Appendix 2 – Description of scientific achievements

Mammal Research Institute
Polish Academy of Sciences

Karol Zub

The effect of body mass and metabolic rates variation on mortality of small mammals

Białowieża 2015

Name: Karol Zub

Date and place of birth: 3rd May1968 r., Mońki

Adress: Mammal Research Institute PAS, ul. Waszkiewicza 1, 17-230 Białowieża
Tel. +48 85 6827792, fax: +48 85 6812289; e-mail: karolzub@ibs.bialowieza.pl

Education and academic degrees

1. 2006: PhD; Biology Institute, University in Białystok; dissertation title: „Factors affecting variation of body size in weasel *Mustela nivalis*” (supervisor: Prof. Marek Konarzewski)
2. 2002: master of science; thesis „Factors affecting selection of breeding sites and diet of the Lesser Spotted Eagle *Aquila pomarina* in the Nizina Północnopodlaska” (supervisors: Prof. Marek Konarzewski and Prof. Bogumiła Jędrzejewska)
3. 1998-2002: University in Białystok, Faculty of Biology and Chemistry
4. 1988-1991: Warsaw University of Life Sciences, Faculty of Forestry
5. 1983-1988: Forestry School in Białowieża

Employment

1. Form July 2006: Mammal Research Institute, Polish Academy of Sciences, assistant professor
2. July 2002 - July 2006: Mammal Research Institute, Polish Academy of Sciences, junior scientist
3. August 1990 – July 2002: Mammal Research Institute, Polish Academy of Sciences, laboratory technician

SUMMARY OF PROFESSIONAL ACCOMPLISHMENTS

I was born in 1968 in Mońki, where I attended primary school. In 1983 I started education in the Forestry School in Białowieża. In 1983-1988 I regularly participated in scientific expeditions organised in Biebrza Marshes by scientist from the Mammal Research Institute PAS in Białowieża and the Biology Institute, Branch of Warsaw University in Białystok, as well as in scientific work conducted by MRI PAS staff in the Białowieża Forest. I was involved in studies on species composition of small mammals communities, as well as in studies on population dynamics of small mammals and moose. In 1988-1991 I studied at Faculty of Forestry, Warsaw University of Life Sciences (from 1990 as external student). In 1990 I started to work as laboratory technician in the Mammal Research Institute PAS in Białowieża. From 1998 I continued education as full-time student at University in Białystok, Faculty of Biology and Chemistry, where I completed a master degree in biology in 2002. I defended my doctoral thesis „Factors affecting variation of body size in weasel *Mustela nivalis*" and got a PhD in biology in 2006. Since 2006, I have been working in the Mammal Research Institute Polish Academy of Sciences as an assistant professor. In 2007 I was on 6-months scholarship at Aberdeen University (Scotland), working in the research group of Prof. John Speakman. In 2009 I was on 2-month scholarship at University of Edinburgh (Scotland), in the research group of Prof. Loeske Kruuk. In 2011 I spent again 2 months at Aberdeen University, working with Prof. John Speakman and Prof. Xavier Lambin.

In 2013 together with Dr. Paulina Szafrańska and Prof. Marek Koanrzewski we received an Award of Biology and Agricultural Science Faculty II, Polish Academy of Sciences, for series of publications on factors affecting variation in body size and metabolic rates of weasels *Mustela nivalis*.

I am an author or co-author of 36 scientific papers, of which 31 are on ISI Master Journal List [Appendix 3]. Some of these were published in highly ranked and prestigious journals such as: *Journal of Animal Ecology*, *Molecular Ecology*, *Proceedings of the Royal Society of London*, *Journal of Experimental Biology*, *Functional Ecology*, *Ecology* and *Science*. In total my papers were cited 452 times (source: Web of Science, 08.01.2015). The Average Citation Rate of my articles was 14.6. The h-index (source: Web of Science, 08.01.2015) was 11, and cumulative impact factor (IF) for all published articles was 106.3 [Appendix 3]. I carried out my scientific tasks by raising funds for research and by taking part in the international cooperation [Appendix 4]. In total I contributed to 11 scientific projects (national and international), including 3 as a project leader.

The results of my research were presented at national and international conferences (e. g. in UK, Russia and Czech Republic). In total I participated in 6 conferences [Appendix 3]. I disseminated my knowledge and results of my research in periodicals such as *Łowiec Polski*, *Las Polski*, *Parki Narodowe*, *Matecznik Białowieski*, *Sekrety Nauki*, *Poznaj Swój Kraj*. I was also frequently interviewed by the Polish newspapers, e. g. *Gazeta Wyborcza* [Appendix 4].

Based on my scientific experience I prepared several expert opinions, including management plan for mammals in the Białowieża National Park and National Park "Bory Tucholskie", management plans for mammal in the nature reserves in the Knyszyn Forest and Protection Plan Tasks for NATURA 2000 site "Puszcza Knyszyńska". I also participated in preparation of the environmental impact report for local airport in the Podlasie province and environmental assessment report for the Implementation Document for Transport Development Strategy until 2020. In 2012-2014 I prepared three expert opinions on food resources for the Lesser Spotted Eagle for the LIFE project concerning protection of this species. I also prepared report concerning diversity and distribution of mammals and birds in the NATURA 2000 site "Murawy w Haćkach" [Appendix 3].

I have also some experience in education. In 2003-2010 I conducted laboratory trainings and lectures at "Summer Schools", in projects BIOTER and BIOSEB organized by Mammal Research Institute for master and PhD students form all over the Europe and financed form UE sources. I also taught primary and secondary school students, tourist guides, Białowieża National Park staff, etc. I have been a tutor of four master's thesis and co-supervisor of one master's thesis, so far [Appendix 4].

During my work I also engaged myself in the activities related to the organization of science: I reviewed manuscripts for scientific journals, e.g. *Proceedings of the Royal Society of London*, *Functional Ecology*, *Journal of Animal Ecology*, *Biology Letters*, Behav*ioral Ecology and Sociobiology*, *Physiology and Behavior*, *Oecologia*, Mammalian Biology, *Forest Ecology and Management*, *Journal of Mammalogy*, *Oikos*, *Acta Theriologica* (36 reviews in total). I also reviewed 2 grants and evaluated 43 proposals for the National Science Centre, as a member of experts team. In 2007-2008 I was responsible for organization of scientific seminars in the Mammal Research Institute and " Białowieża Scientific Seminars". I was a member of the Scientific Council of the Mammal Research Institute (2011-2014) and Local Ethical Committee in Białystok (2014) [Appendix 4].

In 2005-2013 I was an Associate Editor in *Acta Theriologica* (currently *Mammal Research*) and from 2013 I am an Editor-in-Chief of this journal.

For many years I cooperate with scientist from Biology Institute of the University in Białystok (Prof. Marek Konarzewski, Prof. Anetta Borkowska and Dr. Aneta Książek) and Forestry Research Institute (Prof. Jerzy M. Gutowski and Dr. hab. Zbigniew Borowski). I have develop my scientific experience in the laboratories supervised by eminent specialists such as Prof. John R. Speakman, Prof. Xavier Lambin and Prof. Stuart Piertney (Univeristy of Aberdeen, Scotland), and Prof. Loeske Kruuk and Dr. Jarrod Hadfield (University of Edinburgh, Scotland). I have been cooperating also with Prof. Mark Chappell (Univeristy of California, Riverside, USA), Dr. Allan McDevitt (University College Dublin, Ireland), Dr. Dina Dechmann and Dr. Scott LaPoint (Max Planck Institute, Radolfzell, Germany).

From the beginning of my scientific work I conducted studies at the intersection of different fields – ecology, physiology, evolutionary biology and genetics. I am mainly interested in morphological, physiological and behavioural adaptations of mammals to seasonal and long-term changes in the environment, affected by climate, food resources, competition and predator-prey interactions. However, classical ecology is still important part of my research, e. g. population dynamics, habitat selection or variation of diet. In my studies I use different field, laboratory and experimental techniques, e.g. radio-tracking, estimation of energy expenditures, GIS and statistical modelling, genetic analyse of quantitative traits.

As school-age student (1983-1988) I participated in collaborative studies in the Biebrza Marshes, conducted by the Mammal Research Institute PAS in Białowieża and Biology Institute of the Warsaw University Branch in Białystok. This research concerned species composition of small mammal communities and population dynamics of the root vole. During this time I acquired experience in scientific field work and identification of small mammals. Since 1985 I participated also in the research on community of predators and prey conducted in the Białowieża Forest by the team led by Prof. Włodzimierz Jędrzejewski and Prof. Bogumiła Jędrzejewska. This work allowed me to learn more about biology of mammals. In 1990 due to family considerations I had to interrupt my education at the Forestry Faculty in Warsaw and got a job as laboratory technician in the Mammal Research Institute PAS in Białowieża. From the beginning of my work I participated in the long-term studies on population dynamics of small mammals, which resulted in two publications on this subject [20, 25 – numbers in the square bracket refer to publications listed in Appendix 3]. I also participated in the radio-tracking studies of weasels, which revealed that those predators are active almost exclusively at day-hours, much longer during breeding season and during summer, but in winter their activity is limited to 2-4 hours daily [9]. Later I also took part in research on ecology of wolves. In two publications [8 and 11], we demonstrated that red deer is preferred prey of wolf in the Białowieża Forest. Predation of wolves on red deer was higher during periods characterized by deeper snow cover, which was probably related to deteriorated condition of prey. Mean daily consumption by wolves averaged almost 6 kg of meat per individual. This research demonstrated also that wolves are able to reduce number of their prey, but are not affecting population dynamics, which is dependent on various factors (e.g. climate and hunting harvest). During this time I also analyzed pattern of territory marking by wolves and demonstrated, that density of markings was highest in the territory centres (neighbourhood of breeding den) and in peripheral areas, which bounded other territories. This study showed that due to temporal and energetic constrains wolves have to concentrate on marking areas most important for territory defence [12]. I also published several papers [6, 7, 33 i 34] on diet and other aspects of biology of owls and birds of prey. Among others I described relationship between prey size of the Lesser Spotted Eagle and locations of nests of this species, what was the subject of my master's thesis [17]. In 2002, when I became a staff researcher of the Mammal Research Institute PAS, I began studies on variation of body size in weasels *Mustela nivalis* and other aspects of biology of this species. These studies were conducted in cooperation with Prof. Marek Konarzewski and Dr. Paulina Szafrańska from MRI PAS, and Prof. John R. Speakman from Aberdeen University (Scotland). Using radio-tracking data we demonstrated that spatial distribution of weasels was related to the availability of prey. Moreover due to thermoregulation constrains those predators selected for resting more dry and warmer sites, when compared to random locations. They also avoided areas covered by low vegetation, what may reduce their impact on the population of prey [15]. Most important part of these studies concerned energy expenditures of weasels under laboratory conditions – resting metabolic rates (RMR) and daily energy expenditures (DEE), measured in free-ranging animals using the Doubly Labelled Water (DLW) method. This method, based on different rates of decline in enrichment of the stable isotopes of oxygen and hydrogen in body water, was used only for the second time in Poland. Results of these studies confirmed that resting metabolic rates of weasels are two times higher than in other species of similar body size, whereas daily energy expenditures are on comparable level. However, RMR in weasels averaged in some cases over fifty percent of their daily energy expenditures, thus they were not able to spend more energy for other needs (e.g. search for mates). This is main reason why weasels reduce their daily activity, especially in winter [16]. Most probably those energetic constrains cause that body mass of weasels is determine by body size of their prey. This means that individuals hunting on larger prey are able to gain more energy at the same time unit and are able to allocate more energy for body growth, in comaprison to individuals hunting on smaller prey. This could be very important adaptation strategy of weasel males, because due to strong sexual selection observed in this species, larger individuals should be characterized by higher reproductive success. We never tested strength of sexual selection directly, but enormous sexual dimorphism observed in this species (females are 2-3-times smaller than males), indicate that this type of selection should play very important role. Body size variation in weasel males in relation to habitat and body size of prey was a subject of my doctoral thesis.

The results collected during studies on constrains imposed by the body size on ability to satisfy energy needs became source of additional analyses [1, 2, 3 and 4] and initiated new research projects [5]. These studies became part of my selected research achievement and are presented below in details.

SUMMARY OF PUBLICATIONS THAT MAKE UP SELECTED RESEARCH ACHIEVEMENT

The effect of body mass and metabolic rates variation on mortality of small mammals

The selected research achievement consists of five articles [1, 2, 3, 4, 5]. In two of them I directly analyzed the effect of body mass and metabolic rates variation on winter mortality of weasels [1] and root voles [5]. I demonstrated that ability to dissipate heat at high ambient temperatures constrains activity and metabolic rates of male weasels, what may directly affect their survival during summer [4]. Next publication [3] was concerning heritability of body mass and metabolic rates in weasels, and thus potential for natural selection. Finally, results presented in article [4] demonstrated, that variation of phenotypic traits may limit gene flow in the weasel population, and in presence of environmental barriers, can speed up microevolution of body mass. These studies present cutting-edge research in reference to applied methods (estimates of field metabolic rates, estimates of heritability of morphological and physiological traits in free-ranging species), concepts (analyses of the effect of morphological and physiological traits on mortality of wild animals, analyses of relationship between phenotypic traits and gene flow in population, testing assumptions of the heat dissipation limit hypothesis under natural conditions). Moreover, these studies became part of relatively new idea about complex relations between ecological and evolutionary processes (Schoerner 2011).

Scientific problem

Body mass and metabolic rates are two traits closely related to variation of life histories of animals (Stearns 1992, Roff 2002). Most probably this relationship is result of a compromise between sexual selection and other types of natural selection. It is commonly accepted that individuals characterized by larger body mass and/or higher metabolic rates have higher reproductive success, but is also associated with elevated energy needs, which may reduce survival in the situation when environmental conditions deteriorate (Clutton-Brock et al. 1983, Wikelski and Trillmich 1997). On the other hand there are not many examples how these traits affect main components of fitness – reproduction and mortality (Jackson et al. 2001, Boratyński and Koteja 2009, 2010). Moreover, many studies report ambiguous results, because both body mass and metabolic rates are affected by external conditions and change over time. Analyses of survival in the populations of wild animals are not easy task, because usual it is difficult to separate effect of migration from true mortality (Hayes and O'Connor 1999, Jackson et al. 2001, Boratyński and Koteja 2009). Most studies focused on winter mortality so far, because this is most demanding period when costs of thermoregulation (low ambient temperatures) are considered. Moreover, this period is usual characterised by limited possibilities to satisfy elevated energy needs (decrease of quantity and/or quality of food resources). This is why most small mammals, exposed to the harsh winter condition, exhibit many morphological, physiological and behavioural adaptations, which enhance their chance to survive those unfavourable conditions. Usual smaller organisms are characterized by lower energy expenditures, thus natural reaction to lower food availability is reduction of body size (Hayes et al. 1992, Wikelski and Trillmich 1997). This phenomenon was observed in many species of small mammals (Hansson 1990, Aars and Ims 2002). On the other hand larger individuals are less susceptible to negative impact of low temperatures and more resistant to short-term food deficiency (Jackson et al. 2001), therefore some species develop larger body mass in winter (Gower et al. 1994). Accurate estimates of the effect of body mass and metabolic rates on winter mortality is often hampered by high phenotypic plasticity of these traits observed in small mammal under natural conditions (Ergon et al. 2004).

Our knowledge about the effect of high ambient temperatures on fitness of animals under natural conditions is even more limited. Recently formulated Heat Dissipation Limit (HDL) hypothesis (Speakman and Król 2010a) shed new light on the evolution of life histories of ectothermic organisms. According to this concept maximum energy expenditures are limited not only by availability of resources, but also by ability to dissipate heat generated by body, e.g. during lactation or elevated physical activity (Król et al. 2007, Grémillet et al. 2012). This phenomenon may arise additional conflict between fitness, expressed as number of offspring, and survival, because usual larger individuals are characterized by higher fecundity, but at the same time they encounter more problems with heat dissipation (Speakman and Król 2010b).

To assess the impact of directional selection on body mass and metabolic rates, it is important to estimate additive genetic variance associated with these traits, because this is only way to separate effect of phenotypic plasticity from microevolutionary changes (Gienapp et al. 2008). This is particularly important when animals are facing rapid climatic changes, because high additive genetic variance of traits directly affecting fitness enable quick phenotypic response. Apparently, genetic variance of many traits, observed in wild population, is high enough to produce rapid evolutionary changes, when selection pressure is strong (Husby et al. 2011). On the other hand despite of high genetic variance associated with quantitative traits, which affect directly fitness, evolutionary changes of those traits are relatively seldom observed (Merilä et al. 2001, Morrissey et al. 2012, Teplitsky et al. 2014). Usual it is attributed to negative genetic correlation among traits, which are subjected to natural selection acting in opposite directions, and in consequence evolution of single trait is limited (Wilson et al. 2006, Walsh and Blows 2009, Teplitsky et al. 2014). Equally important are also relationships between ecological and evolutionary processes, because level of additive genetic variance is related to population density, which is changing under different environmental conditions (Coulson and Tuljapurkar 2008, Schoener 2011). This is why changes of local ecological conditions may, on the one hand constrain evolutionary response, but on the other hand, they may increase rate of new adaptations. At the present time particularly important are human-induced transformations of the environment, e. g. changes of species composition due to selective harvest, introduction of invasive species, and landscape fragmentation (Reznick andi Ghalambor 2001, Schmidt and Jensen 2003, Hendry et al. 2008).

The aim of the published articles presented as a selected research achievement was to:

1. Analyse effects body mass and metabolic rates variation on winter mortality of small mammals.
2. Determine effect of constrains associated with ability to dissipate heat on activity and metabolic rates of small mammals.

3. Estimate variation of genetic and environmental components affecting body mass and metabolic rates, and their susceptibility to natural selection.
4. Identify effect of body mass and metabolic rates variation on spatial and genetic structure of small mammal populations.

ZUB K., Szafrańska P.A., Konarzewski M., Speakman J.R. 2011. Effect of energetic constraints on distribution and winter survival of weasel males. ***Journal of Animal Ecology*** 80: 259-269. [1]

In this paper was tested hypothesis that winter mortality of male weasels is related to body mass. Larger individuals have higher food requirements, thus when prey availability decreases also survival rates of these animals should be lower. Moreover, longer activity time of larger individuals, imposed by higher energy needs, make them more susceptible to predation. Based on estimates of daily energy expenditures (DEE), obtained using doubly labelled water (DLW) method, I constructed an energetic model predicting how individuals of different size are able to balance their energy budgets feeding on large and small prey while minimizing time spent hunting, thereby reducing their own exposure to unfavourable conditions and predation. The range of body mass in weasels predicted by our model corresponded very well with the distribution of prey body mass in different habitats. Larger individuals were able to compensate for higher food requirements by using habitats with larger prey species than those available to smaller male weasels. This effectively offset the expected negative association between body mass and winter survival predicted from considerations of energy balance. Additionally, I estimated body fat using TOBEC method and demonstrated, that larger individuals are able to stay inactive much longer (over 3 days) than smaller individuals, relaying solely on subcutaneous fat reserves. This strategy allows to reduce additional costs related to exposure to low temperatures. Analysis of body mass distribution of male weasels in different season revealed that during reproductive season (spring-summer) it was significantly higher than in autumn-winter. This may indicate that during summer larger individuals were characterize by higher mortality. Results of this study demonstrated that directional natural selection on body mass could be much weaker than expected, because body mass distribution is related to spatial and temporal variation of food resources.

ZUB K., Borowski Z., Szafrańska P.A., Wieczorek M., Konarzewski M. 2014. Lower body mass and higher metabolic rate enhance winter survival in root voles, *Microtus oeconomus*. ***Biological Journal of the Linnean Society*** 113: 297-309. [5]

The main aim of this study was to estimate the effect of individual body mass and metabolic rates on mortality of the root vole. This species inhabit periodically flooded river valley, thus we assumed that winter survival should be enhanced by higher peak metabolic rates (RMR), but lower body mass and resting metabolic rates (RMR), because quantity and quality of food available for plant-eating voles drastically decrease after growing season [31]. During four consecutive years smaller individuals were characterized by lower mortality, but only during early winter (November-January), whereas from February to March better survived larger individuals. Contrary to our expectations higher body mass-corrected RMR positively affected survival, but direction of PMR influence on mortality varied among years. Diverse directionality and strength of the effects of body mass and metabolic rates on winter survival of voles was caused by variation of these traits among different cohorts. At the beginning of winter voles born in spring and early summer exhibited reduced body mass and metabolic rates, whereas animals born later maintained lower body mass and RMR. Moreover body mass and metabolic rates varied significantly among consecutive years, according to changing quantity and quality of food resources. This study demonstrated that estimation of strength and directionality of natural selection on body mass and metabolic rates could be challenging, because of ability of animals to adjust those traits to changing environmental conditions.

ZUB K., Fletcher Q.E., Szafrańska P.A., Konarzewski M. 2013. Male weasels decrease activity and energy expenditure in response to high ambient temperatures. ***PLoS One*** 8: 1-7. [4]

Most of studies concerning the effect of environmental factors on functioning of homoeothermic animals focus on low range of ambient temperatures, whereas recently formulated HDL (heat dissipation limit) hypothesis (Speakman and Król 2010), proposes that maximal energy expenditure is not constrained by the availability of resources in the environment, but only by the capacity of animals to dissipate body heat. According to predictions of this hypothesis free-ranging mammals should reduce activity time and metabolic rates in response to high ambient temperatures, to avoid the negative effects of hyperthermia. To test this hypothesis we used extensive data collected on male weasels and demonstrated that those animals in response to warm temperatures reduce daily energy expenditures, resting metabolic rates (RMR) and duration of daily activity. These results support the HDL hypothesis and prove that constrains related to ability to dissipate body heat may significantly affect fitness of male weasels. Larger individuals or those characterized by higher RMR could face more problems with body heat dissipation, what may not only constrain their activity, and thus ability to satisfy high energy needs, but also reduce chance to find reproductive partner. Therefore such individuals may not only suffer from higher mortality, but also have lower reproductive success during years, when ambient temperatures are elevated. At the same time those males could be forced to select different habitats (e.g. characterized by higher humidity or better protection against high ambient temperatures), than smaller males or those having lower metabolic rates. The avoidance of overheating may also constrain body size of females due to high energy expenditures during lactation. This could be additional factor limiting increase of body size in this species, despite of strong sexual selection acting on this trait.

ZUB K., Piertney S.B., Szafrańska P.A., Konarzewski M. 2012. Environmental and genetic influences on body mass and resting metabolic rates (RMR) in a natural population of weasel *Mustela nivalis*. ***Molecular Ecology*** 21: 1283-1293. [2]

Body mass and metabolic rates have potentially fundamental adaptive value for homoeothermic animals, particularly in the context of rapid climatic changes. However, disentangling the evolutionary and phenotypic (plastic) changes of these traits is challenging without detailed information about genetic variation underlying those responses. We aimed to estimate amount of additive genetic variance associated with body mass and resting metabolic rates (RMR) in weasels, because both traits have potentially significant effect on modification of life histories of this species. We used microsatellite markers to construct a pedigree and then the ‘animal model’ to separate genetic and environmental components of body mass and RMR of weasels. The estimates of heritability of body mass were high and significant in males ($h^2 = 0.61$), but low and not significantly different from zero in females. The estimate of heritability of RMR was lower ($h^2 = 0.45$ and $h^2 = 0.54$ for whole body and body mass-corrected RMR, respectively), but significantly different from zero. Moreover, there was negative phenotypic and genetic correlation between body mass and body mass-corrected RMR. Lower estimates of heritability of RMR suggests that metabolic rates are characterized by higher phenotypic plasticity. Therefore weasels are able to respond to seasonal changes of environmental conditions by adjusting RMR, what we demonstrated in another study [26]. Significant genetic correlation between body mass and RMR indicate that these traits may evolve independently, what also may constrains response to natural selection. On the other hand relatively high heritability of both traits can facilitate rapid evolutionary changes.

McDevitt A.D., Oliver M.K., Piertney S.B., Szafrańska P.A., Konarzewski M., **ZUB K.** 2013. Individual variation in dispersal associated with phenotype influences fine-scale genetic structure in weasels. ***Conservation Genetics*** 14: 499-509. [3]

However, the main purpose of this study was to present how phenotypic traits affect dispersal and genetic structure of weasel population, but obtained results also demonstrated complexity of interactions between evolutionary and ecological processes. Our analyses revealed presence of two clusters in the studied population, associated with different habitats and different body size of individuals. First group formed weasels inhabiting river valley, which were larger than weasel from second group, inhabiting forest areas and transitional zone (meadows on the forest edge). We also demonstrated that gene flow between those two groups was limited. On one hand is was caused by presence of anthropogenic barriers (build-up area), on the other hand by selection of different habitats, which satisfy energy needs of weasels of different size. Our analyses also showed that the maximum extent of movement was achieved by weasels of medium body size, whereas the smallest and largest individuals exhibited higher site fidelity. Most probably larger weasels were not able to survive in the habitats characterized by lower food resources, whereas smaller individuals were displaced by larger ones. This distribution pattern, in combination with high heritability, may influence rapid evolutionary adaptations and fixation of body mass. Most probably such a process took place in the European river valleys, where introduction of an invasive predator, the American mink, has caused declines in stoat populations, simultaneously releasing weasels from competition with the stoat (Sidorovich and Solovej 2007). This has lead to increased numbers of weasels in the river valleys, where they could hunt on larger prey and satisfy higher energy needs. In consequence mean body mass of weasel in the river valleys increased. According to data collected in the Mammal Research Institute PAS in Białowieża, mean body mass of weasels (after adjusting for differences among habitats) was significantly lower in the past (K. Zub, unpublished data). This results indicate that body mass in this species, regardless of proximate factors, may be subjected to rapid evolutionary changes.

Summary

Presented studies proved that body mass and metabolic rates may significantly affect mortality of small mammals, which is one of basic components of fitness. However, accurate estimation of the effect of those traits on winter mortality is not straightforward due to various adaptations allowing animals survival this critical period. In the first place this is phenotypic plasticity, which is manifested in reduction of body mass and metabolic rates in situation when costs of thermoregulation increase and quantity and/or quality of food resources decrease. Moreover, some species are able to select more rich habitats, which better satisfy their energy needs. During reproductive season high ambient temperatures could be also an important factor constraining physiological performance of small mammals. Those limiting factors, in combination with seasonal and long-term changes of environmental conditions, modify strength and direction of natural selection. In consequence, despite of high additive genetic variance associated with body mass and metabolic rates, rapid evolutionary changes are relatively seldom under natural conditions. Those changes might be slower than expected also due to negative genetic correlation among traits. Environmental disturbances, particularly those caused by human activity or climate change, may, on the one hand, constrain evolutionary responses, but on the other hand they may accelerate appearance of new adaptations. A good example of such a process is the increase of body mass of weasels inhabiting river valleys. However, also density and body mass of voles, undergo seasonal and long-term changes, and can significantly modify phenotypic response of feeding on them weasels. Results of above presented studies allow better understanding of complex relationships between ecological and evolutionary processes.

Cited literature

Aars J., Ims R.A. 2002. Intrinsic and climatic determinants of population demography: the winter dynamics of tundra vole populations. Ecology 83: 3449–3456.

Boratyński Z., Koteja P. 2009. The association between body mass, metabolic rates and survival of bank voles. Functional Ecology 23: 330–339.

Boratyński Z., Koteja P. 2010. Sexual and natural selection on body mass and metabolic rates in free-living bank voles. Functional Ecology 24: 1252–1261.

Clutton-Brock, T.H., Guinness, F.E. & Albon, S.D. 1983. The costs of reproduction to red deer hinds. Journal of Animal Ecology 52: 367–384.

Coulson, T., Tuljapurkar, S. 2008. The dynamics of a quantitative trait in an age-structured population living in a variable environment. American Naturalist 172: 599–612.

Ergon T., Speakman J.R., Scantlebury M., Cavanagh R., Lambin X. 2004. Optimal body size and energy expenditure during winter: why are voles smaller in declining populations? American Naturalist 163: 442–457.

Gienapp P., Teplitsky C., Alho J.S., Mills J.A., Merila J. 2008. Climate change and evolution: disentangling environmental and genetic responses. Molecular Ecology 17: 167–178.

Gower B.A., Nagy T.R., Stetson M.H. 1994. Pre- and postnatal effects of photoperiod on collard lemmings (*Dicrostonyx groenlandicus*). American Journal of Physiology 267: R879-R887.

Grémillet D., Meslin L., Lescroöl A. 2012. Heat dissipation limit theory and the evolution of avian functional traits in a warming world. Functional Ecology 26: 1001–1006.

Hansson L. 1990. Ultimate factors in the winter weight depression of small mammals. Mammalia 54: 397–404.

Hayes J.P., O'Connor C.S. 1999. Natural selection on thermogenic capacity of high-altitude deer mice. Evolution 53: 1280–1287.

Hayes J.P., Speakman J.R., Racey P.A. 1992. The contributions of local heating and reducing exposed surface area to the energetic benefits of huddling by short-tailed field voles (*Microtus agrestis*). Physiological Zoology 65: 742–762.

Hendry A.P., Farrugia T.J., Kinnison M.T. 2008. Human influences on rates of phenotypic change in wild animal populations. Molecular Ecology 17: 20–29.

Husby A., Visser M.E., Kruuk L.E.B. 2011. Speeding up microevolution: the effects of increasing temperature on selection and genetic variance in a wild bird population. PLoS Biology 9: e1000585.

Jackson D.M., Trayhurn P., Speakman J.R. 2001. Associations between energetics and over-winter survival in the short-tailed field vole *Microtus agrestis*. Journal of Animal Ecology 70: 633–640.

Król E., Murphy M., Speakman J.R. 2007. Limits to sustained energy intake. X. Effects of fur removal on reproductive performance in laboratory mice. Journal of Experimental Biology 210: 4233–4243.

Merilä J., Sheldon B.C. Kruuk L.E.B. 2001. Explaining stasis: microevolutionary studies in natural populations. Genetica 112-113: 199-222.

Morrissey M.B., Walling C.A., Wilson A.J, Pemberton J.M., Clutton-Brock T.H., Kruuk L.B.E. 2012. Genetic analysis of life-history constraint and evolution in a wild ungulate population. American Naturalist 179: E97-E114.

Reznick D.N., Ghalambor C.K. 2001. The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. Genetica 112–113: 183–198.

Roff, D.A. 2002. Life History Evolution. Sinauer Associates, Sunderland, MA.

Schmidt N.M., Jensen P.M. 2003. Changes in mammalian body length over 175 years -adaptations to a fragmented landscape? Conservation Ecology 7: 6.

Schoener T. W. 2011. The Newest Synthesis: understanding the interplay of evolutionary and ecological dynamics. Science 331: 426–429.

Sidorovich V.E., Solovej I.A. 2007. The stoat *Mustela ermine* population decline in northern Belarus and its consequences for weasels *Mustela nivalis*. New Zeland Journal of Zoology 34: 9–23.

Speakman J.R., Król E. 2010. Maximal heat dissipation capacity and hyperthermia risk: neglected key factors in the ecology of endotherms. Journal of Animal Ecology 79: 726–746.

Speakman J.R., Król E. 2010a. The heat dissipation limit theory and evolution of life histories in endotherms - time to dispose of the disposable soma theory? Integrative and Comparative Biology 50: 793–807.

Stearns, S.C. 1992. The Evolution of Life Histories. Oxford University Press,Oxford.

Teplitsky C., Tarka M., Møller A.P., Nakagawa S., Balbontín J., et al. 2014. Assessing multivariate constraints to evolution acrossten long-term avian studies. PLoS ONE 9: e90444.

Walsh B., Blows M.W. 2009. Abundant genetic variation + strong selection = multivariate genetic constraints: a geometric view of adaptation. The Annual Review of Ecology, Evolution, and Systematics 40: 41–59.

Wikelski, M., Trillmich, F. 1997. Body size and sexual dimorphism in marine iguanas flactuate as a result of opposing natural and sexual selection: an island comparison. Evolution 51: 922–936.

Wilson A.J., Pemberton J.M., Pilkington J.G., Coltman D.W., Mifsud D.V., Clutton-Brock T. H., Kruuk L.E.B. 2006. Environmental coupling of selection and heritability limits evolution. PLoS Biology 4: E216

Białowieża, 11.03.2015 r.

Place and date

Signature