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Ecology and Evolution of Cuckoo Bumble Bees

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Abstract

Most social insect lineages contain socially parasitic cheater species that, rather than produce their own workers, infiltrate the nests of closely related social species and force the hosts to rear their offspring. These parasites have often lost social traits, like the ability to rear and produce workers, while retaining abilities for reproductive control and exhibiting novel parasitic innovations to capitalize on host resources. Given their close relationships with their hosts, social parasites are particularly informative to understand antagonistic coevolution and the essential components of sociality. Bumble bee social parasites are well suited to inform such evolutionary questions as they exhibit a gradation from facultative to obligate parasitism in their three independent origins of social parasitism, while also exhibiting a diverse obligately socially parasitic lineage, the subgenus *Psithyrus* Lepeletier, that varies across species in host use and invasion strategies. Despite the insights it can provide, cuckoo bumble bees, like most social parasites, are rare to encounter, and as such represent some of the most poorly understood bumble bee lineages. In this review, we bring together the state of our knowledge on the ecology and evolution of these rare cuckoo bees, to set a framework for further study, while also highlighting our current gaps in knowledge. In particular, we describe patterns of host breadth, geographic range, behavioral and morphological innovations, and social invasion strategies utilized across these bees to varying success. Considering their rarity, we highlight the pressing need to study these social parasites given conservation threats posed by host species declines.

Key words: *Psithyrus*, social parasitism, inquilinism, *Bombus*

Parasitism is one of the most common lifestyles on earth (Thompson 1994) and its natural history has fascinated scientists for centuries. Among the different forms of parasitism that have evolved, 'brood parasitism' has been of particular interest as hosts and parasites in these systems are usually phylogenetically closely related and traits between hosts and brood parasites are thus similar. Compared to most microparasites (e.g., viruses, fungi, bacteria) and macroparasites (e.g., ticks, nematodes, parasitoid wasps), brood parasites essentially have evolved as cheaters within their own systems and exploit the resources of close relatives for their own gain, and as such both parasites and hosts have evolved sophisticated invasion and counter-invasion strategies. For these reasons, brood parasitism, although a rare phenomenon, has been intensively studied as a model system to study antagonistic coevolution (reviewed in Kilner and Langmore 2011).

Brood parasites exploit the brood care behavior of their host. Such parasites have arisen multiple times in birds (aka. cuckoo birds), with around 1% of all bird species laying their eggs in nests of other bird species and forcing their host to rear their offspring (Davies 2011). Brood parasites have also arisen several times in social insects, especially in social hymenopterans (e.g., ants, wasps, and bees), but remain rare in the wild compared to their free-living relatives. Contrary to birds, brood parasites of social hymenopterans not only dump their eggs in the nests of others, but they also exploit the social system of their hosts, thus they are referred to as social parasites.

There are different forms of social parasitism in insects depending on the level of integration into the social functioning of the host. Some species, known as xenobiotics, live and feed within the host colony but rear their own offspring (Hölldobler and Wilson 1990). Other species exploit the labor force of their hosts temporarily or facultatively, but are still able to produce their own workers (Nash and Boomsma 2008). Finally some species, referred to as obligate social parasites, are totally dependent on their hosts to complete their life cycle. In the most extreme form, the parasitic females produce only reproductives of both sex and have lost the ability to produce a worker caste. They are thus totally dependent on the workers of their host to raise their offspring (Alford 1975, Cervo 2006, Buschinger 2009).

In this review, we focus on the multiple origins of social parasitism within bumble bees, emphasizing the different aspects of their ecology that might have promoted social parasitism. We then focus more specifically on the obligately socially parasitic subgenus _Psithyrus_ Lepeletier and provide a detailed review of the current state of knowledge about their natural history. We highlight the value of this system for understanding multiple aspects of evolution while emphasizing the gaps in our knowledge of the ecology and behavior of _Psithyrus_ in need of further study.

Social Parasitism in Bees (Hymenoptera: Apoidea: Anthophila)

It is estimated that obligate social parasitism appeared independently at least 24 times during bee evolution: 14 times in Xylocopinae (tribe Allodapini; Smith et al. 2007, 2013), 5 times in Apinae (tribes Bombini and Euglossini; Cameron et al. 2007, Michel-Salzat et al. 2004) and 5 times in Halictinae (tribe Halictini; Gibbs et al. 2011) (Table 1 and references therein). Most of these species are considered social parasites because they remain in the nest of their social host, however some species parasitize only semi- or subsocial hosts (tribes Halictini and Euglossini, respectively) and most of them do not actually functionally replace the host queen but merely cohabit with their hosts. The species _Braunsapis kaliago_ Reyes and Sakagami and cuckoo bumble bees exhibit the most extreme form of social parasitism (Batra et al. 1993), whereby the parasite replaces a social queen and takes control over its offspring, and the parasites have lost behavioral and morphological traits for living independently of their hosts. Obligate social parasitism has three independent origins in the bumble bee lineage (Table 1; Cameron et al. 2007, Hines and Cameron 2010): in the subgenus _Alpinobombus_ with _Bombus hyperboreus_ Schönherr/_Bombus natvigi_ Richards, in the subgenus _Thoracobombus_ with _Bombus inexspectatus_ (Tkalcu) and in the subgenus _Psithyrus_ consisting entirely of workerless social parasite species. In no other case in bee evolution has a socially parasitic bee lineage exhibited a species radiation to the magnitude of _Psithyrus_ (28 species).

The Evolution of Social Parasitism in Bumble Bees (Apidae: _Bombus_)

In this section, only the elements of bumble bee biology that have favored the appearance and evolution of social parasitism are considered. Many works offer a more detailed description of general

Table 1. Bee social parasites and their hosts (adapted from Michener 2007)

Obligate social parasites	Hosts	Bibliographic references
Family Halictidae		
Sub-family Halictinae (5)		
Tribe Halictini		
*_Sphecodes_[a]	_Halictus_	Knerer 1980
*_Microsphecodes kathleenea_	_Lasioglossum (Dialictus)_	Eickwort and Eickwort 1972
Lasioglossum (Dialictus) platyparium group	_Lasioglossum (Dialictus)_	Gibbs et al. 2011
Lasioglossum (Dialictus) cephalotes group	_Lasioglossum (Dialictus)_	Gibbs et al. 2011
Megalopta	_Megalopta_	Biani and Wcislo 2007
Family Apidae		
Sub-family Xylocopinae (14)		
Tribe Allodapini		
Allodape greathеadii p	_Allodape_	Michener 2007
Allodapula guilarmodi p	_Allodapula_	Michener 2007
Braunsapis kaliago + _B. breviceps_	_Braunsapis_	Michener 2007
Braunsapis bislensis	_Braunsapis_	Michener et al. 2003
Braunsapis falcata + B. hirsuta	_Braunsapis_	Michener 2007; Smith et al. 2013
Braunsapis Malaysia (undescribed)	_Braunsapis_	Smith et al. 2013
Braunsapis natalica	_Braunsapis_	Michener 2007
Braunsapis Mysore (undescribed)	_Braunsapis_	Smith et al. 2013
Braunsapis scorpius p	_Braunsapis_	Packer 2018
*_Eucondylops_	_Allodapula_	Michener 2007
*_Effractapis p_	_Braunsapis_	Michener 2007
*_Inquilina_	_Exoneura_	Michener 2007
Macrogalea	_Macrogalea_	Michener 2007; Smith et al. 2013
*_Nasutapis_	_Braunsapis_	Michener 2007; Smith et al. 2013
Sub-family Apinae (5)		
Tribe Bombini		
Bombus (*_Psithyrus_)	_Bombus_	Cameron et al. 2007
B. hyperboreus + B. natvigi	_Bombus_	Cameron et al. 2007
B. inexspectatus	_Bombus_	Cameron et al. 2007
Tribe Euglossini		
*_Aglae_[a]	_Eulaema_	Michel-Salzat et al. 2004
*_Exaerete_[a]	_Eulaema and Eufriesea_	Michel-Salzat et al. 2004

The numbers between brackets represent the probable number of origins of social parasitism.
The species that functionally replace the host queen are in bold.
* Indicate the entire lineage is parasitic
[a] Indicate that the taxon parasitizes semi- or subsocial hosts
p probable parasite based on morphology but not known from host nest

bumble bee natural history (Sladen 1912, Alford 1975, Sakagami 1976, Heinrich 1979, Plowright and Laverty 1984, Goulson 2009).

The Social Condition: The Bumble Bee Life Cycle

To understand how social parasitism in bumble bees evolved, it is first necessary to understand some key facets of social bumble bee biology. Bumble bees are primitively eusocial insects (as defined by Michener 1974) with an annual life cycle (Fig. 1). This cycle is divided into three distinct phases: 1) a solitary phase involving courtship behavior, hibernation of future queens, and the foundation of the nest, 2) a multiplicative phase during which the founding queen produces workers, and finally 3) a reproductive phase during which males and gynes are produced (Fig. 1). In early spring, the queens emerge from hibernation and search for a nesting site. The choice of nesting sites varies across species (Alford 1975, Svensson et al. 2000, Kells and Goulson 2003, Osborne et al. 2008) with most species nesting underground, such as in abandoned rodent nests. Emergence from hibernation varies by species, occurring from February to June in the north temperate zone.

Once the nesting site is found, the queen collects and brings back pollen and nectar to its nest to mass provision brood cells. Its first eggs are laid upon the food store in a wax cell which she incubates to a temperature of 30–32°C (Heinrich 1979). The energetic constraints associated with brood care and foraging required for larval development make this stage the most critical of the bumble bee life cycle, vulnerable to limitations in floral resources and climatic hazards (Iserbyt and Rasmont 2012). The mortality rate of a colony before hatching of the first clutch of workers has been observed to be between 50 and 86% (Cumber 1953, Richards 1975, Müller and Schmid-Hempel 1992), with the survival rate increasing thereafter.

The first batch of workers emerge after 4–5 wk and contains ~6–17 workers depending on the species (Sakagami 1976). Queens that emerge late in the season, as well as northern species (e.g., *Alpinobombus*) generally produce a larger first batch of workers (Richards 1973, 1975). There is also an important interspecific variability in the total number of workers produced and in the duration of the multiplicative phase before the production of workers ceases and sexuals (gynes and males) begins ('the switch point'; Duchateau and Velthuis 1988). A colony of *Bombus terrestris* (Linnaeus) is capable of containing up to several hundreds of workers (Alford 1975) while some arctic species such as *Bombus polaris* Curtis, or mountain species such as Bombus *gerstaeckeri* Morawitz, produce only a single batch of a few workers before producing sexuals (Richards 1931, Ponchau et al. 2006). Even in the same habitats, species can vary substantially in how long their colonies last (e.g., in Europe, *Bombus hortorum* (Linnaeus) and *Bombus pratorum* (Linnaeus) colonies last ~14 wk but *Bombus pascuorum* (Scopoli) colonies last ~25 wk; Goodwin 1995).

In bumble bees, queens behaviorally and chemically inhibit the reproduction of workers, which as unfertilized females, are capable of producing male eggs (reviewed in Amsalem et al. 2015). In large colonies, behavioral inhibition (aggression and destruction of eggs) may not be sufficient, requiring chemical inhibition through fertility signals (reviewed in Ayasse and Jarau 2014). In *B. terrestris*, the absence of the queen rapidly leads to the development of worker ovaries (Röseler and van Honk 1990). This ovarian development leads to a competition between workers for reproduction, which is accompanied by the laying of male eggs but also oophagy and the ejection of the larvae (Zanette et al. 2012). To maintain control and prevent ejection, it is therefore necessary for the queen to impose its dominant status. For this, the *B. terrestris* queen is likely to produce

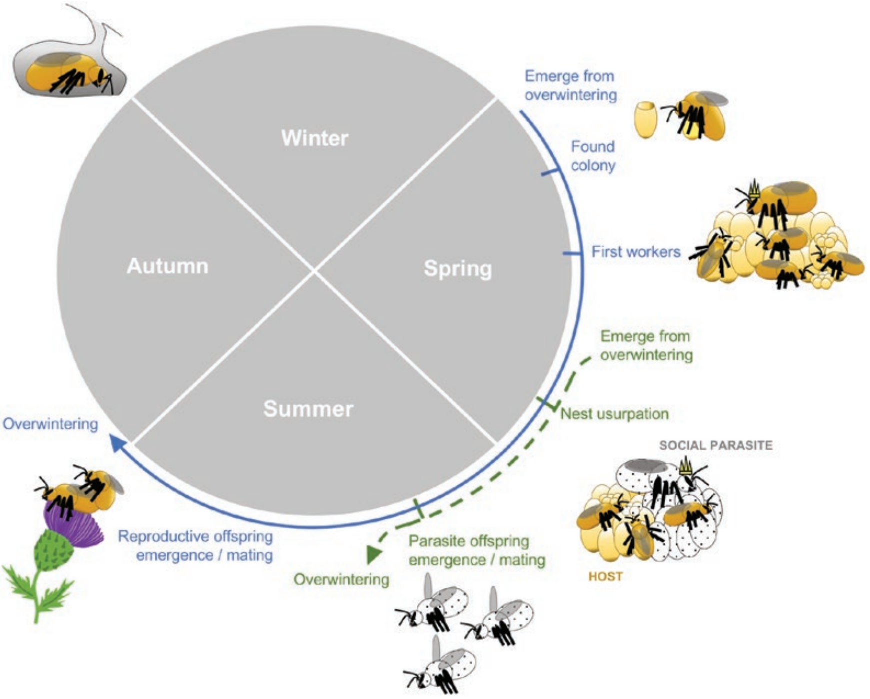

Fig. 1. The life cycle of social (solid line) and cuckoo (dashed line) bumble bees. Bumble bee queens have a solitary phase, as a queen emerges alone from hibernation in early spring, finds a nest, and provisions her first batch of worker brood. Once these workers emerge in mid- or late spring, they will take over nursing (brood care) and foraging for numerous subsequent worker generations. At the end of the summer, these colonies transition to producing reproductive males and females (gynes). These solitary gynes leave the nest, mate, and hibernate from early Autumn. Cuckoo bumble bee females emerge later in spring and usurp nests usually once the first batch of host workers is produced. Their life cycle is much shorter as they produce only reproductive males and females from early to mid-summer. Like their host, these solitary gynes then leave the nest, mate, and hibernate.

chemicals inhibiting ovarian development of workers (van Honk et al. 1980, Röseler et al. 1981, Sramkova et al. 2008).

Queen-Queen Conflicts

Bumble bee queens that have just established a nest do not tolerate the presence of other queens in their nest (Sladen 1912, Plowright and Jay 1966). However, considering the nest mortality rate in bumble bees (Richards 1975), one may wonder why polygyny is not more common. The benefits of an association between queens are well documented in ants and social wasps, where foundress females have been shown to increase their reproductive success through collaboration (Gibo 1978, Queller and Strassmann 1988, Tibbetts and Reeve 2003). In the wild, polygynous nests have only occasionally been observed in the bumble bee *Bombus atratus* Franklin in tropical America (Garofalo et al. 1986), which initiate nests by solo queens and then go through periods of polygyny. The observation of polygynous nest initiation in arctic bumble bees *B. polaris* and *Bombus glacialis* Friese, has been explained as a strategy to ensure a minimum amount of heat in the nest for brood survival in the permafrost (Berezin 1994).

Facultative Social Parasitism

Queen conflict among bumble bees has favored the evolution of important defense abilities. Numerous examples of dead queens found in nests with a living queen attest to this (Sladen 1912, Frison 1930, Plath 1934, Voveikov 1953, Bohart 1970). Despite this, the usurpation of an existing colony is a common strategy among bumble bees. The intruder usually enters the nest and kills the resident queen, then takes possession of the nest and adopts the brood. The majority of cases of facultative social parasitism involve queens of the same species, or closely related species (reviewed in Sakagami 1976)—such as between queens of *Bombus affinis* Cresson and *Bombus terricola* Kirby (Plath 1934) and *B. terrestris* on *Bombus lucorum* (Linnaeus) (Sladen 1912). Sometimes multiple invasions can occur in a single colony. For example, Richards (1975) observed four usurpations within a nest of *Bombus occidentalis* (Greene), three by conspecifics and one by *Bombus frigidus* Smith. Using microsatellite analysis of *Bombus hypnorum* (Linnaeus) worker genotypes, Paxton et al. (2001) demonstrated the presence of non-queen produced workers in more than 50% of the nests studied. Although the authors did not exclude potential worker drifting among nests, they considered that the most plausible explanation was that these workers were the offspring of former queens whose place was usurped.

Four main hypotheses have been proposed to explain the evolution of facultative social parasitism in bumble bees:

1) Facultative social parasitism is a consequence of queens being at a disadvantage compared to other queens of the same species, for example due to a delay in establishing their own nest or due to the destruction of their own nest. They then attempt to take another queen's nest as a means of compensating for their loss (Alford 1975). Late emerging species such as *Bombus rufocinctus* Cresson or *Bombus veteranus* (Fabricius) are known to display high rates of facultative social parasitism (Voveikov 1953, Hobbs 1965).
2) Facultative social parasitism is a consequence of the competition for nesting sites and is nest density-dependent. The year-to-year fluctuation in queen abundance drives reduced nest availability in peak years, leading to a higher proportion of facultative usurpations (Sladen 1912, Alford 1975, Akre et al. 1976, Archer 1982). Sladen (1912) observed successive invasions of several queens in the same nest during the years where *Bombus lapidarius* (Linnaeus) and *B. terrestris* queens were abundant.
3) Facultative social parasitism is a consequence of a 'bimodality in queen body size' (Voveikov 1953). Within a species, smaller queens are expected to emerge from hibernation earlier because of their lower body fat mass. Voveikov (1953) suggested that these early nests would be more fragile, because of the smaller size of these queens. Thus, later queens, larger and better armored than small queens, should have better reproductive success by usurping the nest of small queens. To date, no data supports this hypothesis.
4) Facultative social parasitism is a consequence of 'bimodality in queen behavior' with queens being naturally inclined towards usurpation or nest-making (Plowright and Laverty 1984). According to this hypothesis, both behaviors coexist within a population, and on average, would achieve equivalent reproductive success. Richards (1975) and Fisher (1987b) have shown that the success rate of a usurper queen is almost equal to the success rate of a nest-making queen.

Does usurpation behavior result from the selective advantage to the usurper or is it the result of the important competition between queens for nesting sites? Could a trade-off between nest survival rate and usurpation success explain the coexistence of different nesting behaviors in a population? Further study and more field data are needed to answer these questions, but a field study on *Bombus ignitus* (Smith) in Japan seem to support the idea of a fitness advantage of facultative usurpation. When given the choice between orphan nests and empty cavities, queens of *B. ignitus* had a strong preference for takeover of an orphan colony (Matsumaya and Ono 2018). The same authors also showed that the usurper queens reproduced more quickly and produced more reproductives than nest-making queens.

Evolution Towards Obligate Social Parasitism

Certain lineages of bumble bees have taken their usurpation strategies and exploitation of social and food resources to an extreme by canalizing the parasitic lifestyle to become obligate social parasites.

Richards (1927) noted that cuckoo bumble bees have a north temperate-biased distribution and suggested that obligate social parasitism in bumble bees evolved in areas where southern species of bumble bees occur in the northern edge of their range. Here, southern species tend to emerge later in the spring and overlap with earlier-emerging northern species which have already started a nest. Richards (1927) suggested that in these areas the southern species are disadvantaged because of the suboptimal climatic conditions and may benefit by usurping the nest of the northern species. This might explain facultative interspecific social parasitism of *B. affinis* on *B. terricola* (Plath 1934) and *B. terrestris* on *B. lucorum* (Sladen 1912) as both usurper species have more southern distribution than their facultative hosts.

There might also be a phylogenetic signal in a queen's ability to express facultative social parasitism (Hines and Cameron 2010). For example, bumble bees of the subgenus *Thoracobombus*, the sister group of the exclusively parasitic bumble bee lineage *Psithyrus*, are known to be particularly predisposed to facultative nest usurpation (Voveikov 1953, Sakagami and Nishijima 1973). *Bombus sylvarum* Linnaeus and *B. veteranus*, two sister species of the obligate social parasite *B. inexspectatus*, as well as the more distant species *B. ruderarius* (Müller), are all known to be frequent usurpers of nests of conspecifics or heterospecifics (Voveikov 1953). Hines and Cameron (2010) suggested that the obligatory parasitic behavior of *B. inexspectatus* could be inherited from the general parasitic tendency of species of the subgenus *Thoracobombus*.

Although the origin of obligate social parasitism remains obscure, the diversity of usurpation behaviors across independent origins in bumble bee social parasitism shows a gradation towards obligatory social parasitism that may be indicative of the evolutionary steps that have occurred:

1) Usurpation-prone social *Bombus* (e.g., *B. veteranus*): Usurp nests of their own or related species and recruit emerging workers of hosts to rear their offspring, but the parasite can still collect its own pollen, feed its larvae, and produce its own workers (Voveikov 1953).
2) *B. hyperboreus*/*B. natvigi*: This species/species complex (Williams et al. 2015) relies on workers of the host to rear their reproductive brood in most cases, but some females have been observed to produce a worker caste and they retain the potential to collect pollen to feed larvae (Gjershaug 2009).
3) *B. inexspectatus*: The usurper has reached a point of no return, as it is no longer able to produce a worker caste, thus relying exclusively on host workers to rear their offspring. Corbiculae are present but reduced and likely nonfunctional, preventing the usurper from collecting pollen for its offspring (Müller 2006).
4) Subgenus *Psithyrus*: Taking their social loss one step further, the usurper has not only lost the worker caste but has lost her corbiculae entirely, making her completely incapable of collecting pollen (Alford 1975).

Obligate Social Parasitism (non-*Psithyrus*)

Facultative nest usurpation is common among bumble bees, occurring in nearly 10% of the nests studied by Richards (1975). This widespread alternative nesting behavior might have contributed to the evolution of two taxa of obligate/semiobligate socially parasitic species outside of the subgenus *Psithyrus*: *Bombus* (*Alpinobombus*) *hyperboreus*/*Bombus* (*Alpinobombus*) *natvigi* and *Bombus* (*Thoracobombus*) *inexspectatus*.

In the Arctic region, the breeding season for bumble bees is very short. This lack of time forces most Arctic species to emerge simultaneously and synchronously, within 24 h after the first appearances of willow flowers (Vogt et al. 1994). This forces species to have very few workers before producing reproductives, perhaps skipping worker production entirely (Richards 1931). This shortened life cycle likely explains why *B. hyperboreus* and its sister taxon *B. natvigi* have acquired a largely socially parasitic lifestyle. *B. hyperboreus* was considered to have a circumpolar distribution, but recent genetic evidence suggests it is restricted to the Palearctic (Scandinavia and Russia), and that Nearctic (Canada and Greenland) specimens belong to a separate species *B. natvigi* (Williams et al. 2015), thus requiring a reanalysis of previous research in light of the new taxonomic evidence. *B. hyperboreus* primarily usurps other members of its subgenus *Alpinobombus* (Table 2), with its primary host considered to be *B.* (*Alpinobombus*) *polaris* (Løken 1973, Berezin 1990). *Bombus* (*Alpinobombus*) *balteatus* Dahlbom has also been observed to be parasitized by *B. hyperboreus* (Gjershaug 2009). *B.* (*Alpinobombus*) *alpinus* (Linnaeus) has been suggested to be a host (Stenström and Bergman 1998) although no parasitized nest has ever been observed. *B. hyperboreus* has also been observed to parasitize bumble bees of the subgenus *Pyrobombus*, notably *Bombus jonellus* (Kirby) (Bergwall 1970) and *B. glacialis* (Berezin 1994). In the Nearctic, *B. natvigi* has only been observed to usurp *B. polaris* (Friese 1935, Milliron and Olivier 1966, Richards 1973).

In the Arctic zone of Canada, *B. natvigi* seems to be an obligate inquiline species since there has never been any observation of workers (Milliron and Olivier 1966, Richards 1973, Pape 1983). On the other hand, potential workers of this species (it is possible they are small parasitic females; Michener 1974) have been found below the arctic circle in Greenland (Milliron 1973). *B. hyperboreus* have also been observed with workers below the arctic circle in Scandinavia, Finland, and Russia (Enwald 1881, Skorikov 1922, Elfving 1960, Løken 1973). *B. hyperboreus* queens are able to collect pollen, and thus are capable of provisioning their own nests (Yarrow 1970, Ranta and Lundberg 1981). Both species, however, have yet to be observed founding colonies on their own (Berezin 1994).

Outside of the subgenus *Psithyrus*, only *B. inexspectatus* is considered with certainty to be an obligate inquiline since no worker of this species has ever been observed to date. *B. inexspectatus* is a social parasite of *B. ruderarius* (Table 2; Yarrow 1970, Müller 2006), a very closely related species. Unlike *B. hyperboreus* and *B. natvigi*, the complete absence of pollen loads on the legs of all observed *B. inexspectatus* queens, as well as significantly reduced corbiculae, indicates that *B. inexspectatus* is at an advanced stage in its physiological and behavioral loss of social traits (Müller 2006). Morphological and behavioral traits that attest to the obligate parasitic lifestyle of *B. inexspectatus* include: 1) the absence of a worker caste; 2) the reduction of wax glands; 3) the reduction of the pollen collecting apparatus; and finally, 4) the absence of pollen collecting behavior. In addition, like *Psithyrus*, *B. inexspectatus* has an expansion of the region between the eyes and the pronotum considered to be defensive adaptation against host worker attacks (Yarrow 1970).

The Subgenus *Psithyrus*

Social parasitism in bumble bees reaches its pinnacle with the subgenus *Psithyrus*, which consists exclusively of obligate socially parasitic species. *Psithyrus* species, commonly known as cuckoo bumble bees, have no pollen-collecting apparatus on their hind legs, are unable to produce a worker caste, and produce insufficient wax for the construction of a nest. These species are totally dependent on their hosts to rear their offspring.

Taxonomy and Phylogenetic Relationships

The morphological specificities of cuckoo bumble bees were first described by Kirby (1802). Later, Illiger (1806) suspected they had different habits than other *Bombus* species and separated them from the 'true bumble bees' and Newman (1835) later separated them into the genus name *Apathus*. This genus name was used for over 40 yr, when it was discovered that Lepeletier (1832) had priority in naming the group *Psithyrus*. While long recognized as a monophyletic socially parasitic genus (Gaschott 1922) it wasn't until molecular phylogenetics were performed that *Psithyrus* was determined to be a derived lineage within *Bombus* (Plowright and Stephen 1973, Pekkarinen et al. 1979, Ito 1985, Williams 1985, Pamilo et al. 1987, Cameron et al. 2007), leading to its current recognition as a subgenus of *Bombus* (Williams 1991, Williams et al. 2008). There are currently 28 species of *Psithyrus* worldwide (Williams 1998; Table 2, Fig. 2), however more than 350 specific or subspecific names have been proposed to date (Williams 1998), highlighting the taxonomic confusion remaining within *Psithyrus* subgroups (Lecocq et al. 2011). This confusion is complicated by the rarity of many of the species, which has resulted in it being the most poorly sampled subgenus (19 of 28 spp) in the most recent phylogenetic work (Cameron et al. 2007; Fig. 2).

Psithyrus is fairly isolated phylogenetically as it has a very long branch subtending it that separates it from its sister lineage, the large Holarctic *Thoracobombus* subgenus (Cameron et al. 2007). It separated from this lineage ~20 mya, a deep split considering that

Table 2. The cuckoo bumble bees, their biogeographic ranges, and hosts

Social parasites	Biogeographic range	Hosts	Main bibliographical references
Alpinobombus			
B. natvigi	Arctic, Nearctic	***B. (Alpinobombus) polaris****	Milliron and Olivier 1966, Richards 1973
B. hyperboreus	Arctic, Palearctic	***B. (Alpinobombus) polaris****	Løken 1973, Berezin 1990
		*B. (Alpinobombus) balteatus**	Gjershaug 2009
		B. (Alpinobombus) alpinus	Stenström and Bergman 1998
		B. (Pyrobombus) glacialis	Berezin 1994
		B. (Pyrobombus) jonellus	Bergwall 1970
Thoracobombus			
B. inexspectatus	Palearctic	***B. (Thoracobombus) ruderatus****	Yarrow 1970, Müller 2006
Psithyrus (citrinus group)			
B. citrinus	Nearctic	***B. (Pyrobombus) vagans****	Plath 1934, Salked 1978, Fisher 1983a
		B. (Pyrobombus) impatiens*	Plath 1922, Plath 1934, Fisher 1983a
		B. (Pyrobombus) bimaculatus	Plath 1934
		B. (Bombias) nevadensis	Bequaert and Plath 1925
		B. (Cullumanobombus) griseocollis	Frison 1921
		B. (Thoracobombus) pensylvanicus	Salked 1978
		B. (Bombus) terricola	Plath 1922
B. insularis	Nearctic	*B. (Subterraneobombus) appositus**	Craig 1953, Hobbs 1966
		*B. (Pyrobombus) flavifrons**	Sladen 1915
		*B. (Pyrobombus) ternarius**	Sladen 1915, Craig 1953
		B. (Pyrobombus) impatiens	Pelletier 2003
		B. (Pyrobombus) huntii	Strange et al. 2014
		B. (Pyrobombus) bifarius	Hobbs 1966, Strange et al. 2014
		*B. (Bombias) nevadensis**	Hobbs 1965
		B. (Cullumanobombus) rufocintus	Hobbs 1965
		*B. (Thoracobombus) fervidus**	Hobbs 1966
		B. (Bombus) occidentalis	Frison 1926
		B. (Bombus) terricola	Sladen 1915
		B. (Pyrobombus) mixtus	Sladen 1915, Leech 1947
B. variabilis	Nearctic, Neotropical	***B. (Thoracobombus) pensylvanicus****	Frison 1916, Webb 1961
		B. (Bombus) terricola	Frison 1926
		B. (Bombias) auricomus	Frison 1926
Psithyrus (rupestris group)			
B. branickii	Palearctic, Oriental	*B. (Melanobombus) friseanus*	Williams et al. 2009
		B. (Melanobombus) keriensis	Williams 1991
B. rupestris	Palearctic, Oriental	***B. (Melanobombus) lapidarius****	Hoffer 1889, Sladen 1912, Reinig 1935, Bols 1939
		B. (Melanobombus) sichelii	Bullman 1953, Løken 1984
		*B. (Thoracobombus) pascuorum**	Haeseler 1970
		B. (Thoracobombus) pomorum	Pouvreau 1973
		B. (Thoracobombus) ruderarius	Voveikov 1953
		B. (Thoracobombus) sylvarum	Höppner 1901, Voveikov 1953, May 1959, Løken 1984
		B. (Pyrobombus) pratorum	Voveikov 1953
B. cornutus	Oriental	*B. (Megabombus) trifasciatus*	Maa 1948
B. chinensis	Oriental	*B. (Melanobombus) pyrosoma*	Reinig 1935
B. tibetanus	Oriental	Unknown	
B. turneri	Oriental	Unknown	
B. monozonus	Oriental	Unknown	
B. expolitus	Oriental	Unknown	
B. novus	Oriental	Unknown	
Psithyrus (campestris group)			
B. campestris	Palearctic	***B. (Thoracobombus) pascuorum****	Harter 1887, Hoffer 1889, Cumber 1949, Pouvreau 1973, Løken 1984
		*B. (Thoracobombus) humilis**	Hoffer 1889, Pouvreau 1973, Løken 1984
		*B. (Thoracobombus) pomorum**	May 1937, Løken 1984
		B. (Thoracobombus) muscorum	Pouvreau 1973
		B. (Thoracobombus) ruderarius	Pouvreau 1973
		B. (Thoracobombus) sylvarum	Pouvreau 1973
		B. (Thoracobombus) veteranus	Hoffer 1889
		*B. (Pyrobombus) pratorum**	Pouvreau 1973, Løken 1984
		B. (Megabombus) hortorum	Pouvreau 1973
B. morawitzianus	Palearctic, Oriental	Unknown	
B. ferganicus	Palearctic, Oriental	*B. (Melanobombus) keriensis*	Williams 1991
B. bellardii	Oriental	*B. (Megabombus) trifasciatus*	Maa 1948

Table 2. Continued

Social parasites	Biogeographic range	Hosts	Main bibliographical references
Psithyrus (bohemicus group)			
B. suckleyi	Nearctic	***B. (Bombus) occidentalis****	Fisher 1985
		B. (Bombus) terricola	Hobbs 1968
		B. (Cullumanobombus) rufocinctus	Williams et al. 2014
		B. (Bombias) nevadensis	Hobbs 1965
		B. (Thoracobombus) fervidus	Williams et al. 2014
		B. (Subterraneobombus) appositus	Hobbs 1966
B. ashtoni	Nearctic	***B. (Bombus) affinis****	Plath 1934, Fisher 1983b
		B. (Bombus) terricola*	Plath 1934, Salked 1978, Fisher 1984a
		B. (Bombus) occidentalis	Williams et al. 2014
		B. (Pyrobombus) bimaculatus	Plath 1934
		B. (Pyrobombus) vagans	Salked 1978
B. bohemicus	Arctic, Palearctic, Oriental	***B. (Bombus) lucorum****	Sladen 1912, Reinig 1935, Cumber 1949, Pouvreau 1973, Løken 1984
		B. (Bombus) terrestris	Kreuter et al. 2010
		B. (Bombus) cryptarum	Kreuter et al. 2010
		B. (Bombus) magnus	Edwards and Broad 2006
B. vestalis	Palearctic	***B. (Bombus) terrestris****	Sladen 1912, Reinig 1935, van Honk et al. 1981, Fisher 1988
		B. (Thoracobombus) pascuorum	Hoffer 1889
B. coreanus	Oriental	Unknown	
Psithyrus (barbutellus group)			
B. barbutellus	Palearctic	***B. (Megabombus) hortorum****	Sladen 1912, Ball 1914, Müller 1936, Cumber 1949, Postner 1952
		B. (Megabombus) ruderatus	Pittioni and Schmidt 1942, Ornosa 1984, Rasmont and Adamski 1996
		B. (Megabombus) argillaceus	Reinig 1935, Pittioni and Schmidt 1942, Pouvreau 1973
		*B. (Pyrobombus) hypnorum**	Hasselrot 1960, Pouvreau 1973
		*B. (Pyrobombus) pratorum**	Voveikov 1953, Pouvreau 1973
		B. (Pyrobombus) jonellus	Schenck 1859, Schmiedeknecht 1883, Skorikov 1922
		B. (Subterraneobombus) subterraneus	Knechtel 1955
		B. (Subterraneobombus) distinguendus	Hoffer 1889, Popov 1931
		B. (Thoracobombus) pascuorum	Hoffer 1889, Skorikov 1922, Popov 1931, Cumber 1949
		B. (Thoracobombus) ruderarius	Skorikov 1922, Voveikov 1953
Psithyrus (sylvestris group)			
B. fernaldae	Nearctic	*B. (Subterraneobombus) appositus*	Fisher 1985
		B. (Bombus) occidentalis	Fisher 1985
		B. (Cullumanobombus) rufocintus	Hobbs 1965, Thorp et al. 1983, Laverty and Harder 1988
		B. (Pyrobombus) perplexus	Laverty and Harder 1988
		B. (Thoracobombus) fervidus	Fisher 1985
B. flavidus	Arctic, Palearctic	***B. (Pyrobombus) jonellus****	Brinck and Wingstrand 1951
		*B. (Pyrobombus) lapponicus**	Pittioni 1942
		B. (Pyrobombus) monticola	Richards 1928, Lundberg and Svensson 1977, Pekkarinen et al. 1981
		B. (Pyrobombus) pyrenaeus	Rasmont 1988
		B. (Pyrobombus) cingulatus	Pekkarinen and Teräs 1993
B. quadricolor	Palearctic	***B. (Kallobombus) soroeensis****	Hoffer 1889, Richards 1928, Reinig 1935, Løken 1984
		*B. (Pyrobombus) pratorum**	Sladen 1912, Pouvreau 1973
		B. (Pyrobombus) jonellus	Cederberg 1976
		B. (Thoracobombus) ruderarius	Pouvreau 1973, Pekkarinen and Teräs 1993
B. norvegicus	Arctic, Palearctic, Oriental	***B. (Pyrobombus) hypnorum****	Röseler 1972, Cederberg 1976, Løken 1984
		B. (Pyrobombus) jonellus	Brinck and Wingstrand 1951
B. sylvestris	Palearctic, Oriental	***B. (Pyrobombus) pratorum****	Pouvreau 1973, Küpper and Schwammberger 1995, Løken 1984
		B. (Pyrobombus) jonellus	Richards 1928, Reinig 1935, Løken 1984
		B. (Pyrobombus) hypnorum	Pouvreau 1973, von Hagen and Aichorn 2003
		B. (Pyrobombus) monticola	Edwards and Broad 2005
		B. (Megabombus) hortorum	von Hagen and Aichorn 2003
		B. (Kallobombus) soroeensis	Edwards and Roy 2009
B. skorikovi	Oriental	Unknown	

Main hosts are in bold; the potential hosts that have never been recorded in a nest are in gray text

*Cuckoo female observed breeding.

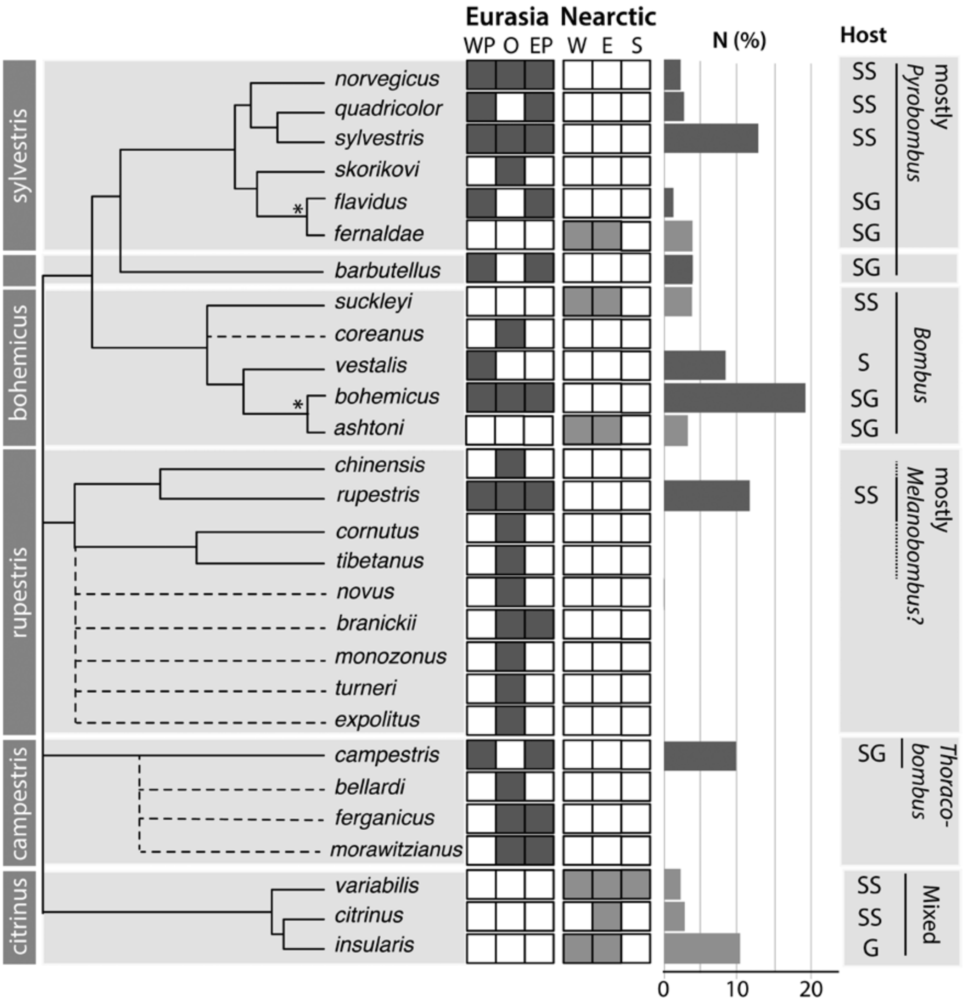

Fig. 2. *Psithyrus* phylogeny with mapping of biogeographic distribution, relative abundances, and general host characteristics. Host classification is generalized based on limited existing information and is thus subject to change with additional data; classification is as follows: SS = semispecialists, SG = semigeneralists, S = Specialists, G = Generalist. N% = Percent of all *Psithyrus* records on GBIF belonging to that species and boxes to the left are filled based on the distributional range of the species (medium gray = Nearctic [W = West, E = East, S = South]; dark gray = Eurasia [WP = West-Palearctic, O = Oriental, EP =East-Palearctic]). The phylogeny is derived from that presented in Cameron et al. (2007). Lineages not analyzed in that study are presented with dashed lines. Dashed lines are placed based on taxonomic assignment and general morphological affinity and have not been analyzed molecularly. Groups at left represent general species groups as defined by Williams et al. (2008). **B. fernaldae-B. flavidus* and *B. ashtoni-B. bohemicus* have recently been considered conspecific, but are represented here separately to better represent the differences between the populations.

the bumble bees are estimated at 34 my old (Hines 2008). Extant *Psithyrus* on the other hand are fairly closely related to each other, with an estimated ancestor that is ~9 my old. This long branch is interesting to consider: perhaps it reflects large amounts of genomic change that occurred in concert with parasitism. This would not be surprising considering that *Psithyrus* deviates from other species substantially in chromosome numbers, exhibiting 26 chromosomes in the two divergent species tested, while all other bumble bees exhibit between 16 and 19 (Owen and Plowright 1983). Alternatively, a parasitic lifestyle may be predisposed to extinction given that they essentially occupy a higher trophic level and thus tend to be less abundant than their hosts.

Geographic Distribution and Population Trends

Psithyrus has a largely Holarctic distribution (Williams 1998). It has a particularly broad range relative to many other subgenera, containing three independent sublineages that have spread to the Nearctic from Palearctic ancestors (Hines 2008; Fig. 2). With the exception of South America, *Psithyrus* are found in most geographic regions where bumble bees are naturally present. Like most parasites, however, species have a more restricted distribution than their host (Fig. 3). They generally live at lower altitudes and latitudes (Alford 1975, Pekkarinen et al. 1981, Løken 1984) and are also rare at low elevations in warmer regions (Rasmont and Adamski 1996). In general, the distribution of cuckoo bumble bees is restricted by the geographic distribution and population density of their hosts (Lundberg and Svensson 1977, Antonovics and Edwards 2011). At the global scale, they do not occur in the extremes of the geographical distribution of other bumble bees, neither the Arctic nor in the intertropical regions (Hines 2008; Fig. 3).

Psithyrus comprises ~11% of all bumble bee species, however, relative population abundances represent less of the overall bumble bee population: of all preserved specimen records of *Bombus* deposited in the Global Biodiversity Inventory (gbif.org, 27 February 2018; Fig. 2) only 5.8% of the >1 million bumble bees databased are *Psithyrus*. Focusing on the two areas with the most specimen records, in the western Palearctic *Psithyrus* comprises 15% of species but only 6% of the abundance of georeferenced specimens on

Fig. 3. Generalized distribution of all bumble bees (medium gray) compared to only *Psithyrus* (dark gray), showing that while *Psithyrus* is a broadly distributed subgenus, it does not reach the climatic extremes of social bumble bees. Distributional ranges are approximated based on literature and gbif.org records and thus are not meant to be accurate at a fine scale.

GBIF, while in the Nearctic north of Mexico they comprise 12.5% of species but 3.8% of abundances. Overall, most community level data suggest that while *Psithyrus* can reach fairly high frequencies in some communities, particularly for some species like *Bombus vestalis* (Geoffroy) (Fig. 4a) (Carvell et al. 2008, Erler and Lattorff 2010), *Bombus bohemicus* Seidl (Fig. 4b) (Müller and Schmid-Hempel 1992) or *Bombus insularis* (Smith) (Fig. 4h) (Strange et al. 2014), they generally are uncommon to encounter (Koch et al. 2015, Williams et al. 2014). The absence of a worker caste, which usually comprises the majority of preserved bumble bees, can partially explain their lower abundances. Their abundance, however, should also be impacted by their higher trophic position given their reliance on other bumble bee species.

In fluctuating environments, such as those subject to climate change, habitat reduction, and introduced pathogens, some bumble bee species have been observed to decline rapidly. Given their reliance on host bumble bees and their natural rarity given their parasitic strategy, *Psithyrus* are potentially more vulnerable to species declines and extinctions (Sheffield et al. 2013; Suhonen et al. 2015, 2016). Bumble bee sampling and databasing is more extensive in North America and Europe, thus allowing more assessment of species status even among typically rare species. No European species are listed among the red listed species, with species listed either as least concern or data deficient (Nieto et al. 2014) due to relative natural rarity. The non-*Psithyrus* cuckoo *B. inexspectatus*, however, is listed as endangered (Nieto et al. 2014). Three North American species are considered critically endangered (*Bombus ashtoni* (Cresson), *Bombus suckleyi* Greene and *Bombus variabilis* (Cresson) (Hatfield et al. 2014). In North American populations, *B. ashtoni* and *B. suckleyi* have suffered an important decline of more than 90% in the last decade like their respective hosts *B. terricola, B. affinis*, and *B. occidentalis* (Hatfield et al. 2014). The Committee on the Status of Endangered Wildlife in Canada suggests that the decline of *B. ashtoni* is likely directly linked to the declines of its two hosts (COSEWIC 2014). *B. variabilis* is also considered one of the rarest of all North American bumble bee species with very few records in the last decade (Williams et al. 2014, Hatfield et al. 2014). Its decline is also likely impacted by the decline in the past 15 yr in the abundance of its primary host *Bombus* (*Thoracobombus*) *pensylvanicus* (De Geer) (Cameron et al. 2011). Suhonen et al. (2015, 2016) empirically demonstrated that the extinction risk of cuckoo bumble bee species was higher if their hosts were also threatened, and that the risk of extinction of cuckoos was always higher than that of their most common hosts, with specialist cuckoo bumble bees being most at risk (Suhonen et al. 2015).

As evidenced by examining the geographic distribution of sister taxa (Hines 2008), bumble bees tend to speciate vicariantly. Most bumble bee species tend to be contained within major world regions of endemicity, and while several sister species result from Nearctic/Palearctic vicariance, few species obtain a distribution that spans both the Palearctic and Nearctic. A few that do so include a few migrants into Alaska from the Palearctic (*B. jonellus, Bombus distinguendus* Morawitz), the circumarctic *Alpinobombus* species *B. polaris*, and the Holarctic species *Bombus cryptarum* (Fabricius) (Williams et al. 2012). The other two species which potentially have such a wide range without speciation are contained within *Psithyrus*. Morphological and genetic data suggest potential conspecificity between *B. ashtoni* (Nearctic) and *B. bohemicus* (Palearctic), and between *Bombus fernaldae* (Franklin) (Nearctic) and *Bombus flavidus* Eversmann (Palearctic) (Cameron et al. 2007, Williams et al. 2014). If these are indeed confirmed to be conspecific, this gives them the widest Holarctic species range of all bumble bees. Although more information is needed to understand the status of these species, it is interesting to contemplate how a social parasite manages to achieve a wider distribution than any one social bumble bee species. Perhaps a parasitic life style may offer a greater ease of occupying new regions than experienced by host species, which must find the right conditions for starting and maintaining nests. Preferred hosts of both socially parasitic species would have already established in both continents (e.g., *B. cryptarum* for *B. ashtoni*; *Pyrobombus spp.* for *B. flavidus*), easing parasite establishment.

Regarding relative diversity of these sister taxa, it is interesting to note as well that while *B. bohemicus* is the most successful W. Palearctic *Psithyrus* species (Fig. 2), reaching highest abundances among databased *Psithyrus* specimens (GBIF), the Nearctic sister taxon *B. ashtoni* reaches much lower abundances, an observation that may reflect its history or perhaps the lower abundances of host species in the Nearctic than the W. Palearctic, where *B.* (*Bombus*) *lucorum* is one of the most successful species. In contrast, *B. flavidus* in the W. Palearctic is much more rare while in the New World it is

Fig. 4. Some females of cuckoo bumble bees (subgenus *Psithyrus*); (a) *Bombus vestalis* (Geoffroy 1785) (England, UK; Photo S. Falk); (b) *Bombus bohemicus* Seidl 1838 (England, UK; Photo S. Falk); (c) *Bombus rupestris* (Fabricius 1793) (England, UK; Photo S. Falk); (d) *Bombus campestris* (Panzer 1801) (France; Photo E. Léglise); (e) *Bombus barbutellus* (Kirby 1802) (England, UK; Photo S. Falk); (f) *Bombus sylvestris* (Lepeletier 1832) (England, UK; Photo S. Falk); (g) *Bombus citrinus* (Smith 1854) (MN, USA; Photo S. King); (h) *Bombus insularis* (Smith 1861) (NM, USA; Photo B. Reynolds).

one of the more successful species. This could again be a reflection of its evolutionary history, or alternatively the varying success of *Pyrobombus* in these respective regions; as the preferred host subgenus of these taxa, *Pyrobombus,* is the dominant subgenus in the Nearctic. Furthermore, the Old World *B. flavidus* may be more host specialized within *Pyrobombus* than the New World populations (Table 2).

The usurpation frequency of nests by *Psithyrus* females seems to be highly variable in time and space (Pelletier and McNeil 2003, Carvell et al. 2008, Antonovics and Edwards 2011). According to Alford (1975), the infestation rate is relatively low, however, high rates of infestation have been frequently observed with recorded usurpation frequencies of 28% of *B. lucorum* nests by *B. bohemicus* (Müller and Schmid-Hempel 1992), 20–40% of *B. lapidarius* nests by *Bombus rupestris* (Fabricius) (Fig. 4c) (Sladen 1912), 33–50% of *B. terrestris* nests by *B. vestalis* (Erler and Lattorff 2010) and 50% of *B. pratorum* nests by *B. sylvestris* (Lepeletier) (Fig. 4f) (Awram 1970). More extreme, Carvell et al. (2008) observed nearly 79% of *B. terrestris* nests parasitized by *B. vestalis*, including about 92% parasitism in above-ground nests placed in oilseed rape fields. The highest rate of nest usurpation was observed by Pelletier and McNeil (2003) in Canada with almost 100% of *B. impatiens* Cresson colonies parasitized by *Bombus citrinus* (Smith) (Fig. 4g) in artificial nests placed above the ground. Parasitism of bumble bee colonies by *Psithyrus* can therefore be a locally common phenomenon and might have negative effects on host populations (Antonovics and Edwards 2011). *Psithyrus* populations may also follow typical predator–prey boom and bust cycles, which may promote high rates and unusual patterns of parasitism in boom years (Strange et al. 2014). On the other hand, *Psithyrus* abundance can be very low in environments that are a priori favorable (e.g., in the Pyrénées-Orientales, Iserbyt et al. 2008), without any explanations being found.

Physiological and Morphological Adaptations

Richards (1928) listed nearly 28 morphological and behavioral traits that separates *Psithyrus* from other bumble bees. Many of them are adaptations that allow cuckoo bumble bees to protect themselves against the attacks of host workers, including larger and stronger mandibles, fusion of the intersegmental membranes of the head, the thorax, and the abdomen, a strongly sclerotized and incurved abdomen, thicker sting with more powerful sting muscles, and an enlarged venom gland. *Psithyrus*, like many parasitic bees, also exhibit a reduction in setal pile on the abdomen, arguably a result of no longer needing the setae to gather pollen. The pollen baskets (corbiculae) of females have also been lost because of disuse, and instead exhibit a similar morphology to that of males. Williams (2008) documented that cuckoos and hosts are significantly more likely to share similar color patterns than would be expected by chance in Europe, but not in North America. This is most probably the result of convergence onto local color pattern complexes as a result of Müllerian mimicry rather than being a host–parasite evasion strategy. Given that bumble bees nest in dark cavities, coloration is not likely to play much of a role in recognition of conspecifics.

Females of *Psithyrus* are not always larger than the queens of the colonies they parasitize. These species present an important body size variability compared to other bumble bees. Plowright and Jay (1977) explain this great variability in *Psithyrus* size as a more plastic adaptation than their hosts to fluctuations in the quantities of food resources. The internal anatomy of *Psithyrus* has been very little studied. Fisher and Sampson (1992) showed that females of *Psithyrus* have an enlarged Dufour's gland, which is believed to produce chemicals that play a role in chemical evasion, and they are also known to have reduced but still functional wax glands (Sramkova et al. 2008, Franzini 2012), but no data show other missing or additional glands compared to other bumble bees. Females of *Psithyrus* also have more ovarioles per ovary than other bumble bees (Fisher and Sampson 1992, Richards 1994). They have 6–18 ovarioles per ovary depending on the species, compared to a fixed 4 in all other *Bombus* species (Cumber 1949), so there is also a great variability in the egg-laying potential in *Psithyrus*. The number of ovarioles per ovary is very plastic, varying within and between species, but also within one individual (Richards 1994). This adaptation may allow females of *Psithyrus* to quickly lay large quantities of eggs during initial takeover of the nest (Richards 1994). The plasticity in this trait may be an adaptive nutritional response, as larger females tend to develop more ovarioles (Richards 1994). Furthermore, it has been shown that egg cells of *Psithyrus* can contain three to four times more eggs than other bumble bees, with *Psithyrus* eggs being longer and thinner to maximize the number of eggs per egg cell (Virostek 1963).

Phenological Adaptations

Like their hosts, females of *Psithyrus* overwinter in the ground, usually in the same types of environments as the queens they parasitize (Frison 1926). However, they emerge from hibernation later than their hosts after which they spend most of their time feeding on nectar and pollen. Cuckoo bumble bees are easily recognizable in the field with their slower and less vigorous flight compared to other bumble bees (Alford 1975). This peculiarity is also at the origin of their name: *Psithyrus* comes from the Greek *Psithyros* which means 'whispering', and refers to the low frequency of their wings vibrations compared to other *Bombus* species (Haas 1967). Once their ovaries have developed enough, the cuckoo females start to look for a host nest. There is great variability among the cuckoo species in their phenology relative to their hosts. Some species (*B. bohemicus, B. suckleyi, B. fernaldae*, and *B. insularis*) emerge very shortly after their hosts (Sladen 1912, Hobbs 1967) while others (*B. rupestris, B. citrinus*, and *B. variabilis*) look for a host nest several weeks after the host queen emergence (Sladen 1912, Plath 1934, Webb 1961, Husband et al. 1980).

The stage of development of the host colony at the time of invasion varies significantly depending on the species of *Psithyrus*. For example, cuckoo females of *B. citrinus* were observed ~46 d after queens of the hosts *B. impatiens* and *B. vagans* Smith, whereas *B. ashtoni* females are observed ~17 d after *B. terricola* host queens and only 2 d after *B. affinis* host queens (Fisher 1984a). Females of *B. variabilis* on the other hand were observed 87 d after host nest initiation (Webb 1961). The European cuckoos *B. vestalis, B. bohemicus, Bombus campestris* (Panzer) (Fig. 4d) and *Bombus barbutellus* (Kirby) (Fig. 4e) (Sladen 1912, Fisher 1984a) and the North American cuckoo bumble bees *B. ashtoni, B. insularis, B. suckleyi*, and *B. fernaldae* (Hobbs et al. 1960; Hobbs 1965, 1968) appear to usurp host nests early after initiation. It is, however, very difficult to estimate precisely when *Psithyrus* females usurp a host nest, because of variability in colony initiation time and variability in search duration by the cuckoos.

Degrees of Host Specialization

Coevolution is a dynamic process whereby selection sometimes favors resource specialists and other times generalists. *Psithyrus* exhibit a continuum from highly specialized species on a single host (van Honk et al. 1981) to broad generalist species parasitizing hosts from different subgenera. The reasons explaining these important differences in host breadth are not clear but ecological constraints as well as physiological and phylogenetic constraints, are all likely to play an important role (Johnson et al. 2009, Poisot et al. 2011).

The level of specialization of a *Psithyrus* species is very difficult to estimate accurately. Host data have been obtained using information that ranges from speculative (correlation in geographic ranges), to suggestive (observing *Psithyrus* in a nest of another species; documenting usurpation potential in the lab), to definitive (behavioral observations of usurped nests collected from the wild). Bumble bee nests in nature are rare to encounter as can be *Psithyrus*, thus the number of observations in support of host choices is limited. Cuckoo bumble bees are thought to occasionally shelter in nests that they will not usurp, complicating the estimate of the number of hosts based on association alone. It is also very difficult to evaluate the degree of specialization of a *Psithyrus* species in the laboratory (Franzini 2013), as even if an inquiline is able to reproduce in the nest of a given host in controlled conditions, this might not be the case in nature. The timing of host nest initiation and reproduction may have been selected in part to counter social parasites (Richards 1975), thus certain species may not be parasitized in the wild even if they otherwise could serve as good hosts. As a result of these limitations, current host data are difficult to interpret. As demonstrated by Table 2, the breadth of hosts is heavily impacted by the types of data we interpret as reliable, as well as the number of host observations, which are few or none in some taxa (Table 2). In particular, most Asian species have few specimen records (Table 2) as several species tend to be rare and/or locally restricted to poorly studied montane areas.

Although speculative, from what can be tentatively inferred, there are some patterns to glean from *Psithyrus* host specificity. Many *Psithyrus* species may potentially usurp multiple species but have a tendency to be found in one possibly preferred host species ('semispecialists', Fig. 2; Fisher 1985). There are other species that have much broader but still phylogenetically-restricted preferences, found in many species within one clade ('semigeneralists', Fig. 2; Fisher 1983b). Some species appear to be much more obligate to a host species. Most notably, there appears to be more specialized parasitism of *B. terrestris* by *B. vestalis*. This is an interesting association to consider given that *B. terrestris* is common across its range but also exhibits larger colony sizes and arguably more sophisticated colony defense than other species. These traits in combination could have been important in driving this strict association. Finally, one species in particular, *B. insularis*, can be considered a broad generalist, as it has been found in nests of many species across the phylogeny (Williams et al. 2014).

Another trend that emerges is that closely related species of *Psithyrus* typically have closely related hosts. For example, the '*sylvestris*' group tend to parasitize *Pyrobombus* spp., although members tend to partition their specialization towards different preferred species. Similarly, the '*bohemicus*' group parasitizes *Bombus s.s.*, with different species affinity. However, host preferences can shift dramatically in a short period of time. This is best exemplified by the '*citrinus*' group, where very closely related species range from more strict specialization on *B. (Thoracobombus) pensylvanicus* in the cuckoo *B. variabilis*, to host preferences on several *Pyrobombus* species in *B. citrinus*, to the most generalized host breadth of all in *B. insularis*.

Brood care strategies among bumble bees are similar across the lineages (Sakagami 1976), thus it seems that most species should have the potential to be able to rear *Psithyrus* brood. Bumble bees are classically divided into two groups according to the way they store pollen and feed their larvae: pollen-storers and pocket-makers (Alford 1975). However, even this does not seem to be a limiting factor in *Psithyrus* brood rearing, as some bumble bees parasitize hosts belonging to both groups. Degree of specialization may be more related to the success rate of usurpation (Fisher 1985).

Chemical and Behavioral Adaptations

Cuckoo bumble bees have several barriers to overcome to parasitize their host and complete their life cycle. They must: 1) locate their host, 2) infiltrate the host colony, 3) integrate into their social system to gain access to the resources (food and workers), and 4) the parasitic offspring must also be accepted by the hosts during development and adult maturation. Different adaptations and strategies are used by *Psithyrus* to overcome each of these different barriers.

Host nest location and selection

Authors have long suggested that *Psithyrus* might be able to locate a host colony using chemicals produced by the host (Sladen 1912, Frison 1930). Plath (1934) noted that excavated nests of *B. bimaculatus* Cresson attracted cuckoo females of *B. citrinus*. Cederberg (1979, 1983) discovered that the cuckoo females of *B. rupestris* find the entrance to the nest of its host *B. lapidarius* using the scent trails left by the workers. Numerous studies have subsequently confirmed the important role of chemical signals left by hosts in nest location by *Psithyrus* (Fisher 1983b, 1985, Fisher et al. 1993, Bunk et al. 2010, Kreuter et al. 2012). The study by Bunk et al. (2010) found that the footprint deposited by a worker is species-specific since the *Psithyrus* female can differentiate the footprint left by a host from nonhosts. The chemical blend detected by *Psithyrus* seems also to vary with the degree of specialization of the parasite. The specialist *B. vestalis* detects a mixture of specific chemical compounds to recognize its host *B. terrestris* while the generalist cuckoo *B. bohemicus* detects only the hydrocarbons common to its three hosts (*B. terrestris, B. lucorum*, and *B. cryptarum*) (Kreuter et al. 2010). Interestingly, Strange et al. (2014) observed many attempts of the cuckoo *B. insularis* to enter honey bee hives, with 47 cuckoo females found dead in front of the colonies. The authors suggested that these could be failed attempts to rob hive resources or that high population densities of *B. insularis* could drive this species to attempt usurpation of new host species. Considering that *B. insularis* is a broad generalist, an alternative explanation could be that females are not able to discriminate nest odors of bumble bees from honey bees as they evolved to detect the compounds common to most bumble bees that may also be common with honey bees.

Once the nest is located, the *Psithyrus* females first assess the size of the host colony. If it is too big, the intruder will be quickly killed or rejected by the workers. If the colony is too small, there will not be enough workers to care for future parasitic larvae. *Psithyrus* females must therefore find the best compromise to maximize its potential reproductive success and minimize its chances of being killed during the invasion (Fisher 1984b, 1987b; Sramkova and Ayasse 2009). The inquiline female must therefore be able to estimate the nest quality (favorable host, stage of development, and nest size) using only information obtained outside or at the entrance of the nest, such as the input / output frequency of workers, their morphology (Cederberg 1983) and their chemical footprints (Wcislo 1986).

Initial host nest infiltration

Once the nest is chosen, the female must infiltrate the nest. This involves overcoming the barrier of recognition set up by the hosts. The response of host workers to the intruder varies within and between species. The workers of *B. pensylvanicus* have not been observed to attack *B. variabilis* parasitic females that enter their nest, regardless of the size of the colony (Webb 1961, Plath 1934). On the other hand, the workers of *B. impatiens* and *B. terrestris* fiercely attack the intruder, sacrificing several workers in the process (Plath 1934, van Honk et al. 1981). At the time of the nest entry, several workers flock to the parasitic female to form a mass around it, each trying to bite and sting the intruder, sometimes even killing each other during the brawl (van Honk et al. 1981, personal observation). Despite this, the death of the parasitic female is rare because they are heavily armored to resist the attacks of the workers (see chapter Physiological and Morphological adaptations).

The size of the host colony also has a huge impact on the infiltration success of the cuckoo bumble bee. Hoffer (1889) introduced cuckoo females of *B. campestris* and *B. rupestris* into host colonies of different sizes and showed that usurpation success increased significantly in small colonies and dropped to zero in colonies of more than 100 workers. Fisher (1984a) showed that in the absence of host workers the usurpation success of the cuckoo *B. citrinus* was

100% and decreased linearly to 20% when the number of workers increased to >40. Similarly in the cuckoo *B. vestalis*, the survival rate of females decreased from 100% when they enter colonies of five workers to 0% in colonies of 50 workers (Sramkova and Ayasse 2009). The same authors determined that under controlled conditions, the highest survival rate was in colonies of about 10–15 workers of *B. terrestris*. The size of the host colony that maximize cuckoo reproductive success might also depend on the ability of the social parasite to chemically control its host. For example, the cuckoo bumble bee *B. variabilis* is known to usurp only mature colonies of its host *B. pensylvanicus* and is hypothesized to invade them only when the host queen's dominance has faded (Webb 1961).

At the time of intrusion into a host colony, the female *Psithyrus* is generally recognized as alien and attacked. Most often the intruder adopts a discreet strategy to avoid contact with its guests and hides under the brood which gives them time to acquire the odor of the colony. As an alternative mechanism, Fisher (1984b) first hypothesized that some *Psithyrus* use allomones to prevent worker attack when entering the nest. This hypothesis was confirmed by Zimma et al. (2003) who showed that females of cuckoo *B. norvegicus* (Sparre-Schneider) protect themselves from host workers' attacks by secreting a repellent molecule, dodecyl acetate, produced by their Dufour's gland. This molecule is also found in *B. vestalis*, *B. bohemicus*, and *B. sylvestris*, where it could have a similar function (Martin et al. 2010).

Some species of *Psithyrus* have a more aggressive strategy and immediately attack any individual hostile to them. Those *Psithyrus* utilizing an aggressive strategy usually eliminate the queen host (e.g., *B. rupestris*, the inquiline of *B. lapidarius* [Sladen 1912, Plath 1934]). Some species have evolved resistance to minimize the impact of cuckoo aggressive behavior and reduce the risk of mortality. This is the case of queens and workers of *Bombus fervidus* (Fabricius) who react to the presence of a female *Psithyrus* by swallowing the provisions accumulated in the honey pots and regurgitating them on the body of the invader (Plath 1922). The parasitic female, stuck in honey, cannot fly away, and usually ends up dying as a consequence. However, it is not clear if this adaptation was selected specifically against *Psithyrus* or if it is used against any type of invaders.

Integration into the host social system

To recognize nestmates and reject intruders, bumble bees use a recognition system based on chemicals shared by all members of the colony. These chemical signals are largely based on cuticular hydrocarbons (CHCs) (Martin et al. 2010).

Psithyrus females have evolved different integration strategies to overcome host recognition systems. Some species, like *B. sylvestris*, use a strategy of chemical insignificance by producing very low amounts CHCs to remain undetectable (Dronnet et al. 2005). The female then acquires host recognition signals passively through contact with nest material and members of the colony, but possibly also actively through dominance behaviors. Such chemical camouflage allows the cuckoo female to avoid the barrier of recognition and thus suppress or reduce hostility of host workers (Fisher 1988, Küpper and Schwammberger 1995). The ability of *Psithyrus* to take over the odor of the nest seems to vary according to the host breadth of the cuckoo bumble bee. The specialist *B. vestalis* perfectly mimics the CHC profile of its host *B. terrestris* (Lückemeyer 2009), whereas the semigeneralist species *B. bohemicus* (parasitizes *Bombus s.s.*) only imperfectly mimics the CHC profile of its same host *B. terrestris* (Kreuter et al. 2012). These cuckoo species, as well as semispecialists *B. campestris* or *B. rupestris*, are likely to synthesize rather than merely passively acquire the recognition signals that mimic their host (Martin et al. 2010).

Most of the time, once integrated into the nest, the inquiline female eliminates the host queen (Sladen 1915, van Honk et al. 1981). There is, however, evidence of prolonged cohabitation with the queen, such as in observations by Hoffer (1889) of the cuckoo *B. campestris* hosted by *B. pascuorum* and those of Awram (1970) on the cuckoo *B. sylvestris* hosted by *B. pratorum*. Their studies showed that cohabitation could result in the production of sexuals of both host and parasite. The observations of Awram (1970) were later confirmed in the laboratory by Küpper and Schwammberger (1995) and Lhomme et al. (2013). Cases of peaceful coexistence between the host queen and the female parasite have also been observed in the cuckoo *B. variabilis* hosted by *B. pensylvanicus* (Webb 1961, Hobbs 1965).

Dominance and parental control

Once accepted as colony member, the cuckoo female usually tears apart the egg-cells of its host (Frison 1926, Plath 1934, Fisher 1987a) and feeds on the eggs and nest provisions. She also often ejects the young host larvae from the nest (Webb 1961). The need for space to lay eggs seems to be the main reason why the female *Psithyrus* destroys the brood of the host, although the cuckoo female can build new wax cells from scratch using nest debris (Plath 1922, personal observation). The destruction of eggs and young larvae might also increase the incubation effort of host workers towards the parasitic eggs. In colonies where the queens and *Psithyrus* female coexist, only eggs of the host queen laid after the first eggs of the female *Psithyrus* are destroyed by the latter (Küpper and Schwammberger 1995).

Since most inquiline females kill the host queen, they must signal their dominant status to keep host workers under control. Although studies on this are few, cuckoo females most likely control host worker reproduction the same way as the host queen (reviewed in Lhomme and Hines 2018). They inhibit worker reproduction and aggressiveness using a combination of aggressive behavior and production of chemicals that inhibit worker ovarian development (Fisher 1983b, Fisher 1984b, Vergara et al. 2003, Kreuter et al. 2012).

Psithyrus exhibit several aggressive behaviors to control workers. The buzzing behavior (wing muscle vibration) seems to be used to warn host workers of their dominant status (Fisher and Weary 1988). They also use 'mauling' behavior, when the female grips the host worker (Fisher 1988), and 'head rubbing' behavior, when the female rubs its head on the body of the worker (Fisher 1984a). According to Fisher (1983b, 1985), these behaviors may allow the female *Psithyrus* to transfer chemical signals that inhibit the host worker's aggression. Indeed, several studies show that *Psithyrus* females can suppress worker ovarian development, but only when they are in direct contact with them (Fisher 1983a, Vergara et al. 2003, Kreuter et al. 2012). The female *Psithyrus* may also use these behaviors to add its own chemical signals to each worker and thus change the smell of the colony, rather than adopting the odor profile of the host. These dominance behaviors are not observed in all *Psithyrus*. They are found mainly in species using an aggressive usurpation behavior, like in the European species *B. vestalis* (van Honk et al. 1981, Lhomme et al. 2013), *B. bohemicus* (Fisher 1988), and the American species *B. ashtoni* (Fisher 1983b, 1987a) and *B. citrinus* (Plath 1934, Fisher 1984a).

At the end of the cycle, it is not uncommon for *Psithyrus* females to lose their dominance in the face of the large number of egg-laying workers. They usually end up getting killed or ejected when the workers start to lay eggs (Fisher 1988). However, there is very little information on how long the female *Psithyrus* remains in the host nest. Hoffer (1889) and Plath (1934) believed that the cuckoo females remain in the host nest until their death, but Webb (1961) also observed females staying in the host nest just long enough to lay a few batches of eggs.

Adaptations of cuckoo offspring

The reason why host workers accept and care for brood of another species is an evolutionary puzzle. Surprisingly, this issue has received very little attention compared to cuckoo bumble bee invasion strategies. Cuckoo offspring also face the challenge of being tolerated and raised by the host workers. Whereas *Psithyrus* females usually infiltrate small colonies consisting of young, small, and mildly aggressive workers, their offspring are born in larger colonies of older and more aggressive workers that are in competition with the cuckoo for reproduction. No study to date has tested whether eggs or larvae of cuckoo bumble bees have evolved particular strategies to manipulate host worker feeding behavior or to avoid their discrimination abilities. Cuckoo females usually spend most of their time moving from one egg cell to another pushing workers away and sometimes mauling host workers if they attempt to open the egg cells (Fisher 1983b). However, once the cuckoo larvae hatch it seems that the cuckoo female tolerates host workers presence and lets them feed its larvae.

Kreuter et al. (2012) have shown that newly emerged gynes of the cuckoo bumble bee *B. bohemicus* exhibit a CHC profile that mimics egg-laying cuckoo females and host queens. Furthermore, young cuckoo males of *B. vestalis* have been shown to produce secretions that repel host workers, probably to reduce aggressive interactions (Lhomme et al. 2012, 2015). Lhomme et al. (2012) also showed that parasitized nests are more tolerant towards alien individuals, possibly due to a decrease of host worker recognition abilities that could facilitate cuckoo offspring acceptance, a pattern also found in *Polistes* social wasps (Lorenzi 2003).

Premating and Mating Behaviors

Voveikov (1953) noticed that unlike other bumble bees, once out of the host nest, the *Psithyrus* female does not return to the nest nor make orientation flights upon leaving it. Male *Psithyrus* exhibit patrolling behavior very much like other bumble bee males (Kullenberg 1973, Svensson 1979, Cederberg 1983), but can be recognized distinctly from their hosts during premating by different patrolling habitats and flight paths (Bringer 1973, Cederberg 1983) and clear differences in the composition of their marking pheromones (Cederberg 1983, Urbanova et al. 2004, Lhomme et al. 2012). Chemical marking pheromones are also distinct in two non-*Psithyrus* cuckoo bumble bees from their hosts (Brasero et al. 2018).

Mating behavior of cuckoo bumble bees is poorly documented, however Lhomme et al. (2013) noticed that the copulation time of hosts *B. terrestris* and *B. pratorum* was substantially longer than their respective cuckoos *B. vestalis* and *B. sylvestris* (~26 vs. ~3 min.). The long duration of copulation behavior in nonparasitic bumble bees is hypothesized to be due to an active role of males in facilitating sperm migration into the female spermatheca, potentially to form mating plugs or guard the mate (Djegham et al. 1994). Without further studies on bumble bee copulation behavior, it is difficult to explain such a large difference in copulation duration between parasitic and nonparasitic bumble bees. *Psithyrus* species also vary in sex ratios, with some strongly male-biased such as *B. sylvestris*, *B. vestalis* (Lhomme et al. 2013, Vergara et al. 2003), *B. insularis*, and *B. flavidus* (Lhomme and Hines, unpublished data), and others exhibiting a female-biased sex ratio such as *B. bohemicus* (Vergara et al. 2003), *B. ashtoni*, and *B. citrinus* (Fisher 1992).

Hibernation

Once mated, females will start to look for hibernation sites like other bumble bee species. It has been argued in bumble bees that the location of the hibernaculum can influence emergence time. Plath (1927), Bols (1939), and Alford (1969) dug up many species of bumble bees from their hibernaculum, including several *Psithyrus* species, and found no difference in hibernation sites (location and depth) between parasitic and nonparasitic bumble bees. Although hibernation in *Psithyrus* seems to be like that of any other bumble bee, they must have evolved certain traits enabling them to hibernate much longer, as certain cuckoo species hibernate almost a third longer than other bumble bees (Webb 1961).

Conclusion

Bumble bees not only exhibit multiple origins of social parasitism, but also contain the especially diverse obligately socially parasitic lineage, *Psithyrus*, thus they provide ample opportunity to understand how social parasitism has evolved and is maintained. We have provided a fairly comprehensive review of ecological and evolutionary traits in this lineage, highlighting among other things the patterns of host breadth, geographic range, behavioral and morphological innovations, and social evasion strategies utilized in this lineage to enable their varying success.

Although the patterns highlighted are intriguing, they are limited by a paucity of data. *Psithyrus*, as most parasites, are rare to encounter, thus the ecology of half of them is totally unknown, with no bumble bee host recorded (Table 2). The remaining species are also poorly understood relative to non-parasitic bumble bees. European species *Bombus vestalis*, *B. bohemicus*, and *B. sylvestris*, and North American species *B. citrinus* and *B. ashtoni*, are the only species that have been more thoroughly investigated in laboratory conditions, providing many of the valuable insights reviewed herein. There is also a gap of knowledge on basic taxonomy and phylogeny of cuckoo bumble bees. This is affecting our understanding of species delimitation in this group but also ultimately affects our conservation policy and decision-making concerning species protection.

Although some more generalized *Psithyrus* have acquired exceptionally broad geographic ranges, many *Psithyrus* depend on a single or a few host species and are much more geographically restricted. Because the cuckoos have smaller population sizes and depend on their host for survival, they are especially susceptible to extinction (Suhonen et al. 2015). Exemplifying this, two of the host specialist North American species have suffered substantial decline in the past two decades as a result of the decline of their host species. The need to understand this lineage better is thus altogether more pressing.

Cuckoo bumble bees, like cuckoo birds, are major models to better understand host–parasite antagonistic coevolution and the complex series of adaptations and counter-adaptions evolving in the process (Kilner and Langmore 2011). Bumble bee social parasites have provided, and continue to provide, perspective into a variety of research questions, such as on the evolution of insect sociality (Cini et al. 2015; Smith et al. 2015), social communication (Martin et al.

2010, Guillem et al. 2014), reproductive skew (Green et al. 2016), and reproductive dominance (Lhomme and Hines 2018). We hope that this review will stimulate interest in these species and promote further research to better understand the ecology and evolution of these social parasites.

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