



## Comparative measurements of terrestrial and aquatic locomotion in *Mustela lutreola* and *M. putorius*

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Through the evolutionary history of mammals, the transition to a semi-aquatic way of life led to different morphological adaptations and behavioural adjustments facilitating more particularly the locomotion in water (LESSERTISSEUR and SABAN 1967; ALEXANDER 1982; RENOUS 1994). However, the requirements of locomotory adaptation to an aquatic habitat directly affected terrestrial mobility (SCHMIDT-NIELSEN 1972; TARASOFF et al. 1972; RENOUS 1994).

Different studies on the American mink *Mustela vison* have stressed that the semi-aquatic way of life of this mustelid resulted from a compromise among these contradictory requirements (POOLE and DUNSTONE 1976; DUNSTONE 1978; KUBY 1982; WILLIAMS 1983 a). Ethological adaptations to the exploitation of water habitats allowed this species to adapt to an ecological niche between the Lutrinae and the more terrestrial weasels (BURT and GOSSENHEIDER 1952; HALL et al. 1959; HALLEY 1975; WILLIAMS 1983 a). In the Palearctic, two autochthonous mustelids, the European polecat *Mustela putorius* and the European mink *Mustela lutreola*, were intermittent to respective niches of typical terrestrial mustelids, such as the stoat *Mustela erminea* and more aquatic ones such as the otter *Lutra lutra* (BOURLIERE 1955; SAINT-GIRONS 1973; BROSSET 1974; GRZIMEK 1974). Although morphologically very similar, *Mustela lutreola* is a characteristic semi-aquatic animal, whereas *Mustela putorius* is to a greater extent considered to be a mainly terrestrial predator (SAINT-GIRONS 1973; STUBBE 1993; LODÉ 1997). Both mustelids frequent marshes and forest brooks (HEPTNER et al. 1974; DANILOV and RUSAKOV 1969; BLANDFORD 1987; PIKULIK and SIDOROVICH 1991; BRZEZINSKI et al. 1992) but the home-range of the European mink remains rather linear along water courses (PALAZON and RUIZ-OLMO 1993), whereas the activity area of the polecat is more strongly determined according to the surface (WEBER 1989; LODÉ 1993, 1994). One might reasonably suppose that the semi-aquatic way of life would have led to important behavioural modifications when compared to *Mustela putorius*. The aim of this study was to evaluate the locomotory abilities of these two species, mainly the mode of moving on ground and swimming in water.

The study took place in western France, in Sévérac and Chizé Zoorama in summer 1995 and concerned four *Mustela putorius* (two adult females, body weight 800 g and 850 g and two adult males, 1 450 g and 1 550 g) born in the laboratory, and one *Mustela lutreola* (adult female, body weight 700 g) which was live-trapped in a wooden-box trap in the southwest of France (D. P.N. authorisation 1995). Additionally, the author viewed a video on the locomotory behaviour of a *Mustela lutreola* male when it was released. The

other animals were individually kept in 10 to 16 m<sup>2</sup> large open-air enclosures provided with a pool, a converted shed, and a resting place under normal photoperiod conditions. Food and water were supplied ad libitum.

The aquatic locomotory behaviour of the female mink and a polecat couple was studied in an open-air pool (2.0×1.5×0.9 m) with a transparent side. The second polecat couple was observed in a smaller pool (1.9×1.0×0.75 m). The water temperature was 20 to 21 °C, the outdoor temperature 19° to 24 °C. Visual marks were set along the transparent sides of both pools every 10 cm for measurements. Swimming behaviour was video-recorded with additional light and linear movement was timed to measure the progression speed. The number of swimming strokes was counted. The degree of body inclination was measured in relation to the horizontal axis. ALEXANDER (1982) proposed the calculation of the ratio between the length and the largest diameter of the body providing an indicative value for the resistance degree of body in the water. Thus, the ratio of the larger diameter of the body to its length (tail not included) was calculated in order to account for the drag resulting from movements.

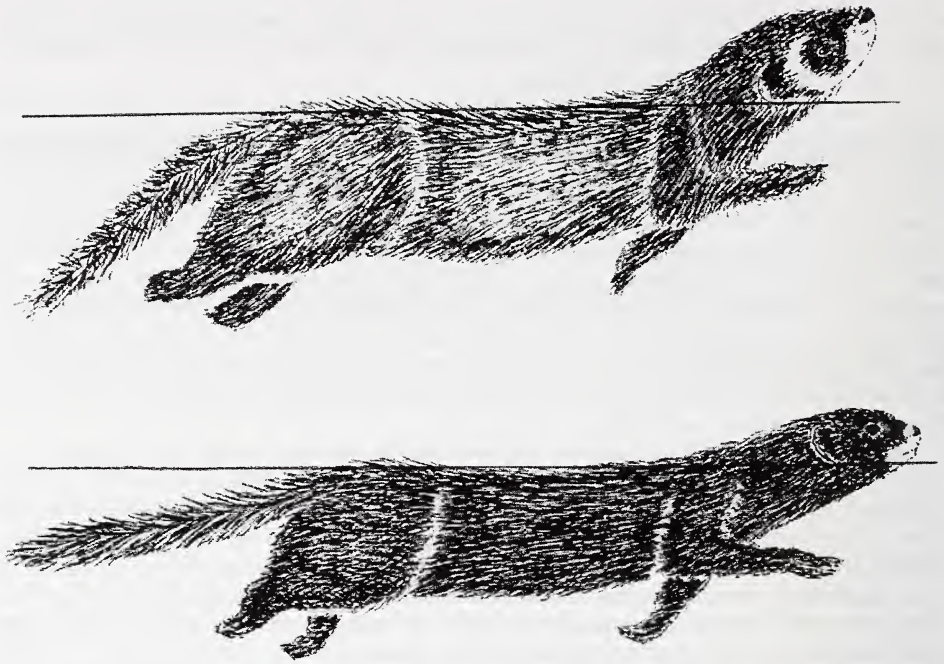
Concerning terrestrial locomotion, the mink and one polecat couple were studied in a 3.8×3.6 m outside enclosure. The second polecat couple was studied in another outside enclosure (3.9×1.5 m). Only linear trajectories, walking or jumping, were taken into account in this study. The sequences were video-recorded (8 mm film) and timed to differentiate between walk and bounds (WILLIAMS 1983 b).

A progressive discriminant analysis was performed (PCSM program, D<sup>2</sup> of Mahalanobis) to assure differences in locomotion between the two species. The degree of freedom (df) depended on the number of experiments carried out.

Terrestrial locomotion: Walking was done as slow speed by *M. lutreola* (0.60 m/s, sd = 0.06) as well as *M. putorius* (female 0.61 m/s, sd = 0.06, males 0.62 m/s, sd = 0.07). No differences resulted between the females of both species ( $t = 0.13$  df 34;  $p > 0.9$ ), between the males ( $t = 0.88$ , df 29,  $p > 0.5$ ), and also not between polecat males and females ( $t = 0.73$ , df 29,  $p > 0.5$ ). Increase in speed led to a moving mode of bounds with a speed of 1.21 m/s (sd 0.12) for *M. lutreola*, 1.21 m/s (sd 0.10) for *M. putorius* females, and 1.23 m/s (sd 0.13) for males. No significant difference resulted (*M. lutreola* versus *M. putorius* females  $t = 0.14$ , df 24,  $p > 0.9$ , males  $t = 0.46$ , df 21,  $p > 0.8$ , polecat females versus males  $t = 0.37$ , df 21,  $p > 0.7$ ).

Aquatic locomotion: The average swimming speed at the surface was 0.44 m/s (sd 0.03, n = 16) for *M. lutreola*, 0.42 m/s (sd 0.06, n = 16) for female polecats and 0.43 m/s (sd 0.04, n = 13) for males. The velocity did not differ between the females *M. lutreola* and *M. putorius* ( $t = 1.77$ , df 30,  $p > 0.08$ ) and males ( $t = 0.63$ , df 23,  $p > 0.6$ ), as well as male and female polecats ( $t = 0.89$ , df 18,  $p > 0.4$ ). The four limbs were used alternatively during the propulsion although the hind limbs moved at a slower average rhythm (*M. lutreola* 2.70 strokes per sec. sd 0.26, female *M. putorius* 2.74 st/s sd 0.11, males *M. putorius* 2.81 st/s sd 0.12) with no significant differences (*M. lutreola* versus *M. putorius*,  $t = 0.51$ , df 20,  $p > 0.4$ ; *M. lutreola* versus male *M. putorius*  $t = 0.97$ , df 15  $p > 0.3$ ; female versus male *M. putorius*  $t = 1.06$ , df 15,  $p > 0.3$ ). The average rhythm of the forelimb movements was 3.50 st/s (sd 0.284) in *M. lutreola*, 3.64 st/s (sd 0.28) in *M. putorius* females and 3.80 st/s (sd 0.14) in *M. putorius* males. Also here, no significant differences occurred (*M. lutreola* versus *M. putorius* females  $t = 1.23$ , df = 27,  $p > 0.2$ ; *M. lutreola* versus *M. putorius* males  $t = 1.96$ , df 17,  $p > 0.8$ , females versus males *M. putorius*  $t = 0.97$ , df 18,  $p > 0.3$ ; Fig. 1).

The speed of motion was clearly correlated with the mean number of forelimb movements in both species (*M. lutreola*  $r = 0.650$ , df 12,  $p < 0.012$ ; female *M. putorius*  $r = 0.602$ ,  $p < 0.018$ , Fig. 2), whereas no correlation was ascertained between speed and the rhythm of hind limbs (*M. lutreola*  $r = 0.520$ ,  $p > 0.5$ ; *M. putorius* females  $r = 0.219$ ,  $p > 0.5$ ; *M. putorius*  $r = 0.433$ ,  $p > 0.5$ ). Most probably the propulsion is mainly dependent on fore-



**Fig. 1.** The aquatic locomotory sequence: body inclination during swimming in *Mustela putorius* (top) and in *Mustela lutreola* (bottom).

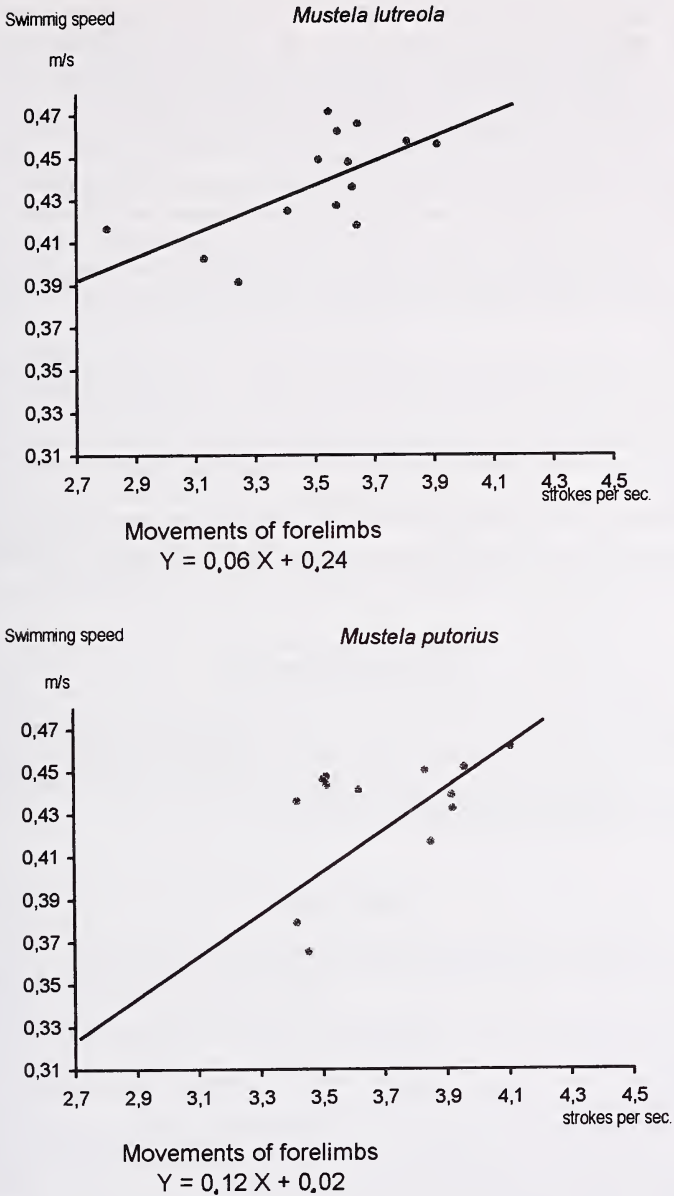
limb movements. However, it was also interesting to note that in spite of a slower rhythm of forelimb movements during swimming, *M. lutreola* moved quicker than *M. putorius*. Thus, including “rhythm of forelimbs” as a co-variant, the variance analysis revealed a significant difference of velocity between *M. lutreola* and *M. putorius* females ( $F = 6.84$ ,  $df\ 1,26$ ,  $p < 0.02$ ; parallelism difference  $F = 2.51$ ,  $p > 0.5$ ).

During swimming, the body position showed a mean inclination angle of  $7^{\circ}2'$  (sd  $2^{\circ}8'$ , range =  $2^{\circ}5' - 12^{\circ}1'$ ) for *M. lutreola*. This was significantly smaller ( $t = 4.33$ ,  $df\ 28$ ,  $p < 0.001$ ) compared with *M. putorius* females (average  $12^{\circ}0'$ , sd  $3^{\circ}6'$ , range  $6^{\circ}3' - 18^{\circ}6'$ ) or versus *M. putorius* males ( $t = 3.59$ ,  $df\ 19$ ,  $p < 0.002$ ; average  $12^{\circ}1'$ , sd  $2^{\circ}2'$ , range  $8^{\circ}9' - 15^{\circ}7'$ ). Concerning this degree of inclination, however, no difference occurred between females and males of *M. putorius* ( $t = 0.04$ ,  $df\ 17$ ,  $p > 0.05$ ). The diameter to length ratio of the body was 0.11 in *M. lutreola*, 0.12 in *M. putorius* females and 0.12 in males. In both species, the head and body dorsum remained above water.

A further progressive discriminant analysis revealed that only the degree of inclination (Mahalanobis  $D^2 = 2.12$ , 100% increase,  $p < 0.001$ ) contributed to distinguish significantly between the locomotory behaviours of both species. Swimming speed differed to a lesser extent ( $D^2 = 2.54$ , 19.9% increase,  $p < 0.002$ ), walk ( $D^2 = 2.63$ , 3.7% increase,  $p > 0.05$ ) and bounds ( $D^2 = 2.64$ , 0.4% increase,  $p > 0.05$ ) not at all.

European mink and polecat differed only in their body position in the water, the mink showing a smaller degree of inclination. Terrestrial mammals often stand vertically in the water (LESSERTISSEUR and SABAN 1967). FISH (1993) noted also that the swimming behaviour was associated with a smaller inclination angle for the aquatic opossum *Chironectes* compared with terrestrial species. The quality of the fur improved floating (JOHANSEN 1962; LING 1970; DAGG and WINDSOR 1972) and the fur density in American mink was  $780\text{ cm}^2$  (KUBY 1982). In *Mustela lutreola*, fur density reached about  $600/\text{cm}^2$  and





**Fig. 2.** Linear regression of swimming speed and mean number of forelimb movements in *Mustela lutreola* and *Mustela putorius*.

guard hair length averaged 23 mm, whereas fur density was only 300/cm<sup>2</sup> in polecat and guard hair length was up to 35 mm.

The European mink did not show ethological adaptations which were characteristic of species living in water habitat. Thus, the bipedal propulsion increased considerably the moving speed, and characterised the specialisation to the liquid element (TARASOFF et al. 1972; FISH 1984, 1993; HILDEBRAND 1989; RENOUS 1994). Furthermore, in the otter, the

undulations of the body perceptibly ameliorated moving speed (TARASOFF et al. 1972; CHANIN 1985). In European mink and polecat, the aquatic locomotion was of a typical paraaxial mode and the propulsion was made by oscillatory movements in which the four limbs alternated. This pectoropelvic paddling was also noted in terrestrial carnivores (ALEXANDER 1982; BRAUN and REIF 1985; RENOUS 1994). Swimming employing four limbs considerably affected the propulsion (TARASOFF et al. 1972; FISH 1984, 1993) and functioned at high metabolic cost (WILLIAMS 1983 a). The American mink showed a more efficient swimming behavior (from 0.46 m/s to 0.70 m/s, POOLE and DUNSTONE 1976; DUNSTONE 1978; WILLIAMS 1983 a). KUBY (1982) observed that *Mustela vison* swam mainly with an alternating movement of forelimbs, only occasionally using the hind limbs, KRUSKA and KUBY (pers. comm.) noted that forelimbs were used about twice as fast compared with hindlimbs.

In mustelids, walk consisted of a symmetrical gait in which the forelimb took off after the hindlimb from the same body side (GOETHE 1964). Terrestrial mobility did not differ between European mink and polecat and the speed increase was associated with an adaptation of the locomotory behaviour, namely bounds (GOETHE 1964; WILLIAMS 1983 b). The slow walk constituted the characteristic gait of the foraging behaviour in polecat (WEBER 1989; LODÉ 1993, 1994) and this type of locomotion mainly improved the olfactory search for food (WÜSTEHUBE 1960; WEBER 1989). In fact, the locomotory behaviour of the European mink differed very slightly from the polecat and consequently, could only partially reply to the constraints imposed by the exploitation of freshwater habitat.

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