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TERRESTRIAL MAMMALIAN PREDATOR/PREY SYSTEMS: NORTHERN HEMISPHERE RATIOS, SPECIES RICHNESS, AND SPECIES COMPOSITION

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In the Neoarctic Biogeographic Region, Pre-Columbian terrestrial mammalian ecosystems were re-constructed to approximately 1400 AD* and terrestrial mammalian predator/prey species lists were developed for each macro-community in each biome. Faunal assemblages for the Palearctic Biogeographic Region were re-constructed to approximately 1000 AD and macro-communities associated with the various biomes ranged from Western Europe to eastern Siberia. From these data, it was concluded that: (1) terrestrial mammalian "species richness" increases from north to south in the northern hemisphere, (2) terrestrial mammalian "species composition" changes in all macro-communities in all biomes and (3) the mean terrestrial mammalian predator/prey ratio remains constant approximating 0.75 in all macro-communities in all the biomes of the Neoarctic and Palearctic Biogeographic Regions and appears to be universal macro-ecological pattern throughout the entire Northern Hemisphere, (4) the evolution of optimal foraging strategies associated with a 0.75 predator/prey ratio represents the mean upper limit of specialization that terrestrial mammalian predators can attain in the northern hemisphere, where prey populations cycle and primary prey availability varies widely. Changes in macro-ecological patterns in the terrestrial mammalian predator/prey systems from the 0.75 ratio in the Northern Hemisphere have implications for conservation biology and wildlife management related to sustaining ecological equilibrium.

***Keywords*: mammalian predator/prey ratios, species richness, species composition, Northern Hemisphere.**

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INTRODUCTION

Communities are natural occurring assemblages of plants and animals living in the same environment and interacting in many ways. These interactions can be direct or indirect and community structure evolves from all the various interactions among species and populations and creates emergent properties of the community (Begon et al., 1996).

For many years, community ecologist and wildlife managers have tried to understand the way resources are allocated throughout communities. This approach was accomplished by studying assemblages of species that used particular resources or clusters of resources in a functional and similar manner. As members of guilds interact strongly with each other and often weakly with the rest of the community (Giller, 1984), comparative research has been done to understand the differences in interactions of such parameters as competition and predation.

Another approach was to try to understand how species richness at one trophic level resulted in constraints on species richness in adjacent trophic levels by analyzing the interactions of predators and their prey. This can be studied using the predator/prey ratio, which is a measure of the number of predators to the number of prey. Cohen (1977) identified a repeating pattern, which seemed to confer a degree of organization on communities. Working with food webs, he found a remarkable constancy in the number of prey to the number of predators. Similarly, Evans, Murdoch (1968) analyzing grassland insect communities found a constant ratio between the numbers of entomophagous and herbivorous insects. Briand and Cohen (1984) analyzed 62 food webs and showed that the number of prey was roughly proportional to the number of predators and suggested that this constancy in the predator/prey ratio reflected an underlying trophic community pattern. In contrast, Cole (1980), Mithen and Lawton (1986), and Wilson (1995) rejected these conclusions and suggested that these ratios were arithmetic artifacts.

"Macro-ecology" has developed in the last decade in an attempt to unify traditional disciplines with the purpose of identifying statistical regularities

* Anno Dominu - наша эра

and patterns in the distribution of ecologically relevant variables found among approximately equivalent biological entities. Brown and Maurer (1989) first used the term macro-ecology to describe large scale entities and since then numerous macro-ecological patterns have been reported (Brown, Maurer, 1989; Damuth, 1998; Brown, 1999; Kindlmann et al., 1999; Schmid et al., 2000; Brown et al., 2001; Smallwood, 2001; Darveau et al., 2002; Carbone, Gittleman, 2002). Brown and Mauer (1989) hypothesized that these patterns reflected the operation of natural laws that governed the organization of the ecological world. However, our understanding of macro-scale interactions and community structures and behaviour remains limited. Unlike much traditional ecology, which focused on the attributes of one or a few species, the goal of macro-ecology is to understand assemblages involving many species at the macro-scale.

The objectives of this investigation were to analyze the relationship between terrestrial mammalian predators and their terrestrial mammalian prey in macro-communities that had evolved in different biomes throughout the Neoarctic and the Palearctic biogeographic regions. It was hypothesized that mammalian predator/prey ratios would remain the same in all macro-communities although species composition and richness vary. By examining this relationship in different macro-communities and biomes, a search for regularities and common principles of organization for macro-ecological systems was possible.

Assumptions made were that: (1) terrestrial mammalian predators and their terrestrial mammalian prey had co-evolved since the Eocene (Vaughan, 1972; Pielou, 1991; Van Valkenburgh, Janis, 1993), (2) the Post-Pleistocene ecosystem had reached dynamic ecological equilibrium by the end of the Pre-Columbian period (approx. 1400 AD) and terrestrial mammalian predator/prey systems were intact (McArthur, Wilson, 1967; Vaughan, 1972; Pianka, 1978), (3) humans (*Homo sapiens)* were part of the ecosystem (Kay, 1998; Pielou, 1991), (5) the Post-Columbian settlement of North America resulted in ecological dis-equilibrium with the associated extirpations, extinctions, habitat loss and the introduction of exotic species, (6) species of the Orders Insectivora and Chiroptera were an incidental part of the terrestrial mammalian prey system, (7) plants, invertebrates and other vertebrate taxa were incidental in the terrestrial mammalian predator/prey system and (8) other terrestrial mammalian predators were seldom consumed by terrestrial mammalian predators.

METHODS

Data Collection

Biogeographical studies have shown that all continents contain a series of biomes, where specific assemblages of life forms (plants and animals) vary as the result of climatic conditions and historical events (Odum, 1971; Pianka, 1978; Pielou, 1991). Shelford (1963) considered biomes to be distinct and real entities in nature defined by characteristic plant and animal species that formed unique communities within the biome, rather than artificial and arbitrary human constructs. Evidence indicates that each biome contains communities with terrestrial mammalian predators and terrestrial mammalian prey that have coexisted for thousands of years and which have evolved complex and intricate interrelationships (Odum, 1971; Pianka, 1978; Mallory, 1987; Pielou, 1991; Van Valkenburgh, Janis, 1993). In the Neoarctic Biogeographic Region, 14 macro-communities in 11 different biomes were selected for analysis and species lists were developed, excluding species from neighbouring biome extensions. Macro-communities were defined areas in the center of biomes without any influence from ecotonal areas that are transitional areas between biomes and house species from both biomes. For comparison, 17 macro-communities in nine different biomes ranging from Western Europe to eastern Siberia were also analyzed in the Palearctic Biogeographic Region (Table 3). In both regions, Insectivora, Chiroptera and other predators were excluded from the prey lists, as they have been shown to be minimally present in terrestrial mammalian diets.

In the Neoarctic Biogeographic Region, Pre-Columbian terrestrial mammalian ecosystems were re-constructed to approximately 1400 AD from the ecological literature. Terrestrial mammalian predator/prey species lists were developed for each macro-community in each biome, taking into consideration distribution patterns and species ecology. North American terrestrial mammalian species lists included the countries of Canada, United States and Mexico. Data from Burt and Grossenheider (1976), Hall (1981), Chapman and Feldhamer (1982) were used to identify the mammals of the United States and Canada, while Mexican species identification and distributions were obtained from Aranda et al. (1980), Hall (1981), Ramirez-Pulido et al. (1982), Ceballos, Galindo (1984), Aranda (2000), Rios and Alvarez-Castaneda (2002). For more southern macro-communities in Mexico, Coates-Estrada and Estrada (1986), Aranda and March (1987) and Emmons (1990) were used. Terrestrial mammalian species were separated into predators and prey based on food habits and in some instances, sibling prey species were considered as one species due to taxonomic inconsistencies, especially in the southern part of the continent (Robbins, 1983; Giller 1984).

Faunal assemblages for the Palearctic Biogeographic Region were reconstructed to approximately 1000 AD and macro-communities associated with the various biomes ranged from Western Europe to eastern Siberia from the literature on historical ranges (Flint et al., 1970; Mitchell-Jones et al., 1999).

Statistical Analysis

Predator/prey ratios were calculated at the macro-community scale. SPSS 9.0 for Windows

was used for correlation analysis, using the data from all Neoarctic and Palearctic locations, with the number of prey on the x-axis and the number of predators on the y-axis. The equations for the lines-of-best fit were calculated for predator/prey ratios in each biogeographic region and the intercept and the slopes with their associated r values and significance values were attained.

Using the Neoarctic data only, a goodness-of-fit test was done using all predators and prey from the different macro-communities to evaluate whether statistically significant differences existed among the predator/prey ratios (Sokal, Rohlf, 1995). Chi-square analyses were used to compare predator/prey ratios to random (Zar, 1999).

RESULTS

Species Richness and Species Composition in Neoarctic Macro-communities

Detailed information on species richness and composition in each macro-community from the different Neoarctic biomes show that terrestrial mammalian predator and prey species richness and composition changed with macro-community and that species richness generally increased from north to south (Tables 1–2).

Generally, both terrestrial mammalian predators and terrestrial mammalian prey species increased in species richness from the High Arctic of Canada to the Tropical Humid Forest of Mexico and species composition was different in each macro-community studied. The exception was the Desert Biomes of the southwest, which had lower species richness than the more northerly Great Basin and Prairie Biomes. When terrestrial mammalian predator/prey ratios were calculated for each macro-community in the Neoarctic Biogeographic Region, all predator/prey ratios approximated 0.75, although species richness and species composition differed in all locations (Table 2).

A preliminary analysis of terrestrial mammalian predator/prey systems in the Palearctic Biogeographic Region associated with various biomes from western Europe to eastern Siberia, produced similar results and although species richness composition differed at each location, terrestrial mammalian predator/prey ratios approximated 0.75 (Table 3).

The correlation coefficient for the Neoarctic data showed that the number of terrestrial mammalian predators and prey have a significant and constant relationship in all macro-communities in all biomes ($r = 0.992$; $P < 0.0001$). The slope of the line-of-best fit ($b = 0.748$) describing the relationship between the number of mammalian predators and the number of mammalian prey represents the mean predator/prey ratio for all locations (Fig. 1) and is a ¾ power relationship. The goodness-of-fit tests showed that there were no statistically significant differences among the ratios for the different biomes ($P < 0.001$). The Chi-square test ($X^2 = 8.18$; $P < 0.05$) indicated that the observed ratios were significantly different from random.

The correlation coefficient for Palaearctic Biogeographic Region faunal assemblages also showed that the number of terrestrial mammalian predators and prey had a constant and significant relationship ($r = 0.985$; $P<0.0001$). In addition, the slope of the line-of-best fit ($b = 0.743$) representing the mean predator/prey ratio for all macro-communities in all biomes, also approximated the ¾ power relationship found in the Neoarctic data (Fig. 2).

DISCUSSION

Through evolutionary time, communities should evolve to optimize the use of all available resources and be as rich and complex as possible, within the constraints established by limiting factors often set by climate, evolution and historical events. The emergent characteristics of communities represent the outcome of complex ecological interrelationships and evolutionary change in the populations and assemblages that compose the community (Pianka, 1978; Giller, 1984). In this study, the increase in species richness of both terrestrial mammalian predators and terrestrial mammalian prey in macro-communities from the High Arctic to the Tropical Humid Forest reconfirmed conclusions reached by previous researchers, that latitudinal diversity gradients exist in many taxa (Wallace, 1878; Simpson, 1969; Brown, Gibson, 1983). Brown (1995) noted that nearly universal latitudinal macro-ecological patterns of species diversity (richness) have been found in mammals, birds, reptiles, fish, grasshoppers, vascular plants and marine invertebrates. However, the fact that the more southerly macro-communities in the Desert Biomes of the Neoarctic Biogeographic Region had lower species richness, than the more northerly Great Basin and Prairie Biomes supports the conclusion that other factors are involved besides latitude.

Pimm (1991) noted that energy inputs to communities increased as one moved towards the tropics. The species-energy hypothesis proposes that biodiversity (species richness) is correlated with primary production and that more productive environments supported greater numbers of species (Wright, 1983; Currie, 1991). The results from this study on terrestrial mammalian predators and terrestrial mammalian prey support this hypothesis, although other factors such as water appear to be involved and the process is likely more complex.

The results of this study also showed that species composition was different in all macro-communities from the High Arctic to the Tropical Humid Forest and that these changes can be attributed to changes in climate, primary productivity and evolutionary history. Animals and plants in each community have specific morphological and physiological traits through which they have adapted to regional physical and social environments (Begon et al., 1996; Smith, Smith, 2001).

Table 1. **Terrestrial mammalian predator and prey species in the Neoarctic**

Таблица 1. **Виды наземных млекопитающих-хищников и жертв в Неоарктике**

Prey	Predators
High Arctic Biome	
Rangifer tarandus	*Canis lupus*
Ovibos moschatus	*Vulpes lagopus*
Dicrostonyx groenlandicus	*Mustela erminea*
Lepus arcticus	
Low Arctic Biome	
Rangifer tarandus	*Canis lupus*
Ovibos moschatus	*Vulpes lagopus*
Urocitellus parryii	*Gulo gulo*
Clethrionomys rutilus	*Mustela erminea*
Dicrostonyx groenlandicus	*Ursus arctos*
Lemmus trimucronatus	*Homo sapiens*
Microtus pennsylvanicus	
Lepus arcticus	
Boreal Forest Biome	
Alces alces	*Canis lupus*
Rangifer tarandus	*Vulpes vulpes*
Glaucomys sabrinus	*Lynx canadensis*
*Eutamias minimus**	*Gulo gulo*
Marmota monax	*Lontra canadensis*
*Tamias striatus**	*Martes americana*
Tamiasciurus hudsonius	*Martes pennanti*
Castor canadensis	*Mustela erminea*
Peromyscus maniculatus	*Mustela nivalis*
Erethizon dorsatum	*Neogale vison*
Clethrionomys gapperi	*Mephitis mephitis*
*Microtus chrotorrhinus**	*Procyon lotor*
Microtus pennsylvanicus	*Ursus americanus*
*Microtus xanthognathus**	*Homo sapiens*
Ondatra zibethica	
Phenacomys intermedius	
Synaptomys borealis	
Napaeozapus insignis	
Zapus hudsonius	
Lepus americanus	
Eastern Deciduous Forest Biome	
Cervus elaphus	*Canis lupus*
Odocoileus virginianus	*Canis lycaon*
Glaucomys volans	*Urocyon cinereoargenteus*
Marmota monax	*Lynx rufus*
Sciurus carolinensis	*Puma concolor*
Sciurus niger	*Lontra canadensis*
Tamias striatus	*Mustela frenata*
Castor canadensis	*Neogale vison*
Neotoma floridana	*Mephitis mephitis*
Peromyscus leucopus	*Spilogale putorius*
Peromyscus maniculatus	*Procyon lotor*
Microtus pennsylvanicus	*Ursus americanus*
Ondatra zibethica	*Homo sapiens*
Pitymys pinetorum	
Synaptomys cooperi	
Zapus hudsonius	
*Sylvilagus floridanus**	
*Sylvilagus transitionalis**	
Coastal Plain Biome	
Odocoileus virginianus	*Canis lycaon*
Glaucomys volans	*Urocyon cinereoargentus*
Sciurus carolinensis	*Lynx rufus*
Sciurus niger	*Puma concolor*
Castor canadensis	*Lontra canadensis*
Neotoma floridana	*Mustela frenata*
Oryzomys palustris	*Neogale vison*
Peromyscus gossypinus	*Mephitis mephitis*
Peromyscus nuttalli	*Spilogale putorius*
Peromyscus polionotus	*Procyon lotor*

Continuation of table 1

Prey	Predators
Sigmodon hispidus	*Ursus americanus*
Neofiber alleni	*Homo sapiens*
Reithrodontomys humulis	
Geomys pinetis	
*Sylvilagus aquatics**	
Sylvilagus floridanus	
*Sylvilagus palustris**	
Great Basin Biome (Utah)	
Antilocapra americana	*Canis latrans*
Odocoileus hemionus	*Canis lupus*
Ammospermophilus leucurus	*Vulpes macrotis*
Eutamias minimus	*Lynx rufus*
Spermophilus townsendi	*Puma concolor*
Microdipodops megacephalus	*Lontra canadensis*
Neotoma lepida	*Mustela erminea*
Perognathus longimembris	*Mustela frenata*
Perognathus parvus	*Neogale vison*
Peromyscus maniculatus	*Taxidea taxus*
Lagurus curtatus	*Memphitis memphitis*
Ondatra zibethica	*Spilogale putorius*
Onychomys leucogaster	*Procyon lotor*
Reithrodontomys megalotis	*Ursus arctos*
*Thomomys bottae**	*Homo sapiens*
*Thomomys talpoides**	
Dipodomys microps	
Dipodomys ordi	
Zapus princeps	
Lepus californicus	
Sylvilagus idahoensis	
Great Basin Biome (Oregon)	
Antilocapra americana	*Canis latrans*
Odocoileus hemionus	*Canis lupus*
Ammospermophilus leucurus	*Vulpes macrotis*
Eutamias minimus	*Lynx rufus*
*Spermophilus richardsoni**	*Puma concolor*
*Spermophilus townsendi**	*Lontra canadensis*
Castor canadensis	*Mustela erminea*
Microdipops megacephalus	*Mustela frenata*
Perognathus longimembris	*Neogale vison*
Perognathus parvus	*Taxidea taxus*
Peromyscus maniculatus	*Mephitis mephitis*
Lagurus curtatus	*Spilogale putorius*
Ondatra zibethica	*Procyon lotor*
Onychomys leucogaster	*Ursus arctos*
Reithrodontomys megalotis	*Homo sapiens*
Thomomys townsendi	
Dipodomys microps	
Dipodomys ordi	
Lepus californicus	
Lepus princeps	
Sylvilagus idahoensis	
Central Prairie Biome (Kansas)	
Antilicapra americana	*Canis latrans*
Bison bison	*Canis lupus*
Cynomys ludovicinus	*Vulpes velox*
Sciurus carolinensis	*Urocyon cinereoargenteus*
Sciurus niger	*Lynx rufus*
Spermophilus franklini	*Puma concolor*
Spermophilus spilosoma	*Lontra canadensis*
Spermophilus tridecemlineatus	*Mustela frenata*
Neotoma floridana	*Mustela nigripes*
Perognathus flavescens	*Mustela nivalis*
Perognathus flavus	*Neogale vison*
Perognathus hispidus	*Taxidea taxus*
Peromyscus maniculatus	*Mephitis mephitis*
Sigmodon hispidus	*Spilogale putorius*

Continuation of table 1

Prey	Predators
Castor canadensis	*Procyon lotor*
Microtus ochrogaster	*Ursus americanus*
Ondatra zibethica	*Ursus arctos*
Onychomys leucogaster	*Didelphis virginiana*
Reithrodontomys megalotis	*Homo sapiens*
Reithrodontomys montanus	
Synaptomys cooperi	
Dipodomys ordi	
Geomys bursarius	
Lepus californicus	
Lepus hudsonius	
Sylvilagus auduboni	
Central Prairie Biome (North Dakota)	
Antilocapra americana	*Canis latrans*
Bison bison	*Canis lupus*
Cynomys ludovicianus	*Vulpes velox*
Sciurus carolinensis	*Vulpes vulpes*
Sciurus niger	*Lynx rufus*
Spermophilus franklini	*Puma concolor*
Spermophilus richardsoni	*Gulo gulo*
Spermophilus tridecemlineatus	*Lontra canadensis*
Neotoma cinerea	*Mustela freneta*
Perognathus fasciatus	*Mustela nigripes*
Perognathus flavescens	*Mustela nivalis*
Perognathus hispidus	*Neogale vison*
Peromyscus maniculatus	*Taxidea taxus*
Castor canadensis	*Mephitis mephitis*
Microtus ochrogaster	*Spilogale putorius*
Microtus pennsilvanicus	*Procyon lotor*
Ondatra zibethica	*Ursus americanus*
Onychomys leucogaster	*Ursus arctos*
Reithrodontomys megalotis	*Homo sapiens*
Thomomys talpoides	
Dipodomys ordi	
Geomys bursarius	
Zapus hudsonius	
Lepus townsendi	
Sylvilagus auduboni	
Desert Biome (Chihuahua)	
Odocoileus virginianus	*Canis latrans*
Pecari tajacu	*Vulpes macrotis*
Spermophilus leucurus	*Lynx rufus*
Spermophilus mexicanus	*Panthera onca*
Spermophilus variegatus	*Puma concolor*
Neotoma albigula	*Mustela frenata*
Neotoma mexicana	*Taxidea taxus*
Perognathus penicillatus	*Conepatus mesoleucus*
Peromyscus eremicus	*Memphitis macroura*
Sigmodon hispidus	*Spilogale gracilis*
Onychomys torridus	*Bassariscus astutus*
Reithrodontomys megalotis	*Nasua narica*
Dipodomys merriami	*Homo sapiens*
Dipodomys ordi	
Lepus californicus	
Sylvilagus audubonii	
Sylvilagus floridanus	
Desert Biome (Baja California)	
Antilocapra americana	*Canis latrans*
Odocoileus hemionus	*Vulpes macrotis*
Ammospermophilus leucurus	*Urocyon cinereoargenteus*
Neotoma lepida	*Lynx rufus*
Perognathus baileyi	*Puma concolor*
*Perognathus fallax**	*Taxidea taxus*
*Perognathus spinatus**	*Spilogale putorius*
Peromyscus eremicus	*Bassariscus astutus*
Peromyscus manicualtus	*Procyon lotor*

Continuation of table 1

Prey	Predators
Thomomys bottae	*Homo sapiens*
Dipodomis agilis	
Dipodomis merriami	
Lepus californicus	
Sylvilagus auduboni	
Pine Forest Biome (Mexican Neovolcanic Belt)	
Odocoileus virginianus	*Didelphis virginiana*
Pecari tajacu	*Canis latrans*
Glaucomys volans	*Canis lupus*
Sciurus aureogaster	*Urocyon cinereoargenteus*
Sciurus oculatus	*Lynx rufus*
Spermophilus variegatus	*Puma concolor*
Baiomys musculus	*Lontra longicaudis*
Neotoma mexicana	*Mustela frenata*
*Oryzomys alfaroi**	*Taxidea taxus*
*Oryzomys fulvescens**	*Conepatus mesoleucus*
*Oryzomys melanotis**	*Mephitis macroura*
*Peromyscus aztecus***	*Spilogale putorius*
*Peromyscus boylii***	*Bassariscus astutus*
*Peromyscus difficilis***	*Nasua narica*
*Peromyscus furvus***	*Procyon lotor*
*Peromyscus leucopus***	*Homo sapiens*
*Peromyscus maniculatus***	
*Peromyscus melanotis***	
*Peromyscus truei***	
Sigmodon leucotis	
Lyomys irroratus	
Microtus mexicanus	
Neotomodon alstoni	
*Reithrodontomys chrysopsis****	
*Reithrodontomys fulvescens****	
*Reithrodontomys sumichrasti****	
Thomomys umbrinus	
Pappogeomys merriami	
Dasypus novemcinctus	
Romerolagus diazi	
Sylvilagus cunicularius	
Sylvilagus floridanus	
Tropical Dry Forest Biome (Oaxaca)	
Chironectes minimus	*Didelphis virginiana*
Tamandua mexicana	*Canis latrans*
Odocoileus virginianus	*Urocyon cinereoargenteus*
Pecari tajacu	*Herpailurus yagouaroundi*
Glaucomys volans	*Leopardus pardalis*
Marmosa canescens	*Leopardus weidii*
Marmosa mexicana	*Panthera onca*
Sciurus aureogaster	*Puma concolor*
Baiomys musculus	*Eira barbara*
*Liomys irroratus**	*Lontra longicaudis*
*Liomys pictus**	*Mustela frenata*
Neotoma mexicana	*Conepatus mesoleucus*
*Orizomys alfaroi***	*Spilogale putorius*
*Orizomys melanotis***	*Spilogale pygmea*
*Oryzomys palustri***	*Bassariscus astutus*
*Peromyscus boylii****	*Bassariscus sumichrasti*
*Peromyscus evides****	*Nasua narica*
*Peromyscus leucopus****	*Procyon lotor*
*Peromyscus megalops****	*Homo sapiens*
*Peromyscus melanophrys****	
*Peromyscus mexicanus****	
*Reithrodontomys fulvescens*****	
*Reithrodontomys mexicanus*****	
*Reithrodontomys sumichrasti*****	
Tylomys nudicaudis	

End of table 1

Prey	Predators
Coendou mexicanus	
Nyctomys sumichrasti	
*Sigmodon alleni******	
*Sigmodon mascotensis******	
Orthogeomys graudis	
Dasypus novemcintus	
Sylvilagus cunicularis	
Sylvilagus floridanus	
Ateles geoffroyi	
Tropical Humid Forest Biome (Yucatan)	
Marmosa mexicana	*Didelphis marsupialis*
Philander opossum	*Didelphis virginiana*
Tamandua mexicana	*Canis latrans*
Dasypus novemcintus	*Urocyon cinereoargenteus*
Mazama americana	*Herpailurus yagouaroundi*
Odocoileus virginianus	*Leopardus pardalis*
Tapirus bairdi	*Leopardus weidii*
Tayassu pecari	*Panthera onca*
Tayassu tajacu	*Puma concolor*
Agouti paca	*Eira barbara*
Sciurus deppei	*Galictis vittata*
Scuirus yucatanensis	*Lontra longicaudis*
Peromyscus yucatanicus	*Mustela frenata*
Heteromys spp	*Conepatus semistriatus*
Oryzomys spp	*Bassariscus sumichrasti*
Coendu mexicanus	*Nasua narica*
Dasyprocta punctata	*Procyon lotor*
*Otonyctomys hatty**	*Homo sapiens*
*Ototylomys phyllotys**	
Reithrodontomys spp	
Sygmodon hispidus	
Orthogeomys sp	
Sylvilagus floridanus	
Alouatta pigra	
Ateles geoffroyi	
Potos flavus	

* Were considered sister species.
** Were considered sister species.
*** Were considered sister species.
**** Were considered sister species.

Despite the range in species richness and community composition from north to south in both the Neoarctic and Palearctic macro-communities, the ratio between terrestrial mammalian predators and terrestrial mammalian prey remained relatively constant at 0.75.

Cohen (1977) who described a similar relationship in food webs was criticized by Pimm (1982) because top predators were described to "species", while the organisms at the lowest trophic levels were often described generally, as "plants" or "phytoplankton". Cole (1980), as well as Mithen and Lawton (1986), had different concerns and suggested that the ratios were maintained due to the random association of arbitrary numbers of predator and prey species.

In this study, there were just two categories of organisms, terrestrial mammalian predators and terrestrial mammalian prey and placement of each species into one of the two categories was based on the analysis of diet. Diets were analyzed as percent occurrence and percent biomass, where data were available. Robbins (1983) noted that prey items consumed by carnivores can vary greatly in energy content, with larger individuals providing more energy to predators. Because of the variability in prey characteristics, analyzing diets by percent occurrence tends to be less accurate than percent biomass (Delibes, 1980; Kruuk, 1986; Cumberland et al., 2001).

The results of the analysis in both the Neoarctic and Palearctic Biogeographic Regions indicated that a significant and constant relationship between the number of terrestrial mammalian predators and terrestrial mammalian prey existed. The validity of this relationship is supported by the goodness-of-fit test, which showed no statistically significant differences among the Neoarctic macro-communities, although the number of predators and prey were different in every macro-community. In addition, the Chi-square test indicated that the observed ratios were significantly different from random. Both of these analyses support the conclusion that these results represent a natural phenomenon characteristic of terrestri-

Table 2. **Species richness, numbers of terrestrial mammalian predators and terrestrial mammalian prey species and the predator/prey ratios for 14 macro-communities in 11 biomes of the Neoarctic Biogeographic Region**

Таблица 2. **Видовое богатство, численность наземных млекопитающих-хищников и видов-жертв наземных млекопитающих и соотношение хищник/жертва для 14 макрообществ в 11 биомах Неоарктического биогеографического региона**

Biome	Species Richness	Number of Prey	Number of Predators	Predator/Prey Ratio
High Arctic	7	4	3	0.75
Low Arctic	14	8	6	0.75
Boreal Forest	31	17	14	0.82
Deciduous Forest	30	17	13	0.76
Coastal Plain	28	16	12	0.75
Great Basin	35	20	15	0.75
Great Basin	35	20	15	0.75
Central Prairie	45	26	19	0.73
Central Prairie	44	25	19	0.76
Desert	30	17	13	0.76
Desert	23	13	10	0.76
Pine Forest	37	21	16	0.76
Tropical Dry Forest	42	23	19	0.82
Tropical Humid Forest	46	25	18	0.72

Table 3. **Species richness, numbers of terrestrial mammalian predator and mammalian prey species and the predator/prey ratio for 17 macro-communities associated within nine biomes in the Palearctic Biogeographic Region**

Таблица 3. **Видовое богатство, численность видов наземных млекопитающих-хищников и млекопитающих-жертв и соотношение хищник/жертва для 17 макросообществ, связанных в пределах девяти биомов Палеоарктического биогеографического региона**

Biome	Species Richness	Number of Prey	Number of Predators	Predator/Prey Ratio
Montane Tundra (Finland)	14	8	6	0.75
Arctic Tundra (Taimyr Peninsula)	13	7	5	0.71
Boreal Forest (Finland)	21	12	9	0.75
Boreal Forest (Arkhangelsk)	30	17	13	0.76
Boreal Forest (Ob River)	25	14	11	0.79
Montane Boreal Forest (Pamirs)	30	16	14	0.88
Deciduous Forest (South Norway)	20	11	9	0.82
Deciduous Forest (Central Germany)	27	15	12	0.80
Mixed Deciduous Forest (Primorye)	43	24	19	0.79
Grassland (Hungarian Plain)	29	17	12	0.71
Crimean Steppe	36	21	15	0.71
Poor Steppe (Mary)	42	24	18	0.75
Poor Steppe (Caspian Depression)	38	22	16	0.73
Poor Steppe (Turkistan)	37	23	14	0.61
Mediterranean (Spain)	23	13	10	0.77
Mediterranean (Italy)	18	10	8	0.80
Mediterranean (Greece)	21	12	9	0.75

al mammalian predator/prey systems in the northern continents, rather than a mathematical artifact. The preliminary analyses of macro-communities in the Palaeoarctic Biogeographic Region further support the conclusion that terrestrial mammalian predator/prey systems in the northern hemisphere, share underlying macro-ecological patterns.

The 0.75 ratio of terrestrial mammalian predators to terrestrial mammalian prey represents a macro-ecological pattern that may reflect how energy is partitioned between trophic levels and among species. The constant ratio may have several explanations. Since terrestrial mammalian predators represent an assemblage of species that primarily use terrestrial mammalian prey in a functionally similar manner, competition among predators, niche divergence, prey specialization and constraints such as metabolic rate at the level of the individual may all be implicated.

For many years, community ecologists have used the predator/prey ratio to explain how energy flow in one trophic level places constraints on adjacent trophic levels. The constancy of the terrestrial mammalian predator/prey ratios in northern continents may reflect such a constraint. Through evolutionary time, communities should evolve to optimize the use of available resources and terrestrial mammalian predators represent assemblages of species that utilize terrestrial mammalian prey in a functionally similar manner, potentially generating strong com-

petitive interaction with one another (Giller, 1984). Within any area, terrestrial mammalian prey are utilized differentially by terrestrial mammalian predators and competition will occur when the interaction of two or more species affect each other negatively (Pianka, 1978). Because this type of interaction has an adverse effect on all predators using the resource, prey specialization is likely to evolve in relation to prey occurrence and biomass and 0.75 may represent the optimal degree of specialization that has evolved. The data indicated clearly that in no macro-community had terrestrial mammalian predator/prey ratios approached 1.00, which would have indicated that each predator had specialized in a single prey species. The mean terrestrial mammalian predator/prey ratio may indicate that terrestrial mammalian predators that specialize above 0.75 over time tend to starve and become extinct when their prey populations crash to low densities, while terrestrial mammalian predators that specialize below 0.75 cannot compete with more specialized predators and succumb to competitive exclusion.

According to Smith (1996), the predator must find an equilibrium among many factors to attain an optimal diet, which will support growth, maintenance and reproduction. This should include: (1) a preference for the most profitable prey, (2) feeding selectively to obtain the greatest net energy gain, (3) the inclusion of less profitable prey when the most profitable prey are scarce and (4) the avoidance of unprofitable prey when profitable prey are abundant. At the interspecific level, the coexistence of two or more predators depends on the range of resources used by each one and the amount of overlap tolerated (Hespenheide, 1975).

Brown and Nicoleto (1991) suggested that in any given assemblage of species, those of the same size tend to not co-exist and they replace each other from habitat to habitat, generating the competitive exclusion of species of similar sizes within the same habitat. The body size distribution of preda-

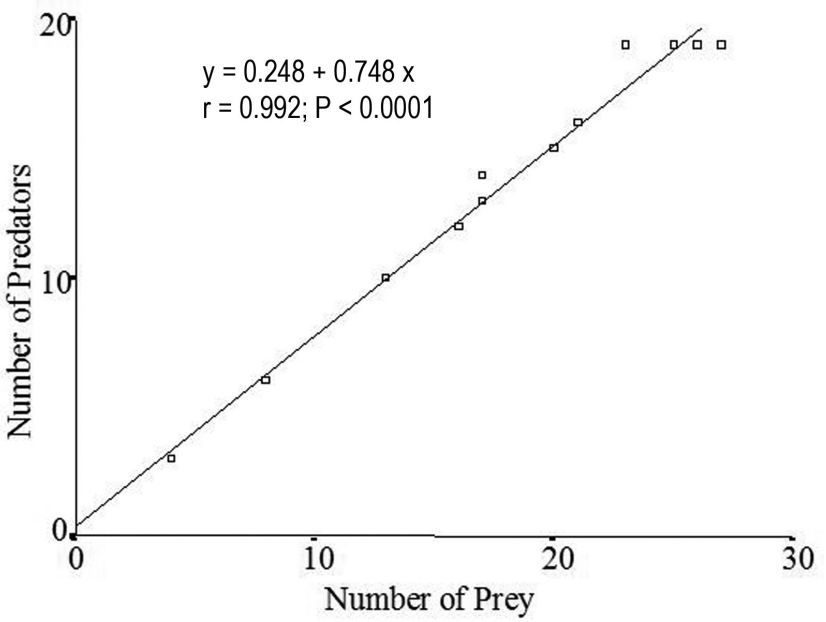

Fig. 1. Relationship between the number of terrestrial mammalian predators and terrestrial mammalian prey in different macro-communities associated with biomes throughout the Neoarctic Biogeographic Region.

Рис. 1. Взаимосвязь между численностью наземных млекопитающих-хищников и добычей наземных млекопитающих в различных макросообществах, связанных с биомами по всему Неоарктическому биогеографическому региону.

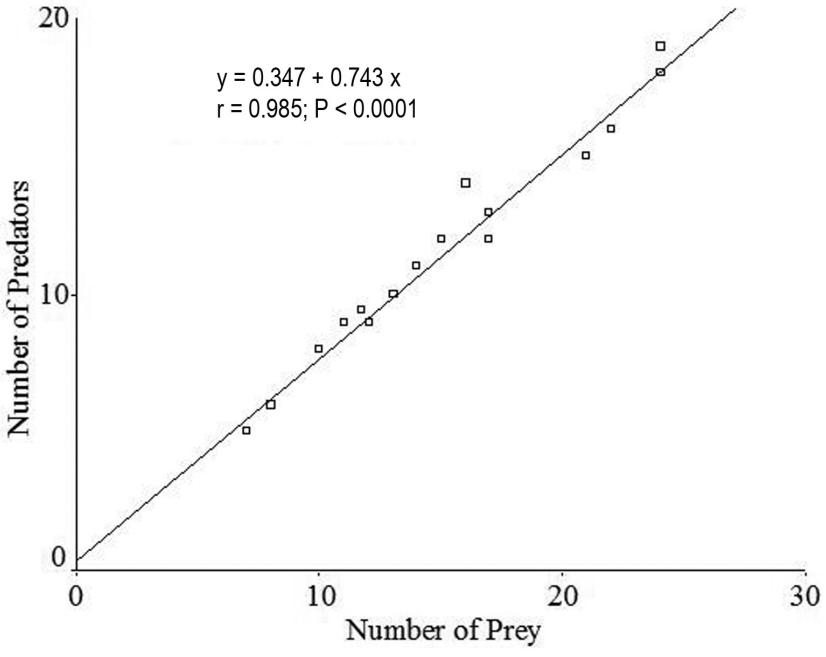

Fig. 2. Relationship between the numbers of terrestrial mammalian predators and terrestrial mammalian prey in different macro-communities associated with biomes in the Palearctic Biogeographic Region.

Рис. 2. Взаимосвязь между численностью наземных млекопитающих-хищников и наземных млекопитающих-жертв в различных макросообществах, связанных с биомами в Палеоарктическом биогеографическом регионе.

tors can be dependent also on the nature and size of their prey (McArthur, Levins, 1967) conferring differences in predator diets, which would allow coexistence in a competitive environment. The variation in the degree of specialization and the partitioning of resources of the different predators in every biome may reflect how limited energy is partitioned among predators and why the predator-prey ratio remains constant.

Metabolic rate and food habits may also influence this ratio. Metabolism is the process by which energy and materials are transformed within an organism and exchanged between the organism and its environment (Gillooly et al., 2001). Brown (1999) has hypothesized those fundamental constraints at the level of the individual drive phenomena in nearly all aspects of ecology. Kleiber (1932) first described the allometric relationship between mammalian basal metabolic rate (BMR) and body mass (M) with the equation (BMR = aMb), where (a) represents a constant and the scaling exponent (b) is ¾ or 0.75. However, the basal metabolic rate used in Kleiber's model is affected by the food habits of each mammalian predator. McNab (1989) has shown (1) that mammalian predator species that feed principally on flesh have a mean basal metabolic rate greater than Kleibers' curve, (2) that mammalian predator species with mixed diets generally have intermediate mean basal metabolic rates and (3) that mammalian species with mixed diets that include little flesh generally have basal metabolic rates below Kleiber's curve. This variation in basal metabolic rate related to different food habits may further explain how terrestrial mammalian predators share and specialize on limited resources and prey.

From this study, it was concluded: (1) that terrestrial mammalian species richness increases from north to south in the northern hemisphere, although the relationship is not totally latitude driven, (2) that terrestrial mammalian species composition changes in all macro-communities of all biomes studied, (3) that the mean terrestrial mammalian predator/prey ratio remained constant approximating 0.75 in all macro-communities in all the biomes of the Neoarctic and Palearctic Biogeographic Regions and appears to be universal macro-ecological pattern throughout the entire Northern Hemisphere and (4) that the amount of deviation from the mean terrestrial mammalian predator/prey ratio (0.75) may be used as a measure of the degree of environmental degradation that has been occurred in ecosystems due to disturbance.

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СИСТЕМЫ ХИЩНИК/ЖЕРТВА СРЕДИ НАЗЕМНЫХ МЛЕКОПИТАЮЩИХ СЕВЕРНОГО ПОЛУШАРИЯ: ВИДОВОЕ РАЗНООБРАЗИЕ И СОСТАВ ФАУНЫ

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В неоарктическом биогеографическом регионе наземные экосистемы млекопитающих доколумбовой эпохи были реконструированы примерно до 1400 г. н. э., составлены списки видов млекопитающих-хищников и жертв для каждого крупного сообщества в каждом биоме. Фаунистические комплексы для палеоарктического биогеографического региона были реконструированы примерно до 1000 г. н. э. для крупных сообществ, связанных с различными биомами от Западной Европы до Восточной Сибири. На основе этих данных был сделан вывод, что: (1) «видовое богатство» наземных млекопитающих увеличивается с севера на юг, (2) «видовой состав» наземных млекопитающих изменяется во всех крупных сообществах во всех биомах и (3) среднее соотношение хищников и жертв среди наземных млекопитающих остается постоянным, приближаясь к 0.75 во всех крупных сообществах во всех биомах неоарктического и палеоарктического биогеографических регионов, и, по-видимому, представляет собой универсальную макроэкологическую закономерность во всем Северном полушарии, (4) эволюция оптимальных стратегий поиска пищи, связанных с соотношением хищник/жертва 0.75, представляет собой средний верхний предел специализации, которого могут достичь наземные млекопитающие-хищники в Северном полушарии, где популяции жертв цикличны, а основная доступность жертв сильно варьирует. Отклонения от соотношения 0.75 в системах хищник/жертва среди наземных млекопитающих в Северном полушарии имеют последствия для сохранения и управления популяциями в дикой природе, связанные с поддержанием экологического равновесия.

***Ключевые слова*: соотношение хищников и жертв у млекопитающих, видовое богатство, видовой состав, северное полушарие.**