

Locomotor Activity of Terrestrial Predators and Its Consequences

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Goszczyński J., 1986: Locomotor activity of terrestrial predators and its consequences. *Acta theriol.*, 31, 6: 79—95 [With 4 Tables & 1 Fig.]

The relations between body mass (M) and daily movement distance (DMD), daily food consumption (DFC) and home range size (HR) were examined in three families of *Carnivora*. The relative locomotion costs of these animals and intensity of penetration of their home ranges were estimated, and it was shown that during the course of 24 hours *Mustelidae* cover greater distances than *Canidae* and *Felidae* possessing the same body mass. In the case of the largest representatives of the families examined relative locomotion costs may be as much as 30—40% of their DFC . In all the families studied intensity of movement over the home range decreases together with increase in body mass. The energetic advantages of movement do not depend on body mass in the case of *Mustelidae*, whereas *Canidae* and *Felidae* increase advantage with increase in body mass.

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1. INTRODUCTION

Increased interest has been manifested in recent years in problems of utilization of space by animals, particularly the relations between body mass and home range size (McNab, 1963; Schoener, 1968; Harestad & Bunnell, 1979; Gittleman & Harvey, 1982). Little attention has been paid to comparative analysis of daily movements, the successive records of which make up the animal's home range. Garland (1983) was the first to point out the relation between the animal's body mass and its daily movement distance, describing from this aspect 76 species of mammals. His paper also contains a large number of important findings on the ecological cost of mammals' transport. Although he also took predators into consideration, the number of their species (13) discussed is too small to make it possible to arrive at any general conclusions.

In the present study the problem of locomotion has been dealt with in greater detail, but is limited to the order of *Carnivora* only. It appeared desirable to analyze the activity of predators for the following reasons: (1) The different families of *Carnivora* differ as to hunting strategy and therefore analysis of distance of movement could supply infor-

mation as to the effectiveness of hunting and locomotion costs of animals belonging to these families, (2) a knowledge of the relation between body mass and daily movement distance would make it possible to grasp differences in intensity of movement over a given area by both large and small animals, the degree of overlapping of home ranges and possibilities of variations in activity.

2. METHODS

Data in literature were collected on daily movement distance (*DMD*), daily food consumption (*DFC*) and home range (*HR*) of various European, Asiatic (from Soviet Union territory) and North American predatory species (Table 1). In one

Table 1

Relation between body mass (*M*) and: daily movement distance (*DMD*), home range size (*HR*) and daily food consumption (*DFC*). Numbers in brackets indicate successive papers in references.

Species analyzed	M, kg	DMD, km/day	HR, km ²	DFC, kJ/animal ¹
<i>Mustelidae</i>				
<i>Mustela nivalis</i>	0.075 (3, 46, 122) ²	1.1 (72, 83, 112)	0.07 (24, 46, 59, 70, 72, 77, 83, 112)	199 (122)
<i>Mustela frenata</i>	0.165 (39)		1.1 (94, 95)	365 (13)
<i>Mustela erminea</i>	0.182 (25, 49, 111, 122)	2.8 (4, 74, 112)	0.6 (4, 25, 72, 74, 112)	434 (122)
<i>Mustela altaica</i>	0.261 (122)	1.5 (112)		581 (122)
<i>Mustela sibirica</i>	0.566 (55, 122)	5.0 (42, 74, 112, 122)	2.2 (42, 74, 112, 122)	700 (9)
<i>Mustela eversmanni</i>	0.855 (1, 122)	6.7 (1, 112, 122)	3.0 (112)	859 (107)
<i>Mustela putorius</i>	1.000 (3, 21, 89, 122)	4.8 (21, 112)	7.3 (1, 21)	971 (107)
<i>Martes americana</i>	1.043 (39)	4.8 (41, 62)	9.0 (28, 41, 62, 68, 69, 117)	
<i>Martes zibellina</i>	1.068 (73)	6.4 (42, 73, 88, 112)	9.7 (42, 73, 112)	945 (42)
<i>Martes martes</i>	1.142 (80, 89)	7.2 (34, 50, 73, 78, 91, 112)	13.5 (34, 50, 73, 91, 112)	1050 (92)
Hybrid <i>M. martes</i> × <i>M. zibellina</i>	1.100	7.6 (73)		
<i>Martes foina</i>	1.462 (1, 42)	6.4 (42, 58, 125)	5.2 (42, 58)	1309 (73)
<i>Martes pennanti</i>	2.640 (86)	9.7 (86)		
<i>Martes pennanti</i>	3.459 (39)		203.4 (23)	
<i>Martes flavigula</i>	3.473 (73)	14.4 (73)	250.0 (73)	
<i>Gulo gulo</i>	14.800 (42)	25.3 (37, 96, 112)	1007.0 (42, 54, 71, 96, 112)	5775 (42)

Species analyzed	M, kg	DMD, km/day	HR, km ²	DFC, kJ/animal ¹
<i>Canidae</i>				
<i>Vulpes corsac</i>	2.60 (42)		1.8 (42)	1610 (42)
<i>Alopex lagopus</i>	3.50 (22, 42, 44)		17.5 (22, 42, 44, 60, 113)	2380 (108)
<i>Urocyon cinereo-argenteus</i>	4.70 (51)		4.7 (40, 124)	
<i>Vulpes fulva</i>	5.40 (39)		4.1 (106)	
<i>Nyctereutes procyonoides</i>	5.90 (22)	8.9 (22)	6.5 (22)	2870 (22)
<i>Vulpes vulpes</i>	6.10 (22, 29, 61)	9.1 (22, 42, 88)	9.7 (22, 42, 44, 57)	3465 (101, 104)
<i>Canis aureus</i>	9.50 (42)	12.0 (42)	15.5 (42)	
<i>Canis latrans</i>	16.00 (30)	16.0 (16)	66.0 (11, 79, 114)	4763 (27)
<i>Canis lupus</i>	37.00 (22, 42, 39)	25.7 (15, 22, 42, 47, 66, 81, 82, 93)	217.0 (5, 18, 22, 42, 48, 65, 67, 82, 115, 116, 123)	14000 (42)
<i>Felidae</i>				
<i>Felis margarita</i>	2.70 (43)	3.2 (43)		1750 (43)
<i>Felis libyca</i>	3.30 (43)		4.3 (43)	2800 (43)
<i>Felis manul</i>	3.50 (43)		1.8 (43)	
<i>Felis catus</i>	3.80 (3)		4.0 (56)	2450 (3)
<i>Felis euphilura</i>	4.80 (43)	3.3 (43)	9.0 (43)	
<i>Felis silvestris</i>	5.60 (43)			2697 (43)
<i>Felis chaus</i>	6.60 (43)	4.8 (43)		
<i>Lynx rufus</i>	9.10 (39)	7.0 (35, 85, 99)	17.8 (38, 87, 99)	5256 (33)
<i>Lynx canadensis</i>	11.60 (39)	6.8 (102, 112)	26.3 (7, 12, 75, 102)	5225 (12)
<i>Lynx lynx</i>	18.00 (22, 37, 63, 76)	10.2 (22, 37, 76, 88, 118)	71.0 (22, 36, 37, 53)	8312 (22)
<i>Panthera uncia</i>	41.00 (43, 84)		138.0 (84)	15400 (43)
<i>Panthera pardus</i>	46.00 (43, 110)	17.5 (2)	171.0 (2, 43, 110)	17500 (110)
<i>Felis concolor</i>	67.00 (39)	20.0 (109, 127)	170.0 (14, 98, 109)	19051 (97)
<i>Panthera leo</i> ♀	120.00 (8)			35000 (103)
<i>Panthera tigris</i>	230.00 (43)	35.0 (43)	783.0 (43, 119, 126)	57538 (119)

¹ In cases when DFC has been given in grams of meat consumed, this value has been multiplied by 7 (mean energetic value of 1 g of the prey's tissue in kJ, after Ryszkowski 1982).

² Use has also been made of the author's own estimates (Goszczyński, unpublished).

case data from outside the above regions (Africa) were used. The analysis was limited to three families: *Mustelidae*, *Canidae* and *Felidae*, most numerous represented in the above mentioned areas. The following representatives of *Mustelidae* from aquatic habitats have, however, been omitted: *Mustela lutreola*, *Mustela vison*, *Lutra lutra* and *Enhydra lutris*. These species differ from other representatives of their family by their different way of locomotion, utilization of space and composition of their food (Gerell, 1970; Chanin, 1972; Jenkins, 1980; Erlinge & Jensen, 1981; Birks & Linn, 1982).

Information on *DMD* originating from the Soviet Union, although the most abundant in the world (the Russians use such data for estimating supplies of fur-bearing animals), is almost unknown outside the boundaries of that country. Its inclusion adds considerably to the initial material for the present study. *DMD* was estimated almost solely on the basis of winter tracking and as implied by the term, means the distance covered by a given animal over the course of 24 hours. *DMD* as reported by a given author was taken as a unit, regardless of the number of movements investigated. The *DMD* value used for analysis is thus the mean value of estimates given by different authors for the given species. In the case of *DFC* use was made of data from long-term feeding experiments carried out in enclosures or in zoological gardens. *DFC* illustrates the average amount of food consumed during a 24-hour period. *HR* value was estimated primarily by means of winter tracking, radiotelemetry and less often, trapping.

In order to define the relation between body mass (*M*) and *DMD*, *DFC* and *HR* values, linear regressions were calculated for double-logarithmically transformed data within the various families. For the exponents of different equations a $\pm 95\%$ confidence interval has been calculated.

The incremental cost of locomotion (*ICL*) expressed in units of energy used to cover a unit of distance is independent of the speed with which the animal covered the route (Taylor, 1980 a). Taylor (1980 b) gives the following equation defining the locomotion costs of mammals (with body mass from 0.01 to 260 kg):

$$ICL (kJ/km) = 10.678 M^{0.70} \quad (1)$$

in which *M* — body mass in kg. Relative cost of locomotion (*RCL*) was defined in this paper as the ratio of energy expenditure by the animal on daily locomotion to the amount of daily food consumption. This equation is a slight modification of the equation given by Garland (1983), who instead of *DFC* used *DEE* (daily energy expenditure):

$$RCL (\%) = \frac{ICL (kJ/km) \cdot DMD (km/day)}{DFC (kJ/day)} \cdot 100 \quad (2)$$

The ratio of *DFC* to *DMD* may be defined as energetic advantage (*EA*) of the animal covering a unit of distance of its route:

$$EA (kJ/km) = \frac{DFC (kJ/day)}{DMD (km/day)} \quad (3)$$

On the other hand the ratio of *DMD* to *HR* was taken as a measure of intensity of movement (penetration) over a unit of home range (*IP*):

$$IP \text{ (km/km}^2 \text{ day)} = \frac{DMD \text{ (km/day)}}{HR \text{ (km}^2\text{)}} \quad (4)$$

IP is therefore expressed in km of route covered by an animal within 1 km² of *HR*.

EA and *IP* for different families of *Carnivora* may be calculated directly by relating the appropriate values *DMD*, *HR* and *DFC* characteristic of the given species to equations (3) and (4). This results in calculating regression *EA* and *IP* to *M* within the given family. As this method requires the full set of parameters (*M*, *DMD*, *HR* and *DFC*) for each species this greatly reduces sample size. Another way consists in defining the relation between *M* and other parameters: *DMD*, *HR* and *DFC*, within the given predator families and relating the equations obtained to equations (3) and (4). In this second case, although we have a greater amount of data, such procedure makes it necessary to accept the assumption that variances for the different variables round regression lines are independent.

Both these ways of calculating *EA* and *IP* have been given parallel presentation in this paper.

List of abbreviations used:

- M* — body mass (kg)
DMD — daily movement distance (km/day)
DFC — daily food consumption (kJ/day)
HR — home range (km²)
RCL — relative cost of locomotion (%)
EA — energetic advantage of locomotion (kJ/km)
IP — intensity of penetration of *HR* (km/km²).

3. DAILY MOVEMENT DISTANCE, RELATIVE COST OF LOCOMOTION AND ENERGETIC ADVANTAGE OF LOCOMOTION

In the regressions calculated for different families, describing the relation of *DMD* to *M*, the exponent was approximately 0.60 (Table 2).

Table 2

Least squares linear regression of log₁₀ transformed *DMD*, *DFC* and *HR* versus body mass (data from Table 1).

Data set	Linear regression estimate of <i>DMD</i> , <i>DFC</i> and <i>HR</i> = $a(\text{mass})^b$				
	<i>a</i>	<i>b</i> ± 95% C.I.	<i>r</i> ²	<i>n</i>	
<i>Mustelidae</i>	<i>DMD</i>	5.758	0.60 ± 0.11	0.92	14
	<i>DFC</i>	1037	0.60 ± 0.06	0.98	11
	<i>HR</i>	9.381	1.79 ± 0.33	0.93	13
<i>Canidae</i>	<i>DMD</i>	3.227	0.58 ± 0.02	0.99	5
	<i>DFC</i>	835	0.73 ± 0.24	0.95	6
	<i>HR</i>	0.500	1.65 ± 0.69	0.82	9
	<i>HR</i> ¹	0.247	1.90 ± 0.29	0.99	8
<i>Felidae</i>	<i>DMD</i>	1.693	0.58 ± 0.08	0.98	9
	<i>DFC</i>	890	0.76 ± 0.06	0.99	12
	<i>HR</i>	0.810	1.34 ± 0.22	0.96	11

¹ Excluding *Alopex*.

Analysis of the covariance shows that regressions for the three families under consideration differ from each other and it is therefore impossible in this case to apply one equation with a common slope b ($t=55.4$, $p<0.001$). *Mustelidae* thus move over greater distances than *Canidae* and *Felidae* with the same body mass (Fig. 1).

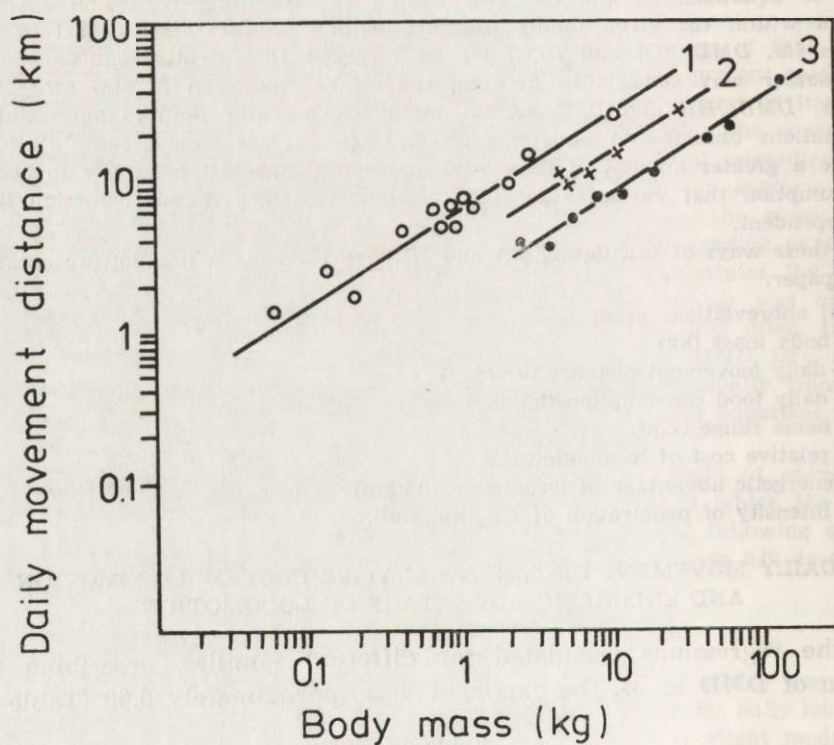


Fig. 1. Relation between body mass (M) and daily movement distance (DMD) for three families of *Carnivora*.

1 — *Mustelidae*, 2 — *Canidae*, 3 — *Felidae*.

The following equations for RCL were obtained for the three families (*Mustelidae* — M ., *Canidae* — C ., *Felidae* — F .) on the basis of regression equations from Table 2 and equation (2):

$$RCL_M = 5.930 M^{0.70}$$

$$RCL_C = 4.127 M^{0.55}$$

$$RCL_F = 2.013 M^{0.52}$$

Although the largest representatives of the three families considered differ greatly in respect of body mass (wolverine about 15 kg, wolf about 40 kg and tiger about 230 kg) the costs they have to bear are similar and form about 30–40% *DFC*. A similar boundary is thus reached by animals differing in size, representing different intensity of locomotion.

EA, that is, advantage expressed by the number of energy units obtained during movement of a distance of one kilometer, is the lowest in the case of *Mustelidae*, intermediate in *Canidae* and highest in *Felidae* (Table 3). The equations obtained, regardless of whether they were cal-

Table 3

Least squares regression analyses of \log_{10} transformed energetic advantage versus body mass data. Respective values *a* and *b* obtained from relating equations from Table 2 to equation (3) are given in brackets.

Data set	Linear regression estimate of $EA = a(\text{mass})^b$			
	<i>a</i>	<i>b</i> ± 95% C.I.	<i>r</i> ²	<i>n</i>
<i>Mustelidae</i>	182.2 (180.0)	0.00 ± 0.19 (0.00)	0.00	10
<i>Canidae</i>	231.2 (259.0)	0.19 ± 0.50 (0.15)	0.41	4
<i>Felidae</i>	434.1 (526.0)	0.22 ± 0.07 ¹ (0.18)	0.94	7
<i>Canidae</i> + <i>Felidae</i>	276.3	0.29 ± 0.22 ¹	0.51	11

¹ Slope (*b*) significant at $p < 0.05$.

culated on the basis of unprocessed data (from Table 1), are characterized by similar coefficients *a* and *b* (Table 3). *EA* in the case of *Mustelidae* is independent of the animal's size, and in the case of *Felidae* and *Canidae* treated jointly, advantage increases with increase in body mass (Table 3).

4. INTENSITY OF PENETRATION OF THE HOME RANGE BY PREDATORS

The value of the exponent in relations *HR* versus *M* exceeds the value of the exponent of equations for the relation *DMD* versus *M* (cf. Table 2), which means that the value of *HR* increases more rapidly than *DMD* with increase in body mass. Intensity of penetration of *HR* thus decreases with increase in the predator's size and this decrease is observed within all the three families considered (Table 4). *Canidae* penetrate their *HR* most intensively ($F = 27.5$, $p < 0.001$).

5. DISCUSSION

Mustelidae are characterized by the greatest length of *DMD*. Over a 24-hour period they cover a far greater distance than *Canidae* and *Felidae* with the same body mass. This is in itself astonishing, since representatives of *Canidae* have so far been considered as typical "runners".

This is probably connected with the hunting methods used by predators belonging to the particular families. *Mustelidae* actively search over an area, hunting singly for prey which they catch in burrows, nests or sheltering places. This type of hunting necessitates covering con-

Table 4

Least squares regression analyses of \log_{10} transformed intensity of penetration of HR versus body mass data. Respective values a and b obtained from relating equations from Table 2 to equation (4) are given in brackets.

Data set	Linear regression estimate of $IP=a(\text{mass})^b$			
	a	$b \pm 95\% \text{ C.I.}$	r^2	n
<i>Mustelidae</i>	0.740 (0.614)	-1.25 \pm 0.31 (-1.19)	0.90	11
<i>Canidae</i>	11.760 (13.065)	-1.30 \pm 0.52 (-1.17)	0.95	5
<i>Felidae</i>	2.514 (2.090)	-0.80 \pm 0.37 (-0.76)	0.86	6

siderable distances and has low productivity from the energy aspect. Although some representatives of this family use other hunting methods (e.g. *Martes flavigula* sometimes hunts in groups of several individuals (Hepther & Naumov, 1967) and *Martes pennanti* may specialize in catching specific prey (Powell, 1980), these are somewhat exceptional. It may be that their lack of speed, although compensated for by their agility, does not permit of their applying a more varied range of hunting techniques.

Canidae, although also hunting for prey in burrows and nests, in addition makes considerable use of chasing. *Felidae*, on the other hand, have specialized in hunting by stealth, in hunting by driving their prey to a desired spot, in stalking etc. (Curio, 1976). In the case of *Canidae* (Bekoff et al., 1981) and also *Felidae*, the size of the group increases with increase in body mass, thus increasing the possibilities of group hunting which may prove more productive. This probably provides the explanation of increase in energetic advantage of locomotion observed in representatives of these two groups. Specific habitat conditions, making stealthy approach to potential prey possible, and high density of

prey in *HR* may also play some part, particularly in the case of large representatives of *Felidae* leading a solitary way of life.

Analyses of data in literature on *DMD* shows that some of the most important factors affecting diversity of movement are:

1. Food supply in the given area. The importance of this factor is particularly strongly emphasized by Soviet authors (Heptner & Naumov, 1967; Nasimovič, 1973; and others) who have shown that length of movements greatly increases with lesser accessibility of prey.

2. Differences in body mass in males and females, particularly distinct among *Mustelidae* and *Felidae*. The distance covered by females, which are characterized by lesser body mass, is usually shorter than that of males (cf. Pulliainen, 1980 a).

3. Weather conditions. For example, reduction in daily distance covered by stoats was observed after snowfall or thaw (Nasimovič, 1977). There are also cases of reduction in *DMD* during periods of severe frosts (Kraft, 1966).

Analysis of data in literature also shows that *DMD* varies to a lesser degree than *HR*. Values of the coefficient of variation for *DMD* and *HR* (only those papers in which these two parameters were estimated simultaneously have been used for calculations) are for example:

<i>Mustela erminea</i>	$C.V._{DMD} = 49^0/0$,	$C.V._{HR} = 104^0/0$
<i>Martes martes</i>	$C.V._{DMD} = 31^0/0$,	$C.V._{HR} = 84^0/0$
<i>Martes zibellina</i>	$C.V._{DMD} = 35^0/0$,	$C.V._{HR} = 88^0/0$
<i>Gulo gulo</i>	$C.V._{DMD} = 17^0/0$,	$C.V._{HR} = 109^0/0$

It would therefore appear that *DMD* may be widely used for estimating density of predators everywhere where weather conditions make this possible. At the present time this method is not used except in the Soviet Union (e.g. Priklonski, 1965) and Scandinavia (Pulliainen, 1979). Radiotelemetric techniques may, however, be currently employed in order to obtain a very accurate definition of *DMD* and its variations. This is possible by means of increasing the number of the animal's locations, application of automatic recording or by comparison of successive radiolocations with the route covered by the animals in the field, as Powell (1980) has done.

Analyses of relations between the predator's body mass and home range size shows that the exponent b in the equation $HR = a M^b$ is far higher than $b = 0.75$ suggested by McNab (1963) and close to $b = 1.36$ given in the paper by Harestad & Bunnell (1979). *HR* reflects the accessibility of prey to predators in the habitat and would also appear to reflect the effectiveness of the predator's hunting activity. With increase

in body mass predators change the composition of their food from small to larger prey which, however, is far more scattered, more active and less productive than small prey. The mean values of *HR* for the same or similar Eurasian and North American species (Harestad & Bunnell, 1979) are similar (wolf: 231 km² and 203 km² respectively; *Martes flavigula* — 250 km², *Martes pennanti* — 203 km²). Greater divergences may be caused primarily by differences in accessibility of food which, as shown by Gittleman & Harvey (1982), may exert a very strong influence on the size of the *HR* exploited.

Analysis of the way in which hunting grounds are used by predatory mammals shows that larger species penetrate their territory less intensively. Large species thus have lower probability of directly or indirectly recording their presence (by marking with urine, faeces or olfactory substances) and protecting the boundaries of their territory. It is therefore to be expected that in the case of large predators home ranges overlap to a great extent. Data in literature on *Mustelidae* provide confirmation of this assumption, that small predators, e.g. weasels (Lockie, 1966), stoats (Erlinge, 1977) are more territorial than larger species, e.g. martens (Pulliainen, 1980 a).

The majority of the species within the families under consideration are characterized by small body dimensions, animals exceeding 5 kg body mass among *Mustelidae* forming exceptions (Heptner & Naumov, 1967; Cowan & Guignet, 1978), 15 kg among *Canidae* (Heptner & Naumov, 1967) and 100 kg among *Felidae* (Heptner & Naumov, 1972). The majority of the species are thus distinguished by locomotion costs below 15–20% of *DFC*. It must be emphasized that *RCL* is a measure of the costs borne not only in localizing and obtaining food, and thus typical hunting activity, but also costs borne in marking territory and sometimes in certain forms of sexual activity. The fact deserves mention that large representatives of the above families have similar *RCL*, which may mean that there is an upper limit to worthwhile costs of locomotion.

In view of the relatively low energy losses involved in locomotion by small predators it is probable that they may exhibit considerable variations in *DMD* in comparison with large species. The *C.V.* values given above for *Mustelidae* are actually greater in the case of small animals. On the other hand small *Carnivora* may experience proportionately greater losses of energy during their movements over snow than large predators. In addition to energy losses connected with locomotion, small predators (chiefly *Mustelidae* and *Canidae*) lose a large amount of energy in the actual process of obtaining food. This kind of hunting activity (digging through snow, digging out the nests of rodents, etc. is very

costly from the energy aspect (Segal *et al.*, 1976) and consequently may reduce their potentially great activity.

Acknowledgements: The author wishes to express his gratitude to Doc. dr hab. Joanna Gliwicz for her assistance with English terminology, and also to the anonymous reviewers for their valued comments on the typescript of this paper.

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Accepted, September 5, 1985.

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LOKOMOTORYCZNA AKTYWNOŚĆ LĄDOWYCH DRAPIEŻNYCH
I JEJ KONSEKWENCJE

Streszczenie

Analizowano zależności między masą ciała zwierzęcia (M) a: długością dobowej wędrówki (DMD), wielkością areалу (HR) i dobową konsumpcją pokarmu (DFC) w obrębie trzech rodzin z rzędu *Carnivora* (Tabela 1). Analiza dotyczyła gatunków euroazjatyckich i północnoamerykańskich.

Stwierdzono, że lasicowate w ciągu doby przemieszczają się na większe odległości niż psowate i kotowate o tej samej masie ciała (Tabela 2 i Ryc. 1).

Względne koszty lokomocji zwierzęcia wyliczono wg wzoru:

$$RCL (\%) = \frac{DMD \cdot 10,678 \cdot M^{0,70}}{DFC} \times 100$$

Koszty te wzrastają ze wzrostem masy ciała zwierzęcia. Potwierdza to wcześniejsze ustalenia Garlanda (1983). W przypadku największych przedstawicieli analizowanych rodzin koszty lokomocji stanowią 30–40% ich DFC .

Zyski energetyczne zwierzęcia (EA) mierzone stosunkiem DFC do DMD są w przypadku *Mustelidae* niezależne od masy ciała, natomiast *Felidae* i *Canidae* zwiększają zysk ze wzrostem masy ciała (Tabela 3).

Intensywność penetracji (IP) własnego areалу (stosunek DMD do HR) spada ze wzrostem wielkości drapieżnika (Tabela 4). Wśród analizowanych rodzin najsilniej penetrują swój areal psowate (Tabela 4).

Wykazano, że DMD jest mniej zmienna niż HR . Omówiono konsekwencje różnicowania RCL i IP w przypadku dużych i małych drapieżnych.