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#### WATER AS A POTENTIAL BARRIER TO DISPERSAL IN *MICRODIPODOPS*

The geographic range of kangaroo mice (genus *Microdipodops*) covers approximately 250,000 square kilometers in the Great Basin region of North America (Hall and Kelson, 1959). In addition to innumerable seasonal streams in this area, there exist approximately 8200 kilometers of rivers, which act as potential barriers throughout the year to the dispersal of these animals. The purposes of our studies were 1) to compare the swimming ability of *M. megacephalus* and of *M. pallidus* when individuals of each species were involuntarily placed in water, 2) to relate this ability to the size of geographic range of each species, and 3) to evaluate several factors (for example, degree of inflation of bullae, cheek pouch contents, and water temperature) that are significant to swimming and buoyancy studies, but to our knowledge, have not been previously investigated.

We studied individuals of *M. megacephalus* ( $N = 18$ ) and *M. pallidus* ( $N = 10$ ) that were live-trapped on 13 and 14 June 1974. The animals were eased individually into a porcelain tank of placid tap water and notes were taken on behavior. An animal was considered minimally exhausted when its nose dipped below the surface of the water, at which point it was quickly removed from the tank. The dimensions of the tank were approximately 1.5 by 0.5 by 0.3 meters and contained water of sufficient depth (150 millimeters) to insure that test animals could neither touch the bottom nor reach the upper rim. The desired water temperature was maintained constant ( $\pm 1^\circ \text{C}$ ) throughout each phase of the study. Although other investigators have made similar studies involving animals with external cheek pouches, no previous publication has made mention of the condition of the pouches during experimentation. In our preliminary tests, it was observed that cheek pouches containing seeds added significantly to the buoyancy of the animal. Therefore, care was taken to insure that the cheek pouches were empty before placing an animal in the experimental tank.

Palmén (1944) noted that the endurance of dispersing insects in water depended, among other factors, on the temperature of the water. On the assumption that water temperature might play a significant role in the metabolism of a swimming mammal, we designed a series of experiments using both species at a water temperature of  $30 \pm 1^\circ \text{C}$ , and, additionally, tested *M. pallidus* at  $20 \pm 1^\circ \text{C}$  and  $10 \pm 1^\circ \text{C}$ . As there was no significant change in the endurance of *M. pallidus* at the lower temperatures, similar tests were not conducted for *M. megacephalus*.

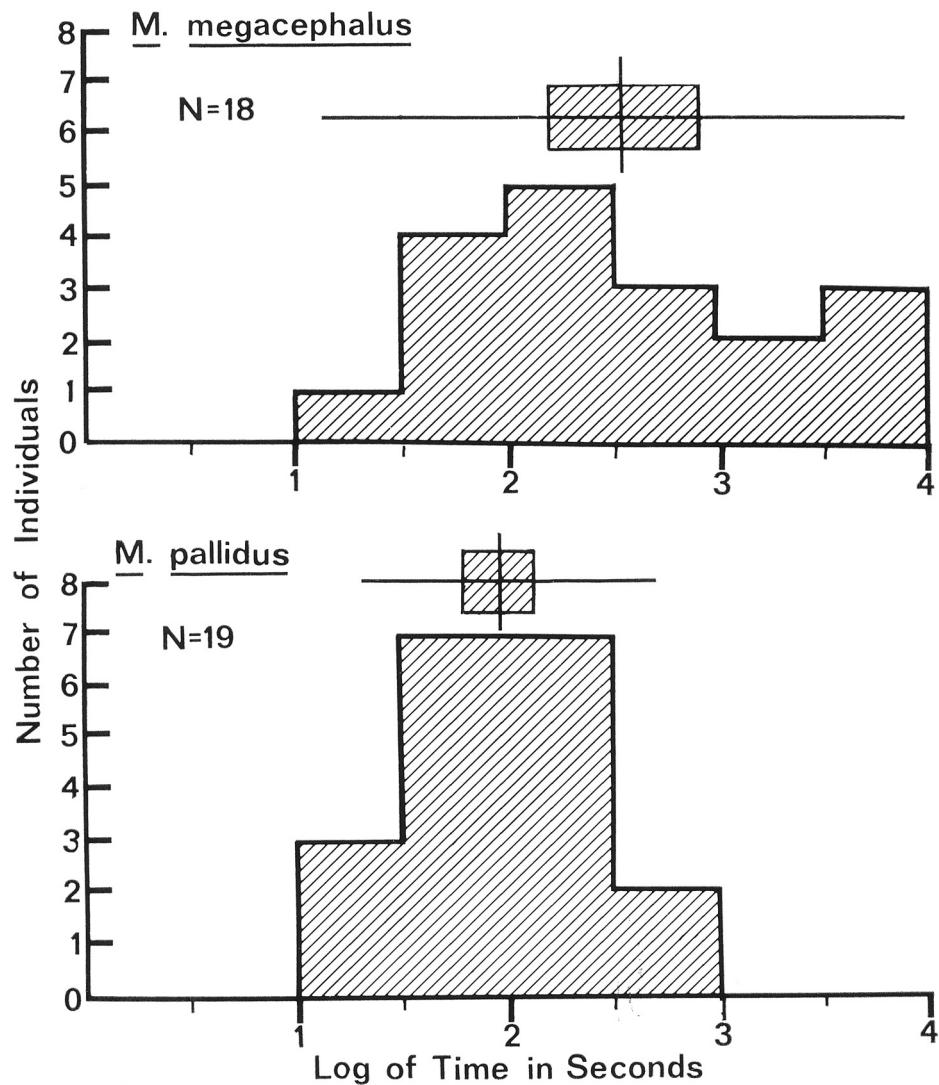


FIG. 1.—The log time in seconds spent in water by two species of *Microdipodops* before minimal exhaustion. The histograms represent the number of individuals per time interval. The horizontal line represents the range; vertical line, the mean; rectangle represents 95 percent confidence limit.

The results of our studies at  $30 \pm 1^\circ\text{C}$  approximate a log normal distribution and are presented on a logarithmic scale (Fig. 1). *M. megacephalus* spent both the shortest (14 seconds) and the longest (more than 2 hours) periods in the water [geometric mean  $337 \pm 5.90$  (standard deviation) seconds]. Observations on *M. pallidus* showed a tight grouping with a range of 20 to 435 seconds (geometric mean  $88.1 \pm 2.64$  seconds). The log means were found to be significantly different by the Student's *t*-test ( $t = 2.876$ ,  $P < .005$ , degrees of freedom = 35).

The ordered swimming phases (swim, float, uncoordinated swim) reported by Schmidly and Packard (1967) for *Perognathus* and similarly reported by Stock (1972) for *Dipodomys* were not observed in *Microdipodops*. *M. pallidus* and *M. megacephalus* displayed remarkably different behavioral patterns in the water. All individuals of *M. pallidus* had a period of rapid, high-intensity swimming followed by a period of lower-intensity swimming, the head soon thereafter dipping below the surface. Individuals of *M. pallidus* floated only occasionally and for brief periods. *M. megacephalus* showed remarkable variability in behavior. One animal swam at high intensity for 14 seconds and immediately sank, whereas most appeared "relaxed" in the water and alternated swimming with floating.

In both species of *Microdipodops*, the forelegs were used in dog-paddle fashion. The hind legs were used in synchrony during periods of high-intensity swimming, and with alternate strokes at lower intensities. During floating periods, one hind leg was extended laterally at 90° from the main axis of the body and appeared to act as a stabilizer. The tail moved in a disoriented fashion, often trailing behind or being thrust above the water and recurred over the back, and not as a rudder as reported for *Perognathus* (Schmidly and Packard, 1967). The entire behavioral sequence shown by each species in the water can be divided into a swimming period and a floating period. *Microdipodops* shows little deliberate oriented movement in the water as the word "swimming" implies, and moreover the extended floating periods of *M. megacephalus* has caused us to refer to the entire behavioral sequence not as "swimming ability" alone, but as the ability to keep the head above water.

Schmidly and Packard (1967) found a positive correlation between "swimming ability" and size of geographic range in four species of *Perognathus* and their discussion aptly noted the hazard of explaining differences in size of geographic range on the basis of one dispersal mechanism alone. Nevertheless, *M. megacephalus* not only can maintain its head above water for longer periods than can *M. pallidus*, but also has a geographic range about three times the size of the latter. Whether or not a causal relationship exists has yet to be shown, however, it appears reasonable that the remarkable floating ability of *M. megacephalus* could be of adaptive significance to the species. Interestingly, in addition to the high degree of behavioral variation we observed in *M. megacephalus*, this generalized species also exhibits a great amount of morphological variation (Hall, 1941; Schitoskey, 1968; personal observation).

The highly inflated bullae and small body size of *Microdipodops* undoubtedly explain the animal's buoyant nature. *M. pallidus*, having slightly more inflated bullae than *M. megacephalus*, should theoretically have more inherent buoyancy resulting in a greater mean swimming and floating time. As this is not the case, we suspect that an ethological factor, rather than a morphological factor, may account for the significantly greater mean test time for *M. megacephalus*.

If it could be hypothesized that a member of this genus were to (accidentally) enter a river at a point where it is 30 meters wide and swim towards the opposite bank at a maximum observed rate of approximately 150 millimeters per second, the river could be crossed within a period of some 200 seconds (within the observed ability of both species). As *Microdipodops* is a weak swimmer, and shows little oriented movement in water, perhaps it is more realistic to view the genus as a passive disperser in water, the direction of movement being determined more by water currents than goal oriented swimming. Nevertheless, in view of the lengthy floating periods we observed for *M. megacephalus*, this species should prove more successful than *M. pallidus* at crossing water barriers.

Specimens used in this study were taken from: *M. megacephalus*, 4 km. NE Larkin Lake, Alkali Valley, 34.5 km. S, 17 km. W Hawthorne, 2091 m., Mineral Co., Nevada; *M. pallidus*, 27.5 km. S, 8 km. E Yerington, 1524 m., Lyon Co., Nevada.

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