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Unreliable population inferences from common trapping practices for freshwater turtles



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ABSTRACT

Fundamental questions in ecology and conservation require reliable data about population size and structure. For freshwater turtles, such data are often obtained via mark-recapture trapping, but commonly used trap types are biased in the sex and age classes they sample although these biases are seldom quantified. We present data from 11 populations of Western painted turtles (Chrysemys picta bellii; 1107 turtles total, n caught per pond 6-322) captured in hoop traps, dip-nets, and basking traps to examine bias in captures and the impact on estimates of population size and sex/age ratios. Hatchlings and juveniles were primarily captured in dip-nets, while hoop nets had the lowest capture rates for adults. Most turtles were caught only once; among recaptures, the majority were recaptured in the same trap type. Estimates of population size and sex/age ratios varied strongly when we calculated results from each trap type separately versus combining all captures. These results show clearly that turtle sampling that uses only one trap type will almost certainly mis-estimate population size and sex/age ratios. These results are troubling in the light of current practice: of population studies of North American turtles published during 2009–2014, 45% used only one trap type, and 49% of studies did not even mention possible sampling biases. The conservation implications are serious, as current trapping efforts probably result in erroneous population estimates and sex/age ratios, which may encourage management actions that are not needed or may obscure actions that are in fact necessary for viable populations.

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1. Introduction

Turtles are globally in decline, with the IUCN classifying 47% of 331 described turtle species as Vulnerable, Endangered, or Critically Endangered (Van Dijk et al., 2012). For semi-aquatic turtle species, declines are due largely to land-use changes and habitat destruction (Gibbons et al., 2000; Lesbarrères et al., 2014), and even turtle species that were once quite common are becoming at-risk and are in need of population monitoring. Lovich and Ennen (2013) reviewed the state of our conservation knowledge for North American turtles, finding that most imperiled turtles have inadequate research to support conservation efforts meaningfully.

Unfortunately, it is hard to obtain reliable population data for freshwater turtles. Low and variable rates of capture are common in turtle studies (Bluett, 2011), and if not enough turtles are recaptured, or if the traps capture certain groups preferentially, inferences about population status will be misleading (Gamble, 2006; Koper and Brooks, 1998; Lindeman, 1990). It is therefore critical to focus on developing better methods and study designs to capture more turtles and to reduce biased sampling of the populations, thus improving inferences about the populations (Bluett, 2011; Jackson et al., 2008).

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Further, population density of adults alone is not a reliable indicator of population stability in turtles, although adults are easier to capture than are hatchling or juvenile turtles (Pike et al., 2008). Without high quality demographic data for all sexes and ages, there could be significant time lags between the start of recruitment failure and detectable population decline among adult turtles. Freshwater turtles are long-lived, often with high mortality rates for eggs and hatchlings, intermediate survival rates for juveniles, and low adult mortality (Griffin, 2007). Population sizes, sex-ratios, age structures, and stage-specific mortality rates are thus of great value to any monitoring program. Adult sex ratios have also recently become an important piece of demographic information for studies examining whether roads near ponds induce higher mortality of females, as females may need to cross roads to access nesting habitat (Aresco, 2005; Dorland et al., 2014; Marchand and Litvaitis, 2004a; Steen and Gibbs, 2004).

Common capture methods for freshwater turtles include baited hoop nets, baited and non-baited basking traps, and dipnets. Captures in each trap type are biased by behavioral differences among turtles and between size classes and sexes (Cagle and Chaney, 1950; Frazer et al., 1990; Gamble, 2006). Females may be more attracted to basking traps as they have higher energetic demands due to larger body size and egg production (Carrière et al., 2008; Lefevre and Brooks, 1995). Hatchling and juveniles often elude the hoop nets and basking traps that are successful with adults (Congdon, 1993; Mali et al., 2013; Ream and Ream, 1966; Sexton, 1959). Hoop nets may be male-biased, with hypothesized mechanisms that males are attracted to captured females (Cagle and Chaney, 1950; Frazer et al., 1990) or that females are more likely to escape (Brown et al., 2011).

Biases among trap types have been known for decades, as Ream and Ream (1966) recommended combining data from multiple trap types to minimize bias. Koper and Brooks (1998) compared capture results from hoop nets and dip-nets to the assumed population size of a well-studied population of adult painted turtles, *Chrysemys picta marginata* in a 1.7 ha pond (total *N* caught = 78); even when they applied analytical and statistical techniques thought to improve accuracy, most results underestimated the number of known marked adults by more than 10%. Using multiple trap types simultaneously would, in theory, capture more turtles, assuming that traps were biased in different ways (Koper and Brooks, 1998). It might also help negate trap-shy responses as animals caught initially in one trap type would not have been exposed to other trap types, thus potentially increasing recapture rates.

Here, we address sampling strategies for populations of the western painted turtle, *Chrysemys picta bellii* in southwestern British Columbia, Canada, near the northwestern edge of their geographic range. Painted turtles are nationally listed as Special Concern in this region (COSEWIC, 2006), and as Endangered in coastal BC. Painted turtles are semi-aquatic, depending on lakes, ponds, or slow-moving water bodies for foraging, mating, and hibernation, as well as upland habitats for nesting (Steen and Gibbs, 2004). In addition to suitable nesting habitats, painted turtles require connectivity between habitats, with connected ponds serving as drought refugia and sources of genetic variation. We deliberately sampled across the spectrum of local pond types (e.g. elevation, surrounding environment, size) to assess how these common trap types performed in the face of this variability and to see how trapping-based demographic estimators performed for very different population sizes of painted turtles. This design mimics sampling that might occur for a conservation assessment or landscape study in a region.

Our objectives were to (a) evaluate performance of three common turtle capture methods for painted turtles, (b) quantify the impact of combining data from all the trap types on population estimates and their variability, and (c) contextualize our results in the light of current trapping practices used in studies of North American freshwater turtles. We used hoop nets, basking traps, and dip-nets to catch western painted turtles in 11 separate locations, then we used mark-recapture analyses to assess how each method performed. We also analyzed the value of each trap type for capturing different age classes and sexes. We used multi-state modeling to determine transition probabilities of turtles among trap types, to see whether using multiple trap types increases the likelihood of recapture, which would increase the confidence in mark-recapture estimates.

2. Materials and methods

We trapped turtles in the Okanagan Valley of southcentral British Columbia, Canada, between May and September, 2009. The Okanagan Valley is semi-arid, with large lakes on the valley bottom bordered by low-sloped hills of open canopy ponderosa pine (*Pinus ponderosa*) forest, sagebrush (*Artemisia tridentata*) dominated shrub-steppe, and grasslands. Western painted turtles were trapped at 11 ponds throughout the valley, ranging in elevation from the valley bottom at 298–924 m (Table 1). Ponds ranged from urban to rural and were selected to represent the range of known turtle habitats in the Okanagan. Each pond was trapped for a single session of 3–8 days (we trapped longer at sites with low recapture rates; trapping duration was not linked to numbers caught per pond, Table 1). Trapping was done only on sunny days. Three trapping methods were used at each pond: basking traps, hoop nets, and captures with dip-nets. Three hoop nets (76.2 cm diameter, 3.81 cm² mesh, Memphis Net and Twine, Tennessee, USA) were secured with steel posts in the vegetated shallows of each pond and baited by dangling a pierced can of cat food inside the middle hoop. Three basking traps (Sun Deck Turtle Trap, Heinson's Country Store, Texas, USA) were also set at each pond. These traps were made of wire ramps attached to a floating PVC frame with a submerged wire basket; we secured traps in areas of the pond where we observed high numbers of basking turtles and we baited them with cat food. All traps were set within a 50 m diameter of a central point in the pond.

We also used fish landing nets from shore or canoe to scoop turtles from the open water or mud. To keep this effort similar across ponds, all dip-net captures were completed by the same 4 people. Basking traps and hoop nets were set in the

Pond attributes and trapping data for *Chrysemys picta* captures in the Okanagan Valley of southcentral British Columbia in 2009. The "context" column identifies urban ponds (developed on all sides, within city limits), suburban ponds (not developed on all sides, within city limits), sub-rural ponds (not developed on all sides, outside city limits), and rural ponds (not developed on all sides, outside city limits), and rural ponds (not developed on all sides, outside city limits), and rural ponds (not developed on all sides, outside city limits), and rural ponds (not developed on all sides, outside city limits), and rural ponds (not developed on all sides, outside city limits), and rural ponds (not developed on all sides, outside city limits), and rural ponds (not developed on all sides, outside city limits), and rural ponds (not developed on all sides, outside city limits), and rural ponds (not developed on all sides, outside city limits), and rural ponds (not developed on all sides, outside city limits), and rural ponds (not developed on all sides, outside city limits), and rural ponds (not developed on all sides, outside city limits), and rural ponds (not developed on all sides, outside city limits), and rural ponds (not developed on all sides, outside city limits), and rural ponds (not developed on all sides, outside city limits), and rural ponds (not developed on all sides, outside city limits), and rural ponds (not developed on all sides, outside city limits), and rural ponds (not developed on all sides, outside city limits), and rural ponds (not developed on all sides, outside city limits), and rural ponds (not developed on all sides, outside city limits), and rural ponds (not developed on all sides, outside city limits), and rural ponds (not developed on all sides, outside city limits), and rural ponds (not developed on all sides, outside city limits), and rural ponds (not developed on all sides, outside city limits), and rural ponds (not developed on all sides, outside city limits), and rural ponds (no

Pond	Elevation (m)	Area (ha)	Context	Turtles captured	Population estimate N (95% CI)	Trap days
Skaha Marina	340	0.6	Urban	6	7 (5-8)	5
Chichester Pond	397	0.2	Urban	38	43 (35-51)	5
Oliver	298	0.3	Suburban	11	15 (8–21)	8
Blair Pond	519	1.5	Suburban	211	400 (313-486)	7
Eastside Road	340	0.3	Suburban	7	9 (5-13)	7
Green Lake	490	13.3	Sub-rural	65	93 (70–117)	7
Yellow Lake	749	34.7	Sub-rural	70	83 (71–94)	5
Vaseux Lake	322	258.2	Sub-rural	152	313 (221-404)	8
Ripley Lake	924	4.5	Rural	69	124 (82-167)	6
White Lake	649	0.9	Rural	156	179 (164–194)	4
Burnell Lake	731	16.4	Rural	322	595 (471-718)	3

afternoon before the first day of each session. Turtles were hand captured for the first 1.5 h of each sampling day, starting between 09:00 and 10:00, after which the basking traps and hoop nets were emptied.

Turtles were uniquely marked after initial capture using a DremelTM rotary tool and the shell filing system set out in Cagle (1939). Small juveniles were marked using nail clippers as their shells were not fully ossified. Hatchlings were given unique numbers with a Sharpie marker on their plastrons and carapaces. Plastron length was measured using digital calipers. We followed Griffin (2007) to assign age classes: hatchlings had plastron lengths \leq 50 mm, juveniles had plastrons 50–104 mm, and adults had plastrons \geq 105 mm. Turtles were classified as adult males if they had a plastron \geq 105 mm and had noticeably elongated foreclaws and a lengthened pre-cloacal tail region, with the cloaca located beyond the edge of the carapace; adults lacking these features were classified as females (Frazer et al., 1990).

2.1. Analytical methods: recapture histories by trap type

To analyze trapping success by each method, data from all 11 ponds were pooled. Captures were analyzed by trap method, with 95% binomial confidence intervals. Analysis of variance (ANOVA) was used to determine differences in mean plastron lengths of turtles caught in each trap type. The Tukey–Kramer HSD post-hoc test was used to determine significant differences among means.

A multi-state transition model was built for the turtle capture histories as a way of describing how individuals moved among trap types during the capture period. The model was built using the MSM package (V. 0.7.4 2007) for R 2.10.1 (Jackson, 2011), and included four states: not caught, caught in basking trap, caught in hoop net, and caught in dip-net. The model permitted transitions between any of the four states, as well as allowing turtles to remain in a state by being caught in the same trap type in the next sampling interval, or by remaining uncaught. There are thus 16 possible transitions between capture states. The data were assumed to represent the exact transition movements of the turtles, as it was extremely unlikely that a turtle would have been caught in one trap type, escaped, and then been caught in another trap type. Initial values for the transition matrix were set to equal probability of moving between each of the states. The data were fit to the model using maximum likelihood estimates. Transition probabilities and 95% confidence intervals were calculated by bootstrapping the data. The model was run with all age and sex classes combined and then run for each class separately.

2.2. Demographic estimates

Four population estimates were calculated for each pond: one estimate each for capture data from each trap type by itself, and one estimate using the capture histories from all three trap types combined. All estimates were calculated using the Lincoln–Petersen model with the Chapman correction for small sample sizes. Recapture rates were calculated for each trap method separately and using all three trap methods combined. Similarly, we calculated sex and age ratios for turtles caught by each trap type separately as well as calculating a combined estimate.

2.3. Analysis of turtle trapping methods currently in use

We analyzed recent scientific papers to examine current trapping practices for North American turtles (excluding *Terrapene*, which is mostly terrestrial, and the sea turtles, but including the estuarine genus *Malaclemys*). In October 2014, we used Web of Science to locate recent papers that used turtle trapping to examine population parameters (e.g. N, sex ratios, age ratios); we excluded studies that captured turtles primarily for other purposes (e.g. to deploy radio-transmitters, obtain genetic samples, or detect pollutants or parasites). We excluded studies focused on nest sites or hatchlings; we also excluded reviews. For each search, we specified publication dates of 2009–2014, then used the genus name to locate papers. For each paper that met these criteria, we extracted data on (a) species trapped, (b) trap type(s) or other capture methods

Western painted turtles captured in 11 ponds in British Columbia in 2009. Turtles were split into four age and sex categories, according to plastron lengths (PL) and absence/presence of male secondary sex characteristics (SSCs): hatchlings (PL \leq 50 mm, SSCs absent), juveniles (PL 50–104 mm, SSCs absent), males (PL \geq 105 mm, SSCs present), and females (PL \geq 105 mm, SSCs absent).

	Number of turtles	Total captures	Turtles caught more than once (%)	Turtles caught in two trap types (%)	Turtles caught in three trap types (%)	
Hatchlings	41	62	36.5	2.4	0	
Juveniles	297	429	32.3	15.4	1.7	
Males	273	385	29.3	17.6	1.5	
Females	496	768	36.0	22.2	1.4	
All turtles	1107	1644	33.5	20.0	1.5	
	0.6 5 5 5 5 6 7 6 7 6 7 7 7 7 7 7 7 7 7 7		2 Number of times cau	B Hatchling Juvenile Male Female Jemale 3		

Fig. 1. Recaptures of western painted turtles by age and sex class. Results are pooled across all basking trap, hoop net, and dip-net captures across 11 ponds. Ten of the 11 ponds were trapped for > 3 days; of the 785 turtles able to be trapped four times, only 34 turtles were (4.3%). Five turtles were caught five times each and one turtle was caught six times. We caught 1107 turtles: 41 hatchlings, 229 juveniles, 273 adult males, and 496 adult females.

used, (c) population parameters reported, and whether the paper mentioned any possible biases in the trapping methods. For studies that addressed multiple species, we extracted data for each species for which at least 20 turtles were captured (or for all species if the focus of the paper was presence/absence data). For *Chrysemys*, there is recent discussion regarding whether *C.p. dorsalis* warrants species status as *C. dorsalis* (Crother, 2012; Jensen et al., in press); we lumped any *Chrysemys* work into the single taxon of *Chrysemys picta*.

3. Results

We captured and marked 1107 turtles; we recaptured 375 of the marked turtles 912 times (Table 2). Nearly half of the captured turtles were adult females and <4% of the turtles captured were hatchlings. Over 60% of all turtles in each class were captured only a single time. Likelihood of recapture was statistically similar across age and sex classes (G = 2.79, d.f. = 3, P = 0.425), ranging from 29.3% recaptured of adult males to 36.5% of hatchlings. Most recaptured turtles were recaptured only once (Fig. 1). Only 7% of turtles were caught three times, and fewer still caught four or more times, a trend consistent across all age and sex classes. Females were most likely to be caught in two different trap types and hatchlings were the least likely (Table 2). No hatchlings, and fewer than 2% of each of the other classes, were caught in all three trap types.

Nearly all hatchlings (95%) were captured in dip-nets (Table 3), with just a single hatchling captured in a basking trap and two captured in hoop nets. Similarly, the majority of juvenile captures (67%) were in dip-nets. The remaining juvenile captures were evenly split among hoop and basking traps. More females were caught in dip-nets than using the other two capture methods, although the distribution among trap types was not statistically significant (G = 2.29, d.f. = 2, P =0.32). Significantly more males were caught in basking traps than either dip-nets or hoop nets (G = 11.54, d.f. = 2, P =0.003). These capture patterns resulted in differences in the mean plastron length of turtles caught in each trap type; turtles caught in dip-nets were significantly smaller ($108.3 \pm 1.9 \text{ mm}$) than those caught in hoop nets (138.8 ± 1.9) or basking traps (137.6 ± 1.6 ; $F_{2,1104} = 92.4$, p < 0.001). When hatchlings and juveniles were removed from this analysis, the same pattern occurred but the differences in body size were much smaller (dip-net: 143.2 ± 1.6 , hoop: 149.9 ± 1.6 , bask: 146.3 ± 1.3 ; $F_{2,766} = 4.73$, p = 0.009).

Fig. 2 illustrates the transition probabilities between trap types or not being caught. Regardless of the initial state, turtles were most likely to be uncaptured at the next sampling interval. Within the transitions that reflect recaptured turtles, turtles were most likely to be recaught in the same type of trap. For example, a turtle caught in a hoop net was six times more likely to be recaught in a basking trap at the next sampling interval. This pattern also occurred with turtles originally caught in basking traps and was especially pronounced when the original capture was by dip-net, as turtles were ten times more likely to be recaught in a dip-net than to be recaptured by either of the other methods. Turtles not caught on one day were most likely to remain uncaught on the next day. Turtles that were captured at time t + 1 after being not caught at time t were more likely to be caught in dip-nets than in hoop or basking traps.

Proportion of captures of Western painted turtles by each of the three capture methods. Upper and lower 95% binomial confidence intervals are in parentheses. Data are pooled across 11 ponds trapped in 2009.

	Hoop net	Basking trap	Dip-net
Hatchlings	0.03 (0.00, 0.11)	0.02 (0.00, 0.09)	0.95 (0.87, 0.99)
Juveniles	0.15 (0.11, 0.18)	0.18 (0.14, 0.22)	0.67 (0.63, 0.71)
Males	0.25 (0.21, 0.30)	0.39 (0.35, 0.45)	0.36 (0.31, 0.41)
Females	0.26 (0.22, 0.28)	0.32 (0.29, 0.35)	0.42 (0.39, 0.46)



Fig. 2. Transition probabilities for Western painted turtles captured across all ponds. Bars represent the likelihood of being caught by each method of capture at time t + 1 following initial capture state as shown by bar color (e.g. turtles trapped by a hoop trap, clear bars, were most likely to not be caught at the next time, and, if captured, were most likely caught again in a hoop trap). Error bars are bootstrapped 95% confidence intervals.

The pattern of being more likely to be recaught in the same trap type as the original capture holds for juveniles, males, and females, for all trap types (Fig. 3). Hatchlings were the exception, as they were more likely to be caught and recaught in dip-nets than in the other two trap types, and the small sample size of hatchlings resulted in very large confidence intervals for nearly all possible transitions. Juveniles that did transition between two trap types were more likely to be recaught in dip-nets than in the other trap types. Both hatchlings and juveniles were much more likely to be caught in a dip-net after having not been caught, but had similar probabilities of being caught in basking traps as hoop nets. Both males and females were slightly more likely to be caught in basking traps than hoop or dip-nets after having not been caught.

3.1. Population inferences from each trap type

Recapture rates were usually highest when using the combined capture data (Fig. 4). The combined recapture rate was often 2–3 fold higher than recapture rates by a single trap type. In four cases, a single trap type had a higher recapture rate than the combined captures did; two cases came from ponds with our fewest over-all turtles, ponds with 6 and 7 individuals captured. In a third case, only two turtles were caught in hoop traps in the second trapping period and both were recaptures. In the final case, only 14 turtles of 69 turtles were recaptured and 12 of these were recaptured in dip-nets, yielding a higher recapture rate for dip-nets than for the over-all estimate. Recapture rates were lowest for basking traps, with an average of 14.8%; 5 of the 9 ponds where turtles were captured in basking traps had no recaptures within basking traps.

Not surprisingly, population estimates from a single trap method were typically smaller than the population estimate calculated by combining data from all three trap methods (Fig. 5). These deviations were often large (Fig. 6), with average underestimates of 31% for hoop nets, 30% for basking traps, and 25% for dip-nets. These values include the six cases in which the single trap type had a higher estimate that the combined estimate (3 hoop trap cases, two for basking traps, and one for dip-nets). If we consider just the negative cases, the average underestimates are 51%, 58%, and 31%. Ponds with lower combined population estimates often had the highest deviations between the combined and single trap estimates.

Estimates of sex and age ratios (omitting hatchlings) also varied with trap type (Fig. 7). For example, in our largest pond (322 turtles captured, population estimate 595), turtles caught only in basking traps yielded an estimate of 13.3% juveniles, whereas dip-nets yielded 66.4% (a spread of 53.1%); the estimate from all captured individuals was 32.3%. Across all ponds, the spread in values of juveniles (maximum-minimum estimate) ranged from 11.6 to 53.0%. For adults, the percentage of females showed even a worse spread among methods across ponds, ranging from a spread of 0 (a pond where 6 turtles were caught, none of them female) to 69.2% (33 females and 14 males caught total, but basking traps caught only one turtle, a male).



Fig. 3. Transition probabilities for age and sex classes of Western painted turtles. Panels represent transitions between method of capture at time t and method of capture at time t + 1. Error bars are bootstrapped 95% confidence intervals.



Fig. 4. Recapture rates for different trap types for Western painted turtles. Population estimates were calculated using combined capture data from hoop nets, basking traps, and dip-nets.

3.2. Current trapping practices for North American turtles

We located 56 recent papers with live-trapping data for turtles; some studies addressed multiple species, so we had 84 cases to analyze (Table 4). On average, studies used 1.9 methods of capture, but 45% of all studies used only one method; another 29% used only two methods. Out of 162 turtle-method combinations, only 70 were the hoop, basking, and dip-net methods we analyzed, although methods such as 'by hand' or 'snorkel' (40 cases) are related to dip-netting as active hunting techniques, as opposed to the passive traps. Over-all, 46.4% of studies used an active method, 82.1% used a passive trap type, and 31.0% used at least one active and one passive method. Only 43 of 84 studies mentioned any sort of trap bias, with mentions ranging from single sentences in methods to full paragraphs in the discussion to data analysis. Fewer than half of the studies (40 of 84) provided population estimates (Table 5); another 24 provided indices of abundance. Adult sex ratios



Fig. 5. Population estimates when calculated from capture histories including only a single trap type versus the combined estimate from all three trap types. Error bars are 95% confidence intervals. The reference line shows a 1:1 relationship. In panels A and C, one upper CI in each panel was truncated for the sake of figure clarity and consistent *y*-axes among panels.

were provided in 71.4% of studies, and estimates of percent juvenile in 35.7%. Body size data were presented in 47.6% of cases.

4. Discussion

Western painted turtles were not caught similarly by hoop nets, basking traps, and dip-netting. Instead, all methods showed significant bias in the size and age of turtles they captured. Individual turtles that were recaptured were typically recaught by the same method, suggesting that studies using only one method of capture are missing an unknown but possibly high number of individuals for whom the chosen method is ineffective. Using the three capture methods together typically resulted in the highest recapture rates and about two-thirds of the time gave population estimates with smaller



Fig. 6. Percent deviation of trapping estimates from single trap types relative to the combined estimate. The percent deviation was calculated as (100*(single trap estimate – combined estimate)/combined estimate); negative values thus indicate the single trap estimate was below the combined estimate. Two sites for basking traps are not shown, as these sites had no turtles captured with basking traps.



Fig. 7. Estimates of age and sex structure of Western painted turtle populations derived from the different trap types. Hatchlings were omitted for this analysis. Population estimates were calculated using combined capture data from hoop nets, basking traps, and dip-nets. (A) The proportion of juveniles (plastrons <105 cm) in each population. (B) The proportion of females out of turtles identified as adults (females were >105 cm and lacked male secondary sexual characteristics).

confidence intervals than estimates from captures via a single trap method only. Population inferences based on single methods of capture were often quite different from the estimates derived from all of our captures; these problems in inference applied to population estimates, body size, and sex and age ratios.

These trapping results indicate strongly that it is dangerously misleading to rely on a single capture method to obtain population inferences about freshwater turtles (Tesche and Hodges, in press). Our survey of recent population studies of North American turtles unfortunately suggests that nearly half of these efforts used only one method of capture, and only 23.8% used more than 2 methods. For painted turtles, despite being a comparatively well-studied species with repeated calls

Capture methods used in recent population studies of turtles in North America. We surveyed the 2009–2014 literature for papers that used live-captures to infer population parameters. We have grouped turtles into taxa that gave >10 papers per group, except for *Apalone* spp. and Chelydridae, which did not group comfortably into higher taxa. The values are counts of papers that focused on each species, or, for papers that addressed multiple species, had \geq 20 captures of a given species. We found 56 papers addressing 84 cases.

Taxon	n studies	Average <i>n</i> methods	Ноор	Bask	Fyke	Dip-net	Seine	By hand	Snorkel	Other ^a	Mention of trap bias ^b
Chrysemys picta	12	1.9	9	3	3	1	0	3	0	4	6
Trachemys scripta	14	1.8	11	1	1	1	1	3	2	3	7
Emydinae	12	2.3	1	0	1	5	0	8	0	10	4
Deirochelyinae	18	2.1	5	5	1	5	3	8	7	3	11
Apalone spp.	3	2.7	3	1	1	0	0	2	0	1	3
Chelydridae	8	1.6	7	1	2	0	0	1	0	2	4
Kinosternidae	17	1.6	10	1	3	0	2	3	3	6	8
Total	84	1.9	46	12	12	12	6	28	12	29	43

^a Other traps are: minnow or crawfish traps (7 cases), crab pots (1 study), drift fences with pitfall traps (6 cases), or trap types with descriptions we could not confidently assign to one of the other categories (e.g. home-made wire mesh traps, box traps, folding nylon nets; 15 cases).

^b Methods or discussion had sentences justifying the capture method or addressing its possible biases. We were very generous in this category, so even one sentence addressing this topic counted as a 'yes' for this column.

Table 5

Population data reported in recent population studies of turtles in North America. We surveyed the 2009–2014 literature for papers that used live-captures to infer population parameters. We grouped turtles into taxa that gave > 10 papers per group, except for Apalone spp. and Chelydridae, which did not group comfortably into higher taxa. The values are counts of papers that focused on each species, or, for papers with multiple species, had \geq 20 captures of a given species. We found 56 papers addressing 84 cases.

Taxon	n studies	Presence/ absence ^a	Index of N ^a	Estimate of N ^a	Sex ratio ^b	Age ratio ^c	Body size ^d	Survival ^e	Dispersal ^e
Chrysemys picta	12	2	3	4	8	3	4	2	1
Trachemys scripta	14	1	6	6	9	3	7	2	1
Emydinae	12	1	2	5	7	6	4	3	1
Deirochelyinae	18	1	4	12	14	8	10	4	3
Apalone spp.	3	0	2	1	2	1	1	0	0
Chelydridae	8	1	4	3	7	3	5	1	0
Kinosternidae	17	4	3	9	13	6	9	2	1
Total	84	10	24	40	60	30	40	14	7

^a For abundance, each turtle species studied is counted only once in the three columns presence/absence, index of N, and estimate of N. In a few cases, both presence/absence and index data were presented (n = 3; counted in the index of N column) or presence/absence and estimates of N were presented (n = 3, counted in the estimate of N column). For 10 turtle studies, papers did not clearly present information on the number of turtles captured or any sort of population index or estimate. The **index of** N column includes studies presenting total captures (includes recaptures), number of turtles caught (excludes recaptures), catch-per-unit-effort or other trap-based but not recapture-based values. The **estimate of** N column includes only studies that estimated population size in some way, e.g. using Lincoln–Petersen, Jolly–Seber, or related metrics.

^b Sex ratios apply to adult turtles only.

^c For age ratios, we considered only adults versus juveniles. Very few studies captured hatchlings. Although some studies reported the numbers of adults and juveniles captured, very few had estimation of age ratios as a primary research aim.

^d For body size, we included studies that reported any or all of the following: plastron length, carapace length, or body mass.

^e Survival and dispersal columns are based on live-trapping data and models, rather than from radio-collars or other methods.

for using multiple methods to address low recapture rates and trap biases (Koper and Brooks, 1998; Ream and Ream, 1966), 7 of 12 recent studies used only one method and only half of the studies even mentioned possible trap biases. It is therefore likely that many inferences about turtle populations are faulty because they are based on methods that are almost certainly biased and unreliable.

4.1. Trapping biases

Hatchling captures were very rare and occurred at only 5 of 11 ponds, almost all via dip-netting. We suspect most or all of the ponds did have hatchlings and we simply did not catch them; all ponds had juveniles and the cryptic nature of turtle hatchlings is well documented (Mazerolle et al., 2007; Pike et al., 2008; Ream and Ream, 1966). The majority of the hatchlings (71%) were captured at a single pond, where hatchlings were found hiding at the base of emergent reeds, rather than in the mud. Shore disturbance by cattle that had dislodged hatchlings from the mud likely accounted for an additional 10% of hatchling captures. These observations suggest dip-netting is unlikely to be useful for hatchlings in ponds unless typical hatchling habitat (muddy shallows) is disrupted or unavailable. Because hatchlings cannot swim very effectively, and were smaller than the mesh of the hoop and basking traps, the single captures we had of hatchlings in these trap types were likely accidental. Specialized trap methods designed for hatchlings are almost certainly necessary for reliable inference about this cohort; terrestrial drift fences (Todd et al., 2007) and nesting surveys (Marchand and Litvaitis, 2004b; Samson et al., 2007), provide better hatchling estimates than do aquatic trapping efforts.

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Juveniles were also most often caught in dip-nets, with two-thirds of their captures via this method. They can swim and dive in open water, but they lack the speed of adult turtles and are thus relatively easy to catch with dip-nets. Although basking traps and hoop nets accounted for 33% of all juvenile captures, it is unlikely that good estimates of juvenile abundance and size would come from these methods alone because of these low capture rates.

Hoop nets were the least successful of all trap types for both males and females, although they accounted for 25% of captures. Adult females were most likely to be captured via dip-net (42% of captures). Basking traps were not the best trap for females, which is surprising given that females bask longer and more often than males, especially during egg development (Carrière et al., 2008; Krawchuk and Brooks, 1998; Lefevre and Brooks, 1995). Egg development for turtles in British Columbia occurs in late spring through summer and corresponds to this study's field season (COSEWIC, 2006). Males were caught slightly more often in basking traps than in dip-nets (39% versus 36%).

We recaptured only 33.5% of turtles, which is actually relatively high for turtle trapping studies (many studies report rates <20%, e.g. Glorioso et al., 2010). By far the majority of recaptured turtles were recaught in the same type of trap as the original capture, a trend consistent across all age and sex classes. For the hoop nets and basking traps, which were both baited, the increased likelihood of being recaught in the same trap type could indicate a positive trap response. A positive trap response does not explain the trend for dip-netting, however, as all turtles tried to avoid the dip-net. Only <2% each of juveniles, males, and females were caught in all three trap types. Despite the small number of turtles caught in all three trap types, recapture rates were usually highest when trap methods were combined. Taken altogether, these data indicate that choosing not to use one of the three trap types would have left some turtles completely unsampled. This finding supports Ream and Ream (1966) in their original assertion that researchers should use multiple trap types and combine the data as it will sample more turtles and likely increase the accuracy of the population estimates.

4.2. Population inferences from biased trapping

The net effect of the biases in each capture method is that population inferences suffer badly when only one method was used as the basis for the inferences. Population size estimates from a single trap type were biased low by an average of 29%, but with a wide range of values and 18% of cases where the single-trap estimate exceeded the combined estimate. Variance in population estimates was not consistently higher for single-method estimates than for the combined estimate, which derives from the over-all low rate of recaptures; in some ponds, single-method estimates had higher recapture rates than the combined estimate did, thus contributing to lower variance even when the population estimates were quite different.

Problematic inference also occurred for estimating sex and age ratios. Here, the results were simply scattered rather than suggesting a systematic bias. For ponds with low numbers of individual turtles captured (\sim 20 or fewer), any sex or age estimates are suspect anyway simply because catching even one or two more turtles would have a big impact on the calculation of sex/age percentages; stochastic variation affecting which turtles are caught is important for these low density populations. For the ponds with high numbers of captures, the substantive variation in these estimates across trap types is more worrying because it is more plainly a trap effect. Quite simply, the different trap types were sampling largely independent segments of the turtle population, so the best pond-wide estimates of sex and age structure really do derive from the use of multiple traps as that increases the numbers of turtles captured.

Our analysis was based on separating the captures by trap type from the same days of trapping. This design could lead to fewer individuals captured per trap type than would have occurred if we had used only a single trap type at a time, since turtles caught in one trap type could not be simultaneously captured in another type. The major alternative design for these questions would be to trap each pond for several days using only one trap type, then switch to another trap type. This alternative design would merely trade potential problems, since it would add temporal variability (e.g. water temperatures, hours of sunlight on trap days) as well as extending the number of days each pond had trappers present, thus increasing the disturbance to the turtles. We do not think our design leads to faulty inferences: the basking and hoop nets were up for hours, with dip-netting occurring at the very end of each trapping period. Turtles caught in dip-nets thus had many more hours in which to be captured by the fixed traps and it is low probability that they would have been captured in the other traps during the 1.5 h of dip-netting. Further, by far the majority of recaptured turtles were recaught in the same trap type, which strongly suggests turtles were differentially attracted to particular trap types.

The only way to truly assess whether combining trap types would reduce bias and improve accuracy would be to compare sampling results to a population with known true values, which by its nature is impossible. Koper and Brooks (1998), working with a well-known population of marked adult painted turtles, also suggested that combining capture methods improved estimates by increasing the number of turtles caught, but they found that population estimate error was still too high for either management of populations or ecological research. This conclusion seems unnecessarily pessimistic to us. All of their population size estimates were negatively biased (as were the majority of our single-trap estimates compared to the combined estimates). From a wildlife management perspective, it would be more precautionary to use an underestimate than an overestimate, although the degree of underestimation is important when determining conservation status or management activities. Regardless of the population estimate, a sampling design that used multiple capture methods would provide stronger inference for age categories and sexes, numbers that are of value in a population survey or monitoring program.

4.3. Recommendations

Our analysis demonstrates that using multiple trap types increases painted turtle captures and recaptures, leading to better inference about population parameters. Our scan of recent population surveys for North American freshwater turtles unfortunately suggests that nearly half of the researchers are instead using single trapping methods. We urge researchers to expand the number of trapping methods they use; we think current practice runs serious risks of faulty inference, especially in cases where researchers are evaluating things like male versus female survival or recruitment from their trapping data. Because most turtles that were recaptured were found in the same trap type, simply extending trapping efforts with one trap type is unlikely to catch these other individuals.

We also encourage more methodological development for turtle trapping. We expect that there is some difference among species in terms of how they react to different traps, and we also suspect that wide-ranging turtles may vary in their trap responses in different locations throughout the range. We also think it would be fruitful to conduct further studies on the efficacy of additional capture methods beyond those we assess here, the seasonal timing of trap efforts vis-à-vis recapture rates, trapping results for lotic and lentic systems, and measures of pond productivity or size that might influence turtle behavior in relation to trappability.

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