

## Diverse Methods for Diverse Systems: A Large-Scale Comparison of Reptile Sampling Methods

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**ABSTRACT:** Reptiles play a crucial role in maintaining biodiversity and ecosystem health, yet many species face increasing threats because of various anthropogenic factors. To enhance our understanding of reptile diversity and habitat use, evaluation of the effectiveness of diverse survey techniques is necessary. The relative efficacy of different methods may vary significantly across regions or communities, highlighting the need for a comprehensive approach using multiple survey methods over extensive spatial and temporal scales. In this study, we compared the effectiveness of seven survey methods—pitfall traps, funnel traps, spotlighting, arboreal cover boards, incidental encounters, camera traps, and passive acoustic monitoring (PAM)—for assessing reptile biodiversity over several years across an extensive spatial range in open eucalypt woodlands in eastern Australia. Pitfall and funnel traps were the most effective methods for detecting reptiles across all sites and latitudes. A combination of pitfall and funnel traps accumulated species most quickly, had high detection probabilities, and accounted for nearly 90% of all different reptile species detected in this study. However, with a decrease in latitude reptile diversity increased and other survey methods became necessary to document the full extent of the reptile communities. Reptile assemblages captured by different survey methods varied significantly, except for the communities captured by pitfall and funnel traps. No single method captured all species, and no species was detected by every method. PAM failed to detect any reptiles and may not be viable for assessing reptile biodiversity in Australia. Pitfall and funnel traps proved highly effective for detecting terrestrial reptiles within open eucalypt woodlands in Australia; however, the selection of methods for evaluating reptile biodiversity depended on the objectives and target fauna. When possible, to maximize species richness, survey designs should incorporate an array of concurrently deployed methods, particularly in regions with higher overall species richness. Nevertheless, if resources and time are limited, pitfall and funnel traps, combined with incidental encounters, should capture the majority of species.

**Key words:** Australia; Biodiversity monitoring; Detectability; Species richness; Survey techniques

REPTILES are a critical part of biodiversity. They play a vital role in ecological communities, serving as predators, prey, and even seed dispersers, and contribute to the overall stability and health of ecosystems (Valido and Olesen 2007; Valencia-Aguilar et al. 2013; Dodd 2016). However, they are increasingly threatened because of habitat loss, climate change, and other anthropogenic factors, with every fifth species currently facing the risk of extinction (Cox et al. 2022). Given the importance of reptiles in ecological communities, identifying changes in reptile biodiversity, particularly biodiversity loss, is crucial, and comprehensive monitoring efforts are required (Böhm et al. 2013; Webb et al. 2014).

Numerous sampling techniques have been developed to survey terrestrial reptile communities (McDiarmid et al. 2012; Dodd 2016). These often involve observer-based monitoring methods, such as pitfall traps, funnel traps, visual encounter surveys, and artificial refugia (e.g., Thompson and Thompson 2007; Ribeiro-Júnior et al. 2008; Sung et al. 2011; Michael et al. 2012). The effectiveness of these methods varies across taxa, and their use can affect the detection of biodiversity patterns (Whitworth et al. 2017). For instance, pitfall traps are widely used and highly effective for capturing small to medium-sized lizards and small snakes, but less effective for medium and large snakes (Greenberg et al. 1994; Todd et al. 2007; McKnight et al. 2015). In

contrast, funnel traps effectively capture medium-sized snakes and lizards but are less effective for small snakes and lizards (Thompson and Thompson 2007; Todd et al. 2007). Common artificial refugia, such as corrugated sheet metal, plywood, or roof tiles, are useful in detecting nocturnal thigmothermic reptiles (Engelstoff and Ovaska 2000; Michael et al. 2012; Kolanek and Bury 2021). Although many of these survey methods target terrestrial species, visual encounter surveys, including diurnal active searches and nocturnal spotlighting, successfully detect many arboreal reptiles (Rodda et al. 1999; Lardner et al. 2013; Vanderduys and Kutt 2013; Nordberg and Schwarzkopf 2015; Kutt and Colman 2023). Additionally, arboreal cover objects and traps have been used to sample arboreal reptiles (Davis et al. 2008; Bell 2009; Nordberg and Schwarzkopf 2015). Despite their varying effectiveness for specific species, most of these sampling methods require considerable labor and can incur high personnel and equipment costs (Garden et al. 2007; Molyneux et al. 2018).

Technological advancements have led to the development of more cost-effective and less time-intensive biodiversity assessment tools, such as remote sensing and environmental deoxyribonucleic acid (eDNA) sampling (Adams et al. 2017; Ezat et al. 2018; Welbourne et al. 2020; Kyle et al. 2022). Camera traps, for example, can offer reduced long-term costs and increase scalability for reptile biodiversity assessments (Ariefiandy et al. 2013; Welbourne et al. 2017; Moore et al. 2020), but face challenges in identifying small reptiles and fail to detect nocturnal species (Welbourne et al. 2015; Richardson et al. 2017). Passive acoustic monitoring (PAM) has demonstrated potential as a noninvasive and cost-effective method for detecting a range of vocal terrestrial vertebrates (Sugai et al. 2019), including reptiles (Yu et al. 2011; Hopkins

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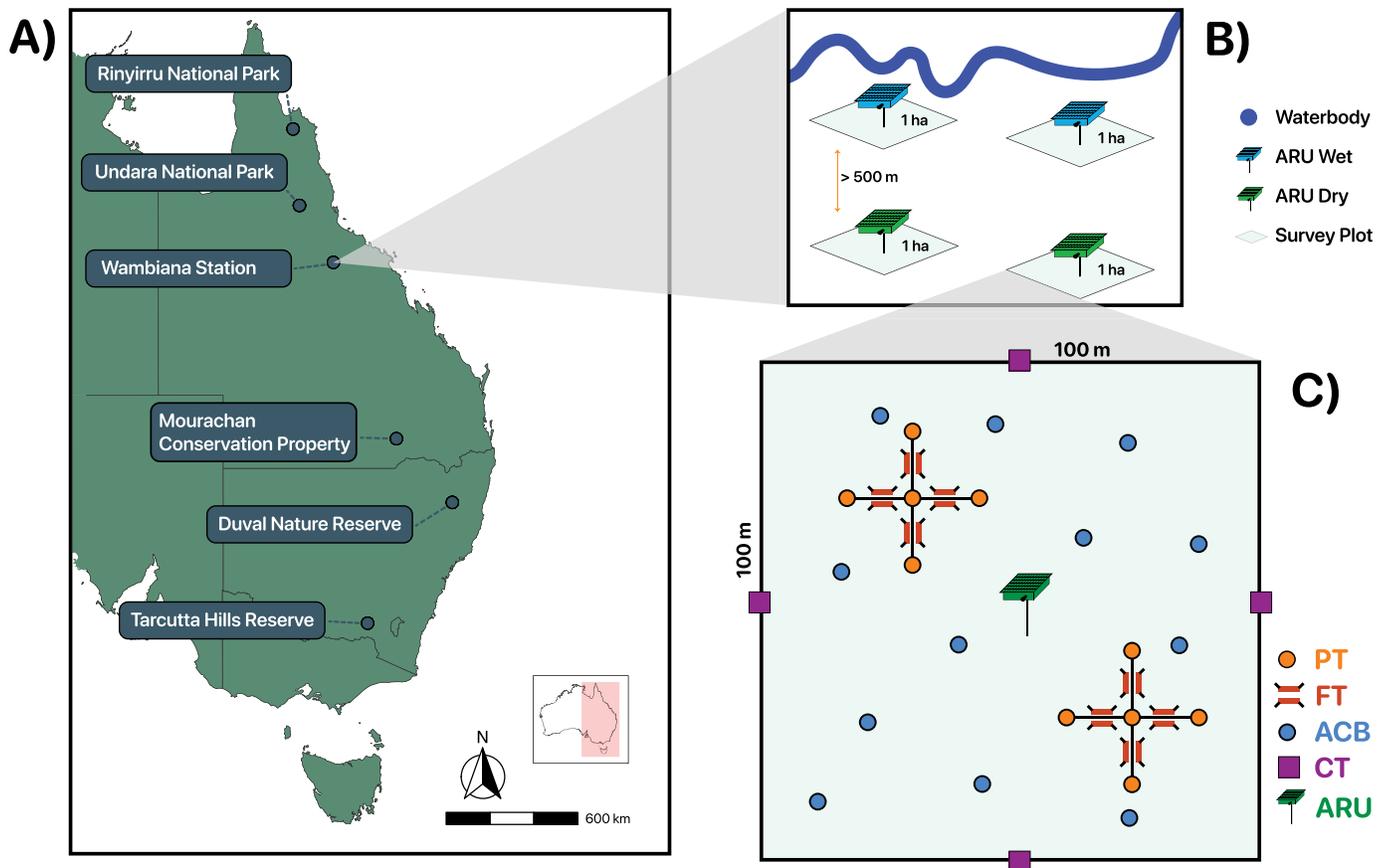


FIG. 1.—Overview of (A) the six field sites across eastern Australia with (B) a schematic of the acoustic setup for each of the field sites and (C) an overview of the survey methods deployed at each survey plot (four per site), targeting reptiles within a 1-ha plot at each ARU. Four ARUs, two within 50 m of a body of water (ARU Wet = blue) and two >500 m from a water source (ARU Dry = green), were deployed in a similar habitat type. PT = pitfall trap, FT = funnel trap, ACB = arboreal cover board, CT = camera trap, ARU = automated recording unit.

et al. 2021), but research on the application of PAM in reptile biodiversity assessments remains limited (McKnight et al. 2015). This limited exploration of PAM in reptile assessments may be attributed to its inability to detect nonvocal species, which are more prevalent among reptiles than other vertebrate taxa (Capshaw et al. 2021). However, it is important to not dismiss the potential of PAM prematurely.

The substantial behavioral and morphological diversity of reptiles and cryptic nature of many species present challenges for accurate biodiversity assessments, resulting in insufficient data for evaluating the conservation status of numerous species (Böhm et al. 2013; Cox et al. 2022). Given the limitations of individual survey techniques, it has been suggested that multiple complementary techniques should be used to assess reptile assemblages (Garden et al. 2007). However, implementing various survey methods simultaneously can increase costs and time spent field sampling (De Bondi et al. 2010; Richardson et al. 2017). Although a variety of studies has compared survey methods for reptiles, most have been conducted in a single area, targeting a single community (often in a single season), and few studies have used replicate surveys over a broad geographic area (Thompson and Thompson 2007). The relative effectiveness of different methods may, however, vary substantially in different areas or for different communities, and studies that take a broader approach would be valuable. To address these knowledge

gaps and inform effective conservation strategies, it is essential to implement reliable and efficient methods for detecting and monitoring reptile communities.

In this study, we aimed to simultaneously compare the effectiveness of seven methods for assessing reptile biodiversity—pitfall traps, funnel traps, spotlight surveys, arboreal cover boards (ACBs), camera traps, incidental encounters, and PAM—over 2 yr and across an extensive spatial scale. Our objectives were to evaluate the performance of each method in terms of species richness, sampling effort, and detectability, while also considering potential biases and limitations associated with each technique. By providing a comprehensive comparison of sampling methods, we contribute to the development of best practices for reptile biodiversity monitoring, ultimately supporting more effective conservation efforts for this ecologically important group of animals.

## MATERIAL AND METHODS

### Study Sites

This study was conducted as part of a large-scale terrestrial vertebrate assessment project, evaluating the efficacy of acoustic monitoring for terrestrial vertebrate biodiversity surveys in Australia. We selected six sites (Fig. 1A) in open eucalypt woodland where acoustic recording units (ARUs) had previously been deployed for the Australian Acoustic

TABLE 1.—Overview of the survey periods and the total number of survey days for each of the six study sites. NA = not applicable.

Site	First survey	Second survey	Third survey	Fourth survey	Total number of survey days
Tarcutta	29 April–6 May 2021	18–25 October 2021	8–15 May 2022	22–29 November 2022	112
Duval	18–25 April 2021	NA	28 April–5 May 2022	12–19 November 2022	70
Mourachan	9–16 May 2021	NA	19–26 June 2022	2–9 November 2022	84
Wambiana	5–12 July 2021	10–17 November 2021	12–19 June 2022	28 September–5 October 2022	112
Undara	3–10 June 2021	28 September–5 October 2021	8–15 May 2022	13–20 October 2022	110
Rinyirru	14–21 June 2021	8–15 October 2021	7–14 August 2022	23–30 October 2022	112

Observatory project (Roe et al. 2021). All six sites were located within natural reserves (Rinyirru, 15.044007°S, 144.242852°E; Undara, 18.187058°S, 144.539753°E; Duval, 30.402213°S, 151.624706°E; datum = WGS84) or private properties (Wambiana, 20.53071°S, 146.113426°E, Lyons family; Mourachan, 27.778986°S, 149.032006°E, Australia Zoo; Tarcutta, 35.368525°S, 147.696893°E, Bush Heritage; datum = WGS84) with no public access. We established a 1-ha survey plot within 50 m of each ARU, resulting in four survey plots (2 × Wet, 2 × Dry) per site (Fig. 1B). Note that throughout we will use the term “site” to refer to the six reserves/private properties and “plot” to refer to the four 1-ha areas surveyed within each site. We used all seven methods simultaneously at each plot over 7 d per survey trip.

### Survey Methods

We conducted surveys to detect terrestrial reptiles in Spring/Summer (September–November) and Autumn/Winter (April–August) in 2021 and 2022 at each site, except for Mourachan and Duval, which were inaccessible during Spring 2021 because of high rainfall (Table 1; Supplemental Table S1, available online). To comprehensively sample the reptile community, we used seven different survey methods within each plot (spatial arrangement shown in Fig. 1C): (1) PAM, (2) pitfall traps, (3) funnel traps, (4) ACBs, (5) nocturnal active area searches or spotlighting, (6) camera traps, and (7) incidental encounters (i.e., animals detected outside of a trap while not conducting active searches such as a lizard observed on the ground while a researcher was walking to a trap).

PAM was conducted to evaluate whether reptile biodiversity in Australia can be assessed via sound. Each site had four ARUs (Frontier Labs Solar BAR), two within 50 m of a body of water (classified as Wet) and two at least 500 m from a water body (classified as Dry). Each recorder was placed at least 500 m from any other to avoid detecting the same individuals across multiple recorders at the same time (Fig. 1B). Each ARU consisted of a solar panel, battery, charge controller, and recorder in a weather-sealed unit equipped with an external Primo EM172 omnidirectional microphone and was installed on a fence post (star picket) with enough clearance to prevent damage from wildlife and livestock. The ARUs recorded in mono at 16-bit 22,050 Hz with FLAC lossless compression in 2-h file blocks stored on two PNY Elite-X secure digital (SD) extended capacity 512-GB SD cards (for more details on the ARU setup and specifications, see Roe et al. 2021). The design and setup of the ARUs enabled a continuous collection of acoustic data for up to 12 mo without maintenance, at which point the SD cards were swapped out and recording resumed.

Inside each plot we set up two drift fences with five pitfall and eight funnel traps each, 12 ACBs, and four camera traps. Drift fences (30 cm high) were installed in a cross design with four 10-m arms, accompanied by five 20-L pitfall traps (one central and four terminal). A pair of funnel traps (Thompson and Thompson 2007) was placed in the center of each arm between the two pitfall traps. We equipped the openings of each funnel trap with additional smaller fences, acting as wings to create a larger funnel and increase capture rates (McKnight et al. 2013). We covered all funnel traps with shade cloth and placed wet sponges in each pitfall and funnel trap to prevent desiccation and overheating of captured animals (McDiarmid et al. 2012). ACBs consisted of soft foam mats (50 × 50 × 1 cm) and were strapped to the trunks of haphazardly selected trees at about 1.5 m above the ground to act as artificial refugia for arboreal species (Nordberg and Schwarzkopf 2015). Additionally, we installed four camera traps (Campark T85, Campark Electronics Co., LTD.) on individual trees about 50 cm above ground between two corners facing into the plot. Each camera trap was baited with a can of sardines and peanut-butter oat balls and set to high sensitivity to take three consecutive photos and one 10-s video when triggered. Camera traps were active for the same 7-d period as the other survey methods. As camera traps were part of the overall vertebrate biodiversity assessment design, their setup followed a more generalized approach (Eyre et al. 2018), rather than a reptile-specific setup (Welbourne et al. 2017); however, baiting camera traps with meat has previously been used for surveying large, active predatory reptiles such as monitor lizards (Ariefiandy et al. 2013; Moore et al. 2020).

Each plot was surveyed by two trained observers familiar with the fauna of the region. Funnel and pitfall traps were checked twice daily (morning and evening) and ACBs were checked each morning. We also conducted active area searches every day after sunset (spotlight survey); for 15 min, two observers searched each entire plot and recorded all individual reptiles detected visually or aurally. To minimize observer bias, members of each search team and the order at which plots were visited were alternated during each survey trip. We marked each captured reptile with a nontoxic permanent marker pen before release to avoid mistaking recaptures for new captures within the survey trip. Recaptures within a survey period were excluded from the data for community analyses.

### Acoustic Data Analysis

To extract information about the presence of vocal reptiles, acoustic data were analyzed using species-specific call recognizers created using monitoR (Katz et al. 2016). To our knowledge, members of the family Gekkonidae are the only Australian terrestrial reptiles producing audible calls for

communication (Capshaw et al. 2021), but only a few species have been witnessed vocalizing. We created call recognizers for three species (*Hemidactylus frenatus*, *Gehyra dubia*, *Heteronotia binoei*) from example calls provided by J. Hopkins, Phongkangsananan et al. (2014), and S. Zozaya, respectively. These call recognizers were subsequently used to analyze the acoustic data for the same 7-d periods we used the other surveys methods. Resulting positive matches were aurally (sound clip) and visually (spectrogram) reviewed and validated by one of the authors to identify and confirm species detections.

#### Camera Trap Data Analysis

We used all camera trapping data available, and images were analyzed using Timelapse2 (Greenberg 2022) and the MegaDetector image recognition pipeline (Beery et al. 2019). There were three stages of analysis to generate species lists from the camera trap data. In the first stage, we used the MegaDetector to classify images as either wildlife or nonwildlife for each site and each survey. In stage two, nonwildlife classifications were validated following the workflow described in the Timelapse Image Recognition Guide (available at <https://saul.cpsc.ucalgary.ca/timelapse/uploads/Guides/TimelapseImageRecognitionGuide.pdf>). In the final stage, all images classified as wildlife were identified and labeled to species level by an expert observer. Each wildlife categorization by MegaDetector comes with a confidence value indicating the certainty of the classification. Although the guide suggests a confidence threshold of 0.8, we opted for a more conservative threshold of 0.5 for validating wildlife classifications. This was done to reduce the likelihood of false negative errors and failing to detect reptiles in our camera trap data.

#### Statistical Analysis

All statistical analyses were carried out in R (v4.2.2) statistical and graphical environment (R Core Team 2023), and the full reproducible code is available at <https://github.com/chelonix/Hoefer2023>. The relationship between species richness and survey method was explored using hierarchical models in a Bayesian framework. Specifically, the total number of species for each survey plot was modeled against the different survey methods assuming a Poisson distribution and weakly informative priors. Additionally, a spatial effect was investigated by including the latitude of each plot as a predictor. The Bayesian models included three chains, each of 5,000 iterations, thinned to a rate of 5, and excluded the first 1,000 iterations (warmup). Several candidate models were compared and the final model was selected on the basis of leave-one-out information criterion values (Vehtari et al. 2017). The best model was well mixed and converged (all  $R_{hat} < 1.05$ ) on a stable posterior and was validated via DHARMA residuals (Hartig 2022). The influence of the priors on the final model outcomes was assessed by visually comparing the prior and posterior distributions via overlaid density plots for each parameter. Specific inferences (comparing differences in species richness for each combination of survey methods at the six survey sites) were explored using exceedance probabilities and post hoc pairwise comparisons. For exceedance probabilities, we calculated the proportion of the posterior distribution above 0 to indicate

the probability that one method is more effective than the other (henceforth referred to as  $P_{(0)}$ ). A  $P_{(0)}$  value of 1 would indicate that 100% of the posterior distribution is above 0, meaning that there is a 100% likelihood of a difference.

**Species accumulation curves and community composition.**—To investigate the sampling effort required to reach an asymptote, we used the vegan package (Oksanen et al. 2022) to calculate species accumulation curves for the total species richness over the course of the 28 survey days (all four plots combined per site). We randomly permuted the order of survey days to provide more robust estimates of species richness by accounting for potential biases introduced by the order of days. Additionally, we performed non-metric multidimensional scaling using Jaccard (presence–absence) and Bray–Curtis (relative abundance) dissimilarities to assess community differences for each survey method at each plot of each survey site. To test for differences in dissimilarity between the survey methods, we performed pairwise permutational multivariate analysis of variance (PERMANOVA) analyses using the vegan (Oksanen et al. 2022) and EcolUtils (Salazar 2022) packages.

**Detectability.**—We calculated the probability of capturing each species at any given survey day for each survey method within each plot for each study site. Our aim was to compare detection probabilities among survey methods and not to conduct occupancy modeling; therefore, for each plot, we only examined species that were confirmed to be present at that plot (i.e., detected at least once by at least one method). To explore the relationship between detection and survey method we used hierarchical models in a Bayesian framework. We modeled the number of days a species was detected at each survey plot against the different survey methods with a negative binomial family and weakly informative priors and investigated a spatial effect by including the latitude of each plot as a predictor. Finally, we were interested in evaluating the efficacy of each survey method for detecting arboreal and ground-dwelling reptiles and distinctions between those species were made following Cogger (2014).

## RESULTS

Overall, we detected 3,323 reptiles of 93 species, including 295 recaptures of 30 species (Supplemental Table S4, available online). An additional 129 reptiles escaped before species-level identification (*Scincidae* = 94, *Gekkota* = 32, *Serpentes* = 3) and were not included in the analyses. Pitfall traps recorded the highest number of reptile observations (978), followed by funnel traps (944), spotlighting (706), ACBs (514), incidental encounters (152), and camera traps (29). We were unable to detect any reptiles in our continuous acoustic recordings and, therefore, removed acoustic monitoring from further analyses.

#### Species Richness

In total, funnel traps recorded the highest species richness (69), followed by pitfall traps (60), incidental encounters (42), spotlighting (28), ACBs (11), and camera traps (5). Funnel traps also detected the highest number of unique species (i.e., species not observed by any other method at a given site) across all plots (33; Supplemental Table S4). Pitfall traps and spotlighting detected the second and third

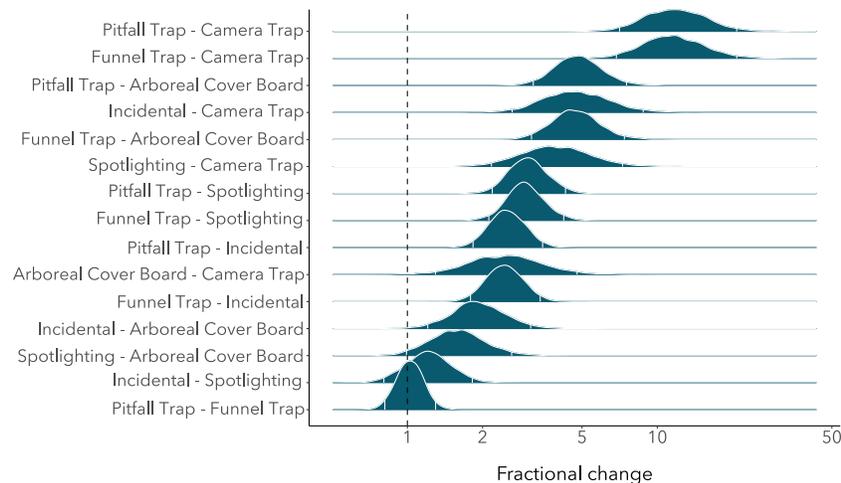


FIG. 2.—Distribution of fractional change in species richness between survey methods across all survey sites. The ridge density plot displays the posterior distribution of the fractional change values for each pairwise comparison of survey methods (i.e., the factor by which the first method detects more species compared with the second), with gradient fill representing the density of the distribution. The x-axis is shown on a log<sub>2</sub> scale, with a vertical dashed line indicating no change in species richness. The lower and upper 95% HDIs are depicted by the solid lines within each ridge.

highest number of unique species (13 and 7, respectively), incidental encounters and camera traps both detected three unique species, and ACBs detected two unique species. We recorded a latitudinal increase in species richness from south to north, with the lowest number of species at Duval (11) and Tarcutta (14) and the highest richness at Undara (42) and Rinyirru (34).

On average, pitfall traps detected 2.49 and 3.04 times more species than incidental encounters and spotlighting, respectively, 4.8 times more than ACBs, and 11.89 times more than camera traps. Similarly, funnel traps yielded 2.45 and 2.96 times more species than incidental encounters and spotlighting, respectively, 4.69 times more than ACBs, and 11.56 times more than camera traps. However, pitfall and funnel traps did not differ significantly from each other (1.02, 95% highest density interval [HDI] = 0.8–1.27,  $P_{(0)} = 0.588$ ; Fig. 2; Supplemental Table S2, available online). Incidental encounters and spotlighting did not differ in the number of species detected (1.21, 95% HDI = 0.79–1.81,  $P_{(0)} = 0.812$ ) but detected up to four times more species than camera traps. ACBs detected about two times fewer species than incidental encounters (1.93, 95% HDI = 1.11–2.97,  $P_{(0)} = 0.997$ ) and spotlighting (1.58, 95% HDI = 0.94–2.56,  $P_{(0)} = 0.966$ ). Camera traps detected the lowest number of species, with 2.5 times fewer species than ACBs (2.48, 95% HDI = 1.14–4.38,  $P_{(0)} = 0.998$ ) and up to 12 times fewer species compared with pitfall traps (11.89, 95% HDI = 6.39–20.14,  $P_{(0)} = 1$ ).

Across all sites, a combination of pitfall and funnel traps recorded 87% of all species. Adding incidental encounters to that combination resulted in a detection of 95% of all species.

To control for the increase in overall species richness from south to north, we also calculated the proportion of the total number of species detected by each method at each survey site. At each survey site, pitfall and funnel traps detected the highest proportion of the total species richness, followed by incidental encounters, spotlighting, ACBs, and camera traps (Fig. 3). At the most southern site (Tarcutta), pitfall and funnel traps detected a combined 74% of the total

species richness, whereas no other method contributed more than 9%. With a decrease in latitude up to the most northern site (Rinyirru), the contribution of incidental encounters, spotlighting, and ACBs to the total species richness increased, whereas the contribution of pitfall traps, funnel traps, and camera traps decreased (see Supplemental Table S2 for a comparison of methods for each survey site).

### Sampling Effort

At all survey sites, species accumulation curves for total number of species did not reach a plateau during our survey period (Fig. 4). Among methods, species accumulation curves for camera traps reached an asymptote at Tarcutta (after 26 d) and Mourachan (after 13 d) but did not at any other site. Curves for arboreal cover boards leveled off only at Mourachan after 20 d of sampling. No other method reached a plateau at any site. The average number of additional species detected after each 7-d survey period varied among sites (Rinyirru, 5.49, 95% confidence interval [CI] = 5.39–5.59; Undara, 8.07, 95% CI = 7.89–8.26; Wambiana, 4.38, 95% CI = 4.29–4.47; Mourachan, 7.67, 95% CI = 7.41–7.94; Duval, 2.72, 95% CI = 2.63–2.81; Tarcutta, 2.9, 95% CI = 2.82–2.99). After 28 d (Rinyirru, Undara, Wambiana, Tarcutta) or 21 d (Mourachan, Duval) of sampling, on average 1.58 times more species had been detected than after the first 7 d of sampling across all sites (Rinyirru, 1.41; Undara, 1.54; Wambiana, 1.49; Mourachan, 1.52; Duval, 1.7; Tarcutta, 1.82). At each site, a combination of pitfall and funnel traps accumulated species more quickly than any method alone, and within 7 d they reached over 50% of their combined total richness (i.e., total richness of pitfall and funnel traps at 28 d; Rinyirru, 0.687; Undara, 0.593; Wambiana, 0.644; Mourachan, 0.548; Duval, 0.595; Tarcutta, 0.516). At each site, pitfall traps accumulated species the quickest, but funnel traps either reached parity with or surpassed pitfall traps within the study period (Fig. 4).

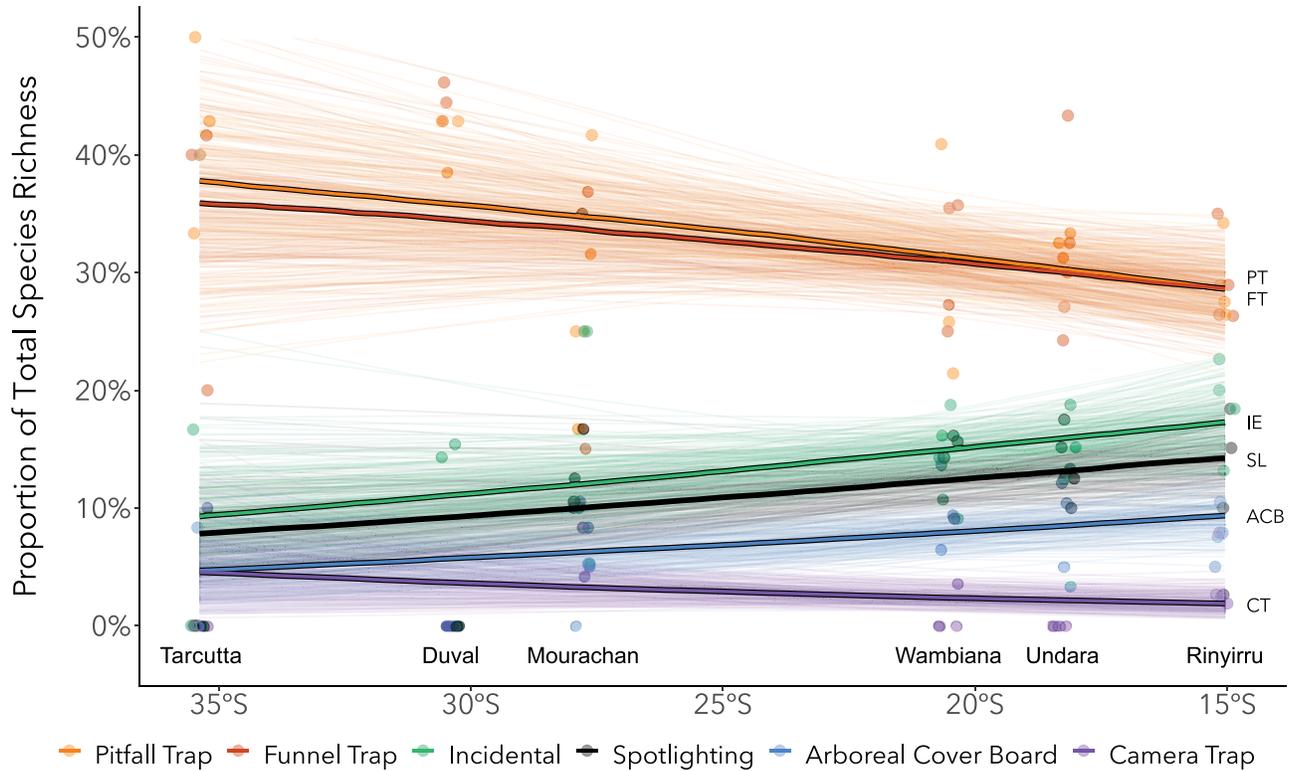


FIG. 3.—Proportion of total species richness across latitudes for different survey methods: pitfall trap (PT), funnel trap (FT), incidental encounter (IE), spotlighting (SL), arboreal cover board (ACB), and camera trap (CT). Observed data points are represented as jittered points; individual model simulations are shown as semitransparent lines. The average proportions for each survey method are depicted as solid lines.

### Community Composition

Over the course of the study period, we detected reptiles across 12 families (Supplemental Table S4). PERMANOVA results evaluating reptile communities detected by each survey method revealed significant differences among methods, except for pitfall and funnel traps. These two methods captured highly similar species assemblages with comparable relative abundances across all sites (Jaccard,  $R^2 = 0.018$ ,  $P = 0.617$ ; Bray–Curtis,  $R^2 = 0.02$ ,  $P = 0.478$ ; Fig. 5; Supplemental Fig. S1, available online). Incidental encounters and spotlighting also recorded a similar community composition but the relative abundances differed (Jaccard,  $R^2 = 0.04$ ,  $P = 0.155$ ; Bray–Curtis,  $R^2 = 0.121$ ,  $P < 0.001$ ; Supplemental Table S3, available online). Variations in relative abundances were driven by incidental encounters of diurnal species, which were rarely detected through spotlighting, and much higher numbers of gecko detections via spotlighting (Supplemental Table S4). Pitfall traps recorded high species richness and captures of *Scincidae* (34 species; 847 captures) and *Agamidae* (5 species; 39 captures) and were the only survey method to record *Typhlopidae* (3 species; 6 captures). Funnel traps recorded high numbers of *Scincidae* (38 species; 810 captures), *Elapididae* (13 species; 39 captures), and *Pygopodidae* (4 species; 12 captures). Spotlighting documented high numbers of *Diplodactylidae* (9 species; 148 captures) and *Gekkonidae* (2 species; 518 captures) and was the only method to detect *Pythonidae* (1 species; 2 captures). Spotlighting and incidental encounters were the only survey methods to detect *Chelidae* (1 species; 3 captures) and *Carphodactylidae* (1 species, 10 captures).

ACBs produced high numbers of *Diplodactylidae* (3 species; 153 captures) and *Gekkonidae* (2 species; 217 captures). Camera traps recorded high numbers of *Varanidae* (3 species; 27 captures) and were the only method to detect *Chlamydosaurus kingii*.

### Detectability

Overall, the average daily detection probability across all sites for each method was highest for pitfall traps (0.076), followed by funnel traps (0.069), spotlighting (0.033), ACBs (0.03), incidental encounters (0.014), and camera traps (0.003). When comparing all methods for all reptiles, pitfall traps and funnel traps were significantly more likely to detect reptiles than any other method, but did not differ significantly from each other (1.11, 95% HDI = 0.83–1.47,  $P_{(0)} = 0.77$ ). Spotlighting (6.81, 95% HDI = 3.64–10.69,  $P_{(0)} = 1$ ), ACBs (5.05, 95% HDI = 2.94–8.04,  $P_{(0)} = 1$ ), and incidental encounters (4.27, 95% HDI = 2.36–6.78,  $P_{(0)} = 1$ ) showed a significantly higher likelihood of detecting reptiles than did camera traps. Spotlighting was significantly more likely to detect reptiles compared with incidental encounters (1.59, 95% HDI = 1.07–2.3,  $P_{(0)} = 0.99$ ), whereas no significant difference was observed between ACBs and incidental encounters (1.18, 95% HDI = 0.75–1.67,  $P_{(0)} = 0.803$ ) or between spotlighting and ACBs (1.35, 95% HDI = 0.9–1.91,  $P_{(0)} = 0.944$ ).

When accounting for differences in lifestyle of reptiles, we found that pitfall and funnel traps were up to 100 times more likely to detect ground-dwelling reptiles compared with any other method, but did not differ significantly from

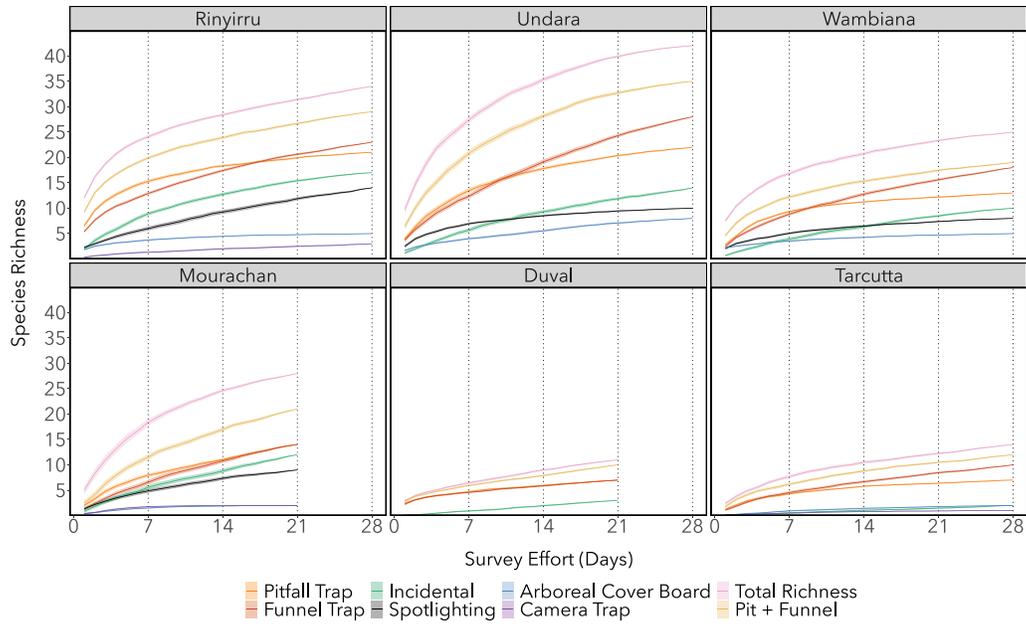


FIG. 4.—Species accumulation curves for reptile communities across six study sites using different survey methods. The x-axis represents survey effort in days and the y-axis shows the estimated species richness. Lines are shown for each method, as well as all methods combined (total richness [pink] and a combination of pitfall and funnel traps [yellow]). The shaded areas represent the 95% CIs for each method. Vertical dotted lines indicate the cumulative effort after each survey.

each other (1.02, 95% HDI = 0.76–1.29,  $P_{(0)} = 0.55$ ; Fig. 6). For ground-dwelling species, incidental encounters and spotlighting were significantly better than ACBs and camera traps but did not differ significantly from each other (1.23, 95% HDI = 0.81–1.78,  $P_{(0)} = 0.839$ ). Camera traps were significantly more likely to record ground-dwelling reptiles compared with ACBs (4.65, 95% HDI = 1.53–10.78,  $P_{(0)} = 1$ ). ACBs and spotlighting were up to 62 times more likely to detect arboreal reptiles compared with any other survey

method but did not differ significantly from each other (1.19, 95% HDI = 0.68–1.81,  $P_{(0)} = 0.766$ ; Fig. 6). Pitfall traps produced significantly higher detectability of arboreal reptiles than funnel traps (3.85, 95% HDI = 1.7–6.62,  $P_{(0)} = 1$ ), incidental encounters (2.98, 95% HDI = 1.52–4.95,  $P_{(0)} = 1$ ), and camera traps (27.93, 95% HDI = 7.01–71.57,  $P_{(0)} = 1$ ), whereas funnel traps were only more likely to detect arboreal reptiles than camera traps (7.26, 95% HDI = 1.54–20.55,  $P_{(0)} = 0.999$ ) but did not

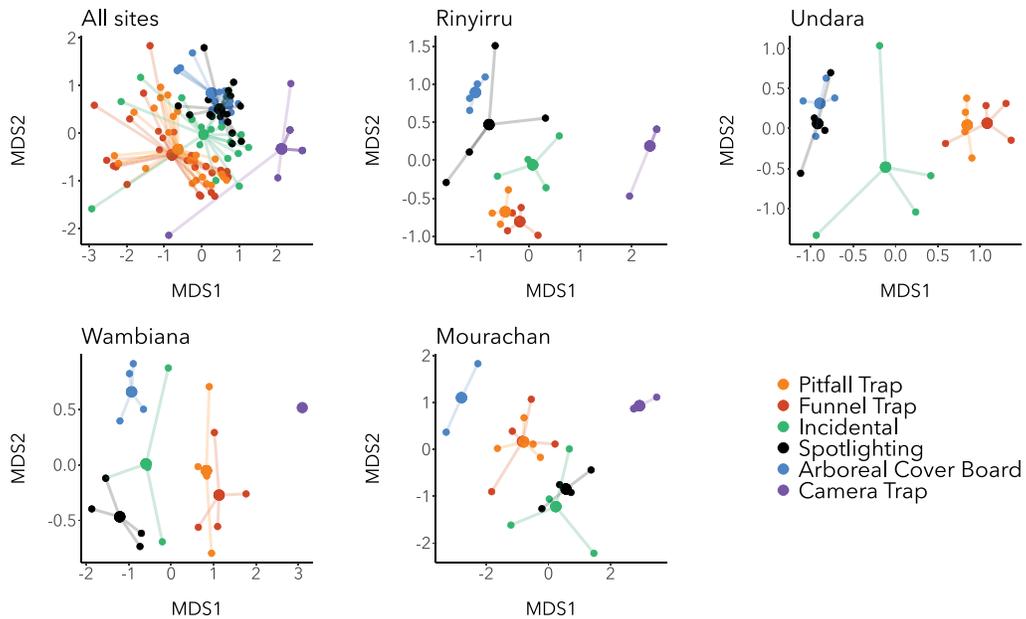


FIG. 5.—Nonmetric multidimensional scaling ordination of reptile communities on the basis of Jaccard dissimilarity (presence–absence), showing the relationships among different survey methods at each survey site. Points represent individual survey plots, colored by the survey method used. Large points indicate the centroids of each survey method and lines connect the centroids to individual plots within each method. Camera traps failed to detect any reptiles at Undara. Tarcutta and Duval were excluded from the plot because of low sample sizes.

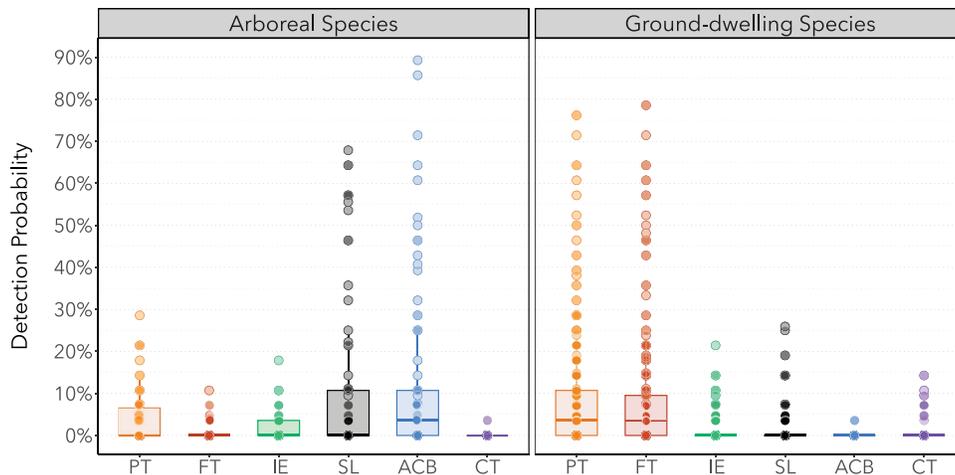


FIG. 6.—Detection probability of arboreal and ground-dwelling reptile species using six different survey methods. The box plots represent the distribution of detection probabilities for each survey method: pitfall trap (PT), funnel trap (FT), incidental encounter (IE), spotlighting (SL), arboreal cover board (ACB), and camera trap (CT). Individual data points are shown as circles and represent daily detection probability of a single species at a single survey plot.

differ significantly from incidental encounters (0.77, 95% HDI = 0.33–1.44,  $P_{(0)} = 0.226$ ). Camera traps were least likely to detect arboreal reptiles (up to 62 times less likely compared with ACBs; 61.5, 95% HDI = 16.59–162.02,  $P_{(0)} = 1$ ). The highest detection probabilities for any species at any plot using any method were for *Amalosia queenslandia* (89% at Undara) and *G. dubia* (86% at Wambiana) using ACBs, followed by *Carlia munda* at Rinyirru using funnel traps (79%) and *Lampropholis guichenoti* at Duval using pitfall traps (76%; Supplemental Table S4).

#### DISCUSSION

In this study, we simultaneously compared seven survey methods—pitfall traps, funnel traps, spotlighting, ACBs, incidental encounters, camera traps, and PAM—to detect reptiles over multiple years and across an extensive spatial scale in open eucalypt woodland across eastern Australia. PAM was ineffective for detecting Australian reptiles, leading to its removal from further analyses. We present insights into the effectiveness of each survey method in terms of species richness, sampling effort, community composition, and detectability. Our results may help with the design and selection of methods for long-term reptile monitoring projects needed for the development of effective conservation and management strategies.

Across all sites, covering a broad range of latitudes, pitfall and funnel traps were the most effective methods for documenting reptiles. Both methods recorded much higher species richness, contributed the highest number of species proportionally to the total richness at each site, recorded the highest number of unique species, and had the highest detection probabilities. This is consistent with previous studies that have compared the effectiveness of pitfall and funnel traps with other sampling methods (e.g., Garden et al. 2007; McKnight et al. 2015; Baumgardt et al. 2021). Even after controlling for a general increase in species richness from south to north, pitfall and funnel traps detected the highest number of species, indicating their relative importance for observing high numbers of reptiles in a wide range of conditions (although their relative importance was greatest at the southern sites). In general, pitfall and funnel traps also

had the highest daily detection probability. This was especially true for ground-dwelling species of the family *Scincidae* such as *C. munda*, *L. guichenoti*, *Eremiascincus pardalis pardalis*, and *Ctenotus spaldingi*.

Although pitfall and funnel traps detected the highest number of species throughout our study sites, we found that the effectiveness of different survey methods varied with latitude. At the southern sites, where species richness was lower, pitfall and funnel traps were responsible for nearly all reptile detections. However, with a decrease in latitude, general species richness increased, and additional survey methods, such as ACBs and spotlighting, became necessary to adequately represent the more diverse reptile community. The different survey methods recorded vastly different assemblages of reptile communities, except for funnel and pitfall traps, highlighting the importance of using multiple methods to capture the true diversity of species present.

Northern sites had higher total species richness, and thus a more diverse array of reptiles, including more large and arboreal species. Previous studies have demonstrated the effectiveness of pitfall and funnel traps in detecting small to medium ground-dwelling species (e.g., Garden et al. 2007; Thompson and Thompson 2007; McKnight et al. 2015; Baumgardt et al. 2021). However, these methods may not be optimal for documenting large and arboreal reptiles and alternative methods have been suggested (Bell 2009; Nordberg and Schwarzkopf 2015). In our study, we found that pitfall and funnel traps were highly effective in detecting small to medium-sized ground-dwelling lizards, such as skinks and dragons, as well as small to medium-sized snakes, such as some species of *Colubridae* and *Elapidae*. However, these traps failed to capture medium to large snakes such as pythons, larger elapids, or large goannas because these species would likely either never enter pitfall or funnel traps or easily escape from the trap (Thompson and Thompson 2007). Larger reptiles were more successfully documented via camera traps or incidentally. Pitfall and funnel traps were also ineffective for most arboreal species except for three species of *Cryptoblepharus*, whereas ACBs and spotlighting proved substantially more effective. For example, we detected *A. queenslandia* on 25 of 28 survey days using

ACBs at a plot at Undara. These methods detected species of Gekkota across four families and 10 genera and achieved the highest daily detection probabilities for any species at any survey plot during our study.

Of importance, these differences in the assemblages detected suggest that our results cannot simply be explained by inherent differences in the scale of sampling effort and, instead, represent true differences in the taxa that can be sampled by each method. In other words, it could be argued that, for example, two drift fence arrays per plot represent an inherently different level of survey effort than 15 min of spotlighting per day and increasing the effort for either method (more fences or longer spotlighting periods) would have changed the results. If that was the case, however, we would expect similar taxonomic or ecological groups to be detected by each method. Additionally, the differences in species accumulation curves (Fig. 4) are pronounced enough that increased survey effort for any one method would be unlikely to substantively change the results.

Observer-based monitoring in the field can be very costly and resources are often limited. Therefore, reptile biodiversity assessments aim to be as comprehensive as possible while keeping cost to a minimum, which can be achieved by reducing the number of simultaneously deployed methods (e.g., Garden et al. 2007; Michael et al. 2012). In our study, a combination of pitfall and funnel traps accounted for the majority of all species detected (87%). When including incidental encounters (i.e., species passively encountered while on the survey plot), the total number of species observed increased to 95% of all species. However, the only unique species documented exclusively through incidental encounters was a turtle (*Chelodina longicollis*), which was detected at night when observers would not be present on the survey plot if only deploying pitfall and funnel traps. Therefore, it is unclear how significant incidental encounters would be if only pitfall and funnel traps were used together. Previous research has highlighted the significance of incidental encounters in biodiversity assessments (McKnight et al. 2015), and although we excluded detections occurring far outside the survey plot boundaries in our analyses, we frequently encountered snake species on the roads and trails away from the plots that we did not detect during our surveys on the plots. Overall, recording incidental encounters is highly recommended, as it involves minimal additional costs and effort while potentially enhancing the overall species richness documented, particularly of cryptic species such as many snakes.

Another factor affecting the cost of biodiversity assessments is the duration of sampling. The recommended sampling duration for reptile biodiversity assessments varies depending on location, habitat, target fauna, and research goal (How 1998; McDiarmid et al. 2012; Michael et al. 2012). Our findings indicate that using a combination of pitfall and funnel traps accelerates species accumulation, yielding results faster than any other method, and capturing at least 50% and as high as 69% of the total species richness within a 7-d sampling period. However, even after 28 d of sampling, including four trips in two seasons over 2 yr, new species continued to be detected at each site, suggesting that additional surveys or an increased number of traps for intensified sampling are required to assess the entire reptile community. In certain cases, sampling the complete community may take up to 5 yr or more (How 1998). This emphasizes the need for long-term monitoring projects to detect particularly elusive species, such as most snakes in Australia.

PAM may not be a viable method for assessing reptile biodiversity in Australia. PAM is a relatively novel monitoring method that, to our knowledge, had only been used indirectly for reptile biodiversity assessments in a single study before (McKnight et al. 2015). In our 2-yr acoustic data set, we were also unable to detect any reptiles using species-specific call recognizers for Asian House Geckos (*Hemidactylus frenatus*), Bynoe's Geckos (*Heteronotia binoei*), and Dubious Dteallas (*G. dubia*). Bynoe's Geckos and Dubious Dteallas have relatively quiet calls, and example calls were obtained from a laboratory environment devoid of background noise (Phongkangsananan et al. 2014). It is possible that these species were vocalizing but at volumes too low to be discernable from ambient sounds. In contrast, Asian House Geckos have loud persistent calls and have been successfully detected in audio recordings previously (Marcellini 1974; Hopkins et al. 2021), and even been identified in recordings from the same type of ARU used in our study (S. Hoefler, personal observation). However, we encountered this species incidentally in the campground at Undara and Rinyirru, with only one individual detected in a funnel trap within a survey plot. This species is currently primarily associated with urban areas, and we think it unlikely that it is established in our survey plots. Instead, we argue that the recorders genuinely did not detect the species because it was absent. In discussing the limitations of our study, we acknowledge that our camera trapping design could be further refined. The design we used followed a more general setup frequently used for mammals (Claridge et al. 2010; Eyre et al. 2018; Burt et al. 2021) and could be enhanced by utilizing camera trap setups specifically targeting small reptiles (Adams et al. 2017; Dundas et al. 2019; Welbourne et al. 2020). Our baited camera traps, a practice highlighted in previous studies for detecting large varanids (Ariefandy et al. 2013; Moore et al. 2020), identified some larger reptiles that were undetected by other methods, demonstrating this design's utility. However, our camera traps failed to detect any small reptiles, for which ground-facing camera trap setups are designed (Welbourne et al. 2017). Ground-facing cameras combined with small drift fences have proven useful for smaller reptiles, but their effectiveness is limited for larger species (Welbourne et al. 2015). Thus, incorporating both camera trap designs could provide a more comprehensive picture and potentially higher species richness. Future studies could use additional methods, such as diurnal active searches (Kutt and Colman 2023), eDNA (Kyle et al. 2022), or artificial refugia (AR) on the ground (Grant et al. 1992). Although some studies have demonstrated the effectiveness of ground ARs (e.g., Engelstoft and Ovaska 2000; Kjos and Litvaitis 2001; Seigel et al. 2002), we only used arboreal ARs in our study. After preliminarily testing corrugated iron and roof tiles at three sites for one survey trip, we detected only one unidentifiable *Carlia* spp. and decided against deploying any ground ARs. Corrugated iron and roof tiles may be less effective in northern Australia for most of the year, as temperatures can become extremely hot and humidity very high, which may lead to a decrease in reptile detections beneath ground ARs (Hoare et al. 2009; McKnight et al. 2015; Lemm and Tobler 2021). Additionally, ground ARs can require extensive effort to establish (Michael et al. 2012).

Overall, our results suggest that pitfall and funnel traps should be prioritized in reptile biodiversity assessments, especially when the primary goal is to quickly accumulate a high number of species. Nevertheless, the relative importance of these methods varies with latitude and overall species richness. In regions

with high species richness, incorporating a broader array of survey methods is crucial to achieve a comprehensive assessment of reptile diversity. Furthermore, although pitfall and funnel traps proved highly effective for ground-dwelling reptiles, they were less successful in detecting arboreal species, for which ACBs and spotlighting were far superior. Using a combination of these survey methods is likely to yield the best results and ensure a comprehensive taxonomic representation of the community.

To prevent the loss of numerous ecologically significant species, there is an urgent need to enhance our understanding of reptile diversity and habitat use worldwide. This necessitates evaluating the effectiveness of various survey techniques for documenting reptiles. Further research is required to investigate the efficiency of using multiple methods concurrently over extended periods and to compare their performance across diverse habitats.

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#### SUPPLEMENTAL MATERIAL

Supplemental material associated with this article can be found online at <https://doi.org/10.1655/Herpetologica-D-23-00022.S1>, <https://doi.org/10.1655/Herpetologica-D-23-00022.S2>, <https://doi.org/10.1655/Herpetologica-D-23-00022.S3>, <https://doi.org/10.1655/Herpetologica-D-23-00022.S4>, <https://doi.org/10.1655/Herpetologica-D-23-00022.S5>.

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