

Bumblebee Vulnerability: Common Correlates of Winners and Losers across Three Continents

PAUL WILLIAMS,* SHEILA COLLA,† AND ZHENGHUA XIE‡

*Department of Entomology, The Natural History Museum, Cromwell Road, South Kensington, London SW7 5BD, United Kingdom
email paw@nhm.ac.uk

†Department of Biology, York University, 4700 Keele Street, Toronto, Ontario M3J 1P3, Canada

‡Laboratory for Biodiversity and Environmental Studies, Department of Environment, Sichuan University, Moziqiao, Chengdu 610065, Sichuan, China

Abstract: *It is widely agreed that in many parts of the world some bumblebee (Bombus) species have declined, and that this has often been driven by land-use changes that cause reductions in the abundance of food plants. There is much less agreement about how changes in food plants affect some bumblebee species more than others. We sought to identify which species' characteristics are generally associated with the relative winners and losers by comparing the 3 independent bumblebee faunas from parts of Britain, Canada, and China. Using available survey data, we assessed species characteristics, including competition with congeners, climatic specialization, proximity to climatic range edge, food specialization, phenology, body size, and range size. Results of our meta-analysis of correlations showed support for the hypotheses that decline susceptibility is generally greater for species that have greater climatic specialization, for species in areas where they occur closest to the edges of their climatic ranges, and for species that have queens that become active later in the year. The latter characteristic may render a species at a particular disadvantage when they have long colony cycles if there are losses of food plants in mid to late colony development.*

Keywords: *Bombus*, climate specialization, community structure, faunal change, pollinator decline, species assemblages, species competition, species' vulnerability

Vulnerabilidad de Abejorros: Correlaciones Comunes de Ganadores y Perdedores en Tres Continentes

Resumen: *Es ampliamente aceptado que en muchas partes del mundo algunas especies de abejorro (Bombus) han declinado y que esto a menudo se debe a cambios de uso de suelo que causan reducciones en la abundancia de plantas que le proporcionan alimento. Hay mucho menos acuerdo sobre cómo los cambios en las plantas afectan más a algunas especies de abejorro que a otras. Buscamos identificar las características que están generalmente asociadas con los ganadores y perdedores mediante la comparación de tres faunas independientes de abejorros de partes de Bretaña, Canadá y China. Utilizando datos disponibles, evaluamos las características de las especies, incluyendo la competencia con congéneres; especialización climática; cercanía al borde del rango climático; especialización alimenticia; fenología; tamaño corporal y rango de tamaño. Los resultados de los meta-análisis de correlaciones mostró soporte a la hipótesis de que la susceptibilidad a la declinación generalmente es mayor en especies que tienen mayor especialización climática; en especies en áreas cercanas al borde de sus rangos climáticos y en especies que tienen reinas que se volvieron activas hacia el final del año. Esta última característica puede constituir una desventaja particular cuando tienen ciclos coloniales largos si hay pérdida de plantas hacia la mitad o final del desarrollo de la colonia.*

Palabras Clave: *Bombus*, cambio de fauna, competencia de especies, declinación de polinizadores, ensambles de especies, especialización climática, estructura de la comunidad, vulnerabilidad de especies

Introduction

Bumblebees (*Bombus*) provide a pollination service that is essential for the sustainability and conservation of natural ecosystems and for multibillion-dollar industries producing commercial crops, including tomatoes, tree fruits, and berries (Dias et al. 1999). It is widely agreed that some bumblebee species have declined in local abundance and in geographical range extent and that this decline has often been driven by land-use changes, especially those that reduce the abundance of preferred food plants and thereby reduce and fragment suitable habitat in Europe (e.g., Williams 1986; Rasmont & Mersch 1988; Kosior et al. 2007), North America (Hines & Hendrix 2005; Gixti et al. 2008), and Asia (Yang 1999; Xie et al. 2008). Recent reviews (Evans et al. 2008; Goulson et al. 2008; Williams & Osborne 2009) emphasize that other factors may also be important, especially pathogens for a few species in North America (e.g., Thorp & Shepherd 2005; Colla et al. 2006; Winter et al. 2006). But whereas land-use changes are thought to be one of the most consistent drivers of declines worldwide, there is much less agreement on how these threats affect some species more than others. As a starting point, we assumed that some threats are broadly similar for most species in bumblebee assemblages, so that the different vulnerabilities of species (measured as declines) are the results of different susceptibilities among species. We sought to identify which characteristics of bumblebee species are generally associated with greater susceptibility to these environmental threats.

Many authors suggest species characteristics they believe are associated with greater susceptibility to decline and extinction (e.g., McKinney 1997; IUCN 2001; Cooper et al. 2008). Among the principal themes for these characteristics are specialization, large body size, and small geographic range size. Nevertheless, these themes are derived from results of studies of vertebrates. For bumblebees there have been other more specific suggestions, which are outlined below.

Close Competitors for Food

During the 1970s and early 1980s, the prevailing paradigm for what governs the presence of particular bumblebee species at a site was competition for food (e.g., Inouye 1977; Ranta 1982). Competition had been demonstrated in the field by competitor-removal manipulations (e.g., Inouye 1978; Plowright & Rodd 1980; Pleasants 1981). Patterns of food-gathering behavior were shown to be governed for bumblebees by their relative tongue lengths, both directly when foraging for nectar (e.g., Brian 1957; Ranta 1984; Inoue & Yokoyama 2006) and indirectly when foraging for pollen (Prys-Jones & Corbet 1987), so that tongue length governs overlap in food use among bumblebee species (e.g., Ranta & Lundberg 1981; Hanski 1982b; Williams 1985). Nonetheless, in the

most direct tests of the effects of this theory on local selective species extirpations, no support was found for food-based competitive exclusion having resulted in a predictable pattern of regular tongue-length spacing within either British or North American assemblages of bumblebee species (Simberloff & Boecklen 1981; Williams 1988).

Climatic Specialization

Williams and colleagues (Williams 1985, 1988, 2005; Williams et al. 2007), in studies of bumblebee declines in Britain, argue on the basis of the idea of climatic niche (constrained by physiological tolerances) that bumblebee species may be most susceptible to reductions in food availability when they have small (specialized) climatic ranges. Analyses of coarse-scale distribution data (e.g., Fig. 1) showed that susceptibility is related inversely to the size of species' European distribution ranges when adjusted for climate for British bumblebee data (Williams 2005) but not for Irish bumblebee data (Fitzpatrick et al. 2007). An improved analysis of more recent and finer-scale (50 × 50 km grid) data for European distributions appears to confirm, at least for 3 British and Irish species, that susceptibility is greater for species that have narrower ranges within a European climatic space (Williams et al. 2007).

Proximity to Edge of Climatic Range

Williams and colleagues (Williams 1985, 1988, 2005; Williams et al. 2007) also propose that bumblebee species may be most susceptible in places where they are proportionately farthest from their climatic optima and closest to their climatic range edges. Initial analyses of coarse-scale data (e.g., Fig. 1) showed no support for this in Britain (Williams 2005) or Ireland (Fitzpatrick et al. 2007). Again, an analysis of finer-scale (50 × 50 km grid) data for European distributions appears to confirm for 3 British species that susceptibility is greater for species in areas farther from the centers of their climatic ranges (Williams et al. 2007).

Food Specialization

Rasmont (1988) and Rasmont and Mersch (1988) studied bumblebee declines in Belgium and France and proposed that rarity and susceptibility are associated with specialization in relatively few food-plant families and species. A similar relationship is suggested for British bumblebees by Goulson and Darvill (2004). Unfortunately, these studies have methodological problems. First, to make valid comparisons of diet breadth, all the included bumblebees must have access to the same range of food-plant choices, a condition not met by these studies, in which data from sites with very different food-plant floras were combined (Williams 2005). Second, it is possible that what appears to be a pattern of rarity (and correlated

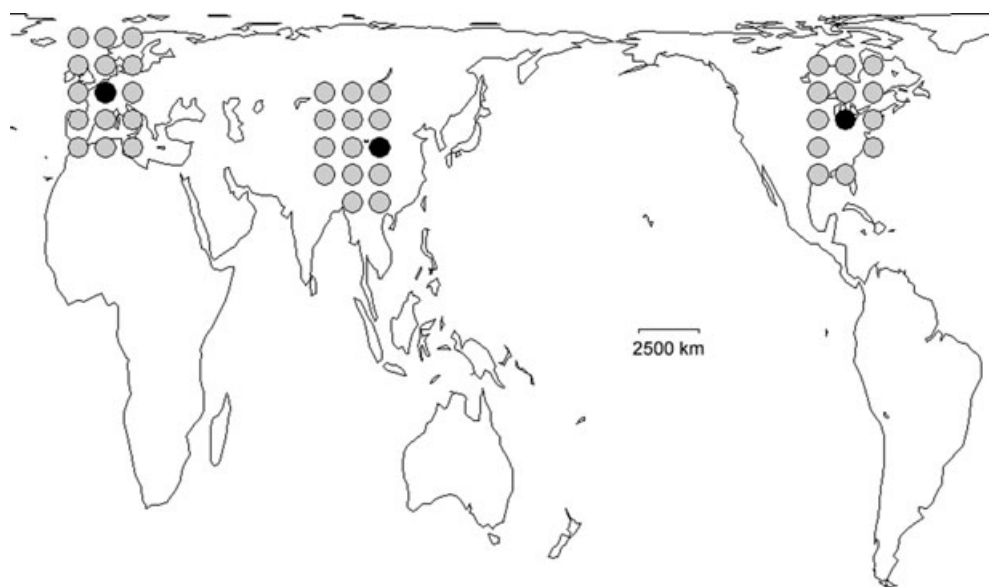


Figure 1. Map of the world, excluding Antarctica, showing coarse-scale equal-area grid cells (area of each approximately 611,000 km²) for counting ranges of bumblebees (Williams 1998). Cells in Britain containing Dungeness (left), in China containing Hongyuan (center), and in Canada containing Guelph (right) are black circles. Neighborhoods of occupied cells selected to provide as far as possible comparable elevational zones for estimating regional ranges and latitudinal range-edge proximity are gray circles. Cells are defined by intervals of 10° longitude (Europe 10°W to 20°E, Asia 80°E to 110°E, North America 100°W to 70°W) and by varying intervals of latitude ranging across 7 rows of cells (20°14', 25°36', 31°13', 37°12', 43°41', 51°00', 59°41', 71°44'N). Cylindrical equal-area projection (the scale bar applies only at the equator).

decline) associated with food specialization may manifest itself in flower-visitation data merely as an artifact of the different numbers of observations available for the different bumblebee species (Williams 1989a). This potential artifact and its correction were demonstrated with British data, and the specialization–decline relationship for data standardized for sample size was then rejected for Britain (Williams 2005) and Ireland (Fitzpatrick et al. 2007). Nevertheless, it is possible there are differences between specialization in nectar and pollen (Kleijn & Raemakers 2008). But if specialization were demonstrated to be associated with susceptibility, then it would also need to be shown whether specialization was a cause or effect of susceptibility.

Specialization in Deep Flowers

Rasmont et al. (2005) and Goulson et al. (2005, 2006, 2008) took Rasmont's (1988) idea further and proposed that the most susceptible bumblebee species have the most specialized diets because they have the longest tongues. Long tongues and apparently narrow diets had been shown to be associated (Prys-Jones 1982; Prys-Jones & Corbet 1987; Rasmont 1988). Nevertheless, when the only suitable, large data set for many species at one homogeneous site in Britain was analyzed with sample sizes standardized among species, susceptibility for

British bumblebees was shown to be unrelated either to tongue length or to diet breadth (Williams 2005).

Late Commencement of Annual Activity

Edwards and Williams (2004) emphasize the observation that the more susceptible species in Britain begin activity later in the summer. They propose that this could give the later species an advantage in some areas where there is a poor early food-plant flora (as in some grasslands). The later bumblebee species may avoid the problem of the lack of early food plants, whereas for the earlier bumblebee species this lack of food plants may constrain their colony growth, thereby reducing their competitive effect on the later bumblebee species later in the year. The idea is only likely to apply in situations where there is a rich food-plant flora later in the season, otherwise all bumblebee species would be expected to suffer reductions. (For another interpretation, see the Discussion.) This correlation is supported for British and Irish bumblebees (Fitzpatrick et al. 2007).

Here we tested for a relationship between each of the factors above and bumblebee susceptibility. We examined the independent bumblebee faunas from Europe (Britain, Dungeness), North America (Canada, Guelph), and Asia (China, Hongyuan). The only overlap between these faunas is that *Bombus humilis* is shared between Britain and Sichuan (Table 1). Testing independent

Table 1. Data for measures of decline and for characteristics that have been suggested to be associated with species' susceptibility.

Species	Decline measure ^a (transformed proportion)	Distance to nearest species' tongue length ^a (transformed proportion)	Regional range size ^{a,b} (transformed proportion)	Latitudinal range-edge proximity ^{a,b} (transformed proportion)	Dietary breadth standardized by rarefaction (no. of plant species/9 visits)	Worker mean tongue length (ln/mm)	Date of early segment of queen records ^c (no. of days into year)	Worker mean body length (ln/mm)	Global range size (ln [no. of cells])
Britain (Dungeness)									
<i>Bombus cullumanus</i>	3.142	—	1.504	1.231	—	—	—	2.485	3.40
<i>B. subterraneus</i>	2.056	0.244	2.056	1.571	—	2.17	193.8	2.515	3.43
<i>B. distinguendus</i>	1.909	0.236	1.772	0.000	—	2.16	—	2.689	3.85
<i>B. soroeensis</i>	1.479	0.231	2.394	1.911	—	1.91	—	2.385	3.61
<i>B. ruderatus</i>	1.416	0.818	2.056	1.571	3.25	2.36	163.8	2.562	2.89
<i>B. humilis</i>	1.270	0.290	2.056	1.571	4.19	2.10	172.0	2.358	3.74
<i>B. sylvarum</i>	1.266	0.188	1.911	1.571	5.02	2.07	170.5	2.359	3.18
<i>B. ruderarius</i>	0.905	0.187	2.214	1.911	4.25	2.08	159.5	2.449	3.30
<i>B. muscorum</i>	0.837	0.279	2.214	1.571	—	2.05	179.8	2.436	4.01
<i>B. monticola</i>	0.815	0.243	2.056	1.571	—	2.01	—	2.416	2.71
<i>B. jonellus</i>	0.784	0.693	1.911	0.841	3.06	1.79	200.0	2.298	4.14
<i>B. lapidarius</i>	0.729	0.295	2.394	1.911	2.52	1.94	165.0	2.424	3.26
<i>B. terrestris</i>	0.269	0.241	2.394	1.911	1.79	2.03	156.5	2.508	3.66
<i>B. hortorum</i>	0.168	0.757	2.394	1.911	3.46	2.51	192.5	2.637	3.99
<i>B. pascuorum</i>	0.000	0.238	2.394	2.301	4.77	2.14	179.0	2.385	4.09
<i>B. pratorum</i>	0.000	0.292	2.056	1.571	3.13	1.96	148.5	2.337	3.58
<i>B. lucorum</i>	0.000	0.233	2.214	1.571	3.51	1.90	117.0	2.467	4.51
Canada (Guelph)									
<i>B. affinis</i>	0.797	0.487	1.648	0.000	4.23	1.93	145.4	2.464	1.95
<i>B. fervidus</i>	0.640	0.091	1.494	0.000	4.67	2.27	159.7	2.458	3.22
<i>B. vagans</i>	0.417	0.451	1.804	0.000	5.34	2.08	157.0	2.308	3.00
<i>B. pennsylvanicus</i>	0.367	0.091	2.139	1.571	—	2.27	162.2	2.628	3.18
<i>B. terricola</i>	0.319	0.559	2.139	1.047	5.19	1.84	122.1	2.392	3.50
<i>B. borealis</i>	0.045	0.290	1.804	0.000	—	2.15	173.0	2.559	2.71
<i>B. perplexus</i>	-0.008	0.295	1.804	0.000	4.19	2.01	140.4	2.394	2.89
<i>B. griseocollis</i>	-0.066	0.309	1.804	1.571	4.73	2.03	154.2	2.565	2.71
<i>B. ternarius</i>	-0.132	0.450	1.648	0.000	—	1.76	131.0	2.310	2.71
<i>B. rufocinctus</i>	-0.155	0.462	1.494	0.000	—	1.71	169.0	2.280	3.22
<i>B. bimaculatus</i>	-0.488	0.293	2.139	1.571	4.66	2.13	116.2	2.495	2.40
<i>B. impatiens</i>	-0.646	0.298	2.139	1.571	4.30	1.98	146.0	2.467	2.48
China (Hongyuan)									
<i>B. humilis</i>	0.674	0.234	1.281	0.000	3.13	2.032	206.3	2.262	3.74
<i>B. filchnerae</i>	0.434	0.164	1.427	0.000	3.38	2.117	203.0	2.434	2.30
<i>B. supremus</i>	0.232	0.733	1.128	0.000	4.00	2.430	202.5	2.667	1.39
<i>B. lemniscatus</i>	0.195	0.465	1.427	0.000	—	1.834	197.5	2.280	2.20
<i>B. laesus</i>	0.062	0.106	1.427	0.000	—	1.913	202.3	2.453	3.74
<i>B. waltoni</i>	0.060	0.265	1.281	0.000	—	2.275	204.5	2.308	1.61
<i>B. impetuosus</i>	-0.009	0.373	1.427	0.000	3.64	2.084	192.5	2.332	1.79
<i>B. sicbelii</i>	-0.125	0.311	1.128	0.000	—	1.886	199.0	2.347	3.71
<i>B. patagiatus</i>	-0.157	0.106	2.014	1.369	—	1.910	194.8	2.573	3.58
<i>B. kashmirensis</i>	-0.168	0.469	1.571	0.841	—	1.979	195.0	2.434	2.20
<i>B. convexus</i>	-0.249	0.263	1.128	0.000	—	2.292	189.0	2.298	1.39
<i>B. rufofasciatus</i>	-0.409	0.164	1.427	0.841	—	2.124	206.0	2.538	2.08
<i>B. friseanus</i>	-0.662	0.232	1.427	0.000	4.00	2.045	192.5	2.433	1.79

^aNegative decline values represent relative increases; proportion data for decline measures and for the first three predictor variables are transformed by twice the arcsine of the square-root (Draper & Smith 1998).

^bWith adjustments for comparable elevations (see Methods).

^cUsing the threshold to the earliest 20% of the records for Canada and to the earliest 25% for Britain and China; accepting records only for >3000 m elevation for Sichuan.

faunas is advantageous because it informs us about susceptibility among bumblebees in general, rather than replicating studies across, for example, Europe, which only informs us about susceptibility within one particular set of species. In all 3 regions, bumblebee-species assemblages have declined in species richness and abundance (Williams 1986; Colla & Packer 2008; Xie et al. 2008).

Methods

Measuring Susceptibility and Decline

We measured susceptibility from the relative declines of bumblebee species, either in their frequency of occurrence or in their abundance. For Britain we measured declines as recorded by the Bumblebee Distribution Maps Scheme (Alford 1980) between species' geographical

ranges before and after 1960, a time of rapid decline (Williams 1986). Declines were measured as the decrease in frequency of 50×50 km grid cell occupancy relative to the starting occupancy (i.e., proportional change in regional range, following Williams 2005). For Canada we measured declines between 2 surveys of sites near Guelph in Ontario (1971–1973 and 2004–2006) by Macfarlane (1974) and by Colla and Packer (2008). They were measured as the change between time periods in proportional abundance relative to the total sample in each period. This was necessary because the sampling effort could not be standardized between the 2 surveys. For China we measured declines between spatially separated but simultaneous summer-ungrazed and summer-grazed rangeland transects near Hongyuan in Sichuan surveyed by Xie et al. (2008). This formulation of the measure followed that used for Canada to facilitate comparison. Doubts have been expressed regarding comparing the results of surveys made at different spatial and temporal scales (e.g., Braithwaite et al. 2006). Our data were collected in different ways in different regions: temporal versus geographical comparisons, frequency of occupancy among sites versus abundance at sites, and 50×50 km grid cells versus 100×2 m transects. Nevertheless, these measures are in each case correlated for bumblebees, at least within Europe (Hanski 1982a; Williams 1985).

Close Competitors for Food

If species experience interspecific competition for food of sufficient intensity to cause selective local extirpations, then this competitive pressure should be inversely related to the distance between the species along what from available evidence is the principal resource axis (flower depth). For a bumblebee species, this can be measured as the distance between its tongue length and the tongue length of the most similar species at the same site. This distance was expressed as a proportion of the species' tongue length because it is the proportional difference in length that is important for competition (Hutchinson 1959). For Britain tongue-length measurements were those compiled in Williams (1985), mostly from Medler (1962a, b), as the combined lengths of prementum and glossa. For Canada tongue-length measurements were taken from Medler (1962b). For China we measured tongue lengths for 15 workers of each species.

Climatic Specialization

The breadth of the climatic niche of a species might be expected to be related broadly to its total geographic range size. The range size of a species was measured as a count of the large equal-area grid cells (each approximately $611,000 \text{ km}^2$) occupied by all historical indigenous records (Williams 1998). Ideally this range size would be measured only among areas at similar elevations to the study sites. But in practice, total geographic range

size might be confounded as a measure of climatic niche breadth in 2 ways because simple latitudinal climatic gradients are complicated by high mountain ranges and by deserts. First, nearer the equator, mountains may act as conduits, extending the ranges of some species southward at high elevations (e.g., southern Appalachians, Himalaya). Second, farther north, mountains or deserts may act as barriers to dispersal, especially when they run from north to south and constrain some longitudinal ranges (e.g., Urals, Rockies). Therefore, the latitudinal extent of the part of the range within the continental region neighboring the study area should be a better indication of climatic niche breadth (1) because regional range can be more easily adjusted to allow for the elevational complications to climate caused by mountains and (2) because it is less likely to be complicated by barriers to longitudinal dispersal (Williams 2005).

We measured this latitudinal range within a window of 3 columns of 5 large, equal-area grid cells (Fig. 1). European range size was measured for 3 complete columns of 5 grid cells spanning Dungeness (Fig. 1). We measured eastern North American range size for 3 columns of 5 grid cells spanning Guelph, but excluded one cell that contained nothing but ocean and one cell with the southern Appalachians (because several species extend along this north-south mountain range into the south only in the high mountains and not at comparable low elevations; Fig. 1). We measured Asian range size for 3 columns of 5 grid cells extending westward from Hongyuan, but excluded one cell in lowland India with no bumblebees (a westward span from Hongyuan was chosen to increase the comparability of the high-elevation [3500 m] habitat around Hongyuan with high-elevation habitats across the Tibetan plateau, Fig. 1; Williams et al. 2009).

Proximity to Edge of Climatic Range

We expected proximity of a study area to the edge of a species' climatic niche to be related to the closeness of that area to a latitudinal range edge. Just as for our hypothesis for climatic specialization, we measured latitudinal ranges within a window of large, equal-area grid cells (Fig. 1). We measured range-edge proximity for a species from the n occupied cells out of the total of N accepted cells in the 2 rows north of each focal (black) cell in Fig. 1 and the s occupied cells out of a total of S accepted cells in the 2 rows south of each focal (black) cell as the minimum of $(n/N, s/S)$. Therefore, a species with a latitudinal range edge at the focal cell scored zero, and a species without a range edge within the window scored one.

Food Specialization

We measured food specialization as the inverse of dietary breadth for worker bumblebees. We used rarefaction to estimate the number of food-plant species and families

expected to be visited by a bumblebee species for a standardized number of flower visits (Williams 2005). For Britain we used data on from one site (Dungeness) from Williams (1989b) to measure dietary breadth. Dungeness has the only large British data set from one homogeneous site in which many predecline species were co-occurring. For Canada we measured dietary breadth with data from several predecline sites (but most data from one site and all sites shared the same food-plant flora) from Macfarlane (1974). For China we measured dietary breadth with data from multiple predecline transects that shared the same food-plant flora (Xie et al. 2008).

Specialization in Deep Flowers

We measured tongue length with data for workers because workers gather most of the food for colonies (Heinrich 1979). Mean tongue length was logarithmically transformed because it is the proportional differences in length that are important (Hutchinson 1959).

Late Commencement of Annual Activity

We measured the timing of the beginning of annual activity from the day of the year corresponding to an early segment of spring-queen records for each species. For Britain we used the day of the year corresponding to the end of the early quartile (25%) of queen records for each species in data for Dungeness from Williams (1989b). For Canada data have been published only for the date of the end of the early 20% of queen records for each species (Macfarlane 1974). For China we measured the beginning of annual activity as the end of the early quartile of queen records, but including only records from above 3000 m within Sichuan (data from Williams et al. 2009). An elevational threshold was applied to avoid the effects of a trend toward earlier activity at lower elevations found for some bumblebee species in Sichuan (Williams et al. 2009), which would be unrepresentative of Hongyuan (at 3500 m).

Large Body Size

We used data for workers because they are the majority of the foragers for the colony in summer. We measured body lengths (from the anterior margin of the vertex of the head to the posterior margin of metasomal tergum 6 from the lateral aspect) for 15 workers of each species. Mean body lengths were logarithmically transformed.

Small Geographic Range Size

We measured global range size of a species as a count of the large, equal-area grid cells (each approximately 611,000 km²) occupied by all historical indigenous records (Williams 1998).

We transformed the proportion data (Table 1) and calculated correlation coefficients (Table 2). We measured

the strength of the common effect of each predictor across regions (Table 2) from a meta-analysis of these correlations (with CMA2 software; Borenstein et al. 2008). Meta-analysis is used widely in ecology to combine evidence from standardized statistics, such as correlation coefficients across any number of studies while taking into account the sizes of those studies (Gurevitch et al. 2001). Because in this case the number of regional studies was small, we used the fixed-effect model, and heterogeneity among studies could not be assessed with precision (Borenstein et al. 2007).

Results

Significant correlations from the meta-analysis across the 3 regions (Table 2) supported the hypotheses that among bumblebee species greater susceptibility is generally associated with (1) narrow climatic specialization, (2) localities where species are closer to the edges of their climatic tolerances, and (3) species with queens that begin activity later in the year. The results for the specialization hypothesis were not significant, irrespective of whether specialization was measured among plant species (Table 2) or among plant families ($r = -0.041$, $p = 0.44$, threshold 0.04). The statistical significances of the common effects were unchanged if the smaller Chinese sample was excluded, except that the effect of a late commencement of annual activity was then no longer significant ($r = 0.348$, $p = 0.06$, threshold 0.02).

Discussion

Our results supported (Table 2) the hypotheses of (1) narrow climatic specialization, (2) edge of climatic tolerance (Table 2), and (3) late commencement of annual activity. Therefore, we infer that bumblebee species' susceptibility depends at least in part on the narrowness of climatic specialization, on proximity to species' range edges, and on colonies that commence development later in the season. The lack of support for the food-plant specialization hypothesis does not mean bumblebees do not show some food-plant specialization; rather, it means we have no evidence that it affects the susceptibility of some species more than others.

Caveats

Our results should be seen as preliminary because our data from diverse surveys are not ideal. Unfortunately, it will be difficult to increase the power of the analysis by obtaining data from larger samples within each region (species have already been lost or areas are currently inaccessible), or from additional species from within each region (no more species are available), or from other

Table 2. Correlations (r) between measures of decline and characteristics of species from Table 1^a.

Species characteristics with suggested links to susceptibility	Surrogate measure	Expected direction of relationship	Britain (Dungeness) Pearson correlation with frequency reduction (no. of valid observations)	Canada (Guelph) Pearson correlation with abundance reduction (no. of valid observations)	China (Hongyuan) Pearson correlation with abundance reduction (no. of valid observations)	Meta-analysis: effect size correlation with reduction (1-tailed probability, probability threshold) ^b
Close competitors for food	distance to nearest species' tongue length	—	−0.066 (16)	0.000 (12)	0.168 (13)	0.026 (0.56, 0.04)
Climatic specialization	regional range size	—	−0.718 (17)	−0.374 (12)	−0.188 (13)	−0.499* (0.001, 0.006)
Proximity to edge of climatic range	latitudinal range-edge proximity	—	−0.462 (17)	−0.449 (12)	−0.345 (13)	−0.424* (0.005, 0.019)
Food specialization (species)	dietary breadth standardized by rarefaction	—	0.246 (11)	0.226 (8)	−0.772 (5)	0.074 (0.61, 0.05)
Specialization in deep flowers	worker mean tongue length	+	0.131 (16)	0.242 (12)	0.050 (13)	0.138 (0.22, 0.03)
Late start to annual activity	day of early segment of queen records	+	0.419 (13)	0.264 (12)	0.540 (13)	0.419* (0.008, 0.013)
Large body size	worker mean body length	+	0.238 (17)	0.038 (12)	−0.228 (13)	0.043 (0.40, 0.03)
Small geographic range size	global range size	—	−0.376 (17)	0.169 (12)	0.282 (13)	−0.033 (0.42, 0.04)

^aAll relationships are approximately linear; proportion data from Table 1 do not share the same variables in the denominator or numerator between predictor and response variables.

^bProbability thresholds for simultaneous tests are calculated with Hommel's sequential Bonferroni correction (Wright 1992). * = significant result.

regions with independent faunas (many of the species are widespread across entire continents, e.g., across Europe and northern Asia).

It remains likely that there are other important causes of decline than reductions in food plants and that these drivers differ between bumblebee species, especially in North America, and that they differ between continents, such as between North America and Europe (Colla et al. 2006; Williams et al. 2007; Colla & Packer 2008). For example, it has been suggested that declines in 2 Canadian species, *B. affinis* and *B. terricola*, may be due to their susceptibility to pathogens (Thorp & Shepherd 2005; Winter et al. 2006). Indeed, removing these 2 species from our analyses increased the strength of all the Guelph correlations in Table 2, except those with ranges near the edge of their climatic range (third row). There is increasing concern about declines of bumblebees in North America (e.g., Winter et al. 2006; Berenbaum et al. 2007) and in Europe (e.g., Settele et al. 2005; Kosior et al. 2007), so it will be important to update and extend our analyses if more information becomes available.

Characteristics of the Relative Winners and Losers

Species that are susceptible to decline owing to reduced abundances of their most suitable food plants, according to our results, will tend to be those bumblebee species that have narrower climatic ranges (Williams et al. 2007), are nearest to the edges of their climatic ranges (Williams et al. 2007), and become active later in the season (Edwards & Williams 2004). In contrast, species that may do relatively well where reductions in food plants drive other species to pronounced declines will tend to be those bumblebee species with broad climatic ranges that occur away from the edges of their climatic ranges and that become active early in the season. We found no significant effect of total global range size, presumably for the reasons described for the climatic specialization hypothesis. The climatic specialization relationship in Table 2 may be weakened in Asia because of the lack of sufficiently high mountains to the south and east of Sichuan and the presence of extreme deserts to the north and west, which reduces the availability of suitable habitat for mountain-meadow species like *B. rufofasciatus* and

B. friseanus (Williams et al. 2009). Climatic specialization of the different species might also interact with some other factors (e.g., pesticides) that reduce local abundance to make species more susceptible to changes in food-plant availability in smaller climatic ranges or toward the edges of their climatic ranges (Williams et al. 2007).

For the more susceptible species that start colonies later in the season, in addition to the mechanism proposed by Edwards and Williams (2004), a simpler explanation is that later species have a shorter remaining maximum-available season length in which to rear reproductive offspring for the following year. With reduced food-plant availability, these species would be exposed to a greater risk of failing to produce sufficient reproductive offspring to maintain their populations. For example, food resources can be lost in the summer as habitat dries out both at high (Bowers 1985) and low elevations (Williams 1991). But late commencement of activity is not the whole story because there are exceptions. For example, *B. hortorum* becomes active and initiates colonies relatively late each summer in Britain (e.g., Williams 1989b), and yet it remains among the most common and widely distributed species (Williams 2005). This species has a relatively short colony-development period (Prys-Jones & Corbet 1987). In contrast, the closely related, late-emerging, and declining *B. ruderatus* (Williams 1989b) has a long colony-development period (Hagen & Aichhorn 2003; Benton 2006). So it may be that it is the combination of late commencement of activity and long colony development that may put species at greater risk of failing to rear enough reproductive individuals when food is in short supply. This contrasts with Goulson and Darvill (2004), who suggest that the rarer and the more in decline a species is, the shorter the colony cycles.

The most invasive of bumblebee species (e.g., *B. terrestris*; Winter et al. 2006) as well as the species least susceptible to food-plant reductions, are, according to our results, among those that have broader climatic ranges and become active earlier in the year. It is therefore possible that an enhanced ability to cope with a broad range of climatic conditions enables them to be active in both the cool early spring and in the hot summer. This may allow colonies to start earlier and grow for longer and may be part of the reason these species have greater reproductive success, resilience, and invasiveness in changing environments compared with other bumblebees.

Recommendations for Conservation Plans

If the aim of conservation plans is to prevent the total extinction of each bumblebee species from throughout its entire range, then on the basis of our results (Table 2) the best plans should target those species with the narrowest climatic ranges and increase food-plant availability partic-

ularly in areas where species occur near the centers of their climatic ranges. In most cases total extinction across the entire range is not an imminent threat, but it may still be that some more peripheral populations are under threat of local extirpation, which could reduce genetic variation within the species. In such areas, conservation plans may stand the best chance of success if they target bumblebee species by increasing food-plant availability particularly later in the season when colonies of late-emerging species are beginning to rear sexual broods. Nevertheless, the best timing of increasing food-plant availability will need to be assessed with experimental tests.

Acknowledgments

We thank M. Brown, M. Kuhlmann, R. Macfarlane, L. Manne, M. McKinney, C. Moncrieff, J. Osborne, L. Packer, Y. Tang, and referees for discussion. S.C. was funded by a Natural Sciences and Engineering Research Council of Canada Discovery Grant to L. Packer. Z.X. was funded by a National Science Foundation of China grant to Y. Tang and by the Chinese Scholarship Council.

Literature Cited

- Alford, D. V. 1980. Atlas of the bumblebees of the British Isles. Institute of Terrestrial Ecology, Cambridge, United Kingdom.
- Benton, T. 2006. Bumblebees, the natural history & identification of the species found in Britain. Collins, London.
- Berenbaum, M., et al. 2007. Status of pollinators in North America. The National Academies Press, Washington, D.C.
- Borenstein, M., L. Hedges, and H. Rothstein. 2007. Meta-analysis fixed effect vs. random effects. Biostat, Englewood Cliffs, New Jersey. Available from www.meta-analysis.com (accessed February 2008).
- Borenstein, M., L. Hedges, J. Higgins, and H. Rothstein. 2008. Comprehensive meta-analysis. Version 2. Biostat, Englewood Cliffs, New Jersey. Available from www.meta-analysis.com (accessed February 2008).
- Bowers, M. A. 1985. Bumble bee colonization, extinction, and reproduction in subalpine meadows in northeastern Utah. *Ecology* 66:914-927.
- Braithwaite, M. E., R. W. Ellis, and C. D. Preston. 2006. Change in the British flora 1987-2004. Botanical Society of the British Isles, London.
- Brian, A. D. 1957. Differences in the flowers visited by four species of bumble-bees and their causes. *Journal of Animal Ecology* 26:71-98.
- Colla, S. R., and L. Packer. 2008. Evidence for decline in eastern North American bumblebees (Hymenoptera: Apidae), with special focus on *Bombus affinis* Cresson. *Biodiversity and Conservation* 17:1379-1391.
- Colla, S. R., M. C. Otterstatter, R. J. Gegear, and J. D. Thomson. 2006. Plight of the bumble bee: pathogen spillover from commercial to wild populations. *Biological Conservation* 129:461-467.
- Cooper, N., J. Bielby, G. H. Thomas, and A. Purvis. 2008. Macroecology and extinction risk correlates of frogs. *Global Ecology and Biogeography* 17:211-221.
- Dias, B. S. F., A. Raw, and V. L. Imperatriz-Fonseca. 1999. International Pollinators Initiative: the São Paulo declaration on pollinators. Report on the recommendations of the workshop on the conservation

- and sustainable use of pollinators in agriculture with emphasis on bees. Brazilian Ministry of the Environment, Brasília.
- Draper, N. R., and H. Smith. 1998. Applied regression analysis. John Wiley and Sons, New York.
- Edwards, M., and P. H. Williams. 2004. Where have all the bumblebees gone, and could they ever return? *British Wildlife* June:305–312.
- Evans, E., R. Thorp, S. Jepson, and S. Hoffman Black. 2008. Status review of three formerly common species of bumble bee in the subgenus *Bombus*. The Xerxes Society for Invertebrate Conservation, Portland, Oregon.
- Fitzpatrick, Ú., T. E. Murray, R. J. Paxton, J. Breen, D. Cotton, V. Santorum, and M. J. F. Brown. 2007. Rarity and decline in bumblebees—a test of causes and correlates in the Irish fauna. *Biological Conservation* 136:185–194.
- Goulson, D., and B. Darvill. 2004. Niche overlap and diet breadth in bumblebees: are rare species more specialized in their choice of flowers? *Apidologie* 35:55–63.
- Goulson, D., M. E. Hanley, B. Darvill, J. S. Ellis, and M. E. Knight. 2005. Causes of rarity in bumblebees. *Biological Conservation* 122:1–8.
- Goulson, D., M. E. Hanley, B. Darvill, and J. S. Ellis. 2006. Biotope associations and the decline of bumblebees (*Bombus* spp.). *Journal of Insect Conservation* 10:95–103.
- Goulson, D., G. C. Lye, and B. Darvill. 2008. Decline and conservation of bumble bees. *Annual Review of Entomology* 53:11.11–11.18.
- Grixti, J. C., L. T. Wong, S. A. Cameron, and C. Favret. 2009. Decline of bumble bees (*Bombus*) in the North American Midwest. *Biological Conservation* 142:75–84.
- Gurevitch, J., P. S. Curtis, and M. H. Jones. 2001. Meta-analysis in ecology. *Advances in Ecological Research* 32:199–247.
- Hagen, E. v., and A. Aichhorn. 2003. Hummeln: Bestimmen, Ansiedeln, Vermehren, Schützen. Fauna-Verlag, Nottuln, Germany.
- Hanski, I. 1982a. Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* 38:210–221.
- Hanski, I. 1982b. Structure in bumblebee communities. *Annales Zoologici Fennici* 19:319–326.
- Heinrich, B. 1979. Bumblebee economics. Harvard University Press, Cambridge, Massachusetts.
- Hines, H. M., and S. D. Hendrix. 2005. Bumble bee (Hymenoptera: Apidae) diversity and abundance in tallgrass prairie patches: effects of local and landscape floral resources. *Environmental Entomology* 34:1477–1484.
- Hutchinson, G. R. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist* 93:145–159.
- Inoue, M. N., and J. Yokoyama. 2006. Morphological variation in relation to flower use in bumblebees. *Entomological Science* 9:147–159.
- Inouye, D. W. 1977. Species structure of bumblebee communities in North America and Europe. Pages 35–40 in W. J. Mattson, editor. *The role of arthropods in forest ecosystems*. Springer-Verlag, New York.
- Inouye, D. W. 1978. Resource partitioning in bumblebees: experimental studies of foraging behavior. *Ecology* 59:672–678.
- IUCN (International Union for the Conservation of Nature). 2001. IUCN red list categories and criteria. Version 3.1. IUCN Species Survival Commission, Gland, Switzerland, and Cambridge, United Kingdom.
- Kleijn, D., and I. Raemakers. 2008. A retrospective analysis of pollen host plant use by stable and declining bumble bee species. *Ecology* 89:1811–1823.
- Kosior, A., W. Celary, P. Olejniczak, J. Fijał, W. Król, W. Solarz, and P. Plonka. 2007. The decline of the bumble bees and cuckoo bees (Hymenoptera: Apidae: Bombini) of western and central Europe. *Oryx* 41:79–88.
- Macfarlane, R. P. 1974. Ecology of Bombinae (Hymenoptera: Apidae) of southern Ontario, with emphasis on their natural enemies and relationships with flowers. Ph.D. dissertation. University of Guelph, Guelph, Ontario, Canada.
- McKinney, M. L. 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annual Review of Ecology and Systematics* 28:495–516.
- Medler, J. T. 1962a. Morphometric analyses of bumblebee mouthparts. *Transactions of the 11th International Congress of Entomology* 2:517–521.
- Medler, J. T. 1962b. Morphometric studies on bumble bees. *Annals of the Entomological Society of America* 55:212–218.
- Pleasants, J. M. 1981. Bumblebee response to variation in nectar availability. *Ecology* 62:1648–1661.
- Plowright, R. C., and F. H. Rodd. 1980. The effect of aerial insecticide spraying on hymenopterous pollinators in New Brunswick. *Canadian Entomologist* 112:259–269.
- Prys-Jones, O. E. 1982. Ecological studies of foraging and life history in bumblebees. Ph.D. dissertation. Department of Applied Biology, University of Cambridge, Cambridge, United Kingdom.
- Prys-Jones, O. E., and S. A. Corbet. 1987. Bumblebees. Cambridge University Press, Cambridge, United Kingdom.
- Ranta, E. 1982. Species structure of North European bumblebee communities. *Oikos* 38:202–209.
- Ranta, E. 1984. Proboscis length and the coexistence of bumblebee species. *Oikos* 43:189–196.
- Ranta, E., and H. Lundberg. 1981. Resource utilization by bumblebee queens, workers and males in a subarctic area. *Holarctic Ecology* 4:145–154.
- Rasmont, P. 1988. Monographie écologique et zoogéographique des bourdons de France et de Belgique (Hymenoptera, Apidae, Bombinae). Ph.D. dissertation. Faculté des Sciences agronomiques de l'Etat, Gembloux, Belgium.
- Rasmont, P., and P. Mersch. 1988. Première estimation de la dérive faunique chez les bourdons de la Belgique (Hymenoptera, Apidae). *Annales de la Société Royale zoologique de Belgique* 118:141–147.
- Rasmont, P., A. Pauly, M. Terzo, S. Patiny, D. Michez, S. Iserbyt, Y. Barbier, and E. Haubruge. 2005. The survey of wild bees (Hymenoptera, Apoidea) in Belgium and France. Food and Agriculture Organisation, Rome.
- Settele, J., et al. 2005. ALARM: assessing large scale environmental risks for biodiversity with tested methods. *GAIA—Ecological Perspectives in Science, Humanities, and Economics* 14:69–72.
- Simberloff, D., and W. Boecklen. 1981. Santa Rosalia reconsidered: size ratios and competition. *Evolution* 35:1206–1228.
- Thorp, R. W., and M. D. Shepherd. 2005. Profile: subgenus *Bombus* Latreille, 1802 (Apidae: Apinae: Bombini). Page 5 in M. D. Shepherd, D. M. Vaughan, and S. H. Black, editors. *Red list of pollinator insects of North America*. The Xerxes Society for Invertebrate Conservation, Portland, Oregon.
- Williams, P. H. 1985. On the distribution of bumble bees (Hymenoptera, Apidae) with particular regard to patterns within the British Isles. Ph.D. dissertation. Department of Applied Biology, University of Cambridge, Cambridge, United Kingdom.
- Williams, P. H. 1986. Environmental change and the distributions of British bumble bees (*Bombus* Latr.). *Bee World* 67:50–61.
- Williams, P. H. 1988. Habitat use by bumble bees (*Bombus* spp.). *Ecological Entomology* 13:223–237.
- Williams, P. H. 1989a. Bumble bees—and their decline in Britain. Central Association of Bee-Keepers, Ilford, United Kingdom.
- Williams, P. H. 1989b. Why are there so many species of bumble bees at Dungeness? *Botanical Journal of the Linnean Society* 101:31–44.
- Williams, P. H. 1991. The bumble bees of the Kashmir Himalaya (Hymenoptera: Apidae, Bombini). *Bulletin of the British Museum (Natural History) (Entomology)* 60:1–204.
- Williams, P. H. 1998. An annotated checklist of bumble bees with an analysis of patterns of description (Hymenoptera: Apidae, Bombini). *Bulletin of The Natural History Museum (Entomology)* 67:79–152. Available from www.nhm.ac.uk/research-curation/projects/bombus/ (accessed December 2008).

- Williams, P. H. 2005. Does specialization explain rarity and decline among British bumblebees? A response to Goulson et al. *Biological Conservation* **122**:33–43.
- Williams, P. H., and J. L. Osborne. 2009. Bumblebee vulnerability and conservation world-wide. *Apidologie*: in press.
- Williams, P. H., M. B. Araújo, and P. Rasmont. 2007. Can vulnerability among British bumblebee (*Bombus*) species be explained by niche position and breadth? *Biological Conservation* **138**:493–505.
- Williams, P. H., Y. Tang, J. Yao, and S. Cameron. 2009. The bumblebees of Sichuan (Hymenoptera: Apidae, Bombini). *Systematics and Biodiversity* **7**:in press.
- Winter, K., L. Adams, R. W. Thorp, D. W. Inouye, L. Day, J. Ascher, and S. Buchmann. 2006. Importation of non-native bumble bees into North America: potential consequences of using *Bombus terrestris* and other non-native bumble bees for greenhouse crop pollination in Canada, Mexico, and the United States. A White Paper of the North American Pollinator Protection Campaign, San Francisco, California.
- Wright, S. P. 1992. Adjusted *p*-values for simultaneous inference. *Biometrics* **48**:1005–1013.
- Xie, Z., P. H. Williams, and Y. Tang. 2008. The effect of grazing on bumblebees in the high rangelands of the eastern Tibetan Plateau of Sichuan. *Journal of Insect Conservation* **12**:695–703.
- Yang, D.-R. 1999. The status of species diversity and conservation strategy of bumble bees, a pollination insect in Lancang River Basin of Yunnan, China. *Chinese Biodiversity* **7**:170–174.

