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Variation in Detection of Smooth Greensnake (*Opheodrys vernalis*) Nests and Adults with Artificial Cover Object Material

Smooth Greensnakes (*Opheodrys vernalis*) are small-bodied oviparous colubrids, dependent on prairie, savanna, and meadow habitats in much of their range (Redder et al. 2006). The species is experiencing range-wide population declines, range contractions, and apparent extirpations due to habitat loss (Mitchell 2006, Redder et al. 2006). *Opheodrys vernalis* are protected in several range states, lack recent distributional or demographic data in many historic locales, and their status illustrates the need for identification of extant populations for monitoring, improving knowledge of persistent threats, and conservation management (Redder et al. 2006; Sacerdote-Velat et al. 2014). Small-bodied snakes are challenging to monitor because of cryptic behavior, morphological limitations to long-term tracking, and variation in activity with environmental conditions and season (MacKenzie et al. 2003; Willson and Dorcas 2004; Mazerolle et al. 2007; Durso et al. 2011). These challenges have led to an increased use of sampling approaches that incorporate detection probabilities and occupancy estimates for habitat patches when encounter rates are insufficient for mark-recapture and detection probability is low (Steen 2010; Durso et al. 2011; Ward et al. 2017; Mitrovich et al. 2018; King and Vanek 2020). Because of their small body size and excellent camouflage, *O. vernalis* is an exemplar of a detection challenge, especially in sites with reduced population densities, as is typical in small remnant natural areas surrounded by urban and suburban matrix (Mitrovitch et al. 2018). Further, *O. vernalis* often exhibit clumped distributions within occupied sites, using communal nesting and denning sites (Cook 1964; Fowler 1966; Fritts 1968; Sacerdote et al. 2012) and maintaining high densities within small habitat patches (Seibert 1950; Sacerdote-Velat et al. 2014). Similar clumped distributions are exhibited by their congeners, *O. aestivus* (Plummer 1990).

Some *O. vernalis* populations will use a variety of artificial cover objects (ACOs) as thermal refugia, including plywood, chipboard, rubber mats, corrugated tin, corrugated fiberglass, asphalt, and acrylic (Seibert and Hagen 1947; Seibert 1950; Redder et al. 2006; Cox et al. 2009; Sacerdote-Velat et al. 2014; King and Vanek 2020). Despite their use of ACOs, annual and within-season variation in environmental conditions, daily survey timing, and seasonal survey timing often yield low encounter rates for *O. vernalis* (Redder et al. 2006; Cox et al. 2009). Therefore, this variation requires numerous site visits to reliably conclude that the species is absent from a site (Steen 2010; Ward et al. 2017).

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While assessments of site occupancy and detection probability often rely on encountering individuals of a given species, survey methods may use other signs of species presence to confirm that a site is occupied. For example, the presence of desert tortoise scat, burrows for ground squirrels, hair snares, scat of large carnivores, or bird nests may provide recent evidence of species presence within a site (Nichols et al. 1986; Long et al. 2011; McHenry et al. 2016; Jiang 2020). During our *O. vernalis* surveys in six occupied sites between 2015 and 2020 for a recovery project in Illinois, USA, we regularly observed *O. vernalis* nests beneath wooden ACOs and occasionally beneath rubber ACOs (Table 1). In portions of their range where rapid site assessment is warranted to examine current distribution of breeding populations, nest surveys can provide a useful approach. By focusing on the presence of nests, the survey window is narrowed down between late June and early August while eggs are present, with some expected variation in timing with latitude. Once a nest is present, barring predation events, detection of nests should exceed detection of snakes since the eggs are present regardless of survey conditions. Further, the presence of eggs demonstrates that reproduction is occurring in an occupied site. Because *O. vernalis* have variable incubation lengths (Stille 1954; Sexton and Claypool 1978; Sacerdote et al. 2012) with nesting occurring at any time between late June and August, repeated surveys throughout this time window may maximize nest detection.

The objectives of this study are to: 1) examine efficacy of wooden chipboard versus plywood for nest detection; 2) identify the optimal survey timing for rapid assessment of site occupancy using nests as an indicator of presence of breeding populations; 3) examine within-season variation in detection probability for adults with rubber, plywood, and chipboard ACOs; and 4) compare detection probabilities of adult *O. vernalis* to nest detection.

While *O. vernalis* adults will make use of wooden ACOs (Seibert and Hagen 1947; Cox et al. 1992; King and Vanek 2020), their selection of cover for nesting sites may vary with attributes of cover materials. Plywood and wooden chipboard (also called

Table 1. Study site county, area (ha), acquisition years, number of artificial cover object (ACO) transects, wooden ACOs, and rubber ACOs per site during long-term monitoring from 2015–2020.

Site	County	Area	Years Acquired	Transects	N Wood	N Rubber
Site 1	DuPage	1407	1965–1974	8	40	6
Site 2	DuPage	145	1979	6	30	6
Site 3	DuPage	55.4	1998–1999	2	10	6
Site 4	Lake	219	1974–1976	10	50	6
Site 5	Lake	110	1976–1986	4	20	6
Site 6	Lake	200	1989–2000	4	20	6

oriented strand board) may vary in the degree of moisture retention or hydric and thermal buffering properties. We hypothesized that detection of *O. vernalis* nests would be greater beneath chipboard than plywood, as it more closely resembles rotting logs in its retention of moisture (Grant et al. 1992). Further, we expected that nest detection would exceed detection of adult *O. vernalis*, thus requiring fewer surveys during peak detection windows to confirm species presence in a site. We expected that adult *O. vernalis* would make use of chipboard, plywood, and rubber, but that detection beneath rubber would be greatest early in the active season when ambient temperatures are cooler, with decreased use during the hotter summer months. We expected detection of adults beneath chipboard to be greatest during late June and July when females are seeking nesting sites with greater moisture, and we expected detection beneath plywood to exceed that of rubber in June and July as temperatures increase.

Table 2. Number of *Opheodrys vernalis* nests (nests per number of cover objects) beneath wooden and rubber ACOs from 2015–2020.

Year	Wood (N = 170)	Rubber (N = 36)	Total (N = 206)
2015	22 (0.12)	1 (0.03)	23 (0.11)
2016	11 (0.06)	1 (0.03)	12 (.058)
2017	32 (0.18)	1 (0.03)	33 (0.16)
2018	33 (0.19)	1 (0.03)	34 (0.17)
2019	61 (0.35)	0 (0.00)	61 (0.29)
2020	53 (0.31)	1 (0.03)	54 (0.26)
TOTAL	212	5	217

Materials and Methods

Long-term Monitoring Sites.—We surveyed six long-term monitoring sites in Lake and DuPage counties, Illinois, USA from 2015–2020. The study sites are located within the traditional territories of the Kickapoo, Peoria, Potawatomi, Myaamia, and Océti Šakówin peoples. The long-term study sites are all suburban natural areas with remnant tallgrass prairie or marsh amidst restored grasslands, and are near active or historic railroad lines, where presence of old field vegetation has maintained a corridor over time. Sites 1–3 are located within DuPage County, Illinois, ca. 65–70 km west of Chicago and are owned and managed by the Forest Preserve District of DuPage County (FPDDC). Sites 4–6 are within Lake County, Illinois, ca. 65–72 km north of Chicago and are owned and managed by the Lake County Forest Preserve District (LCFPD). The sites range in size from 55.4–1407 ha, and were acquired for conservation between 1965 and the mid-2000s (Table 1). Site 1 is composed of several parcels, fragmented by two-lane roads and railroads. Despite multiple parcels having suitable habitat, only a single 141-ha parcel within the preserve has produced *O. vernalis* captures in six years of surveys. Site 1 contains a mixture of marsh, sedge meadow, tallgrass prairie, and expanses of old field habitats dominated by Hungarian Brome (*Bromus inermis*). Site 2, bound by two-lane roads and railroads, is composed of tallgrass prairie, marsh, oak savanna, sedge meadow, and old field habitats. Site 3 is a mixture of remnant marsh and restored tallgrass prairie bound by four-lane roads, railroad, and residential development. Site 4 is composed of tallgrass prairie, sedge meadow, old field, woodlands, and turf grass, bound by a railroad and two-lane roads. Site 5 is a mixture of tallgrass prairie, sedge meadow, and woodland, surrounded by two-lane and four-lane roads, and a regional rail trail adjacent to residential development. Site 6 is a remnant savanna with sedge meadow and tallgrass prairie, bound by a railroad, two-lane roads, and residential development.

From 2015–2020, we sampled a total of 34 50-m transects of ACOs located in sites two to three times per week. These sites had 310 transects per site based on available area in suitable grassland habitat (Table 1). Each transect consisted of five wooden ACOs spaced 10 m apart. Wooden ACOs were 60 × 60 × 0.8 cm squares. For a subset of three transects per site, we placed two black rubber ACOs cut from recycled conveyor belt, 10 m from each end of the transect. Rubber mats were cut to ca. 60 × 45 × 1.5 cm. During the long-term monitoring effort, we routinely replaced wooden ACOs as needed with either plywood or chipboard based on availability of project materials. Initially, for the purpose of documenting the incidence of nests beneath ACOs in the long-term monitoring effort, we did not distinguish between the two types of wooden cover. All statistical analyses were carried out in Statistica (v6.1, StatSoft, Inc, 2003). We used a main effects ANOVA to examine variation in the frequency of *O. vernalis* nests beneath wood and rubber, adjusting for the number of ACOs of each material (Table 2).

Comparison of Nest Detection Beneath Plywood and Chipboard.—In 2019 and 2020, to compare nest detection probabilities beneath plywood and chipboard, we established paired ACO transects in Site 1 (N = 3) and Site 2 (N = 5). We established a total of eight 50-m transects, each containing five pairs of wooden ACOs (plywood and chipboard) with 10 m between each set of paired boards for a total of 40 pairs of boards. For each pair, boards were spaced approximately 0.5 m apart. The chipboard and plywood ACOs measured 60 × 60 × 0.8 cm. The minimum distance between transects at either site was 135 m. Transects were sampled for *O. vernalis* nests three times per week between 25 June–9 September in 2019 and 2020. The nest survey window was extensive because nest fates were monitored for collection of vital rates, and *O. vernalis* oviposition timing and incubation length may vary (Blanchard 1933; Stille 1954; Sexton and Claypool 1978; Redder et al. 2006; Sacerdote et al. 2012). For example, from 2015–2020, we observed egg incubation lengths within the two study sites ranging from 4–46 days (mean = 33 days; N = 861), with the earliest new nest encountered on 25 June 2018 and the latest new nest encountered on 30 August 2019.

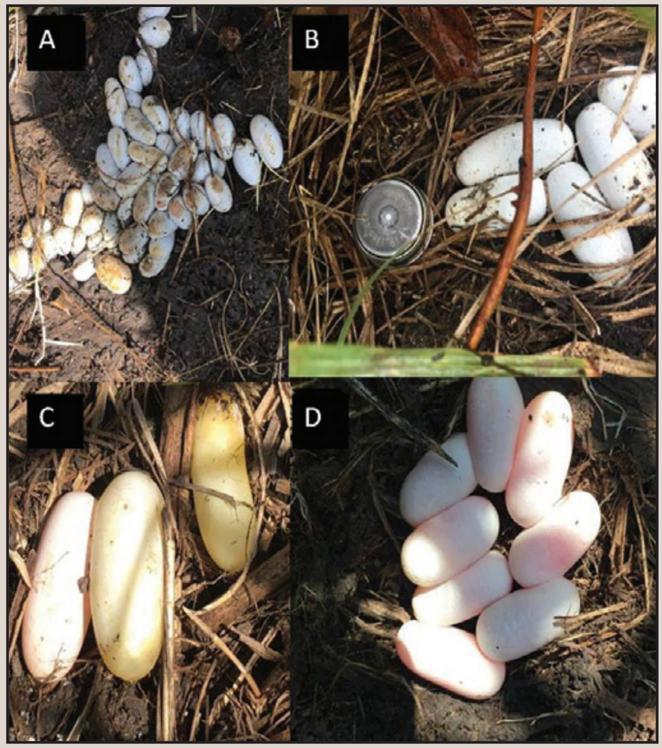
Lee County Inventory Site.—For a separate herpetological monitoring project, we surveyed Green River State Wildlife Management Area (GR), a large grassland site in Lee County, Illinois, USA, using ACOs. We included data from this inventory and monitoring effort to supplement our examination of adult *O. vernalis* detection probability with ACO material and survey month. GR is a 1038-ha preserve consisting of remnant and restored tallgrass prairie, wetland, savanna, and cropland (King and Vanek 2020). GR was set aside by the Illinois Department of Natural Resources in 1943 and is surrounded by row crop agriculture and rural roads.

GR was sampled with weekly ACO checks from May–October 2017, April–October 2018, and April–August 2019. At GR, 12 arrays of ACOs were established, with alternating plywood and rubber mats. ACOs measured 60 × 80 × 1.5 cm. Each array consisted of four rows of eight cover objects separated by 20 m, for a total of 16 plywood and 16 rubber mats per array (384 ACOs in total), with arrays separated by a minimum distance of 400 m (King and Vanek 2020).

Identification of Nests.—Opheodrys vernalis nests may be readily identified by egg size, smooth surface texture, cohesiveness, and general clutch size range (Fig. 1A–D). In our study sites, the only other oviparous snakes include *Lampropeltis triangulum*, *Pantherophis vulpinus*, and in GR, *Heterodon* spp., which all produce larger eggs (≥2.4 cm) with a more granular surface texture. In this study, we followed the fate of all eggs encountered and confirmed that they were *O. vernalis* nests upon hatching. Generally, eggs of *O. aestivus* would be the most challenging to distinguish from those of *O. vernalis*, but *O. aestivus* tends to nest within tree cavities rather than in open grasslands (Plummer 1990). *Opheodrys vernalis* eggs are white and elongate, with dimensions ranging from 2.19 × 1.04 cm (Stille 1954) to 2.48 × 1.20 cm (Blanchard 1933; Fig. 1B). Frequently, an unfertilized egg was present alongside a viable clutch. The unfertilized eggs appear smaller, with a yellow tinge and may be in contact with the rest of the clutch (Fig. 1C). Newly oviposited eggs appear slightly pink but turn white after ca. 24 h (Fig. 1D). Generally, the eggs are completely white and opaque, but Sacerdote-Velat et al. (2020) documented several partially calcified eggs with translucent shells through which the developing embryos were visible until hatching. Reported clutch sizes range from 1–18 eggs, with a mean of 7 eggs (Fowler 1966; Fritts 1968; Sexton and Claypool 1978; Radaj 1981), but larger reported clutch sizes may be the result of communal nesting. In the course of our long-term recovery program, the maximum clutch size confirmed as produced by a single female was 14 eggs.

Water Loss beneath Plywood and Chipboard.—Plywood and chipboard may vary in their hydric buffering properties (Grant et. al 1992) which may affect *O. vernalis* use of each cover type for nesting. We placed plaster of Paris egg models beneath plywood and chipboard ACOs at each transect in the 2019–2020 comparative surveys to monitor water loss in the nest environment. Over the two seasons, 32 models were deployed, with eight beneath plywood and eight beneath chipboard in each year, with one model per transect. Eggs of *O. vernalis* and their congener *O. aestivus*, have flexible shells that readily absorb and lose moisture to the environment (Plummer 1990). Plaster models serve as useful analogs for moisture loss in organisms or life-stages with little resistance to desiccation (Tracy et al. 2007). Plaster egg models were cast using Alumilite Amazing Mold Putty. Once the models were dry, we submerged them for 24 h to saturate the plaster prior to deploying them in the field. Initial model mass was recorded on an electronic balance at the time of placement in the nesting site. During subsequent ACO checks, we recorded the mass of each model to monitor loss or gain of water until the last eggs present in each transect either hatched or failed. We calculated percent water loss between the starting and ending model mass throughout the incubation window. The data were skewed, so we compared mean percent water loss beneath plywood and chipboard pooled across years, using a Mann-Whitney U test.

Canopy Cover.—While the ACO transects were established in grasslands, variation in prescribed burn history, mowing for invasive species management, and presence of encroaching shrubs may affect the height of surrounding vegetation and the degree of shading across transects. Canopy cover quantification allows researchers to obtain precise metrics that elucidate how the related thermal and light environment may affect nest site selection, in a more informative way than categorical classification (Doody et al. 2006a, b). To examine whether canopy cover above ACOs affected nest incidence, canopy photographs were taken at all ACOs in Sites 1 and 2 for the board material comparison (N = 40 plywood, N = 40 chipboard, N = 8 rubber) with the camera resting on the ACOs, pointing skyward. Photographs were between 1000–1100 h with the top of the camera oriented due north. Photographs were converted to binary and the area of black pixels was calculated in ImageJ (Schneider et al. 2012). The percent area of black pixels was used as an estimate of canopy cover. Similar quantification of canopy cover with ImageJ has been used in other grass-dominated systems and forests, with resulting metrics performing similarly to other canopy analysis approaches (Smith and Ramsay 2018; Xiong et al. 2019). We used a nested ANOVA to examine whether percent canopy cover varied between plywood and chipboard ACOs nested within transects. For the supplemental rubber mats, we compared mean percent canopy cover beneath rubber mats with and without nests using a two-tailed t-test.



PHOTOS BY A. SACERDOTE-VELAT

Fig. 1. A) Communal *Opheodrys vernalis* nest; B) *Opheodrys vernalis* nest next to a hygrochron ibutton logger (1.7 cm diameter); C) clutch of *Opheodrys vernalis* eggs with a single opaque, yellowish unfertilized egg at the top; D) newly oviposited *Opheodrys vernalis* eggs have a slightly pink coloration during the first 24 h.

Multi-method Models for Nest Detection.—We used Program Presence v11.5 (Hines 2006) to examine two sets of single season multi-method models for 2019 and 2020 nest survey data. Single season multi-method models simultaneously estimate Ψ (occupancy), θ (availability for detection), and p (detection probability). They assume that sites are closed to changes in site occupancy for the duration of sampling, and detection is independent among sites (Nichols et al. 2008). Multi-method models allow detection probability to vary across different concurrent survey methods. These models include the computation of the parameter θ, availability for detection (= local occupancy), the probability that individuals are available for detection at a finer scale (ACO transect) within the larger site (preserve), given that the site is occupied (Nichols et al.

Table 3. Single season multi-method models of *Opheodrys vernalis* nest occupancy and detection probability with board type as the survey method in 2019 and 2020. Models are ranked by ΔAIC and model weight (w). Models within ΔAIC ≤2.00 are indicated in bold. In 2019, models in bold were included in model averaging to estimate detection probability parameters shown in Fig. 2.

Model	2019 ΔAIC	2019 *w*	2020 ΔAIC	2020 *w*
Ψ, θ (.), p(material+survey)	**0**	**0.715**	**0**	**1.00**
Ψ, θ (site), p(material+survey)	**2.00**	**0.263**	49.11	0
Ψ, θ (.), p(material)	7.68	0.015	28.89	0
Ψ, θ (site), p(material)	12.24	0.001	30.58	0
Ψ, θ (.), p(survey)	50.59	0	24.43	0
Ψ, θ (site), p(survey)	52.29	0	26.25	0
Ψ, θ (.), p(.)	98.29	0	91.84	0

Table 4. Single season multi-method models of *Opheodrys vernalis* adult occupancy and detection in DuPage County, Illinois, USA with wooden chipboard, plywood, and rubber mats as cover objects in 2019. Biweekly survey results were consolidated to monthly detections or non-detections. Models were ranked by ΔAIC and model weight (*w*). Three models within a ΔAIC ≤2.00, indicated in bold, were included in model averaging for parameter estimates of detection probability shown in Fig. 3.

Model	ΔAIC	*w*
Ψ, θ (.), p(material)	**0.00**	**0.407**
Ψ, θ (.), p(survey)	**1.48**	**0.194**
Ψ, θ (site), p(material)	**1.93**	**0.155**
Ψ, θ (.), p(material+survey)	2.77	0.102
Ψ, θ (site), p(survey)	3.48	0.071
Ψ, θ (site), p(material+survey)	4.77	0.037
Ψ, θ (.), p(.)	5.08	0.032

Table 5. Single season multi-method models of *Opheodrys vernalis* adult occupancy and detection at GR in Lee County, Illinois with plywood and rubber mats as cover objects from May-August 2017, 2018, and 2019. Weekly survey results were consolidated to monthly detections or non-detections. Models were ranked by ΔAIC and model weight (*w*). The best-supported models for each year are indicated in bold and were used to generate parameter estimates for detection probabilities shown in Fig. 3.

Model	2017 ΔAIC	2017 *w*	2018 ΔAIC	2018 *w*	2019 ΔAIC	2019 *w*
Ψ, θ (.), p(material+survey)	**0.00**	**0.538**	0.99	0.258	4.82	0.070
Ψ, θ (.), p(material)	2.46	0.157	**0.00**	**0.424**	4.41	0.086
Ψ, θ (.), p(survey)	2.52	0.152	**1.40**	**0.210**	**0.00**	**0.782**
Ψ, θ (.), p(.)	2.53	0.151	2.76	0.106	5.11	0.060

2008). For nest surveys, estimation of θ could provide insight into the proportion of survey plots within an occupied site that may support nesting activity. For each year, within-week nest detections were pooled into 11 weekly surveys per season beginning with the week of 24 June and ending the week of 7 September. Each plywood and chipboard set represented a sampling location. Detections across sampling locations were pooled by board type within transects. We examined a set of seven multi-method models for each survey year, including the null model and global model that included all site and sampling covariates (Table 3). Study site was included as a covariate potentially affecting Ψ and θ; method (board material) and survey week were included as covariates potentially affecting detection probability (p). Models were ranked by Akaike weight (*w*; Akaike 1973) and models within a ΔAIC ≤2.00 were averaged to estimate parameters for occupancy and detection.

Adult Detection Probability by Material and Month.—We examined detection probabilities of adult *O. vernalis* by ACO type and survey month at Sites 1 and 2 in DuPage County, comparing plywood, chipboard, and rubber, and at GR in Lee County, comparing plywood and rubber. We defined adults by snout–vent length (SVL) with females having SVLs ≥225 mm and males having SVLs >200 mm based on the minimum size of gravid females as detected by palpation and of males with cloacal smears containing spermatozoa. In Sites 1 and 2, we used the same paired wooden chipboard and plywood transects from the nest surveys but placed one black rubber mat 10 m from the end of each paired-board transect. In 2019, ACOs in Sites 1 and 2 were sampled three times per week for *O. vernalis* from May through August. In GR in Lee County, the sampling window varied across years. To examine adult detection probabilities across a consistent range of months, we only included detections between May and August in 2017–2019. For each site, total adult detections were pooled by month and ACO material within sampling arrays.

We used single season multi-method model sets to examine variation in detection probabilities for adult *O. vernalis* in DuPage County sites with plywood, chipboard, and rubber (Table 4), and in GR with plywood and rubber (Table 5). The model set for DuPage County sites included seven multi-method models for 2019. Study site was examined as a covariate potentially affecting Ψ and θ; method (board material) and survey month were examined as covariates potentially affecting detection (Table 4). The model sets for GR included four multi-method models per year. Sampling covariates included board material and survey month (Table 5).

Results

At Sites 1–6, from 2015–2020, 98% of 217 nests beneath ACOs occurred beneath wood and 2% occurred beneath rubber. When adjusted by number of coverboards of each type, frequency of nests beneath wooden ACOs was significantly greater than beneath rubber ($F_{1,5}$ = 13.28, p = 0.01; Table 2). Mean percent canopy cover did not significantly differ between rubber mats with and without nests (p = 0.055, t_6 = 2.36), although sample size was small. Mean percent canopy cover was 31.1(± 23.8) for rubber ACOs (N = 3) with nests and 6.4 (± 5.0) for rubber ACOs without nests (N = 5). For the chipboard and plywood ACOs in the 2019–2020 surveys, there was no significant variation in percent canopy cover by board material nested within transects (p = 0.68, $F_{9,6}$ = 0.70), or by transect (p = 0.69, $F_{6,6}$ = 0.64). Since canopy cover did not significantly vary among transects, it was not included as a covariate in the detection probability models.

For nest surveys, we conducted a total of 5280 ACO checks for the paired-board ACO transects in 2019–2020. Surveys produced nest detections beneath 28% of ACOs across years. In 2019 and 2020 combined, 45 of 160 ACOs produced detections of 105 *O.*

vernalis nests within the paired-board transects. Many nests were communal, so the number of boards with nests is not equivalent to the number of nests detected. In 2019, 55 nests were detected beneath 19 ACOs, including five single and 50 communal nests. In 2020, 50 nests were detected beneath 26 ACOs, 10 were single and 40 communal. *Opheodrys vernalis* females demonstrated a clear preference for wooden chipboard over plywood, with 43 of the nest boards across years composed of chipboard, and only two nest boards composed of plywood. In each year, only a single nest was found beneath plywood. While GR was not part of the paired ACO nest detection study, only one nest was encountered beneath plywood in each year from 2017–2019. No nests were encountered beneath rubber ACOs at GR.

At Sites 1 and 2, across 2019 and 2020, water loss from plaster models differed significantly with board material ($U = 44.00$, $Z = 2.01$, $p = 0.04$, $N = 32$) averaging 12.3% (± 3.1 SE, N = 16) for chipboard and 25.6% (± 7.0 SE, N = 16) for plywood.

For the 2019 and 2020 multi-method nest detection models, the best supported models (ΔAIC ≤2.00) held Ψ and θ constant or included site as an occupancy covariate (Table 3). In both years, nest detection probability varied with board material and survey week (Fig. 2). Detection probability was far greater for chipboard than plywood in both years. In 2019, peak detection beneath chipboard occurred between 7 July–10 August with p = 0.88 (± 0.12 SE; Fig. 3). In 2020, peak detection for chipboard occurred earlier, between 30 June–10 August, with p = 0.83 (± 0.17 SE) during the last week of June and p = 1.00 for the successive five weeks. For plywood, detection probability remained low with p ≤ 0.13 (± 0.11 SE) in 2019 and p ≤ 0.17 (± 0.15 SE) in 2020. Peak detection for plywood overlapped with that of chipboard, occurring 14 July–3 August in 2019 and 30 June–13 July in 2020. In both years, nest detection was low at the beginning of nesting season in late June, increased in July, and decreased in August as hatching occurred. Occupancy estimates based on nest detection were greater in 2019 with Ψ = 1.00 than in 2020 with Ψ = 0.75 (± 0.15 SE), but in both years, availability of nests for detection did not differ, with θ = 1.00.

In 2019, we conducted a total of 3696 ACO checks for *O. vernalis* adults and detected a total of 27 adult *O. vernalis*. Captures of adults were greatest during the weeks of 13–17 May (N = 5), 3–7 June (N = 5), and 8–9 August (N = 5). Adult detection probability ranged from 0.10–0.32 (± 0.07–0.11 SE) and varied with coverboard material throughout the season (Figs. 3A–C). Rubber and plywood had the greatest detection probabilities in May, but detection decreased for both materials during June and July, and then slightly increased in August. Chipboard had the greatest detection probability during the nesting window in June and July (Fig. 3A). For DuPage County sites, the model averaged estimate of the proportion of transects occupied by adults was = 0.52 (± 0.16 SE) and availability of adult snakes for detection across surveys, transects, and methods was = 0.57 (± 0.19 SE).

From 2017–2019, we conducted a total of 6144 ACO checks at GR in Lee County during the May–August sampling window. ACO surveys produced a total of 34 adults in 2017, 31 adults in 2018 and 58 adults in 2019. Across years, captures of adults were greatest between 13–19 May (N = 21, mean = 11.5), 3–9 June (N = 20, mean = 6.7), and 22–28 June (N = 9, mean = 4.5). Adult detection probability at GR varied with ACO types, survey months, and years. Detection beneath rubber ranged from 0.17–0.42 (± 0.11–0.14 SE) in 2017, 0.21–0.45 (± 0.14–0.21 SE) in 2018 and 0.21–0.87 (± 0.12–0.13 SE) in 2019 (Fig. 3B). Detection probabilities beneath plywood ranged from 0–0.42 (± 0.14 SE) in 2017, 0.22–0.47 (± 0.15–0.20 SE) in 2018, and from 0.21–0.87 (± 0.12–0.13 SE) in 2019 (Fig. 3C). In 2017, the proportion of arrays occupied was Ψ = 0.80 (± 0.14 SE) with availability of adult snakes for detection, θ = 1.00. For 2018, Ψ = 0.72 (0.15 SE) and the availability of adult snakes for detection was θ = 0.93 (0.19 SE). In 2019, the occupancy estimate Ψ = 0.70 (0.14 SE), and the availability of adult snakes for detection was θ = 1.00. In 2017 and 2018, the best supported models included effects of board material (method) and survey month on detection probability (Table 5). In 2019, only the model that included effects of survey month was within ΔAIC ≤2.00, with peak detection in May and July (Table 5). For all years, detection beneath rubber was greatest in May and decreased in June. In 2017, adult detection beneath rubber remained low through August. In 2018, detection beneath rubber slightly increased in July and decreased in August. In 2019, detection peaked in May and July and decreased in June and August, regardless of ACO material (Fig. 3B). In all years, adult *O. vernalis* detection beneath plywood was greatest in May and July, with decreases in June. In 2017, detection beneath plywood dropped to 0 in August. In contrast, in 2018, detection beneath plywood decreased in June but then increased slightly for July and August (Fig. 3C).

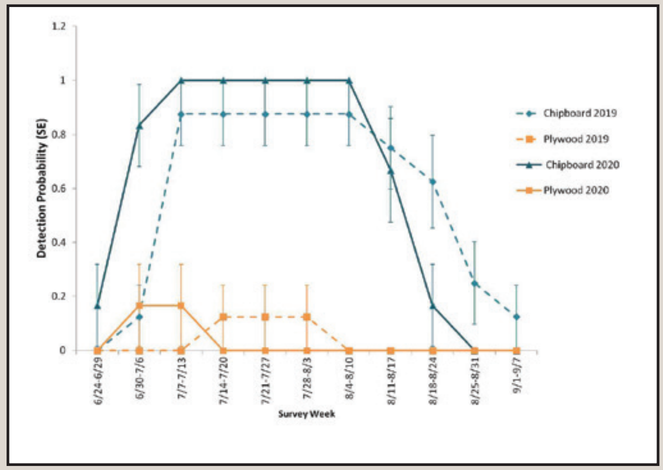


Fig. 2. Nest detection probabilities (SE) in DuPage County, Illinois, USA across transects by survey week, artificial cover object material, and year for 2019 and 2020.

Discussion

Artificial Cover Materials and Nest Detection.—The paired ACO surveys demonstrated a clear preference by *O. vernalis* females for wooden chipboard over plywood as a nesting site, with 54% of chipboard ACOs being occupied by nests across years versus 0.03% of plywood. Nest detection probability beneath chipboard far exceeded plywood and remained >0.8 for five consecutive weeks in each study year, making this approach a reliable method for determining *O. vernalis* occupancy and breeding activity. Plaster egg models beneath chipboard lost less water during the incubation window than models beneath plywood. Chipboard provided a greater buffer to water loss than plywood throughout the nesting season, creating conditions that may be more comparable to rotting logs, which are a natural nesting site for the species if available. This difference in hydric environment likely plays a role in oviposition site selection by gravid *O. vernalis*. Grant et al. (1992) compared amphibian

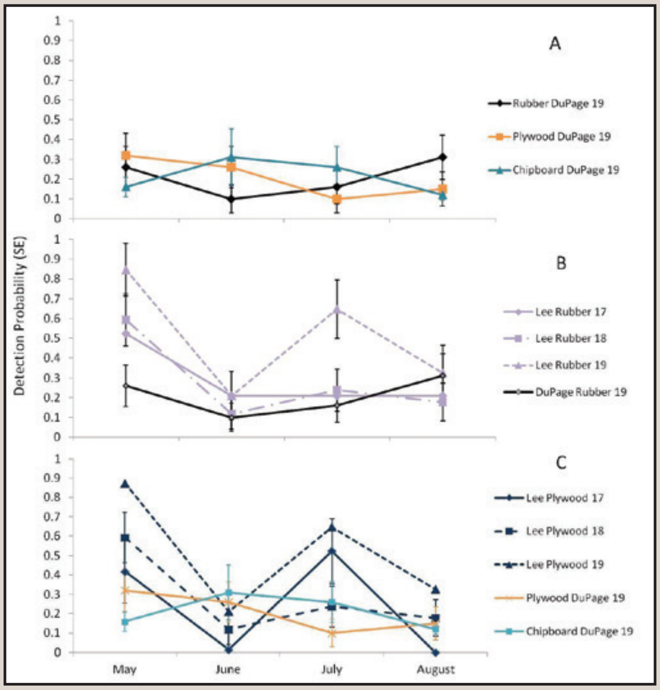


Fig. 3. A) Detection probability (SE) of *Opheodrys vernalis* from a single-season multi-method analysis of 2019 coverboard surveys in occupied DuPage County, Illinois, USA, sites using rubber mats, plywood, or chipboard. Detections across weekly surveys were pooled by month; B) detection probabilities (SE) of adult *O. vernalis* using rubber mats in DuPage County sites in 2019 and Green River in 2017–2019. Detections across weekly surveys were pooled by month; C) detection probabilities (SE) of *O. vernalis* beneath plywood and chipboard in DuPage County sites in 2019 and beneath plywood in Green River in 2017–2019. Detections across weekly surveys were pooled by month.

and reptile capture rates beneath wooden chipboard and tin. They found differences in thermal and hydric environments, litter hydration, and soil moisture with tin and chipboard, with temperatures up to 12°C warmer beneath tin. These attributes made chipboard preferred by amphibians in their study (Grant et al. 1992). Like amphibians, the eggs of *O. vernalis* are susceptible to desiccation, and *O. vernalis* mothers may be selecting ACOs that provide both heat and moisture necessary for embryo development. Plummer and Snell (1988) found that *O. aestivus* females chose nesting substrate with greater moisture in captivity. However, in the field, nest sites of *O. aestivus* ranged considerably in substrate moisture, but nests with drier substrate produced smaller hatchlings (Plummer 1990).

Incidence of nesting beneath rubber was limited to only five occasions beneath three rubber ACOs in our long-term monitoring sites. Our ability to infer any pattern is limited by sample size, however, we observed that the three mats used by nesting mothers were close to shrubs, and in partial shade during the day. While GR had 192 rubber ACOs available, no nests were found beneath them. Although rubber mats may retain some moisture between the substrate, litter, and mat early in the day, they likely exceed a critical temperature for embryo development, such that females will not prefer them as a nesting site, especially if they are not shaded.

Optimal Timing of Nest Surveys.—Opheodrys vernalis nesting tends to occur in several pulses between late June and August in northern Illinois. As such, nest detection probability varied with survey timing. In 2019 and 2020, peak detection beneath chipboard occurred from 7 July–10 August, remaining constant following successive pulses of hatching early in the time window, until hatching commenced. In 2019, northern Illinois had a polar vortex in late January, which was followed by a late spring with two significant accumulating snowstorms during early and late April. With the prolonged cold conditions, snake emergence was later than in other study years and we observed a 7–10 d delay in the commencement of nesting activity, which explains the difference in the onset of peak nest detection probability between 2019 and 2020. While one expects a degree of annual and within-season variation in length and oviposition timing of *O. vernalis*, other reptiles in the region such as Blanding's Turtles also had noticeably delayed nesting activity in 2019 (D. Thompson and G. Glowacki, pers. comm.). Given this delayed nesting activity, the peak detection window for nests observed in 2020, from 29 June–10 August, is more typical of peak activity observed between 2015–2018. For identification of an optimal window for nest surveys, mid-late July produced excellent detection rates in both years, but when conducting surveys at different latitudes, that window may shift later with greater latitude or earlier with lower latitude. However, once the initial bout of nesting has occurred, detection will remain ≥0.80 until hatching occurs.

Once nesting commences in the second week of July, the presence of a nest beneath an ACO may increase the probability that other females will nest beneath an occupied ACO (Gregory 2004). Females may rely on scent trails to find nesting sites and may also choose to nest with the eggs of conspecifics non-randomly (Graves and Duvall 1995; Doody et al., 2009; Scott et al. 2013). In *O. aestivus*, mothers preferentially nested together despite being offered an abundance of identical shelter sites (Plummer 1981), indicating conspecific attraction to eggs (reviewed in Doody et al. 2009). Communal nesting is a frequent occurrence, as evidenced by our observations of 90 communal nests versus 15 single nests of 105 total nests across 2019 and 2020. The age of ACOs may also affect use by snakes, and subsequently, detection. Grant et al. (1992) found that age of tin ACOs affected capture rates such that in the two months following placement, reptile and amphibian captures were low, but captures generally increased during the third month the tin was in place. In the paired-board transects, 45% of chipboard ACOs were occupied in 2019 versus 62% in 2020, showing a general increase in use with board age as boards were not replaced between 2019 and 2020. Peak detection of nests beneath chipboard was greater in 2020 than in 2019 (1.00 vs. 0.81, respectively).

Adult Detection Probability with Cover Material and Survey Month.—Detection probabilities of adult *O. vernalis* varied from 0.10–0.32 (± 0.07–0.11 SE) across the active season and ACO materials in DuPage County. Detection was generally greater at GR in Lee County, a large, rural site, ranging from 0–0.87 (± 0.14 SE) across survey months and ACO types. We found that detection probability for adult *O. vernalis* using chipboard, plywood, and rubber varied by survey month in DuPage County sites. Early in the season, in May, *O. vernalis* were more likely to use rubber and plywood than chipboard. Rubber heats quickly and retains heat for longer periods of time. Plywood may have provided more warmth than chipboard early in the season. Differences in heat retention among ACOs may explain similar apparent preferences for tin over wooden cover demonstrated by Red-bellied Snakes (*Storeria occipitomaculata*) at higher latitudes, along with the preference for cover placed in open canopy fields versus forests (Halliday and Blouin-Demers 2015;

Retemal Diaz and Blouin-Demers 2017). We observed increased detection beneath rubber again in mid-late August. However, these detections tended to be early in the morning (prior to 0900 h). It also appeared that the rubber ACOs may have formed an evaporative barrier between decaying vegetation beneath the ACO and the soil, as the undersides of the rubber ACOs were often wet during August surveys, which may create a preferred microclimate for *O. vernalis* or their invertebrate prey. During June and July, as nesting began, *O. vernalis* shifted use from rubber to wooden ACOs that can retain more moisture. In DuPage County sites, chipboard was a more productive material for adult detections during June and into the July nesting window, with a detection probability of 0.3 vs. 0.1 for plywood.

For GR in Lee County, rubber ACOs were most effective in May in all years, with a decrease in June, leading into nesting season. Detection beneath plywood also decreased in June. In July, plywood had greater detection rates than rubber in all years except 2019 when they did not differ. For August, there was substantial annual variation in patterns of detection probability of adults with board material. For GR, adult detections beneath rubber were limited to the afternoon and the evening, between 1300–2100 h, when air temperatures are generally cooler. Additionally, the late spring in 2019 with delayed emergence and nesting may explain some of the continued use of rubber in the warmer months in that year. Across both counties and years, peak adult captures occurred during 13–19 May and 3–7 June across a combination of rubber and plywood in May, and chipboard, plywood, and rubber in June.

Differences in adult *O. vernalis* detection probabilities between sites in DuPage and Lee counties may be attributable to differences in population size and densities, as well as disparate land use histories, preserve sizes, and surrounding matrix. GR is a large site with little road fragmentation that has been in conservation forty years longer than the DuPage County sites and is surrounded by row crop agriculture rather than additional grassland, pastureland, or development. The lower detection rates in DuPage County likely reflect reduced abundance that may be typical of urban and suburban snake populations where road mortality greatly limits colonization potential and gene flow (Mitrovitch et al. 2018), as well as the tendency of *O. vernalis* to cluster in small areas (Sacerdote-Velat et al. 2014). Additionally, the time of day when surveys were conducted varied by county, with more early morning surveys in DuPage County versus late afternoon and evening surveys in Lee County. Another factor potentially affecting the variation in detection for these counties, and some of the annual variation in detection at GR, may be the differences in prescribed fire interval and fire extent. Differences in fire management affect vegetation presence, density, and height, and thus the need for snakes to use ACOs following burns as the vegetative cover reestablishes through the season. GR is burned on a three-year rotation, while in the DuPage County sites, burn intervals of some management units have reached 10 years, while others have been burned more frequently, or were mowed when burns could not be implemented. In DuPage County, smoke conditions for neighbors and over roads are major constraints in carrying out regular prescribed fire in a suburban area. Future studies examining detection probability of snakes beneath ACOs, along with vegetation monitoring before and after prescribed fire, will inform our understanding of this relationship.

Detection Probability of Adults versus Nests.—The peak detection probabilities of adult snakes occurred in May in DuPage County (p = 0.32) and Lee County (p = 0.42–0.87 across years). The peak adult detection rates were low in comparison to the perfect and near perfect detection of nests with chipboard during July (p = 0.88–1.00). Further, we observed greater annual variation in detection rates of adult snakes at GR. Additionally, multi-method models estimated perfect availability of nests for detection while availability of adult snakes for detection (θ) varied between 0.57–1.00 across counties and years. GR had greater availability of snakes for detection than the suburban DuPage County sites. Although rubber ACOs in GR produced a detection probability of p = 0.87 for adult *O. vernalis* during May surveys, this only occurred in 2019, when survey month rather than board material strongly affected detection probability. This peak in detection was largely driven by captures occurring during 13–19 May. Therefore, the opportunity to conduct surveys of adult *O. vernalis* with peak detection is limited. In 2017 and 2018, peak adult detection beneath rubber in GR was 0.41 and 0.45, respectively. In comparison, once nesting commenced, nest detection probability remained between 0.87–1.00 for five consecutive weeks in both 2019 and 2020 beneath chipboard ACOs. These data support the hypothesis that nests are more readily detectable than adults and would require fewer survey occasions to confirm the species as present and the occurrence of breeding in a site.

Opheodrys vernalis use a variety of ACOs which may facilitate detection in grasslands (Seibert and Hagen 1947; Redder et al. 2006; Cox et al. 2009; Sacerdote et al. 2014; King and Vanek 2020). Over the course of our *O. vernalis* recovery and monitoring program, we have used plywood, chipboard, rubber mats, corrugated fiberglass, and corrugated tin to varied extents. Tin was used in a limited capacity in our 2013–2015 surveys in McHenry County, Illinois where it produced early morning and late afternoon/early evening captures of juveniles, early and late in the active season (early May and early September). We did not observe any nests beneath tin cover objects. Seibert and Hagen (1947) had the greatest percentage of their 90 *O. vernalis* captures beneath tin in an urban site in Illinois described as a defunct subdivision with old field vegetation. Tin produced 41% of their captures, versus 22.8% beneath rocks and only 2.3 % beneath wood. Their remaining captures were either caught in the open or beneath assorted debris including leather shoes, bags, bricks, and glass present in the site. No nests were detected during the course of their study, although adults and hatchlings were encountered at the site. Their peak numbers of adult detections also occurred in May and remained at low levels through the rest of the season. Detections of hatchlings in September and October increased their total number of *O. vernalis* encountered (Seibert and Hagen 1947). However, no encounter breakdown was provided to give a sense of seasonality of captures by cover type, or the availability of various cover materials. Generally, the temperature beneath tin may exceed a critical temperature for embryo development and dry the litter and soil beneath the cover object, promoting egg desiccation (Grant et al. 1992). As an additional practical consideration, tin tends to be cost-prohibitive and in urban and suburban areas, removal of tin for scrap metal is a frequent problem, so we discontinued the use of tin in our study.

Based on the results of our comparative study, we recommend deploying chipboard in spring so that the boards have time to absorb moisture by nesting season, and conducting nest surveys using chipboard during mid-late July for lower effort, rapid assessment of site occupancy by *O. vernalis* and confirmation of breeding activity. However, if after identifying extant populations, the study goal is to conduct mark-recapture or repeated-count abundance estimates, we recommend use of ACO arrays with both rubber and chipboard to maximize encounter rates of snakes throughout the season.

Future studies of *O. vernalis* detection probability should examine detection patterns of hatchlings and juveniles beneath various ACO materials, variation in thermal and hydric properties of various ACO types with time of day and frequency of rainfall events, and variation in detection with time of day and ACO type. Additional studies are needed to examine how *O. vernalis* detection probabilities vary in response to vegetation management such as prescribed burning, mowing, and brush clearing, and how management may influence nesting activity and nest detection. Given the large number of communal *O. vernalis* clutches deposited there, our study reinforces the idea that chipboards would also be useful for addressing questions or hypotheses relating to communal nesting behavior.

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Asymmetry in Reproductive Allocation in Rainbow Water Snakes (*Enhydris enhydris*)

There is extensive literature regarding morphological asymmetry in reptiles (Hoso et al. 2007; Laia et al. 2015; Danaisawadi et al. 2016), and in particular snakes (Oldham et al. 1970; Shine et al. 2000; Perez et al. 2019). For example, many snakes possess only one functional lung (the right lung) while the other is absent or vestigial (van Soldt et al. 2015). In fossorial snakes (Scolecophidians), only the right oviduct is present (Clark 1970; Lock and Wellehan 2015).

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Less well studied is asymmetry in the use and allocation of reproductive investment between paired reproductive organs. Although asymmetry in the size (and perhaps functionality) of reproductive structures in male snakes has received some attention (Shine et al. 2000), little is known about asymmetry in the use of female reproductive organs. Some snakes are known to allocate greater numbers of ova to the right compared to the left oviduct (Shine 1977; Aldridge 1979; Marques and Puorto 1998; Bassi et al. 2018). The reasons for this asymmetry remain unclear. The proximate mechanism(s) for reproductive asymmetry may include inherent differences in the potential fecundity of the right vs. left ovary, or through a process called extra-uterine transfer (the release of ova into the coelomic cavity, where they are taken up by the contralateral oviduct; Shine 1977; Blackburn 1998; Bassi et al. 2018). In addition to disentangling the mechanism(s) that result in this asymmetry, the functional or adaptive significance is also of interest. A better understanding of the snake taxa in which reproductive asymmetry occurs and which it does not (and their ecological traits) is an important first step in answering a broad range of questions around the significance of this pattern (Blackburn 1998). For example, long and thin arboreal snakes may display more pronounced reproductive asymmetry than larger-bodied terrestrial species with less coelomic space restrictions, because of the need to distribute reproductive investment along the body to improve locomotor performance.

We examined reproductive asymmetry in the Rainbow Water Snake (*Enhydris enhyrdis*). *Enhydris enhydris* is a small (<90 cm in length) viviparous homalopsid water snake