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Factors affecting the bird predation of low density gypsy moth egg masses in three types of hardwood forests in southwest Hungary

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Abstract

Bird predation on gypsy moth *Lymantria dispar* L. (Lepidoptera Erebidae) egg masses may have a significant role in the gypsy moth population regulation; therefore the understanding of this process is a key issue to prevent large scale damage. In this paper, we aimed to quantify the winter predation of egg masses by birds and to reveal what factors affect its efficiency in three types of Central European hardwood forests. We detected a predation frequency of 20%, i.e. every fifth egg masses was destroyed at some extent by birds, while the mean percentage of removed surface per attacked egg masses was 35%. We measured the size of egg masses, their location on the trunk and environmental variables. Factors affecting predation frequency as well as the removed surface differed among forest stands characterized by different tree species composition. In beech dominated forest, egg masses located on the north and northeast side of trees were more frequently attacked than egg masses located in any other directions. In hornbeam forests, the predation frequency increased with the height on the trunk, while in Turkey oak forests, only the size of egg masses had a significant positive effect on egg mass predation rate. Egg mass size also affected the percentage of removed surface. Tree species, tree diameter and shrub cover had no significant effect on egg mass predation. Thus, we can conclude that egg mass predation is influenced rather by egg mass location or size than by other habitat characteristics.

Key words: ecosystem service, bird predation, natural enemies, *Lymantria dispar*, climate change, forest management.

Introduction

In the Northern Hemisphere, gypsy moth *Lymantria dispar* L. (Lepidoptera Erebidae) is one of the most serious forest pests, periodically defoliating extensive forested areas of Europe, Asia and North-America. Defoliation cause significant stress to the trees often resulting in serious economic and ecological effects. The loss of leaves decreases the growth rate and seed production (Dulamsuren *et al*., 2010) while increases the vulnerability of secondary pests and diseases (Gerardi and Grimm, 1979; Twery, 1990; Rieske and Dillaway, 2008), and thereby may triggers decline chains resulting in mass tree mortality (McManus and Csóka, 2007; Csóka *et al*., 2015). Climate change scenarios - moreover - foresee more warm and xeric climate which are expected to further increase the frequency of gypsy moth outbreaks (Csóka, 1997; Allstadt *et al*., 2012; Klapwijk *et al*., 2013) as well as the extent of the damaged area (Vanhanen *et al*., 2007). To counteract these environmental changes and keep gypsy moth damage under control, there is an urgent need to study and understand the natural regulatory mechanism acting on gypsy moth populations.

In most habitats, gypsy moth population density fluctuates cyclically: after a latency phase of several years, the population reaches a peak density, then collapses (Luciano and Prota, 1981; Fraval and Villemant, 2009). The major goal of the studies on gypsy moth population regulation is to identify the factors responsible for maintaining gypsy moth populations at low densities and thereby to extend the length of periods between outbreaks (Gould *et al*., 1990). In low-density populations predation has been identified as the major driver of gypsy moth mortality (Campbell, 1975). Predators consume gypsy moth in every developmental stage. For example, larvae and pupae are frequently eaten by small mammals, while egg masses are subject to predation by most birds and predatory arthropods (Brown and Cameron, 1982). As gypsy moth spends more than half of its life cycle (8-9 month) as eggs, the natural enemies of egg masses may have a particularly important role in the regulation of gypsy moth populations. Especially the winter predation by birds needs to be highlighted. Previous studies described that birds frequently feed on egg masses in the absence of other food resources (Higashiura, 1989). For example, Cooper and Smith (1995) showed that the percentage of the destroyed egg masses by birds may reach the 90% during winter period, which may indicates a key role of birds in gypsy moth population regulation. Although egg mass predation by birds has been the subject of several studies throughout the world over the past decades (Reichart, 1959; Higashiura, 1989; Turcani *et al*., 2003; Camerini, 2009, Tabakovic-Tosic *et al*., 2013), we still lack of knowledge on how predation pressure on egg masses can be maintained and improved. To address this question, we attempted a study to quantify bird predation rate on egg masses and to reveal what factors affect its rate in Central European hardwood forests. We aimed to examine the effects of egg mass location as well as some local habitat characteristics on the bird predation rate. Local habitat characteristics - such as shrub density or tree diameter - are known to markedly influence bird communities (Fuller, 2003; Diaz, 2008; Bereczki *et al*., 2014), thus we hypothesized that they have an effect on their predation pressure as well. To get information from a wider range of habitats preferred by gypsy moth, we examined forest stands with different tree species compositions: a Turkey oak *Quercus cerris* L., a hornbeam *Carpinus betulus* L. and a beech *Fagus sylvatica* L. dominated forest stand were chosen to the study.

Materials and methods

Study area and site description

Our study area was situated in the southern part of the Balaton Upland in Hungary, Central Europe (46°56-57'N, 17°38-39'E). The climate of this region is temperate with a mean annual temperature of 9 °C and an average annual rainfall of ca. 600 mm (Dövényi, 2010). The topography consists of slopes and narrow valleys and the elevation is between 250-300 m. The area is covered mainly by deciduous hardwood forests mixed with meadows and agricultural areas. The forest cover exceed one third of the area. Forests are dominated by oak species (*Quercus* spp., mainly Turkey oak *Q. cerris* and sessile oak *Quercus petraea* (Matt.) Liebl.) mixing with hornbeam *C. betulus* and beech *F. sylvatica*. In this area gypsy moth has caused "traditionally" serious defoliation over the last decades. The last series of outbreaks began in 2003 and reached their peak in 2005, when the damaged area of this region exceeded the 50,000 ha (Csóka and Hirka, 2009). Since the population collapsed in 2006, a low but increasing density has been observed. Between 2007 and 2009: no egg mass was detected in the area; in 2010: low egg mass density (<500 egg masses/0.1 ha) was observed in 1 ha; in 2011: low egg mass density (<500 egg masses/0.1 ha) was observed in 20 ha (Source: Forest damage database of the Hungarian Forest Research Institute); in 2012: low egg mass density (<500 egg masses/0.1 ha) was observed in 390 ha and medium egg mass density (500-1000 egg masses/0.1 ha) was observed in 49 ha (Source: National Forest Damage Inventory System - NÉBIH-EI).

To study predation pressure on gypsy moth egg masses, three middle aged forest stands were selected within the study area. The selected stands represented different forest types with markedly different mixture ratio. Stand 1 represented a beech dominated forest type, stand 2 was a hornbeam dominated forest, while in stand 3 Turkey oak was the dominant species. The mixture ratio and the mean habitat characteristics are shown in table 1. All of the selected stands were managed for timber using shelterwood silvicultural system with a rotation period of 100-120 years.

Data collection

Within the selected forest stands, we conducted a survey to measure egg mass predation and reveal the effect of local factors on the predation pressure. During the autumn of 2011 each stand was systematically searched visiting each tree and recording all egg masses. The trees with recorded egg masses were located with GPS and egg masses were let on the trees undisturbed to check winter predation. During the first survey of egg masses we recorded the following variables: the size (maximum length, maximum width) of the egg masses, their height on the trunk and the cardinal direction of egg mass on the tree. To check predation, each recorded egg mass were re-visited in the March of 2012, shortly before larval hatching. Thus, we were able to express the total annual predation on egg masses. To quantify predation, we measured the size (maximum length and maximum width) of the surface removed by natural enemies. Predation rate was expressed as the percentage of the removed surface from the total egg mass area (Higashiura, 1980).

In relation to the egg mass predators, we can conclude that the experienced sign of predation was most likely caused by birds. Indeed, egg masses that showed any sign of predation were significantly destroyed and there were missing eggs in every case. This type of predation probably indicates the feeding activity of birds. The sign of predatory arthropods is completely differed from bird predation because arthropods, such as the larder beetle (*Dermestes lardarius* L.), do not destroy egg masses, but suck the nutrients from the eggs. We did not detect any sign which can be joined to arthropods.

Table 1. The main characteristics of the three selected forest stands based on the Hungarian Database of forest stands.

	Mixture ratio	Stand age (year)	Canopy closure (%)	Mean DBH (cm)	Stand size (ha)
Beech dominated forest stand	beech: 48% hornbeam: 30% Turkey oak: 20% sessile oak: 2%	51	95	26.95	3.228
Hornbeam dominated forest stand	hornbeam: 40% beech: 30% Turkey oak: 15% pedunculate oak: 10% Scots pine:5%	59	94	23.59	4.653
Turkey oak dominated forest stand	Turkey oak: 60% hornbeam: 25% sessile oak: 5% red oak: 5% field maple: 5%	34	100	12.81	4.646

Table 2. Egg mass density, egg mass size, and the height on the trunk of gypsy moth (*L. dispar*) egg masses in three forest types in Hungary during the winter of 2011-2012.

Forest type	Egg mass density (number/ha)	Size of egg masses (cm^2) mean (± SE)[1]	Height on the trunk (cm) mean (± SE)
Beech dominated forest	86.65	8.10 (3.97)	76.77 (72.11)
Hornbeam dominated forest	122.15	7.69 (3.17)	68.36 (83.52)
Turkey oak dominated forest	112.90	7.67 (3.57)	80.23 (82.48)

[1]Egg mass size was calculated as the multiplication of the maximum length and maximum width of the egg mass.

During the summer of 2012 a vegetation assessment was carried out to measure the local habitat characteristics potentially affect egg mass predation. All trees with egg masses were re-visited and the species of the tree as well as the diameter at breast height (DBH) were recorded. In addition to these data, we recorded the exact location and the total extent of every shrub patches within the whole area of the selected stands. Shrub patches were located with GPS, and the total shrub cover (m^2) was calculated around each tree within a circular plot with a radius of 5 m.

Data analysis

The predation on egg masses was analysed in two steps: each egg mass was categorized as whether bird predation was observed or not, and if predation occurred, the percentage of removed surface was expressed as the percent of removed surface (see above). Thus, we were able to separately analyse (1) what factors influence whether natural enemies find egg masses (i.e. predation frequency), and (2) what factors affect the percentage of removed surface on egg masses found by natural enemies.

To examine the effect of egg mass location and habitat characteristics on predation frequency, logistic regression models were built separately in the three forest stands. In these models the dependent variable was binary (predated or not), and the explanatory variables were the follows: egg mass size, height on the trunk, cardinal direction on the tree, tree species, tree diameter at breast height and shrub cover around the trees in 5 m radius. Prior to modelling, conditional density plots were used to describe how the binary dependent variable changes over each potential explanatory variable. In the case of categorical variables (e.g. cardinal direction, tree species) multiple comparisons with Tukey post hoc tests were used to reveal the differences among each level of the variables.

In the second step of the analysis, we examined only those egg masses on which some predation was occurred, and we express the predation as the percentage of the removed surface from the egg masses. To examine the relationship between the percentage of removed surface and the explanatory variables, linear regression models were built. In the linear models, the potential explanatory variables were the same as in the logistic regression models (egg mass size, height on the trunk, cardinal direction, tree species, DBH, shrub cover). The dependent as well as the potential explanatory variables were evaluated for normality using Kolmogorov-Smirnov one sample test, and if necessary were transformed by log-transformation (in the case of the height on the trunk and shrub cover). Prior to modelling, we carried out pairwise correlation analysis and graphical explorations between the dependent variable and the potential explanatory variables. Only explanatory variables that significantly correlated with dependent variables and had homogenous scatterplots were retained in the model selection. During model evaluation, we took into account the graphical diagnostics of the models in addition the results of statistical tests.

The shrub cover around the trees was calculated using QGIS 2.0. The analysis was carried out in R 2.13.0 environment (R Development Core Team, 2011). We used the package "multcomp" (Bretz *et al*., 2010) for the multiple comparisons.

Results

Egg mass density, size and distribution patterns

We detected a total of 1372 egg masses in the tree studied forest stands. More than one egg masses was observed on 235 trees, while 1135 trees contained only one egg masses. The main egg mass density of the study area was 107.09 (± 18.30) egg masses per ha and was variable among forest stands with different tree species composition (table 2). The mean size and the mean aboveground height of the egg masses in the three forest stand are also shown in table 2.

The frequency distribution of egg masses in relation to cardinal direction is shown in figure 1. Based on χ^2 test, the female moths tend to lay their eggs on the southern sides of the trees in all examined forest stands ($\chi^2 = 507.37$, df = 8, $P < 0.001$). In addition to the cardinal direction, the tree size also influenced the egg mass distribution. Namely, trees with egg masses had significantly lower DBH than trees without egg masses considering the three forest stands (Welch two sample t-test, $t = -4.63$, df = 287.66, $P < 0.001$).

Egg mass predation by birds

The predation frequency (i.e. the mean percent of attacked egg masses by birds) was 20.10% throughout the study area and was variable among forest stands characterized by different tree species composition. The highest predation frequency was detected in the Turkey oak dominated forest stand (table 3). The removed surface on attacked egg masses expressed as the mean percentage of area removed from an individual egg mass was 35.30%. However, if we consider all egg masses (i.e. attacked and not attacked egg masses were pooled) the

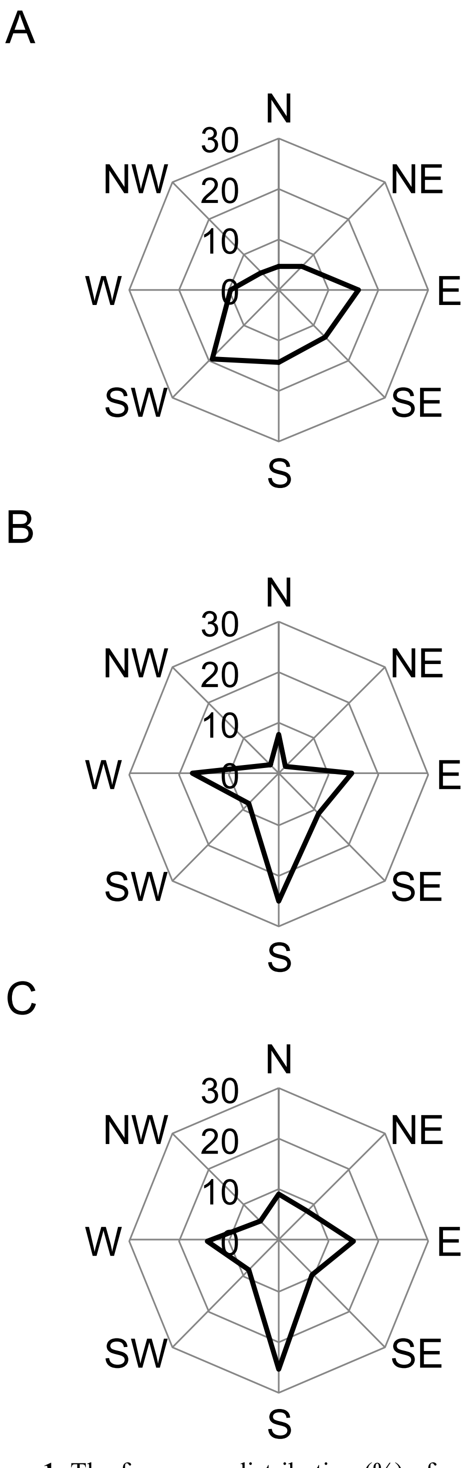

Figure 1. The frequency distribution (%) of egg masses in relation to cardinal direction on the trees in a beech dominated (A), a hornbeam dominated (B) and a Turkey oak dominated (C) forest stand in Hungary.

removed surface was only 7.39% (± 22.53). Less than 10% predation was measured on 87.20% of egg masses and only 3.93% of egg masses were completely destroyed.

Effects of local factors on egg mass predation

Predation frequency

The factors affecting whether egg masses were damaged or not differed among the forest stands characterized by different tree species composition.

In beech dominated forest, the egg mass predation was influenced by the cardinal direction of egg mass on the tree. Egg masses located on the north and northeast side of trees were more frequently eaten than egg masses located in any other directions (figure 2 and table 4). According to logistic models, other local variables had no effect on predation in beech forest (P = 0.229-0.905, all NS).

In hornbeam dominated forest, the predation rate was positively affected by the height on the trunk (figure 3) and negatively by the width of the egg masses, while other variables had no effect on predation (P = 0.260-0.989, all NS) (table 4).

In the Turkey oak dominated forest, the predation was significantly affected by the length of the egg masses; i.e. egg masses with higher length were more frequently attacked (table 4). Furthermore, multiple comparisons of the cardinal direction on the tree revealed a marginally

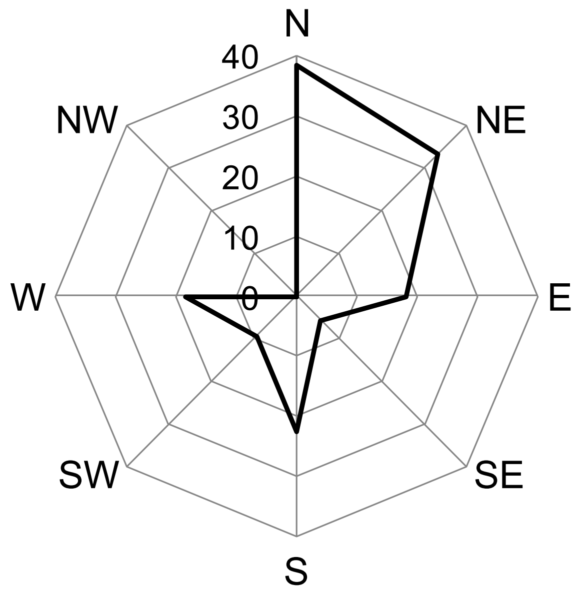

Figure 2. The percentage (%) of destroyed egg masses by birds on the main cardinal directions in beech a dominated forest stand in Hungary.

Table 3. The predation frequency by birds and the percentage of removed surface of gypsy moth (*L. dispar*) egg masses in three forest types in Hungary during the winter of 2011-2012.

Forest type	Predation frequency (%)[1]	Percentage of removed surface[2]
Beech dominated forest	18.72	31.00
Hornbeam dominated forest	17.38	48.66
Turkey oak dominated forest	27.50	26.25

[1]The predation rate is expressed as the frequency of egg mass damage.
[2]The predation rate is expressed as the percentage of removed surface from each predated egg masses.

Table 4. The results of logistic regression models built for the relationship between bird predation frequency[1] of gypsy moth (*L. dispar*) egg masses and potential explanatory variables in three forest types characterized by different tree composition in Hungary during the winter of 2011-2012. Significant values are in bold.

Logistic regression model	Beech dominated forest			Hornbeam dominated forest			Turkey oak dominated forest		
	d.f	*z*	*P*	d.f	*z*	*P*	d.f	*z*	*P*
Height on the trunk	278	−0.587	0.557	533	−3.408	**<0.001**	518	−0.218	0.828
Cardinal direction on the tree	244	3.266	**<0.001**	488	0.019	0.985	498	−1.880	0.060
Tree species	278	−1.203	0.229	534	0.013	0.989	518	0.299	0.765
DBH of the tree	244	−0.992	0.321	493	−0.512	0.609	505	−1.346	0.178
Egg mass number on the tree	278	8.105	**<0.001**	534	11.60	**<0.001**	518	8.534	**<0.001**
Shrub cover	278	0.120	0.905	535	−0.774	0.439	519	−0.880	0.379
Length of the egg masses	278	−0.834	0.404	535	−1.127	0.260	519	−2.699	0.006
Width of the egg masses	278	0.232	0.816	535	2.696	0.007	519	0.447	0.657

[1]The predation rate is expressed as the frequency of egg mass damage.

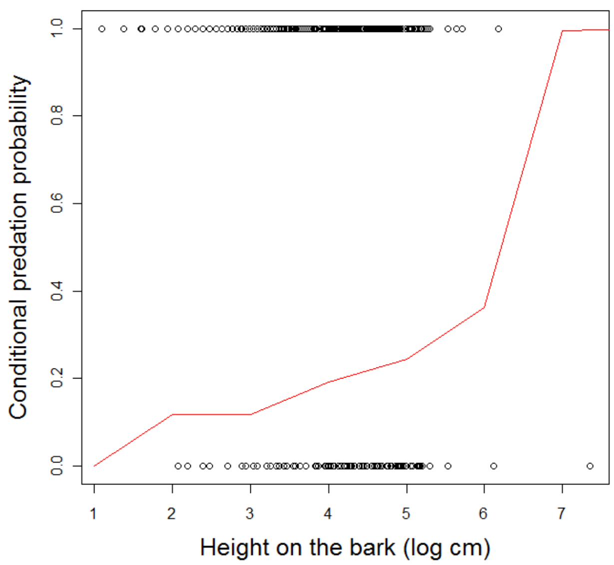

Figure 3. Conditional density plot showing the effect of the height on the trunk on the bird predation frequency of gypsy moth egg masses in a hornbeam dominated forest stand in Hungary.

significant difference in predation between the north and south direction (P = 0.06). As in beech dominated forest, egg masses on the north were attacked more frequently than egg masses located on the south side of the tree (figure 2 and table 4).

Moreover, it should be noted, that egg masses situated on trees which contained more than one egg masses were more frequently attacked by natural enemies, than egg masses situated on tree with only one egg mass (table 4). The tree species, the DBH of the tree and the shrub cover did not affected predation frequency.

Percentage of removed surface

Among the potential explanatory variables, the egg mass size had a significant effect on the percentage of removed surface in each forest stand. Namely, larger egg masses were destroyed to a smaller extent, than the smaller egg masses. In the hornbeam and Turkey oak dominated forest stands, egg masses with larger width were predated to a smaller extent (table 5). In beech dominated forests, the egg mass length was a negative effect on the removed surface, although this effect was only marginal (table 5). In addition to the egg mass size,

Table 5. The results of linear regression models built for the relationship between the percentage of removed surface[1] by birds on attacked egg masses of gypsy moth (*L. dispar*) and the potential explanatory variables in three forest types characterized by different tree composition in Hungary during the winter of 2011-2012. Significant values are in bold.

Linear regression model	Beech dominated forest			Hornbeam dominated forest			Turkey oak dominated forest		
	d.f	*z*	*P*	d.f	*z*	*P*	d.f	*z*	*P*
Height on the trunk	42	0.125	0.725	91	1.397	0.240	141	0.404	0.526
Cardinal direction on the tree	33	1.172	0.345	74	0.295	0.954	129	0.884	0.522
Tree species	38	1.003	0.429	88	0.665	0.618	138	0.330	0.857
DBH of the tree	38	0.113	0.738	83	0.428	0.515	136	0.007	0.930
Egg mass number on the tree	42	0.058	0.809	91	6.561	**0.011**	141	0.667	0.414
Shrub cover	42	3.072	0.087	91	3.838	0.053	141	0.087	0.768
Length of the egg masses	42	3.947	0.053	91	0.352	0.554	141	1.487	0.225
Width of the egg masses	42	0.013	0.908	91	10.406	**0.002**	141	8.921	**0.003**

[1]The predation rate is expressed as the percentage of removed surface from each predated egg masses.

the number of egg masses on the tree had a positive effect on egg mass predation rate, but only in the hornbeam dominated forests. In the hornbeam forest, the shrub cover also had a marginally significant positive effect on egg mass predation. The other variables had no effect on the percent removed surface by natural enemies (P = 0.08-0.95, all NS).

Discussion and conclusions

Egg mass predation by natural enemies - especially by birds - may have an important role in the regulation of gypsy moth population (Gould *et al*., 1990). Thus, any study aiming to understand the underlying mechanisms and to identifying factors influencing bird predation efficiency is a key concern to prevent large scale damage caused by gypsy moth caterpillars during outbreaks. We presented here the results of a study on the winter predation by birds of more than one thousand egg masses. We concentrated to the factors affecting predation pressure rather than to the long-term changes in predation rates. Therefore, we cannot conclude to the long-term control of gypsy moth population, but the large amount of the examined egg masses as well as the wide range of the environmental variables let us to make some conclusion about the influencing factors of bird predation on egg masses.

At first, we can conclude, that the chance of the predation is higher on trees containing more than one egg masses, which result may indicate a density dependent response of birds at tree level. Other factors affecting predation differed among forest stands characterized by different tree species composition, indicating strong site specificity. In beech dominated forests, for example, predation frequency was related to the cardinal direction of egg masses on the tree. Namely, egg masses situated to the north were attacked significantly more frequently by birds, than egg masses in the southern and western directions. This predation pattern may be traced back to the different light conditions associated to the different cardinal directions. The light conditions, in turn, may influence the foraging behaviour of natural enemies, especially in the case of passerines. Indeed, passerines tend to avoid foraging sites with strong shining light to minimize risk being predated (Villén-Perez *et al*., 2013). The other factor influenced predation frequency was the height on the trunk, but only in the hornbeam dominated forest stand. In this stand, egg masses situated higher on the trunk were attacked more frequently than egg masses situated near to the ground. This result overlaps with previous studies by Higashiura (1980; 1989), who observed that in winter, birds began to forage on the higher part of the trunks and they extend their foraging site to the lower part of the trunks in early spring (Higashiura, 1989). Besides the cardinal direction and height on the trunk, egg mass size also had an effect on predation frequency. In Turkey oak forests egg masses with smaller length were more frequently predated, while in hornbeam forests, wider egg masses were more often attacked. From this result we can conclude, that egg masses with closely circular shape can be easily noticeable for birds especially in forest stands dominated by oaks, which bark surface are characterized by strong longitudinal pattern.

Considering the removed surface of attacked egg masses, our results show that larger egg masses were destroyed to a smaller extent in all examined forest stands. This result coincides with the previous observations by Reichart (1959), which showed that in smaller egg masses 80-100% of the eggs were destroyed while in larger egg masses this percentage was between 33-89%. We should also highlight the effect of shrub cover on the percentage of the removed surface. Previous studies on winter foraging behaviours showed that passerines - the main predators of egg masses - tend to spend more time with foraging and hence consume more food near to the shrubs, which provide refuge from the predators (Walther and Gosler, 2001; Carrascal and Alonso, 2006). In our case, however, the effect of shrub cover on the egg mass predation was only marginally significant.

Summarizing our results, we can conclude that egg mass predation is influenced rather by egg mass location than by other habitat characteristics in our study area, contrary to our hypothesis. As a consequence, we cannot recommend any kind of management intervention to improve natural pest control potential of birds on egg masses in winter. Forestry and habitat management may have larger effect on other aspect of gypsy moth population regulation such as the predation of pupae by small mammals (Liebhold *et al*., 2005), the spread of gypsy moth among sites (Foster *et al*., 2013) or the susceptibility of forest stands to gypsy moth damages (Kleiner and Montgomery, 1994). However, habitat management has been proved to have an important role to maintain the suitability of forests to the population of birds (Bereczki *et al*., 2014), who's presence and foraging mean a significant mortality to gypsy moth eggs.

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References

ALLSTADT A. J., HAYNES K. J., LIEBHOLD A. M., JOHNSON, D. M., 2013.- Long-term shifts in the cyclicity of outbreaks of a forest defoliating insect.- *Oecologia*, 172:141-151.

BERECZKI K., ÓDOR P., CSÓKA G., MAG Z., BÁLDI A., 2014.- Effects of forest heterogeneity on the efficiency of caterpillar control service provided by birds in temperate oak forests.- *Forest Ecology and Management*, 327: 96-105.

BRETZ F., HOTHORN T., WESTFALL P., 2010.- *Multiple comparisons using R*.- CRC Press, Boca Raton, USA.

BROWN M. W., CAMERON E. A., 1982.- Natural enemies of *Lymantria dispar* (Lep.: Lymantriidae) eggs in Central Pennsylvania, U.S.A., and a review of the world literature on natural enemies of *L. dispar* eggs.- *Entomophaga*, 27: 311-322.

CAMERINI G., 2009.- Factors affecting *Lymantria dispar* mortality in a willow wood in northern Italy.- *Bulletin of Insectology*, 62: 21-25.

CAMPBELL R. W., 1975.- The gypsy moth and its natural enemies.- *Information Bulletin 381*. USDA, Washington.

CARRASCAL L. M., ALONSO C. L., 2006.- Habitat use under latent predation risk. A case study with wintering forest birds.- *Oikos*, 112: 51-62.

COOPER R. J., SMITH H. R., 1995.- Predation on gypsy moth (Lepidoptera, Lymantriidae) egg masses by birds.- *Environmental Entomology*, 24: 571-575.

CSÓKA G., 1997.- Increased insect damage in Hungarian forests under drought impact.- *Biologia*, 52: 1-4.

CSÓKA G., HIRKA A., 2009.- Gyapjaslepke legutóbbi tömegszaporodása Magyarországon [The last outbreak of Gypsy Moth in Hungary].- *Növényvédelem*, 45: 196-201.

CSÓKA G., PÖDÖR Z., NAGY G., HIRKA A., 2015.- Canopy recovery of pedunculate oak, Turkey oak and beech trees after severe defoliation by gypsy moth (*Lymantria dispar*): case study from Western Hungary.- *Forestry Journal (Lesnicki Casopis)*, 61: 143-148.

DIAZ L., 2008.- Influences of forest type and forest structure on bird communities in oak and pine woodlands in Spain.- *Forest Ecology and Management*, 223: 54-65.

DÖVÉNYI Z., 2010.- *Magyarország Kistájainak Katasztere* [Cadastre of Hungarian regions].- MTA Földrajztudományi Kutatóintézet, Budapest, Hungary.

DULAMSUREN C., HAUCK M., LEUSCHNER H. H., LEUSCHNER C., 2010.- Gypsy moth induced growth decline of *Larix sibirica* in a forest-steppeecotone.- *Dendrochronologia*, 28: 207-213.

FOSTER J. R., TOWNSEND P. A., MLADENOFF D. J., 2013.- Spatial dynamics of a gypsy moth defoliation outbreak and dependence on habitat characteristics.- *Landscape Ecology*, 28: 1307-1320.

FRAVAL A., VILLEMANT C., 2009.- Three successive regulation patterns of gypsy moth (Lepidoptera, Lymantriidae) populations in the Mamora cork oak forest (Morocco).- *Le Courrier De L'Environment De L'Inra*, 13 March 2009 [online] URL: http://inra.fr/dpenv/ld-dyn-e.htm

FULLER R. J., 2003.- *Bird life of woodland and forest*.- Cambridge University Press, Cambridge, UK.

GERARDI M. H., GRIMM J. K., 1979.- Physiological stress to trees as a result of defoliation, pp. 101-105. In: *The history, biology, damage, and control of gypsy moth* Porthetria dispar *(L.)* (GERARDI M. H., GRIMM J. K., Eds).- Fairleigh Dickinson University Press, London, UK.

GOULD J. R., ELKINTON J. S., WALLNER W. E., 1990.- Density-dependent suppression of experimentally created gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), populations by natural enemies.- *Journal of Animal Ecology*, 59: 213-233.

HIGASHIURA Y., 1980.- Analysis of factors affecting bird predation on gypsy moth egg masses by using Holling's Disc-Equation.- *Researches on Population Ecology*, 22: 147-162.

HIGASHIURA Y., 1989.- Survival of eggs in the gypsy moth, *Lymantria dispar*. I. Predation by birds.- *Journal of Animal Ecology*, 58: 403-412.

KLAPWIJK M. J., CSÓKA G., HIRKA A., BJÖRKMAN C., 2013.- Forest insects and climate change: long-term trends in herbivore damage.- *Ecology and Evolution*, 3: 4183-4196.

KLEINER K. W., MONTGOMERY M. E., 1994.- Forest stand susceptibility to the gypsy moth (Lepidoptera, Lymantriidae) - Species and site effects on foliage quality to larvae.- *Environmental Entomology*, 23: 699-711.

LIEBHOLD A. M., RAFFA K. F., DISS A. L., 2005.- Forest type affects predation on gypsy moth pupae.- *Agricultural and Forest Entomology*, 7: 179-185.

LUCIANO P., PROTA R., 1981.- La dinamica di popolazione di *Lymantria dispar* L. in Sardegna. I. Indicatori della gradazione ricavati dalle ovideposizioni [Gypsy moth population dynamics in Sardinia. I. Gradation indicators from egg-cluster].- *Studi Sassaresi*, 27 (1979): 137-160.

MCMANUS M., CSÓKA G., 2007.- History and impact of gypsy moth in North America and comparison to the recent outbreaks in Europe.- *Acta Silvatica et Lignaria Hungarica*, 3: 47-64.

R DEVELOPMENT CORE TEAM, 2011.- R*: A language and environment for statistical computing*.- R Foundation for Statistical Computing, Vienna, Austria.

REICHART G., 1959.- A gyapjaspille (*Lymantria dispar* L.) tojásait pusztító madarak [Birds that destroying gypsy moth (*Lymantria dispar* L.) egg masses].- *Aquila*, 66: 283-287.

RIESKE L. K, DILLAWAY D. N., 2008.- Response of two oak species to extensive defoliation: tree growth and vigor, phytochemistry, and herbivore suitability.- *Forest Ecology and Management*, 256: 121-128.

TABAKOVIC-TOSIC M., GEORGIEV G., MIRCHEV P., TOSIC D., CURGUZ V. G., 2013.- Gypsy moth in central Serbia over the previous 50 years.- *Acta Zoologica Bulgarica*, 65: 165-171.

TURCANI M., LIEBHOLD A., MCMANUS M., NOVOTNY J., 2003.- Preliminary results on predation of gypsy moth egg masses in Slovakia, pp. 115-120. In: *Proceedings: ecology, survey and management of forest insects* (MCMANUS M. L., LIEBHOLD A. M., Eds), 2002 September 1-5, Krakow, Poland.

TWERY M. J., 1990.- Effects of defoliation by gypsy moth.- USDA Gypsy Moth Research Review, USA.

VANHANEN H., VETELI T. O., PÄIVINEN S., KELLOMÄKI S., NIEMELÄ P., 2007.- Climate change and range shift in two insect defoliators: gypsy moth and nun moth - a model study.- *Silva Fennica*, 41: 621-638.

VILLÉN-PÉREZ S., CARRASCAL L. M., SEOANE J., 2013.- Foraging patch selection in winter: a balance between predation risk and thermoregulation benefit.- *PLoS ONE*, 8: e68448.

WALTHER B. A., GOSLER A. G., 2001.- The effects of food availability and distance to protective cover on the winter foraging behaviour of tits (Aves: *Parus*).- *Oecologia*, 129: 312-320.

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