

Article

# A Surfeit of Studies: What Have We Learned from All the Box Turtle (*Terrapene carolina* and *T. ornata*) Home Range Studies?

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**Abstract:** Home range (HR) studies are a particularly common approach to investigations of animal habitat use, resource availability, and response to management manipulation such as relocations. *Terrapene carolina* (Eastern box turtle) and its sister taxon *T. ornata* (Ornate box turtle) are especially popular subjects of HR studies because they are relatively easily tracked. *Terrapene* HR studies have revealed a wide variation in HR sizes within and between populations, due to factors such as differences in ecoregion and analytical approach (e.g., minimum convex polygons, kernel analysis, bivariate normal, multivariate Ornstein–Uhlenbeck stochastic process, harmonic means). We performed a meta-analysis of the available literature, including unpublished work to avoid bias due to under-publication, to explore the causes for variation in HR size. We found 19 studies reporting *T. carolina* HR sizes and seven studies reporting *T. ornata* HR sizes; the resulting meta-analysis revealed patterns that are not visible in the individual studies. We found important differences between the species: female *T. ornata* had smaller HRs than males, whereas the opposite is true for *T. carolina*, and *T. ornata* HRs were influenced by ecoregion, while *T. carolina* HRs were not similarly influenced. Not surprisingly, we found that choice of analysis technique affected HR estimate; analyses using ellipses resulted in larger HR estimates than all the other techniques, while kernels were smaller than minimum convex polygons. Although not indicated by individual studies, our meta-analysis showed that the HRs of relocated *T. carolina* females were significantly larger than those of non-relocated females. Although the number of individual turtles in studies varied from three to 25, the sample size did not significantly affect HR size.

**Keywords:** home range; radio telemetry; minimum convex polygons; kernel analysis; bivariate normal; harmonic mean method; latitude; relocation; sample size; relocation

## 1. Introduction

Home range (HR) studies have a long, complex, and contentious history, in part because the concept of home range is attractive yet ambiguous. One of the earliest HR studies defined HR as “the area an individual uses to carry out its life functions” (e.g., feeding, mating, overwintering, etc.) [1]. This broad definition, along with the lack of a generally accepted subsequent narrowing of this definition, has led to a wide range of uses for the term HR, which is reflected in the varied methods that are used for calculating home ranges. For example, Kernohan et al. [2] described HR as an area where an individual is most likely to be present during a given period of time, which is a probability density also referred to as the utilization distribution (UD) [3]. Some studies attempt to include all the

normal activities that subject animals perform in an annual cycle (e.g., [4,5]), while others explicitly integrate activities such as nesting forays [6].

HR studies necessarily involve numerous decisions regarding what exactly will be measured. The duration of animal movement studies typically span only a small portion of the individual's life, and HR may change in size and location from season to season. That is, an individual may use different areas, each year, as the locations of available resources change. Animals that live in two different geographic locations (e.g., migratory birds) are often considered to have at least two "ranges", and each one is very important to their survival and reproduction.

The lack of a clear definition, differences in what is actually measured, the variety of measurements and analytical techniques, and numerous other differences between studies makes comparisons of HRs between and among studies difficult. Most reviews (e.g., [7,8]) simply list HR studies and draw non-quantitative conclusions about the potential impacts of different factors, such as sampling methods, habitat quality, and age/sex of individuals tracked, on HR. However, a failure to decipher what can be learned from past research can result in new studies that simply repeat previous work, a failure to detect large scale patterns, and little progress overall.

Box turtles (*Terrapene* sp.) are appealing targets for such an analysis because they have been subjects of a large number of both published and unpublished HR studies. Their popularity as subjects of HR studies comes in part because (1) they are of conservation concern in much of their range (reviewed by Kimble et al. [9]), (2) they are conversely relatively common elsewhere, (3) they are terrestrial and have fairly small ranges, and thus (4) they are relatively easy to track using a variety of techniques (reviewed below). Box turtle HR studies include some of the earliest scientific studies of animal movements (e.g., [10,11]) and these predate the use of radio telemetry—which is commonly used today—by decades.

We chose to study *Terrapene carolina* (Eastern Box Turtle) and *T. ornata* (Western box turtle) because despite broadly similar habitat requirements, together they span a wide range of habitats, they are congeneric taxa—thus reducing phylogenetic conflicts—and because few HR studies have been conducted on the other members of the genus. Both are primarily terrestrial and omnivorous species, with highly domed shells and little sexual dimorphism. They are similar in size; *T. carolina* typically range from 11.5 to 15.2 cm in length and *T. ornata* are typically 10.0 to 12.5-cm long [12]. *T. carolina* is primarily a woodland species whose habitat ranges through much of the eastern United States from Maine to Florida and west into the eastern Great Plains. *T. ornata* typically inhabits more xeric, sandy soil prairie grasslands of the Great Plains.

Previous studies measuring *Terrapene* HRs have reported wide variation in HR sizes within and between populations, possibly due to factors such as differences in habitat, demography, and the life history of individuals being tracked. The HR of the males of some terrestrial turtle species are typically larger than females [13,14], presumably because they are seeking females. In contrast, female HR of some species may be larger (e.g., [15]), which is perhaps because of extended excursions for oviposition.

In the past, animal locations for *Terrapene* HR studies sometimes used the results of targeted searches for marked individuals, sometimes involving dogs or string trailers. These were mapped using compasses and measurements to mapped landmarks; the early radio telemetry studies predate high-accuracy portable Global Positioning System units. Some studies used a variety of these techniques. *Terrapene* HR studies in recent decades have nearly always used radio telemetry or GPS technology, permitting the collection of hundreds or thousands of locations. We wanted to test whether tracking technique affected HR size estimation.

*Terrapene* HR have been analyzed using a multitude of HR estimators, including minimum convex polygons (MCP), kernel analysis, bivariate normal, multivariate Ornstein–Uhlenbeck stochastic process (M.O.U), and harmonic means. They also have different sample sizes, all of which may contribute to differences in HR. Similar to studies of other herpetofauna, HR data on box turtles are often characterized by low sample sizes and high spatial autocorrelation in locations of repeated, heavy use, such as basking sites [16,17]. Harmonic mean and kernel density estimates of HR are

especially sensitive to data with low sample size and autocorrelation, often inflating the HR estimate as compared to minimum convex polygon techniques [16,18–20]. However, MCP estimates lack information on centers of activity that other estimators provide, including kernel density, harmonic mean, and 95% ellipses.

Dodd [7] listed 10 *T. carolina* HR studies and nine *T. ornata* HR studies, but there has never been a systematic review, including all the studies with HR data, to quantitatively compare what is known about HR size for these well-studied species. We conducted a meta-analysis of data (Table S1) from these papers to quantify the effect of sex, latitude, sample size, tracking method, analysis method, and habitat on *T. carolina* and *T. ornata* HR size. We also considered the effects caused by relocation, which is a conservation technique that is often used with *Terrapene*.

## 2. Method—Meta-Analysis Outline

In 2014, we used a variety of approaches to locate studies that reported HR for either *T. carolina* or *T. ornata*. We used the terms and various combinations of the terms “terrapene”, “carolina”, “ornata”, “home range”, and “homerange” using Google Scholar. We obtained all papers cited as containing home range data from Dodd [7]. We also searched for PhD dissertations and master’s theses in the ProQuest Dissertations and Theses database, and searched for published papers that resulted from theses and dissertations. Where theses and dissertations were not published, we used the original studies. We examined the literature cited sections of all the studies that we found for additional studies.

We selected all the studies that reported HR for either adult *T. carolina* or adult *T. ornata* and provided a mean, variance, and sample size, or the data for which these could be calculated. For two studies [21,22], we emailed authors to clarify and supplement data. We used mean estimates of home range data as reported, or we calculated these from individual data as reported. Where other forms of variance were reported (e.g., standard error), we converted them to standard deviation for analysis. Study sites were found on Google Maps, and the GPS coordinates for each site were plotted in ArcMap. We used the Level II Ecoregion shapefiles (EPA.gov) [23] to identify the ecoregion for each study. Sex was used as reported: “male”, “female”, or “mixed” where sex specific data was not specified. We attempted to collect the appropriate data to test for the effect of length of study and number of locations/individual.

We also noted whether turtle locations were determined through radio telemetry, visual search, or string trailers. However, all the studies with appropriate data used radio telemetry, so this factor was left out of the analysis. We placed all the HR studies into one of four categories based on analytical technique: kernel (95% kernel), minimum convex polygon (minimum convex polygon, 95% minimum convex polygon, minimum area, minimum polygon, or convex polygon), ellipse (95% bivariate normal or 95% ellipse), and harmonic mean (harmonic mean or 95% harmonic mean). If a paper reported results for more than one gender, location, or analytical technique, we included all the HR estimates and controlled for non-independence by including a random term (Author/paper ID) in the model.

### Meta-Analysis

All the calculations and statistical analyses were executed using functions included in the *metafor* package (version 2.0-0; [24]) of the R open-source software environment (version 3.4.1; [25]) within RStudio (version 1.0.153; [26]). We provide all the data, codes, and output used in this experiment as digital appendices [see Supporting Information]. We used the raw means, standard deviations, and sample sizes of *Terrapene* home range estimates that were extracted from the literature to calculate the sampling variance needed for weighting the outcomes in the meta-analysis. We used the `measure = “MN”` argument within the `escalc()` function for this purpose. Unlike many traditional meta-analytical effect sizes such as Hedge’s *d* or log odds, the raw mean home range (ha) is retained as the effect size response rather than a zero-centered and/or transformed response.

Using restricted maximum likelihood (REML) estimation in the function `rma.mv()`, we ran multi-level random-effects (MLRE) models to understand relationships between *Terrapene* HR sizes

and intrinsic or extrinsic factors. Many factors (e.g., population genetics, researcher error, and climate) are more likely to be similar within than across experiments and locations. MLRE-type meta-analytical models are specifically designed to account for non-independence among effect sizes by allowing for the addition of a random term in the model [24,27]. We included “Author” as a random term in each model to account for the potential lack of independence among effect sizes derived from the same article and/or the same experimental infrastructure. Where appropriate, we used the *glht()* function in the *multcomp* package (version 1.4-8; [28]) to perform post hoc multiple comparisons using the Holm–Bonferroni method. Heterogeneity among effect sizes within datasets was assessed using the *Q*-statistic. Large *Q* values suggest that differences between effect sizes within a dataset do not estimate a common population mean, and thus could vary for reasons other than sampling error (e.g., due to some environmental factor; [29]). We tested for the significance of *Q* using a  $\chi^2$  distribution.

We tested for publication bias using Egger’s regression test [30,31] by modifying the MLRE models to include the standard error of the effect sizes as a moderator. When the intercept of this regression test significantly deviates from zero, the overall relationship between the precision and size of studies included in the dataset is considered asymmetrical, and therefore biased [31]. We considered analyses to be biased if the intercept differed from zero at  $p = 0.10$  (as in [30]).

Parameter estimates in meta-analyses, similar to other regression-based tests, are sensitive to outliers and influential data points. However, diagnostic tests for identifying—and rules for excluding—these types of cases are still evolving, particularly for multivariate/multi-level meta-analytical models [32]. We evaluated the sensitivity of our analyses as in Habeck and Schultz (2015) [33] by comparing fitted models with and without effect sizes that we defined as influential outliers. We considered influential outliers to be effect sizes with hat values (i.e., diagonal elements of the hat matrix) greater than twice the average hat value (i.e., influential) and standardized residual values exceeding 3.0 (i.e., outliers; [32,34,35]). Finally, we used the function *lme* in the package *nlme* (version 3.1-131.1; [36]) to test whether the sample size of experiments influenced *Terrapene* HR sizes.

### 3. Results

#### 3.1. Data Set

We found 23 publications that reported *T. carolina* HR estimates, and eight publications that reported *T. ornata* HR estimates. Five of these did not report sufficiently detailed HR data. We extracted 72 *Terrapene* HR estimates (*T. carolina* = 50, *T. ornata* = 22) from the remaining 26 publications ([21,22,37–60]). The original experiments were conducted within 10 Level II ecoregions as defined by Omernik [61] and the U.S. Environmental Protection Agency. Only 42 (58.3%) of the HR estimates were from published studies, 22 (30.6%) were from unpublished undergraduate and master’s theses or PhD dissertations, and eight (11.1%) were from unpublished government agency reports. All the studies that met our criteria for HR mean, variance, and sample size, or the data for which these could be calculated, used radio telemetry as their tracking technique. We were unable to collect meaningful data to test for the effect of length of study or number of locations/individual because very few publications reported these data in sufficient detail.

#### 3.2. Analysis

Previously reported *T. carolina* HR sizes ranged from 0.205 ha (males only, [54]) to 28.370 ha (mixed sexes, [50]), which is a factor difference of 138. The overall mean of the 50 studies, including those in which turtle sex was identified and those in which sex was not identified, was 7.54 ha (95% CI = 5.86 to 9.21 ha). Previously reported *T. ornata* HR sizes ranged from 0.825 ha (females only, [49]) to 19.097 ha (females only, [40]), which is a factor difference of 23. The overall mean of the 22 reports included was 4.94 ha (95% CI = 2.69 to 7.19 ha).

Home range size did not differ between *T. carolina* and *T. ornata* (Table 1). However, within species, home range size differed between males and females (Table 1). For *T. carolina*, the female home range

was 27% larger than that of the males. For *T. ornata*, the female home range was 6% smaller than that of the males.

**Table 1.** Raw mean home range (HR) estimates with standard error (SE) and 95% confidence intervals (C.I.L (=lower limit of confidence interval) and C.I.U (=upper limit of confidence interval)) for *T. carolina* and *T. ornata* by species and sex, using only studies where turtle sex was identified. Superscript letters show within-species differences between females and males, based on Holm–Bonferroni pairwise post hoc comparisons.

Species	HR Estimate	SE	C.I.L	C.I.U
<i>T. carolina</i>				
Overall	4.50	0.83	2.88	6.12
Female <sup>a</sup>	4.82	1.24	2.40	7.24
Male <sup>b</sup>	3.80	1.24	1.37	6.22
<i>T. ornata</i>				
Overall	4.61	1.37	1.93	7.29
Female <sup>a</sup>	4.37	1.63	1.18	7.56
Male <sup>b</sup>	4.67	1.63	1.48	7.86

For *T. carolina*, HR size did not differ among ecoregions (Table 2). The HR size of *T. ornata* within the west-central semi-arid prairies and western Sierra Madre piedmont ecoregions differed from all other ecoregions (Table 3). HR size differed among home range estimator techniques. HR estimates calculated using the ellipse technique were larger than those calculated using all other techniques, and MCP estimates differed from kernel estimates (Table 4).

**Table 2.** Raw mean HR estimates with standard error (SE) and 95% confidence intervals (C.I.L and C.I.U) for all *T. carolina* studies, by ecoregion.

Ecoregions	HR Estimate	SE	C.I.L	C.I.U
Central USA plains	18.32	12.43	−6.05	42.69
Mississippi alluvial and southeast USA coastal plains	4.64	1.71	1.29	8.00
Mixed wood plains	3.51	2.06	−0.54	7.55
Ozark/Ouachita-Appalachian forests	2.04	1.53	−0.96	5.05
Southeastern USA plains	5.16	0.91	3.37	6.95

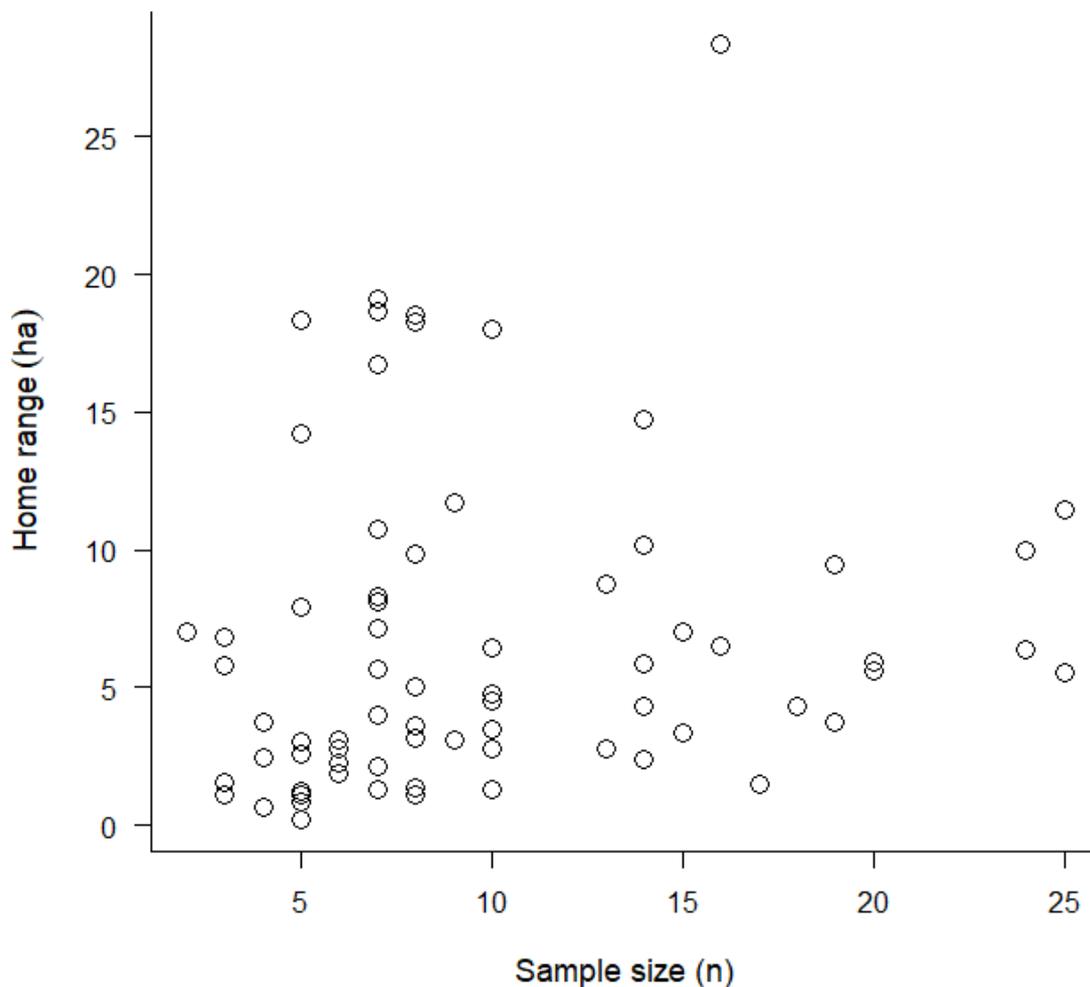
**Table 3.** Raw mean home range estimates with standard error (SE) and 95% confidence intervals (C.I.L and C.I.U) for all *T. ornata* studies by ecoregion. Superscript letters show differences among ecoregions, based on Holm–Bonferroni pairwise post hoc comparisons.

Ecoregions	HR Estimate	SE	C.I.L	C.I.U
Central USA plains <sup>a</sup>	2.55	1.00	0.58	4.52
Cold desert <sup>a</sup>	1.58	1.02	−0.42	3.57
South-central semi-arid prairies <sup>s</sup>	2.32	1.01	0.35	4.30
Temperate prairies <sup>a</sup>	0.86	0.99	−1.08	2.79
West-central semi-arid prairies <sup>b</sup>	18.81	3.02	12.90	24.72
Western Sierra Madre piedmont <sup>c</sup>	6.97	1.01	5.00	8.94

**Table 4.** Raw mean home range estimates with standard error (SE) and 95% confidence intervals (C.I.L and C.I.U) for all *Terrapene* studies by HR technique. Superscript letters show differences among estimators, based on Holm–Bonferroni pairwise post hoc comparisons. MCP: minimum convex polygons.

HR Calculation Technique	HR Estimate	SE	C.I.L	C.I.U
Ellipse <sup>a</sup>	8.29	0.91	6.50	10.08
Harmonic mean <sup>b</sup>	4.13	0.83	2.50	5.75
Kernel <sup>bc</sup>	3.48	0.72	2.08	4.88
MCP <sup>bd</sup>	4.59	0.70	3.21	5.96

The number of turtles in studies varied from three to 25 individuals (mean = 9.85, s.d. = 7.54). The sample size in experiments did not influence either *Terrapene* HR size ( $t = 0.54$ ,  $df = 45$ ,  $p = 0.59$ , Figure 1) or the s.d. of HR ( $\beta = -0.061$ ,  $t = -0.316$ ,  $df = 45$ ,  $p = 0.754$ , Figure 2).



**Figure 1.** Raw mean HR estimates as a function of study sample size. The relationship was not significant ( $\beta = 0.077$ ,  $df = 45$ ,  $t = 0.542$ ,  $p = 0.591$ ).

Relocation status influenced HR size in *T. carolina*, and there were no appropriate data for *T. ornata*. Individuals that were relocated had a HR that was on average 50% larger than individuals that were not relocated (Table 5).

**Table 5.** Raw mean home range estimates with standard error (SE) and 95% confidence intervals (C.I.L and C.I.U) for *T. carolina* by relocation status. Superscript letters show differences among estimators.

Relocated	HR Estimate	SE	C.I.L	C.I.U
Yes <sup>a</sup>	6.13	0.80	4.56	7.70
No <sup>b</sup>	4.07	0.67	2.76	5.38

## 4. Discussion

### 4.1. HR of *T. Carolina* and *T. Ornata*

In agreement with our expectations, HR did not differ between *T. carolina* and *T. ornata*, which was due both to their similar mean HR values and to a wide HR variation within both species (Table 2). The sister taxa are ecologically similar, although adult *T. carolina* are typically slightly larger than *T. ornata* [12]. The species have broad differences in typical habitat: *T. carolina* primarily inhabits woodlands, and *T. ornata* primarily inhabits prairies. However, both are habitat generalists and broadly omnivorous. They are sympatric over eastern Texas and Oklahoma and parts of Missouri and Illinois, where they can be found in the same microhabitat and sometimes hybridize [62–64].

### 4.2. Do the HRs of Male and Female *Terrapene* Differ in size?

Males have larger HRs than females in many species of terrestrial turtles ([13], Lawson 2006); in some species, the female HR is larger (e.g., [15]), and in some species, there is no difference [65]. In contrast, some *T. carolina* HR studies have found that females have larger HRs than males (e.g., [54]), while others have found that males have larger HRs than females (e.g., [49]). Dodd [7] reviewed *Terrapene* HR studies and concluded that male and female *Terrapene* sp. HRs are “similar in size”. However, we found that within species, the HR size differed significantly between males and females (Table 2). In *T. carolina*, the average female HR was 27% larger than that of males, while for *T. ornata*, the average female home range was 6% smaller than that of males. This surprising difference between these closely related species has not been previously detected, and should be investigated where they are in sympatry and allopatry.

### 4.3. Is HR Influenced by Ecoregion?

Numerous researchers have found that the HRs of some species are influenced by resource availability (e.g., olive baboon (*Papio anubis*): Barton et al. [66]; grizzly bears (*Ursus arctos*): Edwards et al. 2013 [67]; African striped mice (*Rhabdomys pumilio*): Schoepf et al. 2015 [68]). Dodd [7] suggested that local resource levels and habitat structure might influence *Terrapene* HR. These data were not available to us, so we used ecoregions as crude proxies. While we found no significant difference in *T. carolina* HR among the five ecoregions they inhabit (Table 3), we note that the average *T. carolina* HR in the central USA plains ecoregion is 3.6 times larger than that of the ecoregion with the next highest average *T. carolina* HR. However, this unusually high HR is because of a single *T. carolina* HR study in the central USA plains ecoregion [58]. In contrast, the average *T. carolina* HR in the other four ecoregions was very similar.

In contrast, the average *T. ornata* HR size in the west-central semi-arid prairies and Western Sierra Madre piedmont ecoregions was significantly larger than that in the other four ecoregions for which we had data (Table 4). The mean HR for the west-central semi-arid prairies ecoregion was exceptionally large, 2.7 times larger than that of the western Sierra Madre piedmont ecoregion. This again was the result of a single HR study from that ecoregion [56].

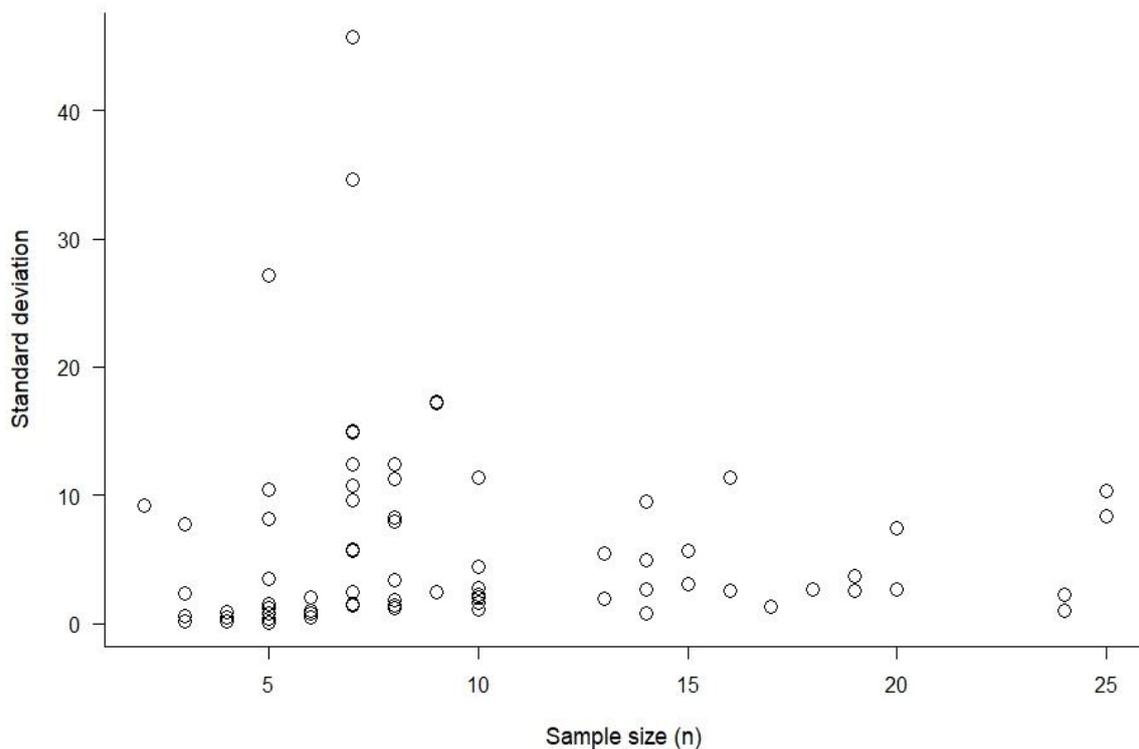
### 4.4. How Does Choice of Analysis Technique Affect HR Estimate?

The analytical approaches that are used for HR size estimation have gone through numerous changes since Burt [1]. There has been vigorous discussion over the optimal approach to the analysis

of individual location points (e.g., [20,69–71]). Since *Terrapene* have been the subjects of numerous HR studies since the 1920s, *Terrapene* HRs have been estimated using a wide variety of techniques. We combined *Terrapene* HR studies into four major categories (kernel, minimum convex polygon, ellipse, and harmonic mean), and found that HR studies that used ellipse techniques had significantly larger HRs than those that used any other techniques, and further, that MCP estimates indicated, on average, significantly larger HRs than kernel estimates (Table 5). These results show that studies using different HR analysis techniques cannot be combined in a single analysis without adjusting for these differences.

#### 4.5. Does Sample Size Affect HR Size Estimation?

We hypothesized that sample size (number of turtles) would affect the HR size and the standard deviation of HR size, because small samples sizes can increase the relative effect of individuals with unusual HR. We found that differences in sample sizes among experiments did not influence mean HR size (Figure 1) or the standard deviation of HR sizes (Figure 2). This suggests that typical sample sizes (mean = 7.85 individuals) for *Terrapene* HR studies are adequate. We were unable to test for the effect of length of study and number of locations/individual because these data were rarely reported. This is unfortunate because, despite the relative ease of *Terrapene* HR studies, resource use could be optimized if these aspects of study design were better understood.



**Figure 2.** Standard deviation of the HR estimates as a function of study sample size. The relationship was not significant ( $\beta = -0.061$ ,  $df = 45$ ,  $t = -0.316$ ,  $p = 0.754$ ).

#### 4.6. Do Relocated *Terrapene* Have Larger HR?

Studies of relocated turtles often attempt to test whether they have a HR size that is different from non-relocated turtles (e.g., [51,72–74]). Testing for this relationship is often difficult, because usually only small numbers of relocated individuals and resident individuals can be tracked in any single study. Typically, the HRs of both relocated and non-relocated turtles are highly variable, raising the probability of Type 2 errors. Meta-analysis can address both of these problems. We only found appropriate data for relocated *T. carolina*, which had considerably higher HR than those that had not

been relocated. We recognize that this is a fairly crude analysis, because a better analysis would be to compare the HRs of relocated turtles to the HRs of local conspecifics that were not relocated. However, this test clearly shows a dramatic difference due to relocation, which is an effect that had not been shown consistently in the individual studies.

## 5. Conclusions

Individual HR studies of *T. carolina* and *T. ornata* contributed a more thorough understanding of the habitat use and behaviors of individuals within local populations. Combining these studies within a meta-analysis allowed us to reveal larger patterns in HR across *T. carolina* and *T. ornata* populations, and between these two species, patterns that were often not detected in individual studies. For example, meta-analysis revealed an increase in HR in relocated *T. carolina* compared to those not relocated. This analysis also revealed species-level differences regarding the influence of sex and ecoregion on *Terrapene* HR, with sex affecting the HR in both species but in opposite directions, and ecoregion playing a larger role in *T. ornata* HR than *T. carolina* HR. Furthermore, our meta-analysis revealed that while tracking technique (number of locations) did not affect HR, the HR estimators (MCP, ellipse, etc.) did affect HR. We note that we were unable to test whether the study length or number of locations/individual affected HR size; however, we suggest that the raw data from an unusually long-term study with very large sample sizes (e.g., [21,45]) or novel studies using current GPS-tracking technology create samples that vary frequently and with high accuracy (e.g., [75,76]) could be sub-sampled to address these questions, as well as to address important issues of spatial autocorrelation. As shown in this study, meta-analysis is a powerful tool that can detect large-scale patterns across studies and provide evidence for or against conclusions made about species within individual studies.

**Supplementary Materials:** The following are available online at <http://www.mdpi.com/1424-2818/11/5/68/s1>, Table S1: Turtle meta-analysis data and code.

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