Great spotted woodpecker (*Dendrocopos major*) and red squirrel (*Sciurus vulgaris*) prefer different cone features of European larch (*Larix decidua*)

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Abstract

Specialized conifers-seed-eating animals, such as crossbills (*Loxia* spp.), woodpeckers (Picidae), squirrels (Sciuridae), nutcrackers (*Nucifraga* spp.) and many of insects (e.g., Pyralidae and Tortricidae) exert phenotypic selection on different features of the coniferous cones. In response to such selection, many conifers invest resources in various physical and chemical seed defenses. The study was conducted in mixed mountain forests in West Sudetes (50°55'N 15°46'E), southwest Poland. We selected 10 anvils for great spotted woodpecker and 12 foraging places for the red squirrel. We collected 350 foraged larch cones from each anvil and feeding place for both species and also 50–100 unforaged larch cones within a 15 m radius at each site. In this study, we documented different selection pressures on European larch (*Larix decidua*) cones exerted by great spotted woodpecker (*Dendrocopos major*) and red squirrels (*Sciurus vulgaris*). The great spotted woodpecker preferred foraging on cones with thinner peduncles resulting in selection for thicker peduncles. However, red squirrels preferred feeding on small and medium larch cones, favoring trees producing large cones. Different foraging behaviors influence the form of selection exerted by these two seed-eating species.

Keywords Great spotted woodpecker · Red squirrel · European larch · Pre-dispersal seed predation · Phenotypic selection

Introduction

Herbivores have favored the evolution of plant defenses (Phillips and Croteau 1999; Barclay 2015). One of the steps of antagonistic interactions between animals and plants is seed predation which has an adverse effect on reproductive success and population dynamic of many plants (Janzen 1971; Hulme 1996). A strong selection pressure exerted on plants results in investment on defenses such as secondary metabolites or additional tissue to protect the seeds (Bazzaz et al. 1987; Coffey et al. 1999). This situation leads to the co-evolution described especially in case of pre-dispersal seed predation by crossbills on many conifers species (e.g. Benkman and Parchman 2009; Benkman 2010; Mezquida and Benkman 2010). Selection pressure by conifers-seed-eating animals, influence on

different cone features (Siepielski and Benkman 2008; Garcia et al. 2009; Myczko and Benkman 2011). For that reason many cones and seeds traits are heritable (references in Benkman et al. 2010). Different seed predators species who are foraging on the same coniferous species may prefer various morphological cone features (Summers and Proctor 1999; Mezquida and Benkman 2014) therefore, this created multidirectional adaptations. Hence, different morphological and reproduction features (e.g., spines, cone mass, cone length, thicker scales, produce empty seeds) may be prevented from seed predation, depending on technique/way of feeding of the seed-eating animals used to obtain seeds from closed cones.

Two common pre-dispersal seed predators in Central Europe are the great spotted woodpecker (*Dendrocopos major* Linnaeus, 1758) and red squirrel (*Sciurus vulgaris* Linnaeus, 1758) (Hogstad 1971; Kędra and Mazgajski 2001; Lurz et al. 2005). During winter these species forage on seeds in closed cones of mainly Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and European larch (*Larix decidua*). Additionally, woodpeckers and squirrels use different methods to remove cones from branches and to extract seeds from the closed cones. Great spotted woodpeckers remove the

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cone from the branches by twisting it in their bill, and then carry the cone to an anvil where the cone is secured, and then hammered with the bill to access the seeds (Pulliainen 1963; Myczko and Benkman 2011). Red squirrels gnaw through the cone peduncle, and then hold the loose cone with their forefeet and bite off successive cone scales to expose the underlying seeds (Bosch and Lurz 2012; Dylewski et al. 2016).

The European larch is a pioneer, long-lived and widely planted coniferous tree species distributed in the central and eastern mountains of Europe. Its elevation range varies between 180 m in Poland to 2500 m in central and southwestern Alps (Da Ronch et al. 2016). European larch produces small cones (19–60 mm long) with thin scales (1–2 mm) but with relatively strong and thick peduncles (Bonner and Karrfalt 2008; Da Ronch et al. 2016). The reproductive success of population from the Alps are strongly affected by specific insect seed predators (mainly three cone fly species *Strobilomyia* sp.) which can damage 60–90% of seeds able to germination (Roques 1993; Turgeon et al. 1994). Seed predation by insects on this tree was directly affected by variable cone production, climate condition and altitude (Poncet et al. 2009).

In this study, we showed different preferences on larch cones features by two vertebrate pre-dispersal seed predators. The extent to which woodpeckers and red squirrels exert selection on European larch cone structure is unknown. Because great spotted woodpeckers and red squirrels have different techniques for removing cones and extracting seeds, we hypothesized that (1) great spotted woodpecker show preference to the cone peduncle diameter but not to the cone length and (2) red squirrel show preference to the cone length but not to the cone peduncle diameter.

Materials and methods

Study area

Our study was conducted in mixed mountain forests in West Sudetes (50°55'N, 15°46'E), southwest Poland. The elevation varied between 380 and 560 m a.s.l. The means of precipitation and temperature in study areas varied between seasons: December–February 74 mm (−3 °C); March–May 74 mm (7 °C); June–August 104 mm (20 °C); September–November 63 mm (8 °C). The sites were managed forests dominated by mature Norway spruce (60%) with co-occurring Scots pine (25%) and European larch (5%) and with 10% addition of deciduous species mainly European beech (*Fagus sylvatica*), pedunculate oak (*Quercus robur*) and silver birch (*Betula pendula*).

Data collection

Firstly, in winter 2013/2014 we attempted to locate as many woodpecker anvils and red squirrel foraging places as possible. From these, we selected ten woodpecker anvils where woodpeckers foraged only on larch cones, and 12 red squirrel foraging places where we found stripped larch cones. To minimize recording the same individuals, the minimal distance in case woodpecker's anvils were 500 m, in case red squirrel's foraging places were at least 1 km apart. In April 2014, we collected 350 cones from each woodpecker anvils and 350 from each red squirrel feeding locations. At each site, we randomly collected 50–100 unforaged larch cones within a 15 m radius. The unforaged cones were randomly collected from larch green branches felled by a strong wind in March 2014. We measured cone length and peduncle diameter of cones foraged on by woodpeckers. We measured the length of all collected cones foraged on by squirrels but, we were able to measure peduncle diameter for only 944 cones.

Data analysis

We used the mixed general additive models (Mixed GAM's) with binomial errors with third-degree polynomial to test which cone features were correlated with larch cone predation, separately for great spotted woodpecker and red squirrel. In both models, we used cone length, peduncle diameter, and interaction between peduncle diameter and cone length as fixed effect predictor and foraging sites (in case woodpecker were anvils, in case red squirrels were feeding locations) as a random effect. We use a cubic spline to visualize the probability of woodpecker and red squirrel predation to the predictor variables. All analysis were performed in R 3.3.1 (R Development Core Team 2016) using the mgcv package (Wood 2015) and lattice package (Sarkar 2008).

Results

Peduncle diameter was related to the probability of predation by great spotted woodpeckers ($p < 0.001$, Table 1). The graphical visualization using a cubic spline showed that the woodpecker preferred cones with thinner peduncles (Fig. 1d).

Cone length ($p = 0.006$) and the interaction between cone length and peduncle diameter ($p < 0.001$) were related to the probability of predation by squirrels (Table 1). In all models, a random effect (feeding location) was significant ($p < 0.01$). The probability of foraging was most notable on short cones (Table 1) and for cones with the thinnest peduncles (Fig. 1).

Table 1 GAM's results on the probability of seed predation by great spotted woodpecker and red squirrel on European larch cone features

Fixed effect	Great spotted woodpecker					Red squirrel				
	Mean($\pm$ SE)	edf	Ref.df	Chi sq	<i>p</i>	Mean($\pm$ SE)	edf	Ref.df	Chi sq	<i>p</i>
Cone length (CL)	26.92($\pm$ 3.88)	1.99	1.99	4.28	0.121	26.69($\pm$ 2.46)	1.00	1.00	8.07	0.005
Peduncle diameter (PD)	3.82($\pm$ 0.50)	1.99	2.00	28.95	<0.001	4.09($\pm$ 0.36)	1.00	1.00	0.61	0.432
Interaction CL*PD		3.97	15.80	23.42	0.105		10.94	12.58	151.39	<0.001
Random effect		0.95	1.00	20.00	<0.001		0.99	1.00	197.28	<0.001

Abbreviations: *edf* effective degrees of freedom, *Ref.df* reference number of degrees of freedom used for hypothesis testing

Discussion

We found that great spotted woodpeckers and red squirrels exert selection on larch cones. Woodpeckers preferred foraging on cones with thinner peduncles that should cause selection favoring trees producing cones with thicker peduncles. Woodpeckers grasp the cone with their bill and twist the cone to break the peduncle. Presumably, woodpeckers need to spend more time to remove cones having thicker peduncles. However, producing thicker peduncles could come at a cost to

the tree of producing fewer seeds. Red squirrel preferred foraging on medium-sized larch cones. However, in the case of Scots pine and Norway spruce, red squirrel prefer feeding on a larger cone with more seeds (Summers and Proctor 1999; Molinari et al. 2006). Mezquida and Benkman (2005) presented that, large cones of Aleppo pine (*Pinus halepensis*) with thick scales are avoided by red squirrel, and they preferred foraging on small cones with thinner scales. But in the case of European larch both large and small cones have very thin scales in comparison to Aleppo pine.

Fig. 1 The probability of seed predation by both studied species on European larch cone features. The **a** and **b** represent the probability of seed predation by red squirrel in relation to cone length (**a**) and diameter of cone peduncle diameter (**b**). The **c** and **d** represent the probability of seed predation by great spotted woodpecker in relation to cone length (**c**) and diameter of cone peduncle diameter (**d**). The solid curves are based on cubic splines and the dashed lines indicate the range of SE

In contrast to the great spotted woodpecker, we do not find any direct preferences on cone peduncle size by red squirrels. However, we find a significant interaction between cone length and peduncle diameter. Red squirrels preferred to forage on medium sized cones with thick peduncle but they avoid large cones with thicker peduncle (Fig. 1a and b). However, we do not know how peduncle thickness is related to other cone traits, including the size and quantity of seeds. Based on our data we are not able to determine whether this preference is the result of competition with the great spotted woodpecker. Previously study showed that red squirrel might forage on a variety of conifers cones, which some of these have a large cone peduncle (see Krauze-Gryz and Gryz 2015). The red squirrel has strong teeth with hard enamel (Bosch and Lurz 2012) which are useful for gnawing many hard cones and fruit structure (e.g., cone scales, walnut and hazelnut nutshell) therefore, in accordance with our results, differences in larch cones peduncles does not have a significant impact on the choice of cones by foraging red squirrels.

There are many described examples of phenotypic selection exerted by pre-dispersal seed predators that affect different features of cones in different coniferous species (Siepielski and Benkman 2008; Garcia et al. 2009; Myczko and Benkman 2011; Dylewski et al. 2017). For example, Myczko and Benkman (2011) showed that great spotted woodpecker avoids Scots pine cones with large apophyses and preferred medium-sized cones with smaller apophyses. Another research showed that great spotted woodpecker preferred foraging on medium Norway spruce cones and avoiding smaller and larger cones (Dylewski et al. 2017). The role of cone peduncle was taken into consideration only on species who do not remove cones from the branches in order to eat seeds (see Siepielski and Benkman 2007). However, large cone peduncle provides a physical barrier against seed predators, especially for woodpeckers who transport cones to the special foraging place.

Previous research indicated that seed predation has a strongly significant negative impact on plant recruitment (Janzen 1971). Seed predation effects on population growth rate and spatial distribution of many plant species (Hulme 1998). However, the climate has a direct impact on mast seeding and specific seed predators (Poncet et al. 2009). European larch is typical for mountain sites and strongly threatened in future by climate change (Dyderski et al. 2018). Meier et al. (2012) showed that seed dispersal strongly modifies the observed patterns of climate change-based migration rates. Linking effect by specific insect and vertebrate seed predators, competition and climate change could affect natural regeneration of European larch and can determine its future distribution range.

We documented that the great spotted woodpecker and red squirrels are the selection agents of European larch cones based on morphological features. But their selective pressures

apply to different traits of cones. Great spotted woodpecker exerts a selection pressure based on cone peduncle diameter, favoring European larch individuals producing thicker peduncles. In contrast, red squirrels seed predation favored individuals producing small and larger cones. However, the direct explanation of reasons of red squirrel preference to foraging on medium-sized larch cones and avoiding large cones require further research.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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