AN ABSTRACT OF THE THESIS OF

ROBIN W. TYSER (Name of student) for the MASTER OF SCIENCE (Degree)

in General Science (Biological Science) (Major) presented on May 16, 1974 (Date)

Title: TAXONOMY AND REPRODUCTION OF MICROTUS CANICAUDUS

Abstract approved: Redacted for privacy

(Dr. Larry G. Forslund)

The taxonomic status of Microtus canicaudus was compared with that of a morphologically similar vole, Microtus montanus. Four means of comparison were utilized: hybridization experiments, comparative karyology, growth distinctions (total length and body weight), and qualitative behavioral observations. The hybridization experiments indicated that, while the incidence of pregnancy of M. montanus x M. canicaudus was similar to one of the control groups (M. montanus x M. montanus) and was even greater than the other control group (M. canicaudus x M. canicaudus), the litter size and survival of hybrid offspring until weaning was significantly less than both control groups. Therefore, reduced reproductive compatibility between the two species is indicated. The karyotypes of the two species (M.

canicaudus from Benton County, Oregon; M. montanus from Moran, Wyoming, Red Butte Canyon - near Salt Lake City, Utah, and the Columbia River Gorge, Oregon) showed consistent interspecific differences. Karyotypes of male and female hybrids exhibited chromosome "mis-matching". Growth comparisons between Benton County M. canicaudus and Red Butte M. montanus demonstrated that M. canicaudus was significantly shorter and weighed less. Behavioral interactions between a group of seven individuals of each species housed in a network of interconnected cages revealed that 77% of the agonistic interactions noted were interspecific. These results lend support to the hypothesis that M. canicaudus deserves species status.

In addition to the taxonomic study, the breeding records of M. canicaudus yielded information concerning its gestation period and trends in sizes of consecutive litters. The most common gestation interval was 21 days. Temporal patterning of successive litters led to speculation on the presence of a 21 day pseudopregnancy. Evidence was presented which suggests that the sizes of first litters were relatively smaller than the mean size of litters two through four.

Taxonomy and Reproduction of *Microtus canicaudus*

by

Robin W. Tyser

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

June 1975

APPROVED:

Redacted for privacy

Assistant Professor of Biology
in charge of major

Redacted for privacy

Head of Department of General Science

Redacted for privacy

Dean of Graduate School

Date thesis is presented May 16, 1974

Typed by Lyndalu Allison Sikes for Robin W. Tyser

ACKNOWLEDGEMENTS

Several persons deserve recognition for their advice and assistance in making this study possible. From field trapping to laboratory maintenance of the voles, Dr. Larry Forslund gave much of his time in assisting me in all phases of this investigation. I am especially grateful for his help in procuring M. montanus individuals from the University of Utah and for sharing the data collected in his previous studies. Jim Weil was instrumental in many of the trapping excursions. Dr. Robert Storm generously loaned his traps to me on several occasions. Dr. Dennis McDonald is to be thanked for his advice in the construction of the experimental setup utilized for behavioral observations. Dr. Robert Baker was kind enough to familiarize me with the basic procedures involved in karyotyping. Finally, I wish to acknowledge the assistance which my wife, Kathie, provided in typing and photographic preparations.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

TAXONOMY AND REPRODUCTION OF *MICROTUS CANICAUDUS*

INTRODUCTION

Microtus canicaudus Miller, commonly known as the gray-tailed vole, is described as being endemic to the lower elevations of the Willamette River valley of western Oregon and the Clark County region of southern Washington (Anderson, 1959). Stemming from this rather limited distribution, comparatively little factual information has been firmly established regarding this vole. The following represents a brief summary of the material published concerning its natural history, distribution, and taxonomic status.

Microtus canicaudus has been observed most frequently in open valley grasslands, especially those in association with farmland (Bailey, 1936; Goertz, 1964). Goertz (1964) implies that the advent of farming has encouraged the presence of this species. *M. canicaudus* constructs elaborate branching runways (or "tunnels") in open grasslands, pastures, and in fields (especially alfalfa fields). Pearson (1972) described two general types of runways. The first is heavily traveled and worn to bare ground; this type usually extends from one nest hole to another or from one complex of nest holes to another complex. Runways of the second type are not so heavily traveled and have matted grass or moss growing in them. These

runways end abruptly and, since they often contain grass clippings, are assumed to be used in feeding excursions.

Gray-tailed voles are strict herbivores, their food being the low lying ground cover through which their runways are constructed. Among food types are clover, grass, alfalfa (Goertz, 1959), wild onion, and false dandelion (Maser and Storm, 1970). During high densities, M. canicaudus inflicts considerable damage on grasses grown for seed and grain (Maser and Storm, 1970) and pastures of clover and grass (Goertz, 1964).

Although M. canicaudus may construct their nests under hay bales or other debris found in fields (Maser and Storm, 1970), it appears as though subterranean nests are more common (Goertz, 1959). The Townsend mole (Scapanus townsendi) and the Camas pocket gopher (Thomomys bulbivorus) open up extensive underground runway systems that are occupied by M. canicaudus when the burrows are evacuated by their original occupants. They are capable of constructing their own subterranean burrow, however. A nest is located about six to twelve inches below the ground surface and several exits lead to the surface from each nest (Goertz, 1959).

Pearson (1972) showed that M. canicaudus has a relatively high rate of water consumption and is comparatively susceptible to water stress. Behavioral experiments, conducted under artificial laboratory conditions, indicated that "... each individual lives a

relatively solitary life in a complex of holes eight feet from the nearest neighbor..." (p. 46). This "antisocial" behavior is supposedly adaptive in that it results in an adequate water source (succulent plants and dew) during periods of dryness (Pearson, 1972).

Relatively little is known about reproduction and growth in M. canicaudus. Field notes from Maser and Storm (1970) indicate that this species breeds year round and that litter sizes range from two to eight, averaging between four and six. Total length varies from 127 to 157 mm, while adult weight is reported to range from 19 to 52 grams (Maser and Storm, 1970).

The taxonomic position of this vole has not been clearly established, and it is to this problem that the major thrust of this study is directed. From a morphological standpoint M. canicaudus and Microtus montanus (the latter commonly named the montane vole) appear quite similar. Anderson (1959) reports that M. canicaudus is slightly smaller and more brownish than M. montanus, indicating that some qualitative differences exist. The size measurements mentioned above (Maser and Storm, 1970), while indicating M. montanus is the slightly larger of the two voles, do show that much size overlap does occur in adult animals. M. montanus has a fairly widespread distribution in western North America, but is restricted to areas east of the Cascades (Maser and Storm, 1970). The

Columbia River Gorge would logically represent a potential channel of communication between M. canicaudus and M. montanus.

Anderson (1959) suggests that M. montanus originated in the general areas which it now occupies. This species, along with M. californicus, M. mexicanus, M. townsendi and M. oeconomus, theoretically evolved from a common ancestral stock (Anderson, 1959) in the Pleistocene. M. canicaudus, then, would supposedly represent an offshoot of M. montanus.

Miller (1897) originally classified M. canicaudus as a distinct species. Hall and Kelson (1951), after examining museum specimens, concluded that M. canicaudus was a subspecies of M. montanus (Peale). Anderson (1959) described M. canicaudus as one of sixteen subspecies of M. montanus. Johnson (1968), however, noted consistent differences in the electrophoretic patterns of secondary globulin banding in eight specimens of M. canicaudus and 35 specimens of various subspecies of M. montanus. Hsu and Johnson (1970) noted a difference between the karyotypes of M. canicaudus and M. montanus. Both species had an identical chromosome number (2N=24), the most salient morphological difference being that M. montanus' sex chromosomes are acrocentric while the "X" and "Y" chromosomes of M. canicaudus are metacentric and submetacentric, respectively. These last findings indicate that perhaps species status should be "awarded" to M. canicaudus.

None of the above authors has, however, undertaken breeding experiments to see if Microtus canicaudus is potentially "reproductively isolated" from M. montanus. By conducting breeding trials, thus testing for reproductive compatibility, Mayr's (1942) criterion of a species, defined as a reproductively autonomous group of actually or potentially interbreeding populations, may be at least partially fulfilled. Johnson's electrophoretic work (Johnson, 1968) in itself does not constitute conclusive evidence since it is theoretically possible that M. canicaudus represents a localized polymorphic variant of M. montanus and hence does not constitute a separate species. Hsu and Johnson (1970) karyotyped eight specimens of M. canicaudus from Benton County, Oregon (five males and three females) and cited eight karyotype preparations of M. montanus (one female from Jefferson County, Oregon, one male from Deschutes County, Oregon, one male and two females from Douglas County, Oregon, one female from Yakima County, Washington, and one male and one female from near Salt Lake City, Utah). Two criticisms can be made regarding this study: 1) no voles were karyotyped from the Columbia River Gorge (where morphological intergradation was noticed in the report by Hall and Kelson, 1951), and 2) the geographical representations of M. montanus show very small sample sizes.

As noted by Baker (1970), karyology is a particularly good tool in taxonomic studies because chromosome configuration is a relatively

conservative and consistent morphological characteristic. One section of this investigation was devoted to a more thorough karyological analysis of M. canicaudus and particularly of M. montanus than Hsu and Johnson's (1970) study. That is, an effort was made to increase sample sizes and strategically increase geographical representation in constructing karyotypes for these two voles.

As mentioned above, some differences in size between M. canicaudus and M. montanus have been noted from field observations. Growth data (total length and body weight) were gathered from M. canicaudus and were compared with previously established growth patterns for M. montanus (Forslund, 1972) in order to quantify comparisons.

The extent of interspecific behavioral compatibility could logically influence interspecific reproductive success and distribution patterns, should these voles exist in sympatric situations. Therefore, intra- and interspecific agonistic interactions were qualitatively studied in an artificial laboratory setting.

Thus, this study is basically a taxonomic one with four investigational techniques being utilized: breeding trials, comparative karyology, growth comparisons, and qualitative behavioral observations. In addition some elementary aspects of the reproductive life history of M. canicaudus (litter size patterns, gestation period) were determined as "offshoots" of the breeding experiments.

MATERIALS AND METHODS

Field Techniques

In order to obtain animals to initiate laboratory stocks of Microtus canicaudus, three areas of Benton County, Oregon were live-trapped at various times from March to August, 1973. A grassy slope in McDonald Forest, located a few miles north of Corvallis, Oregon, and a grassland adjacent to the headquarter buildings of William L. Finley National Wildlife Refuge, located 12 miles south of Corvallis, were subjected to live-trapping in the spring of 1973. Comparatively few animals were captured as vole populations were very low during this period. A third area, an alfalfa field, located approximately 11 miles south of Corvallis and two miles to the east, was then trapped during the summer of 1973. In addition to these areas, one trap site was chosen just north of Eugene, Oregon (Lane County).

Mayer State Park (eight miles east of Hood River, Oregon) situated in the Columbia River Gorge, was selected for trapping purposes in order to examine possible karyotypic intergradation between M. montanus and M. canicaudus. In addition two groups of M. montanus were obtained from established laboratory colonies, housed under the supervision of Dr. Norman Negus at the University

of Utah. One group stemmed from specimens trapped in Red Butte Canyon, located near Salt Lake City, Utah (Forslund, 1972); the other group was derived from individuals captured at the University of Wyoming Research Station, Moran, Wyoming (Negus and Pinter, 1965).

Sherman collapsible live traps, with a cotton ball inserted in the back of each trap, were used to capture the voles. Each trap was placed in a runway and baited with rolled oats. Traps were routinely checked twice each day: once at midnight and once around 7:30 A. M.

Laboratory Techniques

In order to standardize breeding procedures, captured animals were regularly mated in permanent pairs. Each expectant female was checked daily during the latter stages of pregnancy via palpation. Breeding records were established for each pair, yielding dates of parturition, litter sizes, and inter-parturition time periods. Young were weaned at 18-19 days of age, toe-clipped for identification, and housed in groups of three to five according to sex. Mating pairs were selected so that outbred conditions were maintained: siblings and "first cousins" were not mated.

All animals were housed in Bo-Kay fiberglass planter boxes (24" x 6" x 6") fitted with wire hardware cloth. The floor of each box was covered with approximately one-half inch of sawdust, and

cotton batting was provided for nesting material and cover. Cages were changed as deemed necessary, usually at one to two week intervals for the group housed individuals and at the weaning period for the breeding pairs.

Animals were maintained at temperatures of 68°-72°F. and under standard lighting conditions of 16L-8D. Noting the importance of green vegetation in optimizing reproductive performance (Negus and Pinter, 1966), fresh lettuce clippings were provided twice a week to breeding pairs. Purina Rat Chow, Purina Rabbit Chow and tap water were provided ad libitum.

Breeding Trials

During this portion of the investigation the reproductive capabilities of M. montanus and M. canicaudus were ascertained. Laboratory reared offspring between eight and ten weeks of age, were used to form breeding pairs. M. canicaudus was newly colonized, so that most individuals were first and second generation offspring. The M. montanus utilized were propagated from Red Butte Canyon individuals and have been colonized since 1970-1971 (Forslund, 1972).

Three groups of breeding pairs were formed. M. montanus mated with M. montanus (designated as Group I) and M. canicaudus mated with M. canicaudus (designated as Group II) formed the two control groups. M. canicaudus mated with M. montanus formed the

third, or experimental, group. (Group IIIA indicated male M. montanus mated with female M. canicaudus and Group IIIB pairings consisted of the reversed matings.) The reproductive performance of these groups was ascertained at 25, 50, and 80 day intervals. Except where otherwise noted, Student t-tests were routinely used to analyze results (reproductive performance and growth determinations) throughout this study.

Karyology

This section of the investigation addresses itself to the objections raised above with respect to the karyotyping done by Hsu and Johnson (1970), namely that M. montanus sample sizes were quite small and that inappropriate geographical representation was involved. The following is a summary of sample sizes and localities utilized in this study: five males and five females of M. canicaudus, captured in the aforementioned trapping sites in Benton County, five males and five females from the Red Butte stock of M. montanus, five males and five females of M. montanus from the Wyoming stock, and five females and five males of M. montanus from the Columbia River Gorge region.

In addition, karyotypes of hybrid offspring were made. Five male and one female karyotypes were constructed. In order to procure the female, it was necessary to remove some of the newly born hybrids and place them with intraspecifically mated females which were lactating.

The karyotyping procedure was modified after that of Baker's (1970). The steps involved in this procedure are as follows:

1. Intraperitoneal injection of a 0.05% (wt. / vol.) colchicine solution, 0.1 ml. of solution per gram of body weight.

2. After two hours the animals were killed by cervical dislocation and both femurs extracted. The bone caps at each end of the shaft were removed and the bone marrow was flushed out into a beaker using a hypodermic syringe filled with a 0.9% solution of sodium citrate. Two to three ml. of solution were used for each femur.

3. The bone marrow extraction was vigorously pipetted to form a homogeneous mixture. After 30 minutes, this solution was poured through a double thickness of cheese cloth to remove any hair or bone chips. This was followed by six to seven minutes of centrifugation at approximately 800 rpm's.

4. As much of the supernatant as possible was pipetted off, leaving the "button" of cells undisturbed. Three ml. of Carnoy's fixative (three parts of absolute methanol with one part of glacial acetic acid) was pipetted in so that a homogeneous "suspension" results. After eight to ten minutes, the suspension was centrifuged for five minutes.

5. The supernatant was removed, and the button of cells was resuspended with one ml. of fixative and centrifuged for four minutes. This step was repeated two additional times.

6. After the final centrifugation, the button was resuspended with one ml. of fixative. Four to eight drops of the suspension were pipetted onto a glass slide and ignited. After the flame died, the residue was shaken off. Usually four slides were made for each animal.

7. The slide preparation was stained with Giemsa stain (freshly prepared by adding one part of Giesma stock solution with eight parts of water) for 15 minutes.

8. The slides were passed through two baths of acetone, one bath of one part acetone and one part xylene, and then two baths of xylene.

9. Following staining, slides were mounted using "Permount".

The water used throughout the procedure was double-distilled and buffered to a pH of 7.0. Baker (1970) emphasizes that care must be taken to use absolute methanol and freshly prepared sodium citrate solution.

Chromosome clusters were photographed with 35 mm Kodak Plus X film at a magnification of 800X. Three by five inch prints were made using high contrast (F-5) Kodak paper. Chromosomes were cut out and paired according to length and centromere position. Three arbitrary chromosome categories were designed: acrocentric (centromere terminally located), metacentric (centromeres positioned in the center of the chromosome), and submetacentric (centromere positioned between acrocentric and metacentric locations).

Growth Determinations

Total length and body weight measurements for each sex were taken on a weekly basis through eight weeks of age for M. canicaudus. Length was determined by placing the ventral surface of the animal along a metric rule and measuring, to the nearest mm, the distance from the tip of the nose to the end of the tail. Body weights, determined to the nearest 0.5 gram, were measured with a triple beam balance.

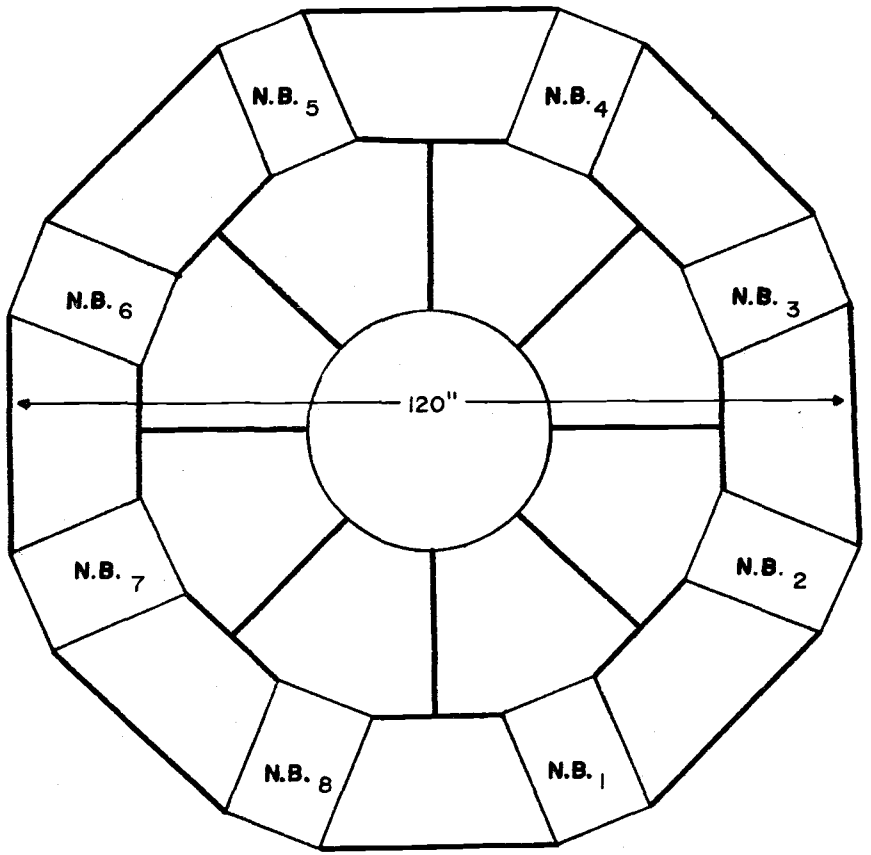
The results obtained above were compared to similar information collected by Forslund (1972) for M. montanus. Laboratory procedures and housing were identical to the ones listed in this study, one exception being that no Purina Rat Chow was used in Forslund's (1972) study.

Behavior Observations

A series of "nest boxes" with interconnecting runways was constructed so that behavioral interactions between groups of M. canicaudus and M. montanus could be observed. The impetus for such an undertaking stemmed from the procedure used by Reimer and Petras (1967) to investigate territoriality and distribution patterns in an artificially created laboratory population of Mus. The general layout, with dimensions, are diagrammed in Figure 1.

The runways were large enough (1 1/2" wide, 2" high) to permit a large adult to quickly reverse directions. Runway floorboards were constructed from 1/8" thick plywood, with hardware cloth forming the roof and sides. Eight nest boxes (8" x 8" x 12") were constructed from 1/4" plywood with one exit hole leading from each corner. Thus an animal could not be "cornered". Cotton batting was provided for nesting material and covering, and a layer of sawdust covered the floors. The central "arena" was built from hardware cloth and lined along its bottom edge with a six inch strip of sheet metal. White construction paper lined the remaining portion of the arena.

Figure 1. Positioning of nest boxes and runways used in behavioral observations.



—— = RUNWAYS

N.B. = NEST BOX

Water was provided at each nest box, and, at the initiation of the experiment, Purina Rat and Purina Rabbit Chow were placed in each nest box and in the central arena. As the experiment progressed, all food (Purina Rat and Purina Rabbit Chow, lettuce clippings) was introduced into the arena only. Standard lighting (16L-8D) and temperature conditions (68-72°F.) were maintained.

Seven animals of each species (three males and four females) were fur-clipped, enabling sex and species determination at a distance, and ear-tagged using color codes, so that individuals could be recognized by a "discerning" eye. Ages varied from six to twelve weeks, with individuals chosen so that interspecific counterparts were of the same age. Animals were observed with a pair of 7 x 35 binoculars while the observer was positioned approximately eight feet from ground level and slightly off to one side of the cage network. Two mirrors attached to ringstands enabled the observer to see "hidden" corners which were otherwise not readily visible.

Prior to the initiation of the experiment each of the 14 voles was allowed to individually familiarize itself with the experimental layout. Each animal was placed in the central arena and allowed ten minutes of unrestricted movement. The experiment was initiated by assigning each animal a number and placing them randomly and in rapid succession into the arena.

The voles were observed for 30 to 60 minute periods at various times during the light cycle during the following 14 day period. General observations were made and the frequencies of typical 'thrust and nip" agonistic encounters were scored. This "thrust and nip" encounter was arbitrarily defined as any situation where one vole would suddenly lunge forward and bite another. Only those encounters where it was fairly certain that physical contact occurred were scored. As the ear tags were fairly hard to distinguish, only the sex and species of the antagonists could be consistently determined.

Miscellaneous Reproductive Determinations

From the breeding trials, the gestation periods of *M. canicaudus* and *M. montanus* were determined by noting time intervals between successive litters. Breeding records of wild *M. canicaudus* which were mated in the laboratory were also utilized during this phase of the investigation.

Post partum estrus is known to occur in at least seven species of *Microtus*, including *M. montanus* (Asdell, 1964), and is assumed to characterize *M. canicaudus* as well. Therefore, the most frequently occurring interval between parturitions in *M. canicaudus* represents its gestation period. In addition, the sizes of second, third, and fourth litters were averaged together and compared with the average size of first litters in order to determine if first litters were significantly smaller.

RESULTS

Breeding Trials

Data obtained from the breeding trials are listed in Tables 1-5. It should be noted that the information in Tables 1-4 is presented in a cumulative form. For example, in Table 1, 75% of Group II pairs achieved parturition at least once during the 80 day interval.

Table 1. Cumulative percentage of breeding pairs achieving parturition.

	N	DAYS 25	50	80
Group I	20	45.0	85.0	85.0
Group II	20	15.0	60.0	75.0
Group III	22	18.2	50.0	50.0
Group IIIA	15	20.0	53.3	53.3
Group IIIB	7	14.3	42.8	42.8

N = sample size

The percentage of Group II pairs reaching parturition was less than that of Group I, but was greater than that of the crosses (Group III) at the 50 and 80 day intervals (see Table 1). These results are not statistically significant ($p>0.05$), however. Considering Groups I, II, and III at the 80 day period, the Chi-square value is only 2.590.

The patterns of the number of litters per "active female" (those females which dropped at least one litter during the 80 day period) are generally consistent at the 25, 50, and 80 day intervals (see Table 2). Group I performed significantly better than Group II ($p<0.05$) at the 25 and 50 day intervals. Group IIIA also demonstrated a greater reproductive output than Group II ($p<0.05$) at the 50 day period. Group III females showed a higher rate of parturition than Group II, but due to small sample sizes the differences were not significant ($p>0.05$) at any interval. The performance of Group I compared with that of Group III was indistinguishable ($p>0.05$) at each interval.

Table 2. Mean number of cumulative litters per active female.

	N	DAYS		
		25	50	80
Group I	17	0.59±0.12*	1.41±0.12	2.23±0.14
Group II	15	0.20±0.11	0.93±0.12	1.87±0.19
Group III	11	0.36±0.15	1.45±0.16	2.27±0.24
Group IIIA	8	0.38±0.18	1.50±0.19	2.50±0.19
Group IIIB	3	0.33±0.33	1.33±0.33	2.00±1.00

* X±SEM

The trends of litter sizes for active females (see Table 3) were consistent throughout the 80 day period. At the 50 and 80 day intervals, the same patterns of statistical differences exist: the

differences of mean litter sizes for Group I vs. Group II were indistinquishable ($p>0.05$), and statistical differences ($p<0.05$) were apparent for Group I and Group II compared with all Group III categories. Thus, the cross pairings demonstrated a greatly reduced reproductive performance with respect to litter size.

Table 3. Mean litter size (cumulative) per active female.

	N_{25}	25 DAYS	N_{50}	50 DAYS	N_{80}	80 DAYS
Group I	8	4.12±0.23*	24	4.37±0.26	38	4.79±0.21
Group II	3	4.00±0.58	12	3.17±0.25	29	4.45±0.20
Group III	4	3.00±0.91	16	2.75±0.37	26	2.42±0.28
Group IIIA	3	3.67±0.88	12	3.17±0.42	20	2.80±0.32
Group IIIB	1	1.00±0.00	4	1.00±0.00	6	1.17±0.17

$N_{(\ )}$ = sample size at each time interval
* X±SEM

Patterns in total number of offspring per active female (see Table 4) were similar at the 25, 50, and 80 day periods. With one exception (Group II at the 80 day period) Group I females parturiated significantly more offspring per active female ($p<0.05$) than any of the other groups at the 50 and 80 day intervals. Group II females dropped more offspring per active female than Group III females at the 80 day period; however, due to small sample sizes no statistical differences ($p>0.05$) could be shown. At the 80

day interval, significant differences ($p<0.05$) were apparent for Group II vs. Group IIIB females, but were not apparent ($p>0.05$) for Group II vs. Group IIIA females.

Table 4. Mean number of offspring (cumulative) per active female.

	N	DAYS 25	50	80
Group I	17	1.94±0.52*	6.17±0.49	10.70±0.70
Group II	15	0.80±0.44	3.93±0.72	8.27±1.00
Group III	11	1.09±0.55	3.82±0.84	5.54±1.02
Group IIIA	8	1.38±0.73	4.75±0.96	7.00±0.92
Group IIIB	3	0.33±0.33	1.33±0.33	2.33±0.88

*X±SEM

The most clear-cut results (see Table 5) showed hybrid mortality to be drastically greater than that of M. canicaudus and M. montanus groups individually. In several litters of Group IIIA and Group IIIB pairings, malformed young were found immediately following parturition. A commonly observed external malformation was a fusion of toes, so that two to three "bunches" of toes resulted.

The relatively small sample sizes involved in analysis of the cross matings prohibit "sensitive" statistical analysis. Generally it appeared that Group IIIA matings show greater reproductive success than Group IIIB matings (see Tables 1-5). The mean

litter size at the 80 day period and the number of offspring at the 50 and 80 day intervals for Group IIIA are significantly larger ($p<0.05$) than those of Group IIIB (see Tables 3 and 4).

Table 5. Percentage of offspring surviving until weaning.

Breeding Pairs	N	% Survival at Weaning
Group I	168	90.4
Group II	112	93.7
Group III	55	9.0
Group IIIA	48	10.4
Group IIIB	7	0.0

N=number of offspring born.

It should be mentioned that it is possible the number of offspring and the litter sizes reported for Group III pairings are low. Partially eaten young were frequently observed and it is possible that some young were consumed entirely before recordings could be made. By monitoring each female's pre-parturitive progress, it is believed that the impact of this type of error would not substantially offset the above findings.

Karyology

The respective karyotypes of M. canicaudus and M. montanus were consistent, regardless of geographical origin, and were

also in accordance with the previously published karyotypes of these two voles (Hsu and Johnson, 1970). The specimens taken from the Columbia River site show the characteristic M. montanus pattern (see Figure 2). The most salient interspecific difference occurs in the sex chromosomes (compare Figures 2, 3, and 4 with Figure 5). The sex chromosomes of M. canicaudus show a fairly large metacentric "X" chromosome and a smaller submetacentric "Y" chromosome. The sex chromosomes of M. montanus are both acrocentric. The autosomal chromosomes show some subtle interspecific differences, in that M. canicaudus appears to have more metacentric to submetacentric chromosomes than does M. montanus.

The karyotypes of the male and female hybrids are arbitrarily aligned and show definite autosomal "mis-matchings" (see bottom rows of chromosomes in Figure 6). The sex chromosomes of the female hybrid are obviously incongruous.

Growth Comparisons

Growth comparisons of M. canicaudus and M. montanus (Figures 7,8, 9, and 10) show that, in terms of total length and body weight, M. canicaudus is the "smaller" of the two voles. Statistical differences ($p<0.05$) between M. canicaudus males and M. montanus males appear at week one (total length) and week three (body weight). Statistical differences ($p<0.05$) between M. canicaudus females and

Figure 2. Karyotypes of male and female Microtus montanus from near Hood River, Oregon vicinity.

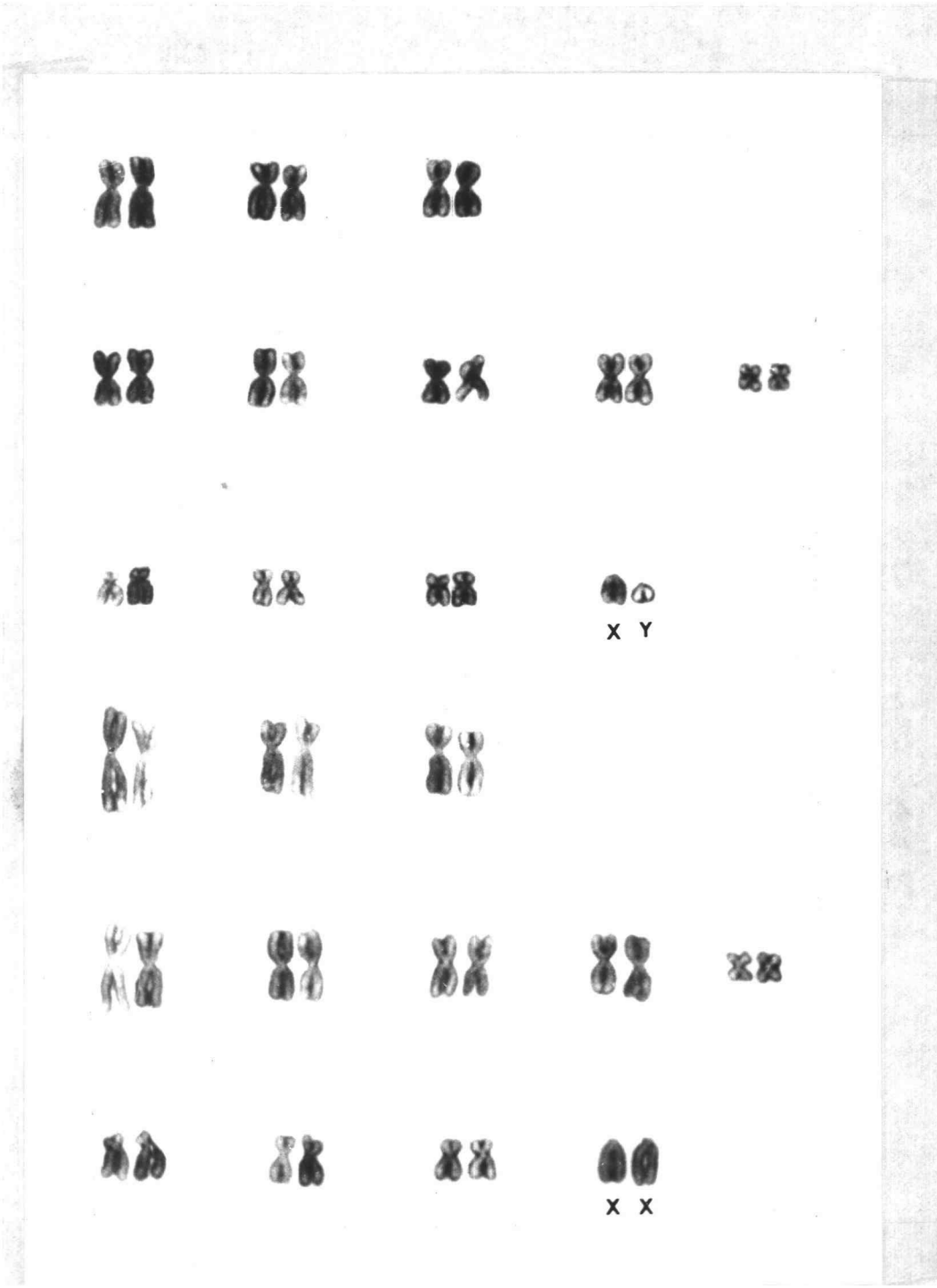

X Y
X X

Figure 3. Karyotypes of male and female Microtus montanus from the Red Butte Canyon (Utah) site.

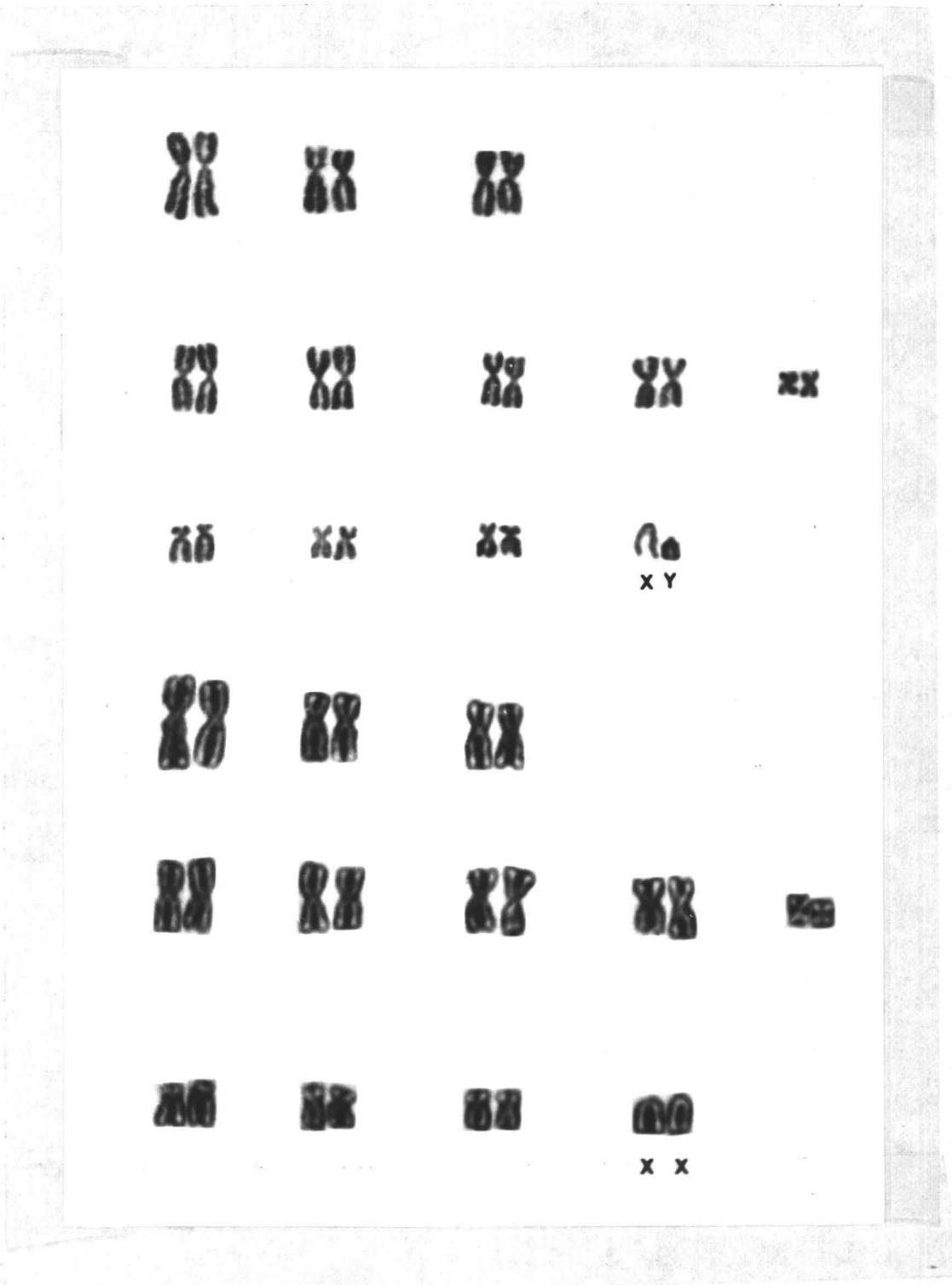

X Y
X X

Figure 4. Karyotypes of male and female Microtus montanus from the Moran, Wyoming vicinity.

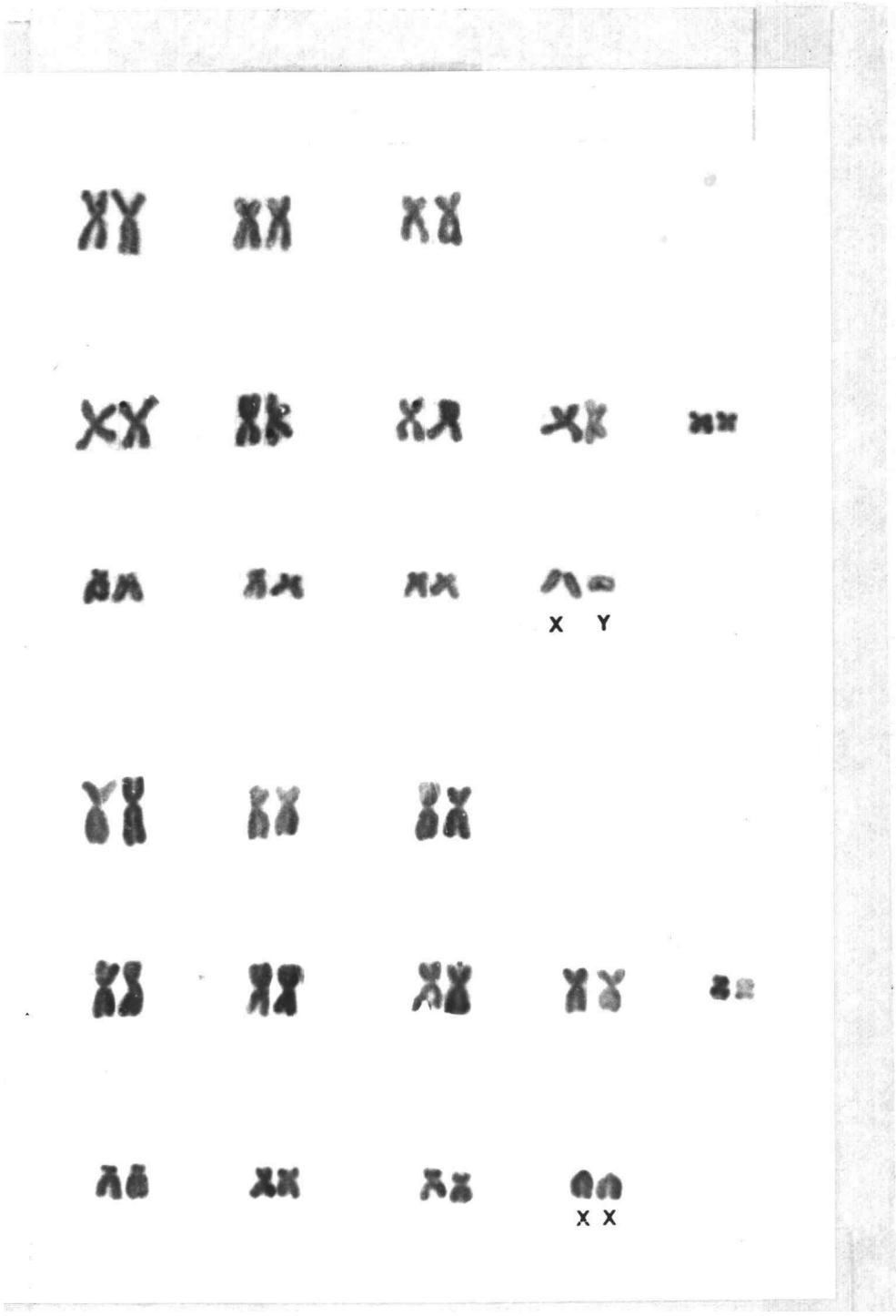

X Y
X X

Figure 5. Karyotypes of male and female Microtus canicaudus from Benton County, Oregon.

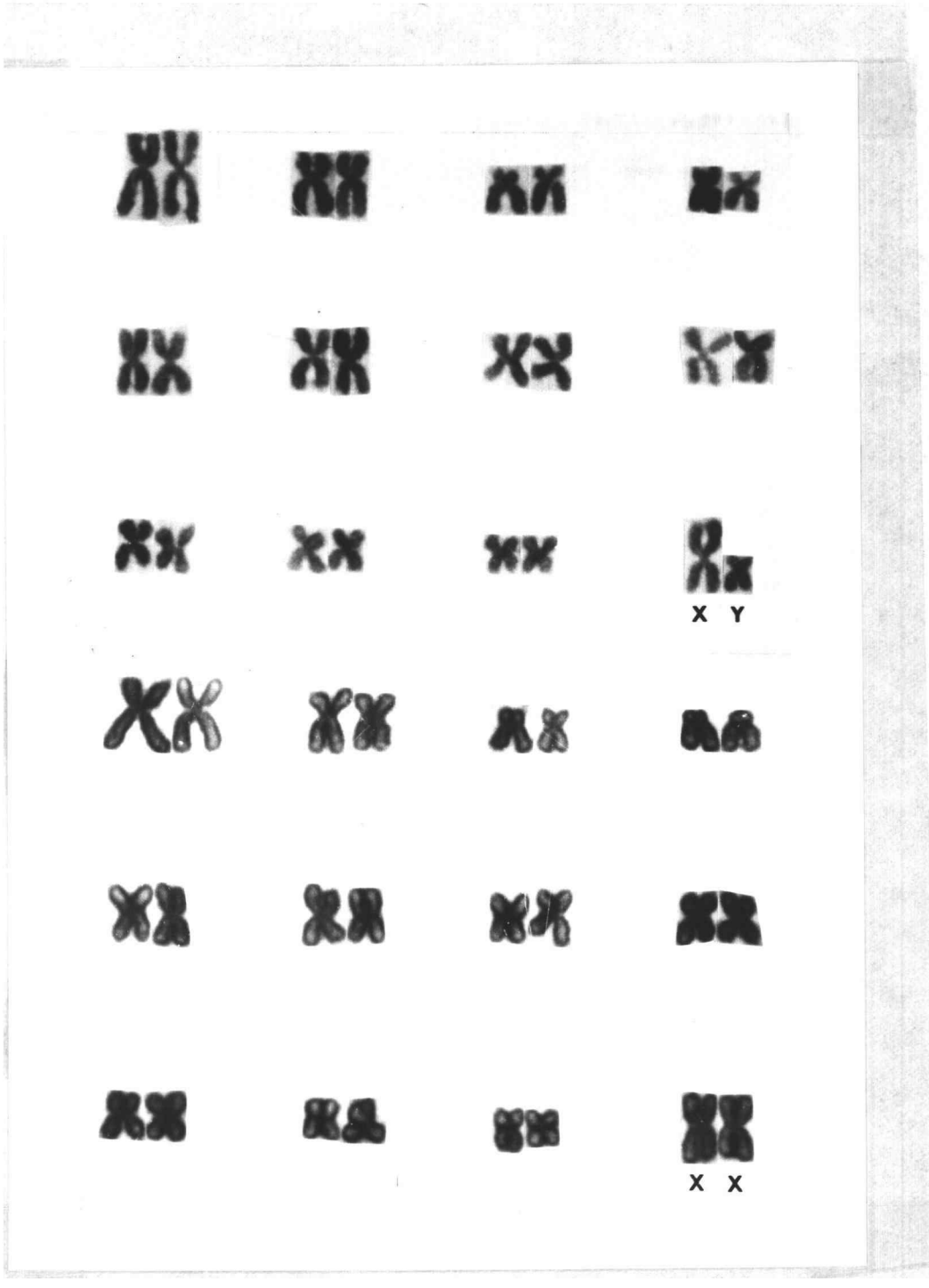

X Y
X X

Figure 6. Karyotypes of male and female hybrids.

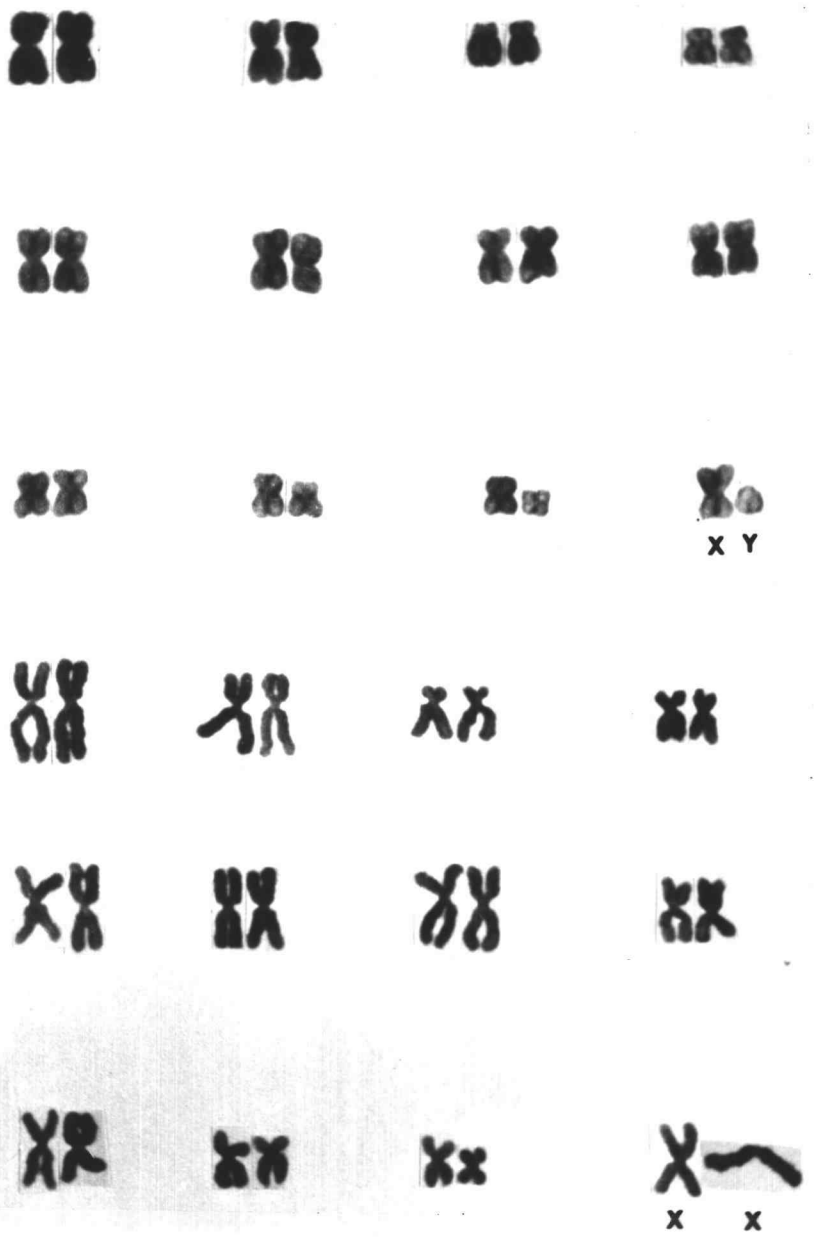

X Y
X X

Figure 7. Growth (body weight) of M. montanus and M. canicaudus males Arrow denotes the presence of significant ($p < 0.05$) dimorphism. Vertical lines represent means ± one standard error. The curves were fitted by eye. For complete weekly data, see Appendices I and II.

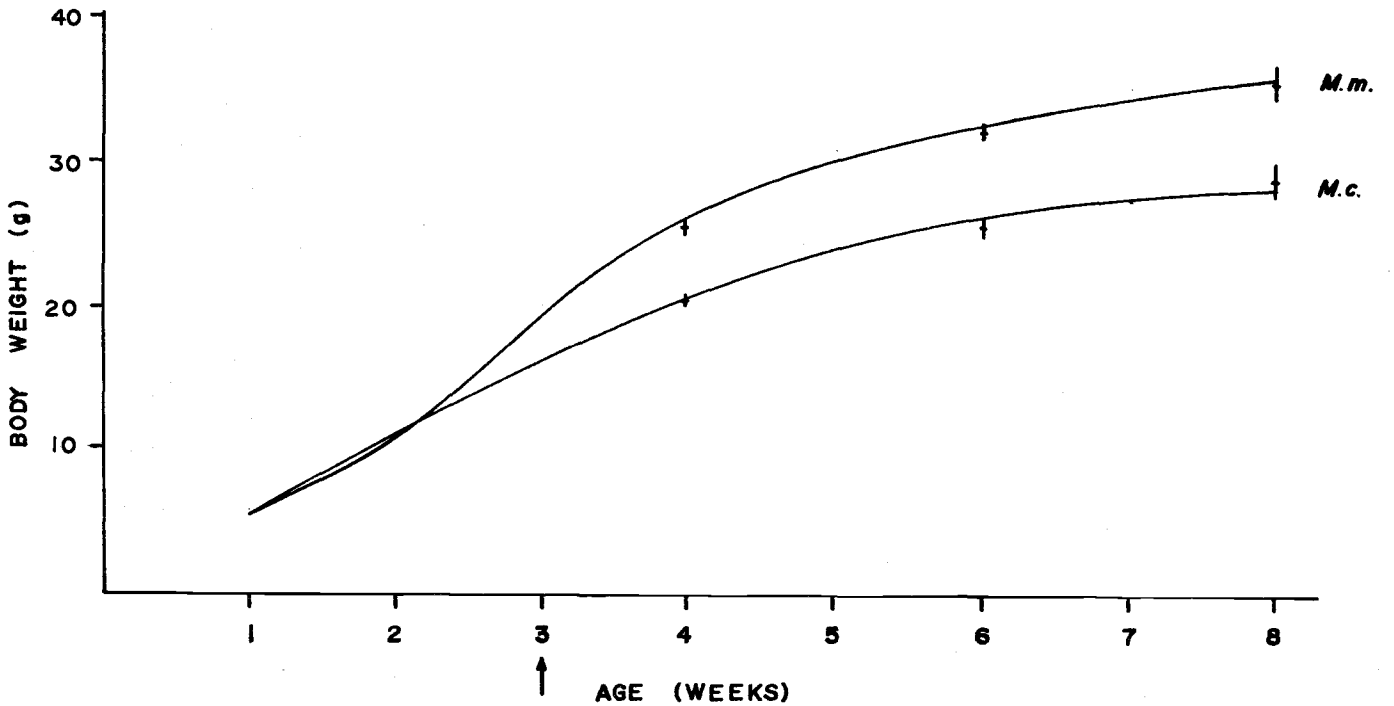

40
30
20
10
BODY WEIGHT (g)
M.m.
M.c.
1
2
3
4
5
6
7
8
AGE (WEEKS)

Figure 8. Growth (body weight) for M. montanus and M. canicaudus females. Arrow denotes the presence of significant ($p<0.05$) dimorphism. Vertical lines represent means ± one standard error. The curves were fitted by eye. For complete weekly data, see Appendices I and II.

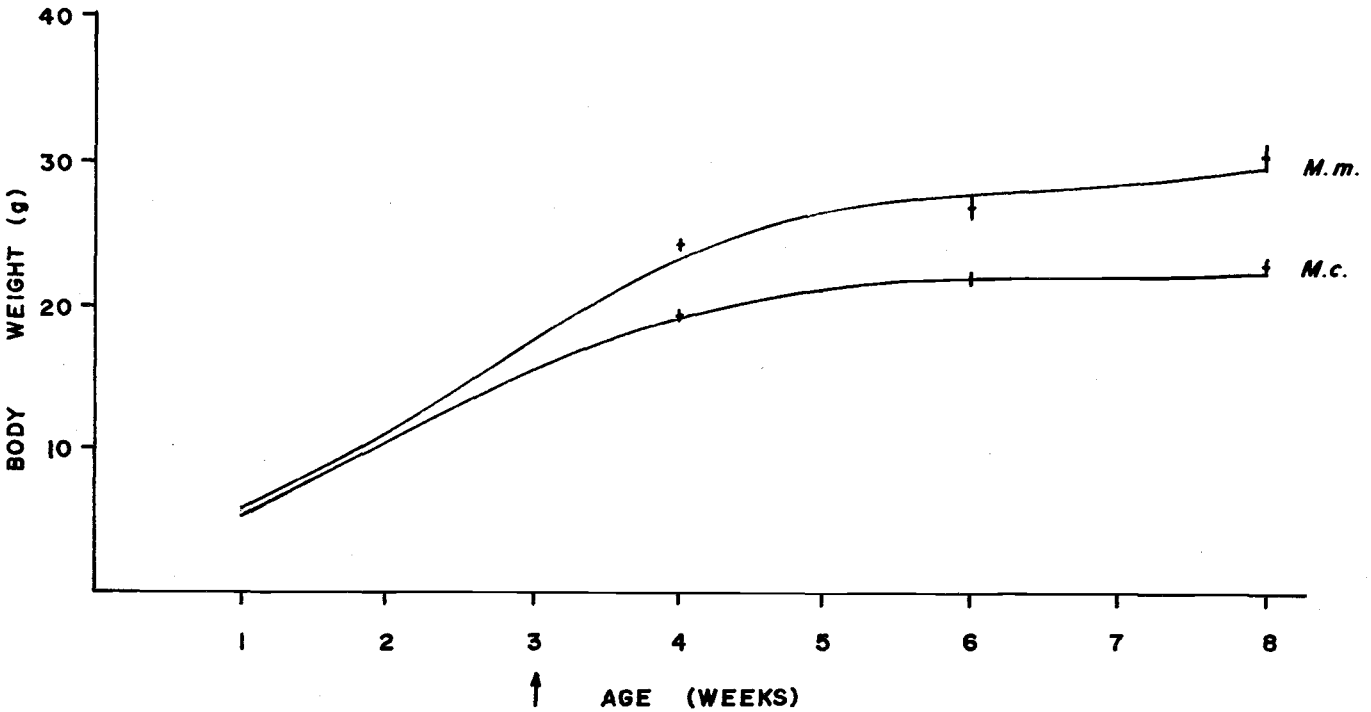

40
30
20
10
BODY WEIGHT (g)
M.m.
M.c.
1
2
3
4
5
6
7
8
AGE (WEEKS)

Figure 9. Growth (body length) for M. montanus and M. canicaudus females. Arrow denotes the presence of significant ($p<0.05$) dimorphism. Vertical lines represent means ± one standard error. The curves were fitted by eye. For complete weekly data, see Appendices I and II.

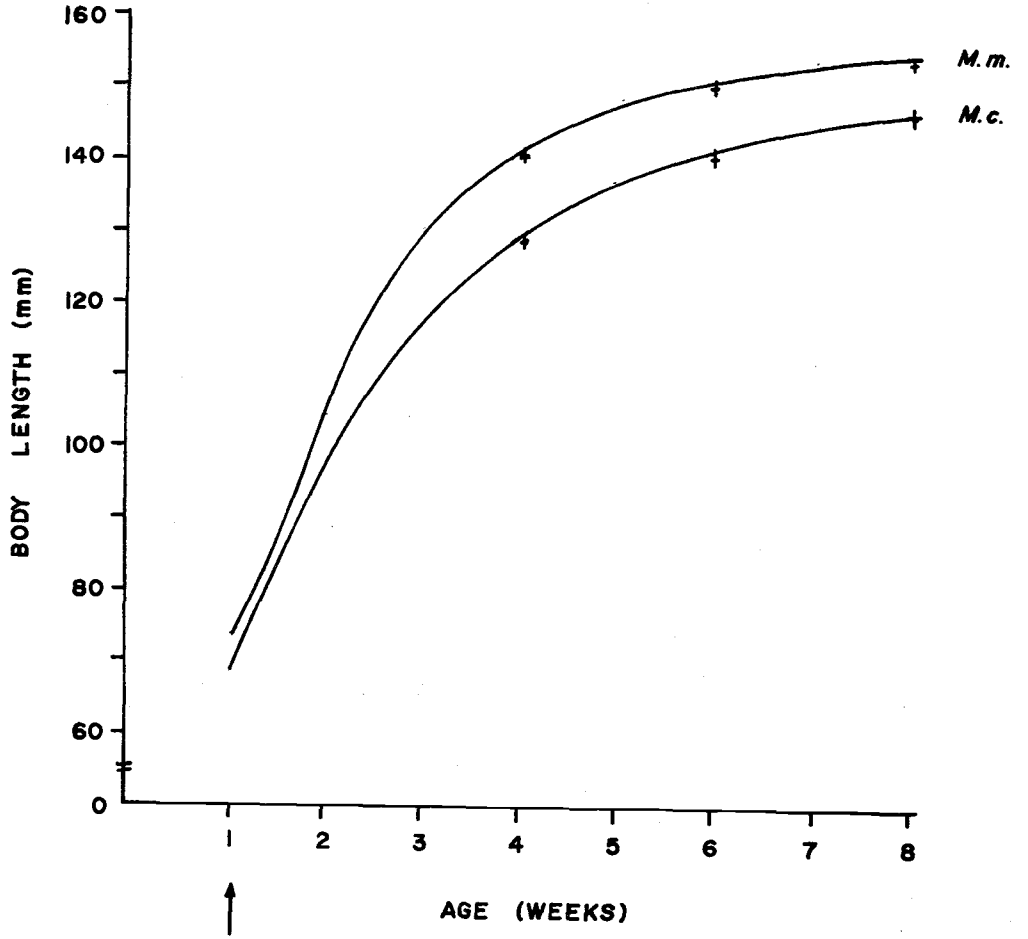
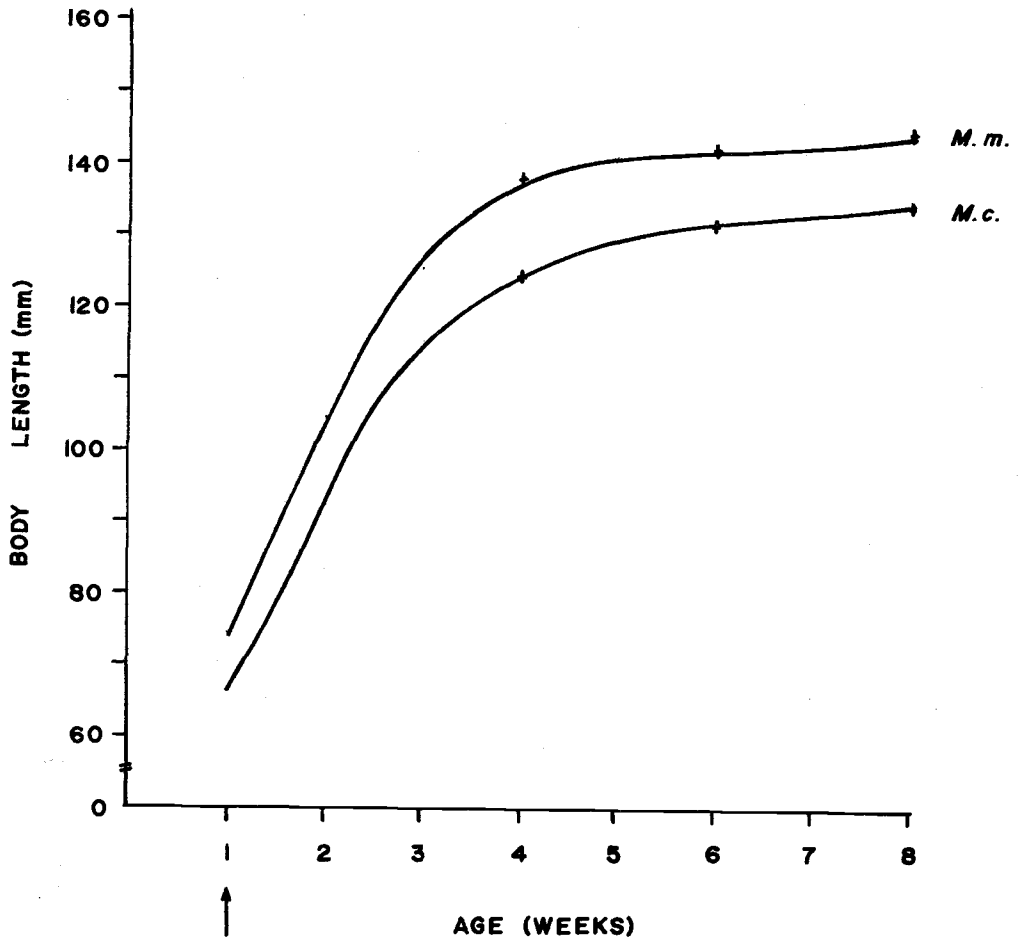

160
140
120
100
80
60
0
BODY LENGTH (mm)
M.m.
M.c.
1
2
3
4
5
6
7
8
AGE (WEEKS)

Figure 10. Growth (body length) for M. montanus and M. canicaudus females. Arrow denotes the presence of significant ($p < 0.05$) dimorphism. Vertical lines represent means $\pm$ one standard error. The curves were fitted by eye. For complete weekly data, see Appendices I and II.


160
140
120
100
80
60
0
BODY LENGTH (mm)
M. m.
M. c.
1
2
3
4
5
6
7
8
AGE (WEEKS)

M. montanus females appear at week one (total length) and week three (body weight). Therefore, definite interspecific growth differences are indicated. Sexual dimorphism ($p<0.05$) in M. canicaudus appears at week two in both body weight and length.

Behavioral Observations

During the relatively short time the behavioral interactions within the cage network were observed, no discreet, stable runway or nest box territories were discernible. However, due to inadequacies mentioned below, the absence of any territorial tendencies cannot be concluded from the brief, limited observations involved in this investigation. Most individuals apparently had unrestricted movement throughout runways and nest boxes. Nesting pockets within the nest boxes appeared to be "defended" over short periods of time, however.

A summary of agonistic encounters scored are listed in Table 6. Out of a total of 151 interactions identified, 117 were interspecific (about 77%). In addition, the two categories which show the most agonistic interactions are those involving interspecific encounters of female M. montanus (see Table 7).

Table 6. Summary of agonistic encounters.

	Interspecific	Intraspecific
Male x Male	48	22
Female x Female	46	2
Male x Female	23	10
Total	117	34

No deaths occurred during this portion of the investigation, but most individuals (the exceptions being a female M. montanus and a female M. canicaudus) were found to have some scarring of the back and rump when the experiment was terminated. Some males, presumably subordinates, were heavily scarred; generally less scarring was present on M. montanus individuals.

Miscellaneous Reproductive Data

The observed gestation patterns of M. canicaudus and M. montanus are shown in Figures 11 and 12. The most commonly occurring period between successive litters seems to be 21 to 23 days for M. canicaudus and 20 to 22 days for M. montanus. In each case the mode is 21 days, indicating the most common gestation period.

Table 7. Tabulation of the number of agonistic encounters for each pair combination.

	Male x Female				Male x Male			Female x Female			
Observation Periods	M. m. x M. m.	M. c. x M. c.	M. m. x M. c.	M. c. x M. m.	M. m. x M. m	M. c. x M. c.	M. m. x M. c.	M. m. x M. m.	M. c. x M. c.	M. m. x M. c.	Unknown
8:00-9:00 AM (1 hr.)[a]	3	1	3	8	1	1	3	0	0	3	0
1:00-6:00 PM (5 hrs.)[a]	5	10	4	31	0	8	16	1	1	36	9
8:00-10:00 PM (1 hr.)[a]	0	3	0	2	0	0	4	0	0	7	3
TOTAL	8	14	7	41	1	9	23	1	1	46	12

[a]Number of hours of observation time within each observation period.

Figure 11. Inter-litter time intervals for Microtus canicaudus.

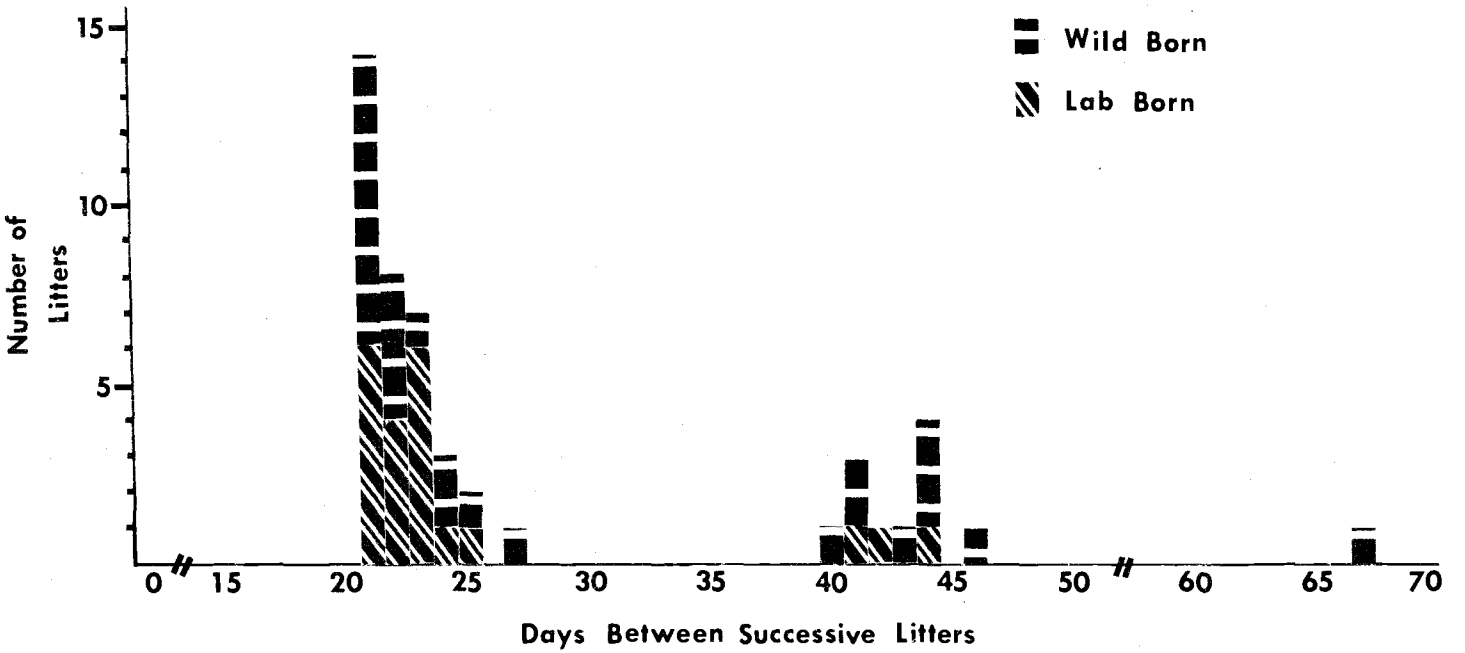

Wild Born
Lab Born
Number of Litters
15
10
5
0
15
20
25
30
35
40
45
50
60
65
70
Days Between Successive Litters

Figure 12. Inter-litter time intervals for Microtus montanus.

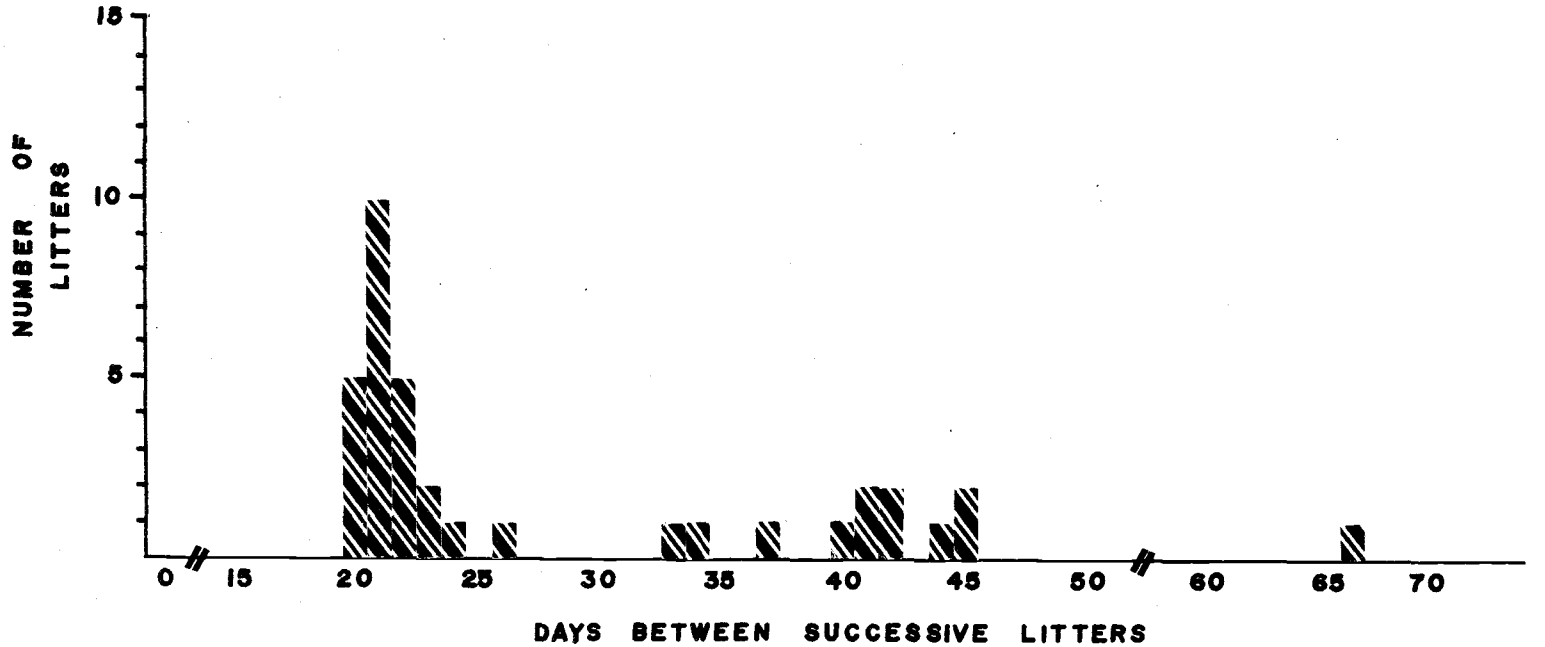

NUMBER OF LITTERS
15
10
5
0
15
20
25
30
35
40
45
50
60
65
70
DAYS BETWEEN SUCCESSIVE LITTERS

Table 8 indicates that, on the average, first litter sizes are significantly smaller ($p<0.05$) than the grouped mean litter size of litters two through four. Thus one would expect sexually mature females to increase their reproductive output as they went through successive parturitions (at least for the first few litters).

Table 8. Litter size comparisons.

Mean Size of 1st Litter		Mean Size of 2nd-4th Litters	
N	$\bar{X}\pm$SEM	N	$\bar{X}\pm$SEM
18	4.18±0.23	21	4.90±0.24

DISCUSSION

Taxonomic Speculations

The results from the breeding trials indicate that the reproductive success of the cross matings is, at best, marginal. The strongest argument in support of this statement is the relatively high degree of hybrid mortality (Table 5). Generally, Group I demonstrated the most successful reproductive performance of the breeding groups, probably in part reflecting M. montanus' longer period of colonization.

Although no statistical significance was shown, a lower percentage of Group III pairings reached parturition when compared to Group I and Group II pairings (Table 1). General interspecific physiological incompatibility is offered as a speculation suggesting intra-uterine selection against gametes, selection against hybrid embroys, or perhaps some type of reproductive behavioral incompatibility. The following observations suggest that intra-uterine selection against hybrid embryos occurred: 1) malformed young were observed in both IIIA and IIIB pairings, 2) periodic palpation of Group III pregnant females implied that hybrid embryos would often undergo initial development and then undergo resorption.

Table 2 shows that those crosses which were capable of producing at least one litter had the capability of producing litters at a

"normal" frequency. Evidently interspecific behavioral or physiological incompatibilities did not interfere with the frequency of litter formation in these pairings. The greater frequency of Group III litter formation compared with that of Group II may be attributed to the fact that Group III pairings had individuals (Microtus montanus) which had been colonized longer.

Table 3 demonstrates that Group IIIA and Group IIIB litter sizes were significantly smaller than the homogeneous pairings, assuming that cannibalization of hybrid young is negligible. This, once more, indicates some kind of intra-uterine selection against gametes or hybrid embryos in the cross pairings, or, if multiple copulations must occur to produce normal litter sizes, that some of inter-specific behavior incompatibilities might exist.

The total number of offspring born per active female (Table 4) is a function of litter size and the number of litters produced. The relatively good performance of Group IIIA reflects the comparatively high frequency at which parturition was reached. A more detailed analysis of the comparative reproductive performances will be deferred until the behavioral data have been discussed.

The karyotypes indicate consistent differences between M. canicaudus and M. montanus. Karyotypic differences have been noted to occur within species (Lee and Zimmerman, 1969) but more often chromosome differences designate species differences, such as in

Peromyscus (Hsu and Arrighi, 1968), Perognathus (Patton, 1967), and Microtus (Matthey, 1957 as cited by Zimmerman, 1970). Therefore, the karyotypic differences noted in this study suggest that M. canicaudus and M. montanus are separate species. This hypothesis is supported by the reproductive incompatibilities of the crosses, mentioned above, and inter-specific behavior patterns, mentioned below.

The interspecific size differences do not, in themselves, warrant a definitive taxonomic "ruling". Size variations have been noted for various subspecies of M. montanus (Anderson, 1959). At best the size and growth differences supplement the other evidence presented in this study.

Several criticisms can be made with respect to the behavioral data collected (Table 6 and 7). As the ear tags were extremely difficult to see, it is possible that the agonistic encounters involved only a small proportion of the total numbers of individuals present in the cage network. If this is indeed true, it is possible that the few individuals involved in generation of the data might not be adequately representative of normal species interactions. In addition, the voles were only observed in daylight and over the comparatively short time period of 14 days. Therefore, whether or not the data collected accurately reflects circadian or long term behavioral patterns must be questioned.

With these drawbacks in mind, the following speculations may be offered. Generally speaking, the higher rate of interspecific encounters suggests interspecific behavioral incompatibility. If, in fact, the data gathered in Tables 6 and 7 are not artifacts of the experimental situation and general interspecific behavioral incompatibility actually exists, consequences other than a reduced reproductive output for certain mated pairings might be foreseen. Perhaps the agonistic actions represent a kind of behavioral isolating mechanism, potentially resulting in interspecific segregation in nature. One wonders if other behavioral isolating mechanisms are present, such as food and habitat selection, activity patterns, etc.

It is interesting that the Group IIIA encounter pairings showed comparatively few agonistic encounters; in fact it was comparable to the frequency of encounters shown in the intraspecific categories. If this is not the product of experimental bias (as well it might be), and, in view of this pairing's comparative reproductive "success", some limited kind of interspecific behavioral compatibility is indicated.

The behavioral data shed light on the reproductive success of Group IIIA and Group IIIB pairings. In every category, Group IIIA deomonstrated more enhanced reproductive performance. These differences lack statistical substantiation in most cases because of small sample sizes, but the litter sizes and number of offspring produced per active female were significantly larger for Group IIIA.

The inferior reproductive performance of Group IIIB pairings might very well stem from female M. montanus and male M. canicaudus behavioral incompatibilities.

Helmreich's (1960) study, correlating an increased rate of embryo resorption with enlarged adrenal glands of crowded deer mice, and Southwick's (1964) study which demonstrated the essential role that incompatibility (or "stressful" interactions) assumes in eliciting adrenal responses in Peromyscus leucopus, suggest that behavioral incompatibility of Group IIIA pairings could explain their relatively poorer reproductive performances.

The fertility or non-fertility of the few hybrid offspring which do survive to maturity remains to be determined. Mammalian hybrids are often, but not always, fertile when parental chromosomes are indistinguishable in number and morphology (Bernirschke, 1967). Failure of gametogenesis appears to be due to incomplete synapsing (caused by parental chromosomal variation) at the first meiotic division (Bernirschke, 1967). Because fertile hybrid offspring from parents with dissimilar karyotypes (Peromyscus polionotus x P. maniculatus) have been observed (Dawson, 1965), predictions as to the presence or absence of fertility of the Microtus hybrids might be tenuous.

While viable hybrids have been produced from six different Microtus mating combinations involving some seven species, only

one pairing (M. arvalis x M. orcadensis) was noted to result in fertile hybrids (Gray, 1972). However, even if the hybrid offspring are found to be fertile, it is believed that this would not alter what seems to be indicated by the aforementioned evidence, namely that M. canicaudus appears to be a separate species. It has been unfortunate, as Mayr (1963) mentions, that hybrid fertility has been used as an indication of conspecificity. Furthermore, he states, "The mere possibility of hybridization in captivity proves nothing as far as species status is concerned" (p. 112). Hybrid sterility represents only one of many potential isolating mechanisms. Differential habitat preferences, activity patterns, and reproductive behavioral isolating mechanisms are some examples of mechanisms which could feasibly act to isolate sympatric populations of similar species.

The strength of the evidence from the breeding trials, which strongly suggests interspecific reproductive incompatibility, and the consistent interspecific karyotype dissimilarities, lend support to the hypothesis that M. canicaudus deserves species status. The two other means of investigating this issue (body growth rates and inter-and intraspecific agonistic observations), while being of dubious value by themselves, do offer supplementary, "circumstantial" evidence. Ideally, the breeding trials should be repeated to see if the results are reproducible, and a greater geographical

representation of M. canicaudus karyotypes (preferably from the northern Willamette River valley and the portion of the Columbia River Gorge west of Hood River, Oregon) should be obtained in order to give more conclusive evidence to M. canicaudus' taxonomic status.

Comments on Miscellaneous Reproductive Findings

The most frequent gestation period for M. montanus has been established at 21 days (Negus and Pinter, 1965). Twenty-one day gestation periods have been established for other species of Microtus as well, namely M. ochrogaster (Richmond and Conaway, 1969), and M. californicus, M. oeconomus, and M. pennsylvanicus (Asdell, 1964). The results of this investigation, assuming that post partum estrus occurs, indicate the most probable gestation period for M. canicaudus to be 21 days.

It is interesting to note that three peaking patterns are suggested in Figures 11 and 12. The first and most obvious peak occurs at 20-24 days between consecutive litters, a second, reduced peak is present at approximately 41-45 days between litters, and a third, much smaller "spike", is suggested at the 63-66 day interval. Admittedly, not enough data are present here to justify designating the presence of the third peak, but in a similar study (Richmond and Conaway, 1969) a much larger sample size was used and a similar

peak was noticed at the 63 day interval. Note that these patterns are multiples of 20-22 days.

Richmond and Conaway (1969) did not comment on the significance of the 63 day interparturitive interval but did offer a hypothesis explaining the cluster of litters occurring at the 40-44 day interval. Supposedly, a certain portion of voles do not achieve fertile copulation in the post partum estrus immediately following parturition. During the ensuing lactation period, estrus is hypothesized to cease or lessen in cases where the adults are permanently paired. Approximately 21 days after the litter was dropped, a new estrus period is theoretically initiated (presumably as suckling decreases) so that fertile mating occurs and a second litter is born about 42 days following the birth of the first one.

Several objections can be raised with respect to this explanation. If the male is removed just before parturition and then replaced several days after parturition, fertile copulation usually occurs immediately (Richmond and Conaway, 1969). Thus, the postulated lactational anestrus (mentioned above) would have to be relative and ill defined. Secondly, Breed (1969) provides evidence that suggests, in the case of M. agrestis, a lactational anestrus does not exist. One wonders if this might characterize other species of Microtus as well. Thirdly, and most significantly, this hypothesis does not explain the reduction of births during the 45-63

day period following the birth of the first litter. Since lactation in many voles is terminated approximately 12-14 days after parturition (Breed, 1969) there could be no lactation anestrus explaining the lack of births during this 45-63 day period.

An alternative hypothesis, involving pseudopregnancy, seems to offer a more theoretically convincing explanation to the gestation patterns shown in Figures 11 and 12. Pseudopregnancy, first noted by Lee and Boot (1956), is a condition involving anestrous, weight gain, and mammary development, symptoms usually associated with pregnancy (Dewar, 1959). It is initiated by an appropriate stimulus, often sterile copulation. Pseudopregnancy in the rat typically lasts twelve days, compared with the normal gestation period of 22 days (Heap, 1972). However, pseudopregnancy in some mammals, such as the ferret and dog, may last as long as the normal gestation period (Heap, 1972).

It is hypothesized that pseudopregnancy lasts approximately 21 days in, at least, M. canicaudus, M. montanus, and M. ochrogaster. Thus, fertile matings normally take place in post partum estrus and hence most litters are born at 21 day intervals. A smaller proportion of matings, however, are infertile, and pseudopregnancy "sets in"; 21 days later, pseudopregnancy has elapsed and another "post partum" estrus occurs. Most matings at this time are fertile and litters are dropped at the 40-44 day interval.

Evidently a small portion of matings during this second estrus period are once more infertile, and a second consecutive pseudopregnancy results. Forty to forty-four days following the birth of the reference litter, another "post partum" estrus occurs, and again the majority of matings are fertile. Thus, a small wave of litters is dropped at the 63-66 day interval.

Admittedly this is a highly speculative hypothesis, but it could by substantiated fairly easily by using vasectomized males paired with females and determining the duration of pseudopregnancy. If pseudopregnancy differed significantly from 20-22 days in length, an alternative hypothesis must be developed. The potential role of pseudopregnancy in the cyclic population fluctuations of voles has not been assessed. It has been suggested that pseudopregnancy is a product of high density housing conditions in laboratories (Sadlier, 1972). Might pseudopregnancy function as a population regulation mechanism in population cycles of microtines?

An alternative, more direct explanation than the phenomena of pseudopregnancy may be offered to explain the patterns of litter intervals shown in Figures 11 and 12. In several cases embryos were detected (via palpations), seemingly in the latter stages of pregnancy. Later examination, however, showed no embryos and no newborn young to be present. This indicates: 1) the embryos underwent rapid resorption or 2) parturition occurred but the new

born were immediately consumed. In a few cases, smears of blood were observed on the sawdust-covered floor, suggesting that the second alternative is a viable one.

In the majority of parturitions occurring after the normal 21 day intra-litter interval, palpation did not indicate the presence of embryos. However, as palpation is not infallible, this does not conclusively demonstrate that embryos were not present. Thus the occurrence of a 21 day pseudopregnancy is at best a largely unsubstantiated suggestion. It is thought to offer significant heuristic value as the role of pseudopregnancy in microtine populations dynamics has not heretofore been considered.

Studies have shown that litter sizes are a function of reproductive age. In M. montanus (Negus and Pinter, 1965) and M. pennsylvanicus (Poiley, 1949) average litter sizes increased until the fifth litter and then declined. These findings, along with those presented in Table 8, suggest a similar phenomenon may occur in M. canicaudus. This emphasizes the need to consider the breeding history of females when looking at microtine population cycles. Perhaps precipitous decreases in population numbers reflect a predominance of young females rather than an increase in stress, selection, agonistic encounters, or other possible explanations.

SUMMARY

A tentative conclusion of this investigation indicates that Microtus canicaudus should be elevated to species status. The demonstrated reproductive incapabilities of interspecific crosses of M. canicaudus and M. montanus provide the primary supportive evidence for this assertion, with interspecific cytological distinctions, growth differences, and behavior incompatibilities lending supplementary support. This conclusion is contingent upon the reproducibility of the breeding trial results and a demonstrated absence of chromosomal integration in Columbia River Gorge populations of M. canicaudus.

The most common gestation period for M. canicaudus was established at 21 days. The pattern of inter-litter intervals led to the speculation of a 21 day pseudopregnancy in M. canicaudus and M. montanus, which, if this hypothesis is substantiated, has implications on the population biology of microtines. Evidence indicating significantly reduced first litter sizes for M. canicaudus was demonstrated, pointing out the need to consider reproductive maturity when studying microtine population cycles.

BIBLIOGRAPHY

Anderson, Sydney. Distribution, variation, and relationships of the montane vole, Microtus montanus. University of Kansas Publications (Museum of Natural History) 9:415-511. 1959.

Asdell, S. A. Patterns of mammalian reproduction. 2nd ed. Ithaca, New York, Cornell University Press, 1964. 670 p.

Bailey, Vernon. The mammals and life zones of Oregon. 1936. 416 p. (U. S. Department of Agriculture, Bureau of Biological Survey, North America Fauna no. 55).

Baker, Robert J. The role of karyotypes in phylogenetic studies of bats. In: About bats, ed. by B. H. Slaughter and D. W. Walton, Dallas, Southern University Press, 1970. p. 303-312.

Benirschke, K. Sterility and fertility of interspecific mammalian hybrids. In: Comparative aspects of reproductive failure, ed. by K. Benirschke, Berlin, Springer-Verlag, 1967. p. 218-234.

Breed, W. G. Oestrus and ovarian histology in the lactating vole (Microtus agrestis). Journal of Reproduction and Fertility 18: 33-42. 1969.

Dawson, W. D. Fertility and size inheritance in a Peromyscus species cross. Evolution 19: 44-55. 1965.

Dewar, A. D. Observations on pseudopregnancy in the mouse. Journal of Endocrinology 18: 186-190. 1959.

Forslund, Larry Gene. Endocrine adjustments in Microtus montanus populations from laboratory and natural environments. Doctoral dissertation. New Orleans, Tulane University, 1972. 122 numb. leaves.

Goertz, John William. The habitat requirements and ecological relationships of Microtus oregoni (Bachman), Microtus townsendii (Bachman), and Microtus montanus (Peale) in Benton County, Oregon. Master's thesis. Corvallis, Oregon State University, 1959. 90 numb. leaves.

Goertz, John William. Habitats of three Oregon voles. Ecology 45:846-848. 1964.

Gray, Annie P. Mammalian hybrids. 2nd ed. Edinburgh, R. & R. Clark, 1972. 262 p.

Hall, E. Raymond and Keith R. Kelson. A new sub-species of Microtus montanus from Montana and comments on Microtus canicaudus Miller. University of Kansas Publications (Museum of Natural History) 5: 73-79. 1951.

Heap, R. E. Role of hormones in pregnancy. In: Reproduction in mammals. Book 3. Hormones in pregnancy, ed. by C. R. Austin and R. V. Short, London, Cambridge University Press, 1972. p. 73-105.

Helmreich, R. L. Regulation of reproductive rate by intra-uterine mortality in the deer mouse. Science 132:417-418. 1960.

Hsu, T. C. and F. E. Arrighi. Chromosomes of Peromyscus (Rodentia, Cricetidae) I. evolutionary trends in 20 species. Cytogenetics 7:417-445. 1968.

Hsu, T. C., and Murray L. Johnson. Cytological distinction between Microtus montanus and Microtus canicaudus. Journal of Mammalogy 51: 824-826. 1970.

Johnson, Murray L. Application of blood protein electrophoretic studies to problems in mammalian taxonomy. Systematic Zoology 17: 23-30. 1968.

Lee, M. R. and E. G. Zimmerman. Robertsonian polymorphism in the cotton rat Sigmodon fulviventer. Journal of Mammalogy 50: 333-339. 1969.

Lee, S. van der and L. M. Boot. Spontaneous pseudopregnancy in mice II. Acta Physiologica et Pharmocologica Neerlandica 5:213-215. 1956.

Maser, Chris and Robert M. Storm. A key to Microtinae of the Pacific Northwest (Oregon, Washington, Idaho). Corvallis, Oregon, O. S. U. Bookstores, 1970. 162 p.

Matthey, R. Cytologie comparée, systematique et phylogenie des Microtinae (Rodentia-Muridae). Revue Suisse de Zoologie 64:33-71. 1957. (Cited in: Zimmerman, Earl G. Karyology, systematics and chromosomal evolution in the rodent genus, Sigmodon. Publications of the Museum, Michigan State University 4:385-454. 1970.)

Mayr, E. Systematics and the origin of species from the viewpoint of a zoologist. New York, Columbia University Press, 1942. 344 p.

_____ Animal species and evolution. Cambridge, Massachusetts, Harvard University Press, 1963. 797 p.

Miller, Gerrit S. Jr. Description of a new vole from Oregon, Proceedings of the Biological Society of Washington 11:67-68. 1897.

Negus, Norman and Aelita J. Pinter. Litter sizes of Microtus montanus in the laboratory. Journal of Mammalogy 46:434-437. 1965.

_____ Reproductive responses of Microtus montanus to plants and plant extracts in the diet. Journal of Mammalogy 47:596-601. 1966.

Patton, J. L. Chromosome studies of certain pocket mice, genus Perognathus (Rodentia: Heteromyidae). Journal of Mammalogy 48:27-37. 1967.

Pearson, John Philip. The influence of behavior and water requirements on the distribution and habitat selection of the gray-tailed vole (Microtus carnicaudus) with notes on Microtus townsendii. Ph. D. thesis. Corvallis, Oregon State University, 1972. 56 numb. leaves.

Poiley, Samuel M. Raising captive meadow voles (Microtus pennsylvanicus) Journal of Mammalogy 30:317-318. 1949.

Reimer, J. D. and M. L. Petras. Breeding structure of the house mouse, Mus musculus, in a population cage. Journal of Mammalogy 48:88-99. 1967.

Richmond, M. and C. H. Conaway. Induced ovulation and oestrus in Microtus ochrogaster. Journal of Reproduction and Fertility Supplement No. 6:357-376. 1969.

Sadier, R. M. F. S. Environmental effects. In: Reproduction in mammals. Book 4. Reproductive patterns, ed. by C. R. Austin and R. V. Short, London, Cambridge University Press, 1972. p. 69-93.

Southwick, Charles H. Peromyscus leucopus: an interesting subject for studies of socially induced stress responses. Science 143:55-56. 1964.

Zimmerman, Earl G. Karyology, systematics and chromosomal evolution in the rodent genus, Sigmodon. Publications of the Museum, Michigan State University 4:385-454. 1970.

APPENDIX I

Growth Data for Microtus canicaudus

	Week	N_L	Total Length*	N_W	Body Weight*
A. Males	1	30	68.67±1.08	30	5.98±0.15
	2	25	97.48±1.42	25	11.00±0.27
	3	40	117.50±0.75	40	16.49±0.37
	4	35	129.48±0.74	35	21.00±0.37
	5	35	136.91±0.99	35	24.59±0.55
	6	30	140.93±1.26	30	26.08±0.74
	7	30	144.83±1.16	30	27.57±0.87
	8	30	146.90±1.40	30	28.78±0.98
	Week	N_L	Total Length*	N_W	Body Weight*
B. Females	1	30	65.97±0.80	30	5.48±0.13
	2	30	92.17±0.86	30	10.28±0.22
	3	40	114.77±0.65	40	15.21±0.32
	4	40	124.12±0.54	40	19.30±0.30
	5	40	128.98±0.68	40	21.29±0.33
	6	40	131.05±0.67	40	22.18±0.35
	7	30	132.57±0.78	30	22.05±0.44
	8	30	134.27±0.81	30	22.82±0.45

*$\bar{X}$±SEM

$N_{(\ )}$ = sample sizes for length and weight

APPENDIX II

Growth Data for Microtus montanus[a]

	Week	N_L	Total Length*	N_W	Body Weight*
A. Males	1	42	73.76±0.47	42	5.78±0.13
	2	40	104.25±0.84	40	10.63±0.21
	3	32	130.63±0.93	32	20.31±0.41
	4	33	140.94±1.05	33	25.95±0.59
	5	25	148.52±1.22	25	31.38±0.70
	6	24	149.92±0.99	24	32.19±0.60
	7	21	153.81±1.24	24	35.60±0.94
	8	25	153.96±0.94	25	36.04±0.86
	Week	N_L	Total Length*	N_W	Body Weight*
B. Females	1	40	74.33±0.42	40	6.03±0.14
	2	41	104.20±0.86	41	10.81±0.26
	3	39	124.97±1.07	40	17.41±0.56
	4	46	138.09±0.83	46	24.22±0.46
	5	25	140.68±0.82	25	26.11±0.54
	6	22	141.91±0.94	24	26.70±0.57
	7	25	141.64±0.84	25	26.59±0.71
	8	25	144.40±1.09	25	31.30±1.01

*$\bar{X}$±SEM

$N_{(\ )}$ = sample size for length and weight

[a]Data from Forslund (1972)