

Decline of bumble bees (Bombus) in the North American Midwest

Jennifer C. Grixti^{a,*}, Lisa T. Wong^a, Sydney A. Cameron^b, Colin Favret^a

^aCenter for Biodiversity, Illinois Natural History Survey, 1816 S. Oak Street, Champaign, IL 61820, USA ^bDepartment of Entomology, 320 Morrill Hall, 505 S. Goodwin Avenue, University of Illinois at Urbana-Champaign, Urbana, IL 61801, USA

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ABSTRACT

Declines in many bumble bee species have been documented in Europe raising several ecological and economic concerns. The nature and extent of bumble bee decline in North America is poorly understood due mainly to a lack of baseline and long-term data. Museum collections provide excellent sources of information on past and current species distributions, which can be used to infer changes in the composition of insect communities. Using the Illinois Natural History Survey's electronic database of Hymenoptera and a recent biodiversity survey of historically sampled localities, we were able to examine changes in the richness and distribution of the bumble bee fauna of Illinois over the last century. We found that bumble bee species richness declined substantially during the middle of the century (1940-1960). Four species were locally extirpated: Bombus borealis, Bombus ternarius, Bombus terricola and Bombus variabilis. The ranges of Bombus affinis, Bombus fraternus, Bombus pensylvanicus and Bombus vagans have also decreased in Illinois. Our analyses also indicated that current bumble bee diversity is highest in northern Illinois, where conservation efforts would be most productive. Our study demonstrates that half of the bumble bee species found historically in Illinois have been locally extirpated or have suffered declines, supporting observations of broader declines in North America. Major declines in the bumble bee fauna coincided with large-scale agricultural intensification in Illinois between 1940 and 1960. Attempts to conserve bumble bees in Illinois should involve wildlife-friendly approaches to agriculture, such as increasing agricultural land set-asides and hedgerows, and employing integrated pest management.

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1. Introduction

Bumble bees (Bombus) provide the vital ecosystem service of pollination in both natural and managed systems (Corbet et al., 1991; Kevan, 1991; Buchmann and Nabhan, 1996; Goulson, 2003; Memmott et al., 2004; Pywell et al., 2006; Goulson et al., 2008), and declines in their abundance and distribution have serious ecological and economic ramifications (Corbet et al., 1991; Biesmeijer et al., 2006; Carvell et al., 2006). Numerous studies from Europe have documented recent declines in many species of *Bombus* (Williams, 1982, 1986; Carvell, 2002; Biesmeijer et al., 2006; Goulson, 2006; Rasmont et al., 2006; Fitzpatrick et al., 2007; Kosior et al., 2007), and such declines were often observed in areas where anthropogenic changes in habitats have occurred, such as agricultural intensification and urbanization (Pywell et al., 2006).

In North America, little is known about the status of native bumble bee species, hampering conservation efforts to

^{*} Corresponding author: Tel.: +1 217 722 5228; fax: +1 217 333 4949.

E-mail addresses: jgrixti@illinois.edu (J.C. Grixti), ltwong2@illinois.edu (L.T. Wong), scameron@life.illinois.edu (S.A. Cameron), ColinFavret@AphidNet.org (C. Favret).

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protect these valuable pollinators (Committee on the Status of Pollinators in North America, 2007). Over the last decade, various North American entomologists have observed (some anecdotally) that some species of once-common bumble bees have declined in abundance and distribution (Thorp, 2005; Thorp and Shepherd, 2005; Colla and Packer, 2008). This prompted the Xerces Society for Insect Conservation to add several presumably declining bumble bees to their Red List of Pollinator Insects of North America (Thorp, 2005; Thorp and Shepherd, 2005). These species belong to a single subgenus (Bombus sensu stricto Latreille) (Williams, 1998; Cameron et al., 2007) and include the eastern Bombus affinis Cresson and Bombus terricola Kirby, and western Bombus franklini Frison and Bombus occidentalis Greene. In addition, the Committee on the Status of Pollinators in North America, (2007) also added two species from the subgenus Thoracobombus Dalla Torre (Williams et al., 2008), the eastern Bombus pensylvanicus (DeGeer) and western Bombus sonorus Say, to their list of bee species in decline. Potential causes cited for the decline of North American bumble bees include land-use changes in the form of urbanization and agricultural conversion (Kremen et al., 2002a,b; Greenleaf and Kremen, 2006; McFrederick and LeBuhn, 2006), extensive pesticide use (Gels et al., 2002; Marletto et al., 2003), and pathogen spillover from commercial bumble bee colonies that contain many parasites (Colla et al., 2006; Otterstatter and Thomson, 2008). A recent study has substantiated the decline in B. affinis in eastern North America, and documented declines in the diversity of the bumble bee fauna during the past 35 years over a small spatial scale (approximately 100 km²) in southern Ontario, Canada (Colla and Packer, 2008). More data, especially over larger spatial and temporal scales, are needed to substantiate a decline of bumble bees in North America.

In Illinois, intensive farming and urban development over the last century have resulted in the loss of most of the state's once vast prairie, forest and wetland habitats (Iverson, 1988; Wang and Moskovits, 2001; Duram et al., 2004). As a result, Illinois ranks second to last of American states in the percentage of natural areas surviving (Jeffords et al., 1995); and nearly 95% of the northern two-thirds of the land area of Illinois is currently used for agricultural purposes (DeWalt et al., 2005). Given our knowledge of land-use changes and bumble bee decline in Europe, it would be expected that intensive farming and urban development in Illinois would have had a negative impact on the bumble bee fauna as a result of the loss of nesting habitat and continuous pollen and nectar sources. A study conducted in Iowa (Hines and Hendrix, 2005), a state with similar land-use changes to Illinois, found bumble bee diversity in prairie remnants to be strongly influenced by the availability of resources in the surrounding area, particularly in grasslands, which provide abundant pollen sources and nesting habitat for bumble bees (Svennson et al., 2000). Hines and Hendrix (2005) suggest that the resources that grassland habitats provide may be limited in agricultural landscapes as a result of mechanical disturbances over large areas. Bumble bees are susceptible to habitat loss due to their relatively limited flight range (Brian, 1954; Walther-Hellwig and Frankl, 2000), long colony cycle (commonly several months), and specific food and nesting requirements (Alford, 1975; Sakagami, 1976; Richards, 1978).

Furthermore, bumble bees, like many other Hymenoptera, have complementary sex determination (van Wilgenburg et al., 2006; Heimpel and de Boer, 2008) which, in small populations, leads to the production of costly diploid males instead of females and this can substantially increase the risk of population extinction (Zayed, 2004; Zayed et al., 2004; Zayed and Packer, 2005).

Documenting the extent and possible causes of species declines requires both historical and current distribution and species richness data. Museum collections provide an excellent source of historical data, but most collections are not electronically catalogued, thus extracting specimen data is extremely time-consuming (Suarez and Tsutsui, 2004). The Illinois Natural History Survey (INHS, Champaign, Illinois) has captured its entire Hymenoptera (ants, bees and wasps) collection (approximately 360,000 specimens) into an electronic database and made them publicly available. A major strength of the Hymenoptera database is its bumble bee database, providing an invaluable source of information on the historical distribution of Bombus in Illinois. In this study, we use the state of Illinois as a model for assessing bumble bee decline over the last century across a state-wide scale (145,934 km²). Illinois is ideal for such a study because it exemplifies a worst case scenario for loss of native habitat to farming and urban development. Further, Illinois has one of the best North American historical records of bumble bee diversity and distribution, dating back to the nineteenth century (e.g., Frison, 1919, 1921, 1923, 1926; Robertson, 1928; Waldbauer et al., 1977). These two factors allow us to examine whether and how the bumble bee fauna has changed in response to changes in habitat over the last century. We achieve this by integrating historical distributions and species richness from the INHS bumble bee database with current bumble bee distribution and species richness data obtained from our recent biodiversity survey.

2. Methods

2.1. Bombus biodiversity survey

In 2007, we conducted a survey of the bumble bee fauna at 56 sites in Illinois previously sampled between 1900 and 1949, 1950 and 1999, and 2000-2006 (Fig. 1, Table 1). Sites ranged in size from 0.05 acres to 2 acres, and were visited at least twice from early April to mid-October (between 9:00 a.m. and 4:00 p.m.). We employed an opportunistic sampling method in which a two-person team spent an average of 1.47 ± 1.09 SD person-hours per visit, and sampling time was increased based on the bumble bee activity observed at the site. We collected bumble bees with an aerial net on flowers or while in flight. We placed each collected specimen in a plastic vial and kept them alive in a cooler on ice until the end of the survey period. We identified the chilled bees to species, determined their caste (i.e. queen, worker or male) and recorded the number of individuals per species. A third of the captured workers and males were killed in cyanide vials for permanent deposition in the INHS insect collection and the remainder were released into the field to minimize destructive sampling of the Bombus fauna. We recorded the date,



Fig. 1 – Bumble bee sampling sites in Illinois. Squares (■) indicate sites sampled in 1900–1949, 1950–1999 and 2000–2007. Triangles (▲) indicate sites sampled in 1900–1949 and 2000–2007. Closed circles (●) indicate sites sampled in 1950–1999 and 2000–2007. Opened circles (○) indicate sites sampled only in 2007. Site numbers correspond to those listed in Table 1.

Table 1 – Location of bumble bee sampling sites in Illinois.							
Site #, site name, county	Region	Site #, site name, county	Region				
1. 4 mi E. Schapville, Jo Daviess	North	33. Mason City, Mason	Central				
2. Algonquin, McHenry	North	34. Muncie, Vermilion	Central				
3. Antioch, Lake	North	35. Near Tomlinson Cemetery ^a , Champaign	Central				
4. Apple River Canyon, Jo Daviess	North	36. Near Welles Cemetery ^a , Champaign	Central				
5. Beach, Lake	North	37. Paxton ^a , Ford	Central				
6. Fulton, Whiteside	North	38. Peoria/Airport region, Peoria	Central				
7. Oregon, Ogle	North	39. Prospect ^a , Ford	Central				
8. Morris, Grundy	North	40. Quincy, Adams	Central				
9. Palos, Cook	North	41. Sand Ridge State Park, Mason	Central				
10. Peru, LaSalle	North	42. Vermilion River Observatory ^a , Vermilion	Central				
11. Savanna, Carroll	North	43. Weldon Springs, DeWitt	Central				
12. Starved Rock, LaSalle	North	44. Alto Pass, Union	South				
13. Volo, Lake	North	45. Ashley, Washington	South				
14. Waukegan, Lake	North	46. Bell Smith Springs, Pope	South				
15. White Pines, Ogle	North	47. Brookport, Massac	South				
16. Allerton, Piatt	Central	48. Burden Falls, Pope	South				
17. Brussels, Calhoun	Central	49. Carbondale, Jackson	South				
18. Carlinville, Macoupin	Central	50. Cottonwood, Gallatin	South				
19. Champaign-Urbana, Champaign	Central	51. Crab Orchard Wildlife Ref., Williamson	South				
20. Charleston, Coles	Central	52. De Soto, Jackson	South				
21. Collin Woods ^a , Champaign	Central	53. Dixon Springs Ag. Center, Pope	South				
22. Forest Glen, Vermilion	Central	54. Dongola, Union	South				
23. Fox Ridge State Park, Coles	Central	55. Emma, White	South				
24. Hanna City, Peoria	Central	56. Fairmont, St. Clair	South				
25. Havana, Mason	Central	57. Freeburg, St. Clair	South				
26. Iroquois Co. C. A., Iroquois	Central	58. Grand Tower, Jackson	South				
27. Jubilee College State Park ^a , Peoria	Central	59. Herod, Pope	South				
28. Kankakee, Kankakee	Central	60. Karnak, Pulaski	South				
29. Kickapoo State Park, Vermilion	Central	61. Metropolis, Massac	South				
30. Lodaª, Iroquois	Central	62. Murphysboro, Jackson	South				
31. Mahomet, Champaign	Central	63. Old Shawneetown, Gallatin	South				
32. Manito, Mason	Central	64. Pine Hills, Union	South				
a Indicates additional sites sampled in Illinoi	s in 2007.						

time, weather conditions, GPS coordinates and the floral host for each captured specimen. Species identifications made in the field were verified in the laboratory using the taxonomic keys of LaBerge and Webb (1962), Medler and Carney (1963) and, for subgeneric features, Williams et al. (2008).

2.2. Databasing of Illinois bumble bees

Approximately 3500 specimens of *Bombus* collected in Illinois and housed in the INHS insect collection had been determined and their locality databased (http://ctap.inhs.uiuc.edu/Insect/search_inhs.asp). Each record was re-examined for accuracy and identifications were confirmed or corrected. The collection localities were retrospectively georeferenced using printed (DeLorme Mapping Company, 2000) and internet-published atlases and geolocator databases (e.g., United States Geological Survey Geographic Names Information System: http://geonames.usgs.gov/, United States Geological Survey maps: http://www.topozone.com/, Google Earth software: http://earth.google.com/).

2.3. Data analysis

We examined changes in the richness and distribution of bumble bee species in Illinois across three time periods (1900-1949, 1950-1999, and 2000-2007). The 1900-1949 and 1950-1999 time periods were chosen because most of the bumble bee specimens from Illinois were collected between 1900 and 1940 and again between 1960 and 1980. The museum specimens included in our analyses were collected by both amateur and professional entomologists using opportunistic methods. It has been suggested that museum collections may over-represent the relative abundance of rare species as a result of collectors preferentially collecting rare over common species in a site, as found in museum collections of birds (Guralnick and Van Cleve, 2005). Although bumble bees may be more difficult than birds for the amateur collector to identify in the field, the potential for bias toward the collection of rare species still exists. Collector bias, however, is only expected to strongly affect relative abundance and not species richness (i.e. the number of species collected in a site); the latter can be biased only if collectors never collect one or more of the common species - an unlikely scenario. Nevertheless, to minimize collector biases that may have resulted at a given site in the historical dataset, we used only presence/absence data in our analyses and grouped sites together over a broad geographic and temporal scale (DeWalt et al., 2005).

We used resampling methods to examine changes in species richness between time periods, as implemented in the computer program ComRAND v 1.4 (Zayed and Grixti, 2005). Species richness is affected by the number of specimens collected (Magurran, 2004). We used ComRAND to randomly sample from the larger 2000-2007 dataset employing the smaller sample size of the historical datasets, in order to remove the confounding effect of sample size when making species richness comparisons. The 2000-2007 dataset mostly represented the 'randomly sampled' specimens collected in 2007 (see Section 2.1), satisfying ComRAND's assumptions. Sampling was conducted with replacement for 1000 iterations (Zayed and Grixti, 2005). For each iteration, species richness (Magurran, 2004) was estimated for the current dataset. To test the null hypothesis of no difference in species richness between the historical and current datasets, we generated *p*-values representing the number of iterations where species richness of the current dataset was equal to or more extreme than, the species richness observed in the historical dataset.

To examine potential declines in the distribution of the 16 species found historically in Illinois, we grouped sites according to Illinois' three major geographic regions (i.e. north, central and south), as defined by the United States Geological Survey, and estimated the proportion of historical regions that a species currently inhabits. This parameter was calculated by dividing the current number of geographic regions where a species is found by the number of geographic regions where the species was historically found. A value of 1 (or 100%) suggests a stable distribution, while a value of 0 suggests local extirpation. Values between 1 and 0 suggest declines in distribution, while values greater than 1 suggest expansion.

To quantify recent (i.e. 2007) bumble bee biodiversity patterns, we estimated species richness (S), the Shannon index (H') and species evenness index (E). H' represents a measure of biodiversity that takes into account both the number of species and their relative abundance, while E measures how evenly spread species are within a community (Magurran, 2004). We used ComRAND to estimate and statistically compare the three parameters between the different geographic regions (north, central and south) sampled in 2007. We also performed a rarefaction analysis, as implemented in BioDiversity Pro (McAleece et al., 1997), to examine if our sampling effort in 2007 was adequate for capturing the species richness of the bumble bee fauna of Illinois.

3. Results

Bumble bee species richness in Illinois declined over the last century despite increased sampling effort. Between 1900 and 1949, 16 species, comprising 1244 individuals were present in the INHS collection. The number of species declined to 11 between 1950 and 1999 as *Bombus borealis* Kirby, *Bombus perplexus* Cresson, *Bombus rufocinctus* Cresson, *Bombus ternarius* Say and *B. terricola* Kirby were absent among the 2674 individuals present in the collection for that time period. Between 2000 and 2007, 12 species were found among the 3763 individuals collected as *B. perplexus* and *B. rufocinctus* were present and *Bombus variabilis* (Cresson) was absent in that time period (Fig. 2). Rarefaction analysis of the 2007 bumble bee survey dataset indicated that we adequately sampled the species



Fig. 2 – The number of bumble bee specimens (bars) and species (line) sampled over time in Illinois.

expected to be found in Illinois, as the species accumulation curve quickly reached an asymptote after approximately 25% of our total sampling effort (Fig. 3).

The declines in species richness over time despite increasing sampling effort indicate that the bumble bee declines are real and not simply an artifact of sampling. Using resampling methods to test the null hypothesis of no difference in species richness between the historic time periods and the current time period, after correcting for differences in sampling effort, species richness was significantly lower in 2000–2007 when compared to 1900–1949 (*p*-value < 0.001). Species richness in the 1950–1999 dataset was also significantly lower when compared to 1900–1949 (*p*-value < 0.001). However, species richness in 2000–2007 was not significantly different when compared to 1950–1999 (*p*-value = 0.473). Therefore, decreases in species richness occurred between the two major collecting periods (i.e. 1900–1940 and 1960–1980) in the historical dataset, between 1940 and 1960.

A total of four species found in the historical time periods were not collected between 2000 and 2007: B. borealis, B. ternarius, B. terricola and B. variabilis. Furthermore, we found that



Fig. 3 – Rarefaction analysis on the 2007 bumble bee survey data indicated that sampling effort was adequate for characterizing the species richness of the bumble bee fauna of Illinois. The species accumulation curve rapidly reached an asymptote with increasing sampling effort.

Table 2 – List of bumble bee species collected from the 56 revisited sites in Illinois, with their presence (+) or absence (–) in the INHS collection.									
Species	Ecological Traits		Presence (+ or $-$) and relative abundance $^{\circ}$ (%)				Distribution ^d		Distribution remaining ^e (%)
	Timing ^a E/I/L	Tongue Length ^b S/M/L	1900–1949	1950–1999	2000–2007	2007 ^f	Past	Current	
B. affinis Cresson	Е	S	+(0.6)	+(0.3)	+(1.4)	50	3	2(N, C)	67
B. auricomus (Robertson)	Ι	L	+(6.9)	+(3.6)	+(8.9)	332	3	3	100
B. bimaculatus Cresson	E	М	+(5.9)	+(7.1)	+(14.7)	547	3	3	100
B. borealis Kirby	L	L	+(0.6)	-(0.0)	-(0.0)	0	1(N)	0	0
B. citrinus (Smith)	L	S	+(0.6)	+(0.5)	+(0.7)	27	3	3	100
B. fervidus (Fabricius)	Ι	L	+(8.3)	+(1.0)	+(2.5)	95	2(N, C)	2(N, C)	100
B. fraternus (Smith)	E	S	+(1.9)	+(0.2)	+(0.2)	4	3	2(N, C)	67
B. griseocollis (DeGeer)	E	М	+(7.8)	+(7.4)	+(29.3)	1118	3	3	100
B. impatiens Cresson	Е	М	+(10.9)	+(52.5)	+(34.7)	1330	3	3	100
B. pensylvanicus (DeGeer)	L	L	+(28.1)	+(23.0)	+(4.4)	160	3	2(C, S)	67
B. perplexus Cresson	E	М	+(0.1)	-(0.0)	+(0.0)	1	1(N)	1(N)	100
B. rufocinctus Cresson	L	S	+(1.3)	-(0.0)	+(0.8)	27	1(N)	1(N)	100
B. ternarius Say	E	S	+(0.2)	-(0.0)	-(0.0)	0	1(C)	0	0
B. terricola Kirby	E	S	+(1.2)	-(0.0)	-(0.0)	0	2(N, C)	0	0
B. vagans Smith	L	М	+(11.3)	+(3.5)	+(2.5)	91	3	2(N, C)	67
B. variabilis (Cresson)	L	S	+(14.3)	+(0.8)	-(0.0)	0	3	0	0

The proportion of the historical distribution remaining was measured by dividing the current distribution by the past distribution. A species is considered to have declined in distribution, if the proportion of the historical distribution remaining is less than 100%.

a E = early emerging, I = intermediate emerging, L = late emerging. Emergence times (i.e. when the first queen of the flight season is observed for a species) were obtained by Medler and Carney (1963).

b S = Short tongue, M = medium tongue, L = long tongue. Tongue lengths were obtained by Medler (1962).

c Relative abundance data was not used in our analyses.

d N = northern region, C = central region, S = southern region.

e Proportion of historical distribution remaining.

f Number of individuals of bumble bees observed from both the 56 revisited sites and eight additional sites.

Table 3 – Current species richness (S), diversity (H'), evenness (E) and sample size (N) for each geographic region in Illinois.

	North	Central	South
S	10	10	7
H'	1.73	1.46	1.46
Е	0.75	0.64	0.75
Ν	1357	1861	564

four bumble bee species were found in fewer geographic regions during the current period when compared to the historical time periods: B. affinis, B. fraternus (Smith), B. pensylvanicus and Bombus vagans Smith (Table 2). This suggests that these species have declined in distribution. Although we do not use relative abundance data in our analyses of bumble bee declines because of the concern that it may be biased in museum datasets (Guralnick and Van Cleve, 2005), most of the species which declined in distribution also declined in apparent relative abundance (Table 2). For example, the historically common B. pensylvanicus (28.1% of all bumble bees sampled between 1900 and 1949) represents only 4.4% of the current (2000-2007) bumble bee fauna. B. affinis declined in distribution, although its relative abundance increased in 2000-2007 (from 0.6% to 1.4%). The increase in relative abundance of B. affinis is, however, misleading because 90% of the 50 workers sampled in 2000-2007 were collected from the same site during the same survey. Finally, eight species were found in all geographic regions in which they were previously recorded: B. auricomus (Robertson), B. bimaculatus Cresson, B. citrinus (Smith), B. fervidus (Fabricius), B. griseocollis (DeGeer), B. impatiens Cresson, B. perplexus and B. rufocinctus (Table 2).

In 2007, we found that the highest diversity of bumble bees in the state were observed in northern Illinois (Table 3). Species diversity (H') was significantly higher in the northern region, when compared to the central (p < 0.001) and southern regions (p < 0.001). Species richness (S) was significantly higher in the northern region when compared to the southern region (p < 0.001), but not the central region (p = 0.66). Species evenness (E) was not significantly different between the northern and southern regions (p = 0.468), but both were significantly higher than the central region (p = 0.002 and p = 0.049, respectively).

Discussion

Bumble bee species, with their varying tongue-lengths (Medler, 1962; Inouye, 1980), ability to forage at lower temperatures (Corbet et al., 1993), and capacity to buzz pollinate (Kevan et al., 1991; King, 1993), are one of the most effective pollinators of wild plants and crops (Goulson, 2003). A large number of wildflowers are pollinated exclusively or predominately by bumble bees (Corbet et al., 1991) and recent work has shown that bumble bees act as important 'hubs' or central connectors in pollination networks (Memmott et al., 2004; Olesen et al., 2007). Therefore, bumble bee declines are expected to have devastating effects on pollination and ecosystem functioning (Memmott et al., 2004; Goulson et al., 2005, 2008; Olesen et al., 2007). Here, we provide quantitative evidence for declines of multiple North American bumble bee species over a large geographic area. Half of the bumble bee species found historically in Illinois have been either locally extirpated or showed declines in distribution. Our findings of declines are similar to those of a study conducted in eastern Canada over a smaller geographic area (Colla and Packer, 2008), as well as those of several European studies (e.g., Berezin et al., 1995; Sarospataki et al., 2005; Kosior et al., 2007), suggesting that bumble bees are declining globally. Our findings confirm previous concerns over the status of *B. affinis*, *B. terricola* and *B. pensylvanicus* in eastern North America (Thorp, 2005; Thorp and Shepherd, 2005; Committee on the Status of Pollinators in North America, 2007; Colla and Packer, 2008); these species have experienced declines in their distribution over time in Illinois.

Three possible reasons have been cited for the decline of bumble bees in North America (Thorp and Shepherd, 2005): (1) habitat loss due to urban and agricultural growth (Kearns and Inouye, 1997); (2) the extensive use of pesticides, such as organophosphates, carbamates, and pyrethroids, (Kevan, 1975; Johansen, 1977), and more recently, neonicotinoids (Marletto et al., 2003); and (3) the spread of pathogens, such as *Nosema bombi* Fantham and Porter and Crithidia bombi Lipa and Triggiani from managed greenhouses to foraging bees nearby (Otterstatter et al., 2005; Colla et al., 2006; Otterstatter and Thomson, 2008) (i.e. 'pathogen spillover').

In Illinois, bumble bee richness declines occurred principally between 1940 and 1960, a period that coincided with major agricultural intensification in the Midwest, during which technological advancements in mechanization and agrichemicals lead to the expansion of existing farms in central and southern Illinois (Mattingly, 1987; Iverson, 1988; Duram et al., 2004). During that time, farms that grew a variety of crops, including temporary and permanent pastures containing wildflowers, switched to growing corn and soybeans (Newman et al., 2003). This conversion resulted in a loss of wildlife habitat within Illinois' agricultural landscape. In Britain and Ireland, it has been suggested that the widespread decline in wildflowers traditionally associated with hay meadows, pasture and hedgerows may have contributed to the decline in British bumble bees (Williams, 1986, 1988; Fitzpatrick et al., 2007) and reports from Europe also suggest that bumble bee declines may be linked to habitat loss and fragmentation, mostly due to urbanization and the intensification of farming practices (Williams, 1986; Goulson, 2003; Goulson et al., 2008). Agricultural intensification may have contributed to the local extirpation and decline of Bombus species in Illinois, where similar land-use changes have taken place.

It has been argued previously that bumble bees that exhibit diet and/or habitat preferences may be more susceptible to anthropogenic changes. One hypothesis proposes that species that exhibit food-plant specialization (e.g., long-tongued species forage primarily on long corolla flowers, such as legumes) are susceptible to declines when losses of the preferred food-plant occur (Goulson and Darvill, 2004; Goulson et al., 2005; Kleijn and Raemakers, 2008). Another hypothesis proposes that niche specialization, including preferred climate and habitat, may interact with food-plant availability to make species at the edge of their distribution more vulnerable to declines (Williams, 1985, 2005). Both specialized diet and habitat are expected to reduce levels of genetic diversity in bee populations (Packer et al., 2005; Zayed et al., 2005), which can increase the risk of extinction from the 'diploidmale production vortex' (Zayed and Packer, 2005). However, a recent study by Fitzpatrick et al. (2007) conducted in Ireland found no evidence of a relationship between rarity and decline in Irish bumble bees and diet specialization. Our study found that both long and short tongued bees were either absent or in decline in Illinois. In our study, lack of a large number of species exhibiting the different natural history traits (e.g., long versus short tongue, and early versus late emerging) precluded statistical testing of the influence of food-plant specialization and declines in the bumble bee fauna. However, most of the species that were locally extirpated or declined were rare and/or at the edge of their distribution (Mitchell, 1962; Milliron, 1971). For example, B. borealis, B. ternarius, B. terricola and B. affinis were both rare and at the edge of their distribution in Illinois. B. fraternus is rare but not at the edge of its distribution. Although the locally extirpated B. borealis (eight bees collected from three sites between 1917 and 1930) and B. terricola (15 bees collected from three sites between 1894 and 1929) were rare in Illinois, they were historically recorded from multiple geographic regions and/or multiple years indicating that they were not transient species. The locally extirpated B. ternarius was very rare (two bees collected from a single site between 1927 and 1929) and may represent a transient species.

The decline and local extirpation of historically common species is of particular concern. *B. vagans* and *B. pensylvanicus* are no longer found in southern and northern Illinois, respectively, while *B. variabilis*, the social parasite of *B. pensylvanicus*, is locally extirpated in Illinois. *B. vagans* was last recorded in southern Illinois in 1975, while *B. pensylvanicus* was last recorded in northern Illinois in 1996. *B. variabilis*, which was historically recorded in all geographic regions, was last recorded in Illinois in 1980. These dates indicate that declines in these common species occurred in Illinois more recently due to novel causes arising later on in the century, and/or due to delayed responses to the earlier land-use changes discussed above.

It is likely that multiple factors are responsible for the decline of these and other bumble bee species in North America. Species-specific resource requirements may explain why we found some species to have declined, while others like B. impatiens and B. bimaculatus continue to persist. Until we gain a better understanding of these resource requirements, efforts to set aside diverse patches of natural habitat for bees throughout Illinois are needed. Because three-quarters of the state is covered by cropland, any attempt at conserving bumble bees must involve a more wildlife-friendly approach to agriculture, including increasing the amount of interspersed or adjacent semi-natural habitat patches, rotating row crops with small grains, grasses and legumes, and employing integrated pest management strategies (Newman et al., 2003). Additional strategies include farm land restoration, use of hedgerows, and agricultural land set-asides.

Our study demonstrates the importance of using museum specimen data – an otherwise underutilized resource – to examine changes in biodiversity over time (Favret and DeWalt, 2002; Suarez and Tsutsui, 2004; DeWalt et al., 2005; Beck and Kitching, 2007; Kleijn and Raemakers, 2008). Museum collections contain valuable baseline data on species distribution and richness (Beck and Kitching, 2007; Tsoar et al., 2007) over large geographic and temporal scales. Once databased, these collections can be used to examine how anthropogenic causes such as habitat destruction and global climate change affect biodiversity (Parmesan et al., 2003; Suarez and Tsutsui, 2004). Our study shows that museum collections, combined with current biodiversity surveys, provide an irreplaceable resource for conservation biology.

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REFERENCES

- Alford, D.V., 1975. Bumblebees. Davis-Poynter, London.
- Beck, J., Kitching, I.J., 2007. Estimating regional species richness of tropical insects from museum data: a comparison of a geography-based and sample-based methods. Journal of Applied Ecology 44, 672–681.
- Berezin, M.V., Beiko, V.B., Berezina, N.V., 1995. Bumblebees of the Moscow region. Entomologist's Monthly Magazine 131, 259– 268.
- Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., Kunin, W.E., 2006. Parallel declines in pollinators and insect pollinated plants in Britain and the Netherlands. Science 313, 351–354.
- Brian, A.D., 1954. The foraging of bumble bees. Part I. Foraging behaviour. Bee World 35, 61–67.
- Buchmann, S.L., Nabhan, G.P., 1996. The Forgotten Pollinators. Island Press, Washington, DC. p. 292.
- Cameron, S.A., Hines, H.M., Williams, P.H., 2007. A comprehensive phylogeny of the bumble bees (Bombus). Biological Journal of the Linnean Society, London 91, 161–188.
- Carvell, C., 2002. Habitat use and conservation of bumblebees (Bombus spp.) under different grassland management regimes. Biological Conservation 103, 33–49.
- Carvell, C., Roy, D.B., Smart, S.M., Pywell, R.F., Preston, C.D., Goulson, D., 2006. Declines in forage availability for bumblebees at a national scale. Biological Conservation 132, 481–489.
- Colla, S.R., Packer, L., 2008. Evidence for decline in eastern North American bumblebees (Hymenoptera: Apidea), with special focus on Bombus affinis Cresson. Biodiversity and Conservation 17, 1379–1391.

- Colla, S.R., Otterstatter, M.C., Gegear, R.J., Thomson, J.D., 2006. Plight of the bumble bee: pathogen spillover from commercial to wild populations. Biological Conservation 129, 461–467.
- Committee on the Status of Pollinators in North America National Research Council, 2007. Status of Pollinators in North America. National Academies Press, Washington, DC.
- Corbet, S.A., Williams, I.H., Osborne, J.L., 1991. Bees and the pollination of crops and wildflowers in the European Community. Bee World 72, 47–49.
- Corbet, S.A., Fussell, M., Ake, R., Fraser, A., Gunson, C., Savage, A., Smith, K., 1993. Temperature and the pollinating activity of social bees. Ecological Entomology 18, 17–30.
- DeLorme Mapping Company, 2000. Illinois Atlas & Gazetteer, third ed. DeLorme, Yarmouth, Maine.
- DeWalt, R.E., Favret, C., Webb, D.W., 2005. Just how imperiled are aquatic insects? A case study of stoneflies (Plecoptera) in Illinois. Annals of the Entomological Society of America 98, 941–950.
- Duram, L.A., Bathgate, J., Ray, C., 2004. A local example of landuse change: southern Illinois – 1807, 1938, and 1993. The Professional Geographer 56, 127–140.
- Favret, C., DeWalt, R.E., 2002. Comparing the Ephemeroptera and Plecoptera specimen databases at the Illinois Natural History Survey and using them to document changes in the Illinois fauna. Annals of the Entomological Society of America 95, 35– 40.
- Fitzpatrick, U., Murray, M.G., Paxton, R.J., Breen, J., Cotton, D., Santorum, V., Brown, M.J.F., 2007. Rarity and decline in bumblebees – a test of causes and correlates in the Irish fauna. Biological Conservation 136, 185–194.
- Frison, T.H., 1919. Keys for the separation of the Bremidae, or bumblebees of Illinois, and other notes. Transactions of the Illinois States Academy of Science 12, 157–165.
- Frison, T.H., 1921. New distribution records for North American Bremidae, with the description of a new species (Hym.). Entomological News 32, 144–148.
- Frison, T.H., 1923. Systematic and biological notes on bumblebees (Bremidae; Hymenoptera). Transactions of the American Entomological Society 48, 307–326.
- Frison, T.H., 1926. Descriptions and records of North American Bremidae together with notes on the synonymy of certain species (Hymenoptera). Transactions of the American Entomological Society 52, 129–145.
- Gels, J.A., Held, D.W., Potter, D.A., 2002. Hazards of insecticides to the bumble bees *Bombus impatiens* (Hymenoptera: Apidae) foraging on flowering white clover in turf. Ecotoxicology 95, 722–728.
- Goulson, D., 2003. Bumblebees: Their Behaviour and Ecology. Oxford University Press, Oxford.
- Goulson, D., 2006. The demise of the bumblebee in Britain. Biologist 53, 294–299.
- Goulson, D., Darvill, B., 2004. Niche overlap and diet breadth in bumblebees: are rare species more specialized in their choice of flowers? Apidologie 35, 55–63.
- Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S., Knight, M.E., 2005. Causes of rarity in bumblebees. Biological Conservation 122, 1– 8.
- Goulson, D., Lye, G.C., Darvill, B., 2008. Decline and conservation of bumble bees. Annual Review of Entomology 53, 191–208.
- Greenleaf, S.S., Kremen, C., 2006. Wild bee species increase tomato production and respond differently to surrounding land use in Northern California. Biological Conservation 133, 81–87.
- Guralnick, R., Van Cleve, J., 2005. Strengths and weaknesses of museum and national survey data sets for predicting regional species richness: comparative and combined approaches. Diversity and Distributions 11, 349–359.

- Heimpel, G.E., de Boer, J.G., 2008. Sex determination in the Hymenoptera. Annual Review of Entomology 53, 209–230.
- Hines, H.M., Hendrix, S.D., 2005. Bumble bee (Hymenoptera: Apidae) diversity and abundance in tallgrass prairie patches: effects of local and landscape floral resources. Environmental Entomology 34, 1477–1484.
- Inouye, D., 1980. The effect of proboscis and corolla tube lengths on patterns and rates of flower visitation by bumblebees. Oecologia 45, 197–201.
- Iverson, L.R., 1988. Land-use changes in Illinois, USA: the influence of landscape attributes on current and historic land use. Landscape Ecology 2, 45–61.
- Jeffords, M.R., Post, S.L., Robertson, K.R., 1995. Illinois Wilds. Phoenix Publishing, Urbana, IL.
- Johansen, C.A., 1977. Pesticides and pollinators. Annual Review of Entomology 22, 177–192.
- Kearns, C.A., Inouye, D.W., 1997. Pollinators, flowering plants, and conservation biology. BioScience 47, 297–306.
- Kevan, P.G., 1975. Pollination and environmental conservation. Environmental Conservation 2, 293–298.
- Kevan, P.G., 1991. Pollination: keystone process in sustainable global productivity. Acta Horticulturae 288, 103–110.
- Kevan, P.G., Straver, W.A., Offer, M., Laverty, T.M., 1991. Pollination of greenhouse tomatoes by bumble bees in Ontario. Proceedings of the Entomological Society of Ontario 122, 15– 19.
- King, M.J., 1993. Buzz foraging mechanism of bumble bees. Journal of Apicultural Research 32, 41–49.
- Kleijn, D., Raemakers, I., 2008. A retrospective analysis of pollen host plant use by stable and declining bumble bee species. Ecology 89, 1811–1823.
- Kosior, A., Celary, W., Olejniczak, P., Fijal, J., Król, W., Solarz, W., Plonka, P., 2007. The decline of the bumble bees and cuckoo bees (Hymenoptera: Apidae: Bombini) of western and central Europe. Oryx 41, 79–88.
- Kremen, C., Bugg, R.L., Nicola, N., Smith, S.A., Thorp, R.W., Williams, N.M., 2002a. Native bees, native plants, and crop pollination in California. Fremontia 30, 41–49.
- Kremen, C., Williams, N.M., Thorp, R.W., 2002b. Crop pollination from native bees at risk from agricultural intensification. Proceedings of the National Academy of Sciences USA 99, 16812–16816.
- LaBerge, W.E., Webb, M.C., 1962. The bumblebees of Nebraska. University of Nebraska College of Agriculture, Agricultural Experiment Station Research Bulletin 205, 1–38.
- Magurran, A.E., 2004. Measuring Biological Diversity. Blackwell Publishing, Oxford.
- Marletto, F., Patetta, A., Manino, A., 2003. Laboratory assessment of pesticide toxicity to bumblebees. Bulletin of Insectology 56, 155–158.
- Mattingly, P.F., 1987. Patterns of horse devolution and tractor diffusion in Illinois, 1920–1982. Professional Geographer 39, 298–309.
- McAleece, N., Lambshead, J., Patterson, G., Gage, J., 1997.
 BioDiversity Pro, Version 2. The Natural History Museum,
 London and The Scottish Association of Marine Science, Oban,
 Scotland.
- McFrederick, Q.S., LeBuhn, G., 2006. Are urban parks refuges for bumble bees *Bombus* spp. (Hymenoptera: Apidae)? Biological Conservation 129, 372–382.
- Medler, J.T., 1962. Morphometric studies on bumble bees. Annals of the Entomological Society of America 55, 212–218.
- Medler, J.T., Carney, D.W., 1963. Bumblebees of Wisconsin (Hymenoptera: Apidae). University of Wisconsin, Madison, WI.
- Memmott, J., Waser, N.M., Price, M.V., 2004. Tolerance of pollination networks to species extinctions. Proceedings of the Royal Society of London B 271, 2605–2611.

- Milliron, H.E., 1971. A monograph of the Western Hemisphere bumblebees (Hymenoptera: Apidae; Bombinae) I. The genera Bombus and Megabombus subgenus Bombias. Memoirs of the Entomological Society of Canada 82 (iii), 80.
- Mitchell, T.B., 1962. Bees of the Eastern United States, volume II. The North Carolina Agricultural Experiment Station.
- Newman, D.S., Warner, R.E., Mankin, P.C., 2003. Creating habitats and homes for Illinois wildlife. Illinois Department of Natural Resources and University of Illinois, Oak Forest, Illinois.
- Olesen, J.M., Bascompte, J., Dupont, Y.L., Jordano, P., 2007. The modularity of pollination networks. Proceedings of the National Academy of Science, USA 104, 19891–19896.
- Otterstatter, M.C., Thomson, J.D., 2008. Does pathogen spillover from commercially reared bumble bees threaten wild pollinators? PLoS ONE 3, e2771. doi:10.1371/ journal.phone.0002771.
- Otterstatter, M.C., Gegear, R.J., Colla, S.R., Thomson, J.D., 2005. Effects of parasitic mites and protozoa on the flower constancy and foraging rate of bumble bees. Behaviour, Ecology, and Sociobiology 58, 383–389.
- Packer, L., Zayed, A., Grixti, J.C., Ruz, L., Owen, R., Vivallo, F., Toro, H., 2005. Conservation genetics of potentially endangered mutualisms: reduced levels of genetic variation in specialist versus generalist bees. Conservation Biology 19, 195–202.
- Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42.
- Pywell, R.F., Warman, E.A., Hulmes, L., Hulmes, S., Nuttall, P., Sparks, T.H., Critchley, C.N.R., Sherwood, A., 2006. Effectiveness of new agri-environment schemes in providing foraging resources for bumblebees in intensively farmed landscapes. Biological Conservation 129, 192–206.
- Rasmont, P., Pauly, A., Terzo, M., Patiny, S., Michez, D., Iserbyt, S., Barbier, Y., Haubruge, E., 2006. The survey of wild bees (Hymenoptera, Apoidea) in Belgium and France. In: Status of the World's Pollinators. Food and Agriculture Organisation of the United Nations, Rome, p. 18.
- Richards, K.W., 1978. Nest site selection by bumble bees (Hymenoptera: Apidae) in southern Alberta. Canadian Entomologist 110, 301–318.
- Robertson, C., 1928. Flowers and insects. List of Visitors to Four Hundred and Fifty-Three Flowers. Science Press Printing Company, Lancaster, Pennsylvania.
- Sakagami, S.F., 1976. Specific differences in the bionomic characters of bumblebees. A comparative review. Journal of the Faculty of Sciences, Hokkaido University, Series VI, Zoology 20, 390–447.
- Sarospataki, M., Novak, J., Viktoria, M., 2005. Assessing the threatened status of bumble bee species (Hymenoptera: Apidae) in Hungary, Central Europe. Biodiversity and Conservation 14, 2437–2446.
- Suarez, A.V., Tsutsui, N.D., 2004. The value of museum collections for research and society. BioScience 54, 66–74.
- Svennson, B., Lagerlöf, J., Svennson, B.G., 2000. Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. Agriculture, Ecosystems and Environment 77, 247–255.
- Thorp, R., 2005. Bombus franklini Frison 1921 Franklin's Bumble Bee (Hymenoptera: Apidae: Apinae: Bombinae). In: Shepherd, M.D., Vaughan, D.M., Black, S.H. (Eds.), Red List of Pollinator Insects of North America. CD-ROM Version 1 (May 2005). The Xerces Society for Invertebrate Conservation, Portland, OR.

- Thorp, R.W., Shepherd, M.D., 2005. Profile: subgenus Bombus. In: Shepherd, M.D., Vaughan, D.M., Black, S.H. (Eds.), Red List of Pollinator Insects of North America, CD-ROM Version 1 (May 2005). The Xerces Society for Invertebrate Conservation, Portland, OR.
- Tsoar, A., Allouche, O., Steinitz, O., Rotem, D., Kadmon, R., 2007. A comparative evaluation of presence-only methods for modelling species distribution. Diversity and Distributions 13, 397–405.
- van Wilgenburg, E., Driessen, G., Beukeboom, L.W., 2006. Single locus complimentary sex determination in Hymenoptera an "unintelligent" design? Frontiers in Zoology 3.
- Waldbauer, G.P., Sternburg, J.G., Maier, C.T., 1977. Phenological relationships of wasps, bumblebees, their mimics, and insectivorous birds in an Illinois sand area. Ecology 58, 583– 591.
- Walther-Hellwig, K., Frankl, R., 2000. Foraging habitats and foraging distances of bumblebees, *Bombus* (Hym., Apidae), in an agricultural landscape. Journal of Applied Entomology 124, 299–306.
- Wang, Y., Moskovits, D.K., 2001. Tracking fragmentation of natural communities and changes in land cover: applications of landstat data for conservation in an urban landscape. Conservation Biology 15, 835–843.
- Williams, P.H., 1982. The distribution and decline of British bumble bees (Bombus Latr.). Journal of Apicultural Research 21, 236–245.
- Williams, P.H., 1985. On the distribution of bumble bees (Hymenoptera, Apidae) with particular regard to patterns within the British Isles. Department of Applied Biology, University of Cambridge, Cambridge. p. 180.
- Williams, P.H., 1986. Environmental change and the distribution 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., 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.
- 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., Cameron, S.A., Hines, H.M., Cederberg, B., Rasmont, P., 2008. A simplified subgeneric classification of the bumblebees (genus Bombus). Apidologie 39, 46–74.
- Zayed, A., 2004. Effective population size of Hymenoptera with complementary sex determination. Heredity 93, 627– 630.
- Zayed, A., Grixti, J.C., 2005. ComRAND: Randomization software for examining community composition change. Version 1.4. http://www.yorku.ca/bugsrus/comrand.htm.
- Zayed, A., Packer, L., 2005. Complementary sex determination substantially increases extinction proneness of haplodiploid populations. Proceedings of the National Academy of Science, USA 102, 10742–10746.
- Zayed, A., Roubik, D.W., Packer, L., 2004. Use of diploid male frequency data as an indicator of pollinator decline. Proceedings of the Royal Society of London B 271, S9–S12.
- Zayed, A., Packer, L., Grixti, J.C., Ruz, L., Owen, R.E., Toro, H., 2005. Increased genetic differentiation in a specialist versus a generalist bee: implications for conservation. Conservation Genetics 6, 1017–1026.