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Searching for rare and secretive snakes: are camera-trap and box-trap methods interchangeable?

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Abstract

Context. Advancements in camera-trap technology have provided wildlife researchers with a new technique to better understand their study species. This improved method may be especially useful for many conservation-reliant snake species that can be difficult to detect because of rarity and life histories with secretive behaviours.

Aims. Here, we report the results of a 6-month camera-trapping study using time lapse-triggered camera traps to detect snakes, in particular the federally listed Louisiana pinesnake (*Pituophis ruthveni*) in eastern Texas upland forests in the USA.

Methods. So as to evaluate the efficacy of this method of snake detection, we compared camera-trap data with traditional box-trapping data collected over the same time period across a similar habitat type, and with the same goal of detecting *P. ruthveni*.

Key results. No differences in focal snake species richness were detected across the trap methods, although the snake-detection rate was nearly three times higher with camera traps than with the box traps. Detection rates of individual snake species varied with the trapping method for all but two species, but temporal trends in detection rates were similar across the trap methods for all but two species. Neither trap method detected *P. ruthveni* in the present study, but the species has been detected with both trap methods at other sites.

Conclusions. The higher snake-detection rate of the camera-trap method suggests that pairing this method with traditional box traps could increase the detection of *P. ruthveni* where it occurs. For future monitoring and research on *P. ruthveni*, and other similarly rare and secretive species of conservation concern, we believe these methods could be used interchangeably by saturating potentially occupied habitats with camera traps initially and then replacing cameras with box traps when the target species is detected.

Implications. There are financial and logistical limits to monitoring and researching rare and secretive species with box traps, and those limits are far less restrictive with camera traps. The ability to use camera-trap technologies interchangeably with box-trap methods to collect similar data more efficiently and effectively will have a significant impact on snake conservation.

Additional keywords: endangered, infrared, monitoring, remote detection, threatened.

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Introduction

As technology advances, researchers gain opportunities to employ new techniques that help better understand and monitor wildlife with less invasive and more time-efficient means (Garden *et al.* 2007; Meek *et al.* 2015; Welbourne *et al.* 2015). Although traditional methods are often proven and dependable, incorporation of new technologies while maintaining efficient study designs can have a significant impact on the conservation of a species (Burton *et al.* 2015; Welbourne *et al.* 2017, 2019). This is especially true for many species of snakes that can be difficult to detect owing to their rarity and/or secretive behaviours (Willson *et al.* 2018). In particular, the federally threatened eastern indigo snake (*Drymarchon couperi*) has been difficult to detect by using various traditional methodologies (Stevenson *et al.* 2003). However, since incorporating camera technology into surveys of potential refuges, substantial information regarding life history and ecology of *D. couperi* has been gained (Hyslop *et al.* 2009, 2014). Additionally, the implementation of new survey technologies could prove to be effective for the management of invasive species. For example, the Burmese python (*Python molorus*) in southern Florida is very difficult to detect because it is extremely cryptic and occupies areas that are often difficult for researchers to access (Reed *et al.* 2011; Hunter *et al.* 2015). Detection of this invasive species will likely increase as the use of additional monitoring methodologies increases or improves.

Another rare and secretive snake of conservation concern is the federally listed Louisiana pinesnake (*Pituophis ruthveni*). Even though monitoring efforts for *P. ruthveni* by using box traps have been substantial, detection rates across the species' historical range are extremely low (Rudolph *et al.* 2018). Reasons for the low detection rates are largely unknown; yet, possibilities include the snake's semi-fossorial behaviour, trap shyness, potential trap escape, or simply the fact that population numbers are extremely low. The actual reason is likely a combination of these factors. Adding a passive monitoring technique that helps control for some of these potential issues to traditional trapping could help determine reasons for low capture rates.

Recent advancements in camera-trap technology have allowed researchers to explore new methodologies that help solve problems associated with trapping (Adams *et al.* 2017; Welbourne *et al.* 2019), but the efficacy of these technologies for surveying snakes appears to depend on target size, habitat, camera-trap design, and elements of the environmental background (Welbourne *et al.* 2016; Richardson *et al.* 2017). Triggering systems using active-infrared (AIR) or passive-infrared (PIR) sensors have shown some success in reptile research, but problems persist (Welbourne *et al.* 2019). For instance, most implementations of infrared (IR)-triggered cameras are species-specific (Bennett and Clements 2014; Welbourne *et al.* 2016). Camera traps using such trigger systems to gather information across poikilothermic taxa can also be limited or inaccurate under different environmental conditions (Kays and Slauson 2008; O'Connell *et al.* 2011; Rovero *et al.* 2013; Meek *et al.* 2014; Welbourne *et al.* 2016).

Despite the above-mentioned limitations of infrared cameras, new applications of camera-trapping technology that accurately and efficiently detect snakes are emerging. Most of the camera traps available can be programmed to trigger over a scheduled time interval, without relying on the use of an infrared trigger system. Here, we report the results of a 6-month camera-trapping study using time lapse-triggered camera traps to detect snakes, in particular *P. ruthveni*, in eastern Texas upland forests. So as to evaluate the efficacy of this method of snake detection, we compared these data with traditional box-trapping data collected over the same time period across a similar habitat type, and with the same goal of detecting *P. ruthveni* (USA Forest Service, J. Pierce, unpubl. data).

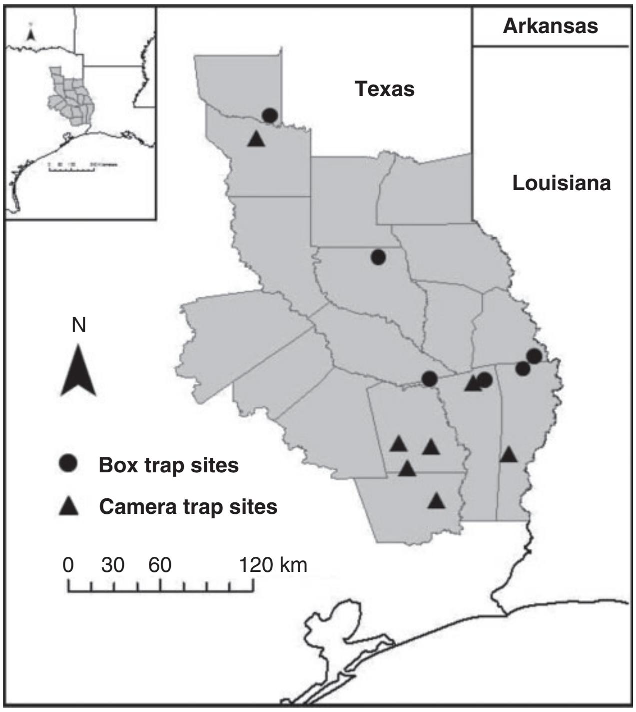

Fig. 1. Map of camera-trap and box-trap sites in eastern Texas. Shaded counties are predicted to have potentially suitable habitat for the Louisiana pinesnake (*Pituophis ruthveni*).

Materials and methods

We selected seven camera-trap sites distributed across five Texas counties, on the basis of available land access within uplands of pine or mixed-pine forests with sandy soils (Fig. 1). At six sites, we deployed four camera traps at least 450 m from each other. At the seventh site, we deployed only two camera traps because of space limitations (total camera traps: 26). For comparative analyses, we used trapping results from 58 traditional box traps deployed across six different sites as part of a large ongoing study to detect *P. ruthveni* on private and National Forest lands in eastern Texas (Fig. 1; Rudolph *et al.* 2018). The number of box traps per site was determined by the amount of potentially suitable habitat available for *P. ruthveni*, while maintaining at least 100-m separation from the nearest box trap ($n = 20$, 16, 8, 5, 5 and 4 at each site). The habitat is similar between the camera and box trap sites and the sites are in general proximity to one another (Fig. 1).

Because the target species of the study was a large, diurnal snake, two aspects of the sampling design for both camera and box traps might be different from other sampling designs focussed more generally on other herpetofauna. First, we set each camera and box trap at the centre of four drift fences arranged in a '+' shape and constructed of 6.4-mm-mesh hardware cloth, ~15 m in length and 61 cm in height, and buried 10 cm deep (Fig. 2; Burgdorf *et al.* 2005; Rudolph *et al.* 2018). We used 121.9 × 121.9 × 45.7 cm box traps

Fig. 2. Camera trap mounted facing the ground in the centre of four drift fences. Background shows eastern Texas pine savanna, the focal habitat in the present study and potentially suitable habitat for the Louisiana pinesnake (*Pituophis ruthveni*).

custom-made of plywood and 6.4-mm-mesh hardware cloth and equipped with four funnels (5.1-cm inner diameter), one for each fence (see Burgdorf *et al.* 2005 for detailed description). Whereas the mesh size for the fences and box traps is too small for *P. ruthveni* to pass through, some smaller species of snakes can readily pass through and, therefore, may be under-represented compared with other studies using a smaller mesh size.

Second, given the diurnal activity of *P. ruthveni*, we programmed camera traps (Fig. 2; RECONYX, PC800$^{\mathrm{TM}}$; Holmen, WI, USA) mounted ~2 m high and facing the ground to take an image every 30 s during daylight hours, from 0545 hours to 2200 hours, between March and October 2016. The diurnal focus of this camera-trap sampling design can lead to an under-representation of nocturnal snake species compared with studies using camera traps set for full 24-h cycles or box traps, which are generally open for multiple days at a time. We selected a 30-s time interval for camera images on the basis of previous research in this system (Adams *et al.* 2017), which found that many snake species exhibiting normal behaviour would move slowly enough across the camera trap field of view at the centre of the drift fences to be captured in an image. We revisited camera traps every 23 days (i.e. trapping interval) to change the SD memory cards and batteries, rake the trap area clean of any debris, and to perform any necessary maintenance tasks, such as reinforcing the drift fences or repositioning the cameras. After retrieving and replacing the SD memory cards, we downloaded and stored all data on an external hard drive. We manually examined images using RECONYX Mapview Professional version 3.7.2.2 (Holmen, WI, USA), which allowed a single observer to analyse 10 000 photos in roughly 1–1.5 h. We recorded species, time of detection and number of images in which an individual occurred for each snake detection.

Box traps at the traditional trapping sites were open concurrently with the camera traps from March to October 2016, and were checked every 2–3 days. We recorded species and date of capture for the box traps. Because the actual start and end dates for both camera and box traps varied with construction and removal timing, we analysed data only during the time frame when all traps were in operation, from 1 April to 30 September 2016. We used two different statistical approaches to compare detection rates across sites for each trapping method over time for focal snake species only (see Results). We used Poisson, or, when appropriate, zero-inflated Poisson (determined using Vuong test, Desmarais and Harden 2013) regression to model detection rates for each focal species, with trapping method and month as potential predictors in the model (R version 3.4.1; package: pscl, https://github.com/atahk/pscl/, accessed 2 June 2020). We also used mixed-model repeated-measures ANOVA to compare average monthly species richness and species' mean monthly detections for focal snake species across replicate traps within each site for each trapping method (IBM SPSS Statistics for Windows, version 24.0, released 2016; IBM Corp., Armonk, NY, USA). Prior to conducting the repeated-measures ANOVA, we tested for sphericity in the dataset by using Mauchly's test of sphericity (Mauchly 1940), and we used Greenhouse–Geisser corrections wherever assumptions of sphericity were violated (Bathke *et al.* 2009). By comparing mean detections with this second statistical approach, we were able to account for differences in the number of traps per site, or sampling effort, across the box-trapping dataset and one site in the camera-trapping dataset. We interpreted the results of both statistical approaches in tandem.

Table 1. Detection numbers and rates (detections per 100 trap-days) of all snake species detected by camera and box traps

Species	Detections		Detection rate (captures per 100 trap-days)	
	Camera	Box	Camera	Box
Agkistrodon contortrix	14	104	0.32	0.87
Agkistrodon piscivorus	4	5	0.09	0.04
Arizona elegans	0	1	0	0.01
Cemophora coccinea	0	5	0	0.04
Coluber constrictor	54	21	1.24	0.18
Crotalus horridus	0	2	0	0.02
Diadophis punctatus	2	0	0.05	0
Farancia abacura	0	1	0	0.01
Heterodon platirhinos	12	14	0.28	0.12
Lampropeltis calligaster	11	1	0.25	0.01
Lampropeltis getula	3	2	0.07	0.02
Masticophis flagellum	195	255	4.48	2.14
Micrurus tener	22	11	0.51	0.09
Nerodia erythrogaster	2	0	0.05	0
Nerodia fasciata	2	0	0.05	0
Opheodrys aestivus	4	0	0.09	0
Pantherophis obsoletus	98	54	2.25	0.45
Pantherophis slowinskii	7	32	0.16	0.27
Storeria dekayi	7	0	0.16	0
Storeria occipitomaculata	1	0	0.02	0
Thamnophis proximus	77	3	1.77	0.03
Virginia striatula	3	0	0.07	0
Unknown	5	2	0.11	0.02
Total	523	513	12.02	4.30

Results

A total of 4352 camera-trap days generated 8 388 078 images over the survey period. These images captured photos of 523 snakes of at least 18 species (one snake detection per 16 038 images on average). At the traditional box-trapping sites, 11 919 trap-days yielded 513 snake detections of at least 15 species (Table 1). Detection rates between the two methods varied substantially, with 12.02 detections per 100 trap-days by using camera traps, compared with 4.30 detections per 100 trap-days by using box traps (Table 1).

Of the 22 identified snake species detected across both the camera-trap and box-trap datasets, 15 were detected infrequently during the trapping period (Table 1). Five small and thin snake species were observed in camera traps only (*Diadophis punctatus*, *Opheodrys aestivus*, *Storeria dekayi*, *S. occipitomaculata*, *Virginia striatula*), most likely because of the large mesh size of the box trap. Five larger snake species were captured once or twice in either box or cameras traps, but not both (box trap: *Arizona elegans*, *Crotalus horridus*, *Farancia abacura*; camera trap: *Nerodia erythrogaster*, *N. fasciata*). An additional species, *Cemophora coccinea*, was detected five times in only three box traps at the same survey site; multiple captures of the same individual cannot be ruled out (Table 1). Four other snake species were detected infrequently in both camera and box traps (*Agkistrodon piscivorus*, *Heterodon platirhinos*, *Lampropeltis calligaster*, *L. getula*; Table 1). No *P. ruthveni* individuals were detected with either method.

We focussed analysis of temporal variation in detection between the two trapping methods on the five species most frequently detected by each trapping method, for a total of seven focal species across both methods. *Masticophis flagellum* was the most commonly recorded species by both trapping methods, with 195 detections by camera traps and 255 detections by box traps (Table 1). *Coluber constrictor* and *Pantherophis obsoletus* were also among the most detected species by both methods. *Thamnophis proximus* and *Micrurus tener* were recorded most frequently by camera traps only. *Agkistrodon contortrix* and *P. slowinskii* were detected most frequently by box traps only (Table 1).

Five of the seven focal snake species detections were modelled using Poisson regression based on results of Vuong tests ($P > 0.05$; Table 2). Only two species detections were best modelled using zero-inflated Poisson regression (Table 3; Vuong tests: *C. constrictor*, z-statistic = 2.14, Akaike information criterion (AIC)-corrected $P = 0.02$; *M. flagellum*, z-statistic = 1.84, AIC-corrected $P = 0.03$), although there were no significant zero-inflated model predictors (e.g. method or month) of detection for *M. flagellum* (Table 3). The trapping method was a significant predictor of detections in all but one species, namely, *M. tener* (Table 2). For *C. constrictor*, trapping method was a significant predictor of detection in the zero-inflated model (Table 3), which suggests that perceived differences in detection owing to trapping method were most likely driven by absence of the species from many box-trapping sites (i.e. the species was not available to be detected or counted at those sites). Month was a significant predictor of detections in all but three species, namely, *C. constrictor*, *P. obsoletus* and *T. proximus* (Tables 2, 3).

Camera traps and box traps detected an average of 3.52 and 3.43 focal species per month respectively (Fig. 3*a*). On the basis

Table 2. Results of Poisson regression with log link for each species
*$P < 0.05$

Species	Coefficient	Estimate	s.e.	z	P
Agkistrodon contortrix	(Intercept)	−1.19	0.36	−3.30	<0.01*
	Method	2.33	0.32	7.33	<0.01*
	May	−1.25	0.46	−2.71	0.01*
	June	0.32	0.29	1.13	0.26
	July	−1.10	0.44	−2.52	0.01*
	August	0.09	0.30	0.30	0.76
	September	0.05	0.31	0.15	0.88
Micrurus tener	(Intercept)	0.48	0.27	1.77	0.08
	Method	−0.54	0.37	−1.46	0.14
	May	−1.22	0.51	−2.41	0.02*
	June	−2.14	0.75	−2.86	0.00*
	July	−2.83	1.03	−2.75	0.01*
	August	−1.22	0.51	−2.41	0.02*
	September	−1.73	0.63	−2.77	0.01*
Pantherophis obsoletus	(Intercept)	0.76	0.22	3.52	<0.01*
	Method	−0.48	0.17	−2.80	0.01*
	May	0.33	0.27	1.21	0.23
	June	0.42	0.27	1.56	0.12
	July	0.08	0.29	0.29	0.77
	August	−0.14	0.31	−0.46	0.65
	September	−0.43	0.33	−1.29	0.20
Pantherophis slowinskii	(Intercept)	−1.52	0.55	−2.79	0.01*
	Method	2.17	0.53	4.08	<0.01*
	May	−0.77	0.49	−1.57	0.12
	June	−2.56	1.04	−2.47	0.01*
	July	−1.47	0.64	−2.29	0.02*
	August	−1.87	0.76	−2.46	0.01*
	September	−0.37	0.43	−0.85	0.40
Thamnophis proximus	(Intercept)	0.58	0.28	2.08	0.04*
	Method	−3.04	0.59	−5.16	<0.01*
	May	0.27	0.37	0.73	0.47
	June	0.14	0.38	0.38	0.71
	July	0.07	0.39	0.19	0.85
	August	−0.08	0.40	−0.20	0.84
	September	−0.96	0.53	−1.82	0.07

of ANOVA results, focal snake species richness was not significantly different between the trapping methods, nor over time, nor was there an interaction between trapping method and time (Table 4). Mean number of detections for *A. contortrix* and *P. slowinskii* was significantly higher, overall, for box traps, whereas the mean number of detections for *T. proximus* was significantly higher, overall, for camera traps (Table 4, Fig. 3*b*, *g*, *h*). No significant differences in the mean number of detections were observed for the remaining species (Table 4, Fig. 3*c*–*f*). The mean number of detections varied significantly over time for *A. contortrix*, *M. flagellum* and *M. tener*, and those temporal trends were similar or statistically indistinguishable across methods (i.e. no significant interaction; Table 4, Fig. 3*b*, *d*, *e*).

The cameras typically functioned as intended; however, there were three trapping intervals in which a camera fell or was dislodged from its original position, and six intervals in which camera batteries died prematurely. One camera from a camera trapping site was stolen in the second-to-last last month of trapping. Another camera was removed at the landowner's request during the final month of trapping. There were also four intervals in which a camera lens was obstructed by condensation or spider activity to the point where images could not be analysed reliably. Furthermore, a single SD memory card for one trapping interval was lost before the data could be downloaded and analysed. Because these intervals were scattered across replicate sites and time within the camera-trapping dataset, we do not believe they biased the larger trends observed in mean differences in focal species richness and detections across trap type and time.

Discussion

No differences in focal snake species richness were detected across the trap methods (Table 4, Fig. 3), although the camera-trap snake-detection rate was nearly three times higher than was the box-trap detection rate (Table 1). Even though neither trap method detected *P. ruthveni* in the present study, the species has previously been detected using both trap methods (US Forest Service, J. Pierce, unpubl. data). The higher snake-detection rate of the camera-trap method suggests that pairing this method with traditional box traps could increase detection of the species

Table 3. Results of zero-inflated Poisson regression

For each species, top block describes results for count-model coefficients using Poisson with log link, and bottom block describes results for zero inflation-model coefficients using binomial with logit link. $^{*}P < 0.05$

Species	Coefficient	Estimate	s.e.	*z*	*P*
Coluber constrictor	(Intercept)	0.55	0.53	1.04	0.30
	Method	0.06	0.37	0.15	0.88
	May	0.33	0.55	0.61	0.54
	June	0.35	0.67	0.53	0.60
	July	−1.06	0.58	−1.82	0.07
	August	−0.13	0.68	−0.20	0.84
	September	0.44	0.56	0.78	0.44
	(Intercept)	−0.25	0.97	−0.26	0.80
	Method	1.71	0.71	2.41	0.02*
	May	−1.30	1.13	−1.15	0.25
	June	0.75	1.17	0.64	0.52
	July	−13.38	717.71	−0.02	0.99
	August	−0.32	1.19	−0.27	0.79
	September	0.28	1.12	0.25	0.80
Masticophis flagellum	(Intercept)	1.67	0.13	12.59	<0.01*
	Method	0.33	0.10	3.26	<0.01*
	May	0.49	0.15	3.23	<0.01*
	June	0.07	0.16	0.43	0.67
	July	−0.44	0.20	−2.20	0.03*
	August	−0.25	0.19	−1.32	0.19
	September	−0.16	0.18	−0.90	0.37
	(Intercept)	−1.28	0.82	−1.57	0.12
	Method	−1.23	0.73	−1.69	0.09
	May	−0.79	1.32	−0.60	0.55
	June	−0.82	1.34	−0.61	0.54
	July	0.44	1.08	0.41	0.68
	August	0.50	1.06	0.47	0.64
	September	0.51	1.06	0.48	0.63

where it occurs. Differences in overall snake-detection rates between the methods could be driven by recaptures. Whereas explicit recaptures by box traps were treated simply as a detection in our analyses, once a snake was captured, it was temporarily unavailable to be detected again until the box trap was checked and the snake was released. Because camera traps yield passive detections, an initial snake detection does not prevent additional detections, which could partially explain the higher detection rate of camera traps compared with box traps.

The two statistical approaches identified trapping method as an important predictor of detections for three of the seven focal species, namely, *A. contortrix*, *P. slowinskii* and *T. proximus*. The first two species were detected more frequently in box traps, whereas the third was detected more frequently in camera traps, on average. These differences in snake-detection rates between the trap methods are likely to be a result of differences in trap design. For example, because low light conditions at night reduce image quality for species identification and the target species is diurnal, camera traps were set to take pictures only during daylight hours. As a result, camera traps were biased against detection of nocturnal snakes such as *A. contortrix* and *P. slowinskii*, which were detected more frequently in box traps that were open continuously 24 h a day (Tables 2, 4, Fig. 3). Alternatively, the box traps showed bias against detection of small-bodied snakes such as *T. proximus*, which were detected more frequently with camera traps. Indeed, five small and thin snake species were observed in camera traps only (*D. punctatus*, *O. aestivus*, *S. dekayi*, *S. occipitomaculata*, *V. striatula*) most likely because of the large mesh size of the box trap, which was designed for detecting large-bodied snakes such as *P. ruthveni* (Burgdorf *et al.* 2005). Both of these trap-design biases can be easily remedied in future studies that are not focussed on detecting *P. ruthveni*. Camera traps can be set to take pictures at night with a flash at the expense of battery life, and box traps can be constructed with smaller mesh sizes.

Trapping method was not an important predictor of detections in either of the statistical approaches for two of the seven focal species, namely, *C. constrictor* and *M. tener*. For two additional species, namely, *M. flagellum* and *P. obsoletus*, the zero-inflated and Poisson regressions (respectively) identified method as an important predictor of detections, but the repeated-measures ANOVA did not. This discrepancy among the statistical approaches for the latter two species was most likely driven by large variation in detection among the camera-trapping sites (Fig. 3*d*, *f*), which could result in a failure to detect a difference between the trapping methods by using ANOVA. Both species, especially *M. flagellum*, are active foraging snakes that could be detected frequently when cameras were set within the home range of the individuals of the species, or undetected if cameras were set outside any home range. The magnitude of and variation in detections for these species would be larger for cameras than for box traps, and, therefore, potentially prevent

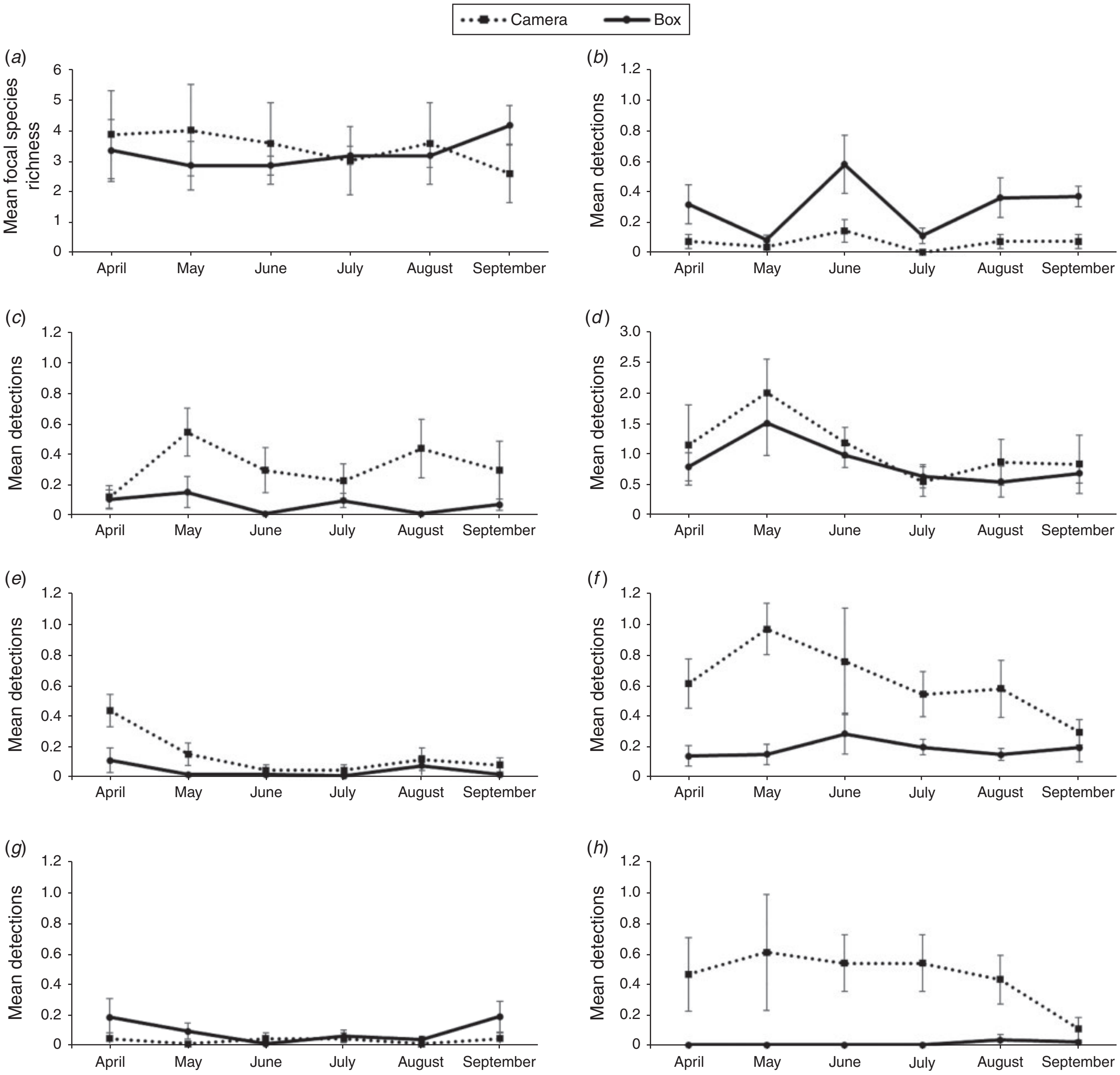

Fig. 3. (*a*) Mean focal species richness over 6 months for box and camera traps. (*b–h*) Mean detections of focal species per month by method: (*b*) *Agkistrodon contortrix*; (*c*) *Coluber constrictor*; (*d*) *Masticophis flagellum*; (*e*) *Micrurus tener*; (*f*) *Pantherophis obsoletus*; (*g*) *Pantherophis slowinskii*; and (*h*) *Thamnophis proximus*. Camera traps are represented by squares and dotted lines, box traps are represented by circles and solid lines. Error bars represent one standard deviation.

recognition of differences between the trapping methods by using ANOVA.

These differences aside, the two trap methods yielded remarkably similar temporal trends in detections, even for species with detections that varied significantly over time. For example, *A. contortrix*, *M. flagellum* and *M. tener* exhibited significant variation in detection rates over time corresponding to changes in seasonal activity in the two species, and that temporal variation was captured using both trap methods and observed with both statistical approaches (Tables 2–4, Fig. 3*b*, *d*, *e*). Both statistical approaches also identified three species, namely, *C. constrictor*, *P. obsoletus* and *T. proximus*, which exhibited no differences in detections over time for either trapping method (Tables 2–4, Fig. 3*c*, *f*, *h*). One species, *P. slowinskii*, exhibited significant variation in detections over time, which was observed using Poisson regressions, but not using the repeated-measures ANOVA (Tables 2, 4). Because this largely nocturnal species was captured predominantly in box traps, this discrepancy between the statistical approaches was most likely driven by the large variation in detections over time among box-trapping sites, on average (Fig. 3*g*). As discussed above, this variation potentially

Table 4. Results of mixed model repeated-measures ANOVA for focal species richness and species' mean monthly detections for each trapping method

Degrees of freedom (d.f.) with decimal values have been adjusted to meet assumptions of sphericity by using the Greenhouse–Geisser correction. Assumptions of sphericity are met for all other d.f. values. ES, effect size (partial eta squared). $^*P \le 0.05$

Response variable	Species	Fixed effect	d.f.	*F*	*P*	ES
Species richness	All focal species	Method	1, 10	0.03	0.87	<0.01
		Month	5, 50	1.11	0.37	0.10
		Method × Month	5, 50	1.54	0.19	0.13
Mean Detections	*Agkistrodon contortrix*	Method	1, 11	9.27	0.01*	0.46
		Month	2.6, 28.7	4.19	0.02*	0.28
		Method × Month	2.6, 28.7	2.58	0.08	0.19
	Coluber constrictor	Method	1, 11	2.13	0.17	0.16
		Month	5, 55	1.28	0.29	0.10
		Method × Month	5, 55	1.02	0.42	0.09
	Masticophis flagellum	Method	1, 11	1.39	0.26	0.11
		Month	5, 55	6.65	<0.01*	0.38
		Method × Month	5, 55	0.28	0.92	0.03
	Micrurus tener	Method	1, 11	1.33	0.27	0.11
		Month	2.1, 23.0	4.90	0.02*	0.31
		Method × Month	2.1, 23.0	0.31	0.75	0.03
	Pantherophis obsoletus	Method	1, 11	2.77	0.12	0.20
		Month	5, 55	1.43	0.23	0.11
		Method × Month	5, 55	0.93	0.47	0.08
	Pantherophis slowinskii	Method	1, 11	5.92	0.03*	0.35
		Month	2.4, 26.5	2.20	0.12	0.17
		Method × Month	2.4, 26.5	2.06	0.14	0.16
	Thamnophis proximus	Method	1, 11	4.87	0.05*	0.31
		Month	2.1, 23.3	0.67	0.53	0.06
		Method × Month	2.1, 23.3	1.42	0.26	0.12

prevented recognition of differences in detections over time by using ANOVA.

These results have highlighted the potential contribution that time lapse-triggered cameras could make towards fine-scale activity monitoring of certain snake species. Researchers can record exact dates, times, temperatures and other weather variables at the moment that snakes are detected using camera traps. Box traps can provide only coarse activity-monitoring data at a resolution that depends on the frequency of box-trap checks, and frequent box-trap checks can be counterproductive to snake detection if they deter snake activity near the trap. Frequent box-trap checks can also be expensive when technicians must be in the field checking and maintaining traps (Kays and Slauson 2008), and difficult in areas where access is challenging (e.g. Burmese python surveys in southern Florida Everglades; Reed *et al.* 2011; Hunter *et al.* 2015). Alternatively, camera traps can be checked every few weeks, which provides a non-invasive and cost-effective method for detecting snakes on private lands, or other properties with limited (e.g. military installations) or difficult accessibility (Adams *et al.* 2017). The cost associated with manually analysing large numbers of images is not trivial, but it can be reduced through volunteer, personal-computing efforts of students or other crowd-sourcing strategies (e.g. Hsing *et al.* 2018) that are not as readily available to reduce the costs of checking traditional box traps in the field. Additionally, the cost of analysing large numbers of images should decrease quickly as computer vision algorithms continue to be developed and deployed to facilitate the use of camera traps for biodiversity research and monitoring (e.g. Yousif *et al.* 2019).

Camera traps offer some advantages to traditional snake-trapping methods, but box traps will always allow researchers to collect data directly from individual snakes captured, such as morphometrics, mark–recapture, genetic material, determining body condition, testing for disease, and obtaining faecal and blood samples (Welbourne *et al.* 2017). Time lapse-triggered camera traps could provide images of an individual that could be used for mark–recapture data based on a physical feature (Treilibs *et al.* 2016), although applications are still largely limited to presence/absence detection data (Burton *et al.* 2015). For species such as *P. ruthveni*, with detection rates across their historical range being extremely low despite substantial monitoring efforts with box traps (Rudolph *et al.* 2018), more presence/absence detection data is exactly what is needed to help understand why detection rates are so low. There are real financial and logistical limits to monitoring and conducting research on this species with box traps, and those limits are far less restrictive with camera traps. For future monitoring and research on *P. ruthveni*, and other similarly rare and secretive species of conservation concern, we believe these methods could be used interchangeably by saturating potentially occupied habitats with camera traps initially and then replacing cameras with box traps when the target species is detected. Advancements in camera-trap technology will continue to provide researchers with a variety of trapping techniques to better understand the species they study, and the ability to use these technologies to collect data more efficiently and effectively will have a significant impact on snake conservation.

Conflicts of interest

The authors declare no conflicts of interest.

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