Grant, B. W., A. D. Tucker, J. E. Lovich, A. M. Mills, P. M. Dixon, and J. W. Gibbons. 1992. The use of coverboards in estimating patterns of reptile and amphibian biodiversity. Pages 379-403 *in* R. Siegel and N. Scott (eds.). Wildlife 2001. Elsevier Science Publ., Inc. London, England.

THE USE OF COVERBOARDS IN ESTIMATING PATTERNS OF REPTILE AND AMPHIBIAN BIODIVERSITY

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Abstract. Reptiles and amphibians play important roles in ecological communities and can be extremely sensitive indicators of environmental change, despite their cryptic and secretive habits. To estimate herpetofaunal community dynamics potentially attributable to either natural or anthropogenic environmental variation, herpetofaunal biodiversity managers will require specific, standardized, and efficient field sampling methods. One such method involves using arrays of wood and tin coverboards and is the subject of this paper. Studies were conducted on the Savannah River Site in the Upper Coastal Plain of South Carolina from January 1988 to August 1991. Compared with a drift fence/pitfall trap array, the coverboard technique requires less maintenance and sampling effort, but only those reptiles and amphibians using the coverboards at the time of an array check could be encountered. In contrast, live-trapping methods integrate over a longer time period and thereby generate many more encounters per trap. Nonetheless, large numbers of encounters with cryptic reptiles and amphibians can result from coverboard sampling depending upon the study site, coverboard age, time of day, and type of coverboard (i.e., wood or tin). Detailed analyses of hydric and thermal microclimates beneath coverboards suggest specific mechanisms to explain observed differences in herpetofaunal coverboard use. We conclude that the coverboard technique can provide a useful means to quantify patterns in herpetofaunal relative abundance and biodiversity. However, array design and sampling protocol should be carefully selected to minimize sampling biases in encounter probabilities due to subtle differences among herpetofauna in their hygrothermal microclimate preferences.

INTRODUCTION

Forecasting the effects of landscape level management practices or impending global climate change on the dynamics of animal populations and community biodiversity

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is a worldwide concern (Wilson 1985, Brussard 1991, Mooney 1991*a*, *b*, Pechmann et al. 1991, Wake 1991, Wake and Morowitz 1991). Such studies are important because naturally occurring levels of biodiversity are critical to preserve, not only because of the potential economic or medical benefits yet to be uncovered, but also because maintaining biodiversity is synonymous with maintaining an intact ecosystem within which we too must live (Soulé and Wilcox 1980, Wilson 1985).

Reptiles and amphibians have long been recognized as major biological components in some habitats (Gibbons and Bennett 1974, Burton and Likens 1975). Due to their low metabolic rates, high energy conversion efficiencies, and astonishing reproductive potentials, herpetofauna provide important links in ecological food chains, the loss of which may be indicative of impending ecosystem destabilization and collapse (Burton and Likens 1975, Vitt et al. 1990). However, reptiles and amphibians are among the more difficult groups to assess in field biodiversity studies because of their small size and fossorial behavior (Gibbons 1988). This necessitates the development and implementation of indirect sampling schemes that exploit patterns of individual activity and microclimate preferences of cryptic herpetofauna to facilitate captures and analyses. Thus, herpetofaunal biodiversity managers will require specific, standardized, and efficient field sampling methods in order to estimate population dynamics potentially attributable to either natural or anthropogenic environmental variation.

Several sampling techniques have been successfully used in the past to census herpetofauna. Many are based upon live-trapping of individuals using funnel traps or pitfall traps typically associated with a fixed drift fence (e.g., Corn and Bury 1990, Pechmann et al. 1991). However, these trapping methods are time and labor intensive and can result in injury to captured individuals either due to physical stress, such as overheating, desiccation, drowning, or to predation (Gibbons and Semlitsch 1981). Another sampling method involves timed opportunistic searching by a trained collector or "time-constrained searching" (Campbell and Christman 1982, Corn and Bury 1990). This method generates encounter rates of herpetofauna in the microclimates (e.g., beneath litter or woody debris) where they naturally occur. However, each observer's speed and efficiency at finding reptiles and amphibians will be complexly determined by physical habitat characters that affect observer movement rate as well as by each observer's ability to develop appropriate search images. Thus, it may prove difficult to compare encounter data among study sites or teams of collectors.

The use of ground cover by reptiles and amphibians is well known, and the collecting technique of searching for individuals under such cover is universal among herpetologists (Stebbins 1966, Conant 1975). However, standardized sampling of fixed arrays of artificial cover, which we refer to as coverboards, has been used in only a few studies even though large numbers of individuals can be encountered (Jensen 1968, Fitch 1987).

The coverboard technique has several advantages over live-trapping methods (funnel or pitfall traps) because a coverboard array does not require comparable levels of maintenance and frequent surveillance, and coverboard use by individual amphibians and reptiles poses a lower injury risk than being trapped (Gibbons and Semlitsch 1981). On the other hand, trapping methods integrate herpetofaunal encounters over a longer time period (depending on the checking frequency) than do the instantaneous encounter methods of either time-constrained or coverboard sampling.

Coverboards are potentially advantageous to time-constrained sampling because there is little or no observer effect on searching, and furthermore it is unnecessary to ransack herpetofaunal microhabitats (such as ripping apart stumps or digging into litter) during searches for reclusive individuals. Coverboards provide fleeting windows to the forest floor that when closed leave little trace of the collector's gaze.

A major objective of this study was to determine the effectiveness of using arrays of artificial coverboards to census cryptic and elusive herpetofauna. In this paper, we compare herpetofaunal encounter rates beneath coverboards deployed in different habitat types on the Savannah River Site (SRS) in the Upper Coastal Plain near Aiken, South Carolina, USA. We also compare herpetofaunal encounter rates from a coverboard array with data from an adjacent drift fence/pitfall trap array. In addition, we varied specific aspects of coverboard array design and checking protocol to see how these affected herpetofaunal encounter rates. Finally, we investigated microclimatic mechanisms potentially affecting coverboard use by individual reptiles and amphibians. Our methods were designed to lead to specific recommendations on the implementation of the coverboard technique in field situations. Clearly, standardized methods are critical to conducting quantitative herpetofaunal biodiversity research.

METHODS

Our artificial coverboards are sheets of plywood chipboard or galvanized roofing tin, each measuring 0.66 m × 1.33 m, individually numbered, and arranged in an array of 60-250 coverboards. By lifting up each coverboard, crews of two or more people can generally check an array of 200 coverboards in less than an hour.

Beginning in 1988, we deployed several arrays consisting of both wood and tin coverboards in a variety of habitats on the SRS that are characteristic of the southeastern Coastal Plain (e.g., margins of Carolina bays, natural pine stands, planted pine stands, clearcut areas, prescribed burn areas, upland hardwood forests, and bottomland hardwood forests [Table 1]). In this region, winters are mild, summers are hot and humid, rainfall averages over 90 cm per year, and the species diversity of reptiles and amphibians is high (more than 100 species on the SRS, Gibbons and Semlitsch 1991).

This paper reports the effects of eight environmental/methodological factors on the encounter rates of herpetofauna beneath coverboards:

(A) Do herpetofaunal encounter rates differ among coverboard arrays in different habitat types?
(B) Do herpetofaunal encounter rates differ between a coverboard array and an adjacent drift fence/pitfall trap array?
(C) Can coverboard age affect the encounter rate?
(D) Can the air temperature during the array check affect the encounter rate?

(E) Can the time of day affect the encounter rate?
(F) Can the type of coverboard affect the encounter rate?

(G) How do coverboards affect hydric microclimates of the litter underneath them?

(H) How do coverboards affect thermal microclimates of the litter underneath them?

Questions (A) to (F) examine coarse scale environmental effects on herpetofaunal encounter rates. Questions (G) and (H) involve fine scale estimates of potential driving mechanisms of coverboard use by individual reptiles and amphibians due to the microclimatic characters associated with wood and tin coverboard types.

TABLE 1. Summary of study locations on the Savannah River Site. Columns indicate the date of array placement, or expansion, the cumulative number of coverboards per array (wood coverboards are 0.66 m × 1.33 m chipboard, and tin coverboards are 0.66 m × 1.33 m roofing tin, except at the pine plantation where they are 0.66 m × 2.66 m), the number of site checks when the array was at each size, and the total number of coverboards checked.

Site	Date Set	Cumulative # boards	# Times checked	# Cover-boards checked
Pine Plantation	Jan 1988	66 tin	62	4092
	Mar 1989	132 tin	94	12 408
	May 1990	132 tin, 66 wood	31	6138
Upland Mixed Forest	Jan 1988	60 tin	62	3720
Dry Bay	Jun 1989	72 tin, 72 wood	30	4320
	Aug 1989	91 tin, 91 wood	66	12 012
Rainbow Bay	Jun 1989	48 tin, 48 wood	66	6336
Lowland Hardwood Forest	Aug 1988	66 tin	33	1980

(A) Herpetofaunal differences among habitats

To illustrate among-habitat variation in herpetofaunal encounter rates beneath coverboards, we report data from three study sites that were censused intensively and fairly evenly during May to August 1990. One site was in a pine plantation, the other two were near Carolina bays (Dry Bay, Rainbow Bay). Site checks occurred during all times of day and under diverse weather conditions. Site descriptions appear in Gibbons and Semlitsch (1991).

(B) Herpetofaunal differences among methods in the same habitat

To illustrate herpetofaunal differences within a habitat due to different sampling methods, we deployed a coverboard array adjacent to a drift fence/pitfall trap array at Rainbow Bay. A long-term study of reptile and amphibian population dynamics has been ongoing at this site since 1979 (Pechmann et al. 1991). We compared herpetofaunal encounter data from both methods for all sampling dates during May to August, 1990.

(C) Effect of coverboard age

To evaluate potential effects of coverboard age on encounter rate, we conducted a multiyear experiment at the pine plantation site. We deployed two sets of tin coverboards 1 yr apart and assessed differences in encounter rate for the old versus the new set of coverboards. The first set of 66 tin coverboards was deployed in pairs along three long rows in January 1988. The pairs were 3 m apart and occurred at 15-m intervals along each row, and rows were 25 m apart. In March 1989, 66 new tin coverboards were deployed in pairs, each of which was 3 m away from each pair of previously deployed tin. This deployment resulted in 33 sets of four coverboards, each of which we refer to as a quad and which forms the experimental unit of this study. All quads were checked several times each month for several months. A standard χ^2 analysis would ignore the quad-wise relationship between old and new tin which is an important structural component of this experiment. Therefore, we estimated the odds-ratio of encounters beneath old versus newly placed coverboards within quads using conditional logistic regression (EGRET 1985, see analysis design in Table 2). An odds-ratio of 1.0 indicates no difference between encounter rates within quads due to coverboard age.

TABLE 2. Illustration of the analysis design for the comparison of encounter probabilities for old tin coverboards (in place since January 1988) versus new tin coverboards (placed next to old tin in March 1989). Pairs of old and new tin were arranged in quads and form the unit of the experiment. For each check of each quad, either (A) no herpetofauna were encountered beneath both age groups, (B) at least one reptile or amphibian was seen only beneath old tin, (C) at least one was seen but only beneath new tin, or (D) at least one was seen beneath both types. We tested for differences in encounter rate between age groups by estimating the odds ratio, B/C, using conditional logistic regression (EGRET 1985). If this ratio is greater than 1.0, then old tin exhibits a higher encounter rate.

		BENEATH OLD TIN		*ODDS RATIO*	
		none	**> 0**	H_0:	B/C = 1.0
BENEATH	**none**	A	B	H_1:	B/C > 1.0
NEW TIN	**> 0**	C	D		

(D) Effect of air temperature

To evaluate potential effects of air temperature on encounter rate, we compared encounter rates from sampling dates under many different ambient temperature conditions during May 1988 to August 1990 at the pine plantation site. Air temperatures were measured (±1°C) using a mercury thermometer affixed to the north side of a large tree.

(E) Effect of time of day

To evaluate potential effects of time of day on encounter rate, we compared encounter rates from array checks during the morning and the afternoon under many different weather conditions during May to August 1990 at the pine plantation site and at Dry Bay.

(F) Effect of coverboard type

To address the question of how coverboard type can affect the encounter rate, equal numbers ($N = 91$) of wood and tin coverboards were deployed at Dry Bay in 1989. Similar to the coverboard arrangement at the pine plantation site, wood and tin coverboards were arranged in discrete quads (one pair of wood and one pair of tin coverboards per quad) along parallel rows radiating from the edge of the bay. Data reported are from array checks under many different weather conditions during May to August 1990.

(G) Hydric microclimates beneath coverboards

We quantified litter hydric microclimates by collecting litter samples beneath 12 wood and 12 tin coverboards at Dry Bay in June 1991. Target coverboards were selected from an evenly spaced checkerboard pattern that encompassed the entire coverboard array. From beneath each selected coverboard, a shallow scoop of litter was taken with a small hand trowel, sealed in a plastic container, and an initial weight (±0.001 g) was recorded. Litter samples were air dried to obtain a final weight measurement, and we calculated the percent water content using [(wet weight - dry weight) / wet weight]. During litter sampling, we noticed that many of the wood coverboards (which had been in place for 3 yr) had rotted and that the number of intact boards differed between the left and right sections of the array ($\chi^2 = 16.3$, df = 1, $P < 0.001$). Upon closer inspection, these sections also appeared to differ slightly in topography which may translate into different soil moisture contents. To test for this difference we included array section (left versus right) as a main effect, along with coverboard type (wood versus tin), in a two-way ANOVA (SAS Institute 1985) on arcsine squareroot transformed (Sokal and Rohlf 1981) water content data.

(H) Thermal microclimates beneath coverboards

To quantify detailed thermal microclimatic effects of coverboards, we examined fine scale spatial patterns in temperature availability for a single pair of wood and tin coverboards placed in a large light gap in a pine plantation. Trios of fine (36 gauge) thermocouples were attached to the top and undersurface of each coverboard to estimate surface temperatures. To estimate thermal gradients above and below each coverboard, additional thermocouples were suspended at 1 cm, 10 cm, and 150 cm above or were buried at 5 cm and 100 cm below each coverboard.

Because bare thermocouples generally provide poor estimates of the environmental temperatures available to ectothermic reptiles (Gates 1980), we implanted additional thermocouples within hollow copper models of the ground skink, *Scincella lateralis*, which is a typical lizard found beneath coverboards on the SRS. Models were painted to match the color, contrast, and pattern of *S. lateralis*. Because these models closely match the surface heat transfer properties of these lizards, model temperatures provide an estimate of the operative environmental temperatures (T_E) available to these lizards (Bakken and Gates 1975, Grant and Dunham 1988, Grant 1990). Trios of models were placed on top of the litter and at the base of the litter under each coverboard (12 models in total). Temperatures were recorded by a datalogger (Campbell Scientific CR-21X) at 3-min intervals during 90 min of full sunlight in the light gap on a cloudless summer day.

Methods just described address how the thermal microclimates of wood and tin coverboards differ but not how each coverboard type differs from adjacent exposed areas. To examine the latter, we used an array of 30 painted copper models of *S. lateralis* and 30 bare thermocouples. These probe types occurred in pairs, with the lizard model on top of the litter and the bare thermocouple at the litter base about 10 cm below. Since the litter base is dark and has little air movement, the bare thermocouples provide an adequate estimate of T_E to fossorial *S. lateralis*. Pairs were placed 2 m apart along six 10-m long transects that radiated from a datalogger. Following placement of all models on the surface and all bare thermocouples below, 10 tin coverboards (0.66 m × 1.33 m) were randomly assigned and placed over one-third of the pairs, 10 same-sized wood coverboards were randomly assigned and placed over another third, and the remaining third was left exposed.

At 3-min intervals, the datalogger recorded maximum, minimum, and average temperatures for all models by treatment (wood, tin, or exposed) and depth (litter surface and base). Temperature data from midday (1100-1500 h) on a cloudless summer day (25 July 1991) were selected because the differences among coverboard types and the exposed areas should be maximal under these conditions.

RESULTS

Between January 1988 and August 1990, coverboard arrays were checked opportunistically at the principal study sites (Table 1), most frequently between March and October. In 444 site checks, we encountered 2878 reptiles and amphibians of 31 different species (Table 3) beneath 51,006 coverboards, with an average encounter rate of about five to six reptiles or amphibians per 100 coverboards.

TABLE 3. Species list from 2878 encounters of herpetofauna beneath coverboards (January 1988 to August 1990).

TAXA SPECIES	*COMMON NAME*	*# ENCOUNTERED*
SALAMANDERS: N = 844		
Ambystoma talpoideum	Mole salamander	21
Ambystoma opacum	Marbled salamander	25
Plethodon glutinosus	Slimy salamander	665
Eurycea quadridigitata	Dwarf salamander	133
ANURANS: N = 86		
Bufo terrestris	Southern toad	65
Hyla chrysoscelis	Gray treefrog	1
Gastrophryne carolinensis	Eastern narrow-mouthed toad	7
Rana clamitans	Green frog (bronze frog)	1
Rana utricularia	Southern leopard frog	12
LIZARDS: N = 1721		
Anolis carolinensis	Green anole	49
Sceloporus undulatus	Eastern fence lizard	91
Cnemidophorus sexlineatus	Six-lined racerunner	3
Scincella lateralis	Ground skink	1367
Eumeces fasciatus	Five-lined skink	33
Eumeces laticeps	Broadheaded skink	72
Eumeces inexpectatus	Southeastern five-lined skink	10
Eumeces spp.	Species unidentified	95
Ophisaurus attenuatus	Slender glass lizard	1
SNAKES: N = 227		
Nerodia fasciata	Banded water snake	2
Storeria occipitomaculata	Red-bellied snake	2
Thamnophis sirtalis	Common garter snake	1
Virginia striatula	Rough earth snake	4
Diadophis punctatus	Ringneck snake	68
Farancia abacura	Mud snake	1
Coluber constrictor	Racer	50
Elaphe guttata	Corn snake	5
Elaphe obsoleta	Rat snake	1
Lampropeltis triangulum	Milk snake	3
Tantilla coronata	Southeastern crowned snake	83
Agkistrodon contortrix	Copperhead	3
Sistrurus miliarius	Pygmy rattlesnake	1
Crotalus horridus	Canebrake rattlesnake	3

(A) Herpetofaunal differences among habitats

Patterns of herpetofaunal biodiversity by taxa were determined among three sites that were censused intensively during May to August 1990 (Fig. 1). Rainbow Bay had the highest encounter rate (90.3 herpetofauna per 1000 coverboards checked) by almost a factor of two over both Dry Bay (49.3) and the pine plantation site (42.3). The herpetofaunal community at Rainbow Bay was clearly dominated by salamanders (of which 97% were slimy salamanders, *Plethodon glutinosus*) whereas at the pine plantation, lizards were dominant (of which 82% were ground skinks). In contrast, the herpetofaunal community at Dry Bay was less dominated by any particular species. Although two-thirds of the Dry Bay encounters were also dominated by salamanders, two species were commonly present. The remaining third of the encounters was divided fairly evenly among four species of lizards and a few other amphibians, lizards, and snakes.

More species were encountered at Dry Bay than at either Rainbow Bay or the pine plantation (14, 11, and 10 species, respectively). According to a widely used index of species diversity, the Shannon index, H' (Pielou 1977), the herpetofaunal community at Dry Bay was nearly twice as diverse as either Rainbow Bay or the pine plantation (H' = 1.87, 0.90, and 0.99, respectively).

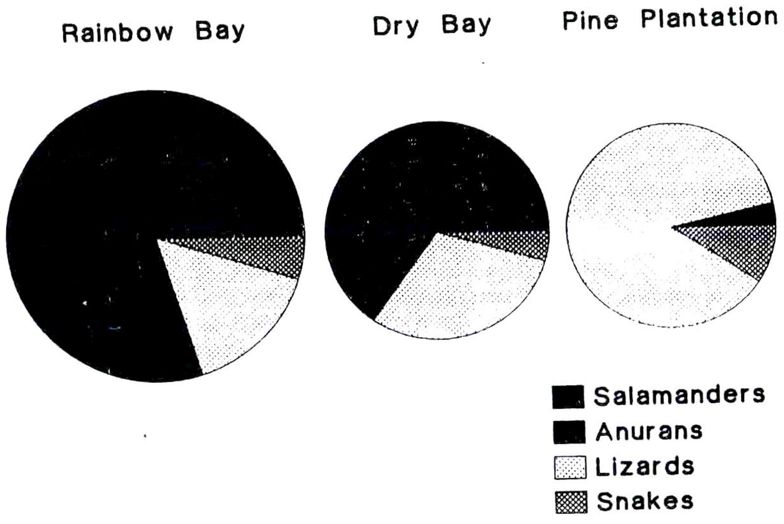

Fig. 1. Pie diagrams of herpetofaunal occurrence beneath coverboards at three study sites on the Savannah River Site during May to August 1990. The area of each pie exactly matches the relative differences among sites in encounter rates per coverboard.

TABLE 4. Species list for all herpetofaunal encounters at Rainbow Bay, during May to August 1990 according to censusing by a drift fence with pitfall traps (total 10,648 pitfall traps checked) or with a coverboard array adjacent to the drift fence (total 3456 coverboards checked).

Taxa Species	Coverboards	Drift fence
SALAMANDERS		
Ambystoma talpoideum	0	170
Ambystoma opacum	7	378
Notophthalmus viridescens	0	1321
Plethodon glutinosus	235	1355
Eurycea quadridigitata	0	166
ANURANS		
Scaphiopus holbrooki	0	658
Bufo terrestris	5	525
Hyla chrysoscelis	0	38
Pseudacris ornata	0	36
Gastrophryne carolinensis	2	1011
Rana catesbeiana	0	9
Rana clamitans	0	171
Rana utricularia	0	1
TURTLES		
Kinosternon subrubrum	0	98
Terrapene carolina	0	110
LIZARDS		
Anolis carolinensis	1	1629
Sceloporus undulatus	0	9
Cnemidophorus sexlineatus	0	82
Scincella lateralis	38	342
Eumeces fasciatus	1	0
Eumeces laticeps	3	65
Eumeces inexpectatus	0	39
Eumeces spp.	5	0
SNAKES		
Storeria occipitomaculata	1	1121
Thamnophis sirtalis	1	0
Virginia valeriae	0	173
Diadophis punctatus	13	41
Coluber constrictor	0	84
Cemophora coccinea	0	21
Tantilla coronata	0	186
TOTALS	312	9839

(B) Herpetofaunal differences among methods in the same habitat

At Rainbow Bay during May to August 1990, the total number of herpetofauna as well as the spectrum of herpetofauna encountered at the coverboard array differed dramatically from those captured at the adjacent drift fence/pitfall trap array (Table 4 and Fig. 2) even though these two methods were sampling from ostensibly the same herpetofaunal community during the same time period. The encounter rate for the coverboard array was less than one-tenth of the rate for the drift fence (90.3 individuals per 1000 coverboards versus 924.0 individuals per 1000 pitfall traps checked). Further, the drift fence data included 27 species in contrast to only 11 species beneath coverboards. Not surprisingly, herpetofaunal biodiversity as estimated by the Shannon index was also much lower from the coverboard array (H' = 0.90) compared to the drift fence data (H' = 2.58).

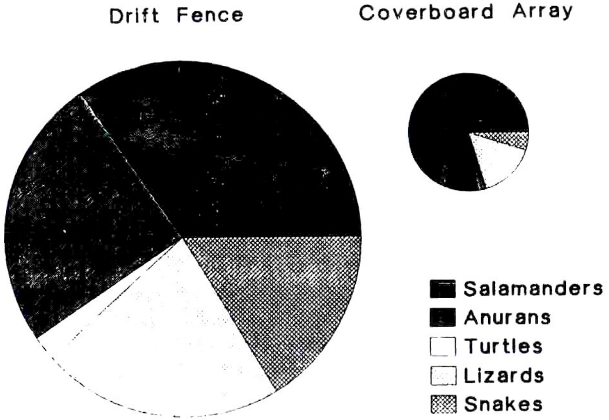

Fig. 2. Pie diagrams of herpetofaunal occurrence at Rainbow Bay during May to August 1990 for the drift fence/pitfall trap array and for the adjacent coverboard array. The area of each pie exactly matches the relative differences among censusing methods in encounter rates per pitfall trap and per coverboard.

(C) Effect of coverboard age

According to conditional logistic regression (analysis design in Table 2), the monthly average of the odds ratio of old to new tin significantly exceeded 1.0 for the first 2 mo following the placement of new tin but was nonsignificant for the third and later months (Fig. 3). In June, despite a trend for a higher encounter rate beneath old coverboards, the odds ratio did not differ significantly from 1.0 ($P = 0.11$). Thus, reptiles and amphibians were either attracted to older tin coverboards or avoided newly placed tin, or both, but only for the first 2 mo.

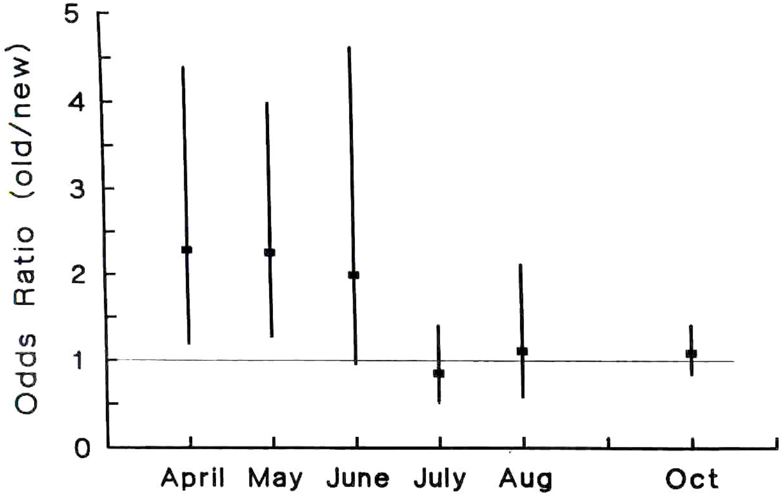

Fig. 3. Monthly average odds ratio (±95% C.I.) defined as the number of quads (two old and two new coverboards) for which at least one reptile or amphibian was seen only beneath old tin divided by the number of quads for which at least one was seen but only beneath new tin (analysis design in Table 2).

(D) Effect of air temperature

Average rates of reptile encounters beneath coverboards at the pine plantation site exhibited a marked unimodal distribution with a peak in the air temperature interval (T_A) of 20-25°C (Fig. 4). Note that Fig. 4 summarizes data from different seasons, different times of day, and different weather conditions. All of the site checks at very low T_A occurred in early morning in spring and fall, during which few reptiles were encountered; however, during these same seasons in afternoons when T_A were within 20-30°C, many reptiles were seen. Conversely in summer, early morning T_A or afternoon cloudy T_A were within 20-30°C and encounter rates were high, but in the afternoon on sunny days, T_A exceeded 30°C and few reptiles were seen.

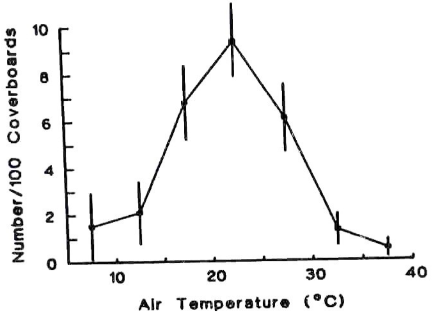

Fig. 4. Average number of reptiles encountered per 100 coverboards checked at the pine plantation site (±1 SE) for 5°C air temperature increments based on site checks from all times of day and under many different weather conditions during March 1988 to November 1990.

(E) Effect of time of day

Data from Dry Bay and the pine plantation site recorded in the morning or afternoon indicated that time of day interacted with site (Fig. 5). At Dry Bay, remarkable similarity existed in the total number of animals encountered (morning = 57.2 individuals per 1000 coverboards versus afternoon = 59.5 individuals per 1000 coverboards) and the relative contributions among different taxa were also almost identical. In contrast at the pine plantation site, encounter rates during the morning period were over 10 times greater than the rates from the afternoon site checks (morning = 66.6 individuals per 1000 coverboards versus afternoon = 5.5 individuals per 1000 coverboards

(F) Effect of coverboard type

Results from a comparison of wood and tin coverboard types at Dry Bay indicated that far more animals were encountered beneath wood (76.3 individuals per 1000 coverboards) than beneath tin (22.3 individuals per 1000 coverboards), and more amphibians were proportionally represented beneath wood as well (Fig. 6). In fact, salamanders dominated the encounters beneath wood coverboards (>75%), whereas lizards dominated beneath tin coverboards (>75%). Despite great differences in the taxonomic composition of herpetofauna among coverboard types, the total number of species was the same (N = 11) and the Shannon estimates of biodiversity were also very similar (H' = 1.57 for wood, and H' = 1.93 for tin). The biodiversity estimate for tin was slightly higher than for wood due to a fairly even contribution by the lizard fauna (*S. lateralis*, *Eumeces fasciatus*, *E. laticeps*, and *Anolis carolinensis*), whereas only two species (*P. glutinosus* and *Eurycea quadridigitata*) dominated the data from beneath wood coverboards.

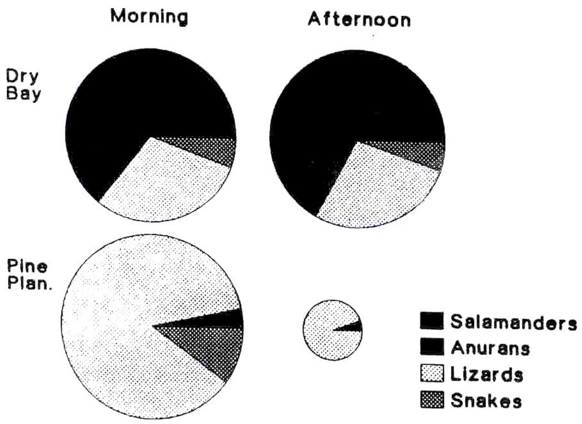

Fig. 5. Pie diagrams of herpetofaunal occurrence beneath coverboards at Dry Bay (upper row) and at the pine plantation site (lower row) for site checks during the morning (left column) and afternoon (right column) during May to August 1990. The area of each pie exactly matches the relative differences among time periods and sites in herpetofaunal encounter rates.

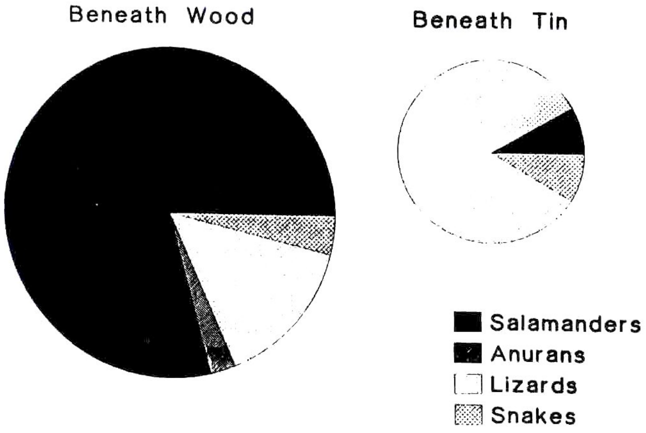

Fig. 6. Pie diagrams of herpetofaunal occurrence beneath coverboards beneath wood coverboards (left) and tin coverboards (right) at Dry Bay during May to August 1990. The area of each pie exactly matches the relative differences among coverboard types in herpetofaunal encounter rates.

(G) Hydric microclimates beneath coverboards

At Dry Bay, the average percentage of litter mass due to water was about 30% more beneath wood than beneath tin (Fig. 7). Further, the averages for wood and tin were both about 10% more in the left section of the Dry Bay coverboard array than in the right. According to a two-way ANOVA on arcsine squareroot transformed data (Sokal and Rohlf 1981), these results were significant (drier litter beneath tin, $F_{1,23}$ = 39.04, $P < 0.001$, and drier on the right section of the array $F_{1,23}$ = 5.84, $P < 0.025$). The effects of array section and coverboard type did not interact ($F_{1,23}$ = 0.30, $P > 0.05$).

Interestingly, the difference in litter moisture between sections of the Dry Bay array was also associated with differences in herpetofaunal encounter rates. In an a posteriori analysis of Dry Bay herpetofaunal encounter data from 1990, significantly more amphibians were encountered beneath coverboards on the wetter section (averaging 42.7 individuals per 1000 coverboards) versus on the drier array section (26.4 individuals per 1000 coverboards), although encounter rates did not differ between array sections for reptiles (Table 5).

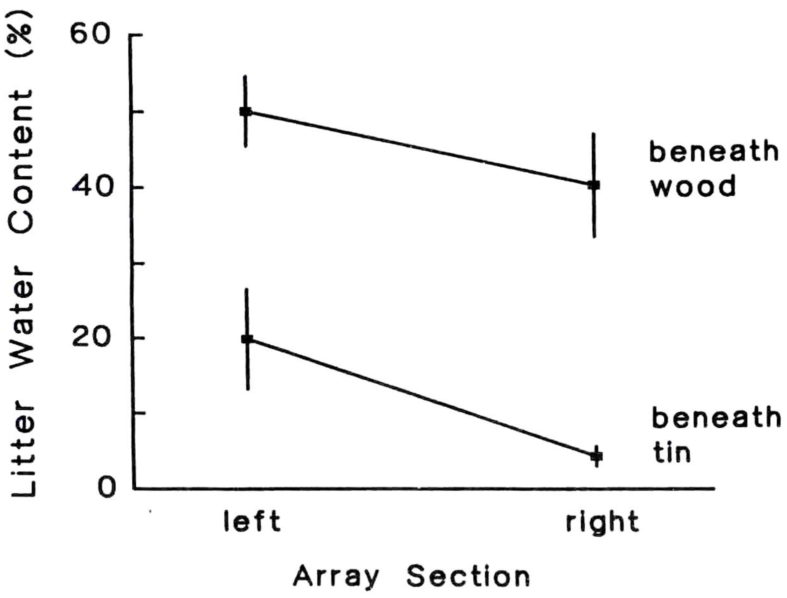

Fig. 7. Average percentages (±1 SE) of litter mass due to water (Litter Water Content = 100% * [wet weight - dry weight] / wet weight) for wood or tin coverboards and for the left or right sections of the Dry Bay array in June 1991.

TABLE 5. Comparisons of the encounter rates for left and right sections of the Dry Bay coverboard array during all site checks in 1990 for amphibians and for reptiles. Numbers in each cell of each table indicate the number of coverboards beneath which at least one reptile or amphibian was, or none were, encountered for the left or right sections of the array.

	AMPHIBIANS			REPTILES	
	LEFT	*RIGHT*		*LEFT*	*RIGHT*
> 0	242	40	> 0	139	35
NONE	5662	1518	*NONE*	5765	1523
	$\chi^2 = 7.95$, $P < 0.005$			$\chi^2 = 0.06$, NS	

(H) Thermal microclimates beneath coverboards

Average temperatures at various heights and depths above and below wood and tin coverboards in full sun in a light gap in a pine plantation appear in Fig. 8. The greatest difference between coverboard types occurred at the under surface of each board. The upper surface of tin was only about 3.5°C warmer than the upper surface of wood; however, this temperature was almost unattenuated across the thickness of the tin coverboard. In contrast, the low thermal conductivity and greater thickness of the wood coverboard resulted in an under-surface temperature of wood which was about 12°C below corresponding temperatures beneath tin. The higher under surface temperature of tin resulted in higher T_E on top of the litter beneath tin than beneath wood. Thermal gradients beneath wood and tin from the litter base to a depth of 100 cm were very similar.

According to our array of copper models of the lizard *S. lateralis* (with each model deployed either in an exposed area, beneath wood, or beneath tin), T_E available to thermoregulating lizards differed greatly with time of day and deployment treatment (Fig. 9). A large number of models in exposed areas and beneath tin exceeded 35°C at midday, but only a few did so beneath wood. According to a multivariate comparison of the average, maximum, and minimum T_E from midday (1300-1600 h), these thermal microclimate types differed significantly (MANOVA on log transformed data, Wilks's Lambda $F_{6,356} = 92.4$, $P < 0.001$), and the T_E of exposed models averaged about 2°C warmer than models beneath tin, which in turn averaged about 2°C warmer than models beneath wood (both least-squared mean differences were with $P < 0.001$). The previous section reported a difference of >12°C between under surface temperatures and model temperatures on the litter surface beneath wood and tin coverboards in the sun. The reduced difference reported here was because many of the exposed models and coverboards were shaded at any particular time.

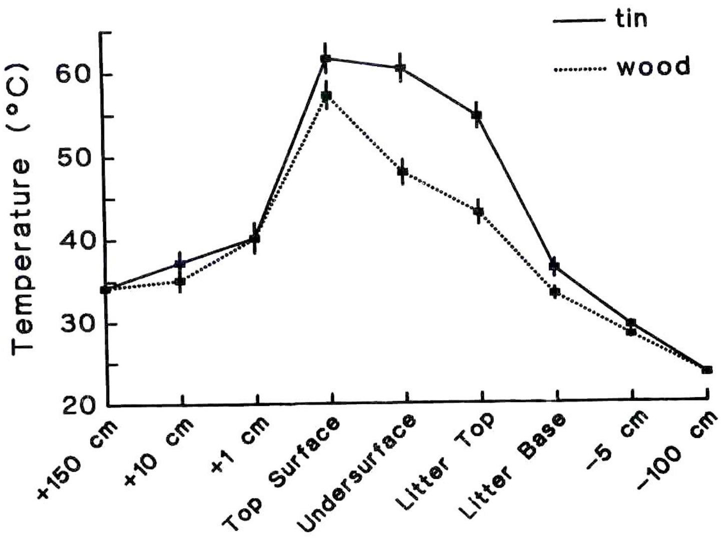

Fig. 8. Average temperatures (±1 SD) of thermocouples at various heights above and depths below wood or tin coverboards. Bare thermocouples were used to estimate all air and soil temperatures (heights and depths listed), and thermocouples were affixed to the top and bottom surfaces of each coverboard using epoxy. Painted copper models of *S. lateralis* were used to estimate operative environmental temperatures (T_E) on top of the litter and at the litter base beneath each coverboard.

A similar multivariate comparison of T_E at the litter base indicated that exposed, tin, and wood microclimates were also significantly different (MANOVA on log transformed data, Wilks's Lambda $F_{6,356} = 365.3$, $P < 0.0001$), as observed in the previous section. However, averages differed by less than 2°C, again due to the large fraction of shaded sampling locations.

A distinct feature of Fig. 9 is that the midday T_E distribution beneath wood exhibited lower variance relative to either the T_E distributions in exposed areas or beneath tin. Average standard deviations in T_E at midday for exposed, tin, and wood were significantly different (3.6°C, 3.1°C, and 1.3°C, respectively, one-way ANOVA on log-transformed standard deviations, $F_{2,180} = 76.9$, $P < 0.001$). This result stemmed from the thermal insulating capacity of wood coverboards.

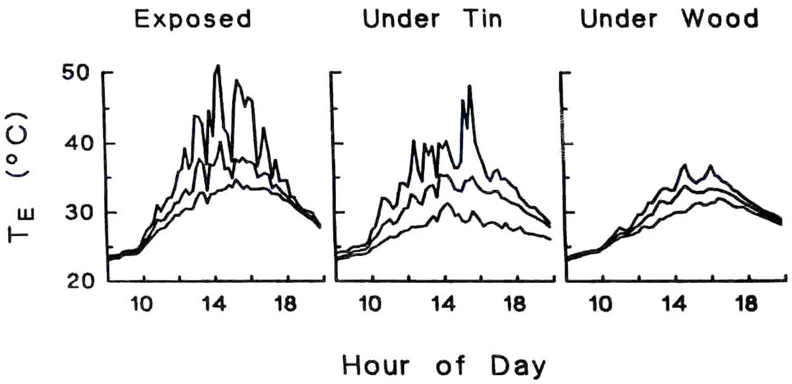

Fig. 9. The distributions of operative environmental temperatures (T_E) for painted copper models of *S. lateralis* deployed on top of the litter in exposed areas (left), beneath tin (center), and beneath wood (right) coverboards for a sunny day on 25 July 1991. In each plot, the upper, middle, and lower curves are the maximum, average, and minimum model temperatures, respectively, for each 3-min scan of the copper lizard array. Values were averaged for plotting at 12-min intervals, so sample sizes are 4 for maxima, 40 for averages, and 4 for minima.

DISCUSSION

Systematic sampling of arrays of artificial coverboards can yield large numbers of reptiles and amphibians, as well as quantitative estimates of relative abundance that include representation by rare species (Table 3). Variation in encounter rates can be associated with differences in every environmental or methodological factor we examined--habitat type, comparison with a drift fence/pitfall array, coverboard age, time of day, air temperature, coverboard type, and litter hydric and thermal microclimates. Detailed studies of the litter microclimate beneath coverboards suggest specific mechanisms by which temperature, humidity, and coverboard type interact to affect herpetofaunal encounter rates.

(A) Herpetofaunal differences among habitats

This comparison indicates that coverboard census data can generate quantitative patterns in herpetofaunal biodiversity to address simple questions about relative differences among sites. However, an assumption of many biodiversity indices such as the Shannon Index is that no individual may be counted more than once in any particular calculation (Pielou 1977). Thus, raw encounter frequencies of herpetofauna beneath coverboards should not be used to calculate biodiversity unless unique individuals are identified. If individuals of a single species were more frequently encountered beneath coverboards (e.g., if they had small home ranges relative to the size of the coverboard array), or were more easily seen relative to other species, then encounter frequencies would be biased toward the conspicuous taxa, which would result in underestimates of biodiversity.

According to a mark-recapture study at the pine plantation site, during May to July 1991 (B. Grant, *unpublished data*), the effect of this bias can be considerable. The ground skink was the most abundant species (75% of 385 encounters were *S. lateralis* with the remaining 25% split among 13 other species), and home ranges of *S. lateralis* were much smaller than the size of the coverboard array (more than 90% of all recaptures were within 10 m of the original capture point). Thus, the encounter data beneath coverboards were heavily biased towards the same individual *S. lateralis*. According to calculations of the Shannon index using all encounters versus only data from unique individual captures, biodiversity estimations were about 20% higher when the appropriately distilled data set was used (H' = 0.87 for all 385 encounters, and H' = 1.04 for 238 unique individuals). This comparison suggests that studies of herpetofaunal biodiversity should include mark-recapture methods to ferret out duplicate encounters of disproportionately conspicuous taxa.

Because the data summarized in Fig. 1 were not associated with mark-recapture studies, we must caution that apparent biodiversity may be underestimated. But, a more important question is to what extent is the spectrum of herpetofauna encountered beneath coverboards an unbiased estimate of the "true" spectrum of herpetofauna in residence at each study site? We may never know this unbiased spectrum because there may be no unbiased censusing scheme, nonetheless some insight may be gained by comparing coverboard-based biodiversity estimates with those from a different sampling scheme at the same time and place.

(B) Herpetofaunal differences among methods in the same habitat

Although the Rainbow Bay coverboard and drift fence/pitfall trap arrays were adjacent and censused during the same time period, the estimated herpetofaunal species composition and encounter rates were vastly different (Table 4 and Fig. 2). These differences are undoubtedly the interactions of properties of these sampling schemes with biological attributes of the individuals that determine encounter probabilities. An obvious example is that no turtles were observed beneath coverboards whereas many were trapped at the drift fence. Turtles, like numerous other reptiles and amphibians, were using Rainbow Bay during a particular stage in their life cycle, and were intercepted by the drift fence in transit to or from the Bay. Amphibians whose reproduction requires standing water were especially numerous at the fence as they migrated into the Bay to mate and oviposit, or emerged from the Bay after reproduction or metamorphosis. The coverboard method was less able to census incoming breeders because many moved nocturnally with less likelihood of an individual stopping beneath a coverboard. Similarly, emigrating amphibians, including recent metamorphs, may disperse quickly to distances beyond the narrow zone of the coverboard array.

These biological effects on encounter probabilities were undoubtedly responsible for the 10 times greater encounter rate at the drift fence than at the adjacent coverboard array (Fig. 2). Another obvious reason for fewer encounters from the coverboard array was that the drift fence integrated captures over a 24-h period (pitfall traps were checked daily), whereas only those herpetofauna using the coverboards at the time of the array check could have been encountered.

Part of the reduction of apparent biodiversity beneath coverboards was due to the predominance of a single salamander, *P. glutinosus*, many of which, according to a mark-recapture study during May to August 1990, appeared to take up residence beneath coverboards (L. Elliot and S. Kemp, *unpublished data*). This illustrates that coverboard deployment creates new microhabitats, and those reptiles and amphibians whose microhabitat preferences matched these newly created microhabitat types were more likely to be encountered.

(C) *Effect of coverboard age*

Many experienced reptile collectors believe that one has a better chance of collecting individuals beneath ancient rather than newly placed debris. Our experiment supports this conclusion to some degree for tin coverboards at our pine plantation site. We do not know the mechanisms by which reptiles detect differences beneath old and new tin coverboards. It could be related to the leaching of volatile chemicals from within the galvanized tin, or perhaps microscopic soil organisms require a few months to colonize the new microhabitat and produce the aroma or taste which reptiles or their prey associate with suitable habitat. However, based on our limited results, herpetofauna made no distinction between old and new coverboards after only a few months. This aspect needs to be investigated more thoroughly before definitive conclusions are drawn.

(D) *Effect of air temperature*

The unimodal pattern of herpetofaunal encounter rate versus air temperature at the pine plantation site (Fig. 4) is driven to a large extent by the activity patterns of a single reptile, the ground skink, which comprised 80% of the encounter data. The thermal ecology of these lizards is poorly known; however, some data (Fitch 1956) suggest that these lizards exhibit a rather low average field active body temperature of 29°C. Hudson and Bertram (1966) also reported an average body temperature in the upper 20°Cs from a laboratory study of thermal gradient.

According to our data from the copper lizard array in a pine plantation, the average difference between the T_E beneath tin coverboards and air temperature at 150 cm at midday is about 3.5°C for a typical sunny summer day. Thus, when the air temperature was within the interval 20-25°C, the thermal microclimates beneath many tin coverboards would have exhibited T_E in the upper 20°Cs and would have been favorable to thermoregulating *S. lateralis*. This suggests that the thermal ecology of individual herpetofauna can play a major role in determining encounter rates.

(E) *Effect of time of day*

The interaction between time of day and site observed in Fig. 5 could have been due to a variety of environmental and herpetofaunal behavioral factors. At the pine plantation site, most of the coverboards were tin (Table 1); and most of the encounters were with a lizard, *S. lateralis* (see previous subsection), the activity of which may be tightly constrained by high environmental temperatures typical in the afternoon beneath tin (Fig. 9). Thus, we suggest that at the pine plantation site, tin coverboard use may have been only by actively thermoregulating *S. lateralis* and thus would not have occurred during typically hot summer afternoons. In contrast, at Dry Bay, most of the encounters at all times of day were with wet-skinned salamanders (typically *P. glutinosus*) beneath wood (Fig. 6). The thermal environments beneath wood exhibited much less diel variation than did those beneath tin (Fig. 9), and individual *P. glutinosus* were repeatedly encountered beneath the same coverboard indicating very small home ranges if not actual residence (L. Elliot and S. Kemp, *unpublished data*). For these individuals, we suspect that both activity and inactivity coincided with coverboard use which could have led to no effect of time of day on encounter rates.

(F) *Effect of coverboard type*

Coverboard type can dramatically affect total as well as taxon-specific encounter rates and, to a lesser degree, it can affect estimates of biodiversity. The preponderance of wet-skinned amphibians beneath wood coverboards and dry-skinned reptiles beneath tin coverboards strongly suggests the importance of microclimatic effects on coverboard use. The apparent dominance of lizards at the pine plantation site (Fig. 1) may be an artifact of the preponderance of tin coverboards at this site.

(G) *Hydric microclimates beneath coverboards*

Our results show the extreme sensitivity of amphibians to litter humidity differences beneath coverboards relative to cohabitating reptiles. Even a relative humidity difference as subtle as the 10% observed between the left and right array sections at Dry Bay (Fig. 7) was associated with a large difference in amphibian encounter rate (a factor of two), but no difference for reptiles (Table 5). Differences in litter hydration beneath wood and tin coverboards were probably caused by the warmer undersurface temperature of tin (Fig. 8) which would have heated the litter surface immediately below and driven soil moisture further underground. Further, unlike tin, the woodchip matrix of wood coverboards tended to absorb and hold water following soaking rains, which would have buffered soil moisture variation immediately below.

(H) *Thermal microclimates beneath coverboards*

High undersurface temperatures beneath tin created a dense infrared radiant environment that impinged on the litter surface below and would have offered high rates of conductive heat flow to objects in contact beneath. Below the litter surface, little heat flow could have occurred because the pine straw litter would have absorbed infrared radiation, conducted heat poorly, and inhibited heat flow by convective air movement. The comparison with exposed areas (Fig. 9) shows that reptiles could have attained slightly higher body temperatures by basking in exposed sunlit areas than beneath sunlit tin. However, an advantage of basking beneath sunlit tin is a decreased risk of predation with only a slight decrease in the rate of heating or the steady-state body temperature relative to basking in an exposed area.

On the other hand, the similarity in T_E between microclimates in exposed areas and beneath tin suggests that one might expect a high correlation between encounter rates beneath tin and actual individual activity rates. This may explain the unimodality between reptile encounters and air temperature (Fig. 4) as well as large time of day effects at sites dominated by tin coverboards as at the pine plantation (Fig. 5). If wood coverboards may be viewed as generally providing insulation from high temperatures, then wood coverboard use might be more associated with reptile inactivity as they take shelter from midday heat. Detailed behavioral studies on reptile activity patterns would address this question.

Both wood and tin coverboards offer the herpetofauna a refuge from visually orienting aerial predators. Although wood insulates any inhabitants beneath from solar radiation, tin coverboards directly convert this visible radiation into infrared below, as well as providing a heated undersurface for conduction. These microclimatic characters provide mechanisms for differences in encounter probabilities between wood and tin. For reptiles, which because of their dry skin generally exhibit higher field active body temperatures than do wet-skinned amphibians (Fitch 1956, Conant 1975), the temperature distributions beneath tin are similar to those found in nearby exposed areas and temporal patterns in reptile activity are likely to match patterns in tin coverboard use. Such a correlation may not be true for amphibians and wood coverboard use.

Implications for biodiversity management

We have shown that the coverboard technique can be used to generate estimates of herpetofaunal relative abundance and biodiversity. Advantages of the coverboard technique, relative to other censusing techniques, include its ease of implementation (materials costs are low and little site preparation is needed) and low maintenance. In addition, coverboards can be checked at the convenience of the investigator with no risk to resident herpetofauna from a failure to check on a frequent and fixed schedule. Disadvantages of this technique include the extreme sensitivity of encounter probabilities to the diverse and specific microclimatic preferences of individual species.

Major sampling artifacts in herpetofaunal relative abundance and biodiversity can occur due to the interaction of biological characteristics of amphibians and reptiles with the types of coverboards used and subtle spatiotemporal differences along environmental hygrothermal gradients. This is not surprising since herpetofauna are ectothermic and their heat, water, and energy budgets are tightly coupled to characters of their immediate biophysical environments. The importance of microclimate effects are much greater on the activity, life history, and ecology of ectotherms than would be true for endothermic birds and mammals.

This argues strongly that population models of the effects of specified management practices or of climate change on herpetofauna must examine the precise mechanisms by which individuals interact with their environment. Models must include how the specific management regime or climate change affects interactions between individuals and their perturbed microclimates.

To use the coverboard technique most effectively, we offer three recommendations:

(1) deploy as many different coverboard types as possible, especially both metal and wood, and wait at least 2 mo before beginning the census program;

(2) check coverboard arrays under as many different times of day and weather conditions as possible so that all taxa in residence will be encountered. If encounter rates are to be compared among sites, insure that the array of times and weather conditions during which site checks occurred is identical; and,

(3) all encounters of herpetofauna should be accompanied by capture and marking (cohort or individual) because biodiversity estimates, such as the Shannon, should use only one datum per individual.

We believe that the principal utility of the coverboard technique is in its applicability to large scale experimental designs in which herpetofaunal relative abundance and biodiversity are critical response variables to natural or human-induced environmental changes. In practice, comparisons may occur among different locations, under different experimental treatments, in the same location among different years, or during different stages of regeneration following a perturbation. Given the present concern over global herpetofaunal decline, there should be ample justification and opportunity for the use of this censusing technique.

ACKNOWLEDGMENTS

We appreciate the field assistance of many participants, including J. Greene, E. Wiltenmuth, J. Reardon, M. Bradford, A. Groat, S. Kemp, L. Elliot, P. Mahaney, S. Swenson, K. Hayden, J. Martin, M. Mills, H. Berna, P. Turner, M. Gibbons, and T. Lynch. The manuscript was improved by comments from N. Frazer, J. Greene, J. Pechman, R. Seigel, N. Scott, and an anonymous reviewer. Data collection, analysis, and manuscript preparation were made possible by contract DE-AC09-76SR00-819 between the University of Georgia and the U.S. Department of Energy.

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