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Effects of pollen species composition on the foraging behaviour and offspring performance of the mason bee *Osmia bicornis* (L.)

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Abstract

The effects of floral species composition on offspring performance of solitary bees are rarely studied under conditions where foraging behaviour of mothers is allowed to play a role. In a semi-field experiment, we restricted foraging choices of the polylectic mason bee *Osmia bicornis* L. to flower species belonging to plant families presumably used to different extent: *Borago officinalis* L. (Boraginaceae), *Centaurea cyanus* L. (Asteraceae) and *Brassica napus* L. (*Brassicaceae*). We quantified the foraging behaviour and brood cell production by mother bees, and compared the quality of offspring in pure and mixed flower species stands. Offspring survival in pure stands was expected to reflect the mothers' foraging preferences in the mixed stand. Pure stands of *B. napus* supported highest offspring survival, body mass and fraction of females produced. Offspring survival on *C. cyanus* and *B. officinalis* was very low. Larval mortality occurred earlier in brood cells provided with *B. officinalis* pollen than in brood cells provided with *C. cyanus* pollen suggesting different effects of pollen quality on early larval and later development. The time spent on different foraging activities correlated with lifetime reproductive output. However, in mixed stands, the proportion of time the bees were foraging on the different flower species did not differ significantly. Foraging behaviour may therefore not generally be a good proxy for the quality of floral resources for offspring production. Our results suggest that resources collected from one plant species may influence the usefulness of resources from another plant species. Bees may therefore overcome potentially deleterious effects of the suboptimal resources by mixing low- and high-quality resources. This may help generalist bees, such as *O. bicornis*, to cope with an unpredictable environment.

Zusammenfassung

Die Effekte der Artenzusammensetzung von blühenden Pflanzen auf das Gedeihen der Nachkommen von solitären Bienen werden selten unter Bedingungen untersucht, die zulassen, dass das Sammelverhalten der Mütter eine Rolle spielt. In einem Semi-Freilandexperiment, beschränkten wir die Sammeloptionen der polylektischen Mauerbiene *Osmia bicornis* L. auf Blütenarten aus vermutlich unterschiedlich stark genutzten Familien: *Borago officinalis* L. (Boraginaceae), *Centaurea cyanus* L.

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(Asteraceae) und *Brassica napus* L. (*Brassicaceae*). Wir bestimmten das Sammelverhalten und die Brutzellenproduktion von Bienenweibchen und verglichen die Qualität der Nachkommen bei reinem und gemischtem Blütenangebot. Die Überlebensrate der Nachkommen bei Angebot von nur einer Blütenart sollte die Präferenz der Mütter in gemischten Blütenbeständen wiederspiegeln. Reine Bestände von *B. napus* ergaben die höchste Überlebensrate, Körpermasse und den höchsten Weibchenanteil bei den Nachkommen. Bei *C. cyanus* und *B. officinalis* war die Überlebensrate sehr gering. Die Larvensterblichkeit setzte in mit *B. officinalis* verproviantierten Brutzellen früher ein als in Brutzellen mit *C. cyanus* als Proviant. Somit sollte es unterschiedliche Effekte der Pollenqualität auf die frühe larvale und die spätere Entwicklung geben. Die für die verschiedenen Sammelaktivitäten aufgewendete Zeit korrelierte mit der Gesamtproduktion an Nachkommen einer Mutterbiene. Indessen unterschieden sich die Zeitanteile, die bei gemischtem Angebot mit dem Sammeln an unterschiedlichen Blütenarten verbracht wurden, nicht signifikant voneinander. Das Sammelverhalten könnte deshalb kein guter Indikator für die Qualität von Blütenressourcen für die Produktion von Nachkommen sein. Unsere Ergebnisse legen nahe, dass Ressourcen, die von einer Pflanzenart gesammelt wurden, den Nutzen der Ressourcen von einer anderen Art beeinflussen könnten. Die Bienen könnten somit mögliche abträgliche Effekte einer suboptimalen Ressource durch das Mischen von qualitativ hoch- und minderwertigen Ressourcen kompensieren. Dies könnte Generalisten wie der Mauerbiene *O. bicornis* helfen, mit einer nicht vorhersagbaren Umwelt zurechtzukommen.

Keywords: Floral resource; Food quality; Offspring performance; Foraging behaviour; *Osmia bicornis*; *Brassica* pollen

Introduction

Herbivore growth, survival and reproduction are not only determined by the abundance of available resources, but also by their quality. Plants generally have a low nutrient content and often contain toxic allelochemicals and thus may represent suboptimal food sources for herbivores (Jermy 1984; Schoonhoven, van Loon, & Dicke 2005). Most of our understanding of the role of plant quality in plant-invertebrate herbivore interactions originates from studies on folivorous insects, with much focus on how specialist herbivores deal with constraints imposed by plant defence chemistry (e.g. Zangerl & Berenbaum 2003). Substantially less attention is paid to the effects of food quality on generalist insect herbivores (Bernays & Graham 1988), and especially in pollen feeding species. Recent studies have begun uncovering the role of variation in pollen nutritional quality in wild bee development (Eckhardt, Haider, Dorn, & Müller 2014; Praz, Müller, & Dorn 2008a; Williams 2003), and suggest that variation in pollen quality may have driven both dietary specialisation and generalism in plant – pollinator systems (Müller & Kuhlmann 2008; Roulston & Goodell 2011; Sedivy, Dorn, Widmer, & Müller 2013).

Pollen has been viewed as a nutrient-rich food source, where diet choices of bees were thought to be predominantly shaped by flower morphology and resource accessibility, and nutritional chemistry has been considered to play a secondary role (Roulston & Cane 2000). However, across different plant species, pollen shows large variation in nutritional properties like concentrations of essential amino-acids and fatty acids, and vitamin content (Roulston & Cane 2000). Besides nutrients, the amount and composition of pollenkitt may influence the pollen digestibility and thus nutrient uptake in the insect alimentary tract (Dobson & Peng 1997). Members of the family Asteraceae, for example, possess pollen that is difficult to digest and may contain low levels of essential amino-acids (Nicolson & Human 2013). Pollen may also contain a range of allelochemicals such as alkaloids and glucosides, which may negatively affect pollinator survival (Detzel & Wink 1993). For example, the pollen and nectar of some members of Asteraceae, Boraginaceae, Ranunculaceae and Fabaceae contain allelochemicals with a purportedly defensive function (Dodson & Stermitz 1986; Haider, Dorn, & Müller 2014; Reinhard et al. 2009; Sedivy, Müller, & Dorn 2011). While several studies report deleterious effects of pollen due to suboptimal nutrient content or allelochemistry on managed honeybees, studies began only recently to quantify the effects of pollen quality on life-history traits of solitary bees.

While specialist herbivores often detoxify or sequester allelochemicals, or physiologically adapt to assimilate food of low nutrient content, generalist herbivores have to deal with suboptimal food in other ways. Polylectic bees may exhibit large variation in their ability to develop on different pollen species (Eckhardt et al. 2014; Sedivy et al. 2011). As a result, mixing unsuitable and suitable pollen to balance nutrients or dilute toxins may increase both offspring survival and reproductive output (Eckhardt et al. 2014; Singer, Bernays, & Carriere 2002). On the other hand, specialising in terms of flower handling (i.e. flower constancy), may be beneficial over diet mixing because it allows more efficient resource harvesting. To date, existing studies have tested the effects of pollen quality on bee development and survival by artificially controlling the mixture and composition of pollen provided to bee larvae.

The effects of food quality on survival and development ultimately depend on the foraging decisions that mother bees make when allocating provisions into brood chambers. As provisioning rates impact offspring survival and quality (Müller et al. 2006; Roulston & Goodell 2011), natural selection is expected to affect foraging decisions.