richmond, N. D., and H. R. Roslund. 1949. Mammal survey of northwestern Pennsylvania. Final Report P-R Project 20-R. Pennsylvania Game Comm., Harrisburg. 67 pp.

Ritchie, J. C. 1966. Aspects of the late-Pleistocene history of the Canadian flora. *In* The evolution of Canada's flora. Edited by R. L. Taylor and R. A. Ludwig. Univ. Toronto Press. Pp. 66-80.

Roslund, H. R. 1951. Mammal survey of north-central Pennsylvania. Final Report P-R Project 37-R. Pennsylvania Game Comm., Harrisburg. 55 pp.

Rupes, V., and J. O. Whitaker, Jr. 1968. Mites of the Subfamily Labidophorinae (Acaridae, Acarina) in North America. Acarologia, t. X, fasc. 3: 493-499.

Saunders, W. E. 1921. Notes on *Napaeozapus*. J. Mammal. 2:237-238.

Schwentker, V. 1957. The jumping mouse (*Napaeozapus insignis* Miller). *In* The UFAW handbook on the care and management of laboratory animals. Publ. The Universities Federation for Animal Welfare, London. Pp. 300-304.

Seton, E. T. 1909. Life histories of northern animals. An account of the mammals of Manitoba. 2 vols. Scribners, New York. 1267 pp.

Sheldon, C. 1934. Studies on the life histories of *Zapus* and *Napaeozapus* in Nova Scotia. J. Mammal. 15:290-300.

———. 1938. Vermont jumping mice of the Genus *Napaeozapus*. J. Mammal. 19:444-453.

Smith, R. W. 1940. The land mammals of Nova Scotia. Am. Midland Naturalist. 24:213-241.

Snyder, L. L. 1924. Some details on the life history and behaviour of *Napaeozapus insignis abietorum* (Preble). J. Mammal. 5:233-237.

Soper, J. D. 1923. The rare *Napaeozapus insignis*. J. Mammal. 4:127.

———. 1937. *Napaeozapus* in eastern Manitoba. J. Mammal. 18:369.

———. 1938. Additional note on *Napaeozapus* in eastern Manitoba. J. Mammal. 19:108.

Sprague, J.M. 1941. A study of the hyoid apparatus of the Cricetinae. J. Mammal. 22:296-310.

Stehlin, H. G., and S. Schaub. 1951. Die Trigonodontie der simplicidentaten Nager. Schweiz. Paleontol. Abh. 67:1-385.

Stupka, A. 1934. Woodland jumping mice. Nature Notes from Acadia 3:6.

Surber, T. 1923. The occurrence of the woodland jumping mouse in Minnesota. Fins, Feathers, and Fur 35:106.

Thibault, P. 1969. Activité estivale de petits mammifères du Québec. Canadian J. Zool. 47:817-828.

Townsend, M. T. 1935. Studies on some of the small mammals of central New York. Bull. New York State Coll. Forestry, Syracuse Univ., Roosevelt Wildl. Ann. 4:1-120.

Tullberg, T. 1899. Ueber das System der Nagethiere eine phylogenetische Studie. Nova Acta. Regiae Societatis, Scientiarum Upsaliensis, Seriei Tertiae, Vol. XVIII. 514 pp.

Vinogradov, B. S. 1925. On the structure of the external genitalia in Dipodidae and Zapodidae (Rodentia) as a classificatory character. Proc. Zool. Soc. London. Part 1, pp. 577-585.

———. 1937. Fauna of the U.S.S.R., N.S., No. 13. Mammals, Vol. 3, part 4. Jerboas. (Title translated.) Moscow-Leningrad: Publ. House of the Academy of Sciences of the U.S.S.R. 196 pp. (In Russian, with English summary.)

Walker, E. P. 1964. Mammals of the world. Johns Hopkins Press, Baltimore. 1500 pp.

Whitaker, J. O., Jr. 1962. *Endogone, Hymenogaster,* and *Melanogaster* as small mammal foods. Am. Midland Naturalist 67:152-156.

———. 1963a. A study of the meadow jumping mouse, *Zapus hudsonius* (Zimmerman), in central New York. Ecol. Monographs 33:215-254.

———. 1963b. Food, habitat, and parasites of the woodland jumping mouse in central New York. J. Mammal. 44:316-321.

———. 1966. Clitoris bones of *Zapus hudsonius* and *Napaeozapus insignis.* J. Mammal. 47:127.

Wilson, R. W. 1936. A Pliocene rodent fauna from Smiths Valley, Nevada. Publ. Carnegie Inst. Wash. 473:15-34.

———. 1937. Pliocene rodents of western North America. Publ. Carnegie Inst. Wash. 487:21-73.

———. 1949a. Additional Eocene rodent material from southern California. Publ. Carnegie Inst. Wash., Contrib. to Paleontol. 584:1-25.

———. 1949b. Early Tertiary rodents of North America. Publ. Carnegie Inst. Wash. 584:67-164.

Wrigley, R. E. 1969. Ecological notes on the mammals of southern Quebec. Canadian Field-Naturalist 83:201-211.

INDEX

Age groups: determination, 23-25; development of characters, 25-27; entrance into hibernation, 74; survival during hibernation, 77; breeding, 81, 82, 83; molting, 85; possible age, 88-91
Agkistrodon contortrix, 94
Aggression, 70-71, 101
Air isotherms, 62, 67
Akodon azarae, 22
Alder-willow shrubs, 65, 66, 70, 107
Allactaga williamsi, 18
Arctic ground squirrel, 81
Aspen parkland, 65
Avoidance, 70, 71

Blarina brevicauda, 63, 69
Bog, 65, 66, 70, 107
Botfly larvae, 94
Breeding in captivity, 77, 83
Breeding peaks, 79-81, 83

Cestoda, 95
Cheek pouches, 8
Chromosome preparation, 3
Clethrionomys gapperi, 63, 68, 69, 70-71, 72, 99
Competition, 69-71
Condylura cristata, 63, 69
Cricetidae, 84, 85
Critical temperature, 67
Crotalus horridus, 94

Dentition: wearing of, 23-25
Dipodidae, 6, 7
Dipodoidea, 6, 7, 18
Dipus, 12
Distribution: effect of elevation on, 65; effect of moisture on, 66-67; effect of temperature on, 67
Drowning, 94

Embryos, 80-83
Eozapus setchuanus: distribution, 5; affinities, 6; generic status, 6; ear ossicles, 11; pelage color, 11;

dentition, 13; os penis, 14; phallus, 16

Fat, 73-74, 75, 76, 98
Fleas, 94-95
Food storage, 68, 75
Forest: spruce-fir, 59, 60, 61, 62, 63, 65, 70; deciduous, 59, 60, 65, 107; hemlock–northern hardwood, 61, 62-64, 70, 76, 93, 106; mixed mesophytic, 63, 65; maple-basswood, 65; oak-aspen, 65; oak-hickory, 65; beech-maple, 65, 93; black spruce–tamarack, 65, 107; northern white-cedar, 70, 107; boreal. *See* spruce-fir
Forest-tundra ecotone, 62, 65
"Freezing" behavior, 8-9, 100

Glacial Lake Agassiz, 60
Guard hair, 8, 10

Heterosminthus, 5
Hibernacula, 67, 74-75, 77
Hiberating position, 75
House cat, 94
Hyperthermy, 73
Hystricomorphs, 7

Isolated populations, 65
Isophene maps, 3

Jaculus, 7, 18

Latitude, 78, 83, 88, 92
Life-span, 91

Macrognathomys, 5, 6
Meadow, 66, 93, 107
Measurements, 2, 8, 25-27
Megasminthus, 5, 6, 7
Mephitis mephitis, 63, 94
Metabolic rate, 73
Metatarsals, 14
Microtus ochrogaster, 99
Microtus pennsylvanicus, 99

116

A Note on the Author

Robert E. Wrigley was born in Buenos Aires, Argentina, and raised in St. Lambert, Quebec. He received his B.S. and M.S. from McGill University in Montreal and his Ph.D. from the University of Illinois. He is presently Curator of Higher Vertebrates at the Manitoba Museum of Man and Nature in Winnipeg.