BODY-MASS DIVERSITY IN MARMOTS
РАЗНООБРАЗИЕ МАССЫ ТЕЛА У СУРКОВ
DIVERSITÉ DE LA MASSE CORPORELLE CHES LES MARMOTTES

K.B. Armitage, D.T. Blumstein
К.Б. Армитейдж, Д.Т. Блюмштейн

Department of Systematics and Ecology, The University of Kansas,
Lawrence, Kansas 66045-2106 USA
Факультет систематики и экологии Университета штата Канзас,
Лоуренс, Канзас 666045-2106 США

Abstract

Emergence mass is highly correlated with immergence mass, but explains about 55% of the variation. There is a 2-fold difference in body mass among marmot species. Total mass loss during hibernation is correlated with immergence mass. All measures of mass loss are correlated with each other. Big species may be big because they require the use of considerable mass during hibernation; however, mass loss is not significantly correlated with the length of hibernation. Body mass is related to the age of first reproduction and length of the active season. Environmental harshness may provide a unifying theme that integrates life-history traits and patterns of mass loss. Evidence for environmental harshness is derived from patterns of female reproduction, mass loss following emergence, variation in home-range size, time of mating, and reproductive skipping. The major sources of mass loss are maintenance during hibernation, reproduction, social thermoregulation, and post-emergence environmental stress. The importance of these four sources of mass loss vary among species and should determine the differences in body mass among species of marmots. Patterns of mass loss are related to social systems.

Key-words: mass, mass loss, environmental harshness, immergence, emergence, life-history traits.

Резюме

Масса тела сурков после спячки довольно точно коррелирует с массой тела перед ее началом. Однако, статистически эта корреляция составляет примерно 55%. В то же время показатели веса у разных видов рода Marmota отличаются примерно в два раза. Общие потери веса во время спячки коррелируют с массой тела сурков перед залеганием. Все значения потери массы коррелируют между собой. Крупные по размерам виды являются таковыми, потому что они вынуждены терять много энергии во время спячки. Однако, масса тела не всегда четко коррелирует с продолжительностью спячки. Масса тела в значительной мере определяет возраст наступления реальной половой зрелости у сурков, а также длину и продолжительность активного периода годового цикла. Резкая смена условий окружающей среды может нарушить сложившийся ритм, изменить жизненные циклы и привести к изменению динамики потерь веса. Очевидно, что неблагоприятные факторы окружающей среды могут изменять показатели размножения у самок, потери массы тела после выхода из нор весной, размеры индивидуальных участков, время размножения и частоту размножений по годам. Наибольшие потери веса у сурков происходят во время спячки из-за социальной терморегуляции, размножения и стресса после окончания спячки. Степень действия этих факторов отличается у разных видов животных и должно, по нашему мнению, определять различия массы тела у разных видов сурков.

Ключевые слова: масса, потери массы, изменения окружающей среды, появление после спячки, залегание в спячку, особенности жизненного цикла.

Résumé

La corrélation entre la masse corporelle à la sortie d'hibernation et celle à l'entrée en hibernation est importante, mais n'explique que 55% de la variation. La masse corporelle des espèces de marmottes varie du simple au double. La perte de masse corporelle au cours de l'hibernation est en corrélation avec la masse corporelle lors de l'entrée en hibernation. Toutes les mesures de perte de masse corporelle sont en corrélation entre elles. Les espèces pourraient être de grande taille car elles doivent dépenser une masse considérable pendant l'hibernation ; cependant, la perte de masse n'est pas en corrélation avec la durée de l'hibernation. La masse corporelle est liée à l'âge de la première reproduction et à la durée de la saison d'activité. La dureté du milieu pourrait fournir le cadre unificateur, intégrant les traits d'histoire de vie et les canevas de perte de masse corporelle. L'importance de la sévérité du milieu découle des patrons de reproduction des femelles, des pertes de masse suivant la sortie d'hibernation, de la variation de la taille du domaine vital, du moment de l'accouplement et des arrêts de reproduction. Les principales sources de perte de poids sont dues à l'entretien pendant l'hibernation, la reproduction, la thermorégulation sociale et la pression du milieu après la sortie d'hibernation. L'importance de ces quatre sources de perte de poids varie suivant les espèces et pourrait entraîner les différences de masse corporelle des espèces. Les patrons de perte de poids sont liés aux systèmes sociaux.

Mots clés: masse, perte de poids, dureté du milieu, entrée en hibernation, sortie d'hibernation, traits d'histoire de vie.

Introduction

Marmots are the largest mammals known to be true hibernators. A major advantage of large body size is that energy (fat) storage scales directly with mass (M^1) and the rate that energy (fat) is used at environmental temperatures below the thermal-neutral zone scales with mass ($M^{0.5}$) (French 1986). Thus, a large marmot can accumulate absolutely more mass than a small marmot and use the stored mass at a slower rate. Therefore, a larger marmot could hibernate longer or have more mass available for euthermic activities when food is insufficient to meet energy requirements after emergence.

Body mass undergoes seasonal changes and follows a circannual rhythm in yellow-bellied marmots, *Mamota flaviventris* (Ward & Armitage 1981) and probably in all marmot species (Davis 1976). Minimal body mass occurs at or near the time of emergence from hibernation and may be used as an index of body size (lean tissue, which reflects somatic growth). Maximal mass occurs at the time of immergence into hibernation and includes lean tissue and fat. The difference between the emergence mass and the immergence mass is a measure of mass use during the hibernation phase of the annual cycle.

We extracted body mass and mass loss data from the literature and calculated measures of mass loss from immergence and emergence masses and the length of hibernation (Table 1; see caption for Fig. 1 for references). Although we recognize that mass values may differ for different populations or sub-species of a species, we ignored these differences. Our goal was to look for broad trends and comparisons among species.

Emergence mass is highly correlated with immergence mass, but this correlation explains only about 55% of the variation between these two measures of mass (Fig. 1). For example, *M. olympus* and *M. caligata* have larger immergence masses than would be expected from their emergence masses. There is about a 2-fold difference in body mass among the 13 species included in this analysis. The variation in mass among species and the variation in the relationship between emergence and immergence masses raises the question of what accounts for these differences. Specifically, we address issues related to mass loss as measured by the difference between immergence mass and emergence mass.

Table 1.

Body-mass (g) and mass loss during hibernation for *Marmota*.
IM = immergence mass, EM = emergence mass.

Species	IM	EM	Mass Loss	% of IM lost	Loss (g/d)	Mass specific Loss (mg/g IM/d)	Length of Hibernation
baibacina	5583	3978	1605	28.7	7.64	1.37	7.0
bobak	4120	2910	1210	29.4	5.14	1.25	7.7
caligata	6187	3283	2904	46.9	13.8	2.23	7.5
camtschatica	4748	2900	1848	38.9	7.39	1.56	8.2
caudata	3923	2631	1292	32.9	5.33	1.36	7.6
flaviventris	3431	2422	1009	29.4	3.90	1.14	7.5
himalayana	6420	3445	2975	46.3	12.4	1.93	7.5
marmota	3987	2825	1236	31.0	6.45	1.62	6.5
menzbieri	3760	2321	1439	38.3	5.99	1.99	8.0
monax	4718	3356	1362	28.8	10.1	2.14	4.5
olympus	7100	3350	3750	52.8	16.7	2.35	7.5
sibirica	3960	2550	1410	36.5	7.05	1.78	6.6
vancouverensis	5328	3899	1429	26.8	7.34	1.37	6.5

Mass Loss

Total mass loss during hibernation is correlated with immergence mass (Fig. 2). This correlation explains 83% of the variation between the two variables. The rate of mass loss, measured as g/day, the specific rate of mass loss, measured as mg/g immergence mass, and the percentage of the immergence mass lost are significantly correlated with total mass loss and with each other (r varied from 0.74 to 0.94; p varied from 0.003 to <0.0001). This pattern of relationships suggests that the big species are big because they require the use of considerable

mass during hibernation.

Therefore, we ask the question, is mass loss correlated with the length of hibernation ? No measure of mass loss is significantly correlated with the length of hibernation (Table 2). It seems most likely that the length of hibernation is a factor in mass loss, but that factors other than the use of energy for maintenance during the torpor cycle are important.

Table 2.

Correlations between measures of mass or mass loss and the length of hibernation (months). IM = immergence mass.

	r	p
Immergence mass	-0.016	0.96
Emergence mass	-0.348	0.25
Total mass loss	0.192	0.54
% IM lost	0.368	0.22
mg/gIM/day	-0334	0.27
Mass loss (g/day)	-0.140	0.66

Possibly, mass loss is related to life-history traits. Larger species have longer developmental time and disperse later. These processes are related to length of the active season (Armitage 1981). Emergence mass, as a measure of body size, is poorly correlated with the length of the active season (Fig. 3). However, a pattern emerges when considering the age of first reproduction. *M. monax* is the only species that reproduces at age 1. Although the emergence mass of *M. monax* is among the largest among the species of marmots, the length of the active season is the longest (Fig. 3), which provides sufficient time to reach reproductive maturity in the first year of life. Five species begin reproduction at age 2. *M. caudata caudata* may breed at age 2, but *M. caudata aurea* does not breed before age 3 (Blumstein & Arnold, unpubl. data). Species first reproducing at age 2 have the smallest emergence masses; if large, they have a longer active season (e.g., *M. marmota* and *M. sibirica*). The remaining species are the larger marmots with a short to moderately long active season and first reproduce at age 3. *M. baibacina* stands out as an exception to the pattern; it is the largest species with a moderately long active season and breeds at age 2. However, 2-year old pregnant females are rare (Zimina 1978) and in some populations maturity occurs at age 3 (Bibikov 1996).

Table 3.

Orthogonally rotated factor scores of traits related to mass and mass loss. Only those traits with factor scores > 0.5 are included.

Traits	Factors			
	1	2	3	4
Immergence mass (IM)	0.802		0.573	
Total mass loss	0.956			
% of IM lost	0.900			
Mass loss (g/day)	0.953			
Specific mass loss (mg/gIM/day)	0.888			
Length of active season		-0.939		
Length of hibernation		0.939		
Age of first reproduction		0.743		
Skip reproduction		0.661	0.553	
Emergence mass			0.939	
Litter size				0.949
Time of breeding				0.902
% explained	39.9	30.5	13.0	9.8

The frequency of reproduction of female marmots varies (Armitage 1996) as does the timing of breeding (Bibikov 1996). We asked the question how are various reproductive traits related to body mass and the length of hibernation ? A factor analysis of 12 traits produced four interpretable factors that explained 93.2% of the

variation (Table 3). Factor 1 included the measures of mass and mass loss and was designated a mass factor. Factor 2 was designated a time factor as it included the length of hibernation and age of first reproduction. Skip reproduction (one or more years elapses between successful breeding by an adult female) loaded more heavily on this factor than on the other factors and appears to be a function of how frequently litters are produced by a female. Emergence mass characterizes factor 3 and we designate it the emergence mass factor. Skip reproduction and immergence mass also loaded on this factor. Time of breeding (prior to or after emergence) and litter size loaded on factor 4. We designated factor 4 a breeding factor. The factor analysis suggests that a complex interplay among the traits may account for body size (mass) and mass loss. For example, skip reproduction loaded on factors 2 and 3, which suggests that skipping reproduction may be a function of the interaction of body mass and length of active (or hibernation) season. Environmental harshness is one factor that may provide a unifying theme that integrates all life-history traits.

Environmental Harshness

Environmental harshness, or environmental severity, is not readily defined and can include factors such as environmental temperature, rainfall (drought), predation risk, social stress, and length of the growing season (Barash 1989). In this paper we focus on physical factors, such as length of winter, snow cover, and air temperature that affect survival and reproduction. Because climatic records for the habitats of most species of marmots are unavaiable, we examine five features of marmot biology for evidence of environmental harshness.

The first set of evidence derives from reproduction. Reproductive females accumulate far less fat *(M. baibacina, M. sibirica)* than barren females, embryos may be reabsorbed in bad years *(M. baibacina, M. caudata)*, good feeding in one year makes possible breeding in the following year (*M. camtschatica*), drought affects reproduction and survival (*M. bobak, M. flaviventris*), and reproduction may occur in successive years only if the litter is small *(M. marmota)* (Table 4). Not only do these reproductive characteristics suggest a harsh environment, they also suggest an environment that may vary among years in degree of harshness.

Table 4.

Evidence for environmental harshness based on reproductive characteristics.

M. marmota	Can reproduce in successive years if litter no more than two	Bonesi et al 1996
M. caudata	Up to 48% of embryos reabsorbed when emergence conditions are poor; e.g., a cold spring; in one year no young *M. c. aurea* emerged in the 15 social groups studied	Zimina 1978, Blumstein, Arnold - unpubl. data
M. bobak	Accumulates fat more rapidly in moist years; more juvenile mortality during hibernation following drought	Shubin 1963, Zimina 1978
M. sibirica	Reproductive females accumulate 414g of fat, barren females 747g at hibernation	Zimina 1978
M. baibacina	25% of all embryos reabsorbed in bad years, occurs in one-half of the females; reproductive females accumulate 525g, barren females, 1100g of fat at hibernation	Zimina 1978
M. flaviventris	Summer drought results in high mortality of juveniles and reproductive females in subsequent hibernation	Armitage 1994

Mass loss following emergence suggests environmental harshness. Such loss typically occurs when post-emergence weather conditions are stressful; e.g., snow cover or cold, snowy weather (Table 5). Mass loss probably is associated with the lack of new forage, which would be especially severe during prolonged snow cover.

Home range areas vary widely among species of marmots from as little as 0.13 ha to 13.8 ha (Table 6). Some evidence suggests that the variation in home range size reflects variation in resource availability. The vegetation biomass is much less for those species that have large home ranges (Table 6). However, not all plant species are palatable to marmots and marmots probably select some subset of the available vegetation (Frase & Armitage 1989). The home range must be of sufficient size to provide sufficient palatable food and burrows for the individual or family group. Thus, group size may be associated with home-range size. Interestingly, some evidence suggests that group size is not directly related to home-range area. First, home-range size may not vary much between years when group size varies and home-range size may not be related to group size (Blumstein & Foggin 1997). Second, the average adult member of a *M. camtschatica* family would have 3.7 ha of the 13.0 ha

average family home range (calculated from Mosolov & Tokarsky 1994). By contrast, the average adult member of a *M. flaviventris* matriline would have about 0.15 ha. When the population of *M. flaviventris* increases, the average home range size does not, but the overlap in home ranges is directly related to population density (Armitage 1975). Even if the *M. flaviventris* matriline home range triples, it would still be much smaller than that of *M. camtschatica*. This comparison suggests that large home ranges occur where food is of poor quality and/or scanty. Scattered or low quality food resources suggest another way in which a species' environment may be harsh.

Table 5.

Evidence for environmental harshness based on mass loss after emergence.

M. monax	Lose mass (300g in females) for 6 weeks	Snyder et al. 1961
M. flaviventris	Rare, usually begins gaining mass	Armitage 1996
M. caligata, M. olympus	May lose mass for several weeks in years of heavy snow	Barash 1989
M. bobak	Especially when snow cover lasts or cold, snowy weather occurs	Zimina 1978
M. sibirica	Use fat	Bibikov 1996
M. marmota	Typically lose mass for about 2 weeks when ground snow covered	Arnold per. com.
M. caudata	Lose mass for up to two weeks	Barash 1989
M. baibacina	Lose mass and use fat for 2-2.5 months	Bibikov 1996
M. camtschatica	Pronounced use of fat reserves	Bibikov 1996

Table 6.

Evidence for environmental harshness based on home range area. Data for vegetation biomass, measured as mean dry mass of aboveground herbaceous vegetation at peak growth, from Holmes 1984, except for *M. caudata aurea* from Blumstein & Foggin 1997.

Species	Home range area (ha)	Vegetation bio mass (g/m^2)	Reference
M. monax	0.6-0.7 (predispersal)		Ferron & Ouellet 1989
	1.3		Meier 1985
M. flaviventris	0.13-1.0	383	Armitage 1975
M. olympus	2.0	206	Barash 1973
M. caligata	13.8	117	Holmes 1979
M. vancouverensis	3.0		Heard 1977
M. marmota	1.4-5.7		Sala et al 1992
	2.6		Arnold 1993b
M. caudata aurea	3.1	22-51	Blumstein 1996
M. camtschatica	13.0		Mosolov & Tokarsky 1994

Many species of marmots mate before emergence and some development may also occur before emergence (Table 7). Presumably, mating and development occur before emergence because conditions above ground are unfavorable for activity and the burrow provides a less stressful standard operative temperature (Melcher et al 1990). Mating requires that the animals be euthermic. Euthermy requires a high expenditure of energy, at least a 20-fold increase above the energy used in torpor.

This use of energy is supplied by fat accumulated the previous summer and as a consequence, considerable mass loss occurs at this time and this mass loss is reflected in the emergence mass.

If the environment is harsh so that a female that breeds in one year does not have sufficient time and resources to permit reproduction the following year, the female may skip reproduction for one or more years. Many female *M. flaviventris* reproduce annually (Armitage 1984), but in a high altitude population where snow cover persists much later, no female reproduced in successive years (Johns & Armitage 1979). Many species typically skip one year (Table 8); these species, except *M. olympus*, are relatively smaller. Females may skip two

or more years; these species, except *M. caudata* and *M. menzbieri*, are the larger marmots. *M. menzbieri* may skip reproduction because it has one of the shortest active seasons. By contrast, *M. monax*, one of the larger marmots, has the longest active season and reproductive skipping does not occur.

Table 7.

Evidence for environmental harshness from hibernation and the time of mating
for species of *Marmota*.

After Emergence	*monax* (Snyder & Christian 1960); *flaviventris* (Armitage 1965); *caligata* (Holmes 1984); *olympus* (Barash 1973), *vancouverensis* (Nagorsen 1987); *marmota* (Arnold 1990)
Before Emergence	*baibacina, sibirica* (Zimina 1978)
Development Before Emergence	*bobak*, birth may occur (Zimina 1978); *broweri*, young born 1-2 weeks later (Rausch & Bridgens 1989); *camtschatica*, young half-developed (Kapitonov 1963); *caudata*, young half-developed (Zimina 1978)

Table 8.

Evidence for environmental harshness from reproductive skipping in the genus *Marmota*.

Usually One Year	Often Two or More Years
bobak (Rymalov 1994) *marmota* (Arnold 1993b) *olympus* (Barash 1973) *sibirica* (Bibikov 1996)	*baibacina* (Bibikov 1996) *caligata* (Holmes 1984) *camtschatica* (Yakolev & Shadrina 1996) *caudata* (Blumstein & Arnold, pers. com.) *menzbieri* (Bibikov 1996) *vancouverensis* (Bryant 1996)

Social Thermoregulation

Social thermoregulation has been demonstrated only in *M. marmota* (Arnold 1993b). However, social thermoregulation is likely to be widespread given that most species hibernate in groups (Bibikov 1996). Social thermoregulation is costly; mass loss increases with increased group size when juveniles are present. When juveniles are absent, mass loss decreases with increased group size (Arnold 1993b). Thus, the benefits and costs of group hibernation depend on group composition.

Summary of Mass Loss

There are four major sources of mass loss: (1) maintenance during hibernation, (2) reproduction, especially when initiated before emergence, (3) social thermoregulation, and (4) post-emergence environmental stress. The importance of these four sources varies among the species of marmots. All species must meet maintenance costs of hibernation; these costs form the basis of mass loss and determine the minimal mass needed at immergence. All other sources of mass loss require additional mass beyond that required for basic maintenance. We predict that these additional needs will primarily determine the differences in body size, as measured by mass, among species of marmots.

Mass Loss and Social Systems

Marmots live in four types of social systems that we define based on summer and winter social groups (Fig. 4). *M. monax* females live solitarily and several females may live within the home range of one male. We designate this pattern diffuse harem polygyny in which females and males are not socially integrated and solitary hibernation occurs. Although the percentage of mass lost during hibernation is low, this loss occurs in four months and daily mass loss is relatively high (Table 1); total loss is greater than that of *M. flaviventris, M. caudata, M. marmota*, and *M. bobak*. Woodchucks from a more northerly population with longer hibernation and a shorter active season lost 36.9% (Fig. 4) of their mass (Ferron 1996). *M. monax* relies on its large size and long active season to accumulate sufficient fat for hibernation and early post-emergence activity.

In *M. flaviventris*, females form social groups in the summer to which an adult male attaches to form a harem (Armitage 1991). In this concentrated harem polygyny, males are not integrated into the social group. Hibernation typically is solitary although females in the same matriline may hibernate together and juveniles hibernate as a group (Armitage, unpubl. data, Lenihan & Van Vuren 1996). At higher elevations, all yellow-bellied marmots hibernated socially (Johns & Armitage 1979). Thus, group hibernation in this species is facultative for adults, but may be obligatory for the more vulnerable juveniles. Mass loss is relatively low; thus we predict that their environments are less harsh than those of most other species and that social thermoregulation does not occur, but facultative group hibernation may provide benefits in some environments.

Concentrated harem polygyny occurs in *M. olympus* and *M. caligata* where females live somewhat independently during the summer in association with a territorial male (Barash 1989). All are somewhat socially integrated and hibernate as a group. Mass loss is high, both as a percentage of body mass and as total mass lost (Fig. 2). A social group may have either young or yearlings but not both (Barash 1989). We predict that social thermoregulation occurs in these species, and that the parents bear the cost by losing considerable mass during hibernation. Thus, these two species are among the largest marmots, which make possible the accumulation of sufficient fat for maintenance, social thermoregulation, and post-emergence loss (Table 5).

The remaining species are organized into family groups that are socially integrated in the summer and hibernate as a group. Although monogamy is the prevailing mating system, polyandry may occur in those species that retain non-breeding, adult males in the family group; e.g., *M. marmota* (Arnold 1990), *M. bobak*, and *M. baibacina* (Rymalov 1994), *M. caudata* (Blumstein & Arnold pers. com.). All species in this group lose a high percentage of their mass during hibernation. We predict that social thermoregulation occurs in most, if not all, of these species. Some species lose additional mass because reproduction is initiated before emergence. Mass may be lost post-emergence because of unfavorable weather conditions (Table 5). Reproductive skipping characterizes all of these species.

Conclusions

Heavy energy demands are met by a large body size that permits the accumulation of absolutely more fat and the use of the fat relatively more slowly. Thus, larger species are larger because they both accumulate and use more fat in the annual cycle. Species with high mass loss reduce their frequency of reproduction and delay the age of first reproduction. In order to fully understand the mass cycle of marmots, we need to partition out the various sources of mass loss: maintenance during hibernation, social thermoregulation, pre-emergence reproduction, and post emergence maintenance and reproduction. This analysis requires laboratory studies of the annual cycle of energy use.

We predict that when the costs of hibernation maintenance are measured for all species under identical conditions, larger species will lose relatively less mass than smaller species. We also predict that the largest species live where environmental harshness is more severe. We predict that species that initiate reproduction before emergence use more mass than those that initiate reproduction post-emergence. In those species that hibernate in social groups, we predict mass loss will be less than in those that hibernate singly. However, social thermoregulation of juveniles will lead to relatively large mass loss. Furthermore, mass loss will be related to group size and the age structure of the population (e.g., see Arnold 1993b). We predict that patterns of mass loss will vary within a species based on environmental harshness, e.g., marmot populations at lower elevations or latitudes will lose less mass and skip reproduction less frequently than populations at higher elevations or latitudes. Finally, we predict that marmots from populations within a species will be larger at higher elevations or latitudes than at lower elevations.

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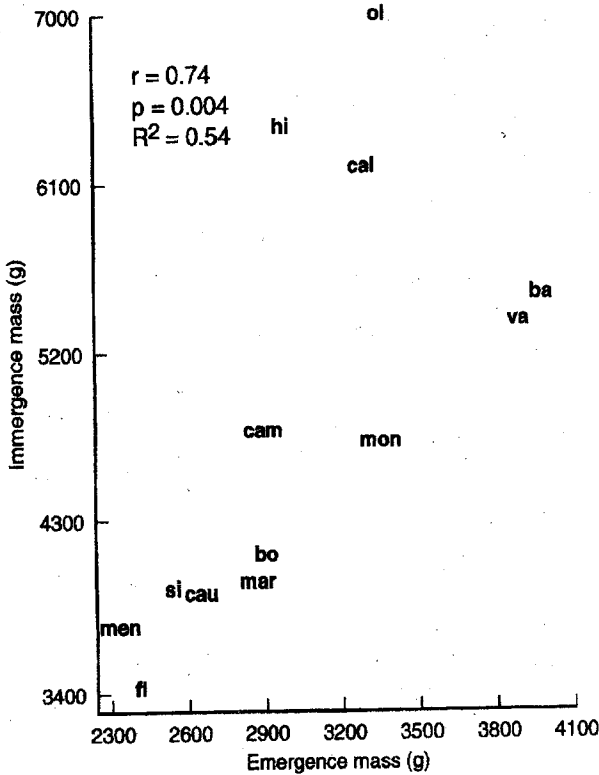
FIGURES / *РИСУНКИ*

Fig. 1. The relationship between immergence mass and emergence mass for *Marmota*. ba = baibacina, bo = bobak, cal = caligata, cam = camtschatica, cau = caudata, fl = flaviventris, hi = himalayana, mar = marmota, men = menzbieri, mon = monax, ol = olympus, si = sibirica, va = vancouverensis. Mass data taken from Armitage unpubl., Arnold 1990, 1993, Barash 1973, 1989, Bibikov 1996, Blumstein 1997, USNM specimens, Bryant pers. com., Ferron 1996, Heard 1977, Mashkin 1982, Snyder et al. 1961.

Рис. 1. *Связь между массами тела до и после спячки у видов рода* Marmota. *ba* = baibacina, *bo* = bobak, *cal* = caligata, *cam* = camtschatica, *cau* = caudata, *fl* = flaviventris, *hi* = himalayana, *mar* = marmota, *men* = menzbieri, *mon* = monax, *ol* = olympus, *si* = sibirica, *va* = vancouverensis. *Данные по массе взяты из: Armitage, unpubl.; Arnold, 1990, 1993; Barash, 1973, 1989; Bibikov, 1996; Blumstein, 1997; USNM specimens; Bryant, pers. com.; Ferron, 1996; Heard, 1977; Snyder et al., 1961; Машкин, 1982.*

Plot 1 (Immergence mass (g) vs Emergence mass (g)):
r = 0.74
p = 0.004
R² = 0.54

Fig. 2. The relationship between mass loss during hibernation and immergence mass. Abbreviations of species names as in Fig. 1.

Рис. 2. *Связь между потерей массы в течение спячки и массой перед спячкой. Обозначения те же, что на рис. 1.*

Plot 2 (Mass loss during hibernation (g) vs Immergence mass (g)):
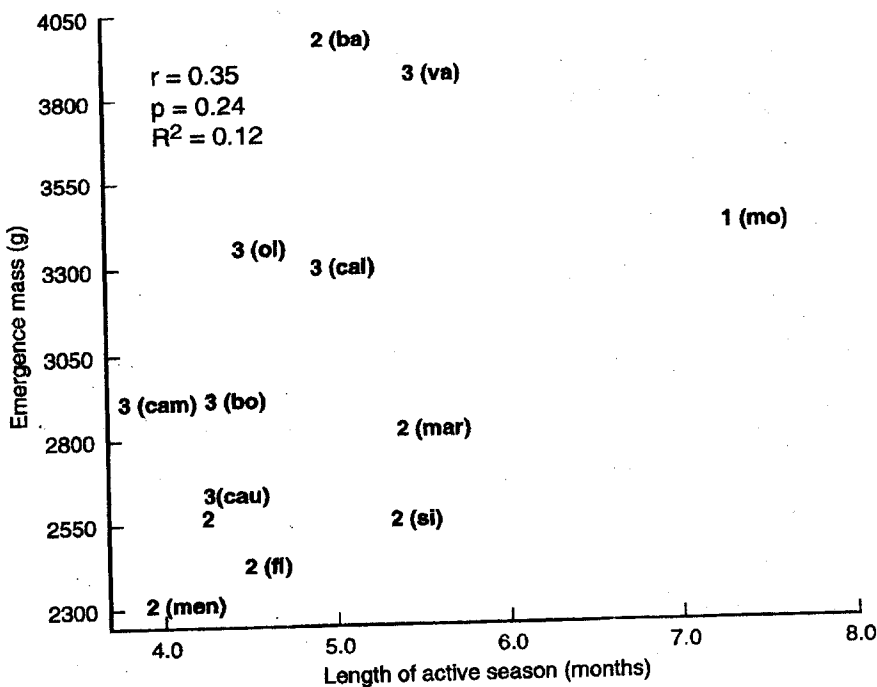r = 0.91
p = <0.0001
R² = 0.82
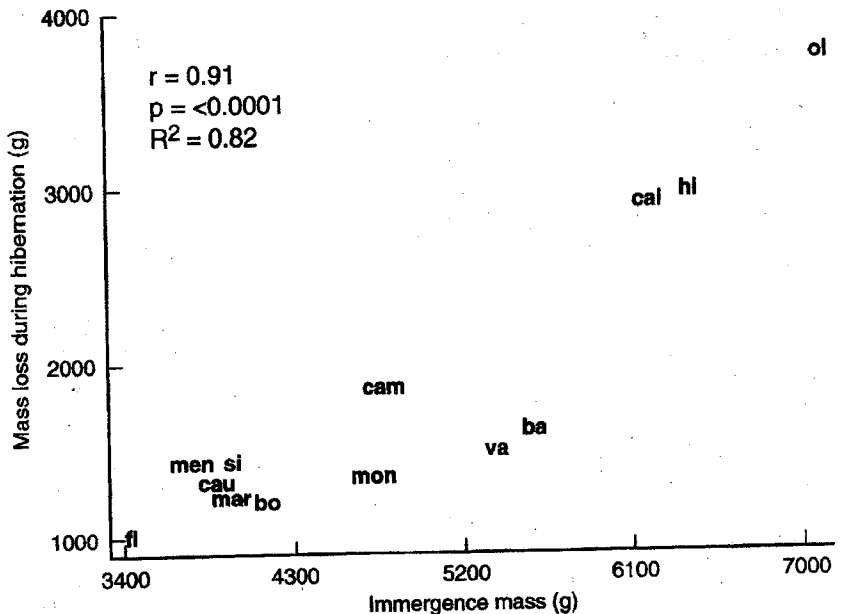
Fig. 3. The relationship between emergence mass and length of the active season. The numbers next to the abbreviation of the species name (as in Fig. 1) refer to the age of first reproduction.

Рис. 3. *Связь между массой тела после спячки и длительностью сезона активности. Цифры после аббревиатур названий видов (см. рис. 1) означают возраст первого размножения.*
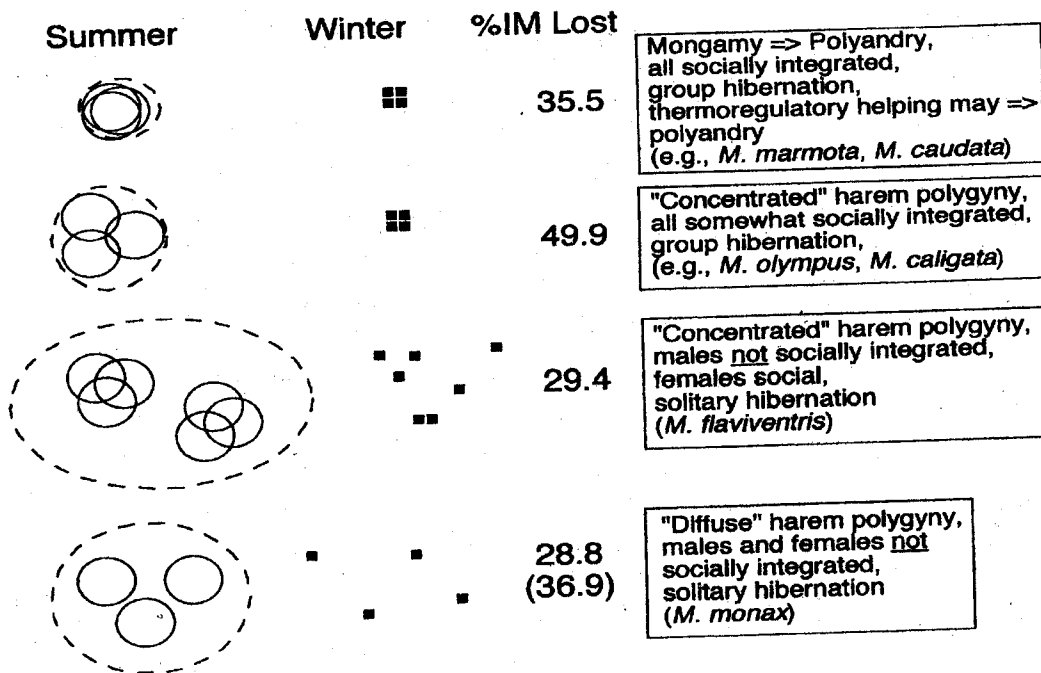

Fig. 4. The relationship between summer and winter dispersion, per cent mass loss, and the social system. Solid circles = female home range, dash circles = male home range, solid square = one hibernating individual, IM = immergence mass.

Рис. 4. *Связь между зимней и летней дисперсией, потерей массы (%) и социальной системой. Черные кружки - участки самок, кружки со стрелкой - участки самцов, черные квадраты - одна особь в спячке, IM - масса перед спячкой*

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Holarctic Marmots as a Factor of Biodiversity (K.B. Armitage & V.Yu. Rumiantsev Eds). - *Proceedings of The 3d International Conference on Marmots, Cheboksary, Russia, 25-30 August 1997*. - Moscow: ABF P.H., **2002**, 411 p.

The results of researches on marmots carried out mainly during the 1990th in Russia and abroad are discussed: theoretical and practical problems of marmots' ecology and ethology, their protection and population management.

The book may be useful for wide range of zoologists, specialists on animals' protection and management, students of biology, etc.