Journal of Insect Conservation (2023) 27:517–522
https://doi.org/10.1007/s10841-023-00462-2

SHORT COMMUNICATION

Concern for cuckoo bumblebees (*Bombus* subgenus *Psithyrus*): addressing our lack of knowledge

Reanne Bower[1] · Mark Bulling[1] · Briony Norton[1]

Received: 29 October 2022 / Accepted: 25 January 2023 / Published online: 17 March 2023

Abstract
Bumblebees (genus *Bombus*) have received increased academic and conservation attention with the recognition of a global pollinator crisis. However, the *Bombus* subgenus *Psithyrus* (cuckoo bumblebees), has been overlooked. *Psithyrus* species parasitise social *Bombus* species and are frequently viewed as being detrimental to their hosts. This lack of attention, combined with the taxon's relatively low abundances and enhanced vulnerability to climate change due to its phenological dependence on *Bombus*, means there is an urgent conservation challenge facing *Psithyrus*. We found that academic literature focused on *Psithyrus* comprised less than 2% of the total works on *Bombus*, despite forming approximately 11% of *Bombus* species. We argue that species of the *Psithyrus* subgenus have key roles in the ecosystem and have been potentially overlooked bioindicator of *Bombus* diversity. We present evidence suggesting that the close phenological ties between *Psithyrus* and its hosts are being impacted by climate change. Going forward, research on *Psithyrus* distributions and phenology will be essential for conserving this subgenus. Additionally, addressing these areas provides broader opportunities to improve our understanding of ecosystem dynamics under climate change and their associated links with ecosystem services.

Implications for Insect Conservation
This article aims to increase awareness of an underappreciated group of insects (the *Bombus* subgenus *Psithyrus*), and to encourage vital research to support targeted conservation efforts.

Keywords *Bombus* · *Psithyrus* · Brood parasites · Climate change · Phenology · Distribution

Introduction

Bumblebees (genus *Bombus*) are key crop and wild vegetation pollinators. Since the recognition that we may be facing a global 'pollinator crisis', the amount of scientific literature regarding bumblebees has increased dramatically, supporting informed and targeted conservation (Goulson et al. 2011). However, the parasitic subgenus *Psithyrus*, or cuckoo bumblebees, receives far less attention than their social bumblebee hosts. They share the conservation threats facing other *Bombus*, with additional risks resulting from their parasitic lifestyle, notably a negative perception of parasites by conservation practitioners and urgent threats from climate change disrupting the host-parasite relationship. Here, we argue that greater attention to this taxon is warranted in order to support its conservation. We firstly evaluate the current state of literature on *Psithyrus*, finding many gaps in our knowledge of their ecology. We then re-examine the perceived threat of *Psithyrus* to their *Bombus* hosts and argue they in fact play a key role in the ecosystem and are potentially overlooked bioindicators of *Bombus* diversity. Finally, we suggest two key areas (species distribution and phenology) on which to focus future research efforts in order to support evidence-based conservation action for *Psithyrus* under climate change.

✉ Reanne Bower
reanneb98@hotmail.co.uk

[1] University of Derby, Environmental Sustainability Research Centre, DE22 1GB Derby, UK

Existing *Psithyrus* literature

Cuckoo bumblebees are obligate brood parasites of non-*Psithyrus Bombus* species, relying on their hosts to raise their offspring. Female *Psithyrus* identify a flourishing *Bombus* nest and overthrow the queen, laying their own eggs for the host workers to raise. Of the 250 *Bombus* species, roughly 28 are *Psithyrus*; they are found in the same areas as the genus as a whole, with the exceptions of South America, the Arctic and intertropical regions (Lhomme and Hines 2019).

Bumblebees avoid some of the taxonomic bias against invertebrates in conservation research and practise because of their ecological significance and aesthetic appeal (Lemelin 2013). Cuckoo bumblebees, however, have characteristics that have contributed to their comparative neglect. Firstly, *Psithyrus* lacks a foraging worker caste and has less dense pile hair, making them less prolific pollinators than social bumblebees (Falk 2015; Lhomme and Hines 2019). Thus, they are not targets of the recent proliferation of research and conservation efforts based around pollinating insects. Secondly, cuckoo bumblebees live in small, fragmented populations (Suhonen et al. 2016), which when combined with the absence of a worker caste, makes them more difficult to find and study than social bumblebees. In turn, accurate field identification can also be negatively impacted from the general lack of exposure to *Psithyrus* species. Particularly for citizen science schemes, where the participants may be less familiar with the features that distinguish *Psithyrus* species. Importantly, cuckoo bumblebees are often perceived as being detrimental to their ecologically and economically valuable hosts as they lower host reproductive output (Lhomme and Hines 2019), and are therefore not treated as a conservation priority. Few works regarding conservation practice feature *Psithyrus*. For example, two reviews focused on bee conservation, *Conservation Evidence*'s synopsis of bee conservation (Dicks et al. 2010) and IPBES's Assessment Report on Pollinators, Pollination and Food Production (IPBES, 2016), rarely mention *Psithyrus*. In both, *Psithyrus* are discussed only as part of the wider bee community or as an obstacle to social *Bombus* conservation, with no specific conservation considerations given to them.

There is a substantial gap in the academic literature addressing the subgenus *Psithyrus*, reflecting the trend in the conservation practice literature. The number of published works focused on *Psithyrus* has increased over time (1971 to 2020; Fig. 1a). However, the increase is minor compared to the boom around *Bombus* (Fig. 1b). Literature on *Psithyrus*, approximately 11% of *Bombus* species, comprises less than 2% of the works on *Bombus*. The amount of literature on *Psithyrus* should not necessarily be proportional, as they are less abundant and do not provide ecosystem services at the same scale, but the disparity is nonetheless concerning and presents additional challenges for the taxon's already limited conservation efforts.

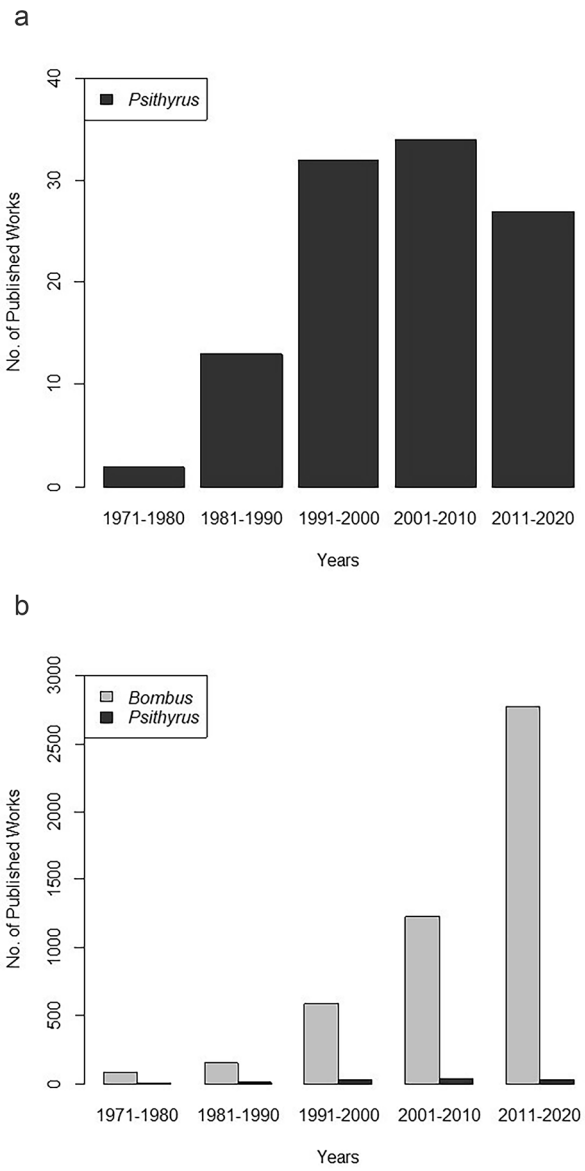

Fig. 1 The number of published works indexed on the Web of Science from 1971 to 2020 (Data source: https://www.webofscience.com/wos/woscc/advanced-search), with (a) cuckoo bumblebees as a "topic" (any of the following key words/ phrases: '*Psithyrus*', 'cuckoo bumblebee', or 'cuckoo bumble bee'), and (b) bumblebees (*Bombus*) as a topic, excluding '*Psithyrus'* (key words: '*Bombus*', 'bumblebee', or 'bumble bee', removing results with the key word '*Psithyrus*'). Graphs were made using R software

The data for Fig. 1 was gathered from the Web of Science core collection in January 2022. No languages or regions were excluded. The query was made in the 'topic' category to include works where *Bombus* and/or *Psithyrus* were the main focus of the literature; see Fig. 1 for all search terms.

Results from irrelevant categories with respect to this article (for example, engineering or literature journals) and non-peer reviewed works have been excluded from both searches.

Do *Psithyrus* threaten or benefit other *Bombus*?

Brood parasites, including *Psithyrus*, can be perceived as a threat to their hosts and potentially warranting control rather than conservation attention. This perception is presumptive and detrimental to *Psithyrus*, particularly given our limited understanding of their ecosystem-wide impacts. Firstly, a relatively small proportion of *Bombus* taxa are parasitised; Europe has 69 social bumblebee species and 78% have no known obligate brood parasites (Suhonen et al. 2016). Secondly, *Psithyrus* may have a relatively minor impact across wider *Bombus* populations, as the number of parasitised nests in an area can vary considerably, often making *Psithyrus* invasions a localised issue (Lhomme and Hines 2019). In addition to this, while brood parasites are a limiting factor to their host's population growth, the hosts, having evolved with this threat, are able to retain a stable population. These dynamics have been demonstrated in the more widely researched avian brood parasites. For example, the removal of the parasitic *Molothrus ater* for host conservation had mixed results; other factors, such as habitat gain, were more significant to recovery, and the species threatened by brood parasitism were the ones that had already experienced population declines from habitat loss (Rothstein and Peer 2005). Indeed, avian brood parasites have been hypothesised to aid ecosystem heterogeneity, by preventing hosts from dominating over less competitive species (Rothstein and Peer 2005), similar to the ecological role of predators. Indeed, the parallels with predators can be valuable in research and conservation. Using predator-prey ecosystem dynamics to inform and direct host-parasite research is established (Raffel et al. 2008), and it would be beneficial to incorporate this into research on *Psithyrus'* ecosystem role. Unlike parasites, the role of predators in ecosystems is generally perceived as positive and they are considered to have an important function in conservation actions (Ritchie et al. 2012). An increased regard for the roles of parasites within ecosystems could be similarly beneficial to their conservation outcomes.

Additionally, *Psithyrus* could be used to provide valuable information about the status of their host species. For example, studies of avian brood parasites (*Cuculus* spp.) have shown that cuckoo species richness is a reliable indicator of overall bird species richness in an area (Møller et al. 2017). Whether *Psithyrus* could also be used as a reliable bioindicator of host diversity needs to be explored; the geographic range and abundance of host and parasitic *Bombus* species are interlinked, and data on the parasite could be informative of the condition of the host (Suhonen et al. 2015). Overall, the impacts of *Psithyrus* invasions at large scales are understudied, and need more attention to clarify their positive and negative effects. Given the potentially significant, but poorly understood, role of *Psithyrus* within the ecosystem, it is important to consider key information gaps about the subgenus that should be filled. Here, we highlight species distributions and phenology as two key areas warranting future research to support evidence-based conservation.

Psithyrus species distributions

Cuckoo bumblebees are restricted within their host's range and are generally less abundant where there is low host abundance, particularly in the marginal areas of the host's range. However, this is variable; the highest parasite abundances are not always where host abundance is highest, and cuckoo bumblebees can be absent from areas where the host species is abundant (Antonovics and Edwards 2011). As such, a stable and healthy host population may not be sufficient to support a cuckoo parasite population, and other factors need exploring to underpin more targeted conservation. For example, the absence of *Psithyrus* from areas where their hosts are established could reflect differences in environmental niches between host and parasite; in the UK, five of the six *Psithyrus* species show more specialised environmental preferences than their most common host (Casey et al. 2015).

The distribution and range of cuckoo bumblebees and their hosts must be considered in the context of climate change. Whilst there will be variation in bumblebee responses to climate change, the majority of European species are predicted to experience range loss (Rasmont et al. 2015). Across continents, bumblebees have generally responded to climate change with southern range loss and limited northwards shift (Kerr et al. 2015). For *Psithyrus*, the predicted range contractions will likely exacerbate their already fragmented populations. This presents particular challenges for species conservation where northward migration potential is limited, such as in the UK. The UK has 17 native social bumblebees and one recent coloniser, alongside six cuckoo bumblebees. Four *Psithyrus* species are rare or absent in northern UK areas, despite host abundance being high in these areas (Falk 2015). This suggests that there are factors restricting northwards migration of *Psithyrus*. A better understanding of the habitat requirements of *Psithyrus* would help to understand patterns in range changes and may

Table 1 Correlations between first sighting of the six UK Bombus (Psithyrus) species and year. BWARS1 data are from 1970 to2019, BeeWalk2 data are from 2009 to 2019. Correlation coefficients are Spearman's rank. * indicates $p < 0.05$, ** indicates $p < 0.01$

	Bombus (Psithyrus) barbutellus	*B. (P.) bohemicus*	*B. (P.) campestris*	*B. (P.) rupestris*	*B. (P.) sylvestris*	*B. (P.) vestalis*
BWARS	-0.106	-0.363**	-0.410**	-0.604**	-0.539**	-0.631**
BeeWalk	-0.429	-0.648*	-0.285	-0.550	-0.773**	-0.818**

[1] Bee, Wasp, and Ant Recording Society dataset (BWARS, 2020) composed of sightings from the public. Data taken from 1970 onwards; dataset available from BWARS, at: https://www.bwars.com/content/bwars-data-download.

[2] BeeWalk is a standardised monitoring scheme for *Bombus*, started in 2009, supported by the public (Comont, 2020; dataset available from Figshare, at: https://doi.org/10.6084/m9.figshare.12280547.v1).

suggest strategies for supporting stronger northward expansion of distribution ranges. Furthermore, it will help identify the areas that are valuable to *Psithyrus* species and need protecting. For example, species distribution modelling of *Bombus (Psithyrus) chinenis* was used to describe its current distribution, possible risks, and priority conservation areas in China, despite low species records (Hu et al. 2022). Linking distribution research with behavioural and ecological studies would help expand this even further, particularly by bringing in the host species. For example, establishing how closely *Psithyrus* species and their hosts follow predator-prey population dynamics, the impact of host population and distributional decline, or how the defence strategies of the host species, if any, restrict *Psithyrus* species distributions (Grüter et al. 2018).

Phenology

Phenological timing is vital for cuckoo bumblebees, as usurpation success is related to host nest progression. The invader needs a nest with enough workers to raise their brood, but one that is not substantive enough to threaten the invader. *Psithyrus* females emerge from hibernation later than their host to facilitate this (Sramkova and Ayasse 2009). Consequently, maintaining phenological timing between emergence of host queens and *Psithyrus* females is crucial to the parasite's success. However, bees are generally experiencing life history events earlier than in previous years in response to rising temperatures (Bartomeus et al. 2011). Consequently, we argue that there is reasonable cause for concern that the parasite-host relationship could be threatened under climate change. Earlier emergence of host species could negatively impact invasion success if not adequately matched by cuckoo bumblebees.

Climate change will potentially affect the environmental stimuli that impact the trigger, maintenance, and end of diapause (Tougeron 2019). Understanding the emergence triggers for species in host-parasite relationships would help predict how each will respond to climate change and whether they are likely to maintain relative emergence times. Currently, it is unclear why some cuckoo bumblebees are faring better than others and differential phenological change could be a possible explanation. Parallels with other Hymenoptera taxa that, like *Bombus*, contain both social insects and obligate brood parasites within the same genus could provide some insights. For example, the wasp, *Polistes sulcifer*, parasitises the social wasp, *P. dominulus*. *P. sulcifer* emerges later to invade an established host nest, and the later emergence is explained by differing hibernation sites, with *P. sulcifer* over-wintering in high-altitude areas to delay emergence (Ortolani et al. 2008). For *Bombus*, however, there are no recorded differences between parasite and host hibernation sites (Alford 1969). With no recent data contradicting Alford (1969), emergence time could be better explained by differing internal trigger thresholds. We know that bumblebee emergence is associated with rising spring temperatures and photoperiod, and that bumblebees have periods of insensitivity and sensitivity to environmental stimuli (Larrere et al. 1993). However, the specifics of the process remain largely unknown, particularly at the species level. Importantly, to our knowledge, there is no research on these aspects regarding *Psithyrus*. Developing a better understanding of the diapause termination process would help to identify which species are at greater risk of a shift in the timing of emergence relative to their hosts.

There are currently no studies specific to cuckoo bumblebees investigating phenological shifts in the subgenus. Preliminary explorations of existing data from the UK (Table 1) suggest that there could be a trend of earlier emergence when using first sightings of female cuckoo bumblebees as a proxy for emergence time. Whilst this is preliminary and there is variation between the two data sets, overall, UK cuckoo bumblebees are showing negative correlations between first sightings and the year, indicating that they are emerging earlier each year.

Conclusion

Cuckoo bumblebees have been overlooked in the scientific literature and in conservation efforts at a time of greatly increased attention on social bumblebees. *Psithyrus*'s enhanced vulnerability to climate change due to its phenological dependence on *Bombus*, combined with the generally negative perceptions of brood parasites, means there is an urgent conservation challenge facing the subgenus. This is an important moment to develop an integrated approach of increased research attention on, and development of, targeted conservation strategies for *Psithyrus*. In part, this will involve a change in perception of parasitic species, drawing on a better understanding of their role in shaping ecological communities and in supporting *Bombus*, which are more traditional conservation icons. *Psithyrus* provides an exciting opportunity to both improve our understanding of ecosystem dynamics under climate change for conservation and ecosystem service outcomes, whilst challenging us to think about our conservation priorities and biases.

Acknowledgements The authors would like to thank Dr Richard Comont at the Bumblebee Conservation Trust for his valuable advice and feedback on this article.

Author contributions The concept for this short communication was drawn from the MSc dissertation of the corresponding author, Reanne Bower, who wrote the first draft. Briony Norton and Mark Bulling, her dissertation supervisors, critically reviewed and helped rewrite the manuscript to produce the final draft. All authors reviewed the manuscript.

Declarations

Competing interests The authors have no competing interests to declare that are relevant to the content of this article.

References

Alford DV (1969) A study of the hibernation of bumblebees (Hymenoptera: Bombidae) in southern England. J Anim Ecol 38(1):149–170

Antonovics J, Edwards M (2011) Spatio-temporal dynamics of bumblebee nest parasites (*Bombus* subgenus *Psythirus* ssp.) and their hosts (*Bombus* spp). J Anim Ecol 80(5):999–1011

Bartomeus I, Ascher JS, Wagner D, Danforth BN, Colla S, Kornbluth S, Winfree R (2011) Climate-associated phenological advances in bee pollinators and bee-pollinated plants. *Proceedings of the National Academy of Sciences*, 108(51), pp.20645–20649

Casey LM, Rebelo H, Rotheray E, Goulson D (2015) Evidence for habitat and climatic specializations driving the long-term distribution trends of UK and Irish bumblebees. Divers Distrib 21(8):864–875

Dicks LV, Showler DA, Sutherland WJ (2010) Bee Conservation: Evidence for the effects of interventions. *Synopses of Conservation Evidence*. Exeter: Pegasus Publishing. Available at: https://www.conservationevidence.com/synopsis/index

Falk S (2015) Family- Apidae. Field Guide to the bees of Great Britain and Ireland. Bloomsbury Publishing, London, pp 368–414

Goulson D, Rayner P, Dawson B, Darvill B (2011) Translating research into action; bumblebee conservation as a case study. J Appl Ecol 48(1):3–8

Grüter C, Jongepier E, Foitzik S (2018) Insect societies fight back: the evolution of defensive traits against social parasites. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1751), p.20170200

Hu X, Ding G, Ma F, Naeem M, Li Y, Huang J, An J (2022) The cuckoo bumble bee, *Bombus chinensis*, has a fragmented habitat, as revealed using the maximum entropy approach (Hymenoptera: Apidae). Apidologie 53(4):1–16

Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) (2016) *The assessment report on pollinators, pollination, and food production*. Potts, S.G., Imperatriz-Fonseca, V.L., and Ngo, H.T. (eds). [online] Bonn: Germany. Available at: https://ipbes.net/assessment-reports/pollinators

Kerr JT, Pindar A, Galpern P, Packer L, Potts SG, Roberts SM, Rasmont P, Schweiger O, Colla SR, Richardson LL, Wagner DL (2015) Climate change impacts on bumblebees converge across continents. Science 349(6244):177–180

Larrere Y, Lavenseau L, Tasei JN, Couillaud F (1993) Juvenile hormone biosynthesis and diapause termination in *Bombus terrestris*. Invertebrate Reprod Dev 23(1):7–14

Lemelin RH (2013) To bee or not to bee: whether 'tis nobler to revere or to revile those six-legged creatures during one's leisure. Leisure Stud 32(2):153–171

Lhomme P, Hines HM (2019) Ecology and evolution of cuckoo bumble bees. Ann Entomol Soc Am 112(3):122–140

Møller AP, Morelli F, Benedetti Y, Mousseau T, Su T, Zhou B, Tryjanowski P, Liang W (2017) Multiple species of cuckoos are superior predictors of bird species richness in Asia. Ecosphere 8(11):e02003

Ortolani I, Turillazzi S, Cervo R (2008) Spring usurpation restlessness: a wasp social parasite adapts its seasonal activity to the host cycle. Ethology 114(8):782–788

Raffel TR, Martin LB, Rohr JR (2008) Parasites as predators: unifying natural enemy ecology. Trends Ecol Evol 23(11):610–618

Rasmont P, Franzén M, Lecocq T, Harpke A, Roberts SP, Biesmeijer JC, Castro L, Cederberg B, Dvorak L, Fitzpatrick Ú, Gonseth Y, Haubruge E, Mahé G, Manino A, Michez D, Neumayer J, Ødegaard F, Paukkunen J, Pawlikowski T, Potts SG, Reemer M, Settele J, Straka J (2015) Schweiger O. Climatic risk and distribution atlas of European bumblebees. *Biorisk*, 10, pp. 1-236

Ritchie EG, Elmhagen B, Glen AS, Letnic M, Ludwig G, McDonald RA (2012) Ecosystem restoration with teeth: what role for predators? Trends Ecol Evol 27(5):265–271

Rothstein SI, Peer BD (2005) Conservation solutions for the threatened and endangered Cowbird (*Molothrus* spp.) hosts: separating Fact from Fiction. Ornithological Monogr 57:98–114

Sramkova A, Ayasse M (2009) Chemical ecology involved in invasion success of the cuckoo bumblebee *Psithyrus vestalis* and in survival of workers of its host *Bombus terrestris*. Chemoecology 19(1):55–62

Suhonen J, Rannikko J, Sorvari J (2015) The rarity of host species affects the co-extinction risk in socially parasitic bumblebee *Bombus (Psithyrus)* species. Ann Zool Fenn 52(4):236–242

Suhonen J, Rannikko J, Sorvari J (2016) Species richness of cuckoo bumblebees is determined by the geographical range area of the host bumblebee. Insect Conserv Divers 9(6):529–535

Tougeron K (2019) Diapause research in insects: historical review and recent work perspectives. Entomol Exp Appl 167(1):27–36