

Swimming ability of the Mediterranean pine vole *Microtus (Terricola) duodecimcostatus*

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We studied the swimming capacity of the fossorial rodent *Microtus (Terricola) duodecimcostatus* (de Selys-Longchamps, 1839), and found it to be a proficient swimmer in comparison with other fossorial species. We determined that main factor affecting swimming ability is the resistance of its hair to water absorption and its small body size. The hypothesis suggesting that insectivore moles are better swimmers than rodent mole is discussed. We find that body size, rather than the taxonomical group (insectivore or rodent), appears to be an important factor affecting swimming ability of fossorial species. The wide distribution of *M. (T.) duodecimcostatus* could be partly explained by its high swimming ability; rivers, therefore, may not be significant geographical barriers to its dispersal.

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Introduction

Rivers may act as a geographical barrier or, alternatively, as a dispersal pathway for terrestrial species distribution, depending mainly on the swimming ability of the species (Hickman and Machiné 1986). For this reason, the study of swimming ability and the corresponding adaptations of small mammals is of much interest. While the study of swimming in aquatic mammals is quite extensive (e.g. Howell 1930), terrestrial forms have received little attention until recent years (Hickman *et al.* 1983).

Fossorial mammals are characterized by poor climbing ability (Hickman 1982, 1983, Hickman *et al.* 1983) and low vagility (Nevo 1979, Vleck 1979, Hickman *et al.* 1983), therefore, rivers may act as dispersal pathways for them (Hickman 1983, 1988), or as barriers between different populations (Kennerly 1963, Savidge 1973, Smith and Patton 1980). For this reason, the study of the swimming ability of

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fossorial mammals is interesting and necessary for understanding their current distribution.

We will use the terms fossorial and/or subterranean in the sense of Contreras and McNab (1990): fossorial for species that usually live in closed burrows and that usually do not venture from their burrows further than their body length, and subterranean for the species that seldom come to the surface. Like Contreras and McNab (1990) have shown, it is difficult to apply these categories, because there is an almost continuous gradient of fossorial to subterranean, and therefore for simplification, in this study we will refer to both categories broadly as fossorial.

With regard to predicting the swimming ability, Hickman (1988) suggests that there are two general trends in subterranean mammals: (1) insectivore moles swim better than rodent moles, (2) smaller species of mole types swim longer than larger mole types. On the other hand, Wilber (1958) proposed a general thesis for rodents: when the logarithm of swimming time in minutes is plotted against the logarithm of body weight in grams, a straight line is obtained. Moreover, Hickman and Machiné (1986) found that six species of African rodents fit the general thesis suggested by Wilber. In order to test the above hypotheses, we describe the swimming ability of a small fossorial rodent, *Microtus (Terricola) duodecimcostatus* (de Sélys-Longchamps, 1839), and compare the results with the swimming ability of other subterranean mammals.

M. (T.) duodecimcostatus is a mole vole who builds complex burrows, throws the excavated dirt on top of the ground in the form of mounds (Vericad 1970, Soriguer and Amat 1980, Soriguer *et al.* 1984, Borghi 1992), and maintains their burrow systems closed. This rodent has a strong skull, adapted for the role of the head in burrowing (Agrawal 1967, Mathias 1990, 1991) and the use of incisors as a digging tool (Giannoni *et al.* 1992). *M. (T.) duodecimcostatus* is widely distributed throughout the Iberian Peninsula (Niethammer and Krapp 1982).

Material and methods

Nine adult females (none of them gravid) and five adult males of *Microtus (T.) duodecimcostatus* were captured in the Aisa valley, Spanish Pyrenees at 1690 m a.s.l. The animals were kept in individual cages with enough soil, natural light, an average temperature of 23°C, and an *ad libitum* diet of carrots and peanuts.

Observations were made in an all-glass aquarium of size 80 × 54 × 24 cm, with a water depth of 39 cm. The frontal glass was marked with a grid to measure swimming velocity during the first minutes of observation. No more than three observations were done for each animal. After each observation, the water was replaced. Observations lasted for 60 minutes as, in spite of the fact that in previous observations some animals had swum for two hours, an unnecessary prolongation of observation time could have caused unjustified cruelty to the animals.

A small perforated plastic box with a hinged lid was used to put the animal smoothly to the water, and also for removal if fatigue appeared. The water temperature was 25 ± 1°C, other experiments being done in cold water (15°C), and in water (at 25°C) with detergent acting as a wetting agent (1 cm³ of 30% industrial detergent in the aquarium). These water temperatures are within the range of the water temperatures in the wild (9°C, 2100 m a.s.l.; 27°C, 340 m a.s.l.; Vilchez-Quero and

Casas-Jimenez 1987). The quantity of water retained by hair was measured by weighing the animal before and after each test.

Observations were recorded on videotape. Measured variables were: total swimming time of each animal (including total time float) (TST), time during which hair was soaked completely (TS), total float time in each experiment (TFT), mean time of float period (MF), maximum float period in each experiment (MAF), quantity of water absorbed by hair during each experiment (WA), and body weight (BW). Time was recorded in minutes (TST, TS), and in seconds (TFT, MF, MAF); and body mass in grams. Statistical methods included are: descriptive statistics, Student's *t*-test, Kolmogorov-Smirnov's test, Kruskal Wallis Anova test, Dunn nonparametric multiple comparison test, Wilcoxon's matched-pairs signed-ranks test, Spearman rank-correlation coefficient, Pearson's correlation and multiple regression (Zar 1984, Siegel 1986).

Results

General swimming performance

When swimming, the body is kept in horizontal position with the back out of the water and the tail freely hanging. The mouth was below the water surface while the eyes, which remained open, and the nares were kept above the water surface. Swimming was done in the so called "dog paddle" style (Dagg and Windsor 1972), with an alternating movement of each pair of members: the foreleg in one side was moved together with the hindleg of the other side. The tail seem to play a part in maintaining balance when swimming. While turning, return movements were managed by the foreleg of the turning side, the other being less active. While turning, the tail was oriented to the other side, and therefore, perhaps served as an stabilizing device.

The median of total swimming time and time during which hair was wetted completely was 60 min. No significant differences between sexes were found (Kolmogorov-Smirnov's test, $p > 0.5$). Mean swimming speed was 23.8 cm/s, and therefore, the whole crossed distance, calculated by multiplying mean speed by mean time (Hickman and Machiné 1986), was 680 m.

When animals were tested for a second time, their total swimming time increased. Difference between first and second total swimming time was significant (one-tailed Wilcoxon's test, $p < 0.025$). On the other hand, there was no significant difference in the body weight between the first and second tests (Wilcoxon's test, $p = 0.938$).

Table 1 shows the result of Spearman's correlations. There is a positive correlation between total swimming time (TST) and float times (TFT, MAF and MF; see Table 1); and a significant negative correlation between the quantity of water absorbed by hair (WA) and total swimming time (TST). Multiple backward stepwise regressions were also calculated among variables. Total swimming time (TST) was the dependent variable, and only two variables, time during which hair was soaked completely (TS) and mean time of float period (MF), were statistically significant as predictors of TST, as shown in Table 2.

Table 1. Spearman rank-correlation coefficients between measured variables: TST – total swimming time including TFT (min), TS – time during which hair was soaked completely (min), WA – quantity of water absorbed by hair during each experiment (g), BW – body weight (g), TFT – total float time in each experiment (sec), MAF – maximum float period in each experiment (sec), and MF – mean time of float period (sec).

Variable	TST		TS		TFT	
	r_s	p	r_s	p	r_s	p
TST	–	–	0.9457	0.0000	0.5960	0.0002
TS	0.9457	0.0000	–	–	0.4944	0.0023
WA	–0.4874	0.0027	–0.4875	0.0027	–0.3766	0.0202
BW	–0.2620	0.1063	–0.1932	0.2336	–0.2341	0.1490
TFT	0.5961	0.0002	0.4944	0.0023	–	–
MAF	0.5216	0.0013	0.3900	0.0162	0.8452	0.0000
MF	0.4123	0.0110	0.2818	0.0824	0.7390	0.0000

Table 2. Results of the Multiple stepwise regressions among the variables; taking total swimming time (TST) as the dependent variable. Only two variables: time during which hair was soaked completely (TS), and mean time of float period (MF), were statistically significant as predictors of TST.

Independ variable	Coefficient	SD	t -value	p
Constant	10.95	2.46	4.44	0.0001
TS	0.79	0.04	16.63	0.0001
MF	2.27	1.02	2.22	0.0320

Floating

When floating, the animal remained generally motionless, with the body in horizontal position, the head somewhat raised and the legs hanging freely under the body. The tail seem to play a part in maintaining balance when floating. Sometimes, if the animal was tired, or the hair soaked, the position was different: the body was curved downwards, with the head and the tail ends raised, and the belly lowered. The legs stretched outwards, making an angle of 45 with the body axis; the tail was vertical, above the water, and the eyes were kept open. Mean time of float period was, on average, 2.47 min (SD = 2.13) for the males and 6.62 min (SD = 6.4) for the females. Difference between sexes in mean time of float period seems to be significant (t -test, $p = 0.016$); thus, females floated the 11.1% of the time spent in water, while males floated only the 5.2% of that time. There is a positive correlation between total float time (TFT) and total swimming time (TST) (Table 1).

Effects of temperature and detergent on swimming ability

The low water temperature and the addition of detergent to water changed the performance of the animals significantly. Table 3 shows that when water temperature was decreased to 15°C, total swimming time (TST), time during with hair was soaked completely (TS) and total float time (TFT) were significantly lower. When detergent was added, all the former variables were significantly lower, and the quantity of water absorbed by hair (WA) increased significantly.

Table 3. *M. (T.) duodecimcostatus* tested for swimming ability in water temperature at 15°C, 25°C, and at 25°C with detergent acting as a wetting agent. Kruskal Wallis ANOVA test to compare all the experiments, and the Dunn nonparametric multiple comparison test to compare water temperature at 25°C vs 15°C (25°-15°) and for water temperature at 25°C vs water with detergent (25°-D); ⁽¹⁾ except for TFT, MF and MAF where we used Kolmogorov-Smirnov test. * $p < 0.001$, ** $p < 0.0001$, ns - not significant. See Table 1 for symbol explanation.

Variable	25°C		15°C		Detergent		25°-15°	25°-D
	mean	SD	mean	SD	mean	SD	<i>p</i>	<i>p</i>
TST	49.39	20.81	10.13	2.33	1.47	0.85 **	0.005	0.0005
TS	46.26	25.15	9.55	3.12	0.03	0.02 **	0.025	0.0005
WA	1.50	0.98	1.64	0.49	4.11	1.50 *	ns	0.0005
BW	25.71	2.83	25.76	2.34	24.15	3.51 ns	-	-
TFT	313.90	334.05	24.82	26.12	-	-	0.001 ⁽¹⁾	-
MAF	13.33	19.30	4.22	3.50	-	-	ns ⁽¹⁾	-
MF	1.66	1.11	1.63	0.91	-	-	ns ⁽¹⁾	-

Insectivore vs rodent moles

To test the hypothesis of Hickman (1988), we compared the swimming time between the studied species of insectivore and rodent moles, and did not find

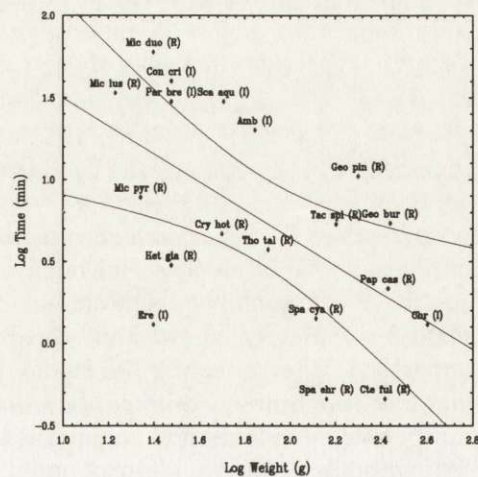


Fig. 1. Regression between body mass (log mean weight in grams) and swimming time (log mean swimming time in minutes), for insectivore moles and rodent moles. See Table 4 for species names. Person's correlation: $r = -0.591$, $p = 0.0077$, $n = 19$, $\text{Log Time} = 2.382 - 0.870 \times \text{Log Weight}$.

Table 4. Fossorial mammals tested for swimming ability, weight (g) and swimming time (min). There was no significant difference in the swimming time between insectivore moles and rodent moles (Kolmogorov-Smirnov test, $p > 0.05$).

Species	Weight	Time	Reference
<i>Insectivora</i>			
<i>Chrysoxalax</i> sp.	400	1.3	Hickman 1988
<i>Eremitalpa</i> sp.	25	1.3	"
<i>Amblysomus</i> sp.	70	20.1	"
<i>Scalopus aquaticus</i>	47	30.0	Hickman 1984
<i>Parascalops breweri</i>	30	30.0	"
<i>Condylura cristata</i>	30	40.0	Hickman 1988
<i>Rodentia</i>			
<i>Pappogeomys castanops</i>	270	2.2	Best and Hart 1976
<i>Geomys bursarius</i>	248	5.4	"
<i>Geomys pinetis</i>	200	10.5	"
<i>Thomomys talpoides</i>	80	4.0	Hickman 1988
<i>Tachyoryctes splendens</i>	160	5.3	Hickman 1983
<i>Spalax ehrenbergi</i>	145	0.5	Hickman <i>et al.</i> 1983
<i>Spalacopus cyanus</i>	130	1.4	Hickman 1988
<i>Ctenomys fulvus</i>	262	0.5	"
<i>Cryptomys hottentotus</i>	50	4.7	Hickman 1978
<i>Heterocephalus glaber</i>	30	3.0	Hickman 1983
<i>M. (T.) lusitanicus</i>	17	34.0	Giannoni <i>et al.</i> (1993)
<i>M. (T.) pyrenaicus</i>	22	7.8	Giannoni (1994)
<i>M. (T.) duodecimcostatus</i>	25	49.4	Present study

significant differences in the swimming time between them (see Table 4; Kolmogorov-Smirnov test, $p > 0.05$). On the other hand, Fig. 1 shows the regression between the logarithm of the swimming time in minutes and the logarithm of the body weight in grams of insectivore and rodent moles. There is a significant negative regression between these variables ($r = -0.63$, $p < 0.005$).

Discussion

Microtus (Terricola) duodecimcostatus could be considered a good swimmer compared with other fossorial mammals (Esher *et al.* 1978, Hickman 1988). The positive correlation between total swimming time and time during which hair was soaked completely, shows that the resistance of hair to water absorption is an important factor affecting the swimming ability (Stock 1972, Hickman 1988). For instance, the hair of litters of *Microtus oeconomus*, which are good swimmers, was rarely soaked (Frank and Zimmermann 1956). We also observed that in *M. duodecimcostatus*, when a wetting agent was added to water, both, the time during

which hair was soaked completely and total swimming time decreased significantly. This experience shows the importance of the fur in trapping air and contributing to the buoyancy of animals while swimming, as other authors have found (Best and Hart 1976, Hickman and Machiné 1986). Also, temperature affects the swimming ability of *Microtus (T.) duodecimcostatus*. On cold water, both total swimming time and total float time in each experiment decreased, and the animal movements became very slow after several minutes (locomotor ataxia). These results agree with those found by other authors, among them Wilber (1958), Hickman (1978), Carter and Merritt (1981) and Hickman and Machiné (1986).

With regard to the swimming performance between insectivore vs rodent moles, we did not find significant difference in the swimming time between them. We therefore do not agree with the hypothesis of Hickman (1988), who suggests that the insectivore moles, as a general rule, are better swimmers than rodent moles, and that none of the rodent moles were able to float. Our disagreement in hypothesis could be because most of the rodent species that were studied by Hickman were of large size, and the observations of Hickman could therefore be a consequence of the body size, rather than differences between groups. Within this framework, *Microtus (T.) duodecimcostatus*, *M. (T.) lusitanicus* and *M. (T.) pyrenaicus* could be examples of fossorial rodents of small size, who are able to float, and to swim for long time (see Table 4).

Additionally, the regression between the logarithm of the body weight and the logarithm of the swimming time of insectivore and rodent moles, suggests that weight is a variable of primary importance to swimming success. Insectivore and rodent moles would seem to fit the general thesis suggested by Wilber (1958) for rodents.

Because of the lack of basic information on swimming ability of fossorial mammals, it would seem necessary to extend the studies to include more species, small rodent moles as well as insectivore moles, and consider body size as an important variable in understanding the possible dichotomy in swimming performance between these groups.

Although the role of swimming ability in the geographical distribution of *Microtus (T.) duodecimcostatus* is entirely speculative, it could be expected that this species, which has a wide distribution, has a high probability of encountering a watercourse in its dispersal way. Therefore, as it is a good swimmer, the probability of crossing this watercourse satisfactorily is high. Hence, our results should suggest that rivers cannot be significant barriers for the Mediterranean pine vole.

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