



Spatial patterns of bee captures in North American bowl trapping surveys

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Abstract. 1. Bowl and pan traps are now commonly used to capture bees (*Hymenoptera: Apiformes*) for research and surveys.

2. Studies of how arrangement and spacing of bowl traps affect captures of bees are needed to increase the efficiency of this capture technique.

3. We present results from seven studies of bowl traps placed in trapping webs, grids, and transects in four North American ecoregions (Mid-Atlantic, Coastal California, Chihuahuan Desert, and Columbia Plateau).

4. Over 6000 specimens from 31 bee genera were captured and analysed across the studies.

5. Based on the results from trapping webs and distance tests, the per bowl capture rate of bees does not plateau until bowls are spaced 3–5 m apart.

6. Minor clumping of bee captures within transects was detected, with 26 of 56 transects having index of dispersion values that conform to a clumped distribution and 39 transects having positive Green's index values, 13 with zero, and only four negative. However, degree of clumping was slight with an average value of only 0.06 (the index ranges from -1 to 1) with only five values >0.15. Similarly, runs tests were significant for only 5.9% of the transects.

7. Results indicate that (i) capture rates are unaffected by short distances between bowls within transects and (ii) that bowls and transects should be dispersed throughout a study site.

Key words. Apiformes, Apoidea, bee bowl, bees, inter-trap distance, North America, pan trap, spatial distribution, trap spacing, trapping web.

Introduction

The influence of anthropogenic activities on the world's biota has been described by many conservation biologists (e.g., Primack, 1993). Policies designed to mitigate the effects of human expansion are aided by focusing our attention on the plight and well-being of groups that are representatives of their communities. Taxa that are also bioindicators of, and/or keystones in,

their natural areas, and that make essential contributions to agricultural ecosystems are especially important targets for study and conservation.

For several reasons, bees (Apiformes) satisfy these (Kevan, 1999) and other of the criteria recommended for selecting taxa for survey and study (Raven & Wilson, 1992). First, bee taxonomy is fairly well-known and is the subject of much current technological effort, including: a new checklist of the bees of the world (Ascher, 2008); plans to obtain DNA barcodes for all species (Packer, 2008); plans to catalogue all major bee collections (Global Biodiversity Information Facility, 2008). Second, bees are important economically. The introduced honeybee

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(*Apis mellifera* L.) is the pre-eminent crop pollinator in the world (Klein *et al.*, 2006 and references therein), and the diverse bee fauna of North America (over 4000 species, Michener, 2007) and other regions becomes more important to crop pollination as the difficulties plaguing honeybee keepers grow (Parker *et al.*, 1987; Allen-Wardell *et al.*, 1998; Klein *et al.*, 2006; Cox-Foster *et al.*, 2007). Third, bees are important ecologically: between 67% and 90% of flowering plants in native ecosystems depend on pollinators for seed production (Axelrod, 1960; Ricklefs & Renner, 1994; respectively) and most of this is accomplished by bees (Kevan, 1999; Michener, 2007). Finally, surveying for bees satisfies the low-cost criteria implied by Raven and Wilson (1992). These characteristics have led to calls for survey and monitoring of the native bee fauna (Committee on the Status of Pollinators in North America, 2007).

Over the past decade, pan, Moericke, or bowl traps (Kirk, 1984; Leong & Thorp, 1999; Cane *et al.*, 2000; Monsevičius, 2004; Toler *et al.*, 2005; Wilson *et al.*, 2008) have become widely used to sample bees. Recently, Westphal *et al.* (2008) concluded that bowl traps were 'the most efficient, unbiased, and cost-effective' of six tested methods for sampling bee diversity. Bowls are also apt tools for the sampling of bees as they are inexpensive, need not be deployed by someone with entomological training, and capture most of the species present in a community.

Previous studies have mostly compared bee 'catch' by trap colour (Leong & Thorp, 1999; McIntyre & Hostetler, 2001; Bartholomew & Prowell, 2005; Toler *et al.*, 2005; Campbell & Hanula, 2007; Romey *et al.*, 2007; Krug & Alves-dos-Santos, 2008; Wilson *et al.*, 2008), and have estimated the efficacy of different collection methods (Jacob-Remacle, 1984; Noyes, 1989; Riemann, 1995; Banaszak & Krzysztofiak, 1996; Cane *et al.*, 2000; Monsevičius, 2004; Bartholomew & Prowell, 2005; Giles & Ascher, 2006; Wells & Decker, 2006; Campbell & Hanula, 2007; Roulston *et al.*, 2007; Hopwood, 2008; Krug & Alves-dos-Santos, 2008; Kwaiser & Hendrix, 2008; Wilson *et al.*, 2008; Westphal *et al.*, 2008). Other important methodological questions remain unaddressed. For example, does distance among traps affect the total number of bees captured (independent of species), and how much impact does trap placement and trap order within a transect or grid have on the total number of bees captured? Here, we present several independent investigations of these questions, describe the dispersion of captures among traps, and provide recommendations for bee inventory and monitoring programs.

Materials and methods

Analysis of the effects of bowl placement on bee captures requires datasets in which captures were recorded by individual bowl, something that is rarely done. Here, we have gathered seven such studies from the shrub-steppe habitats of the Columbia Plateau, Chihuahuan Desert, California Coastal Scrub, and a variety of old field and agricultural habitats from the Ridge and Valley and Coastal Plain provinces of the Mid-Atlantic region of the US. This diversity of sampling localities is useful for comparing the effectiveness of bowl traps across a broad spectrum of bee communities. Unless otherwise noted below, all

bowls were white plastic cereal dishes (3.25 oz, 96 ml; Solo Brand P325), filled with a surfactant (0.13–0.39% Dawn Original Blue dishwashing detergent in tap water), and placed on the ground; bees land in the bowls and are retrieved later that day or after 24 h. Some early experiments used larger bowls until tests demonstrated that there was little difference in capture rates among bowl sizes (S. Droege, unpubl. data). Some experiments used additional colours (i.e., blue, yellow) with demonstrated attraction to bees (e.g., Kirk, 1984; Wilson *et al.*, 2008). Captured specimens were usually stored in 70% alcohol or in a freezer, washed in warm soapy tap water, blown dry with a hairdryer, pinned and labelled.

Statistical analyses were performed using PAST version 1.82b (Hammer *et al.*, 2001) and SYSTAT 10. We analysed the data as the total number of bees captured within individual bowls because capture rates per bowl for individual species were too low for meaningful analyses in all but the Columbia Basin golf courses data set. Low bowl trap capture rates for most regions is the norm [average per bowl captures of all bees collected per date across a season for a set of bowls ranged from 2.3 to 3.2 in western USA (T. Griswold, unpubl. data) and 0.5–1 in Eastern USA (S. Droege, unpubl. data)]. Papers that report and analyse captures by species commonly do so by pooling across bowl traps rather than using data from individual bowls.

Significance levels for all tests were set at $P = 0.05$. Three tests were used to evaluate patterns of dispersion and clumping: (i) a runs test, (ii) an index of dispersion (variance/mean ratio) and (iii) Green's clumping index, a modified form of the index of dispersion that adjusts for differences in number of individuals (Ludwig & Reynolds, 1988). The indices measure the degree of conformity of a series of captures to a distributional series. These indices use a Poisson distribution as the model of random captures (variance = mean). If the variance is significantly lower than the mean, the distribution of bees captured among bowls is considered uniformly distributed; if the variance is significantly higher than the mean, then the distribution of bees is clumped.

Inter-bowl competition for bees

We used trapping webs and paired bowls to explore the effect of bowl proximity on the number of bees captured per bowl.

2007 – Trapping webs. In 2007, three trapping webs (Buckland *et al.*, 1993) were established in fields with low, apparently uniform floral resources on the USDA Agriculture Research Center in Beltsville, Maryland, USA. (latitude, longitude – web 1: 39.0341, –76.8758; web 2: 39.0337, –76.8741; web 3: 39.0331, –76.8730) to estimate the distance at which capture probability among bowls becomes uniform and is no longer affected by neighbouring bowls (i.e., the bowls are no longer competing for captures; Link & Barker, 1994) (note that bee density could not be estimated in this way because of violations to the assumptions of trapping webs (Lukacs *et al.*, 2005).

Bowls in each 24 m diameter web were placed in several concentric rings, along eight equally spaced arms radiating from a central point, and run on consecutive days. Each ring in a web

had an even number of bowls; bowl density was highest in the centre and decreased towards the outside. For web 1, eleven bowls at intervals of 1 m were placed along each of the eight arms from 31 July until 3 August on a regularly mown, but sparse and weedy lawn. The bowls in the innermost ring touched forming a 1 m circle. Webs 2 and 3 were established approximately 100 m apart and were run concurrently from 7 to 9 August in a recently mown meadow approximately 300 m from web 1. In web 2, six bowls were spaced 2 m apart along each leg. In web 3, four bowls were spaced 3 m apart. Captured specimens were pooled by bowl location across all days for each web. Estimates for the distance at which bowls no longer compete used the methods of Link and Barker (1994); Pearson's chi-squared was used to test goodness of fit.

2003 Paired bowls. In 2003, to explicitly test for competition among bowls for captures of bees, three pairs of 177 ml white plastic salad bowls (Solo Brand PB6 0099), whose inner surface was painted fluorescent yellow with Krylon brand spray paint, were set out in Glen Canyon Park, San Francisco, CA, USA. Paired bowls were either touching or spaced 5 or 10 m apart; pairs were at least 50 m from other pairs. Seven trials of each of these three pairs were run from March until early June in various locations in the park. Although the data were distributed normally, the assumption of equal variances was violated and Welch's version of ANOVA which permits unequal variances was used in an analysis of the numbers of bees captured per bowl across the three distances. Following the initial analysis of total number of bees the specimens were inadvertently moved into the general collection and thus the genus level break down is not included in Table 1.

Patterns of captures among bowls

The distribution of captures between peripheral and interior bowls was compared using a series of transects and a grid.

2007 – 25 Bowl transects. In 2007, a series of eleven transects consisting of 25 bowls each, spaced 3 m apart, were established in central Prince George's County, Maryland, USA to examine capture patterns among individual bowls in fields and along roadsides. Transects were run within the first 3 weeks of September.

2004 – Soybean field transects. On July 27, 2004 ten 10-bowl transects (100 bowls) were distributed throughout a 4.43 ha, slightly rectangular, sandy field populated with young soybean plants near Davidsonville, Maryland, USA (latitude 38.9269, longitude -76.6667). Transects were oriented from the field edge to the centre with bowls approximately 9 m apart. Due to lost or spilled bowls eleven bowls were removed from the analysis.

2001 – Desert transects. In May, 2001 a series of eight 30 m transects consisting of 30 bowls each (177 ml, Solo Brand PB6 0099), were established in the Chihuahuan Desert in Arizona, USA and Sonora, Mexico to examine capture patterns

among individual bowls. Samples were taken from four transects on 13 May 2001 at a 1 ha site established in an agricultural field that had been fallow since 1999, from three transects on 7 May 2001 at a 1 ha site established in creosote bush (*Larrea tridentata*) dominated desert scrub habitat, and from one transect on 14 May 2001 established along a dry waterway in undisturbed desert. On each transect, ten yellow, blue and white bowls were alternated 1 m apart. For other details of the region and climate see Minckley (2008).

1997 – Golf course transects. In 1997, three golf courses at the interface of the Columbia Basin and Blue Mountain physiographic provinces of the Pacific Northwest (USA) were sampled weekly: Wild Horse Resort, Pendleton, Oregon (WH), latitude: 45.5971, longitude: -118.6837; Veteran's Memorial, Walla Walla, Washington (VM), latitude: 46.8754, longitude: -118.3404; Horn Rapids, Richland, Washington (HR), latitude: 46.3239, longitude: -119.3199. All are embedded in steppe or shrub-steppe natural vegetation (Franklin & Dyrness, 1988). At each course, a single transect of 45 plastic bowls (355 ml Solo Brand PSB 0099 series) placed at approximately 3 m intervals was set out in the same area each week beginning 1 August. The transect at WH was in a weedy area abutting the golf course proper. At HR, the transect was immediately adjacent to the course in a natural area. At VM, the transect was located in an out-of-play area on the golf course. In each transect, we alternated three plastic bowl colours: white, dark blue, and yellow (see Leong & Thorp, 1999 for spectral reflectances and other details). Bowls were positioned between 0700 and 0800 hours and collected individually between 1500 and 1700 hours. Data were not collected on 24 August and 14 September (WH), 18 September (HR), and 11 October (VM) due to rain. The last sampling dates were 28 August (WH), 2 October (HR), and 18 October (VM). If a bowl was missing or spilled then data for that bowl number was removed from the analysis: consequently, WH had 44 bowls, VM 42, and HR 45 and degrees of freedom for the Chi-square analysis adjusted accordingly.

2001 – 6 × 7 Trapping grid. In 2001, in a study designed to investigate the pattern of captures of bees within a grid of bowl traps, plastic salad bowls (Solo Brand PB6 0099, 177 ml) were placed 3 m apart in a six column, seven row grid in an uncut field of low grass and forbs in Buffalo Gap Community Camp, Capon Bridge, WV, USA (latitude 39.3354, longitude -78.4567). White plastic bowls alternated with dark blue plastic bowls throughout, starting with a white bowl in one corner. The grid was run for 5 days from 15 to 20 July (weather for day 4 was inclement).

Results

The diversity of bees for the five studies in which generic identifications were made is shown in Table 1. They varied in number of bees captured (23–2209) and in number of genera recorded (5–21) primarily due to the number of dates sampled and bowls used. Per bowl captures varied from 0.6 bees per bowl to 6.4. All

Table 1. Total captures of bees by genera in nine pan trap collections across North America.

Genus	Number of bees trapped								
	Web 1	Web 2	Web 3	25B	WH	VM	HR	SBF	CD
<i>Agapostemon</i>	2			5	604	414	48	31	
<i>Andrena</i>				2	2	3			
<i>Anthidium</i>	14		1	4	1				27
<i>Anthophora</i>					38	2	3		
<i>Anthophorula</i>									1
<i>Apis</i>	5	1		16	10	38	8		
<i>Ashmeadiella</i>									27
<i>Augochlora</i>								1	
<i>Augochlorella</i>	7	9	9	6				3	
<i>Bombus</i>	1			1	2	1	1		
<i>Calliopsis</i>	1		1	6	1				14
<i>Ceratina</i>	29	7	5	212	1	1			
<i>Coelioxys</i>				1	1	2	2		
<i>Colletes</i>					6	2	1		
<i>Diadasia</i>					1	2			20
<i>Dianthidium</i>					2	2	17		
<i>Epeolus</i>					1		2		
<i>Eucera</i>									2
<i>Exomalopsis</i>									2
<i>Halictus</i>	9	7	4	18	515	792	43	2	
<i>Hylaeus</i>					2	1			
<i>Lasioglossum</i>	109	4	3	134	889	606	282	311	176
<i>Megachile</i>	3			2	60	56	25	2	5
<i>Melissodes</i>					45	90	29		2
<i>Nomada</i>					2	3			
<i>Perdita</i>							1		35
<i>Sphecodes</i>	1			1	25	18	4	1	
<i>Stelis</i>									3
<i>Tetraloniella</i>									1
<i>Triepeolus</i>							2		
<i>Xeromelecta</i>					1				
Unknown				1					
Total Inds	181	28	23	409	2209	2033	468	351	315
Per bowl	2.1	0.6	0.7	1.5	6.4	4.4	1.2	3.9	1.3
Total genera	11	5	6	13	21	17	15	7	13
% Halictidae	70.7	71.4	69.6	40.1	92.0	90.0	80.6	99.4	55.9

Webs 1–3: trapping webs, Beltsville, MD; 25B: 25 bowl study, Prince George's County, MD; WH, VM, HR: Golf Course Study, Columbia Plateau of Washington and Oregon; SBF: soybean field, Davidsonville, MD; CD: Chihuahuan Desert of Arizona and Mexico. Per bowl, number of captures divided by number of bowl traps.

studies agreed in the preponderance of halictid bees recorded (40.1–99.4%).

Inter-trap competition for bees

2007 – Trapping webs. The three trapping webs suggest that the inter-bowl distance at which competition ceases is between 2.5 and 5 m. For web 1, the calculated distance beyond which bowls no longer competed for bees was 2.67 m (SE = 0.27 m; 95% profile likelihood interval = 2.16–3.18; chi-squared goodness of fit P -value = 0.025) (Table 2). Similarly, the values for web 2 are 3.44 m (0.81 m; 1.88–5.04 m; P = 0.452) and for web 3, 4.78 m (1.29 m; 2.92–8.92 m; P = 0.279).

2003 – Paired bowl. There was a significant effect of distance on the abundance of bees caught in the pairs of bee bowls ($F_{10,33} = 5.002$, $P = 0.030$). While *post hoc* analyses were not significant, bee bowls that were adjacent to one another caught far fewer bees (mean = 4.57) than either the 5 m (mean = 9.71) or 10 m pairs (mean = 8.43).

Patterns of captures among traps

2007 – 25 Bowl transects. For eight transects, bees were independently distributed across bowls; in the three remaining transects captures of bees were more clumped than expected (Table 3).

Table 2. Total number of bees captured within each distance ring of trapping webs 1–3, Beltsville, MD, USA.

Ring	Observed	Modelled
Web 1		
0	2	3.21
1	9	5.71
2	10	8.56
3	6	11.41
4	10	14.26
5	19	17.09
6	13	18.27
7	15	18.27
8	26	18.27
9	29	18.27
10	42	47.67
Web 2		
0	0	1.45
1	3	2.57
2	3	3.86
3	6	5.03
4	8	5.26
5	8	9.84
Web 3		
0	0	2.02
1	4	3.59
2	7	5.39
3	12	12.00

As outer bowls potentially have higher capture rates than inner bowls due to fewer competing adjacent bowls, we repeated the analysis with the outer 2–4 bowls removed. There was no change in the patterns. Green's clumping index was uniformly positive or zero except for one transect; the highest value across transects was only 0.04 (on a scale from -1 to 1, with 1 being most clumped) giving an indication that while clumping may be present it was rather mild (Table 3). When the number of bees

captured in the two end bowls (mean = 2.05, median = 1.00) were compared to those of the interior bowls (mean = 1.44, median = 1.17), a Wilcoxon signed-rank test indicated that end bowls did not capture significantly more bees than inner bowls ($P = 0.248$), although the mean of the end bowls was greater than that of the inner bowls in eight of the eleven transects. None of the runs tests for any of the transects indicated that bowls with either high or low numbers of captures were more likely than chance to occur in clusters near one another.

2004 – Soybean field transects. The dispersion of captures of bees across the bowls indicated that captures at six transects were independent of one another, and that four were more clumped than expected (Table 4). All but two transects had positive values for Green's clumping index with one transect exceeded 0.5 (Table 4).

2001 – Desert transects. The dispersion of bees across bowls indicated that captures on four transects were independent of one another while captures on the other four conformed to a clumped distribution (Table 5). While five of the transects had positive values for Green's clumping index (the other 3 were zero), none of those values exceeded 0.05 indicating that clumping was not great. Only one of the transects gave a significant runs test.

1997 – Golf course transects. Across the three study areas, 4710 individuals of 23 genera were captured (Table 1). The dispersion of captures of bees across the bowls at WH indicated that captures on all seven dates conformed to a clumped distribution of captures across the transect (Table 6). Captures on seven of 11 dates at VM were more clumped than expected; the remaining four were independent of one another. Captures on eight of the nine dates of HR were independent of one another. Across all of the date/transect runs all but one had positive or zero scores for Green's Index (Table 6) and those values were all

Table 3. Trap and dispersion statistics for 11 bee bowl trap transects, Prince George's County, MD, USA.

Transect	Total	Mean per bowl		Index of dispersion	Chi-squared (d.f. = 24)		Green's index	*Chi-squared (d.f. = 22)		†Index of dispersion	†Chi-squared (d.f. = 20)		
		Variance	Dispersion		For ID	Dispersion		For ID	*Dispersion		For ID	†Dispersion	
Site 1	12	0.48	0.43	0.89	27.00	n	0.00	0.93	20.36	n	0.97	19.40	n
Site 2	69	2.76	4.11	1.49	16.13	n	0.02	1.24	27.33	n	1.17	23.43	n
Site 3	14	0.56	0.76	1.35	17.76	n	0.01	1.55	34.00	n	1.50	30.00	n
Site 4	77	3.08	13.49	4.38	5.48	c	0.14	4.21	92.69	c	4.37	87.38	c
Site 5	100	4.00	7.75	1.94	12.39	c	0.04	1.94	42.76	c	2.16	43.22	c
Site 6	31	1.24	2.44	1.97	12.20	c	0.04	2.11	46.34	c	2.19	43.78	c
Site 7	30	1.20	1.33	1.11	21.60	n	0.00	1.21	26.67	n	0.79	15.70	n
Site 8	20	0.80	0.92	1.15	20.95	n	0.01	1.16	25.44	n	1.19	23.76	n
Site 9	31	1.24	1.36	1.09	21.94	n	0.00	1.08	23.67	n	1.18	23.56	n
Site 10	8	0.32	0.31	0.97	24.77	n	0.00	0.77	17.00	n	0.85	17.00	n
Site 11	18	0.72	0.46	0.64	37.57	n	-0.02	0.71	15.63	n	0.80	16.00	n
Pooled	410	16.40	21.08	1.29	18.67	n	0.01	1.22	26.76	n	1.27	25.46	n

Dispersion, n = conforms to normal distribution, c = conforms to a clumped distribution.

*With one bowl removed from each end.

†With two bowls removed from each end.

Transect	Total	Mean per bowl	Variance	Index of dispersion	Chi-square (d.f. = 9)		Green's index
					for ID	Dispersion	
1	24	3.43	5.29	1.54	9.25	n	0.09
2	46	4.60	2.93	0.64	5.74	n	-0.04
3	40	4.00	4.89	1.22	11.00	n	0.02
4	32	3.56	15.28	4.30	34.37	c	0.41
5	36	3.60	4.27	1.19	10.67	n	0.02
6	14	2.00	1.33	0.67	4.00	n	-0.06
7	51	5.10	12.10	2.37	21.35	c	0.15
8	42	4.67	9.50	2.04	16.29	n	0.13
9	46	5.11	13.36	2.61	20.91	c	0.20
10	22	2.75	17.64	6.42	44.91	c	0.77
*Pooled	173	17.30	17.79	1.03	9.25	n	0.00

*Pooled data for each bowl position across all transects with complete data. Dispersion, n = conforms to normal distribution, c = conforms to a clumped distribution.

Table 4. Bee captures and dispersion statistics for 10, 10 bowl trap transects, Davidsonville, MD, USA.

Table 5. Bee captures per bowl and dispersion statistics for eight Chihuahuan desert transects in Arizona, USA and Sonora, Mexico.

Site	Total	Mean per bowl		Index of dispersion	Chi-square for ID (d.f. = 29)	Chi-square 0.975	Chi-Square 0.025	Dispersion	Index of clumping	Green's index
		Variance								
Desert wash	53	1.77	3.84	2.17	63.04	16.05	45.72	c	1.17	0.04
Abandoned field, transect 1	17	0.57	0.81	1.42	41.24	16.05	45.72	n	0.42	0.01
Abandoned field, transect 2	17	0.57	0.60	1.06	30.65	16.05	45.72	n	0.06	0.00
Abandoned field, transect 3	19	0.63	0.59	0.92	26.79	16.05	45.72	n	-0.08	0.00
Abandoned field, transect 4	10	0.33	0.37	1.10	32.00	16.05	45.72	n	0.10	0.00
Desert scrub, transect 1	72	2.40	6.04	2.52	73.00	16.05	45.72	c	1.52	0.05
Desert scrub, transect 2	69	2.30	3.87	1.68	48.83	16.05	45.72	c	0.68	0.02
Desert scrub, transect 3	48	1.60	2.80	1.75	50.75	16.05	45.72	c	0.75	0.03

Dispersion, n = conforms to normal distribution, c = conforms to a clumped distribution.

below 0.10 with the exceptions of one in WH and one in VM of 0.23 and 0.24, respectively. When dates were combined, all three transects had dispersion values that matched that of a clumped distribution. Of the 27 trials only two had significant runs tests and none of the pooled results for the three study areas did.

When the number of bees captured in the two end bowls of WH (mean = 9.21, median = 5.5) were compared to those of the interior bowls (mean = 7.07, median = 7), a Wilcoxon test indicated that end bowls did not capture significantly more bees than interior bowls ($P = 0.467$). On four of the seven dates, the mean of the end bowls was greater than that of the interior. For VM (end: mean = 2.82, median = 2.5; interior: mean = 4.36, median = 3.8) interior bowls caught significantly more bees than end ones ($P = 0.005$) with 10 of the 11 dates having higher interior rather than end means. For HR (end: mean = 1.06, median = 1; interior: mean = 1.16, median = 0.88) captures in end and interior bowls were not significantly different ($P = 1.000$), with six of the nine dates having higher captures in the outer bowls than in the end bowls.

2001 – 6 × 7 Trapping grid. Across the 5 days, 382 bees were captured (captures by day were: 125, 63, 55, 59, 80). The average number of bees/bowl was higher in the interior bowls

than in the peripheral bowls. Per bowl captures for each day with end bowl mean given first, interior second: 2.73, 3.25; 1.14, 1.90; 1.05, 1.60; 1.18, 1.65; 1.64, 2.20. A Wilcoxon test of the pairs neared significance ($P = 0.063$) while a chi-square test was significant ($X_1^2 = 9.45$; $P = 0.002$).

Discussion

Both the trapping web and the paired bowl study explicitly examined competition among bowls for bees, and each demonstrated that bowls placed close together have fewer bees/bowl than those at greater inter-bowl distances. At the extreme, when bowls touch, a foraging bee presumably is simultaneously attracted to either bowl but can only choose one of them. As distance between bowls was lengthened, the rate at which bees were captured increased to a plateau between 3 and 5 m.

While bowls located at the end of a transect or along the periphery of a grid have a higher probability than interior bowls of first encountering a bee, the results of our investigations indicate that the capture rates for outer bowls are not significantly greater, and in some cases are actually lower, than for interior bowls. Consequently, there is preli-

Table 6. Bee captures per bowl and dispersion statistics for 3 multi-day 45 bowl trap transects on the Columbia Plateau of Washington and Oregon, USA.

Date	Total	Mean per bowl	Variance	Index of dispersion	Chi-square		Green's index
					For ID	Dispersion	
<i>Wild horse resort</i>							
8/4	582	13.23	49.58	3.75	161.16	c	0.06
8/10	467	10.61	29.36	2.77	118.94	c	0.04
8/17	333	7.57	23.04	3.04	130.92	c	0.05
8/31	148	3.36	8.14	2.42	104.11	c	0.03
9/7	208	4.73	51.74	10.94	470.62	c	0.23
9/21	302	6.86	22.21	3.24	139.17	c	0.05
9/28	168	3.82	9.45	2.48	106.48	c	0.03
*Pooled	2209	50.20	295.14	5.88	252.79	c	0.11
<i>Veteran's memorial</i>							
8/2	200	4.76	15.99	3.36	137.68	c	0.06
8/9	209	4.98	14.27	2.87	117.56	c	0.05
8/16	230	5.48	6.40	1.17	47.93	n	0.00
8/23	125	2.98	3.83	1.29	52.74	n	0.01
8/30	130	3.10	3.65	1.18	48.34	n	0.00
9/6	146	3.48	5.08	1.46	59.97	n	0.01
9/13	162	3.86	5.93	1.54	63.04	c	0.01
9/20	461	10.98	32.22	2.94	120.35	c	0.05
9/27	161	3.83	41.95	10.94	448.65	c	0.24
10/4	103	2.45	6.79	2.77	113.52	c	0.04
10/18	103	2.45	5.91	2.41	98.84	c	0.03
Pooled	2030	48.40	223.66	4.62	189.45	c	0.09
<i>Horn rapids</i>							
8/1	33	0.73	0.84	1.14	50.18	n	0.00
8/7	116	2.58	2.70	1.05	46.16	n	0.00
8/14	73	1.62	1.69	1.04	45.97	n	0.00
8/21	98	2.18	3.19	1.47	64.55	c	0.01
8/28	54	1.20	1.62	1.35	59.33	n	0.01
9/4	38	0.84	0.77	0.91	40.16	n	0.00
9/11	17	0.38	0.29	0.76	33.29	n	-0.01
9/25	15	0.33	0.41	1.23	54.00	n	0.01
10/2	24	0.53	0.66	1.24	54.75	n	0.01
Pooled	468	10.40	15.79	1.52	66.81	c	0.01

*Pooled across all bowl numbers with complete data. Dispersion, n = conforms to normal distribution, c = conforms to a clumped distribution.

minary evidence that bees may not be captured in the first bowl encountered. Rather, their capture in a bowl may be influenced by the number of bowls nearby much as flower-visitation rates are positively related to flower density (Ohashi & Yahara, 1998).

We expected that the pattern of captures of bees in individual bowls across a transect would show some degree of clumping because of differences in habitat preferences, the vegetation structure along the transect, and the proximity to bee nesting aggregations. If detected, significant clumping would increase both the size of the area required to sample and the number of bowls necessary for an unbiased estimate of the mean relative abundance of a study site. However, while the index of dispersion values from four quite different ecoregions in North America gave evidence for clumping in 26 of 56 transects, clumping was usually slight, with an average value of only 0.06 (Green's index ranges from -1 to 1); only five values exceeded 0.15. Similarly, only three out of the 46 transects, where runs tests were appropriate had significant runs results. Inspection of the patterns of captures

from individual transects in Tables 4-6 indicated that in those transects where the distributions of captures were found to conform to a clumped distribution it was the result of relatively higher and lower numbers of bees captured in bowls across certain stretches of the transects rather than a pattern of high numbers in some sections of the transect punctuated by regions with no bees. Consequently, it seems reasonable that, when laying out bowl surveys in uniform habitats, practitioners need not alter their survey design to accommodate an overly clumped distribution of bees. On the other hand, as these studies only present information about total bee abundance, it remains possible that individual species populations may not be uniformly distributed. Until we investigate the distributions of individual species, it remains wise to disperse bowls and transects throughout a study site rather than assume that species distributions are relatively uniform.

For researchers using bowl traps to conduct status and monitoring surveys, these results indicate that the numbers of bees captured per unit effort is not likely to increase by spac-

ing bowls further than 5 m apart. From a practical perspective, this is useful, as relocating bowls spaced further than 5 m apart without marking their locations each time is often difficult under field conditions. Such short inter-bowl distances decreases travel time and increases the number of bees collected per unit effort.

In this paper, we have evaluated only some aspects of the sampling characteristics of bowl traps: the impacts of inter-bowl distance and bowl position on the capture of bees irrespective of identity. Many other questions remain for study, most obviously, how to best estimate species richness and/or diversity. Trap size, colour and height have been partially studied in past papers (Kirk, 1984; Leong & Thorp, 1999; McIntyre & Hostetler, 2001; Bartholomew & Prowell, 2005; Toler *et al.*, 2005; Campbell & Hanula, 2007; Romey *et al.*, 2007; Krug & Alves-dos-Santos, 2008; Wilson *et al.*, 2008) but low sample sizes for some studies and limited geographic and habitat localities studied warrant more exploration. The number of bowls required to appropriately sample species richness and/or diversity of a site has not been studied and is presently being estimated from datasets where captures and species identifications are tracked for individual bowls. The amount of water, types of surfactants, trap colour patterns, floral scents; and salts, preservatives, and other amendments to the water in traps are also under investigation.

Perhaps the greatest area of need for bowl trap research is a better understanding of how the numbers of bees captured in bowl traps (or any other sampling technique for that matter) relate to the true number of bees in an environment. We do not have a clear picture of whether bowl captures over- or under-represent individuals of different ages, sex, species, nesting status, dispersal status, or their relationship to local habitats and forage opportunities. Consequently, we cannot say that captures of bees in a set of coloured bowls is truly representative of the bee community because we do not have an independent and unbiased assessment of that bee community to compare it to. Studies that experimentally manipulate foraging, nesting, and structural characteristics of bee habitats as well as use marked individual bees are obvious (but costly) next steps in investigating the relationship between bee communities and their capture in bowl traps.

Acknowledgements

SD would like to thank Harold Ikerd for help with identification of specimens, Amy Lohr for running the Soybean Field study and the interns of the Droege lab for their help with specimen preparation and data entry. Leo Shapiro provided a number of insightful comments on early drafts. VJT would like to thank: Melody Mackie Allen, formerly of the Xerces Society, for helping to plan and administer the golf course study; Kimberly Eru-sha and the US Golf Association for funding it; golf course superintendents Sean Hoolahan (WH), Nick Rodrigues (HR) and Joe Towner (WW) for not only putting up with us, but encouraging us; Gretchen Fortner for doing the field and some of the lab work; and Frank Parker and Terry Griswold for identifying the bees.

References

- Allen-Wardell, G., Bernhardt, P., Bitner, R., Burquez, A., Buchmann, S., Cane, J., Cox, P.A., Dalton, V., Feinsinger, P., Ingram, M., Inouye, D., Jones, C.E., Kennedy, K., Kevan, P., Koopowitz, H., Medellin, R., Medellin-Morales, S., Nabhan, G.P., Pavlik, B., Tepedino, V., Torchio, P. & Walker, S. (1998) The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conservation Biology*, **12**, 6–17.
- Ascher, J.S. (2008) *Apoidea Species Guide*. Available from URL: http://www.discoverlife.org/mp/20q?guide=Apoidea_species.
- Axelrod, D.I. (1960) The evolution of flowering plants. *Evolution After Darwin* (ed. by S. Tax), Vol 1, pp. 227–305, The Evolution of Life. University of Chicago Press, Chicago, Illinois.
- Banaszak, J. & Krzysztofiak, A. (1996) The natural wild bee resources (Hymenoptera: Apoidea) of the Wigry National Park. *Polskie Pismo Entomologiczne*, **65**, 33–50.
- Bartholomew, C.S. & Prowell, D. (2005) Pan compared to Malaise trapping for bees (Hymenoptera: Apoidea) in a Longleaf Pine Savanna. *Journal of the Kansas Entomological Society*, **78**, 390–392.
- Buckland, S.T., Anderson, D.R., Burnham, K.P. & Laake, J.L. (1993) *Distance Sampling*. Chapman & Hall, New York, New York.
- Campbell, J.W. & Hanula, J.L. (2007) Efficiency of Malaise traps and colored pan traps for collecting flower visiting insects from three forested ecosystems. *Journal of Insect Conservation*, **11**, 399–408.
- Cane, J.H., Minckley, R.L. & Kervin, L.J. (2000) Sampling bees (Hymenoptera: Apiformes) for pollinator community studies: pitfalls of pan-trapping. *Journal of the Kansas Entomological Society*, **73**, 225–231.
- Committee on the Status of Pollinators in North America. (2007) *Status of Pollinators in North America*. The National Academies Press, Washington, DC.
- Cox-Foster, D.L., Conlan, S., Holmes, E.C., Palacios, G., Evans, J.D., Moran, N.A., Quan, P.-L., Briese, T., Hornig, M., Geiser, D.M., Martinson, V., vanEngelsdorp, D., Kalkstein, A.L., Drysdale, A., Hui, J., Zhai, J., Cui, L., Hutchison, S.K., Simons, J.F., Egholm, M., Pettis, J.S. & Lipkin, W.I. (2007) A metagenomic survey of microbes in honey bee colony collapse disorder. *Science*, **318**, 283–287.
- Franklin, J.F. & Dyrness, C.T. (1988) *Natural Vegetation of Oregon and Washington*. Oregon State University Press, Corvallis, Oregon.
- Giles, V. & Ascher, J.S. (2006) A survey of the bees of the Black Rock Forest preserve, New York (Hymenoptera: Apoidea). *Journal of Hymenoptera Research*, **15**, 208–231.
- Global Biodiversity Information Facility (2008) *Bee Digitization Project*. Available from URL: <http://www.gbif.org>.
- Hammer, Ø., Harper, D.A.T. & Ryan, P.D. (2001) PAST: paleontological statistical software package for education and data analysis. *Palaeontologia Electronica*, **4**, 1.4.
- Hopwood, J.L. (2008) The contribution of roadside grassland restorations to native bee conservation. *Biological Conservation*, **141**, 2632–2640.
- Jacob-Remacle, A. (1984) Etude écologique du peuplement d'Hyménoptères Aculéates survivant dans la zone la plus urbanisée de la ville de Liège. *Bulletin & annales de la société royale d'entomologie de Belgique*, **120**, 241–262.

- Kevan, P.G. (1999) Pollinators as bioindicators of the state of the environment: species, activity and diversity. *Agriculture, Ecosystems & Environment*, **74**, 373–393.
- Kirk, W.D. (1984) Ecologically selective coloured traps. *Ecological Entomology*, **9**, 35–41.
- Klein, A., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. & Tscharntke, T. (2006) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B*, **274**, 303–313.
- Krug, C. & Alves-dos-Santos, I. (2008) O Uso de Diferentes Métodos para Amostragem da Fauna de Abelhas (Hymenoptera: Apoidea), um Estudo em Floresta Ombrófi la Mista em Santa Catarina. *Neotropical Entomology*, **37**, 265–278.
- Kwaiser, K.S. & Hendrix, S.D. (2008) Diversity and abundance of bees (Hymenoptera: Apiformes) in native and ruderal grasslands of agriculturally dominated landscapes. *Agriculture, Ecosystems and Environment*, **124**, 200–204.
- Leong, J.M. & Thorp, R.W. (1999) Colour-coded sampling: the pan trap colour preferences of oligolectic and nonoligolectic bees associated with a vernal pool plant. *Ecological Entomology*, **24**, 329–335.
- Link, W.A. & Barker, R.J. (1994) Density estimation using the trapping web design: a geometric analysis. *Biometrics*, **50**, 733–745.
- Ludwig, J.A. & Reynolds, J.F. (1988) *Statistical Ecology: A Primer on Methods and Computing*. Wiley and Sons, New York, New York.
- Lukacs, P.M., Anderson, D.R. & Burnham, K.P. (2005) Evaluation of trapping-web designs. *Wildlife Research*, **32**, 103–110.
- McIntyre, N.E. & Hostetler, M.E. (2001) Effects of urban land use on pollinator (Hymenoptera: Apoidea) communities in a desert metropolis. *Basic and Applied Ecology*, **2**, 209–218.
- Michener, C.D. (2007) *The Bees of the World*. The Johns Hopkins University Press, Baltimore, Maryland.
- Minckley, R.L. (2008) Faunal composition and species richness differences of bees (Hymenoptera: Apiformes) from two North American regions. *Apidologie*, **39**, 176–188.
- Monsevičius, V. (2004) Comparison of three methods of sampling wild bees (Hymenoptera, Apoidea) in Ėepkeliai Nature Reserve (South Lithuania). *Ekologija*, **4**, 32–39.
- Noyes, J.S. (1989) A study of five methods of sampling Hymenoptera (Insecta) in a tropical rainforest, with special reference to the Parasitica. *Journal of Natural History*, **23**, 285–298.
- Ohashi, K. & Yahara, T. (1998) Effects of variation in flower number on pollinator visits in *Cirsium purpuratum* (Asteraceae). *American Journal of Botany*, **85**, 219–224.
- Packer, L. (2008) *Bee-BOL*. Available from URL: <http://www.bee-bol.org/>.
- Parker, F.D., Batra, S.W.T. & Tepedino, V.J. (1987) New pollinators for our crops. *Agricultural Zoology Reviews*, **2**, 279–304.
- Primack, R.B. (1993) *Essentials of Conservation Biology*. Sinauer Associates, Sunderland, Massachusetts.
- Raven, P.H. & Wilson, E.O. (1992) A fifty-year plan for biodiversity surveys. *Science*, **258**, 1099–1100.
- Ricklefs, R.E. & Renner, S.S. (1994) Species richness within families of flowering plants. *Evolution*, **48**, 1619–1636.
- Riemann, H. (1995) Zur Stechminnenfauna des Bremen Bürgerparks (Hymenoptera: Aculeata). *Naturwissenschaftlicher Verein zu Bremen*, **43**, 45–72.
- Romey, W.L., Ascher, J.S., Powell, D.A. & Yanek, M. (2007) Impacts of logging on midsummer diversity of native bees (Apoidea) in a Northern Hardwood Forest. *Journal of the Kansas Entomological Society*, **80**, 327–338.
- Roulston, T.H., Smith, S.A. & Brewster, A.L. (2007) A comparison of pan trap and intensive net sampling techniques for documenting a bee (Hymenoptera: Apiformes) fauna. *Journal of the Kansas Entomological Society*, **80**, 179–181.
- Toler, T.R., Evans, E.W. & Tepedino, V.J. (2005) Pan-trapping for bees (Hymenoptera: Apiformes) in Utah's West desert: the importance of color diversity. *Pan-Pacific Entomologist*, **81**, 103–113.
- Wells, W. & Decker, T. (2006) A comparison of three types of insect traps for collecting non-formicidae Hymenoptera on the island of Dominica. *Southwestern Entomologist*, **31**, 59–68.
- Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, N., Petanidou, T., Potts, S.G., Roberts, S.P.M., Szentgyörgyi, H., Tscheulin, T., Vaissière, B.E., Woyciechowski, M., Biesmeijer, J.C., Kunin, W.E., Settele, J. & Steffan-Dewenter, I. (2008) Measuring bee diversity in different European habitats and biogeographical regions. *Ecological Monographs*, **78**, 654–671.
- Wilson, J.S., Griswold, T. & Messinger, O.J. (2008) Sampling bee communities (Hymenoptera: Apiformes) in a desert landscape: are pan traps sufficient? *Journal of the Kansas Entomological Society*, **81**, 288–300.

Accepted 16 November 2009

First published online 10 December 2009

Editor: Calvin Dytham

Associate editor: Donald Quicke