

# Effectiveness of Bowl Trapping and Netting for Inventory of a Bee Community

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Environ. Entomol. 40(2): 374–380 (2011); DOI: 10.1603/EN09278

**ABSTRACT** Concern over the status of bees has increased the need to inventory bee communities and, consequently, has increased the need to understand effectiveness of different bee sampling methods. We sampled bees using bowl traps and netting at 25 northwest Indiana sites ranging from open grasslands to forests. Assemblages of bees captured in bowl traps and by netting were very similar, but this similarity was driven by similar relative abundances of commonly captured species. Less common species were often not shared between collection methods (bowls, netting) and only about half of the species were shared between methods. About one-quarter of species were more often captured by one of the two collection methods. Rapid accumulation of species was aided by sampling at temporal and habitat extremes. In particular, collecting samples early and late in the adult flight season and in open and forest habitats was effective in capturing the most species with the fewest samples. The number of samples estimated necessary to achieve a complete inventory using bowls and netting together was high. For example,  $\approx 72\%$  of species estimated capturable in bowls were captured among the 3,159 bees collected in bowls in this study, but  $\approx 30,000$ – $35,000$  additional bees would need to be collected to achieve a 100% complete inventory. For bowl trapping, increasing the number of sampling dates or sampling sites was more effective than adding more bowls per sampling date in completing the inventory with the fewest specimens collected.

**KEY WORDS** bees, inventory, netting, bowl trapping, sampling

Concern over the status of pollinators (National Research Council 2007) has led to increased efforts to document and monitor bee faunas worldwide (Westphal et al. 2008). Development of efficient sampling and monitoring protocols to meet these goals requires quantification of sources of variability in capture of bees during surveys. Progress has been made in this documentation. For example, differences in which bees, and how many bees, are collected from a site by netting versus bowl trapping have been assessed (Roulston et al. 2007, Westphal et al. 2008, Wilson et al. 2008), generally concluding that the two collection methods are partly complementary in the compilation of a complete bee fauna. Bowl trap color (Toler et al. 2005) and trap placement within study plots (Tuell and Isaacs 2009, Droege et al. 2010) affect which, and how many, bees are collected in a survey.

We assess how bees collected using bowl trapping and netting differ and how bowl color affects which bees are collected. However, beyond comparing how bee faunas collected by bowl trapping and netting differ, we attempt to understand how sampling intensity affects the completeness of inventories (Chao et al. 2009). Inventories repeated through time at mul-

multiple locations are one method for monitoring pollinator status. Assessment of inventory completeness is important in designing such monitoring schemes.

Comparisons in this study are based on bee surveys carried out to assess habitat use patterns of bees across a gradient of woody vegetation in upland areas in northwest Indiana, representing the historic grassland to forest transition zone of prairies, savannas, woodlands, and forests that once dominated this region (Grundel et al. 2010). However, the historic northwest Indiana native landscape has been almost completely converted to agriculture and industrial and residential development (Nuzzo 1986) and the three areas surveyed in this study represent a substantial fraction of the remaining grasslands and savannas in the northwest corner of Indiana. Surveys were conducted across months (April–September) when most adult bees were flying. Based on results from this study, museum records, and results of prior and nearby studies (Pearson 1933), we expect our northwest Indiana study sites to have a bee fauna of moderate richness, perhaps 200–300 species. The sampling intensity employed for this study, bowl trapping and netting over the course of an entire flight season, might also be considered moderate in that it covered a complete flight period but did not repeat the surveys over several years. Therefore, the results presented may be looked at as arising from an experimental and ecolog-

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ical situation that might be fairly typical of those outcomes occurring in many locales, surveys, and studies.

### Materials and Methods

We surveyed bees in northwest Indiana at 25 sites within three locations: Indiana Dunes National Lakeshore (41° 38' N, 87° 09' W;  $n = 17$  sites); Tefft Savanna Nature Preserve and Jasper–Pulaski Fish and Wildlife Area (41° 10' N, 86° 58' W;  $n = 7$  sites); and Hoosier Prairie Nature Preserve (41° 31' N, 87° 27' W;  $n = 1$  site) (Grundel and Pavlovic 2007, Haney et al. 2008, Grundel et al. 2010). Sites were located from 0.8 to 80 km from the southern shore of Lake Michigan and averaged  $1.8 \text{ km} \pm 0.7 \text{ SEM}$  between nearest neighbor sites. The sampling sites spanned a range of woody vegetation densities, from nearly treeless, open grasslands and forb dominated habitats to forests. Sampling sites were classified as open (<20% canopy cover measured with a spherical densiometer); savanna (20–50%); woodland (50–90%), scrub (>1,000 woody stems 2.5–10 cm diameter at breast height (dbh)  $\text{ha}^{-1}$ ); or forest (>90% canopy cover and >300 woody stems  $>10 \text{ cm dbh ha}^{-1}$ ) (Grundel and Pavlovic 2007). Five samples of each habitat type were represented by the 25 sites.

At each site, bees were surveyed along a single 270-m transect by netting and along the central 160 m of the transect by capturing in colored bowl traps (Roulston et al. 2007). For netting surveys, we slowly walked the transect line, examining plants for bees and captured any bees observed, over an average observation time of  $88 \text{ min} \pm 3 \text{ (SEM)}$ . For bowl trapping at each site, we placed out nine sets of 178-ml plastic bowls with one bowl of each set painted fluorescent blue, fluorescent yellow, or left as the original white. Bees were attracted to the bowls and drowned in soapy water filling the bowls. Along the transect, bowl triplets (one blue, one yellow, one white) were separated by 20 m. Within a triplet, bowls were separated from each other by 5 m and the triplet was oriented perpendicular to the transect line. During a survey day, bowls were left out for a mean duration of  $303 \text{ min} \pm 3 \text{ (SEM)}$  between 0930 and 1430 hours. At each site, bowl surveys were carried out approximately once every 25 d from 30 May to 17 September 2003 and from 14 April to 8 July 2004 for a total of seven surveys spanning the entire April to September main adult flight season. At each site, netting was also carried out approximately once every 25 d from 14 April 2004 to 9 September 2004, again for seven cycles spanning the flight season. The first three netting cycles were carried out concurrently with bowl surveys. Only bees identified to species (99% of bees collected) were used in the analyses presented here.

We used  $\chi^2$  analysis to assess whether different bee species were more likely to be captured in bowls of certain colors. Because multiple species were tested individually, we used the Benjamini–Hochberg procedure (Benjamini and Hochberg 1995) to adjust probabilities for multiple testing (R Development Core Team 2009).

We compared the similarity of samples collected in bowls and by netting by enumerating the number of shared species collected by the two methods and by computing a Sørensen similarity index, which is based on which species are, and are not, shared between samples, regardless of the abundances of the species (Chao et al. 2005). In this classic Sørensen similarity index, sharing an abundant species will have the same effect on the index as sharing a rare species between samples. However, when trying to determine how many species two samples might have in common, or how similar two samples might be, it is also important to consider the effects that incomplete sampling and abundances can have on the outcome. Chao and colleagues (Chao et al. 2000, 2005) devised a modified Sørensen similarity index that is based on the probability that individuals selected from two samples, such as the sample of all bees we collected by netting and in bowls, are species shared between the two collection methods. They further modified their index to account for species unseen in a sample because of insufficient sampling. We report these modified indices, using the program EstimateS, version 8.20, for calculations (Colwell 2009). These calculations are coverage-based estimators of shared species (Chao et al. 2000); therefore, we included an abundance based coverage estimate (ACE) of species richness in the samples to allow comparison of estimated species richness in samples and the number of species the samples are estimated to share in common.

Chao et al. (2009) present a model for estimating the additional sampling effort necessary for obtaining different percentages of all species estimated to occur at a site but that were not actually encountered during sampling. For this model, the total number of species estimated to occur at a site is calculated using the Chao2 nonparametric estimator, which derives estimated number of species occurring in a sampling area based on the supposition that the greater the number of species occurring in only one or two samples, the more likely it is that additional species are present that have not been encountered during sampling (Gotelli and Colwell 2001). Chao et al. (2009), manipulated the basic equation for the Chao2 estimator to derive a formula (equation 15) estimating additional sampling effort necessary to obtain different fractions of the Chao2 estimate of species present in a sampling area and capturable by a given sampling method.

More species may be found if we put out more bowls for collecting bees. However, new bowls can be added in several ways: bowls can be put out on additional dates, bowls can be put out at new sites or in new habitats, and the size of the transects can be increased by adding more bowl triplet sets to each site. We used the Chao et al. (2009) model to estimate which of these methods of increasing sample size was likely to capture the most additional species with a given level of additional sampling effort.

To evaluate the relative effectiveness of bowl trapping and netting in accumulating species, we pro-

duced species rarefaction (accumulation) curves for the samples collected in bowls and by netting (Colwell et al. 2004, Colwell 2009). Rarefaction curves represent the expected number of species captured ( $Y$ ) for a given number of samples collected ( $X$ ). The  $X$  variable in the curve was expressed as number of bees collected across the sites sampled, as recommended by Gotelli and Colwell (2001) for species richness rarefaction curves. Expected number of species captured for a given number of sites sampled was calculated using the Mao *tau* richness function, which yields the same result as calculating expected number of species via resampling the sites without replacement (Colwell et al. 2004, Colwell 2009). If the 95% confidence intervals of the netting and bowl rarefaction curves do not overlap, we can say that the curves are significantly different from each (Colwell et al. 2004). If their confidence intervals do overlap, a formal significance test is needed to determine whether the curves are, in fact, not significantly different (Schenker and Gentleman 2001). For formal significance testing, we used a randomization test (Manly 2007) in which we resampled the sampling units (e.g., sites), without replacement, 1,000 times and determined how many species would have been collected in bowls or by netting for a specific number of bees (e.g., 500) collected in each of the 1,000 trials. The sampling unit was a site so resampling represented randomly reordering the 25 sites and determining how species accumulated as bees were collected at each successive site. Although the sampling unit was the site, we expressed results in terms of number of bees collected across the sites resampled (Gotelli and Colwell 2001). To evaluate the number of species present at a specific number of bees, we interpolated resampling results so, for example, if, in a specific resample, 450 bees and 30 species were present across six sites and 550 bees and 40 species were present at seven sites, we estimated that 35 species would have been present if 500 bees had been collected. Once we had estimated how many species were present for a given number of bees collected in a resampling, we calculated the difference in number of species between bowl resampling  $i$  and netting resampling  $i$  ( $i$  = resampling run 1-1000) and examined whether the 95% confidence interval for the differences, in this case the interval between the 25th and 975th largest resampling differences, included zero. If the interval did include zero, the difference between species numbers for netting and for bowls at that number of bees collected was not significant at  $P < 0.05$ , otherwise netting and bowls were significantly different in the number of species present for the given number of bees collected.

Optimal species accumulation curves were described by ordering actual samples in a manner that reached the maximum number of species observed with the fewest samples. These optimal curves allowed us to examine which sampling schemes might be most efficient in producing the most complete inventories with the least sampling effort.

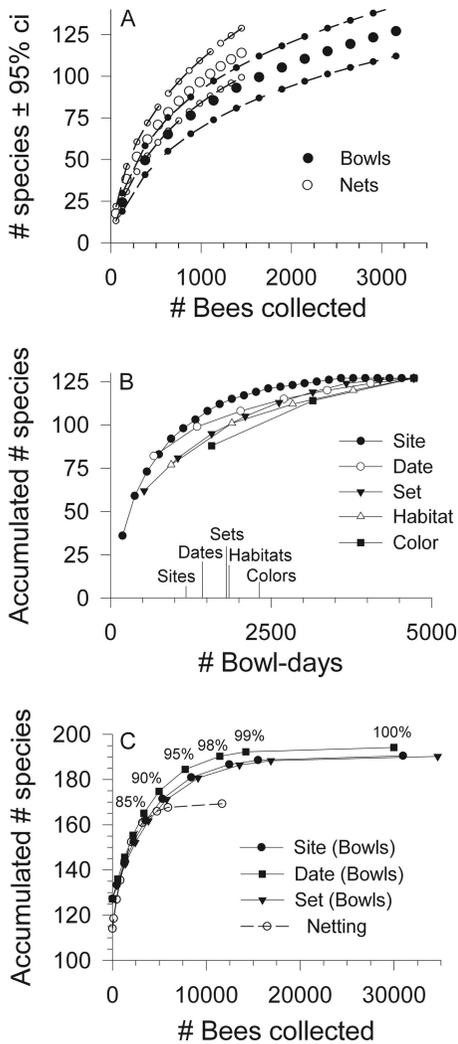
## Results

Of the 171 species identified for this study, 57 (33%) were collected only in bowls; 44 (26%) only by netting; and 70 (41%) by both methods. Overall, 127 species were captured in bowls and 114 by netting. Of the 30 bee species collected at least 25 times, an arbitrary limit designating bees that were relatively common in our surveys, at least 95% of the specimens of seven species were collected either in bowls or by netting: *Perdita bequaerti* (0 collected in bowls:28 by netting), *Bombus impatiens* (1:64), *Apis mellifera* (8:153), *Lasioglossum coeruleum* (38:2), *Colletes inaequalis* (58:0), *Lasioglossum svenki* (29:0), and *Hoplitis producta* (26:0). By family, the percentage of specimens captured in bowls, as opposed to by netting ( $n$  = total number of specimens collected) was: Halictidae (77%,  $n$  = 2798 specimens); Megachilidae (70%,  $n$  = 244); Andrenidae (62%,  $n$  = 254); Apidae (54%,  $n$  = 1050); Colletidae (43%,  $n$  = 283); and Mellitidae (0%,  $n$  = 2).

The number of bees collected in bowls of different colors was blue (1,034); white (1,114); and yellow (970). These frequencies varied significantly among colors ( $\chi^2 = 10.0$ , d.f. = 2,  $P = 0.007$ ). The number of bee species collected in bowls of different colors was blue (87), white (86), and yellow (83). These frequencies were not significantly different among colors ( $\chi^2 = 0.1$ , d.f. = 2,  $P = 0.95$ ). Of the 171 species identified, 23 were captured at least 25 times in bowls. Of these 23, 13 (57%) varied significantly between bowls of different colors ( $\chi^2$  test,  $P < 0.05$ , adjusted for multiple tests [Benjamini and Hochberg 1995]). Because there were three bowl colors, a given species will either be captured equally in all three colors or will be captured more often in one of the colors or less often in one of the colors than expected based on equal capture frequency in each color. Of the 13 bee species with a significant difference, six were found less frequently in yellow bowls than expected based on equal capture across all bowl colors (*Agapostemon virescens*, *Augochlorella aurata*, *Ceratina strenua*, *L. coeruleum*, *Perdita gerhardi*, and *Perdita svenki*); three were found more frequently than based on equal capture in yellow bowls (*Hylaeus mesillae*, *Lasioglossum pilosum*, and *Lasioglossum vierecki*); three were found more frequently than based on equal capture in white bowls (*Ceratina calcarata*, *Ceratina dupla*, and *Osmia pumila*); and one was found more frequently than based on equal capture in blue bowls (*Agapostemon splendens*).

The number of species captured in bowls ( $24.3 \pm 6.3$  SD,  $n = 25$ , range 14-36) and by netting ( $17.6 \pm 10.6$ ,  $n = 25$ , range 1-34), per site across sampling periods, were moderately correlated ( $r = 0.54$ ,  $P = 0.006$ ,  $n = 25$  sites). Based on a randomization test, the estimated number of species captured by netting was significantly greater ( $P < 0.05$ ) than the number of species captured in bowls, at a given number of bees collected, if >905 bees were collected (Fig. 1A).

Abundance coverage estimates (ACE) of richness were 176 for bowls of which the 127 captured repre-



**Fig. 1.** Number of bee species captured in northwest Indiana using different levels of sampling effort. (A) Expected accumulation of species ( $\pm 95\%$  confidence intervals indicated by lines with smaller symbols) with the accumulation of specimens, based on rarefaction, using Mao *tau* richness function (Colwell et al. 2004, Colwell 2009). Sample units are collecting sites. Curves are shown for sampling using bowls and netting separately. These curves are significantly different (randomization test) beyond 905 bees collected. (B) Accumulation of 127 species captured in bowls, over the course of 4,725 bowl-days of sampling, if samples were ordered to achieve most rapid accumulation of species. Sampling units include sites ( $n = 25$ ; 189 bowl-days per site), collecting dates ( $n = 7$  cycles; 675 bowl-days per cycle), number of sets of bowls per transect ( $n = 9$ ; 525 bowl-days per set), habitats ( $n = 5$ ; 945 bowl-days per habitat), and bowl colors ( $n = 3$ ; 1,575 bowl-days per color). Markers on x-axis indicate the number of bowl-days required to capture 100 of the 124 species actually captured for the different sampling units. Order of most rapid species accumulation: Dates: 1) 14 April to 19 May, 2) 20 August to 17 September, 3) 20 May to 13 June, 4) 25 June to 22 July, 5) 15 June to 8 July, 6) 30 May to 23 June, and 7) 23 July to 19 August; Habitats: Open-Forest-Woodland-Savanna-Scrub; Color: Blue-Yellow-White. (C) Predicted number of bees needed to be

sent 72%, 171 for netting of which the 114 captured represent 67%, and 223 overall of which the 171 captured represent 77%. As noted, 70 species (41% of all species actually captured) were in common between the two sampling methods. The number of species estimated to be shared between netting and bowl collections (Chao et al. 2000, Colwell 2009) was 113 out of the 223 species (51%) estimated to be present by the ACE estimator. The Classic Sørensen similarity index, a measure of similarity of species composition between samples, was 0.58 between the overall samples obtained by bowls and by netting across sites and was 0.74 between blue and white bowls, 0.67 between blue and yellow bowls, and 0.73 between white and yellow bowls. Chao's Sørensen abundance-based similarity index (Chao et al. 2005, Colwell 2009) that measures similarity based on species composition and abundance, was 0.90 and, corrected for unseen species, was  $0.97 \pm 0.03$  SE, between bowls and netting samples.

The mean number of bees collected per bowl per day was  $0.66 \pm 1.51$  (SD) (range, 0–20) ( $n = 4,725$  bowl-days) (one bowl-day equals one bowl left out for 1 d of sampling) or  $2.18 \pm 2.05$  ( $n = 1,435$  bowl-days) for bowl-days on which at least one bee was collected in a bowl. The percentage of bowl-days ( $\log_{10}$  transformed) ( $Y$ ) with  $X$  bees captured per bowl was well described ( $R^2 = 0.98$ ) by a quadratic relationship  $Y = (1.621 \pm 0.089[\text{SEM}]) - (0.372 \pm 0.021) X + (0.011 \pm 0.001) X^2$ . All coefficients were significant at  $P < 0.001$  ( $t$ -test,  $n = 21$  categories of number of bees captured per bowl). Most bowl-days ( $n = 3,290$  of 4,725 bowl-days, 70%) had no bee captures and, overall, 84 of the 675 bowls (12%) had no captures across 7 d of sampling between April and September. The number of bowls with no captures differed significantly among habitat types (Open 2, Savanna 15, Woodland 11, Scrub 31, Forest 25;  $n = 135$  bowls per habitat,  $\chi^2 = 35.7$ , d.f. = 4,  $P < 0.001$ ).

The minimum number of transect-days (1 d sampling of one transect of 27 bowls at a site) that could have captured all of the 127 species actually captured by bowls in this study was 40 out of 175 transect-days. Of the 127 species captured in bowls, 18.9% ( $n = 24$  species) were captured in the most species-rich transect in a single day and the fewest transect-days in which more than half (65 of 127) of the species were captured was six. These six transect-days occurred in early season (late April and early May) scrub (two transects with 24 and 12 additional species, respec-

collected to obtain new bee species (beyond the 127 actually captured in bowls and 114 by netting), as calculated by methods of Chao et al. (2009). The bees collected would be additional specimens beyond the 3,159 actually collected in bowls and 1,448 by netting and identified to species. The maximum number of additional species likely to be captured in bowls or by netting was estimated by the Chao2 nonparametric richness estimator (Chao 1987). Each subsequent symbol on a curve represents 70%, 75%, 80%, 85%, 90%, 95%, 98%, 99%, and 100% of the estimated maximum number of species capturable.

tively) and woodland (nine species) transects; a mid-season savanna (eight species); and early season (late May) (seven species) and late season (late August) (five species) open transects.

There are many ways in which new samples can be added. For instance, within the habitats sampled, we can add more triplet sets of bowls to each transect beyond the nine triplets (27 bowls) already deployed, we can add more sites beyond 25, or we can maintain the deployed sites and number of bowls per site but increase the number of sampling dates beyond seven. An arbitrary benchmark of 100 species of the 127 total species collected in bowls can be reached in fewer bowl-days by adding sites than by adding new collecting dates, bowl sets, habitats, or bowl colors (Fig. 1B). Species were collected most rapidly if the samples were collected at the beginning (April and May) and end (August and September) of the season, and in the habitat extremes (open and forest).

Based on the method of Chao et al. (2009) for estimating number of samples required to achieve different proportions of complete inventory, the estimated number of bees needed to be captured to achieve different levels of inventory completeness (for bees collectable in bowls) varied somewhat among the three ways of increasing sampling effort (Fig. 1C). For example, a complete inventory of bees achieved by increasing sampling dates required an estimated 29,998 more bees collected than the 3,159 collected in bowls, while a complete inventory achieved by increasing the number of triplets per transect required an estimated 34,648 bees and captured somewhat fewer species. Regardless of the method of adding samples, the number of additional samples to reach a complete inventory was great, although reaching 100% of bees predicted capturable by netting required many fewer bees than by trapping in bowls, and netting was predicted to capture fewer bee species than did bowls (Fig. 1C).

## Discussion

Several findings important for the design of bee community surveys are suggested by the results of this study. First is the degree of complementarity between bowl trapping and netting surveys. We estimated overall that about half of the species (51%) would likely be found in both bowl and netting surveys so about half would be taken in only one of the survey methods. However, among species that were most prevalent in samples, only about one-quarter of the species were significantly better captured either in bowls or by netting, suggesting that either method is at least somewhat effective in capturing about three-quarters of these more common species. Based on these results overall and from more abundant species, we infer that either bowls or netting are likely to be effective in inventorying most of the common species, but that bowls and netting are likely to be complementary in completing inventories of less common species.

As in other studies (Roulston et al. 2007), Halictidae were, in comparison to other bee families, more likely to be captured in bowls than by netting. Nonetheless, for the more common species tested here, the species that did exhibit a tendency for capture in bowls or by netting often exhibited a different tendency than seen in other regions. For example, Wilson et al. (2008) found that *Perdita* were predominantly collected in bowl traps and *Colletes* were mainly detected by netting in the Great Basin Desert of western Utah. Roulston et al. (2007) also collected *Colletes* mainly by netting. In our study, *P. bequaerti* was common and exclusively captured by netting and *C. inaequalis* was common and exclusively captured in bowls, even though overall the family Colletidae was more prone to be captured by netting than in bowls compared with the other bee families (except Mellitidae, which was only captured twice, both times by netting). Thus, caution should be used when developing generalizations about potential prejudices of different survey methods for bee fauna.

Second, approximately one-quarter of tested species exhibited a preference for, or an aversion to, a particular bowl color, usually yellow. Although much of the benefit of using three bowl colors to document richness may arise from the mere tripling of number of bowls deployed for sampling, color diversification, in and of itself, may account for a quarter of the species richness documented by bowls as suggested by the percentage of species prone to be captured in or avoid a particular bowl color and by the similarity of species composition (0.67–0.74) between bowl colors. Thus, species compositions are moderately complementary among bowl colors. Most bowls (70%) deployed over the course of the study did not capture any bees. For those bowls that did, about two bees per bowl were captured and overall  $\approx 0.66$  bees per bowl were captured per day, when bowls without captures were included. Such data are useful in calculating adequate sample effort for planned studies.

Third, if abundance is taken into account, and especially if unseen species are considered statistically (Chao et al. 2005), the probability is very high (97%) that two randomly chosen individuals, one from the netting samples and one from the bowl samples, both belong to species shared by both sets of samples. However, we also estimated that only about half of the species captured would be shared between bowls and netting. The much higher similarity (97%) between bowls and netting when abundance was taken into account than when it was not (58%) implies that the more commonly collected species were more likely to be shared, resulting in the high abundance based similarity, while many of the rarer species were not shared between collecting methods. Based on estimated richnesses for bowls, netting, and overall, the percentages of all species captured in bowls (176 of 223) and by netting (171 of 223) were similar but each would miss about one-quarter of the species estimated to be present. Although bowl trapping and netting were, in some ways, complementary, species capture rates were higher for netting than for collection in bowls in that

more species were typically present in a collection of a given number of bees from netting than from bowl trapping at the levels of inventory completeness ( $\approx 67\%$  for netting and  $72\%$  for bowl trapping) achieved in this study (Fig. 1A).

Fourth, although more than half of the species present in bowls could be collected in as few as six transect-days, with 27 bowls per transect, it would be difficult to predict exactly which sites and times would need to be employed to achieve this level of completeness with that little effort. However, inclusion of early and late season collecting was important in filling in the inventory with minimum effort (Fig. 1B). The habitats where this efficacious sampling would take place were not necessarily the most species-rich habitats overall. For example, early season sampling in scrub habitats contributed most to rapid initial accumulation of species in an inventory with minimum effort, although overall scrub habitats were more likely than any of the other habitats sampled to have bowls in which no bees were collected. In general, sampling at habitat extremes, open and forest in this study, achieved the most rapid accumulation of species. Thus, for both collection date and collection habitat, collecting at the extremes was central to minimizing sampling effort while moving toward inventory completeness.

Fifth, if the goal of collecting is achieving as complete an inventory as practical, there is a question as to whether each additional unit of sampling effort is best spent by allocating that additional effort to 1) sampling on more days, 2) sampling additional sites, 3) placing out more trapping bowls on a transect, or 4) putting more effort into netting than into bowl trapping. In this study, the rate of species accumulation with accumulation of specimens was higher with netting than with bowl trapping at the levels of inventory completeness achieved in this study (Fig. 1A) and an estimated complete inventory of species likely to be collected by netting required fewer specimens captured than for bowl trapping. However, bowl trapping was estimated to capture more species (Fig. 1C). Adding more sampling dates or sites proved more efficacious than adding more bowls per transect in achieving a complete inventory of bee species likely collected in bowls in that a complete inventory was projected to be achieved with fewer bees collected (Fig. 1C). These results suggest that increasing number of specimens captured by increasing the number of collecting dates is an effective way of accumulating species as is the strategy of collecting at habitat and date extremes.

It is important to note that these examinations of effectiveness of different sampling schemes compare the different schemes on the basis of how many species are collected for a given number of samples obtained. This analysis does not take into account the costs, benefits, and some possible biases associated with different collection methods. For example, an advantage of bowl traps is that collecting bees is not dependent on the skill of the collector, except possibly in determining the placement of the bowls, and a

single collector can often deploy many sets of bowls simultaneously on a given day. Netting, however, is influenced by the collector's skill; different collectors will likely have different rates of bee collection and will likely collect different bees, and a single collector can only collect at one site at a time (Westphal et al. 2008).

Finally, bowl trapping is increasingly recommended as the standard methodology for large scale surveys, in part because of its perceived consistency among collectors (Westphal et al. 2008). In northwest Indiana, completing one cycle of bowl collecting, seven temporal samples in this study, at a single site would yield an average of  $\approx 24$  species, with a range of 14–36 species. Thus, a single sample (one set of bowl samples at one site collected over the course of seven days spread across the bee flight season) might collect  $\approx 10\%$  of the estimated species present across this region. However, the expected effort required to discover  $>98\%$  of species is quite high. For example,  $\approx 72\%$  of species estimated likely to be captured in bowls across our study area were actually captured by bowls at the level of effort expended in this study. To increase that percentage to  $90\%$  would have required us to collect  $\approx 5,000$  more bees in bowls, beyond the 3,159 actually captured (Fig. 1C). To capture an estimated  $100\%$  of the species in bowls would have required adding 30,000 or more bees beyond the 3,159 captured. Thus, a steep price must be paid, in terms of sampling effort, to go from fairly complete inventory to  $100\%$  completion. This raises the question of how complete an inventory is adequate for a given situation. From a statistical viewpoint, this could be addressed by looking at species accumulation curves, such as in Fig. 1, and stopping collection when the curve begins to flatten, if a nearly complete inventory without excessive collection is desired. From an experimental viewpoint, the goal of the project might be paramount in determining when to stop collecting. In this northwest Indiana study, our goal was to compare bee communities among habitat types. In such a study, obtaining a mix of species that represents how assemblages of bees vary among habitat types is adequate, a complete inventory is not necessary, and collecting a moderate percentage of the species present, such as  $\approx 75\%$  in this study, is likely adequate. However, for conservation purposes, the least abundant species will likely be difficult to collect but especially prone to extirpation. In such a case, a more complete inventory, based on tactics such as survey timing outlined in this paper that increase the rates of species accumulation, would be more appropriate, although removing many bees from an area can raise concerns about possible effects of collecting intensity on the local bee fauna.

### Acknowledgments

We thank Sam Droege and Jason Gibbs for assistance in bee identification, Gary Glowacki for assistance in the field, Jan Adams for recommending the randomization test, and Leo Shapiro and Joy Marburger for comments on the manuscript. Support for this project was provided by the USGS

Grasslands Research Funding Initiative and by the National Park Service Inventory and Monitoring Network. Research was conducted with permission and assistance of the National Park Service and the Indiana Department of Natural Resources, Division of Nature Preserves. Specimens used for this publication are currently deposited in the museum of Indiana Dunes National Lakeshore, Porter, IN. This article is Contribution 1610 of the U.S. Geological Survey Great Lakes Science Center.

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Received 30 September 2009; accepted 20 December 2010.