

— Opinion —

## CRITICISM MISMATCHED: RESPONSE TO DE KEYZER ET AL. 2016

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**Abstract**—In a recent paper, we reported on the evolution of shorter tongues in two alpine bumble bee species in response to climate-induced flower deficits. De Keyzer et al. concede that tongue lengths have decreased but criticize the level of support for our claims. Here, we address the alternative mechanisms they proposed, highlight evidence presented in the supplementary material, and elaborate on the support for our claims in the literature. De Keyzer et al.'s criticisms reflect concerns about the misrepresentation of our work in the popular press. To clarify, we do not imply that evolutionary rescue is necessarily a prudent conservation strategy; we illustrate that remote bumble bee populations buffered from other environmental stressors have undergone an adaptive evolutionary response to dwindling resources under climate change.

**Keywords:** *Tongue length evolution, functional mismatch, Bombus, bumble bee, flower density, climate change*

In Miller-Struttmann et al. (2015, henceforth M-S15), we reported the evolution of a functional mismatch between bumble bees and their historic host plants. Our results indicate that declines in flower abundances with climate change favour a generalist foraging strategy and the evolution of an associated foraging trait, shorter tongue length. De Keyzer et al. (2016, hereafter DK16) propose several alternative mechanisms and caveats that warrant more detailed discussion. The authors challenge the potential relevance of our results to global bee declines, citing data from North America where long-tongued species are few (Kawakita et al. 2004). As acknowledged by DK16, demographic and distributional trends in North American long-tongued bumble bee populations, including the species in M-S15, are insufficiently known to discern their status (Williams & Osborne 2009, Fig. 1). Conversely, some of the clearest evidence of bumble bee declines comes from Europe where bumble bees are over 33% more species-rich, have been surveyed over longer periods (e.g., 85 years, Dupont et al. 2011), and show pronounced declines in long-tongued specialists (Goulson et al. 2005; Kleijn & Raemakers 2008; Dupont et al. 2011).

Our paper documented evolutionary decreases in tongue length for two bee species. While selective pressure to produce these changes should exact a demographic cost, we were unable to measure it or infer impacts on population growth rates, because data on historic densities of these alpine bees are unavailable (M-S15, Supplementary Materials). DK16 question how tongue length change in *Bombus sylvicola*, a short-tongued bee, is relevant to declines in populations of long-tongued bumble bees. The decreases

in tongue length we observe over the past 40-50 years imply the action of strong, consistent selection pressure for shorter-tongues in these alpine bumble bee species. Our model suggests that shorter-tongued generalist bees will have a fitness advantage as resources grow scarce (M-S15, Fig. 4), explaining both the evolutionary trend that we see in alpine species (M-S15, Fig. 1) and the range contraction of some more specialized longer-tongued bumble bees elsewhere (Goulson et al. 2005; Dupont et al. 2011). Results cited by DK16 (e.g., Williams et al. 2009) to refute our claims are based on survey data ill-suited for assessing pollinator declines: one with no standardization of sampling effort over time (Alford 1980); another documenting changes in relative (proportional) rather than absolute density (Macfarlane 1974; Colla & Packer 2008); and a third, making a space for time substitution to infer declines from simultaneous surveys of isolated grasslands subject to different management schemes (Xie et al. 2008). We agree with the authors' assertion that the picture is likely more complex, particularly at low altitudes where pesticides, pathogens, and limited nesting sites may contribute to bumble bee declines (Goulson et al. 2015 and references therein). However, there is a large body of evidence demonstrating the consequences of declining floral resources for specialist bees (e.g., Biesmeijer et al. 2006; reviewed in Roulston and Goodell 2011).

DK16 challenge our assertion that “long-tongued pollinators specialize on flowers with deep corolla tubes, whereas shorter-tongued pollinators generalize across tube lengths.” The literature on bumble bee foraging supports our view that long-tongued bumble bees specialize on long-tubed flowers (Goulson & Darvill 2004; Heinrich 2004; Goulson et al. 2008; Huang et al. 2015) and are disadvantaged in comparison with shorter-tongued bees when foraging on shorter flowers (Inouye 1980; Harder 1983) or across a

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range of flower tube depths (Plowright & Plowright 1997; Arabulo et al. 2011; Geib & Galen 2012). We do not claim that long-tongued bees are *incapable* of generalizing; our own data confirm that they do. In previous work (Miller-Struttman & Galen 2014), we reported that the two alpine bumble bee species studied in M-S15 generalized across a guild of predominantly long-tubed flowers, including *Trifolium* spp., *Polemonium viscosum* and *Castilleja occidentalis*. Historically, the short-tongued bee, *B. sylvicola*, visited flowers with a broader suite of tube depths than the long-tongued species (M-S15, Fig. 2). Since then, foraging breadth for both species has more than doubled with the incorporation of shorter-tubed and tubeless flowers into their diets (M-S15, Fig. 2). DK16 reason that because long-tongued *B. balteatus* bees still visit their historic long-tubed hosts a functional mismatch has not emerged, stating that “the range of tube lengths that *B. balteatus* visits has changed little over time”. On the contrary, our results indicate that variance in host plant tube depth increased by 289% for *B. balteatus* (M-S15, Table S3), whereas flower depth has not changed (M-S15, Fig. S2). Pollination services are derived from both *frequency* (reviewed in Knight et al. 2005) and *quality* (reviewed in Ashman and Arceo-Gómez 2013) of visits, not simply presence or absence of an interaction. Our results indicate that both of these components of pollination efficacy may decline for deep-flowered plants as alpine bumbles forage from a greater diversity of host plants.

Our model indicated that generalization is favoured when flowers are sparse, because search time exceeds handling time under resource scarcity (M-S15, Figs. 3 and 4, Table S7). Thus, foraging success is more strongly limited by search time rather than handling time or the prevalence of long-tubed flowers. This analysis (M-S15, Fig. 4) implies that benefits of long-tongued phenotypes have diminished, while costs of resource allocation to tongue construction are unchanged. The studies DK16 cite to refute resource-based selection for shorter-tongued bees ignore the cost of searching for sparse flowers (Harder 1985; Rodríguez-Gironés & Santamaría 2006). Theoretical (M-S15, Fig. 4) and empirical (M-S15, Fig. 3) results in our paper show that this assumption is flawed. DK16 suggest that nectar foraging behaviour should not exert strong selection for shorter tongues, since it (1) does not affect colony growth, disregarding evidence to the contrary (Cartar & Dill 1991; Pelletier & McNeil 2003; Elliott 2009), and (2) is influenced similarly by competition and low flower abundance. They argue that the effects of increased competition and reduced flower abundance are indistinguishable, because nectar resources would be low in either setting. However from the foragers perspective, these are not equivalent (Pleasants 1981). Competition reduces nectar standing crop (Pleasants 1981; Keasar et al. 2008), whereas diminished flower abundance increases the distance traveled between flowers (Chittka et al. 1997; Essenberg 2013). Each has different effects on bumble bee foraging (Dreisig 2011). Competition among bumble bees also leads to higher niche partitioning (Heinrich 1976; Inouye 1978; Brosi & Briggs 2013). If competition were driving shifts in tongue length, theory predicts the upward migration of long-tongued bees and/or the contraction of alpine bumble

foraging niche. We documented the opposite: upward migration of *short*-tongued bees and expansion of foraging niche (M-S15).

DK16 present several alternative hypotheses, which we were unable to address fully in the main text of our paper due to space constraints. First, DK16 suggest that tongue length declines in current bees may reflect selection due to drought in 2012. While we agree in general that selection on fitness-related traits varies from year to year, our analysis of inter-annual variation shows little impact of drought in 2012 on bumble bee tongue length distributions (M-S15, Fig. S2C-D). For both *Bombus* species, comparison of bees from pre-drought matings in 2011 (sampled in 2012) to bees from matings at the end of the 2012 summer (sampled in 2013) shows negligible change in tongue length (M-S15;  $F_{2,16} = 0.77$ ,  $P = 0.48$ ;  $F_{2,36} = 0.64$ ,  $P = 0.53$ ; legend, Fig. S2). Drought is unlikely to account for the changes in tongue length over the past 40 years, because winter precipitation was similarly low in 1977 and 2012 (< 22 percentile over the past century) and high in 1979-80 and 2013-14 (> 70 percentile; Daly et al. 2008). Alternatively, bottleneck events following the 2012 drought could have lead to genetic drift and shorter tongues. However, as they themselves note later in the paper, “because the same trend of tongue length shortening was observed in [multiple populations of] both species, it seems unlikely that random genetic processes are to blame.”

Next they suggest that generalization may only be favoured in our optimal foraging model when deep flowers disproportionately decline. While the proportion of deep flowers available can modify the advantage of being a generalist, its influence diminishes rapidly at low flower density (M-S15, Fig. 4). Specifically when flowers are scarce, generalization is favoured even when deep flowers account for the vast majority (up to 70%) of available flowers. Our long-term surveys of flower abundances on Pennsylvania Mountain show a 66% decline in historical resources for bumble bees at the landscape scale matching forager movement (M-S15, Fig. 4; Geib et al. 2015). Only at the highest sites, where warming is likely countered by cooling impacts of adiabatic lapse rate, has flower abundance of bumble bee host plants been buffered over time (M-S15, Fig. 3). Since high-altitude habitats account for a much smaller portion of the landscape (M-S15, Fig. 3), modest increases in flower abundance at high-altitude are insufficient to compensate for declines in lower altitude habitats. Similar declines in flower density with warming are found elsewhere in the Rocky Mountains and more broadly (e.g., Aldridge et al. 2011; reviewed in Vanbergen & the Insect Pollinators Initiative 2013).

Citing reports of declines in body size with temperature, DK16 suggest that developmental plasticity could result in shorter bumble bee tongues. Bumble bee tongue length shows high among-colony heritability suggesting a limited role of phenotypic plasticity or genetic constraint due to its correlation with body size (Owen & Harder 1995). While the genetic architecture of bumble bee tongue length is not fully known, our analyses, which controlled for known genetic correlates (specifically body

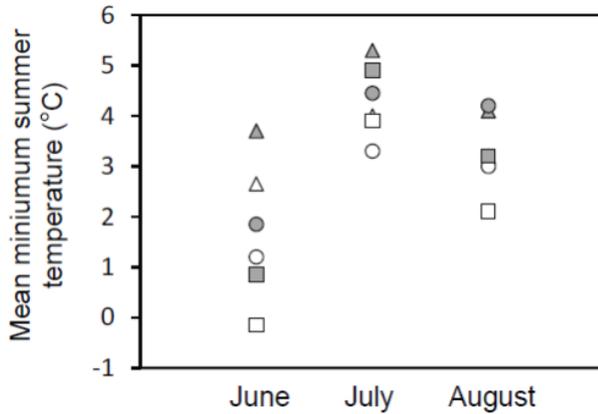


Figure 1. Seasonal and inter-annual variation in mean minimum summer temperatures for Mount Evans (open symbols) and Niwot Ridge (filled symbols) as estimated by PRISM interpolation (Daly et al. 2008). Symbol shape denotes year (2012: triangles, 2013: circles, and 2014: squares). Tongue length phenotype did not vary within or among years (M-S15, Fig. S4) despite significant variation in temperature.

size, M-S15), found no evidence of seasonal plasticity in tongue length (M-S15, Fig. S4), despite substantial seasonal and inter-annual variation in temperature (Fig. 1). This may not be surprising since bumble bees regulate nest temperature behaviourally, both through site selection (e.g. underground in alpine habitats) and via incubation/fanning. Multiple studies of diverse *Bombus* species show that internal nest temperature is maintained between 27 and 33°C despite exposure to ambient temperatures ranging from 10–38°C (Heinrich 1972; Schultze-Motel 1991; Gardner et al. 2007). In a system where average maximum summer temperatures rarely exceed 15°C, it is highly unlikely that heat-induced developmental plasticity is responsible for shorter bumble bee tongues, (Pepin et al. 2002).

Finally, DK16 dispute a misrepresentation of our work in the media. Indeed, we do not imply that “change in tongue length has allowed [bumble bee] populations to thrive or escape decline through evolutionary rescue”. While some bees may have the propensity to adapt to a specific selective pressure in the absence of other stressors, recent global bee declines (Kleijn & Raemakers 2008; Williams et al. 2009; Cameron et al. 2011; Goulson et al. 2015) indicate that *laissez faire* management is insufficient to preserve bee populations. We suggest that in remote habitats buffered from multiple environmental stressors (e.g., habitat destruction, toxins, and pathogens) adaptive evolution is *helping* alpine bees track climate change. Whether this evolutionary process “succeeds” in sustaining bee populations depends on its demographic cost and on future warming (Fig. 2). The efficacy of evolutionary rescue remains poorly known, but an increasing body of evidence suggests that wild populations may harbour genetic variation in traits conferring tolerance to climate change (reviewed in Franks & Hoffmann 2012). Our research suggests that conserving the remote habitats and resource base on which these populations depend should represent a priority for pollinator conservation.

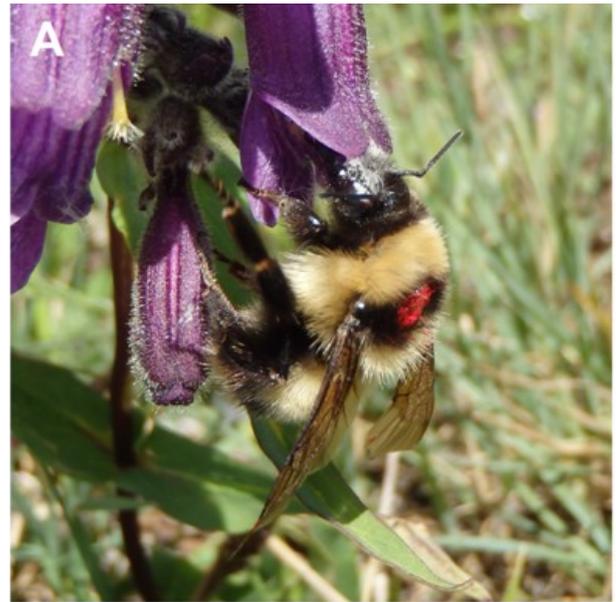


Figure 2. *Bombus balteatus* (A) and *B. sylvicola* (B) studied in (M-S15) are described as uncommon (A) and rare (B) species (Koch et al. 2014). Rapid adaptation to climate change could stabilize their populations if its demographic cost is low and future warming of alpine regions slows. Photographs by Eric Rayfield and Nicole Miller-Struttman, respectively.

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