Diet of the fat dormouse (Glis glis) *on the northern periphery of its distributional range*

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Mammal Research

ISSN 2199-2401
Volume 60
Number 2

Mamm Res (2015) 60:155-161
DOI 10.1007/s13364-015-0213-5

Springer

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ORIGINAL PAPER

Diet of the fat dormouse (*Glis glis*) on the northern periphery of its distributional range

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Received: 30 September 2014 / Accepted: 13 January 2015 / Published online: 29 January 2015

Abstract We studied the seasonal and annual variation in diet composition of the fat dormouse (*Glis glis*) in Lithuania, a locality situated on the northern periphery of the dormouse range and outside of the range of the European beech (*Fagus sylvatica*). After emergence from hibernation, dormice fed on oak acorns (from the previous year), inflorescences of various trees, vegetative parts of plants and food of animal origin (birds, their eggs and insects). In June, soft mast and seeds of birches supplemented the dormouse diet, and diet composition was the most diverse during this period. In July, raspberries and fruits of glossy buckthorn constituted the bulk of dormouse diet, but seeds of birches dominated in a specific year. Hard mast (mainly acorns) dominated the diet of *G. glis* from August until the beginning of hibernation in October. A high prevalence of acorns, comparatively high proportion of birch seeds and low proportion of food of animal origin in the diet, as well as feeding on fruits of glossy buckthorn, are specific features of feeding by *G. glis* in Lithuania. The diet of *G. glis* on the northern periphery of its range resembles its diet on the eastern periphery of the range where beech trees are also absent. According to the composition of *G. glis* diet, feeding conditions in both of these peripheral regions are poorer in comparison to central or southern regions.

Keywords Edible dormouse · Feeding · Faecal analysis · Beech · Oak · Lithuania

Communicated by: Magdalena Niedziałkowska

Electronic supplementary material The online version of this article (doi:10.1007/s13364-015-0213-5) contains supplementary material, which is available to authorized users.

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Introduction

The fat dormouse (*Glis glis*) is the largest member of the dormouse (Gliridae) family and has several specific characteristics. A feature distinctive to dormice, hibernation in *G. glis* can last up to 7–8 months. Before hibernation, dormice accumulate large quantities of body fat by feeding on the most nutritious food sources available in autumn (e.g. Airapetyants 1983; Rossolimo et al. 2001; Kryštufek 2010). Dormice lack the caecum and are less adapted to digest cellulose and use enteric symbionts than other small mammals (Vorontsov 1967). This may be an important trophic limitation, because dormice are less able to exploit abundant foods such as vegetative parts of plants.

The distributional range of *G. glis* extends from northern Spain, Italy and the Balkan Peninsula in the south through central and eastern Europe as far as Lithuania and Belarus in the north, and Ukraine in the east with isolated pockets in Latvia, Russia, the Caucasus, Turkmenistan and Iran (Amori et al. 2008). Across this large range, the dormice live in different habitats, and the composition of their diet seems to vary very much depending on available food (reviewed in Ognev 1947; Vietinghoff-Riesch 1960; Airapetyants 1983; Rossolimo et al. 2001; Kryštufek 2010). *G. glis* feed mainly on vegetable food—soft mast (berries and other soft fruits) in summer and hard mast (nuts and acorns) in autumn; food of animal origin is only supplementary (e.g. Holišová 1968; Samarskij and Samarskij 1980; Nowakowski et al. 2006). The full list of dormouse feeding plant species consists of more than 30 species (e.g. Airapetyants 1983; Lozan et al. 1990; Rossolimo et al. 2001). The list of major hard mast used by *G. glis* for accumulation of fat reserves prior to hibernation is much shorter and includes nuts of beech (*Fagus* spp.) and hazel (*Corylus avellana*), walnuts (*Juglans* spp.) and acorns of oak (*Quercus* spp.) (e.g. Donaurov et al. 1938; Lozan 1959, 1970; Rodolfi 1994).

Beech nuts are an important food of *G. glis* in most parts of its range (Kryštufek 2010). Beech nuts contain high proportions of lipids (41.5 %), proteins (22.8 %) and sugar (9.6 %), and they have elevated nutritional value (Fietz et al. 2005). If beech nuts are present, dormice even start feeding on unripe nuts. These nuts are the main food source until hibernation, and in spring, dormice also consume nuts from the previous year (e.g. Donaurov et al. 1938; Müller-Stiess 1996; Fietz et al. 2005). Dormouse reproduction and population dynamics are closely related to the masting pattern of beech. In years when beech trees do not fruit, dormice skip reproduction (e.g. Bieber 1998; Schlund et al. 2002; Ruf et al. 2006; Pilastro et al. 2003; Fietz et al. 2005; Morris and Morris 2010). The high availability of energy-rich seeds is essential for juvenile dormice to survive the first winter, whereas adult dormice can store enough fat for hibernation on alternative food items such as fruits and other seeds (Fietz et al. 2005; Lebl et al. 2010).

The oak is another tree important for *G. glis*, but acorns of oak are a less favourite food than beech nuts. For example, in a year when the masting of beech and oak was similar in the northern Caucasus, *G. glis* fed on beech nuts, but did not feed on acorns (Donaurov et al. 1938). The energy value of acorns of pedunculate oak (*Quercus robur*) and sessile oak (*Quercus petraea*) (4.5 and 4.4 kcal/g, respectively) is much less than for seeds of European beech (*Fagus sylvatica*) without coats (about 7 kcal/g) (Grodziński and Sawicka-Kapusta 1970). Oak acorns have a significantly lower content of total lipids (3.4 %) and proteins (0.9 %), and rather high content of tannins (Fietz et al. 2005; Shimada and Saitoh 2006).

Lithuania is situated on the northern periphery of the distributional range of *G. glis* and outside the continuous range of the European beech (Bolte et al. 2007). Beech are absent in the forests of Lithuania occupied by *G. glis*. Acorns of pedunculate oak and nuts of hazel are potential food for *G. glis* in autumn in Lithuania. Trees and shrubs providing soft fruits are scarce in Lithuanian dormouse habitats (Juškaitis and Šiožinytė 2008). Therefore, feeding conditions for *G. glis* could be poorer in Lithuania in comparison to southerly situated parts of the range. A higher proportion of animal food in the diet of *G. glis* could be expected in Lithuania, as was found in some other studies (e.g. Franco 1990; Hürner and Michaux 2009).

The diet of *G. glis* has been investigated by several authors across its range (see references above), but not on the northern periphery of the range, outside the range of the beech. The aim of the present study was to investigate diet composition, its seasonal and annual variability in a population of *G. glis* living in a typical habitat on the northern periphery of its range and to compare it with diet studies from across the range of the species.

Material and methods

This study was carried out in Rumšiškės forest in central Lithuania (54° 52′ N, 24° 09′ E). The relief of the terrain is rolling with ravines and rivulets. The study site is covered by mixed forest stands composed of 180-year-old Scots pine (*Pinus sylvestris*), 185-year-old pedunculate oak (*Q. robur*) and 135-year-old Norway spruce (*Picea abies*) with lime (*Tilia cordata*), birches (*Betula pendula*, *Betula pubescens*), hornbeam (*Carpinus betulus*) and aspen (*Populus tremula*). Hazel (*C. avellana*), rowan (*Sorbus aucuparia*), honeysuckle (*Lonicera xylosteum*) and glossy buckthorn (*Frangula alnus*) form the understorey. Bird and black cherries (*Prunus avium*, *Prunus serotina*), elders (*Sambucus racemosa*, *Sambucus nigra*) and wild apples (*Malus sylvestris*) also occur in the understorey, and raspberries (*Rubus idaeus*) are common along forest rides and in small clearings.

The population of *G. glis* studied lives in typical for Lithuania habitat, i.e. mature mixed forest with old pedunculate oaks and old hazels, with the habitat suitable for *G. glis* occupying an area of about 160 ha. The average population density ranged from 0.8 to 2.0 ind./ha in spring and from 1.2 to 4.8 ind./ha in autumn (V. Augutė, unpublished). The highest dormouse abundance was recorded in autumn 2013. In the study site, the annual variation of masting in pedunculate oak, hazel and birches was evaluated visually using four categories: absent or almost absent, low, intermediate and abundant (Table 1).

At the study site, nestboxes have been present since 1990, when 50 nestboxes were placed along forest roads and rides at 30–50 m intervals, and these boxes were inspected in 2011. In June of that year, 93 new nestboxes were set up in a grid with 50 m distances between boxes covering an area of 18 ha, and these were monitored in 2012–2013. About 60 % of the old nestboxes put up in lines also occurred in the area covered by the new nestbox grid. In the course of this study (2011–2013), nestboxes were inspected every fortnight through the activity season of *G. glis* from the first half of May until the end of October.

During every nestbox check, all faeces of *G. glis* found inside or on top of the boxes were collected, and all food

Table 1 Variation of masting in pedunculate oak, hazel and birches in Rumšiškės forest 2011–2013

Species	Masting in scores in different years		
	2011	2012	2013
Pedunculate oak	3	1	3
Hazel	1	1	0
Birches	1	3	0

Masting was evaluated visually using four categories: absent or almost absent (0), low (1), intermediate (2) and abundant (3)

remains were recorded. Faeces from each nestbox were treated as a single sample. Every sample contained droppings left by dormice over the previous 2 weeks, and they could have been left by either single dormouse or several individuals. Droppings that contained only sand or soil (typical of spring) were discarded from all further analysis. In total, 743 samples were collected over the 3 years (125 samples in 2011, 247 in 2012 and 368 in 2013). From every sample, 1–10 droppings (an average 5.3) were selected and weighed. Every dropping (treated as a subsample) was soaked in water, placed on glass, carefully separated with preparation needles and analysed under a microscope (at the magnitude×15–200). In total, 3943 slides were prepared and analysed.

Food remains were identified with the help of our own reference collection. For this purpose, potential food items were collected in the study site and slides were prepared. All food remains were grouped into seven types: hard mast, soft mast, vegetative parts of plants, birch seeds, inflorescences, fungi, and food of animal origin. Percentage of dry faeces weight was used as the estimation method for diet analysis (Litvaitis 2000). The breadth of food niche was assessed using Levins' standardized niche breadth (B_A) according to the seven main food groups for every 2-week period (Krebs 1999):

$$B_A = B{-}1/n{-}1,$$

where B is Levins' measure of niche breadth ($B=1/\sum p_j^2$, where p is a proportion of food group j), and n is number of possible food groups. Levins' standardized niche breadth varies from 0 to 1.

Seasonal (2-week periods) and interannual differences in the diet were analysed by one-way ANOVA and tested for differences using Tukey's honestly significance difference test (HSD) for unequal sample sizes. Statistical analyses were carried out using the STATISTICA 7.0 package (StatSoft, Inc. 2004).

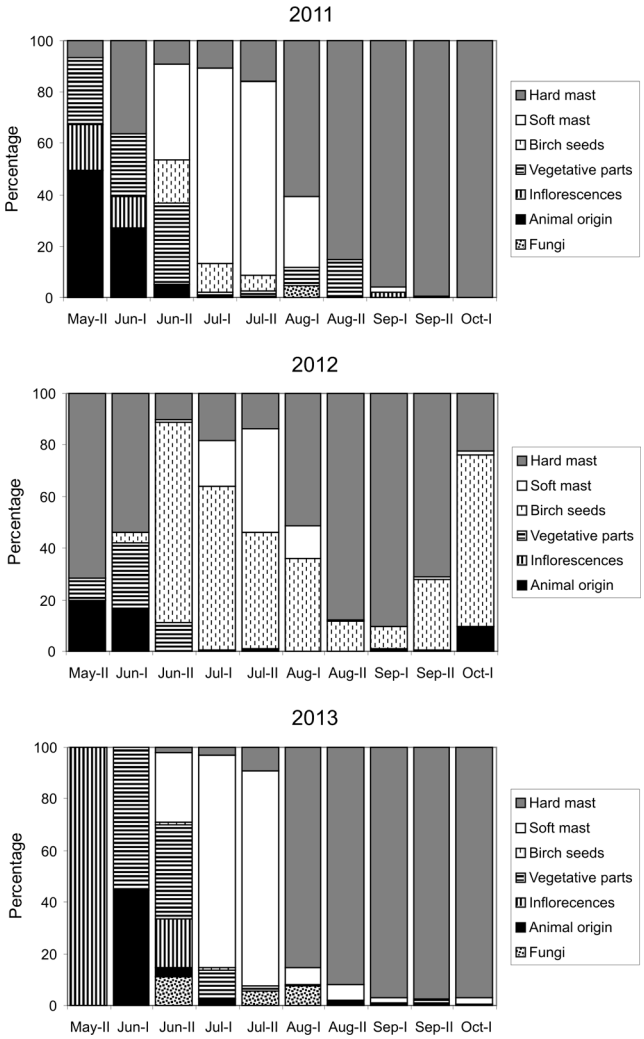

Fig. 1 Seasonal variations in the diet composition of *G. glis* (percent of dry faeces weight) in mature mixed forest in Lithuania sampled at fortnight intervals in 2011–2013

Results

Over the entire activity period, the diet composition of *G. glis* continually changed (Fig. 1). The consumption of all main food groups differed significantly over the course of the 2-week periods (ANOVA test: $F=7.03–166.05$, $p<0.0001$). Emerging from hibernation in the second half of May, the dormice then fed on foods belonging to four particular groups, depending on availability in different years:

1. Oak acorns from the previous year (present in spring 2011 and 2012, but not in 2013)
2. Inflorescences of various trees, mainly pedunculate oak, but also Scots pine, Norway spruce and hornbeam
3. Vegetative parts of plants
4. Food of animal origin (birds, their eggs and insects) (Tables S1–S3)

In June, diet composition was the most diverse of the entire activity season. In comparison to May, the proportion of inflorescences decreased, but two new food groups—soft mast and seeds of birches—contributed. An especially high proportion of birch seeds was recorded in 2012, but this was marginal in 2013. The proportion of animal food, averaging about 20 %, remained rather constant in early June in all three years (Tables S1–S3). In July, the bulk of the dormouse diet was formed by soft mast (raspberries and fruits of glossy buckthorn) in 2011 and 2013, but seeds of birches dominated in 2012. Acorns formed a small proportion of the diet.

Hard mast dominated the diet from August until the beginning of hibernation in October in all 3 years. Due to the

negligible fruiting of hazel during the study period, acorns dominated among hard mast (Table 1). Hazel nuts did however form 20–30 % of the diet in August 2011 and 2012. In the autumn of 2012, dormice largely fed on seeds of birches (Fig. 1). Evidence that *G. glis* ate hornbeam nuts was found in a few nestboxes, but no detectable share of this food type was recorded during the analysis of faeces.

Food remains of *G. glis* were present in some nestboxes during the regular controls. Bird carcasses and destroyed eggs were found in May–July and acorns from the previous year in May–June. Shells of hazel nuts started to appear within nestboxes in July, then prevailed in August and were also found in September. Gnawed acorns of the same year were found in July–August and predominated in September–October samples. Partly eaten fruits of wild apple were recorded in August. Remains of hazel catkins were found inside nestboxes in September and October, as well as gnawed hornbeam nuts, maple (*Acer* sp.) keys and Scots pine cones. Chewed and spat out needles of Norway spruce were recorded throughout the entire activity season.

The annual consumption of the main food groups varied significantly between years from 2011 to 2013 (ANOVA test: $F=13.90–508.86$, $p<0.0001$, except birds, $F=0.25$, $p=0.781$). However, the composition of the dormouse diet was more similar in 2011 and 2013, when only the proportions of soft mast, hard mast, fungi (HSD test: for all cases $p<0.0001$) and insects (HSD test: $p<0.03$) were significantly different. The composition of the dormouse diet in 2012 was influenced by the very high proportion of birch seeds not only in summer, but also in autumn. Food niche breadth varied both between seasons and years (Fig. 2).

Discussion

Generally, the broadest food niche of *G. glis* was typical of June, when the diet was typified by a diverse range of foods. In July and the first half of August, soft mast and hard mast prevailed in the diet and the breadth of food niche became narrower. The third period lasted until the beginning of hibernation, when hard mast dominated the dormouse diet and, consequently, the narrowest niche was determined. Differences in food niche breadth between years might be related to masting patterns of pedunculate oak and birches (Table 1). In 2012, an extremely high abundance of birch seeds and low abundance of acorns were recorded. This can explain the narrow niche recorded at the end of June, when birch seeds comprised almost 80 % of the diet in contrast to the typical diverse diet of this season in 2011 and 2013. By contrast, birch seeds diversified the diet and broadened the niche at the end of the activity season in 2012 as the mast of oak was low.

The diet of *G. glis* on the northern periphery of its range is rather specific when compared to populations situated more southerly. This is due to the absence of beech in Lithuanian dormouse habitats. Acorns of pedunculate oak become the main food source in late summer and autumn, and even in spring after hibernation when acorns from the previous year are present. Hazel nuts would be the preferred dormouse food, but hazel fruits rather irregularly in Lithuania (Juškaitis and Baltrūnaitė 2013a). Under the exceptionally good hazel fruiting conditions in 2007, the highest ever body weights of *G. glis* in this country were recorded (R. Juškaitis, unpublished).

In some years, both hazel and oak do not mast or have very limited seed production in Lithuania. In those years, we did not record any juveniles (R. Juškaitis, unpublished). Therefore, it is very likely dormice in our population skip reproduction in such poor years as has been shown across Europe by Lebl et al. (2011). Mature cones of Scots pine gnawed by *G. glis* were found in nestboxes in September 2010 when hazel nuts and acorns were absent (R. Juškaitis, unpublished). Elsewhere, feeding by *G. glis* on cones of different pine species has been recorded only in some coniferous forests in central and southern Italy (Santini 1978; Rima et al. 2007).

Extensive feeding on the very small seeds of birches is an unusual phenomenon for *G. glis*, and it has been recorded only

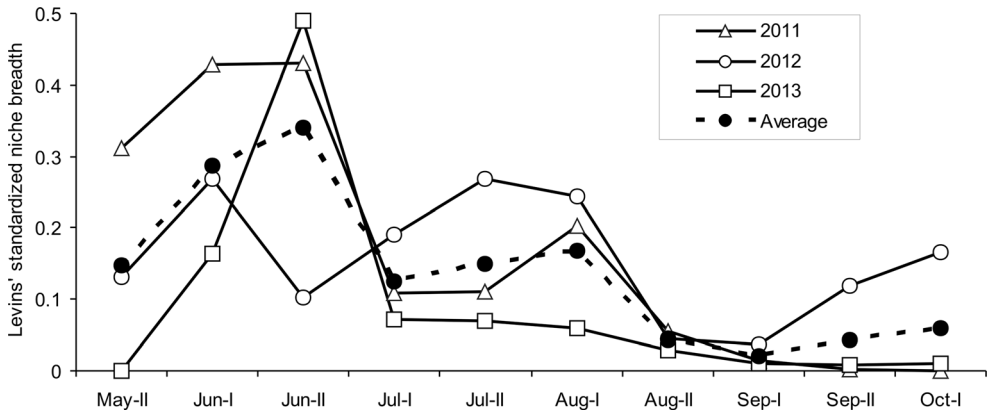

Fig. 2 Seasonal and annual variation of the food niche breadth of *G. glis* (Levins' standardized niche breadth, B_A) in mature mixed forest in Lithuania in 2011–2013

in some peripheral populations. A very high proportion of seeds of birches was found in the diet of *G. glis* in the Lithuanian study site in 2012 when a low mast of both oak and hazel occurred, but the crop of birch seeds was exceptionally good. Similarly, this high proportion of birch seeds in the diet of *G. glis* has been recorded elsewhere only on the eastern periphery of the range (Samara region, Russia, 56.6 % birch seeds by frequency of occurrence). In different years, the proportion of birch seeds was inversely related to the proportion of acorns and nuts in the diet of *G. glis* (Vekhnik 2011). A very small proportion of birch seeds (0.02 % of dry weight in autumn) was recorded in diet of *G. glis* in northwestern Spain (Gigirey and Rey 1998), but in none of the other numerous studies across the entire range.

Feeding on birch seeds was also recorded in the Lithuanian population of the forest dormouse (*Dryomys nitedula*), also situated on the northwestern edge of its range where high-calorific vegetable food is scarce and is present only for short periods (Juškaitis and Baltrūnaitė 2013b). Seeds of birches were not found in the diet of this species at any other site across its large range. We believe that dormice must feed on the very small seeds of birches when other more palatable and more calorific foods are scarce. Very small seeds are generally not eaten by small rodents (Grodziński and Sawicka-Kapusta 1970).

Contrary to expectation, the proportion of food of animal origin was not higher in the diet of *G. glis* in our study when compared to populations to the south. Food of animal origin constituted on average about 20 % of dormouse diet only in the second half of May and in the first half of June. However, when taken over the entire season, it accounted for only 3.5 % by weight estimates and 5.5 % by frequency of occurrence. Meanwhile remains of animal food were found in 41.2 % of stomachs of *G. glis* in Ukraine (Lozan et al. 1990), 23.4 % of stomachs in the northern Caucasus (Donaurov et al. 1938) and 29 % of faecal samples of *G. glis* in Bialowieza forest in Poland (Nowakowski and Godlewska 2006). In Belgium, remains of arthropods and bird feathers were present in 27 and 11 % of the total faecal sample, respectively (Hürner and Michaux 2009).

Feeding by *G. glis* on food of animal origin and on vegetative parts of plants may be related to the temporary absence of preferable vegetable food (Donaurov et al. 1938; Franco 1990). However, food of animal origin is also essential for herbivorous animals for successful breeding (White 2011). Predation on birds in nestboxes by *G. glis* was recorded both in Lithuania (Juškaitis 2006; present study) and in some other parts of the range, e.g. Germany (Vietinghoff-Riesch 1960; Müller-Stiess 1996) and the Czech Republic (Adamík and Král 2008), but only invertebrates were found in dormouse diet in some southern regions, e.g. the Caucasus (Donaurov et al. 1938), Spain (Gigirey and Rey 1998, 1999) and Italy (Franco 1990).

G. glis feeds on very different soft mast across its large range. However, feeding by *G. glis* on fruits of glossy buckthorn has not been recorded anywhere until now, and this is a specific feature of the dormouse diet on the northern periphery of the range. Raspberries were recorded in the dormouse diet only in Germany (Sailer and Fietz 2009). Thus, soft mast used by *G. glis* in Lithuania is not diverse and rather specific in comparison to other parts of the range.

The diet of *G. glis* has also been studied in some other peripheral sites. Differences in the ecology of *G. glis* were expected in Belgian population on the western limit of the distribution in comparison to more central populations. However in general, very small variations were found in the ecology of the species there, and in terms of the diet, only a higher proportion of birds was recorded (Hürner and Michaux 2009). The absence of any significant differences may be related to the presence of beech trees in dormouse habitats in Belgium. The diet of *G. glis* in northern Spain, on the southwestern edge of the range, was also in general in accordance with reports from other parts of the range, but fleshy fruits dominated the total diet (46.5 %). As beech was also absent, acorns of pedunculate oak and hazel nuts dominated the dormouse diet in autumn. Birch seeds appear to be an occasional food item, and animal food was represented only by insects and arachnids (Gigirey and Rey 1998, 1999).

Meanwhile, the diet of *G. glis* is very specific on the eastern periphery of the range (Samara region, Russia) where beech is also absent. Besides acorns and hazel nuts forming the bulk of the dormouse diet, high proportions of birch seeds, fungi and leaves were recorded among the main food categories, but soft mast was absent even among secondary food groups (Vekhnik 2011). According to the composition of *G. glis* diet, the feeding conditions are the poorest there in comparison to the rest of the range.

The diet of *G. glis* in Lithuania, on the northern periphery of its range, is most similar to its diet on the eastern periphery of the range. The prevalence of acorns and hazel nuts, as well as high proportion of birch seeds, in the dormouse diet are general features for *G. glis* populations situated in these peripheral areas. The average body weight of adult *G. glis* individuals prior to hibernation is lower in Lithuania in comparison to more southerly situated sites in Europe, but it is still higher than on the eastern periphery of the range (R. Juškaitis and V. Augutė, submitted). Based on these peculiarities of dormouse diet and body weight, we can state that feeding conditions on the northern and especially eastern peripheries of the range are suboptimal in comparison to central or southern sites where beech trees are present. Despite these facts, *G. glis* survives in these areas but the suboptimal feeding conditions might be the reason for its low abundance in Lithuania and the surrounding regions (Pilāts et al. 2009, R. Juškaitis and V. Augutė, submitted).

Acknowledgments This research was funded by the European Social Fund under the Global Grant measure (grant no. VP1-3.1-ŠMM-07-K-01-026). Peter Adamík and two anonymous reviewers made valuable comments on earlier version of the manuscript. Jos Stratford revised the English of the manuscript.

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