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THE TIMING AND PATTERNS OF MOLT IN
MICROTUS BREWERI

BY

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ABSTRACT

Molt in the beach vole (*Microtus breweri*), an island endemic, was studied in 1972-1973. Observations were made on timing and pattern of molt and their relationship to reproductive activity. Three molt types are recognizable: juvenile, subadult, and adult. Adult molt occurred seasonally, whereas the other two are age-dependent. Two molt patterns were described: dorsad and diffuse (Ling, 1970). Dorsad is a uniform sequence of replacement and diffuse is characterized by an irregular and blotchy pattern of replacement. Juvenile molt is of the dorsad type, whereas the subadult and adult molts are of both dorsad and diffuse types. The diffuse molt pattern in adults seems to be dependent on reproductive activity and the peak molting activity in adults seems to occur when reproductive activity is reduced. Molt patterns in *M. breweri* are compared to those of other members of the genus and the relevance of molt timing and pattern to the energetic demands of reproduction is discussed.

The beach vole, *Microtus breweri*, is indigenous to Muskeget Island, a 1.0 square mile island west of Nantucket Island, Massachusetts. The present population is descended from *M. pennsylvanicus*, the common *Microtus* species on the nearby New England mainland and adjacent islands. The Muskeget Island population has been separated from its neighbors for 2000 to 3000 years (Weatherbee *et al.*, 1972). Although interbreeding between *M. breweri* and *M. pennsylvanicus* has occurred in the laboratory (Weatherbee *et al.*, 1972), there are sufficient differences to warrant retention of specific status for the beach vole (Tamarin and Kunz, 1974).

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Molt is of interest for several reasons. First, age groups are defined by pelage type and it is important to distinguish age-specific molts. Second, molt is an energy-requiring process, and we are concerned about energy demands made on individual animals. Finally we are interested in comparing molt in *M. breweri* with other microtines to determine what, if any, effects insular isolation has produced.

This investigation is part of a study of the population biology of *M. breweri* under the direction of R. Tamarin.

MATERIALS AND METHODS

All animals used in this study were live-trapped on Muskeget Island, Nantucket County, Massachusetts, from June 1972 to May 1973, at monthly intervals excepting December and February. Animals were killed with ether and standard measurements and reproductive data were recorded. Flat skins were prepared of 137 males and 122 females (Lieberman and Lieberman, 1972). These skins and skulls are deposited in the mammal collection, Museum of Natural History, The University of Kansas.

Determination of the molting condition of each animal was made by examination of melanin deposits. In mammals with pigmented hair, melanin is deposited in the dermis prior to growth of a hair shaft. This is visible as areas of black pigmentation on the flesh side. As hair grows, melanin migrates into the cortex of the hair shaft, leaving the skin without pigmentation when the growth of hair has been completed. From these melanin deposits, areas of new hair growth can be easily determined from a specimen preserved as a flat skin. For each specimen an estimate of the fraction of total surface area actively molting was made and descriptive data on replacement patterns were recorded.

The sequence and direction of hair replacement could be determined from the pelage by comparing the relative lengths of the new and old hairs. Short hairs (0.1 mm) usually were nearest the periphery of melanin deposits. No short hairs were found outside this area. Examination of adjacent hairs closer to the center of the melanin deposit revealed that they were of increasing length, up to that of fully-grown hair. The shortest hairs were obviously in early stages of growth and therefore at the leading edge of molt. Those of increasing length up to and including full length were in later stages of growth.

Terminology for molt patterns follows that of Ling (1970).

RESULTS

We recognize three general molt categories: a juvenile molt between juvenile and subadult pelage; a subadult molt between subadult and adult pelage; and seasonal adult molts. A comparison of pelage condition and total length (Fig. 1) reveals that *M. breweri*

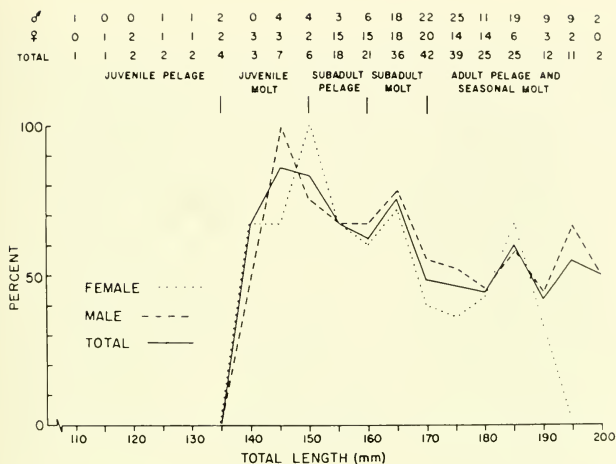


FIG. 1.—Frequency of individuals molting as a function of total length in *Microtus breweri*. Sample sizes are above the graphs.

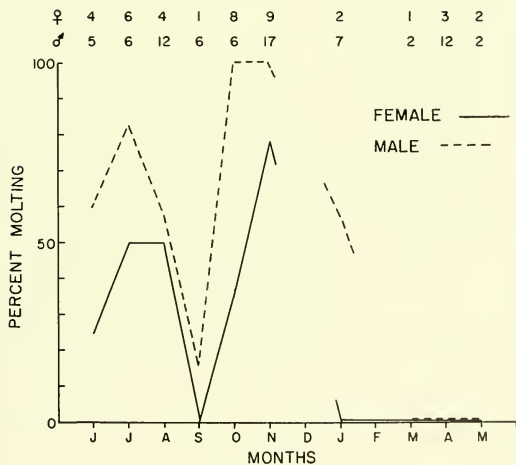


FIG. 2.—Frequency of adults (greater than 170 mm total length) molting as a function of season in *Microtus breweri*. Sample sizes are above the graphs.

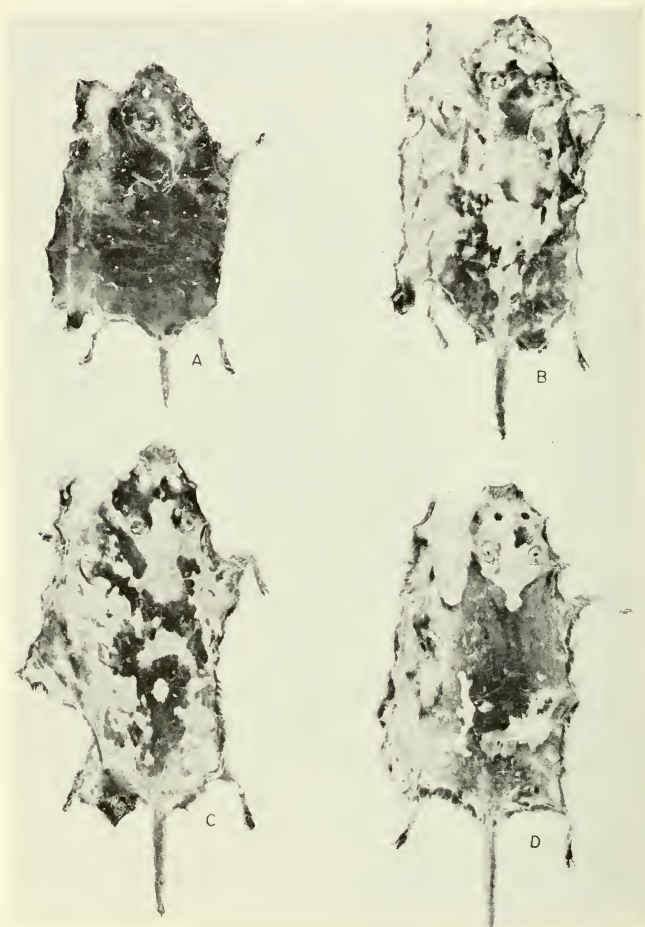


FIG. 3.—Photograph of the underside of flat skins showing molt patterns in *Microtus breweri*; ventral surface is to the left. A: juvenile molt; B, C: diffuse molt showing symmetrical melanin deposits; D: diffuse molt displaying general symmetry only.

retains its juvenile pelage until it reaches a total length of 136 to 150 mm. At this time a juvenile molt occurs, giving rise to a subadult pelage. This pelage persists until a length of 161-165 mm is achieved. At this time the subadult molt occurs, culminating in an adult pelage. The only molts occurring in animals having a total length greater than 165 mm were seasonal. A spring molt was evident from June to August and an autumn molt occurred from October to January (Fig. 2).

Pelage characteristics have been summarized (Starrett, 1958), and it was noted that adult pelage of *M. breweri* is paler than that of *M. pennsylvanicus*. Juvenile pelage in *M. breweri* is similar in

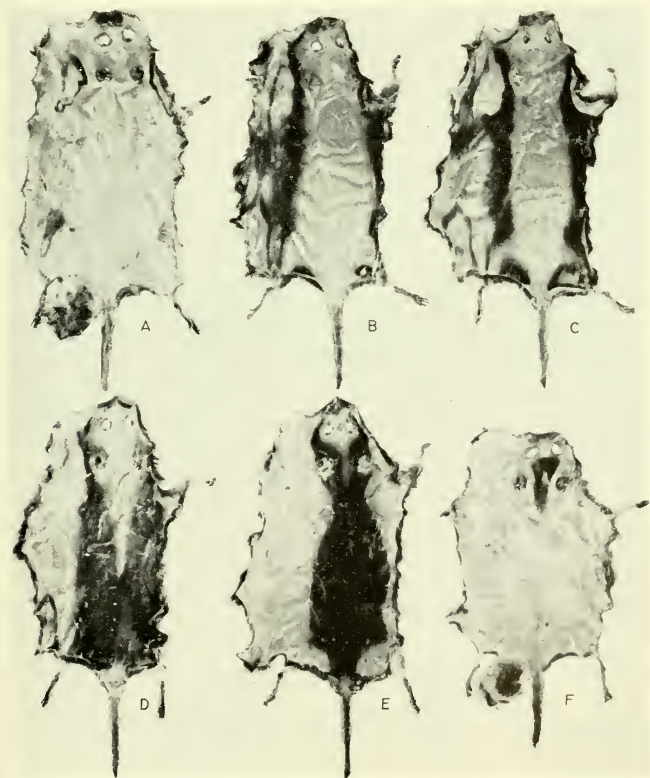


FIG. 4.—Progression of dorsad molt in subadults from the earliest stage (A) through the last stage (F). See legend for Fig. 3.

color to that of the adult, whereas in *M. pennsylvanicus* the young are considerably darker than adults. Juvenile pelage in *M. breweri* is distinct in texture and length from that of older animals, but there is no grossly discernible difference between the subadult and adult pelage when animals captured in the same month are compared.

The sequence of hair replacement in juveniles proceeds from the ventral surface, laterally nearly simultaneously to the dorsal surface, and terminates at the head. This is evidenced both by the melanin deposits in the underside of the skin and by visual examination of the pelage (Fig. 3A). This wave of replacement from ventral to dorsal is termed "dorsad" by Ling (1970).

Two types of subadult molt were seen. The first consists of a dorsad molt, similar and possibly identical to that of the juvenile. This wave begins on the legs, spreads to the ventral surface, moves laterally, and meets on the entire dorsal surface except for an area on the head, which is the last to molt (Fig. 4). In our samples, eighty-one percent of the voles undergoing subadult molt followed the dorsad type. No sexual dimorphism was observed in this pattern. The second type consists of a diffuse distribution of melanin deposits ranging from speckled to blotchy. Ling (1970) refers to this type of molt as "diffuse." In all cases there is a general symmetry to the deposits (Fig. 3D). In 33 percent of those subadults exhibiting diffuse molt, a distinct symmetry in melanin depositions near the mid-dorsal line can be seen (Fig. 3B and C).

Adult seasonal molts are of the same two types as in subadults (dorsad and diffuse). However, eight percent of the molting adults revealed no pigment symmetry.

A comparison of molt with reproductive data reveals a relationship between breeding condition and adult seasonal molt. Molting adults were more likely to follow a dorsad sequence if they were nonbreeding; conversely, if in breeding condition adults were more likely to molt in a diffuse or irregular fashion (Tables 1 & 2). Length

TABLE 1.—RELATIONSHIP BETWEEN MEDIAN AND MEAN TOTAL LENGTH AND TYPE OF MOLT PATTERN (DORSAD AND DIFFUSE) IN MALE AND FEMALE *M. breweri*.

Total length	Female		Male	
	166—180 mm		171—182 mm	
	Dorsad	Diffuse or Irregular	Dorsad	Diffuse or Irregular
Median	172 mm	170 mm	175 mm	174.5 mm
Mean	172	172	176.3	176
N = Total number of animals molting	10	9	11	12

TABLE 2.—A COMPARISON OF MOLT PATTERN AND BREEDING ACTIVITY IN *M. breweri*.¹

	Breeding	Nonbreeding
Dorsad	8	13
Diffuse or Irregular	17	4

¹ Reproductive activity was determined by visible tubules in the cauda epididymides of males and by corpora lutea in the ovaries, perforate vagina, pregnancy, or lactation in females. Chi-square (1 df) = 8.00; $p < 0.01$.

classes of specimens used for comparison in this analysis were selected because within each sex the median and the mean total lengths of those molting were similar, which avoids biasing the data with age differences (Table 1). This is important because several authors think diffuse molt is a function exclusively of age (Ecke and Kinney, 1956; Hatfield, 1935; Zejda and Mazak, 1965; Jameson, 1947). The relationship of diffuse and other non-dorsad molt to reproductive activity in adults is highly significant (Table 2). No significant relationship was found between pregnancy and type of molt in adult females. No such trend was found in subadult females, even though many were in breeding condition while undergoing a subadult molt. This comparison cannot be made in subadult males because breeding in males commenced at 170 mm, which was reached after subadult molt in the year studied.

Seasonal molts in females are delayed relative to those of males in both spring and fall. Males initiate molt in June and again in October, whereas females begin in July and in November (Fig. 2).

Comparisons of molting with lactation and pregnancy were made in females having a total length greater than 155 mm. This length was chosen in order to restrict the analysis to those individuals of potential or actual reproductive activity, both adult and subadult, and thereby eliminate the possible bias of including individuals undergoing subadult molt. Figure 5 shows that peaks in molting activity occur at times different from peaks in pregnancy and lactation.

DISCUSSION

Juvenile and subadult molts have been described in several species of *Microtus*. Hatfield (1935) and Ecke and Kinney (1956) both observed these two molts occurring in *M. californicus*; Jameson (1947), Pinter (1968), and Martin (1973) noted their occurrence in *M. ochrogaster*, *M. montanus*, and *M. chrotorrhinus*. The descriptions given by these authors for juvenile and subadult molting patterns fit into Ling's (1970) dorsad classification. Al-Khateeb and Johnson (1971a) reported dorsad patterns in both juvenile molt and spring molt in adult *M. agrestis* but failed to distinguish between subadult and adult fall molt. Kryltzov (1964) found the same pattern (=sublateral) for *M. arvalis*, *M. mongolicus*, *M. trans-*

caspicus, *M. middendorffi*, *M. hyperboreus*, *M. unguensis*, *M. fortis*, *M. socialis*, *M. brandti*, *M. vinogradovi*, *M. carruthersi*, *M. blythei*, *M. gud*, *M. nivalis*, *M. roberti*, *M. majori*, and *M. linnophilus*. Minor differences in patterns described within the genus may be attributable in part to varied amounts of detail considered by various authors working with different sample sizes. Our findings for *M. breweri*, that there is no sexual dimorphism in molt patterns, concurs with findings for *M. californicus* (Ecke and Kinney, 1956). None of the other authors mentioned sexual dimorphism in the genus *Microtus*.

Hatfield (1935) and Ecke and Kinney (1956) noted that all adult *M. californicus* undergo a diffuse molt with no apparent pattern. Jameson (1947) observed the same for *M. ochrogaster*. Although Al-Khateeb and Johnson (1971a) found a regular dorsad spring molt in adult *M. agrestis*, they observed patchy replacement continuing in these animals throughout the summer. Martin (1973) noted a sacral subtype of the cephalo-sacral molt in adult *M. chrotorrhinus*. This is described by Kryltzov (1964) as commencing in a V-shaped spot on the rump which spreads to the whole back, extends to the belly, and terminates on the head. Diffuse molts in adults are reported in a variety of mammals: *Apodemus sylvaticus* (St. Girons, 1967), *Ondatra zibethica* (Shanks, 1948), *Clethrionomys glareolus* (Zejda and Mazak, 1965), *C. rutilus* (Sealander, 1972). Of these, *A. sylvaticus* and *O. zibethica* are the only species in which some adults molt in a regular sequence and others in a diffuse manner.

Diffuse molt appears to be far more complex than a molt resulting from random distribution of groups of follicles entering the growing stage (anagen). The existence of symmetry in some individuals suggests that there is an intrinsic symmetrical pattern in these animals, rather than a random replacement as suggested by others (Hatfield, 1935; Ecke and Kinney, 1956; Jameson, 1947; Al-Khateeb and Johnson, 1971a; St. Girons, 1967; Zejda and Mazak, 1965). We suspect that more careful examination of diffuse molt in other species may reveal a pattern of symmetry in some specimens.

Our data show a relationship between breeding and the frequency of diffuse molt. This observation is not unique. In a study of *Sylvilagus floridanus* and *S. transitionalis*, Spinner (1940) observed two types of molting: spotted and sheet. The former is characteristic of spring molt and the latter is found primarily in fall molt, and they correspond to our diffuse and dorsad molts, respectively. Spinner assumed a correlation with breeding because he found that, in fall, pregnant females had a spotted molt, whereas nonpregnant females had sheet molt. Shanks (1948) found diffuse molt to be normal in adult muskrats, but noted that six out of seven barren adult females retained the regular pattern found in young

animals. Our data reveal that, for *M. breweri*, it is breeding condition rather than pregnancy that determines the type of molt.

It is of interest that Sealander (1972) observed reversals of hair replacement in autumn and spring molts in *Clethrionomys rutilus*. An autumn molt was characterized by a dorsad pattern, but a spring molt began on the dorsum, spread laterally, and terminated on the venter. This reversal was attributed to possible differences in age groups taken in the two seasons. In our study there was no evidence of seasonal differences in replacement patterns.

Although reproductive hormones have been shown to have effects on various aspects of hair growth and molting in wild and laboratory mammals (Al-Khateeb and Johnson, 1971b; Fraser and Nay, 1953; Nay and Fraser, 1955; Johnson, 1958b), we are not in a position to suggest what causes the diffuse molt during periods of reproductive activity. Laboratory studies in which reproductive hormones can be administered to nonpregnant females during the period of fall molt may suggest answers to this question. Examination of molt sequence could best be accomplished by dyeing the pelage prior to molting and recording the time required to complete

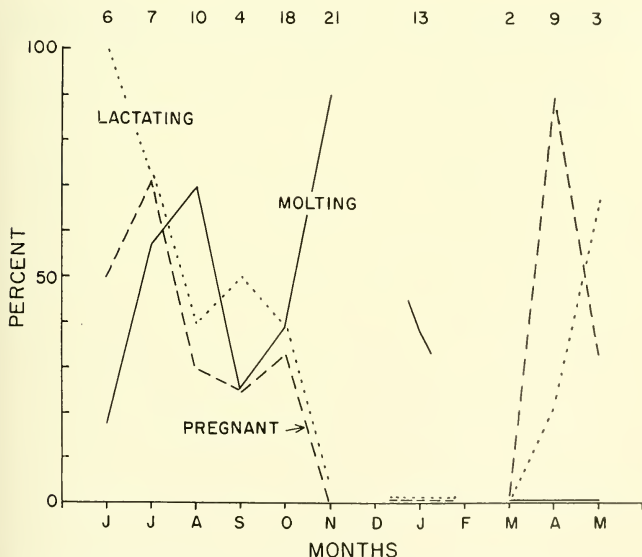


FIG. 5.—Relationship of frequency of females (greater than 155 mm total length) molting, lactating, and pregnant as a function of season in *Microtus breweri*. Sample size is above the graphs.

a molt. The possibility that molt is arrested due to reproductive or other influences cannot be determined from prepared specimens. Arrested molt has been seen during lactation in *Miniopterus schreibersi blepotis* (Dwyer, 1963), and during lactation and pregnancy in *Perognathus parvus* (Speth, 1969).

The general trends in Fig. 5 suggest that molting is timed so that the majority of molting occurs at a time when reproductive activity (pregnancy and lactation) in the subadult and adult female population is low. Although this cannot be extrapolated to what is occurring in the individual animal, laboratory study where pregnant and lactating females could be observed for molt progress may be illuminating.

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