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The effects of overwintering and habitat type on body condition and locomotion of the wolf spider *Pardosa alacris*

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ABSTRACT

Overwintering in temperate regions is a prominent mortality risk for invertebrates and may affect their behaviour and body condition. *Pardosa alacris* is a common ground dwelling spider in central European native and plantation forests, and habitat type and prey availability may play important roles in their overwintering. The effect of overwintering on body condition and behaviour of spiders in semi natural and exotic habitats is relatively unknown. Here we assess the effects of winter on spiders from native poplar and exotic pine plantations. The locomotory behaviour of *P. alacris* (distance covered and speed) was assessed by tracking their movement in a white circular plastic arena. We assessed body condition, body size, and total fat content. Forest type and sex had significant effects on body length. Fat content was significantly higher in the spring than in autumn, and spiders covered larger distances and were faster in autumn than in spring. Fat content had a significant negative effect on average speed. Spiders in native forests were smaller but grew more during the winter than in exotic plantations, possibly due to higher prey availability in native forests. Visually-hunting predators may significantly affect spiders. Fat spiders with better body condition moved less, and were thus less detectable by predators. However the low movement rate may result in a low rate of encountering prey items, thus lowering feeding efficiency.

1. Introduction

Exotic tree plantations can have severe ecological impacts on community compositions (Brockerhoff et al., 2008; Moreira-Arce et al., 2015) and ecosystem functioning (Spirito et al., 2014). Intensivelymanaged short-rotation exotic forest plantations reduces microhabitat diversity and changes vegetation composition. Tree species have a significant effect on understory light incidence and microclimate (Messier et al., 1998). Pine plantations commonly exploited for timber in Europe, generally show lower species richness and diversity of predatory invertebrates than plantations of native tree species (Bonham et al., 2002; Samways et al., 1996).

Spiders are abundant predatory arthropods in nearly all terrestrial ecosystems and play an important role in top-down regulation of the insect populations (Almada et al., 2017; Meissle and Lang, 2005; Schmidt and Tscharntke, 2005). They also play a key role in regulating soil fauna, thus having cascading effects on litter decomposition

(Lawrence and Wise, 2000; Liu et al., 2016). Spiders are generally sensitive to habitat change (Buddle et al., 2000). Habitat structure shapes spider diversity and abundance (Gallé et al., 2014a,b, 2016) may also affect foraging spider body condition. Here, we studied the wolf spider *Pardosa alacris* C.L. Koch, 1833 (Lyosidae, Araneae), a very common species in central European forests (Michalko et al., 2016). This species belongs to the ground-dwelling active hunter guild and shows a sit-and-move hunting strategy (Samu et al., 2003; Cardoso et al., 2011). It has a clear preference for dry deciduous forests with an open canopy and forest steppes (Michalko et al., 2016), but also occurs in pine forests (Gallé et al., 2014a,b).

Large spiders often have higher chances of overwintering survival (Schneider, 1995; Walker et al., 2003), but this correlation is not always clear (Gunnarsson, 1988; Kotiaho et al., 1996). Numerous indices have been proposed to assessing the body condition of invertebrates (Jakob et al., 1996). However, fat reserves are considered good estimators of body condition in arthropods (Contreras-Garduno et al., 2006), since

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age and nutrition intake determine their protein and lipid content (Bednaski et al., 2015; Cappelari et al., 2009). In predators, prey availability is an important factor that limits population size and individual growth rates (Kessler, 1971). Good body condition and rapid growth of an arthropod predator can be due to an increase in the quantity and quality of consumed prey, which is linked to habitat quality. In complex habitats, the amount of prey available to predatory arthropods is oftenhigher than in simple habitats (Copley and Winchester, 2010). Prey availability, together with predation risk influences foraging and microhabitat selection by predatory arthropods (Roume et al., 2011).

Overwintering in temperate regions is a considerable mortality risk for arthropods (Knapp and Saska, 2012). To avoid extremely low temperatures, arthropods overwinter in habitats that buffer temperature fluctuations (Roume et al., 2011). Furthermore, arthropods have several physiological adaptations to survive under low temperatures, such as 'cold-hardiness' (Lee, 2012). Some species may even be active at temperatures below freezing levels and search for food when other species have become inactive (Li and Jackson, 1996). The rate of successful overwintering is determined by body condition and is thus linked to prey availability in the overwintering habitat type (Gunnarsson, 1988; Lee, 2012). Forest patches are likely to be important overwintering habitats for arthropods at the landscape scale (Roume et al., 2011). To the best of our knowledge, the effect of overwintering on spider body condition and behaviour in semi natural and exotic habitats have not yet been studied.

The aim of this study is to test the effects of winter on the behaviour and body condition of spiders collected from native poplar (*Populus alba*) and exotic pine (*Pinus sylvestris*) plantations. We hypothesised that (1) winter has a significant negative effect on the fat reserves of spiders (2) the effect of winter on spiders is mediated by habitat type and (3) the habitat and body condition of the spiders affect their behaviour.

2. Material and methods

2.1. Study area and sampling

Field sampling was conducted in Southern Hungary (46° 42′ N, 19° 36′ E). The study area is characterized by semi-arid, temperate continental climate, with a precipitation range of 550–600 mmyr⁻¹ and a daily temperature range of 0–5 °C in winter and 21–28 °C in summer (Domonkos and Tar, 2003; Török et al., 2003). The basic soil type is calcareous coarse sand, and a large portion of the landscape comprises native and exotic plantations.

The specimens were collected in six forest plantations using the ground hand collecting method (Sorensen et al., 2002). We selected six short-rotation plantations: three native silver poplar (Populus alba) and three non-native pine (Pinus sylvestris). The size of the plantations ranged between 4.2 and 18.1 hectares, and all of them were at commercial maturity. The distance between the sampling sites ranged between 250 and 1200 meters to ensure similar climatic conditions, soil type, and water regime. In each of the sampling sites, we collected 15 sub-adult P. alacris spiders in the second half of November 2016, shortly before overwintering, and again in early March 2017, when the activity of P. alacris increases after winter (Eliašová et al., 2015). The 180 spiders were housed individually in plastic containers (4.5 cm in diameter and 7 cm height) with blotting-paper as substrate. We kept the individuals at a constant temperature of 10 °C and a 12:12 h photoperiod in the climate chamber and provided them with water ad libitum overnight.

2.2. Locomotory behaviour trials

We studied the cursorial locomotion of *P. alacris* by tracking their movements in a white circular plastic arena (25 cm in diameter) at 20 °C. The floor of the arena was covered with blotting-paper. The

spider was placed into a small black plastic cylinder (3 cm in diameter) in the centre of the arena and it was allowed to acclimatise for 60 s before the cylinder was removed. Then, the spider was allowed to freely move in the arena during 180 s. The movement of the spider was recorded with a Fuji^{*} finepix HS 50EXR camera from 100 cm above the arena.

The locomotory activity of individuals within the arena was determined by digitalising their path using the SMART video tracking software version 2.5.2 (Panlab). The following parameters were measured: (1) total distance travelled (cm); (2) total moving time during the 180 s of observation (s); (3) average speed of the individuals when moving (cm/s) (Csata et al., 2017).

2.3. Body size and fat percentage

Spiders were fixed and stored in a freezer at -15 °C. The gender of the spiders was determined and the total body length and prosoma length of spiders were measured using an Olympus SZ40 stereo microscope. Spiders were subsequently dried at 60 °C for four days and then weighted to the nearest 0.0001 g with an OHAUS Explorer^{*} Proscale. The spiders were then moved to glass vials (2 cm diameter), and their fat was extracted with 4 ml petroleum-ether (boiling range 40–70 °C; Molar Chemicals^{*}). We closed the vials with plastic lids and kept them at room temperature. The spiders were left in the petroleumether for three days; we then changed the petroleum-ether, and spiders were kept in the new liquid for three more days. Spiders were subsequently dried again at 60 °C for four days and their weight was measured. The fat content of spiders was quantified as the ratio of final mass to dry mass.

2.4. Data analysis

To test if season (autumn/spring), forest type (poplar/pine), gender and their second order interaction had significant effects on the size or fat content of P. alacris, we used mixed effect linear models and model averaging. We also added percentage fat content as a fixed effect in the models where total distance covered and speed were the dependent variables. We used mixed-effect linear models (lmer function, "lme4" package, Aisenberg et al., 2009) with a Gaussian error term, and the random effect term was "forest ID". For total distance covered and speed models, sex was used as a random effect, in order to control for potential multicollinearity between gender specific locomotory activity and sex (Framenau, 2005). All possible linear combinations of the above fixed effects were considered and ranked according to Akaike's information criteria corrected for small sample sizes (AICc). The models with $< 10 \Delta AICc$ of the best model (i.e. the model with the lowest AICc) were used for model averaging with the R package MuMIn (Barton, 2015).

3. Results

Female spiders (4.77 \pm 0.38 mm; mean \pm SD) were larger than males (4.63 \pm 0.38 mm) and subadult spiders collected from poplar forests (4.57 \pm 0.42 mm) were smaller than those from pine forests $(4.83 \pm 0.30 \text{ mm})$. We found a significant interactive effect of forest type and season on body length, due to a more pronounced effect in poplar forests (autumn: 4.40 ± 0.46 mm; spring: 4.74 ± 0.29 mm) than in pine forests (autumn: 4.78 ± 0.36 mm; spring: $4.89 \pm 0.21 \text{ mm}$). Furthermore, a significant interaction between season and gender indicated that the difference between body length in autumn (4.49 \pm 0.44 mm) and spring (4.76 \pm 0.26 mm) in males was greater than that of the females (Table 1, Fig. 1a) in autumn $(4.67 \pm 0.45 \text{ mm})$ and spring $(4.87 \pm 0.26 \text{ mm})$, respectively. Percent fat content was significantly higher in spring spiders (16.72 \pm 4.21%) than in autumn spiders (fat content: 12.17 \pm 5.15%). Total distance covered (1.04 \pm 0.54 m) and speed (0.022 \pm 0.004 m/s) were

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