

Trophic Impact of Mammals in Terrestrial Ecosystems

Lech RYSZKOWSKI & Norman R. FRENCH

Ryszkowski L. & Fench N. R., 1982: Trophic impact of mammals in terrestrial ecosystems. Acta theriol., 27, 1: 3—24 [With 13 Tables].

Mammals are characterized by a wide range of body sizes and highly variable population densities. They are important in energy flow of ecosystems due to the high energetic cost of homeothermy, due to high turn-over rates in populations of small mammals, and due to low efficiency of production. Biomass of mammals is small in comparison to that of soil invertebrates but exceeds above-ground invertebrates in many grasslands, indicating a high contribution to mineralization rates by mammals. Mammals generally consume only a small amount of the vegetation available, but seed consumption may influence plant species composition in forests, and consumption of invertebrates by small mammals may be important in control of these populations. It was found that the impact of carnivores on prey is between that exerted by small mammals on available plants and ungulate impact on plant cover. Complexity of the mammal community varies with type and availability of food resources. The contribution of mammals to total herbivory in grasslands is between 4% and 38%.

[Dept. of Agrobiolology and Forestry, PAS, Swierczewskiego 19, 60-809 Poznań, Poland and Nat. Resource Ecol. Laboratory, Fort Collins, Colorado 80523, USA]

1. GENERAL FUNCTIONAL CHARACTERISTICS OF MAMMALS

Mammals adapt to any terrestrial habitat from arctic to tropics provided they can obtain food. Generally speaking, production of any component per unit time can be defined as the product of mass times turnover. In a functional analysis of an animal community there are three important components of mass. The first is increment of body sizes resulting from physiological, developmental processes of the individual animal. The second component is population biomass resulting from interplay of production processes within the species population. The third is the biomass of the total mammal community resulting from the interplay of various ecosystem processes.

Adult weight of terrestrial mammals in the world varies approximately by a factor of 2.5 million. The range of weight distribution is marked out by shrews (e. g., *Suncus etruscus* — less than 2 grams) and elephants

(*Loxodonta africana* — over five tonnes). But, the weight distribution actually observed within a majority of ecosystems is narrower and ranges from several grams to tons, or a few hundred kilograms.

Energy turnover is speeded up in mammals due to homeothermy. Using an allometric equation for respiration and body weight Fenchel (1974) estimated that homeotherms have 28 times higher respiration rate than poikilotherms of comparable size. On the other hand, when more specific data are compared the differences could be smaller. For example Dawson (1973) estimated that energy required to maintain the same body size in birds and mammals is about 3.5 times higher than for a reptile of equivalent size. These two results could be supplemented by estimates obtained from comparison of other published bioenergetics characteristics of homeotherms and poikilotherms. In spite of variability among comparisons, these comparisons show that energy cost of maintaining homeothermy is much higher than poikilothermy.

Maintainance of a constant body temperature suitable for optimization of various biochemical reactions is advantageous for a high level of activity sustained in extreme or rapidly fluctuating ambient conditions. This requires higher input of energy, but enables colonization of habitats and niches unavailable to poikilotherms. Homeotherms are more independent of ambient conditions than poikilotherms, at the expense of demanded for more intensive and continuous energy supplies.

Metabolic rate, body temperature, body size and insulative properties are interrelated in homeotherms (Spotila & Gates, 1975). Small mammals rely to the higher degree on fur insulating properties than large ones, and also make substantial use of burrows, holes, and other shelter places having more suitable microclimatic conditions. These adaptation compensate for need of higher energy input caused by increased metabolic rate due to small body size.

The higher turnover rates in small mammal populations result in speeding up of many individual life processes like growth rate, gestation period, ageing etc. (Bourliere, 1975). The opposite situation is true for large mammals. These different strategies result in bimodal weight distributions in terrestrial mammals which are not observed in swimming or flying homeotherms. Thus many terrestrial mammal species cluster between a few grams to a few kilograms and the second cluster is between a few tens to a few hundreds kilograms. All size intermediates can be observed between the smallest and the largest birds and the swimming mammals (Bourliere, 1975). Recently it was shown by French, Stoddart & Bobek (1975) that within small mammal populations one can find two types of strategy for achieving success in exploiting various habitats. The first one is related to high reproduction and rapid growth

to maturity combined with low survival. The second consists of effective survival with low reproduction. Outbreaks in numbers of small mammals having economic importance were reported mainly for those characterized by the first strategy.

The low efficiency of mammal production is apparent when the ratio of net production to food assimilation of homeotherms and poikilotherms is compared. This ratio varies from 10 per cent to about 40 per cent in many poikilotherms (Golley, 1968; Reichle, 1971) but very rarely reaches the value of 6 per cent in mammals, usually below 2 per cent. Only in domesticated mammal species could efficiencies comparable to some poikilotherms be observed due to selective breeding, special diet, and other factors of modern husbandry.

Herbivory in terrestrial mammals tends to increase with body size. Large canids and felids are exceptions and have very low densities. Many mammal species are omnivorous and take advantage of a variety of plant foods, fungi, invertebrate and vertebrate flesh if available. Thus, omnivory could be considered as a link between primary producers and vertebrate predators of the ecosystem. The direct influence of mammals on energy flow is measured by their consumption which is rather small, except during outbreaks, in the overall picture of ecosystem energetics (see for example Golley, Ryszkowski & Sokur, 1975; Goszczyński, Ryszkowski & Truszkowski, 1976). The role of mammals, especially rodents, in mineral cycling is not limited to consumption. Burrowing activity or other forms of matter relocation greatly magnify the role of mammals in mineral cycling beyond the limits set by consumption (Abaturov, 1972; Zlotin & Khodashova, 1974).

In order to summarize this general discussion on functional characteristic of mammals it should be stressed, that although the energy cost of maintaining the homeothermic way of life is higher than the poikilothermic one, but due to higher turnover of energy various organismal processes as well as biomass production are accelerated and more independent of ambient conditions. In consequence, some ecosystem processes could be magnified, extended into more severe environmental conditions, and proceed during the whole year. In the following parts of this paper more detailed documentation of this statement is presented.

2. STRUCTURE OF THE TERRESTRIAL MAMMAL COMMUNITY

Despite many publications on abundance and biomass of particular mammal populations or taxonomic groups there is scanty quantitative information on biomass of the total mammal community. Evaluations of mean values taking into account seasonal changes of total mammal com-

munity supplemented by primary production as well as other animal biomass estimates were obtained only in a few studies on total ecosystem functioning (Satchell, 1971; Zlotin & Khodashova, 1974; Ryszkowski, 1979; French, 1979). When only live weight was provided by the authors then an approximate factor of 0.33 was used to convert published data into dry weight estimates. It is impossible to estimate the contribution of mammal community biomass to total biomass of animals in all basic types of terrestrial ecosystems because of lack of data. Results of site studies on total animal biomass including *Protozoa* indicate the share of mammal community is approximately 4.2% in deciduous forest in England (Satchell, 1971) and 3.2% in agroecosystem landscape in Poland (Ryszkowski, 1979). When biomass of *Protozoa* is neglected then contribution of mammal communities to total biomass of animals vary from 0.1% to 7.7% in various ecosystems under study (Table 1). Apart from

Table 1

Total biomass of animals in forest (Satchell, 1971) and in agroecosystem (Ryszkowski, 1979) mg.d.w/m², desert and grassland's (French 1979).

Soil	Forest ¹	Agro-ecosystem ¹	Desert	Short-grass	Mixed	Tall-grass
<i>Nematoda</i>	200	260	30	430	1323	398
<i>Annelida</i>	1600	2200	0	0	0	—
<i>Arthropoda</i>	1200	173	756	549	787	384
<i>Mollusca</i>	500	0	0	0	0	0
Total soil invertebrates	3500	2633	786	979	2110	782
Above-ground invertebrates	100	133	52	32	372	166
<i>Amphibia</i>	—	0.6	—	—	—	—
Reptiles	—	—	32	2.5	—	—
Birds	—	15	1	7.5	4	4.7
Mammals	165	193	14	40	3	80
Total vertebrates	—	208.6	47	50	7	85
Total animals	3765	2974.6	885	1061	2489	1033
Percentage of mammals	4.4	6.5	1.6	3.8	0.1	7.7

¹ In original papers data on *Protozoa* biomass are shown.

the scanty information it can be assumed in regard with general ecological knowledge that the share of total mammal biomass does not exceed a couple per cent in other types ecosystems. Thus, for example, Chernov, Khodashova & Zlotin (1967) compiling many partial studies assumed the share of vertebrate biomass in total animal biomass to be equal to 0.12% in temperate deciduous forest, about 1% in steppe, from 1.6% to 4% in mixed forest and taiga and up 5% tundra.

In total 24 estimates of the total mammal community biomass were found (Table 2). Most results concern the north temperate regions. Tropical and arctic habitats are not represented practically. The lowest

Table 2

Biomass of total mammal community in various terrestrial ecosystems (mg.d.w./m²)

Alpine tundra	Deserts and semideserts	Grasslands		Forests		Cultivated field landscape
		Alpine	Lowland	Deciduous	Coniferous	
1.2 ^a	2.3 ^a	37.1 ^a	6.0 ^c	165.0 ^f		
	9.9 ^b	37.9 ^a	41.3 ^c	165.0 ^g		
	11.2 ^c	49.5 ^a	42.0 ^d	247.5 ^f	237.6 ^f	192.5 ^h
	16.3 ^c	83.1 ^a	45.1 ^c	330.0 ^f		
	23.1 ^b		155.1 ^e	330.0 ^e		
	46.2 ^b					
	62.0 ^a					
Mean	24.4	55.2		245.8		

References: ^aZlotin (1975) Tian-Shan, Asia, ^bRodin (1977) Karakum, Asia, ^cFrench (1979) North America, ^dLamotte (1975) North Africa, ^eZlotin & Khodashova (1974) Eastern Europe, ^fTurček (1971) Central Europe, ^gSatchell (1971) Western Europe, ^hRyszkowski (1979) Central Europe

biomass of mammal community was recorded in alpine tundra: 1.2 mg d. w/m², and in alpine desert: 2.3 mg d. w/m² by Zlotin (1975) in Tian-Shan mountains. In both situations small mammals (voles and marmots) constituted almost the total community (86 and 91% respectively).

Calculating mean values for desert, grasslands and forests one can find that the mammal biomass in forests is on the average ten times higher than in deserts.

Forest mammal biomass is about 3.5 times higher than grassland. Variability of the total biomass is high in analysed ecosystems. The same is true with major components of the mammal community such as small mammals, lagomorphs (intermediate size class), ungulates, carnivores. Biomass of each component fluctuates greatly, showing even higher variability than biomass of the total mammal community (Table 3).

Table 3

Biomass structure of mammal community at desert, grassland and agroecosystem sites (mg.d.w./m²).

Site	Small mammals	Lagomorphs	Ungulates (wild)	Carnivores	Total
Mojave desert ^a	10.16	0.01	0	1.0	11.17
Desert grassland ^a	9.79	0.94	5.5	0.11	16.34
Southern shortgrass ^a	4.96	0.90	0	0.13	5.99
Northern shortgrass ^a	9.35	32.50	3.24	0.09	45.18
Mixed ^a	2.18	0.53	824.27 ¹	0.08	827.06
Tallgrass ^a	33.20	7.91	0	0.22	41.33
Agroecosystem ^b	55.10	66.00	52.5	18.90 ²	192.50

¹ Unusually high at this location due to river near site, ² High insectivores especially mole (12 mg) populations, ^aFrench (1979), ^bRyszkowski (1979).

It seems that ungulate biomass could attain high levels if predator control is limited and food resources are abundant as in reserves or other protected areas. Thus, comparing ungulate biomass in various zones of USSR Dobrinsky (1975) has shown, that on the average from 10 to 20 times higher biomass is observed in protected than unprotected areas (Table 4). Biomass of large mammals recorded for savanna reserves in Africa are the highest published to date (Bourliere, 1965; Lamprey, 1964; Petrides & Swank, 1965).

Large body sizes coupled with lower turnover rates of energy correlate with slower rate of various life processes like reproduction and growth in comparison to small mammals. Thus, ungulate populations do not fluctuate rapidly like small mammals, and probably approach the food-limiting conditions more consistently than small mammals. It is well known, that in the case of insufficient impact of predators, ungulate populations build up in numbers to the level of vegetation damage (*e. g.* Mohler *at al.*, 1951).

The highest ungulate biomass recorded for unprotected areas by Dobrinsky (1975) was in forests (Table 4) indicating better shelter conditions than in other ecosystems, especially against hunting pressure of man. In protected areas Dobrinsky (1975) recorded the highest ungulate biomass in grasslands (Table 4). Average values of total mammal population biomass evaluated in this paper in three types of ecosystems are lower than values presented by Khodashova (1966) obtained by compilation of separate population studies (Table 4).

In terrestrial ecosystems animal biomass is concentrated in soil invertebrates. Above-ground animal biomass is usually in the order of a few percent of the total. But, considering only the above-ground invertebrates one may find in some grassland ecosystems that total mammal biomass exceeds above-ground invertebrate biomass (Table 5). In these situations enormous number of invertebrate species, especially insects, is balanced by a few species of mammals. The higher biomass of mammals than invertebrates above-ground means that much more covalent bond energy stored in consumer tissue is converted to thermal energy because of higher energy cost in maintaining homeothermy. In other words it means the higher contribution of mammals to above-ground fauna means higher mineralization rate of animal biomass in some grassland ecosystems.

3. CONSUMPTION BY THE MAMMALS

Grassland ecosystems are controlled to a higher degree by climatic factors, especially water, in the sequence of dry and wet seasons, and

Table 4
Recorded ungulate biomass versus total mammal community biomass (mg.d.w./m²)¹.

Community	Location	Type of estimate	Desert	Grass-lands	Forests		Taiga	Tundra	Reference
					Deciduous	Mixed			
Ungulates	Unprotected areas, USSR	minimal	1	3		30	13	7	Dobrin'sky (1975)
		maximal most frequent	66	264		330	165	297	
Ungulates	Reserves, USSR		33	82		132	66	66	
Ungulates	Zoogeographical zones, USSR	average	726	1716		1320	1188 ^a —1023 ^b	858	Dobrin'sky (1975)
Ungulates	Reserves, Africa	compilation	1	16		33	24 ^a —2 ^b	11	Khodashova (1966)
Total mammals	Zoogeographical zones, USSR	average		7986					Bourliere (1965); Peirides & Swank (1965); Lamprey (1964)
				5808					
				4059					
Total mammals	North America	compilation	119	196		169	46 ^a —11 ^b		Khodashova (1966)
		average of ecosystem estimates	24	55	246				this paper

¹ If data published in live weight then factor 0.33 was used to get dry weight, ^aEuropean Taiga, ^bEast Siberian Taiga.

Table 5
Ratio of mammal biomass to above ground invertebrates biomass (mg.d.w./m²).

Tundra ^a	Desert ^a	Desert ^d	Semi-desert ^a	Short-grass ^d	Arid-steppe ^a	Cold-steppe ^a	Steppe meadow ^a	Steppe ^b	Tall-grass ^d	Wet meadow ^a	Agroeco-forest ^b
1.2	2.3	14.0	62.0	46.2	83.1	37.1	37.9	155.1 ¹	80.3	49.5	192.5
9.2	13.5	52.3	14.4	32.2	13.3	15.0	21.9	870	166.1	36.6	133.3
0.13	0.17	0.27	4.30	1.44	5.43	2.47	1.73	0.18	0.48	1.35	1.44
Mammals											
Above ground invertebrates											
Ratio											

^aAlpine ecosystems, Zlotin (1975), ^bZlotin & Khodashova (1974), ^cRyszkowski (1979), ^dFrench (1979). ¹About four or five times more before modern agriculture.

practically all above-ground plant biomass becomes dry or dead and is shed when growing season ends. Thus, consumption of even a large quantity of above-ground vegetation could be accomplished without damage to plant cover, especially because grazing promotes regrowth processes in plants. In forests, where a substantial part of annual above-ground primary production is accumulated in live standing biomass, the amount of vegetation consumed by herbivores could more easily impair photosynthetic capacities of trees.

The data gathered from a variety of ecosystems through the International Biological Programme indicate that usually a very low proportion of herbage is consumed by small mammals (Table 6; Golley,

Table 6
Yearly energy consumption of small mammals as the percentage of available primary production.

Ecosystem	Consumption, %	Reference
Agricultural fields		
Rye	0.5	Trojan (1969)
Alfalfa	0.8	Trojan (1969)
Alfalfa	1.4—21.4	Ryszkowski et al. (1973)
Forest plantations		
Spruce	1.8— 3.1	Hansson (1971)
Mixed	3.1	Gębczyńska (1970)
Coniferous forests		
Pine-lichen dry forest	1.9	Ryszkowski (1969)
Pine-blueberry (40 years)	0.9— 1.2	Ryszkowski (1969)
Pine-blueberry (140 years)	0.6	Ryszkowski (1969)
Pine-oak	0.6— 0.8	Ryszkowski (1969)
Taiga (Alaska)	13.5	Grodziński (1971)
Deciduous forests		
Oak-hornbeam	4.6	Grodziński (1971)
Beach forest	2.4— 6.7	Grodziński <i>et al.</i> (1969)
Alder-ash	2.2	Aulak (1973)
Mixed forest	0.6	Ryszkowski (1969)
Grasslands		
Grass field	1.3	Trojan (1969)
Grass field	1.6	Golley (1960)
Desert shrub	5.5	Chew & Chew (1970)

Ryszkowski & Sokur, 1975). The vegetation is seriously damaged by small mammals only in the case of population outbreak. It seems that quite the contrary situation exists in large herbivorous mammals. The ratio of food consumed to food available is usually much higher than in the case of small mammals (Table 7). These results of studies support the conclusion that ungulates approach the food limiting conditions more consistently than small mammals. One may expect therefore, that the

impact of ungulates on vegetative parts of plants could be substantial, especially when density of predators is limited.

The opposite situation is expected with small mammals in forests. Selection of seeds for food by rodents has a greater influence on the species composition of plant cover in forest ecosystems where seeds play an important role in propagation of vegetation than in grasslands where much of the regrowth is from roots (Dinesman, 1961; Golley, Ryszkowski & Sokur, 1975).

Table 7
Percentage of available energy utilized by large mammals.

Location	Species	Period	Percentage consumed	Source
Grassland, Uganda	<i>Adenota kob thomasi</i>	whole year	10	Buechner & Golley (1967)
Grassland, Uganda	<i>Loxodonta africana</i>	whole year	9.5	Petrides <i>et al.</i> (1968)
Grassland, Tanganika	Ungulates	whole year	28	Wiegert & Evans (1967) acc. to Lamprey data
Deciduous forest, Poland	<i>C. capreolus</i>	whole year	8.4	Bobek <i>et al.</i> (1972)
	<i>C. elaphus</i>	winter	15.7	
Deciduous forest, Poland	as above	growing season winter	19.1 25.5	Bobek <i>et al.</i> (1975)
Deciduous forest, Poland	as above	growing season winter	7.3 15.5	
Coniferous forest, Poland	as above	growing season winter	4.0 12.0	
Deciduous forest, Poland	Ungulates	whole year	5.0	Borowski & Dzieciolowski (1980)

Analysis of the impact of predators on prey in various homeotherm populations indicates that the ratios of biomass consumed to available prey (Table 8) are between those indices observed in small mammals (Table 6) and in ungulate populations (Table 7).

More detailed studies on food habits, diets and bioenergetics have shown that many so called herbivorous species of small mammals actually take advantage of a variety of plant foods as well as insects, other invertebrates, fungi and even vertebrate flesh if available. Most small mammals are omnivorous. In studies on small mammals in various grassland ecosystems in North America carried out within the IBP it was shown that in some arid grasslands carnivory is nearly as important as herbivory (Table 9). Analyses of food utilization indicate that the small mammal impact on herbage food is much smaller than on animal

food (Table 10, French *et al.* 1976). Only in one case nearly 20% of available herbage food was consumed. This occurred during a year of low primary production at the desert site. Annual plants in deserts do not germinate in years of unfavorable growing conditions. Thus, the failure of seed production may have forced high utilization of herbage

Table 8
Predator impact on prey populations.

Predators	Prey	Pressure on prey, %	Reference
Lion	antelope gnu	2.2—3.3	Schaller (1972)
Lion	antelope gnu	1.2	Kruuk & Turner (1967)
Hyena	antelope gnu	1.7—2.7	Schaller (1972)
Hyena	antelope gnu	1.6—2.6	Kruuk (1970)
Hyena	zebra	1.7—2.3	Kruuk (1970)
Hyena	Thompson's gazella	2.2—6.5	Kruuk (1970)
Hyena	zebra	3.2—4.2	Schaller (1972)
Wolf	white-tailed deer	10.0	Kolenosky (1972)
Lynx	snowshoe hare	2.1—6.4	Nellis <i>et al.</i> (1972)
Lynx	red squirrel	1.1—1.6	Nellis <i>et al.</i> (1972)
Fox	European hare	11.0	Pielowski <i>et al.</i> (1974)
Big predators	ungulates	9.0—10.0	Schaller (1972)
Big predators	ungulates	15.5	Foster & Coe (1968)
Total set of homeotherm predators	forest rodents	18.2—55.8	Ryszkowski <i>et al.</i> (1973)
Total set of homeotherm predators	common vole	9.4—47.4	Ryszkowski <i>et al.</i> (1973)

Table 9
Sources of energy utilized by small mammal populations at various grassland sites (French *et al.*, 1976)

Site	Biomass, mg d.w./m ² (avg. for 3 years)	Carnivore, %	Herbivore, %
Tallgrass	33.20	13	87
Midgrass	2.18	53	47
Northern shortgrass	9.35	52	48
Southern shortgrass	4.96	60	40
Desert grassland	9.79	45	55
Mojave desert	10.16	10	90 ¹

¹ Includes 45% granivory.

by small mammals. In desert environments rapid decrease of primary production efficiency could create conditions similar to population outbreak situations even at low mammal population density. French *et al.* (1976) estimate that small mammal pressures on invertebrate components of above-ground animal community were very high at nearly all

sites (Table 10). The one exception was the site with very low small mammal density.

One of the most interesting points emerging from these studies is that estimated impact of small mammals on the epigeic invertebrates is usually much higher than impact of mammal predators on their mammal food resources (compare table 10 and 8). Only the impact of the total set of predators including six mammal predator species and five species of predatory birds, in agricultural landscape approaches the level of pressure exerted by small mammals on epigeic invertebrates in some grassland ecosystems. Thus, the small mammal community may be an important factor in control of above-ground invertebrates.

Table 10

Fraction of available energy utilized by small mammal communities at various grassland sites (after French *et al.*, 1976).

Grassland sites	Year	Herbage	Animal
Tallgrass	1970	0.063	0.88
	1971	0.010	0.38
	1972	0.047	all ?
Midgrass	1970	0.002	0.08
	1971	0.001	0.08
	1972	0.002	0.02
Northern	1970	—	all ?
Shortgrass	1971	—	0.42
	1972	0.005	0.83
Southern	1970	—	0.96
	Shortgrass	1971	0.013
Desert grassland	1972	0.091	0.11
	1970	0.032	all ?
	1971	0.190	all ?
	1972	0.004	0.68

It seems that the granivores predominate in desert ecosystems where they also exert the highest recorded impact on seed numbers (Table 11). Because of high impact evoked by small mammals both on seeds and above-ground invertebrates one may conclude that the abundance of these resources is coupled with small mammal populations at least in some ecosystems. Thus, for example the selection of seeds for food by rodents has substantial influence on the species composition of seedlings in deciduous forest and thus on the composition of forest regrowth (Dinesman, 1961). The following general trophic description of small mammals is based on French *et al.* (1975). The structurally simple habitats have small mammal populations dominated by herbivores, while with increasing degrees of structural complexity the predominant roles are displayed by omnivores, then granivores, and finally carnivores. Tundra habitats may have one to several herbivorous species of micro-

tines, a single omnivore and a single carnivore (Batzli, 1975). The grassland ecosystem generally has a single species of herbivorous small mammal, two to three species of omnivores, none or a single species of granivore, and one carnivore (French *et al.*, 1976). The temperate deciduous forests the small mammals play a very minor role on the forest floor, and may be characterized by a single species each of herbivore, of granivore and of omnivore. Deserts are dominated by granivorous species of small mammals, with perhaps one omnivore and one carnivore, and on occasion an herbivore in addition. Tropical ecosystems, with their many species of small mammals, may have one or two each of herbivore, granivore and omnivore, and generally several

Table 11

Percentage of available seeds consumed by small mammals.		
Ecosystem	Consumption, %	Reference
Old field	12	Odum <i>et al.</i> (1962)
Savanna	9	Poulet (1972)
Desert	95	Soholt (1973)
Desert	85	Chew & Chew (1970)
Bunchgrass		
<i>Sitanion hystrix</i>	1-8	Becker & Balph (1976)
<i>Atriplex confertifolius</i>	4-32	Becker & Balph (1976)
Tallgrass	8	French <i>et al.</i> (1976)
Northern shortgrass	0.2	French <i>et al.</i> (1976)

species that may be partially carnivore and partially scavenger (Fleming, 1975). This is not including the large segment of the tropical small mammal community feeding on insects, the bats (Fleming 1973).

In comparatively simple ecosystems the energy coupling between the small mammals and the producers must be short and direct. For this reason the herbivores dominate in arctic and alpine environments. The high degree of direct dependence upon the resource base has resulted in populations that can rapidly exploit given resources when they become available, fluctuate widely in numbers during a short span of time, in other words, the *r*-selected species. In the more variable environment of grassland, omnivores predominate perhaps because they are capable of switching as resource conditions change. In temperate deciduous forests small mammals have little impact on system energetics, although they may control species composition of forest regrowth. In the desert, on the other hand, there is a fairly reliable source of energy in the form of seeds which are abundantly exploited by granivores. Labile

metabolic characteristics of some of the desert dwelling forms enables them to persist during infrequent periods of unusual scarcity of seed resources. In tropics the carnivore—omnivore category predominates, exploiting the abundant invertebrate and small vertebrate consumers that occur in the system. In the less seasonal environment resources are more constant and there is little need for adaptation toward rapid exploitation of periodically available resources.

With increasing size of mammals herbivory is spread among more mammalian species. Larger herbivorous species have higher impact on vegetative parts of plant cover (browse, grasses) than small mammals. Selective grazing by ungulates is an important determinant of species composition of plant cover especially in grasslands (*e.g.* Clements & Shelford, 1939). Their importance for ecosystem succession was recognized long ago by many pioneers of ecology.

In an attempt to evaluate the importance of different consumer groups in grassland ecosystems French (1980) evaluated consumption of basic functional groups of animals in four grassland ecosystems. Data models, involving use of computer models with field data as input were used on animal groups under question, to obtain estimates of consumption at shortgrass, mixed-grass, tallgrass, and desert grassland sites. Field data included basic microclimatic characteristics and estimates of animal and plant species biomass and densities. The data models use respiration equations, growth equations, assimilation rates, and diet preferences, which are specific to each taxon, to determine consumption. Above-ground animal consumption is only about 3—8% of the total consumption (Table 12). Only 2—7% of primary production is consumed above-ground, but below-ground 7—26% is consumed. Predators consume most of the production of primary consumers, however. Total consumption increase from the shortgrass to the tallgrass sites, and above-ground consumption becomes slightly greater. As primary production above-ground becomes greater between sites, consumers eat a greater proportion of this production, indicating a density—dependent mechanisms of control of plant growth. Plant tissue feeders are more important than plant sap feeders above-ground but the reverse is true below-ground. There may, therefore, be less damage to under-ground parts by consumers. Mammal contribution to the total above-ground consumption varies from 4% (mixed grassland) to as high as 38% at tallgrass site. Although the amount of energy consumed depends mainly on the level of biomass standing crop of animals in question, nevertheless homeothermy magnifies the consumption compared to poikilothermy. The contribution of mammal consumption among secondary consumers varied from 4.2% (mixed) to 42.9% at shortgrass site. Thus, in three out of four analysed grassland

ecosystems mammals are very important components of energy flow at higher trophic levels in the above-ground segment of ecosystems.

These results support the conclusion that mammals may play important roles in elaboration of trophic structure of above-ground segment of ecosystems. The effects of consumption processes may be considered as mechanisms of supplying organic matter to the soil, through spreading over the whole year the fall of clipped but not consumed plant material

Table 12
Consumption ($\text{kcal.m}^{-2} \text{ season}^{-1}$) by consumers at four grassland sites
(after French, 1979).

Consumers	Desert grassland	Short- grass	Mixed	Tall- grass
ABOVE-GROUND				
Primary consumers				
Plant tissue feeders				
Mammals	1.69	0.51	1.60	20.90
Arthropods	8.12	3.54	6.33	6.91
Plant sap feeding arthropods	2.18	2.98	24.72	12.60
Pollen nectar feeding arthropods	0.55	0.59	0.98	6.66
Seed feeders				
Birds	6.51	0.62	0.16	0.59
Mammals	0.70	0.08	0.20	11.28
Arthropods	1.73	0.12	0.17	1.34
Dead plant-litter feeding arthropods	12.36	1.55	9.88	24.35
Secondary consumers				
Predators				
Birds	3.98	1.13	0.88	1.65
Mammals	1.49	1.28	0.20	2.48
Arthropods	2.30	0.55	3.25	6.43
Scavenger arthropods	0.51	0.02	0.34	0.47
BELOW-GROUND INVERTEBRATES				
Primary consumers				
Plant tissue feeders	—	40.22	244.26	69.02
Plant sap feeders	—	192.93	382.38	369.64
Fungal feeders	—	97.60	33.66	215.47
Bacteria feeders	—	101.13	66.53	83.91
Secondary consumers				
Predators	—	28.46	117.83	78.02
Protozoa feeders	—	11.67	31.65	22.36

and by addition of unassimilated food. There are accumulating data indicating that mammals may speed up decomposition processes in ecosystems (e.g. Zlotin & Khodashova, 1974). While the quantity of nitrogen entering the top soil from decomposition of litter produced by mammals is significant only with very high densities, the clipping rate, about which we have little information, may be substantially higher than usually assumed. This would suggest that herbivorous mammals may also serve as regulators of the supply of fresh organic matter made available for decomposition. There is some information that green plant material, such as enters the litter via mammal clipping and mammal

feces decomposes more rapidly than does brown, dry plant material entering the litter from standing dead plants. Thus, mammals are capable of affecting decomposition by altering both the quantity and quality of litter.

4. EVALUATION OF THE MAMMAL'S ROLE IN TERRESTRIAL ECOSYSTEMS

Much of the above information on the trophic relationships was obtained during recent studies on energy flow in ecosystems accomplished by the International Biological Programme. These studies have revealed the intriguing pattern of direct impact of mammals on primary producers as well as on other consumers. Thus, for example, small mammals may play an important role in seed elimination or display serious impact on above-ground invertebrates in some ecosystems. Ungulates may control plant species composition. Mammals accelerate decomposition processes of plant materials. All these impacts of mammals are related to their direct role in energy flow in ecosystems, which is relatively small in comparison to the invertebrate contribution, to say nothing about microbes. Thus, the magnifying effects of homeothermy on energy flow does not surpass the effect of lower density and longer turnover times characteristic of mammals, in comparison to invertebrates. There are suggestions that the role of mammals is mainly expressed in their rate control of several fundamental processes for ecosystem functioning. For example, it has been convincingly argued from a theoretical standpoint that consumers in general, and mammals in particular, fulfill the requirements for regulators of the producer, decomposer system (Golley, 1973; Golley, Ryszkowski & Sokur, 1975). These impacts can be grouped into four main categories related to the following effects of mammals: a) destruction of a component; b) movement of materials or components; c) alteration of the environment, and d) interactions with other consumers. All these effects are not strictly related to magnitude of energy flow and therefore could play the role of feedback mechanisms for the plant-decomposer system.

Thus for example the burrowing activity of small mammals may be the important agent supplying nutrients for plants across the soil profile. This nutrient transfer could be especially important in dry climatic conditions when capillary ascension of ground water does not operate as in dry grassland ecosystems. An increase in small mammal density or in proportion of burrowers results in an increase in rate of nutrient cycling in the ecosystem. When nutrients are tied up in undecomposed organic matter small mammals may influence primary production by dispossing from deep layers new supplies of minerals (Golley, Ryszkow-

ski & Sokur, 1975). Mammals, by changing the relief of ground, influence water runoff, which influences local moisture conditions in soil and may also influence growth of plants. In the case of many plant species mammal grazing has a direct stimulating effect on regrowth processes. Such examples of positive or negative feedback impact of consumers on primary producers or decomposers could be expanded. However, in spite of abundant qualitative information there is very poor quantitative understanding of these feedback effects. This lack of knowledge applies to actions of the mammals and also to the quantitative response of the vegetation or decomposers to these actions. Thus, the knowledge of mammal impact based on processes not strictly related to energy flow is very limited. However, there are published contributions based on meager information. Thus, for example, evaluating the role of small mammals in temperate ecosystems suggested that their highest impact

Table 13

Increase of mammal production due to energy subsidies provided by husbandry.

Species	Location	Net production (kcal.m ⁻² year ⁻¹)	Reference
44 small mammal populations	various natural habitats	up to 0.600	French <i>et al.</i> (1976)
<i>Alces americana</i>	Michigan, USA	0.200	Jordan <i>et al.</i> (1971)
<i>Cervus elaphus</i> <i>Capreolus capreolus</i>	Poland	0.300	Bobek (1974)
<i>Loxodonta africana</i>	Uganda	0.340	Petrides <i>et al.</i> (1968)
<i>Adenota kob thomasi</i>	Uganda	0.807	Buechner & Golley (1967)
Masai cattle	Tanzania	2.650	Deans <i>et al.</i> (1968)
Beef cattle	average for western USA native range	6.500	Cook (1971)
Beef cattle	improved range, USA	140.000	Hull <i>et al.</i> (1971)

is in temperate grassland ecosystems (Golley, Ryszkowski & Sokur, 1975). Under very intensive agriculture small mammals are practically eliminated and, at the other extreme, in mature forest the impact of small mammals on the system is negligible.

The importance of mammals to man is far greater than their relative importance to ecosystem function, because of their available protein, their capacity to attain high densities with resulting damage to agricultural stores, and their ability to serve as reservoirs of disease that affect man. Through specific interactions in the utilization of ecosystems by man conflict with mammals intensifies relationship to structure and

function of ecosystems. These results are obtained by energy subsidies which permit attainment of needed goals. In the case of modern husbandry the results obtained are striking (Table 13).

Consideration of the different types of energy utilization among consumer groups begins to clarify the means and mechanisms of comparative system impact. Mammals display an important role in control of transfer rates of energy and matter in ecosystems like other consumers. Their specific characteristics are related to homeothermy which make them more independent of ambient conditions. Therefore their actions are comparatively less related to the magnitude of energy flow than the effects of invertebrate actions.

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Accepted, July 16, 1981.

Lech RYSZKOWSKI i Norman R. FRENCH

ODDZIAŁYWANIA TROFICZNE SSAKÓW W EKOSYSTEMACH LĄDOWYCH

Streszczenie

Masa ciała ssaków wykazuje dużą zmienność. Najmniejszy ssak lądowy waży około 2 g a największy 5 ton. Dużej zmienności podlega zagęszczenie populacji wielu gatunków ssaków. Skutkiem dużych kosztów energetycznych stałocieplności jak i dużej zmienności zagęszczenia ssaki odgrywają istotną rolę w przepływie energii w ekosystemie. W wielu ekosystemach trawiastych biomasa całego zespołu ssaków równoważy lub nawet jest większa od biomasy wszystkich żyjących na powierzchni ziemi i w nadziemnej warstwie roślinności bezkręgowców. W stosunku do całej biomasy zwierząt stwierdzonej w analizowanych ekosystemach ssaki sta-

nowią od około 0.1 do 7.7% (Tabela 1). W 24 analizowanych ekosystemach średnia masa całego zespołu ssaków wykazała zmienność od 1.2 mg s.m./m² do 330 mg s.m./m² (Tabela 2). Średnio biomasa zespołu ssaków w lesie jest dziesięć razy większa niż na pustyni. W porównaniu od cenionej biomasy ssaków w lasach ich biomasa w ekosystemach trawiastych jest trzy razy mniejsza. Biomasa kopytnych osiąga największe wartości na terenach chronionych, gdzie ograniczona została działalność drapieżników a zasoby pokarmowe są duże (Tabela 4). W niektórych ekosystemach trawiastych biomasa całego zespołu ssaków przewyższa biomasę bezkręgowców epigeionu (Tabela 5).

Tylko mała część dostępnego pokarmu jest zwykle zjadana przez drobne roślinożerne ssaki (Tabela 6). Wyjątek stanowią sytuacje ich masowego pojawu liczebności. Duże kopytne zjadają znacznie większą część dostępnego pokarmu (Tabela 7), dlatego ich liczebność może być ograniczona przez zasoby pokarmowe w większym stopniu niż ma to miejsce wśród drobnych ssaków. Wykazano, że drapieżne ssaki (Tabela 8) zajmują pośrednią pozycję pomiędzy drobnymi ssakami a kopytnymi pod względem wykorzystywania przez nie pokarmu. W przypadku trawiastych ekosystemów drobne ssaki zjadają prawie tyle bezkręgowców co pokarmu roślinnego (Tabela 9). Jednak, jak się wydaje, wpływ drobnych ssaków na bezkręgowce jest większy niż na rośliny (Tabela 10). Drobne ssaki zjadają bardzo duży procent nasion (Tabela 11), przez co oddziałują na skład gatunkowy odrastającej roślinności. Chociaż przeważająca część konsumpcji w ekosystemach trawiastych jest wywołana przez bezkręgowce glebowe, to jednak, gdy rozważać tylko wielkość pokarmu zadanego przez epigeion, okazuje się, że udział ssaków jest znaczny. Ta charakterystyka wykazuje, że ssaki są ważnym czynnikiem w przepływie energii przez epigeion.

Znaczenie ssaków w przepływie energii w całym ekosystemie jest małe w porównaniu do bezkręgowców (Tabela 12). Ich istotna rola w gospodarce ekosystemu polega na regulacyjnym oddziaływaniu na tempo szeregu procesów, takich jak przemieszczanie składników odżywczych roślin, stymulacja tempa rozkładu materii organicznej, uszkodzenie roślin uprawnych oraz rozprzestrzenianie różnych chorób. Oddziałując na szybkość przebiegu tych procesów, ssaki wywierają pośredni wpływ na produkcję ekosystemu i gospodarkę człowieka.