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COMPARATIVE EFFECTIVENESS OF NIGHTTIME VISUAL ENCOUNTER SURVEYS AND COVER OBJECT SEARCHES IN DETECTING SALAMANDERS

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***Abstract.*— I compared numbers of the plethodontid salamanders *Desmognathus fuscus, D. monticola, Eurycea cirrigera, Gyrinophilus porphyriticus*, *Plethodon cinereus*, and *P. glutinosus* detected during nighttime visual encounter surveys to those detected during cover object searches along paired belt transects to evaluate whether individuals of each species were more likely to be detected using one method than the other. Significantly more *P. glutinosus* were detected during visual encounter surveys than during cover object searches of adjacent transects at the same sites. This resulted from higher detection of adult *P. glutinosus* during the visual encounter surveys. There were no significant differences in numbers of individuals detected using the two methods for the remaining species. However, visual encounter surveys were significantly more likely to detect the presence of *G. porphyriticus* and *P. glutinosus* at a site than were cover object searches, and tended to yield more adult *G. porphyriticus* than did cover object searches. Adults of all species used wider cover objects and were found deeper beneath cover than were juveniles, and *P. glutinosus* and *G. porphyriticus*, the two largest species, used deeper cover and wider cover objects than the remaining species. These trends indicate that visual encounter surveys are optimal for detecting large-bodied plethodontids that frequently use large and/or deeply embedded cover objects that restrict access to retreats during cover object searches. Visual encounter surveys and cover object searches were both far superior to searches of arrays of cover boards, which were effective for sampling *P. cinereus*, but none of the other species.**

Key words.—cover object; cover object search; plethodontidae; salamander; survey method; visual encounter survey

INTRODUCTION

Lungless salamanders (Plethodontidae) are often the dominant vertebrate animals, in terms of numbers and biomass, in moist forest ecosystems of North America (Hairston 1987; Petranka and Murray 2001). Plethodontids are sensitive to environmental variation such as spatial and temporal changes in vegetation, cover, soil pH, and environmental moisture (Wyman 1988; Grover 1998; Herbeck and Larsen 1999; Knapp et al. 2003), and have been proposed as ideal indicators of forest ecosystem integrity (Welsh and Droege 2001). In addition, plethodontid populations appear to respond to landscape-level processes such as habitat fragmentation and the influence of matrix habitat (Kolozvary and Swihart 1999; Grover and Wilbur 2002). Furthermore, although long-term data sets are rare, there is evidence that many populations of plethodontid salamanders have undergone recent declines (Highton 2005).

In light of the usefulness of plethodontids as indicator species and the need to assess the status and temporal dynamics of plethodontid populations, the acquisition of accurate survey data and the establishment of long-term monitoring programs are of critical importance. However, because of their moist, permeable skin and reliance on cutaneous respiration, plethodontid salamanders usually restrict their foraging activities in terrestrial habitats to periods of rainfall or high humidity, are active almost exclusively at night, and spend the majority of the time in moist microenvironments beneath cover objects (e.g., course woody debris or leaf litter) or in subterranean retreats (Taub 1961; Feder 1983). Even during favorable conditions, the majority of individuals present in an area are likely to be beneath cover or in subterranean retreats at any given time. Consequently, counts of salamanders encountered or captured during surveys are highly dependent on environmental conditions and are most appropriately used as indices of abundance that are potentially correlated with actual abundances. One way to overcome this limitation is to use mark-recapture or removal sampling to estimate actual abundances of plethodontid species within an area (Petranka and Murray 2001; Bailey et al. 2004). Unfortunately, given the potentially high population densities and low detection probabilities of plethodontids, these methods are generally very time consuming and labor intensive. An alternative is to use counts obtained by searching for active salamanders during periods of optimal environmental conditions or by searching beneath natural cover objects within a survey area. Counts of active salamanders during optimal conditions and counts of salamanders in retreats beneath cover objects tend to be positively correlated with actual abundances (Smith and Petranka 2000; Flint and Harris 2005). In addition, count data obtained from searching beneath cover objects or from visual surveys of active salamanders can be standardized to provide abundance index data if the surveys are conducted during a set time period (time-constrained) or within a defined area (area-constrained). However, much of the variation in count data can be caused by factors other than variation in actual abundances (Dodd and Dorazio 2004).

The use of survey techniques that minimize unexplained variation in detection probabilities is important in studies of salamander population trends and in surveys designed to determine the presence or absence of rare salamander species. Smith and Petranka (2000) advocated the use of area-constrained cover object searches based on data showing a positive correlation between counts from cover object searches and mark-recapture abundance estimates, and the dependence of salamander surface activity on environmental conditions (i.e., temperature and moisture levels). However, surveys of active salamanders at night (nighttime visual encounter surveys) tend to be relatively effective if conducted during optimal conditions for salamander activity, with variation in numbers of salamanders encountered during such surveys being related to variation in actual abundances

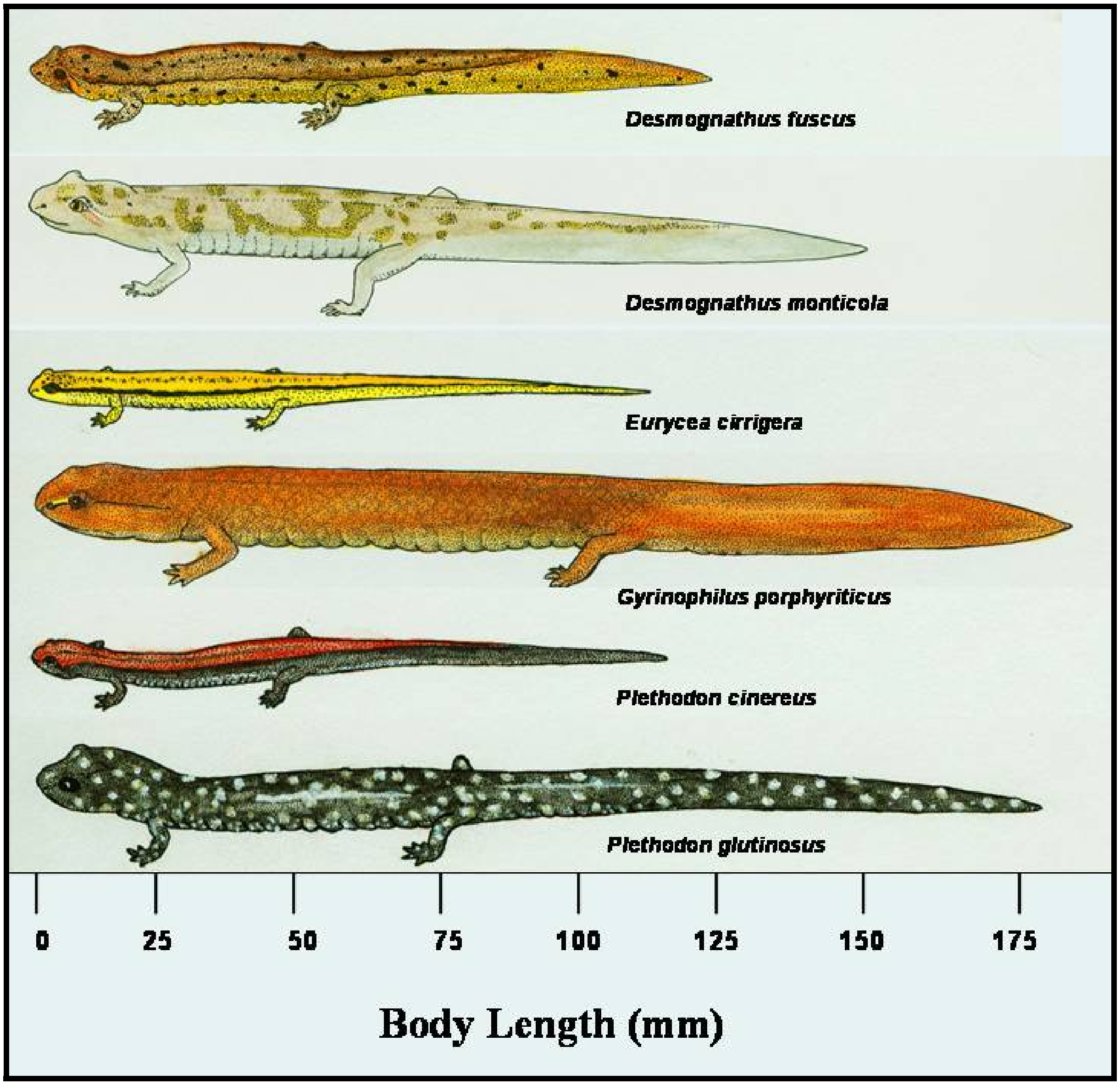

FIGURE 1. The six species of plethodontid salamanders for which data were collected during cover object searches and visual encounter surveys of paired transects. Illustrated by Sherilynn S. Grover.

(Williams and Berkson 2004; Flint and Harris 2005). Furthermore, different species of plethodontid salamanders exhibit significant differences in the depths of their retreat sites and the sizes and types of cover objects that they use (Southerland 1986; Grover 2000). Consequently, the relative numbers of different species of plethodontid salamanders detected in cover object searches could be biased if certain types or sizes of cover objects are more easily searched than others, which is inevitable when large embedded boulders and logs are used as cover by salamanders. In addition, cover object searches may fail to detect species that use retreats within or beneath complex three-dimensional cover, such as talus (Flint and Harris 2005) or arboreal habitats (Spickler et al. 2006). Bias in encounter frequency is probably not limited to cover object searches. Multiple studies have documented that activity levels of small-bodied plethodontids are more strongly curtailed by suboptimal environmental conditions than are activity levels of large-bodied plethodontids (Grover 1998; Petranka and Murray 2001; Bailey et al. 2004). This suggests that species-specific and age-specific biases in detection probabilities are likely in visual encounter surveys if surface activity is at all curtailed by environmental conditions. Thus, both cover object searches and visual encounter surveys have the potential to be limited by sampling bias. However, no formal comparison and assessment of the relative strengths and weaknesses of these two survey methods has been reported.

I evaluated the relative effectiveness of the area-constrained cover object search (COS) method and nighttime visual encounter survey (VES) method by comparing numbers of plethodontid salamanders of six species detected using each method on paired belt transects at eight sites in Giles County, Virginia (Fig. 1). Each of the transects spanned the moisture gradient from stream to upland forest habitat and included habitats of four semi-aquatic species (*Desmognathus monticola*, *D. fuscus*, *Gyrinophilus porphyriticus*, and *Eurycea cirrigera*) and two terrestrial species (*Plethodon cinereus* and *P. glutinosus*). Data on cover objects

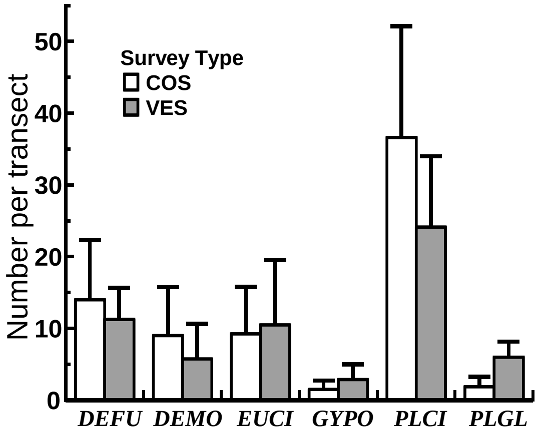

FIGURE 2. Average number (±2 SE) of *Desmognathus fuscus* (*DEFU*), *D. monticola* (*DEMO*), *Eurycea cirrigera* (*EUCI*), *Gyrinophilus porphyriticus* (*GYPO*), *Plethodon cinereus* (*PLCI*), and *P. glutinosus* (*PLGL*) detected during cover object searches (COS) and visual encounter surveys (VES) on paired transects at eight sites in the vicinity of Mountain Lake Biological Station, Giles County, Virginia USA.

and relative numbers of juveniles and adults of each species collected and analyzed to evaluate whether detection probabilities were related to interspecific and age-specific differences in cover object properties, and whether either juveniles or adults of each species were more likely to be encountered using one survey method than the other. I also compared data on the species and relative abundances of salamanders detected during searches of two arrays of artificial cover objects (i.e., cover boards) to VES and COS data from transects near the arrays of cover boards.

MATERIALS AND METHODS

The study was conducted in the Allegheny Mountains in the vicinity of Mountain Lake Biological Station (MLBS), Giles County, Virginia (37º 22’ N; 80º 31’ W). I searched for salamanders on 5 m wide transects, each of which intersected a first order stream and extended 20 m perpendicularly from the edge of the stream into the terrestrial habitat on each side. Two adjacent parallel transects were delineated at each survey site. One of the two transects was surveyed for active salamanders using a VES conducted during optimal conditions (within 24 hours of the most recent rainfall when the relative humidity was close to 100%, leaf litter and surface vegetation were wet or damp, and there was little or no wind). The other was subject to a COS for salamanders in retreats during the day. The VESs and COSs were conducted from 1-5 days of one another at each site. Each transect was searched only once and all area within the transect, including the stream, was searched. There was a total of eight pairs of transects, with two sets of paired transects located at each of four first order streams (Hunters Branch, Pond Drain, Sartain Branch, and Saltpeter Branch). All transects were within 3 km of MLBS at elevations between 1070 and 1220 m. A description of the study area is given in Grover (2000).

Performing a COS on a transect entailed turning over all potential cover objects (rocks, logs, sticks, and bark) and sifting through leaf litter by hand, in areas where substantial leaf letter was present, to find salamanders in retreats. When a salamander was located, the type of cover (litter, wood, or rock) was noted and the depth of the salamander beneath cover was determined by measuring the thickness of cover directly above the salamander to the nearest mm. In addition, when a salamander was found beneath a rock or wooden cover object, the length, width, and thickness of the cover object were measured. The maximum width was measured along an axis running perpendicular to the

TABLE 1. Numbers of individuals of *Desmognathus fuscus*, *D. monticola*, *Eurycea cirrigera*, *Gyrinophilus porphyriticus*, *Plethodon cinereus*, and *P. glutinosus* detected on 5 m wide transects extending 20 m on each side of stream habitat on four headwater streams near Mountain Lake, Virginia. Numbers of juveniles and adults, respectively, are shown in parentheses. Paired transects, one subject to a cover object survey (COS) and one subject to a nighttime visual encounter survey (VES) were located at each survey site. Two survey sites were located on Hunters Branch (HB1 and HB2), two on Pond Drain (PD1 and PD2), two on Sartain Branch (SB1 and SB2) and two were located on Saltpeter Branch (SP1 and SP2).

		STUDY SITE							
Species	Survey Type	HB1	HB2	PD1	PD2	SB1	SB2	SP1	SP2
D. fuscus	COS	17 (5, 12)	3 (0, 3)	12 (5, 7)	20 (3, 17)	1 (0, 1)	5 (1, 4)	37 (23, 14)	17 (8, 9)
	VES	13 (5, 8)	13 (1, 12)	2 (0, 2)	15 (1, 14)	1 (0, 1)	14 (9, 5)	15 (6, 9)	17 (7, 10)
D. monticola	COS	0	1 (0, 1)	27 (13, 14)	3 (0, 3)	10 (6, 4)	19 (13, 6)	9 (5, 4)	3 (2, 1)
	VES	1 (1, 0)	0	8 (2, 6)	1 (1, 0)	15 (3, 12)	17 (6, 11)	4 (1, 3)	0
E. cirrigera	COS	31 (16, 15)	5 (2, 3)	7 (1, 6)	2 (0, 2)	5 (3, 2)	4 (3, 1)	11 (1, 10)	9 (8, 1)
	VES	40 (20, 20)	14 (9, 5)	4 (0, 4)	2 (1, 1)	3 (2, 1)	3 (2, 1)	6 (2, 4)	12 (12, 0)
G. porphyriticus	COS	0	0	0	1 (0, 1)	1 (1, 0)	2 (2, 0)	3 (3, 0)	5 (5, 0)
	VES	1 (1, 0)	1 (0, 1)	1 (0, 1)	1 (0, 1)	5 (3, 2)	4 (3, 1)	1 (0, 1)	9 (9, 0)
P. cinereus	COS	87 (36, 51)	38 (8, 30)	38 (7, 31)	14 (2, 12)	24 (11, 13)	34 (20, 14)	32 (7, 25)	26 (7, 19)
	VES	33 (15, 18)	42 (16, 26)	8 (2, 6)	5 (2, 3)	35 (11, 24)	15 (7, 8)	35 (9, 26)	20 (3, 17)
P. glutinosus	COS	2 (1, 1)	3 (0, 3)	2 (2, 0)	1 (1, 0)	0	1 (1, 0)	6 (5, 1)	0
	VES	7 (3, 4)	3 (1, 2)	9 (1, 8)	11 (0, 11)	2 (2, 0)	5 (4, 1)	7 (3, 4)	4 (1, 3)

TABLE 2. Mean snout to vent length (SVL) and SVL range of juvenile and adult salamanders of each species surveyed on transects. Measurements were taken on salamanders captured during visual encounter surveys of transects and on several additional salamanders captured within the general vicinity of transects.

	SVL (mm)					
	Juveniles			Adults		
Species	**Mean**	**Range**	***n***	**Mean**	**Range**	***n***
D. fuscus	30.63	15.38 – 38.87	18	49.48	37.76 - 65.17	52
D. monticola	35.73	16.78 - 47.47	43	60.79	42.90 - 74.40	81
E. cirrigera	23.67	18.88 - 29.89	36	37.77	25.23 - 44.35	46
G. porphyriticus	61.70	51.11 - 81.03	5	96.14	83.26 - 106.47	13
P. cinereus	26.91	20.14 - 35.03	55	40.98	33.69 - 48.49	102
P. glutinosus	39.69	19.44 - 57.17	26	67.27	56.54 - 78.46	31

axis of maximum length. The maximum thickness was measured along an axis orthogonal to the other two axes.

Each VES involved systematically searching a transect for active salamanders with a headlamp until the entire area of the transect had been inspected. No cover objects were manipulated during a VES, but surface substrates and low-growing vegetation were methodically searched. The location of each salamander sighted during a VES was marked with a numbered flag and, whenpossible, salamanders were captured and placed individually in numbered plastic bags containing wet leaf litter and transported to laboratory facilities at MLBS following the survey. The sex and reproductive status of each salamander was determined by the presence and condition of oviducts or testes, which were visible when the salamander was trans-illuminated using a fiber-optic light. This information facilitated the classification of individuals as either juveniles or adults. In addition, several of the captured salamanders of each species were also were measured (SVL; snout to the posterior edge of the vent to the nearest 0.01 mm) using digital calipers and weighed to the nearest 1 mg on an electronic balance to determine the range of body sizes of juveniles and adults. Captured salamanders were released the following evening at the exact locations at which they were initially detected. Salamanders encountered during cover object searches were not removed from their retreats, but were identified and categorized as juveniles or adults based on size and external appearance.

An alternative survey technique to the COS and VES methods is the use of cover boards as artificial cover objects (ACOs), which can be placed in desired locations to attract salamanders and inspected on one or more occasions (Monti et al. 2000). Results of the VESs and COSs at the two sites on Sartain Branch were compared to the results of searches of two arrays of ACOs, in the form of 20 cm × 20 cm × 2.5 cm oak cover boards, positioned 1-25 m from the stream along transects spanning Sartain Branch and extending perpendicularly into the forest on each side. There were 200 cover boards in each array. The arrays of cover boards were each inspected once and the species and age class of each salamander detected was noted at the time of the search.

For each of the species, I used Wilcoxon signed ranks tests to compare numbers of salamanders detected during COSs and numbers detected during VESs on adjacent transects. The nonparametric Wilcoxon signed ranks tests were used instead of paired *t*-tests because individuals of *D. monticola*, *G. porphyriticus*, and *P. glutinosus* were rarely detected (i.e., 0–1 individuals) on some of the transects. These same analyses were repeated with juveniles and adults of each species considered separately. Values reported for the test statistic in the Wilcoxon signed ranks tests (W) were obtained by subtracting the absolute value of the sum of the negative ranks from the absolute value of the sum of the positive ranks. The probability of obtaining a particular value of W depends on the number of ties subtracted from the total number of pairs (n_{sr}).

I used two-way ANOVA to determine whether species and age-classes differed with respect to the depth beneath cover at which they were found while in retreats. Two-way ANOVA was also used to determine whether individuals belonging to different species and age-classes differed with respect to the sizes of cover objects that they used. Cover object width was the dependent variable in this analysis. Data on cover objects were obtained from the transect searches and from searches of additional plots reported in Grover (2000). These data were used to evaluate whether size differences in cover objects use by individuals of different salamander species or of different age-classes corresponded to interspecific or age-specific differences in encounter frequencies during cover object searches.

RESULTS

Numbers of salamanders of each species detected on the paired transects at each site are shown in Table 1. For most of the species, numbers of individuals detected during COSs were similar to the numbers detected during VESs (Fig. 2). There were no significant differences in numbers of individuals detected during COSs and numbers detected during VESs for each of the four semi-aquatic semi-aquatic species ($P > 0.10$). Among the terrestrial species, there was not a significant difference in the numbers of *P. cinereus* detected during COSs and the numbers detected during VESs ($W = 20$, $n_{sr} = 8$, $P = 0.195$), but significantly fewer *P. glutinosus* were detected during COSs than during VESs ($W = -28$, $n_{sr} = 7$, $P = 0.022$).

When juveniles and adults were considered separately, it was apparent that adult *P. glutinosus* were less likely to be detected during COSs than during VESs ($W = -25$, $n_{sr} = 7$, $P = 0.043$), whereas the difference in numbers of juvenile *P. glutinosus* detected using the two survey methods was not significant ($W = -14$, $n_{sr} = 8$, $P = 0.363$). Adult *P. glutinosus* were not detected on five of the eight COSs, compared to only one of the eight VESs. A similar pattern was evident for *G. porphyriticus*, for which adults were not detected on six of the eight COSs of transects, compared to two of the eight VESs of adjacent parallel transects. In no case did a COS yield more adult *G. porphyriticus* than a corresponding VES. However, due to the small sample size (adults were not detected using either method at two sites), the difference in numbers of adult *G. porphyriticus* detected using the two methods was only marginally significant ($W = -15$, $n_{sr} = 5$, $P = 0.059$). The relatively low encounter rates of adult *G. porphyriticus* and *P. glutinosus* during COSs made COSs less effective than VESs for confirming the presence of these species. VESs confirmed the presence of *G. porphyriticus* and *P. glutinosus* at all eight sites, whereas *G. porphyriticus* was not detected during COSs at three sites and *P. glutinosus* was not detected during COSs at two additional sites. The detection of

Table 3. Mean depth beneath cover and mean cover object width (to the nearest 0.1 cm) used by juvenile and adult salamanders of each species.

Species	Age-class	Depth	*n*	Width	*n*
D. fuscus	Juvenile	4.1	121	11.3	100
	Adult	6.1	231	13.5	213
D. monticola	Juvenile	6.0	57	14.2	52
	Adult	7.3	53	19.9	50
E. cirrigera	Juvenile	4.2	31	9.7	16
	Adult	5.6	68	10.3	53
G. porphyriticu	Juvenile	4.7	5	14.5	4
	Adult	15.2	8	21.0	8
P. cinereus	Juvenile	5.5	119	10.1	86
	Adult	7.5	441	12.3	403
P. glutinosus	Juvenile	8.7	19	11.1	19
	Adult	12.9	20	25.0	19

both *G. porphyriticus* and *P. glutinosus* on all eight VESs but only three of the COSs was unlikely under the assumption that both methods have equal detection probabilities for these species ($P < 0.013$ in a Fisher exact test). Individuals of *G. porphyriticus* and *P. glutinosus* tended to be larger than individuals of the remaining species (Fig. 1; Table 2). This was especially true for adult *G. porphyriticus*, which did not overlap in size with adults of any of the other species. Thus, it is likely that there was a general pattern of lower detection of large adult salamanders during COSs than during VESs. In the case of *P. glutinosus*, this had a significant impact on the total number of individuals detected as well.

The mean depths of surface retreats and widths of the cover objects used by salamanders of each species and age-class are shown in Table 3. Two-way ANOVA revealed that the species exhibited significant differences in the depths of their retreats beneath cover ($F_{5,\ 1160} = 20.93$, $P < 0.001$) and that adults were found beneath deeper cover than juveniles ($F_{1,\ 1160} = 45.80$, $P < 0.001$). There was also a significant species × age-class interaction ($F_{5,\ 1160} = 2.27$, $P < 0.046$), which resulted primarily from *G. porphyriticus* and *P. glutinosus* adults being found beneath deeper cover than adults of all other species (Fig. 3). Likewise, cover object widths differed significantly between species ($F_{5,\ 1011} = 16.35$, $P < 0.001$) and age-classes ($F_{1,\ 1011} = 20.11$, $P < 0.001$), with larger-bodied species using wider cover objects than smaller-bodied species, and adults using wider over objects than juveniles. Again, there was a significant species × age-class interaction ($F_{5,\ 1011} = 3.47$, $P < 0.004$), which was evident in the shift to especially wide cover objects exhibited by adult *P. glutinosus* relative to juvenile *P. glutinosus*. The overall trends were that the three larger-bodied species (*D. monticola, G. porphyriticus,* and *P. glutinosus*) tended to use wider cover objects than those used by the smaller-bodied species, adults used wider cover objects and were found beneath deeper cover than juveniles, and retreats of adult *G. porphyriticus*, and *P. glutinosus* were found beneath particularly deep cover (Fig. 3).

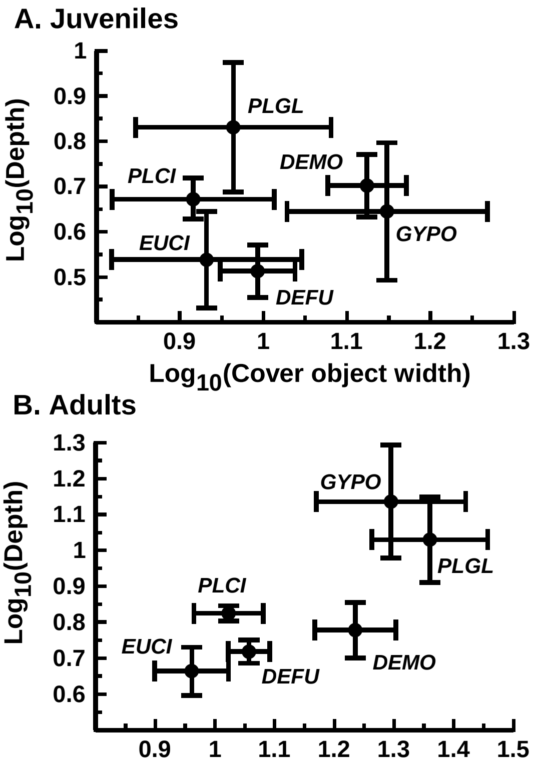

Figure 3. Average width of cover objects and depth beneath cover for juveniles (A) and adults (B) of each of the six salamander species surveyed. Abbreviations are as in Figure 2. Values shown are averages (±2 SE) of $\log_{10}$ transformed data.

The searches of the two arrays of cover boards at Sartain Branch yielded a total of 52 salamanders (27 at one site and 25 at the other), all of which were *P. cinereus* except for a single juvenile *P. glutinosus*. By contrast, all six focal species were detected during both VESs and one of the two COSs of the transects at Sartain Branch, and all species except *P. glutinosus* were detected during the other COS. The total numbers of *P. cinereus* were similar for the three survey methods, with 51 individuals (25 juveniles and 26 adults) detected within the two arrays of cover boards, 58 individuals (31 juveniles and 27 adults) detected during the two COSs, and 50 individuals (18 juveniles and 32 adults) detected on the two transects subject to VESs. The three methods did not differ significantly in the relative numbers of juvenile and adult *P. cinereus* detected during the surveys ($\chi^2 = 3.471$, df = 2, $P = 0.176$). Thus, the use of large numbers of artificial cover objects, in the form of cover boards, was an effective means of sampling *P. cinereus*, the smaller of the two terrestrial species, but failed to detect any of the four semi-aquatic species and was of limited usefulness in detecting *P. glutinosus*.

DISCUSSION

Very few studies have directly compared the relative effectiveness of cover object searches (COSs) and visual encounter surveys (VESs). Hairston (1987) reported that greater numbers of individuals of *Desmognathus quadramaculatus*, *D. monticola*, and *D. ochrophaeus* were detected when plots were searched using VESs than when COSs were employed, but did not formally analyze these differences. The greatest difference was for the largest and most aquatic species, *D. quadramaculatus* (3.75 times more individuals were detected during VESs than COSs), and the smallest difference was for the smallest and most terrestrial of the species, *D. ochrophaeus* (1.65 times more individuals detected during VESs than COSs). By contrast, individuals of *D. aeneus*, a small and secretive terrestrial species, were detected six times more frequently during daytime COSs than during nighttime VESs. This illustrates that the effectiveness of a survey method depends on the size, habitat, and activity patterns of the target species. The choice of one survey method over another may also depend on objectives or logistical constraints. For example, Williams and Berkson (2004) found that *P. cinereus* placed in small mesocosms were more likely to be detected using COSs than nighttime VESs (unless only VES data from within 12 hours of the most recent precipitation were included), but that VES data exhibited less temporal variability, making VESs potentially more useful for repeated sampling aimed at detecting population trends.

In the present study, relative numbers of individuals detected using COSs and VESs were compared for an ecologically diverse assemblage of six plethodontid salamander species at eight sites in the Allegheny Mountains of southern Virginia. The transects at these sites spanned a range of habitats, from stream to upland forest. The use of multiple sites with a range of habitats was important to the scope of the study because habitat features (e.g., vegetation) can have a significant influence on the detectability of plethodontid salamanders (Bailey et al. 2004), and the effectiveness of the two search methods might vary with habitat characteristics. COSs and VESs yielded fairly similar counts on adjacent parallel transects for four of the six species, including three semi-aquatic species found in stream and streamside environments and a fully terrestrial woodland species, *P. cinereus*. The fact that COSs performed as well as VESs for these species, but are less constrained by fluctuating environmental conditions, indicates that COSs might be preferred over VESs when it is difficult or impractical to restrict searches to periods of optimal conditions for salamander activity. However, adults of the largest of the terrestrial species and the largest of the semi-aquatic species were under-represented in COSs. Adults of both of these species used large and difficult to manipulate cover objects, compared to those used by the other species. In addition, both of these species frequently use burrows beneath large and embedded boulders or among tree roots (pers. obs.). Thus, their retreats are often inaccessible during cover object searches tendency for large adults of certain species to escape detection in COSs could potentially lead to three problems: (1) biased demographic information for large-bodied species; with relative abundances of adults being underestimated; (2) underestimates of relative abundances of large-bodied species; and (3) failure to detect rare large-bodied species. The latter problem was evident for *P. glutinosus*, which was not detected on two of the eight COSs, and for *G. porphyriticus*, which was not detected on three of the eight COSs. Both of these species were detected on all transects subject to VESs.

Because aboveground foraging is more strongly curtailed by dry conditions than is the use of surface cover objects (Taub 1961; Jaeger 1980), VESs are likely to be more sensitive than COSs to short-term reductions in environmental moisture (Williams and Berkson 2004). Occasionally, detection of *P. cinereus* appeared to be lower during VESs than during COSs (i.e., the surveys of Hunters Branch Site 1 and both Pond Drain sites), but VESs performed comparably to COSs in detecting *P. cinereus* at other times. Activity levels of small terrestrial plethodontids, such as *P. cinereus*, tend to fluctuate with fluctuating environmental conditions to a greater extent than the activity levels of larger terrestrial species (Grover 1998; Smith and Petranka 2000; Bailey et al. 2004), which is a potential pitfall in using simple count data from VESs to compare relative abundances of species. Conducting VESs only during optimal environmental conditions (i.e., nights when humidity is near 100%, surface substrates are moist, and the temperature is mild) can minimize this problem. Conversely, high moisture levels can cause terrestrial salamanders to move from beneath cover objects into surrounding leaf litter (Jaeger 1980), which could potentially reduce the effectiveness of a COS. Consequently, a COS is likely to be most effective when the search involves sifting through leaf litter in addition to searching beneath solid cover objects.

The strengths and weaknesses of the use of cover boards for surveying terrestrial salamanders have been explored using data on *P. cinereus* (Monti et al. 2000; Marsh and Goicochea 2003; Williams and Berkson 2004). My results confirm that cover boards can be useful for sampling *P. cinereus*, but demonstrate that they can be very ineffective for sampling semi-aquatic and large terrestrial plethodontids. Surprisingly, semi-aquatic species did not use cover boards at all, even when the cover boards were positioned within one meter of stream habitat. The lack of cover board use by semi-aquatic species probably resulted from multiple factors. For example, large semi-aquatic species use a high proportion of rock cover objects and are most often found in retreats in water or within a few meters of water in association with saturated soil, whereas the small terrestrial species *P. cinereus* favors wooden cover objects and is usually found in association with moist, but unsaturated, soil (Grover 2000). Thin wooden cover objects, such as cover boards, probably fail to provide adequate shelter and suitable microenvironments for large semi-aquatic salamanders. Large terrestrial species, such as *P. glutinosus*, tend to inhabit relatively dry retreats (Grover 2000), but their use of wide and thick cover objects as adults minimizes the likelihood that they will be found beneath cover boards. Cover boards attracted numbers of *P. cinereus* that were comparable to numbers detected in VESs and COSs, and there was no evidence that cover board use by *P. cinereus* was demographically biased. However, Marsh and Goicochea (2003) found lower proportions of juvenile *P. cinereus* beneath cover boards than under natural cover objects. A similar pattern has been reported for *P. vehiculum* and *Aneides vagrans* on Vancouver Island, British Columbia (Davis 1996). Thus, cover boards appear to be unsuitable cover objects for many plethodontids, and have the potential to provide demographically biased samples for species known to use them frequently.

The most important trend evident in the comparisons of the VESs and COSs at each of the study sites was the tendency for individuals of the two largest species (particularly adults) to be detected more frequently in VESs than in COSs. The use of relatively inaccessible retreats by these species (*G. porphyriticus* and *P. glutinosus*) is a likely explanation for this trend. I found no definitive evidence that COSs were more effective than VESs for detecting any of the six focal species on my study sites. I recommend using VESs conducted during optimal environmental conditions when surveying large-bodied plethodontid species and entire communities of plethodontids. However, secretive species that seldom forage aboveground and in the open may be detected most efficiently using COSs (Hairston 1987). In addition, COSs can be more practical for surveying populations of small-bodied plethodontids that are especially sensitive to fluctuations in environmental conditions, particularly when surveys must be conducted during a fixed time frame. Thus, the choice of a survey method should be made in light of information regarding the characteristics and habitats of the target species, and may also be dependent on time constraints.

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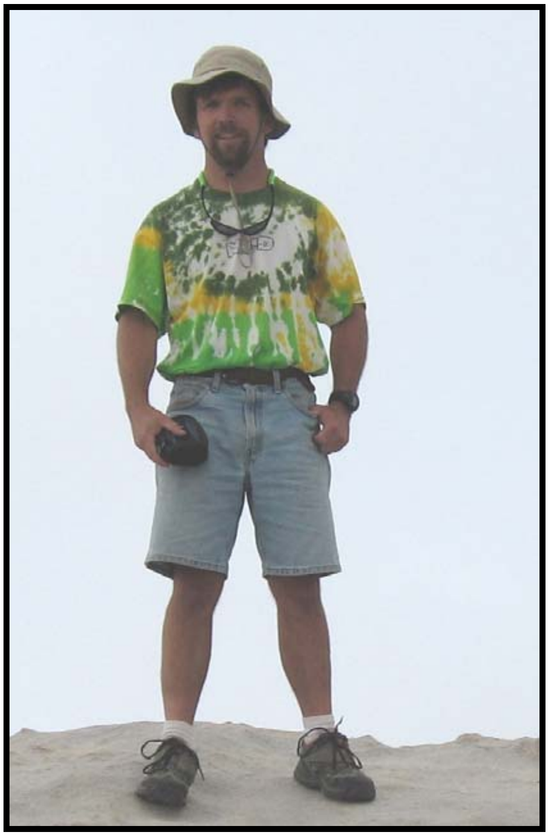

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