Bumble bee forager abundance on lowland heaths is predicated by specific floral availability rather than the presence of honey bee foragers: evidence for forage resource partitioning

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Abstract—Honey bees are being scrutinized for their potential impact upon wild bees. In lowland heath mosaics, a simple but resource rich habitat for pollinators, there is a higher probability of niche overlap for bumble bees and honey bees due to the requirement of similar resources and limited floral diversity. This study assesses i) if there is any evidence of forage competition between bumble bees and honey bees and ii) asks to what extent the number of bumble bee foragers in a lowland heath mosaic over the summer months is affected by floral resource availability in different heath types (wet/dry). Bumble bee and honey bee counts were conducted at 30 wet heath and 30 dry heath 20 m × 20 m sites, in the Poole Basin, UK. The relationships between bumble bee and honey bee forager observations and ericaceous forage availability throughout the summer were evaluated using GLMMs considering presence and abundance of honey bees and specific floral availability as factors.

Only weak correlations of honey bee forager abundance on bumble bee forager abundance were detected. Instead, the most important factors relating to bumble bee numbers were the abundance of specific floral resources within the heath type (wet/dry). Bumble bees and honey bees showed resource use consistent with resource partitioning with bumble bees predominantly using wet heaths and honey bees using dry heaths. These findings provide evidence of the importance of maintaining complex habitat mosaics within broader habitats to promote coexistence between bumble bees and honey bees.

Keywords: Bumble bees, Honey bees, Competition, Lowland Heaths, Coexistence

Introduction

The honey bee (*Apis mellifera*) has long been suspected of competing for resources with wild bees as its populations are artificially modified by humans and their impact per colony is large (See: Goulson 2003b; Paini 2004; Mallinger, Grains-Day & Gratton 2017). This is important as many wild pollinators, such as bumble bees, are already in decline, due to many factors including agricultural intensification and urbanisation (Ghazoul 2005; Vanbergan 2013; Potts et al. 2010; Dicks 2012; Montero-Castano & Vila 2012). Bumble bees have been shown to use habitats in response to different factors including food availability (McFrederick & LeBuhn 2006; Ahrne et al. 2009; Bates et al. 2011; Moron et al. 2014) nest site availability (Osborne et al. 2008; Knight et al. 2009) and competition (Goulson 2003a; Goulson 2003b; Paini 2004). Several studies suggest that the introduction of honey bees disrupts the foraging of native wild bees through nectar depletion, reduction of foraging rates and increasing

competition (Schaffer et al. 1983; Kato et al. 1999; Gross 2001; Paini 2004). Conversely, other studies suggest that honey bees have little or no effect on native bees from nectar depletion (Roubik 1983; Horskins & Turner 1999) and that changes in abundance of wild bees often correspond to changes in habitat induced by human activity with simple or homogeneous habitats having greater pollinator competition (Huryn 1997; Steffan-Dwenter & Kuhn 2003; Herbertsson et al. 2016; Lindström et al. 2016). It is important to consider the impact of the honey bee on wild bees as a reduction in bee diversity can lead to reduced crop yields in agricultural areas where honey bees are not efficient pollinators (Garibaldi et al. 2013) and a reduction in wild plant biodiversity (Biesmeijer et al. 2006).

Heathlands have high floral density and contribute one third of total nectar provision in the UK (not including Northern Ireland) (Baude et al. 2016). In the UK, heathlands are dominated by three ericaceous species (also called "ericoids"), *Calluna vulgaris*, *Erica tetralix* and *Erica cinerea* and as such are comparatively floristically simple (Rodwell 1998). Heathlands consist of a mosaic of different habitat types including dry, wet and mire heath habitats (JNCC 1990). In addition to this, the abundance of available forage in heathlands changes dynamically throughout the summer,

starting before May with (*Ulex europaeus*) then moving through the ericoids, *Erica cinerea*, *Erica tetralix* and *Erica ciliaris*, smaller species of *Ulex* and finishing with *Calluna vulgaris* into September (Forup & Memmot 2005). Ericoids are among the top four largest contributors to national nectar production in the UK, with 50% of the nation's nectar production coming from *Calluna vulgaris* and *Erica cinerea* along with the non-ericaceous *Cirsium palustre* and *Trifolium repens* (Baude et al. 2016). *Calluna vulgaris* has a predicted nectar yield of 147.5 Kg/ha/yr, *Erica cinerea* 160 Kg/ha/yr and *Erica tetralix* 160 Kg/ha/yr potentially making all three very valuable to pollinators (Baude et al. 2016). The long resource availability and presence of rich resources makes heathlands potentially very important to bumble bees. Heathlands also provide a highly economically valuable resource for honey bee keepers around Europe (Descamps et al. 2015). However, potential for niche overlap and competition on heathlands between honey bees and wild bees may be enhanced by the limited floral diversity available at the beginning and the end of the summer.

Bumble bees, especially short tongued bumble bees, have a high likelihood of niche overlap and foraging competition with honey bees due to having similar tongue lengths which dictate the resources that the bees can access (Hawkins 1969; Goulson et al. 2008). This study addresses if there is any evidence of foraging competition between bumble bees and honey bees for forage on lowland heath and explores the possibility of floral resource partitioning by monitoring the abundance of bumble bee foragers on lowland heath mosaics over the summer months in response to i) honey bee forager abundance and ii) floral resource availability in different heath types (wet/dry). If honey bees are competing with bumble bees for forage we expect to see a strong negative correlation between bumble bees and honey bees that cannot be explained by specific floral resource availability.

MATERIALS AND METHODS

Sixty heathland sites were surveyed 17th-23rd July, 17th-26th August and 8th-19th September 2015 across the Poole Basin, Dorset, UK (Fig1, for Grid reference see SI). Site locations were selected at random within heathland areas with the restriction that each site consisted of a 20 × 20 m quadrat patch of homogeneous vegetation that was classified either as dry or wet heath (JNCC 1990). Sites were on average separated by 4494m (with 95% confidence limits of 419-8231m and an absolute minimum of 30m) and showed no spatial autocorrelation found with a Moran's I test for honey bee abundance ($Z = -0.005$, $P = 0,385$) or bumble bee abundance ($Z = -0.010$, $P = 0.729$). Thirty dry heaths were classified as having at least 25% ericaceous or *Ulex* cover with the presence of *Calluna vulgaris*, *Erica cinerea*, *Ulex gallii* and or *Ulex minor* (D1 or E1.8 Phase 1 habitat survey) (JNCC 1990). Thirty wet heaths were classified as having at least 25% ericaceous cover with the presence of *Molinia caerulea*, some *Sphagnum* and *Erica tetralix* (D2 or E1.7 Phase 1 habitat survey) (JNCC 1990).

To calculate the floral abundance of ericoid species in terms of actual available percentage cover of ericoid floral resource, five 2 × 2 m quadrats were sampled haphazardly
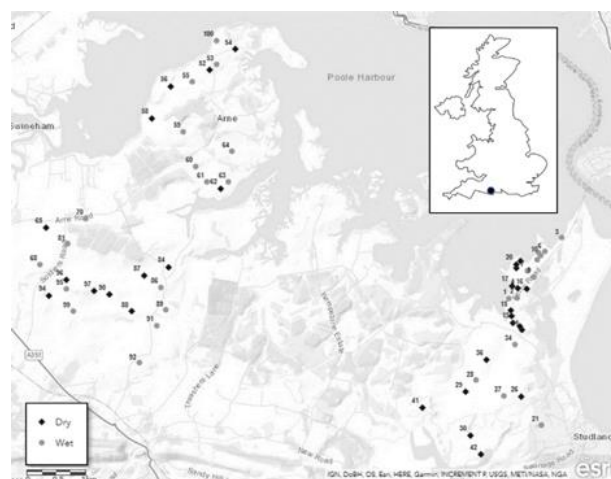

FIGURE 1. Locations of wet and dry heath field sites (grey circles wet sites and black diamonds dry sites) with an inset map identifying the location of the sites within the UK (Grid references in SI.)

(but ensuring no overlap) within the 20 × 20 m quadrat in July, August and September. A record was made of the percentage cover of each ericoid species in full flower and percentage cover of each heather species in partial flower. Actual available % cover of floral resource was calculated as % cover of heathers in full flower + 0.5 (% cover of heathers in partial flower). The foraging interactions between pollinators and ericaceous floral resources were recorded each month on a 10 minute roughly 'W' shaped walk (to reduce resampling) within the 20 × 20 m quadrat to evaluate foraging preferences and site use. All foraging interactions were all observed under good conditions for pollinators, warm (>15°C) and with low wind (Beaufort scale score 0-3). Pollinators were initially identified as *B. terrestris/lucorum* group, *B. lapidarius*, *B. pratorum*, *B. pascuorum* or *Apis mellifera*. Subsequently, due to some low observation counts, the *Bombus* species were considered together as one group. Most were *B. terrestris/lucorum* which together with *B. lapidarius* and *B. pratorum* have similar, relatively short, tongue lengths (Goulson et al. 2008). The remaining species, *B. pascuorum* has a medium tongue length (Goulson et al. 2008) but occurred very infrequently in our dataset.

Analysis

To assess the relationships between bumble bee presence/abundance, specific floral availability and the presence/abundance of honey bees a series of generalised linear mixed models were conducted within the glmmTMB (Magnussun et al. 2018) package in R (2017).

Relationships with the presence of bumble bees were tested with a binomial glmm model with month and site as random intercept factors and the presence of honey bees and the % floral cover of *C. vulgaris*, *E. cinerea*, *E. tetralix* and *E. cilliaris* as factors. Relationships with the presence of honey bees were also tested with a binomial glmm model with month and site as random intercept factors and the presence of bumble bees and the % floral cover of *C. vulgaris*, *E. cinerea*, *E. tetralix* and *E. cilliaris* as factors. Initial models contained

all interactions but these were removed due to their limited effect (S2).

Relationships with the abundance of bumble bees in all sites and those shared with honey bees were tested with a zero inflated, Poisson, glmm model with month and site as random intercept factors and the abundance of honey bees and the % floral cover of *C. vulgaris*, *E. cinerea*, *E. tetralix* and *E. cilliaris* as factors. Relationships with the abundance of honey bees were also tested with a zero inflated, Poisson, glmm model with month and site as random intercept factors and the abundance of bumble bees and the % floral cover of *C. vulgaris*, *E. cinerea*, *E. tetralix* and *E. cilliaris* as factors. Initial models contained all interactions but these were removed due to their limited effect (S3 and S4).

Wet heaths are characterized by the presence of *E. tetralix* and dry heaths with the presence of *C. vulgaris* and *E. cinerea*. As such heath type was co-linear with these relative abundances and not included in the models.

RESULTS

The presence of bumble bees at a site was only significant positively correlated with the percentage floral cover of *E. cinerea*. Honey bee presence was only significantly correlated with the percentage floral cover of *C. vulgaris* (Table 1, Fig 2A).

Bumble bee abundance was positively and significantly correlated with all heather percentage floral cover. Bumble bee abundance showed a significant but weakly negative correlation with honey bee abundance (Table 2, Fig 2A). Honey bee abundance was positively and significantly correlated with the percentage floral cover of *C. vulgaris* and *E. cinereal* and significantly and weakly negatively correlated with bumble bee abundance (Table 2. Fig 2A, Fig 3).

When both bumble bees and honey bees are present at a site, bumble bee abundance was only positively correlated with the percentage cover of *E. cinerea* and *E. tetralix*. Honey bee abundance was significantly and positively correlated with the percentage cover of C. *vulgaris* and *E. cinerea*. and significantly and weakly negatively correlated with bumble bee abundance (Table 3, Fig 2B).
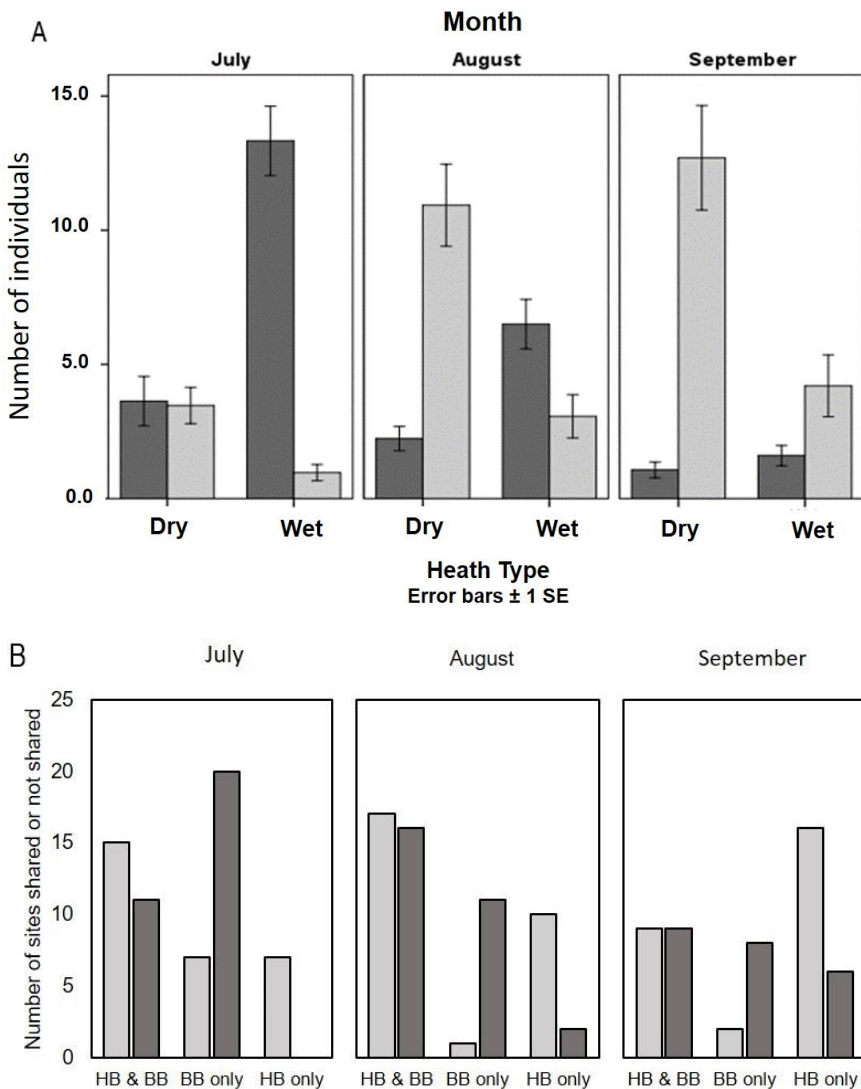

Figure 2. (A) The mean number of bumble bee (dark grey) and honey bee (light grey) observations on wet and dry heaths in July, August and September. Wet heath sites are dominated by *E. tetralix* and dry sites by *C.* vulgaris (Fig. 3). Whiskers display ±1SE.

(B) The number of sites shared by honey bees and bumble bees (HB & BB) and those with only bumble bees (BB only) or only honey bees (HB only) out of a total of 30 sites each month. Dark grey bars represent wet heath sites and dry heaths are light grey.

TABLE 1.   (A) The presence of bumble bees in response to specific heather availability and presence of honey bees. (B) The presence of honey bees in response to specific heather availability and presence of bumble bees. Significance is marked with * at $P \leq 0.05$, ** at $P \leq 0.01$ and *** at $P \leq 0.001$.

Factor	Estimate (log)	Standard error	Z- Value	P
(A) bumble bee presence $N = 180$				
% floral cover *C. vulgaris*	-0.013	0.011	-1.185	0.236
% floral cover *E. cinerea*	0.130	0.073	1.782	0.0747
% floral cover *E. tetralix*	0.176	0.070	2.500	0.0124*
% floral cover *E. cilliaris*	0.086	1.185	0.464	0.6427
Presence of honey bees	0.0152	0.5944	0.026	0.9796
(B) honey bee presence $N = 180$				
% floral cover *C. vulgaris*	0.064	0.022	2.882	0.004**
% floral cover *E. cinerea*	0.022	0.041	0.530	0.596
% floral cover *E. tetralix*	-0.024	0.019	-1.214	0.225
% floral cover *E. cilliaris*	-0.472	0.272	-1.736	0.083
Presence of bumble bees	0.059	0.693	0.086	0.932

TABLE 2.   (A) The abundance of bumble bees in response to specific heather % cover and abundance of honey bees. (B) The abundance of honey bees in response to specific heather % cover and abundance of bumble bees. Significance is marked with * at $P \leq 0.05$, ** at $P \leq 0.01$ and *** at $P \leq 0.001$.

Factor	Estimate (log)	Standard error	Z- Value	P
(A) bumble bee abundance $N = 180$				
% floral cover *C. vulgaris*	0.0126	0.005	2.620	0.009**
% floral cover *E. cinerea*	0.027	0.006	4.507	<0.001***
% floral cover *E. tetralix*	0.223	0.003	6.881	<0.001***
% floral cover *E. cilliaris*	0.040	0.010	3.935	<0.001***
Abundance of honey bees	-0.062	0.014	-4.375	<0.001***
(B) honey bee abundance $N = 180$				
% floral cover *C. vulgaris*	0.020	0.003	6.809	<0.001***
% floral cover *E. cinerea*	0.032	0.009	3.558	<0.001***
% floral cover *E. tetralix*	0.006	0.006	1.031	0.303
% floral cover *E. cilliaris*	-0.420	0.132	-3.190	0.001
Abundance of bumble bees	-0.103	0.021	-5.025	<0.001***

TABLE 3.   (A) The abundance of bumble bees in response to specific heather % cover and abundance of honey bees when sites are shared. (B) The abundance of honey bees in response to specific heather % cover and abundance of bumble bees when sites are shared. Significance is marked with * at $P \leq 0.05$, ** at $P \leq 0.01$ and *** at $P \leq 0.001$.

| Factor	Estimate (log)	Standard error	Z- Value	P
(A) bumble bee abundance – when sites are shared $N = 76$				
% floral cover *C. vulgaris*	0.006	0.004	1.46	0.143
% floral cover *E. cinerea*	0.21	0.001	2.418	0.016*
% floral cover *E. tetralix*	0.025	0.004	6.034	<0.001***
% floral cover *E. cilliaris*	0.077	0.074	1.039	0.299
Abundance of honey bees	-0.020	0.015	-1.401	0.161
(B) honey bee abundance– when sites are shared $N = 76$				
% floral cover *C. vulgaris*	0.019	0.003	5.461	<0.001***
% floral cover *E. cinerea*	0.026	0.010	2.731	0.006**
% floral cover *E. tetralix*	0.002	0.006	0.370	0.711
% floral cover *E. cilliaris*	-0.285	0.183	-7.557	0.119
Abundance of bumble bees	-0.057	0.024	-2.397	0.017*
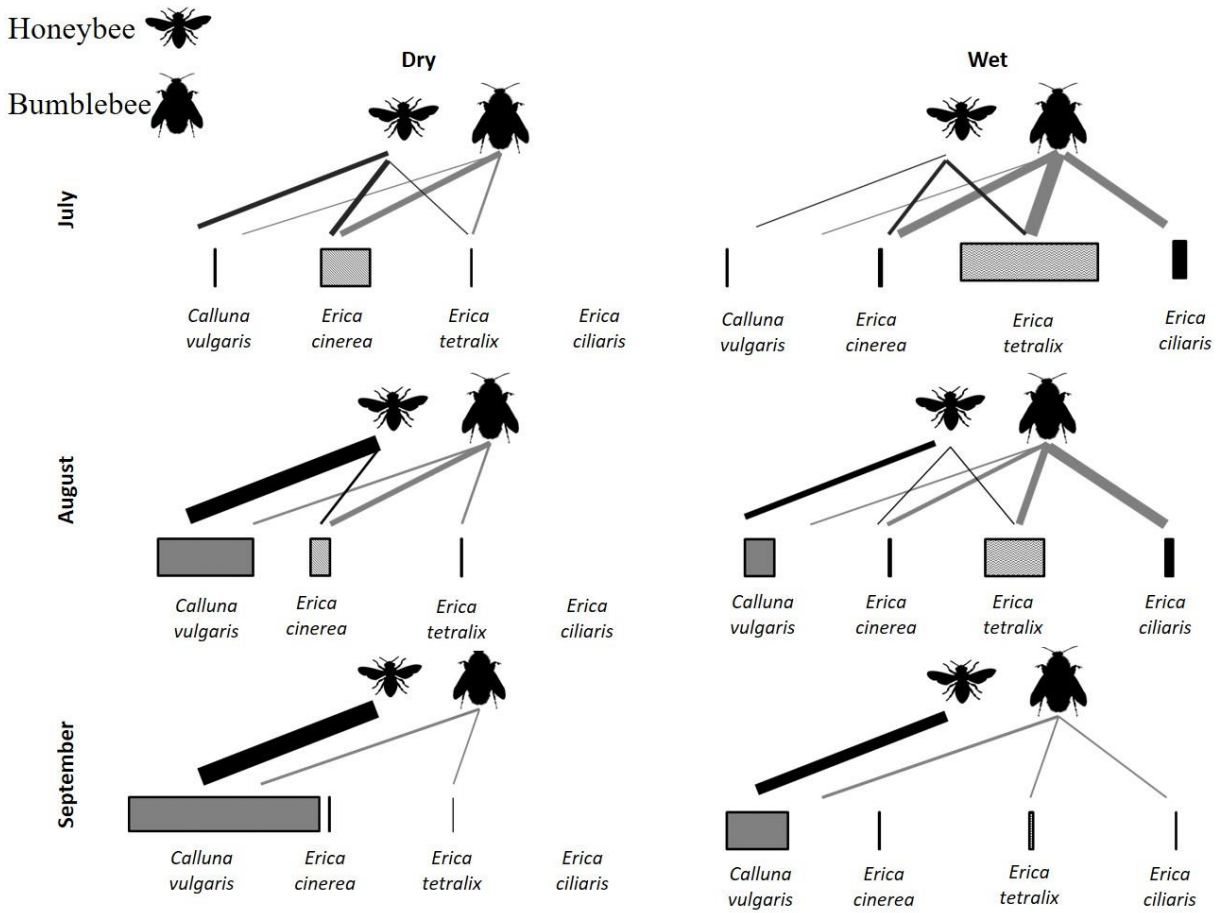
FIGURE 3.   Relative mean forage availability (% cover) of each heather species on dry and wet heath types and mean forager observations on each heather species. Boxes are to the same scale with 1 unit representing 1% floral cover. Lines are to the same scale with each unit representing forager observation honey bees in black and bumble bees in grey.

DISCUSSION

The effect of honey bee forager abundance and any evidence of honey bee competition

This study detected no evidence of forager exclusion between bumble bees and honey bees for forage on lowland heath and demonstrates that where bumble bees and honey bees coexist in lowland heaths, their forager distribution is not highly related to each other's presence but the presence of the specific available forage. This indicates that honey bees are only likely to greatly impact bumble bee forager numbers when they are in very high density, such as close to a honey bee hive (Klemens & Volkmar 2006). This study also put honey bees 'in the spot light' and found that their abundance is also correlated with specific forage plants, mainly *C. vulgaris* and *E. cinerea,* characteristic of dry heaths. They also showed a weak but significant negative correlation with an increase bumble bee abundance even in shared sites but showed no evidence of being excluded by bumble bees. Although, the findings from this study suggest that it is unlikely that there is competition between bumble bees and honey bees for forage on lowland heath sites we cannot conclusively exclude any effect of competition (in either direction) as we have not considered colony fitness in our measures.

The bumble bee foragers in this study did not change their preferred forage plants in response to the presence of honey bee foragers as we found no significant interactions between heather availability and presence of honey bees. Instead bumble bees consistently focus their foraging on the *Erica* species regardless of number of honey bees. This contrasts with the findings of other studies where the presence of honey bees has resulted in a foraging pattern shift of the wild bees (Klemens & Volkmar 2006; Ishii et al. 2008; Magrach et al. 2007). It is probable that on lowland heath mosaics, where the forage heterogeneity exists over longer time periods, that stable resource portioning has the potential to exist.

It is in relatively homogeneous habitats, such as agricultural land, that negative impacts of honey bees on bumble bees have predominantly been reported (Lindström et al. 2016; Herbertsson et al. 2016). In such simple habitats there is limited alternative forage on which bumble bees can escape the competition with honey bees and where heterogeneity exists it is short lived with the presence of mass flowering crops. Our findings concur with those found in a study on woodlands, which also found that when heterogeneity of resources were available honey bees and wild bees demonstrated resource partitioning (Magrach et al. 2017). These authors found that competition and diet switches occurred when the crop the honey bees were feeding

on stopped flowering and the honey bees moved into semi natural areas to find forage (Magrach et al. 2007). This study also supports the findings of Herbertsson et al. (2016) working in open grassland and road verge landscapes, who conclude that lower bumble bee forager abundance was correlated with honey bee abundance only where habitats were homogeneous; when habitats were heterogeneous, no negative effect of honey bee presence was detected. This study additionally provides an explanation for previously detected negative associations between bumble bees and honey bees (Forup & Memmot 2005). Forup and Memmot's (2015) study focused on dry heaths and suggests that their detected negative relationship between honey bees and bumble bees may be a result of honey bees moving into areas not suitable for the bumble bees. The present study confirms that hypothesis with a greater number of bumble bee forager being associated with *Erica* species in wet areas and honey bee foragers on *Calluna* in dry. This highlights the importance of looking beyond a single habitat when considering inter species competition for both potential habitat partitioning, as seen in this study, or in the breakdown of resource partitioning as seen in Magrach et al. (2017).

Lowland heath flowering phenology also correlates with the peak abundances of bumble bees and honey bees (Forup & Memmot 2005). Species in the genus *Erica* flower earlier and are the preferential forage of bumble bees, where *Calluna vulgaris* flowers later in the season and is the preferential forage for honey bees. In this way the potential for competition between these bees on lowland heaths is limited further.

Evidence for resource partitioning and implications for management

This study has demonstrated the crucial role of habitat heterogeneity though the availability of both wet and dry heaths for enabling bumble bees and honey bees to coexist through potentially portioning their use of floral resources. However, to support a diversity of bees within the landscape, connectivity between these spatially separated heath types needs to be maintained within foraging distances. For bumble bees this is likely ~ 1000 m (Walther-Hellwig & Frankl 2000; Knight et al. 2005) and other wild bees this is likely ~ 250 m (Gathmann & Tscharntke 2002). The temporal availability of resource heterogeneity is also important to avoid times of intense competition when resources are limited (Magrach et al. 2007). In agricultural systems where there is a fluctuating availability of mass flowering resources, the creation of floral resources with long flowering phenology may provide the long-term heterogeneity required to support stable resource partitioning as well as pollinator diversity (Albrecht et al. 2007). Habitat heterogeneity is also important for the other habitat requirements of pollinations such as nest site availability and overwintering sites (Osborne et al. 2008; Knight et al. 2009) that were not addressed in this study. In terms of forage, the results show that wet heaths provide better forage for bumble bees and findings from Moquet et al. (2015) suggest that wet heaths provide important early season (April and May) forage for bumble bees. However, wet heaths are likely to become saturated by water and be unfavourable for bumble bee nests of any of the subterranean nesting

bumble bees (*Bombus terrestris, B. lucorum, B. lapidarius* and *B. pratorum*) or the ground surface nesting species like *B. pascuorum* and *B. jonellus* (Prys-Jones & Corbet 1987) and consequently dry heaths may be needed for nesting areas. In addition, if there were only wet heaths the bumble bees come into more competition with honey bees for resources as the favoured honey bee forage plants (*Calluna vulgaris* and *Erica cinera*) would not be as abundant on wet heaths. Management to support the value of heathland as both a wildlife habitat and an economic resource for beekeepers, should therefore aim to maintain connectivity and floral diversity over the duration of the season.

Conclusions

This study found that bumble bee forager abundance is highly related to the floral availability of their favoured *Erica* forage on heathlands rather than honey bee forager abundance which indicates that bumble bees and honey bees may limit competition by resource partitioning. This study highlights that it is important to i) assess habitats for their within habitat heterogeneity when considering inter species interactions to detect resource partitioning ii) consider both sides of a potential competitive relationship and iii) maintain high habitat heterogeneity and forage diversity throughout the season in order to maintain coexistence between species with high potential niche overlap.

APPENDICES

Additional supporting information may be found in the online version of this article:

APPENDIX I.   Grid references of sample site locations, information on glmm models.

APPENDIX II.   Full observational data set.

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