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# The rarity of host species affects the co-extinction risk in socially parasitic bumblebee *Bombus* (*Psithyrus*) species

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In this study, we investigated whether social parasitic species would be more threatened than their host species. Cuckoo bumblebees *Bombus* (*Psithyrus*) (Hymenoptera: Apidae: Bombini) live in naturally-fragmented environments composed of host bumblebee (*Bombus*) colonies upon which they are exclusively dependent. We collected literature data on ten social parasitic cuckoo bumblebee species and their host bumblebee species in Europe. We found that cuckoo bumblebee species are more vulnerable to extinction than their hosts. When we controlled for the host species threat index, extinction risk was unexpectedly lower in specialist than generalist species. Finally, we showed a co-extinction risk of host bumblebee species and their social parasitic species — if a host species was threatened, the cuckoo bumblebee species was also threatened, and *vice versa*. Thus, to lessen the risk of extinction of social parasitic cuckoo bumblebees, it is important to conserve their bumblebee host species.

## Introduction

Co-extinction refers to the loss of one species as a result of the extinction of a species it depends upon (Koh *et al*. 2004, Altizer *et al*. 2007, Dunn *et al*. 2009). Theoretical models predict that parasites will decline or go extinct when host population sizes decreases below a critical threshold value (Lloyd-Smith *et al*. 2005, Altizer *et al*. 2007). In this study, we investigated whether social parasites are more vulnerable to extinction than their host species, whether specialist cuckoo bumblebee species are more vulnerable to extinction than host-generalist species, and whether there are co-extinction risks of social parasitic species and their main host species. We used social insects, bumblebees (*Bombus* spp.) and their social parasites, cuckoo bumblebees of the subgenus *Bombus* (*Psithyrus*) as the study objects. This study system is suitable for co-extinction and host–parasite extinction studies because cuckoo bumblebee species are obligate social parasites of bumblebees. Moreover, bumblebees are vulnerable to modern agricultural practices, introduced pathogens and pesticides, and many species are threatened (e.g., Kosior *et al*. 2007, Winfree *et al*. 2009, Williams & Osborne 2009, Cameron *et al*. 2011, Szabo *et al*. 2012).

Bumblebees are primitive eusocial insects, in which only the queen overwinters and colonies are built throughout the warm season (e.g. Goulson 2003, Benton 2006). Social-insect colony parasitism is a special case, where the parasite does not devour its host, but is dependent on the social organization of the host (e.g. Wilson 1971, Hölldobler & Wilson 1990). A social-insect colony typically consists of a queen, workers, future sexual males and new queens. Workers forage and care for offspring. They are important pollinators and any decline in numbers of species constitutes a significant threat to biological diversity, ecosystem function and worldwide economies (e.g., Kosior *et al*. 2007, Williams & Osborne 2009, Winfree 2010). Most bumblebees live in cold and seasonal habitats (Heinrich 1979). Typically, the colony is started in spring by a large fertile female (the queen), which was inseminated the previous autumn and hibernated underground during winter. Some bumblebee species nest underground, while others nest in tussocks or holes above ground, such as in hollow trees or in bird nest boxes (e.g., Macdonald & Nisbet 2006).

There are about thirty cuckoo bumblebee species globally and they all are obligate social parasites of bumblebee species (Williams 1998). Cuckoo bumblebees live in nests of naturally-fragmented host bumblebee species (Franks 1987). In general, most cuckoo bumblebee species parasitize only one host bumblebee species and only a few cuckoo bumblebee species have more than one host bumblebee species (Williams 2008, Lecocq *et al*. 2011). The life cycles of cuckoo bumblebees differ from that of its bumblebee host. Cuckoo bumblebees awake from winter dormancy later than the host bumblebee queens. When the host bumblebee queen has started its production of workers, the cuckoo bumblebee queen invades the bumblebee colony by using similar pheromones as its host (e.g. Franks 1987, Goulson 2003, Lecocq *et al*. 2011, Ayasse & Jarau 2014). Cuckoo bumblebees are exclusively dependent upon their bumblebee hosts because they lack pollen-collecting apparatus (corbiculae) and do not produce workers (e.g. Söderman & Leinonen 2003). Thus, the cuckoo bumblebee queen uses its host bumblebee colony's workforce to raise their purely sexual offspring. The rate of parasitism varies among host bumblebee species, but in most cases it is less than 50% (e.g., Erler & Lattorff 2010). The tolerance of cuckoo bumblebee species to their host species varies. Some cuckoo bumblebee species are queen-intolerant while others are queen-tolerant, and in some cases cuckoo bumblebee species rear offspring together with its host (e.g. Küpper & Schwammberger 1995, Brandt *et al*. 2005, Lhomme *et al*. 2013, Ayasse & Jarau 2014). Females and males of cuckoo bumblebees emerge in the autumn, and after mating, the males die and the females overwinter. Although both bumblebees and cuckoo bumblebees are widespread across Europe, several species are rare (*see* www.zoologie.umh.ac.be// hymenoptera/page.asp?ID=169).

Our goal was to analyse the extinction risk of parasitic species and their host species using data from publications of cuckoo bumblebees and their bumblebee hosts in Europe (Kosior *et al*. 2007, Williams 2008). Since cuckoo bumblebees are host-dependent, we defined the host bumblebee species as a resource for each cuckoo bumblebee species. In this study, we addressed the following three specific questions: (1) we studied whether parasitic cuckoo bumblebee species are more vulnerable to extinction than their common bumblebee hosts; (2) Whether specialist cuckoo bumblebee species are more vulnerable to extinction than host-generalist species (e.g. Dunn *et al*. 2009); and (3) whether host species and their parasite species display a co-extinction risk. In other words, if a host bumblebee species is threatened, so too is the cuckoo bumblebee species and *vice versa*.

## Material and methods

### The dataset

In this study, we re-analysed the Kosior *et al*. (2007) dataset. Because the evaluation criteria for threatened species changed, we did not include other data in our dataset. We extracted the data on ten cuckoo bumblebee species/subspecies that are classified as obligate workerless social parasites in Europe (Williams 2008). Recently *Bombus* (*Psithyrus*) *barbutellus* and

*B.* (*P.*) *maxillosus* were classified to conspecific taxa, but because both subspecies have different main host species (Lecocq *et al.* 2011), we used both subspecies as independent observations in our statistical analyses to increase statistical power. In total, our data consisted of ten cuckoo bumblebee species/subspecies and their most common host bumblebee species/subspecies (Table 1). To analyse extinction risk of specialists and generalists, we grouped cuckoo bumblebee species into two groups: (i) only one host species (hereafter specialist), and (ii) two or more hosts bumblebee species (generalist) (*see* Williams 2008 for hosts of cuckoo bumblebees). Our data included five specialist and five generalist cuckoo bumblebee species.

### Statistical analysis

In this study, we arcsin-square-root-transformed Kosior's threat index for our statistical analyses. For each bumblebee and cuckoo bumblebee species, an index of overall threat was calculated by dividing the number of countries (in total eleven countries) in which the species was listed in the Red List by the total number of countries in which the species was present. If the threat index was 0, the species did not occur in any of the Red lists in western and central European countries. On the other hand, if the threat index was 1, the species occurred in the Red List of all countries in which the species was present (*see* more details in Kosior *et al.* 2007). If certain cuckoo bumblebee species had more than one host species, we used the less vulnerable host bumblebee species' or subspecies' threat index. Moreover, if some cuckoo bumblebee species had two subspecies, we used the nominal subspecies' threat index.

We tested our hypothesis that cuckoo bumblebees were more threatened than their common host species with a paired *t*-test. Using a *t*-test, we analysed if specialist cuckoo bumblebee species (only one host) were more threatened than generalist cuckoo bumblebee species (two or more hosts). For these two subsets of data, the parasite–host threat index relationship had no significantly different slopes ($F_{1,6}$ = 0.30, $p$ = 0.605), allowing us to use analysis of covariance (ANCOVA). Using ANCOVA, we investigated specialist and generalist species extinction risks and the co-extinction risk (covariate, most common host-bumblebee species threat index) (Kosior *et al.* 2007). The analyses were performed with IBM SPSS for Windows (ver. 20.0).

## Results

The mean ± SD threat index in cuckoo bumblebee species (0.53 ± 0.30, $n$ = 10) was higher than in their common host bumblebee species (0.31 ± 30, $n$ = 10; paired *t*-test: $t_9$ = 2.76, $p$ = 0.022; Fig. 1). Specialist cuckoo bumblebee species were not more vulnerable to extinction (mean threat index 0.51 ± 0.29, $n$ = 5) than generalist cuckoo bumblebees (0.56 ± 0.34, $n$ = 5; *t*-test: $t_8$ = –0.46, $p$ = 0.659; Fig. 1). However, when we controlled for host extinction risk, generalist species had, unexpectedly, a higher risk of extinction than specialist species (ANCOVA: $F_{1,7}$ = 9.09, $p$ = 0.020; Fig 1). Moreover, there was a co-extinction risk between cuckoo bumblebee species and their main bumblebee host species (ANCOVA: $F_{1,7}$ = 15.58, $p$ = 0.006; Fig. 1). Therefore, if the bumblebee host species is threatened, its cuckoo bumblebee species is also threatened and *vice versa*.

## Discussion

Our study has three main results. First, cuckoo bumblebee species were more threatened than

**Table 1.** Ten European social parasite cuckoo bumblebee species/subspecies [*Bombus* (*Psithyrus*)] and their common host bumblebee species/subspecies (*Bombus*).

| Parasite cuckoo bumblebee species | Most common host bumblebee species |
|---|---|
| *Psithyrus barbutellus* | *Bombus hortorum* |
| *P. bohemicus* | *B. lucorum* |
| *P. campestris* | *B. pascuorum* |
| *P. f. flavidus* | *B. jonellus* |
| *P. maxillosus* | *B. r. ruderatus* |
| *P. norvegicus* | *B. hypnorum* |
| *P. q. quadricolor* | *B. soroeensis proteus* |
| *P. rupestris* | *B. pascuorum* |
| *P. sylvestris* | *B. pratorum* |
| *P. vestalis* | *B. terrestris* |

their primary host species because they are exclusively dependent upon their host. Second, specialist cuckoo bumblebee species were not more vulnerable to extinction than generalist cuckoo bumblebees. In fact, when we controlled for the host species threat index, extinction risk was lower in specialist species than in generalist species. Third, there was a co-extinction risk between bumblebee host species and their social parasitic cuckoo bumblebee species: host species and their parasite species extinction risks were positively correlated. There are at least two explanations for our main results: (i) reduced geographical ranges and population sizes of host species, and (ii) less genetic variation of parasite species than their hosts.

Overall, our results support the concept of a parasitic species being more vulnerable to extinction than its host species, also in the special case of social parasitism. This host–parasite extinction study is consistent with the metapopulation theory, which predicts that the more distant the host population is from other populations, the more challenged the parasite will be to colonise the population (Hanski 1999). In previous studies, it has been found that individuals in isolated edge populations harbour fewer parasites (Radomski *et al.* 1991, Brewer & Gaston 2003, Kaunisto *et al.* 2015). This may decrease the probability of persistence of the parasitic population in isolated and marginal populations. Our results are consistent with this, as risk of extinction of cuckoo bumblebee species was higher than that of their host bumblebee species.

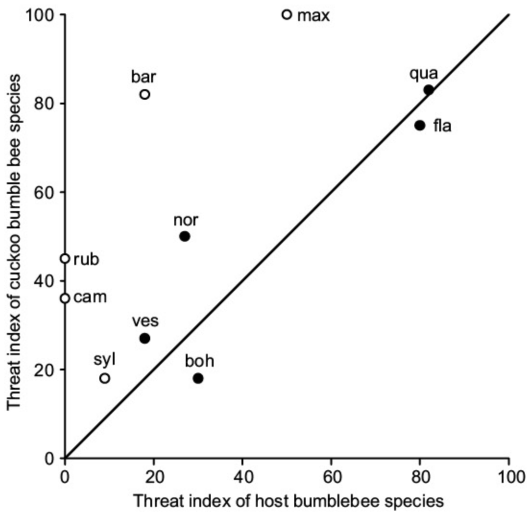


**Fig. 1.** The threat index of ten cuckoo bumblebee species/subspecies and their most common host bumblebee species/subspecies (Kosior *et al.* 2007) in western and central Europe. For the figure, we multiplied Kosior's threat index by 100 and it varied from 0 to 100, indicating low and high extinction risks, respectively. The continuous line is where the threat index is the same in both cuckoo bumblebee species and its most common host bumblebee species. The symbols indicate generalist cuckoo bumblebee species (at least two host bumblebee species, circles) and specialist cuckoo bumblebee species (one host bumblebee species, dots). Symbols above the line represent the situation in which the cuckoo bumblebee species have a higher extinction risk than its most common host bumblebee species and *vice versa*. Species abbreviations: bar = *Bombus* (*Psithyrus*) *barbutellus*, boh = *B.* (*P.*) *bohemicus*, cam = *B.* (*P.*) *campestris*, fla = *B.* (*P.*) *f. flavidus*, max = *B.* (*P.*) *maxillosus*, nor = *B.* (*P.*) *norvegicus*, qua = *B.* (*P.*) *q. quadricolor*, rup = *B.* (*P.*) *rupestris*, syl = *B.* (*P.*) *sylvestris*, and ves = *B.* (*P.*) *vestalis*.

There are also other explanations as to why parasitic species may be more vulnerable to extinction than host populations. Because social parasitic *Bombus* (*Psithyrus*) species parasitize only a subset of all available host colonies (e.g. Erler & Lattorff 2010), their population size should be lower than that of their host. It is a well-known phenomenon that small population size is a high-risk factor for local extinction. Moreover, small population sizes coupled with low dispersal rates may reduce genetic diversity as it was found in *B.* (*Psithyrus*) *vestalis* (Erler & Lattorff 2010). Due to lower dispersal rates and smaller population sizes, cuckoo bumblebee species may be more vulnerable to inbreeding and have reduced resistance against infections and diseases (Erler & Lattorff 2010). In addition, genetic variation was low in a declining host bumblebee species, which was also highly infected by a microsporidian pathogen *Nosema bombi* (Cameron *et al.* 2011). This would lead to local co-extinction vortices of both the host and their parasites as was found in the North American social parasite species *Bombus* (*Psithyrus*) *ashtoni* (Colla & Packer 2008) and both its host species *B. affinis* and *B. terricola* (Cameron *et al.* 2011).

Specialist cuckoo bumblebee species were not more vulnerable to extinction than generalists. In fact, when we controlled for host species threat index, we found that extinction risk was lower in the specialist species than the generalist species. This result disagrees with earlier observations and proposed ecological theory (e.g. Hughes *et al*. 2000, Harcourt *et al*. 2002; but *see* Suhonen *et al*. 2014) that with several sympatric host species, generalist cuckoo bumblebee species can shift to use alternative but closely related host species if its primary host's abundance and/or geographical range area decreases. Contrary to our prediction, specialist species had lower extinction risks than generalist species, probably due to the fact that the suitability of different host bumblebee species varied for generalist cuckoo bumblebees. Our results coincide with the predictions of source–sink theory (Pulliam 1988, Suhonen *et al*. 2010, 2014). So, it seems that different bumblebee host species form low and high quality habitat patches for parasites. However, in order to understand the risk of local population extinctions of parasites, future empirical and theoretical studies thus need to incorporate more detailed information regarding parasite host species requirements, including the quality of the host.

In our main finding, co-extinction refers to the loss of one species as a result of extinction of a species it depends on (Koh *et al*. 2004, Altizer *et al*. 2007, Dunn *et al*. 2009). Our results indicate that the extinction risk of a cuckoo bumblebee species is higher if its host bumblebee species is threatened. There are a number of reasons why several host bumblebee species have declined and have a high risk of extinction. Many bumblebee species are vulnerable to modern agricultural practices, introduced pathogens and pesticides, and thus, many species are threatened (e.g., Kosior *et al*. 2007, Winfree *et al*. 2009, Williams & Osborne 2009, Cameron *et al*. 2011, Szabo *et al*. 2012). For example, there are fewer nesting sites available in modern farmland than in the past (Goulson 2003, Goulson *et al*. 2008, Williams & Osborne 2009, Winfree 2010). In addition, the area of feeding habitat and the quality and quantity of food resources it provides have also decreased (Goulson *et al*. 2005, Fitzpatrick *et al*. 2007, Williams & Osborne 2009, Redpath *et al*. 2010, Winfree 2010). All of these reasons would cause a decline in host population size and its geographical range would decrease as well. Because many bumblebee species are threatened, their social parasites are threatened as well. More support for our co-extinction hypothesis comes from a North American social parasite species *Bombus* (*Psithyrus*) *ashtoni* that strongly declined in recent decades. It seems that this social parasite species was extinct at least in the eastern part of North America (Colla & Packer 2008). The most plausible explanation for its extinction seems to be that both previously widespread host species *B. affinis* and *B. terricola* (Williams 2008) have declined considerably (Colla & Packer 2008, Grixti *et al*. 2009, Williams & Osborne 2009, Cameron *et al*. 2011). On the other hand, in Europe the social parasite *Bombus* (*Psithyrus*) *vestalis* may be increasing its population size and geographical range because the population size and geographical range of its main host, *B. terrestris*, is stable or is slightly expanding (e.g. Williams *et al*. 2009).

In fact, it has generally been found that host distribution affects the distribution of species that are host-dependent (Koizumi *et al*. 1999, Magagula & Samways 2001, Koh *et al*. 2004, Altizer *et al*. 2007, Dunn *et al*. 2009). Our results reflect previous studies and ecological theory (e.g. Purvis *et al*. 2000a, 2000b, Harcourt *et al*. 2002, Dunn *et al*. 2009). The logic behind co-extinction risk in host–parasite systems is certainly reasonable. The carrying capacity and extinction risk of a parasite population may be largely dependent on the dynamics of their host species (Altizer *et al*. 2007, Dunn *et al*. 2009). A species' local abundance has been found to increase with an increase in its geographical range area (e.g. Brown 1984). If the host bumblebee species' range or abundance decreases, then cuckoo bumblebees would also decrease, because they are exclusively dependent upon their bumblebee hosts. This is due to the fact that it may be more difficult for cuckoo bumblebees to find a particular bumblebee host if its abundance and geographical range decreases. On the other hand, species with broad habitat tolerances are more likely to persist than those with narrow habitat requirements.

Theoretical models predict that parasites and diseases will decline or become extinct when the host population size decreases below a critical threshold density (*see* review in Lloyd-Smith *et al*. 2005). As a result of small or decreased host population size, many parasitic species, which live uniquely on threatened host species, are expected to go extinct long before their specific hosts (e.g. Altizer *et al*. 2007, Dunn *et al*. 2009). For example, the most threatened species have small geographical ranges and narrow habitat requirements and they are highly sensitive to environmental changes (*see* Owens & Bennett 2000, Purvis *et al*. 2000a, 2000b). Rapid environmental changes probably lead to high local extinction risks, which may ultimately lead to the loss of species in certain areas. The long-term survival of cuckoo bumblebee populations depends on the distribution of host bumblebee species, because the hosts provide a critical resource for that particular socially parasitic species. In a previous study, it has been found that the geographical ranges of parasite cuckoo bumblebee species are more limited than their bumblebee host species geographical ranges (Antonovics & Edwards 2011).

To conclude, parasites are more vulnerable than their hosts, and this seems to be true also in the case of social parasites. Thus, to lessen the risk of extinction of socially parasitic cuckoo bumblebees, it is important to conserve their bumblebee host species. In addition, this recommendation is likely useful in the conservation of other rare specialist social parasites. Moreover, our results provide more information on the correlation between host and parasite extinction risk. However, long-term datasets and more up-to-date information from larger geographical areas are required to provide more insightful data to understand proximate and ultimate reasons for the risks of extinction of hosts and their parasites.

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