Experimental removal of introduced slider turtles offers new insight into competition with a native, threatened turtle

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The red-eared slider turtle (*Trachemys scripta elegans*; RES) is often considered one of the world's most invasive species. Results from laboratory and mesocosm experiments suggest that introduced RES outcompete native turtles for key ecological resources, but such experiments can overestimate the strength of competition. We report on the first field experiment with a wild turtle community, involving introduced RES and a declining native species of conservation concern, the western pond turtle (*Emys marmorata*; WPT). Using a before/after experimental design, we show that after removing most of an introduced RES population, the remaining RES dramatically shifted their spatial basking distribution in a manner consistent with strong intraspecific competition. WPT also altered their spatial basking distribution after the RES removal, but in ways inconsistent with strong interspecific competition. However, we documented reduced levels of WPT basking post-removal, which may reflect a behavioral shift attributable to the lower density of the turtle community. WPT body condition also increased after we removed RES, consistent with either indirect or direct competition between WPT and RES and providing the first demonstration of RES competing with a native turtle in the wild. We conclude that the negative impacts on WPT basking by RES in natural contexts are more limited than suggested by experiments with captive turtles. However, native WPT appear to compete for food with introduced RES. Our results highlight the importance of manipulative field experiments when studying biological invasions.

Full Title: Experimental removal of introduced slider turtles offers new insight into competition with a native, threatened turtle

Short Title: Competition between introduced sliders and threatened turtles

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Abstract: The red-eared slider turtle (*Trachemys scripta elegans*; RES) is often considered one of the world's most invasive species. Results from laboratory and mesocosm experiments suggest that introduced RES outcompete native turtles for key ecological resources, but such experiments can overestimate the strength of competition. We report on the first field experiment with a wild turtle community, involving introduced RES and a declining native species of conservation concern, the western pond turtle (*Emys marmorata*; WPT). Using a before/after experimental design, we show that after removing most of an introduced RES population, the remaining RES dramatically shifted their spatial basking distribution in a manner consistent with strong intraspecific competition. WPT also altered their spatial basking distribution after the RES removal, but in ways inconsistent with strong interspecific competition. However, we documented reduced levels of WPT basking post-removal, which may reflect a behavioral shift attributable to the lower density of the turtle community. WPT body condition also increased after we removed RES, consistent with either indirect or direct competition between WPT and RES and providing the first demonstration of RES competing with a native turtle in the wild. We conclude that the negative impacts on WPT basking by RES in natural contexts are more limited than suggested by experiments with captive turtles. However, native WPT appear to compete for food with introduced RES. Our results highlight the importance of manipulative field experiments when studying biological invasions.

Introduction

The International Union for Conservation of Nature (IUCN) has labeled the red-eared slider turtle (*Trachemys scripta elegans*; RES) one of the "world's worst invasive species" (Lowe et al. 2000). RES are native to the central United States but are now established on every continent except Antarctica, predominantly because of unwanted pet turtle releases (Kraus 2009; Rhodin et al. 2017). Results from laboratory and mesocosm experiments suggest that RES can outcompete native European and eastern United States freshwater turtles for food and basking sites (Cadi and Joly 2003, 2004; Polo-Cavia et al. 2010, 2011; Pearson et al. 2015). While such controlled experiments are informative, they can also inflate the effects of competition compared to *in situ* field manipulations (Skelly 2002; Winkler and Van Buskirk 2012). Comparing laboratory and mesocosm experiments with field manipulations is a critical step to a more complete understanding of the strength and mechanisms underlying species interactions in nature. However, to our knowledge, no study has experimentally tested for competition between non-native RES and any native turtle species in the wild.

Basking sites are a key resource for thermoregulation, disease control, and reproduction in freshwater turtles (Ernst and Lovich 2009), and previous *ex situ* experiments suggest that basking sites are an important axis of competition between native turtles and introduced RES (Cadi and Joly 2003; Polo-Cavia et al. 2010). Prior work in the University of California, Davis Arboretum waterway (hereafter, UCD Arboretum) found that introduced RES and native western pond turtles (*Emys marmorata*; WPT) sometimes bask at the same sites (Fig 1), although they tend to use basking sites that differ physically and spatially (Lambert et al. 2013). Whether these basking site differences are the result of species-specific habitat choices or competition has never been resolved and requires an experimental approach.

Freshwater turtles, including both WPT and RES, are dietary generalists as adults and consume a broad array of food items (Ernst and Lovich 2009). Even so, laboratory and mesocosm experiments suggest RES might directly interfere with native turtle food consumption through aggressive behaviors or higher food consumption rates (Cadi and Joly 2004; Polo-Cavia et al. 2011; Pearson et al. 2015). Additionally, if turtle densities are high for a given habitat, exploitative competition could limit food availability, both intra- and interspecifically, and therefore decrease growth rates and / or body condition of native species.

Here, we present the results of an *in situ* field experiment in which we substantially reduced the introduced RES population at the UCD Arboretum to test for competition with WPT. For both WPT and RES, the UCD Arboretum represents a closed system that is well suited for experimental manipulations; natural immigration/emigration is not possible for freshwater turtles in this system, although occasional human-assisted transport does occur, particularly with RES released into the waterway. Our experiment is the first to explicitly test whether invasive species removal, a commonly-advocated management practice for invasive species including RES (Gaeta et al. 2015; García-Díaz et al. 2017), influences the basking behavior and body condition of a native turtle in the wild. If the distribution of WPT basking is a result of direct, competitive exclusion by RES from optimal basking sites, then RES removal should result in an increase of post-removal WPT basking at sites previously dominated by RES. Alternatively, if WPT basking activity does not significantly change in this manner after RES removal, then existing behavioral basking differences between the two species likely reflect species-specific habitat preferences, competitive superiority of WPT, or both. We also assessed WPT body condition pre- and post-removal as a proxy for whether removing RES improves WPT access to food resources. If introduced RES compete with WPT for food, then removing RES should result in an increase in WPT body condition. Given the broad overlap of these two species across California (Thomson et al. 2010, 2016; Fisher unpubl.), the range-wide imperilment of WPT (Spinks et al. 2003; Thomson et al. 2016), and the current Status Review for possible WPT listing under the U.S. Endangered Species Act (USFWS 2015), this experiment is directly relevant to ongoing WPT management actions.

Methods

UC Davis IACUC Protocols #15263 and #16227 and California Department of Fish and Wildlife Scientific Collecting Permits #2480, #4307, and #11663 approved this work.

Turtle trapping and RES removal

Across the UCD Arboretum, we deployed baited submersible traps in optimal habitat for both RES and WPT over approximately 900 trap-nights from 10 July–1 August, 2011 and again from 13–29 September, 2011. We supplemented this trapping with dip netting, opportunistic hand captures, a fyke net, and a basking trap. Dip netting and hand captures were targeted at RES but other trapping was not. We removed and euthanized all RES, depositing most specimens at the UC Davis School of Veterinary Medicine, the Natural History Museum of Los Angeles County, or the UC Davis Museum of Wildlife and Fish Biology. We used linear regression to test whether our trapping depleted the RES population over time by regressing cumulative RES captures against trapping day for adult RES. Using likelihood ratio tests to assess model fits, we compared a quadratic model, which would indicate population depletion, to a linear model, which would indicate that the RES population was not leveling off with our removal effort.

WPT Body Condition

To estimate changes in WPT body condition, we trapped for one week the following year from 27 May–2 June, 2012. In both 2011 and 2012 we measured WPT plastron length (notch-to-notch; mm) and body mass (g) (Iverson and Lewis 2018). We used a linear mixed-effects model (function ‘lmer’, R package “lme4”) to test whether WPT body condition (i.e., differences in mass controlling for body length) changed after the RES removal (Cadi and Joly 2003; Schulte-Hostedde et al. 2005; Litzgus et al. 2008). Our model of WPT mass controlled for plastron length and included treatment (pre- or post-removal) and sex as fixed effects and individual WPT (which were uniquely marked with scute notches) as a random effect to control for repeated measures. We used likelihood ratio tests to assess the significance ($\alpha < 0.05$) of fixed effects and removed non-significant variables from our model. We obtained full model conditional R^2 (cR^2) for fixed and random effects combined and a marginal R^2 (mR^2) for the model's fixed effects alone (function 'r.squaredGLMM', package "MuMIn").

Basking Site Monitoring

We conducted binocular surveys of 24 pre-selected basking sites (Fig 1) for 34 total days, including 16 days pre-removal from 18 March–22 April 2010 (Lambert et al. 2013) and 18 days post-removal from 18 March–22 April 2012. Following Lambert et al. (2013), we performed all surveys between 1000 and 1500 hr to coincide with the expected maximum turtle basking activity during this time of year. We surveyed all sites once daily in rapid succession to avoid counting the same turtle at multiple sites. During each survey we recorded the number of species basking at each basking site as well as water temperature because we previously found that basking activity of both species increases with warmer water temperatures, more so than air temperatures (Lambert et al. 2013). We also obtained air temperature data from the UC Davis Russell Ranch Weather Station which is located ~4 km NW of the UCD Arboretum.

Modeling the Effects of RES Removal on Turtle Basking

We tested for changes in the proportion of WPT:RES basking across the UCD Arboretum pre- and post-RES removal using a generalized linear mixed effects model (GLMM) with a binomial family for proportion data (function 'glmer', R package "lme4"). We modeled WPT:RES basking as a function of treatment (pre- or post-removal) and the distance of each basking site from the west end of the UCD Arboretum because turtle basking distributions were previously shown to vary west-east (Lambert et al. 2013). We accounted for repeated measures by treating survey date as a random effect (Lambert et al. 2013). To explore site-specific changes in the proportion of the two species, we also used individual binomial GLMMs for each basking site.

In addition, we modeled the absolute basking abundance of both species pre- and post-removal using Poisson GLMMs for count data. Our approach here was the same as with the binomial GLMM and, if an interaction was significant, we used individual GLMMs for each year to test the pattern and strength of turtle basking distributions across the UCD Arboretum in each year. To test whether certain basking sites made up larger or smaller proportions of total WPT basking observations pre- or post-removal, we used contingency tables, focusing on the five most heavily-used turtle basking sites (combined for both species) pre-removal (P, O, E, Q, and R) and site X, the most heavily-used turtle basking site post-removal.

Results:

Trapping and RES Removal

We removed and euthanized 177 RES (100.6 kg total biomass), including 28 adult males (16.3 kg), 72 adult females (79.4 kg), and 77 juveniles (4.9 kg, defined as ≤ 100 mm carapace length; Ernst and Lovich 2009). A quadratic (rather than linear) model fit our data best (likelihood ratio test $p < 0.0001$, full model $R^2 = 0.95$) and showed RES captures leveling off, signifying we had removed a substantial fraction of the RES population.

We also captured, marked (or re-marked), and released 115 unique WPT (62.7 kg total biomass) comprising 36 females (24.1 kg), 51 males (36.1 kg), and 28 juveniles (2.5 kg, defined as ≤ 110mm plastron length; Holland, 1991). The number of adult RES captures was ca 1.5 times greater than that of WPT. Given the high population size and density of RES, and given we likely removed the majority of the RES population, our RES removal effort was likely substantial enough to exert an effect on WPT if the two species compete for food or basking.

WPT Body Condition

While we trapped a large number of WPT in each year, we trapped 25 unique adult WPT in both 2011 and 2012; we used these 25 WPT for the body condition analysis. The body condition linear model showed no interaction between treatment and sex ($p = 0.92$) and so we removed this interaction from the model. Sex ($p = 0.009$), treatment ($p < 0.001$), and plastron length ($p < 0.0001$) were significant (full model $cR^2 = 0.95$, $mR^2 = 0.86$). For a given plastron length, males were on average 61.54 g (± 23.55 g) heavier than females. Individual WPT varied in the degree of body condition change post-removal (Fig 2A) and, on average, the 25 WPT measured before and after RES removal were 39.80 g (± 9.92 g) heavier for a given plastron length post-removal (Fig 2B). The absence of an interaction between sex and treatment indicates that male and female WPT responded similarly to RES removal.

Basking Site Monitoring

In 2010, we recorded 283 WPT and 645 RES observations, but only 43 WPT and 61 RES observations in 2012. Although the reduction in numbers of observed WPT was unexpected, we do not believe this reflects a decline in the WPT population. From 27 May–2 June 2012, we trapped 54 unique WPT over seven days and a Schnabel population estimate derived from trapping data suggest that ~109 WPT were present in the UCD Arboretum immediately after our post-removal surveys (McKenzie, Screen, and Pauly unpubl.); this estimate is similar to pre-removal estimates of WPT population size. Given these estimates, we are confident that the WPT population was essentially unchanged during our experiment, and thus our focus on the relative proportions of turtles at monitored basking sites meaningfully reflects the impact of our removal experiment and not a catastrophic decline in WPT.

The basking sites most commonly used by WPT pre-removal were generally the same sites used post-removal (Fig 3A, B). We recorded WPT basking at 15 of 24 basking sites pre-removal, but at only 8 of 24 sites post-removal. WPT were absent from 8 sites they used pre-removal (although of these, only 2 were frequently used pre-removal: sites A and N), and were present at one additional site they were not recorded using pre-removal (site B). We recorded RES basking at 17 of 24 basking sites pre-removal, and only 8 of 24 sites post-removal (Fig 3A, B). RES were absent from 9 sites they used pre-removal and were not recorded using new sites post-removal.

Water temperatures were warmer (two-tailed t-test, $p < 0.0001$) in 2010 (17.0 C ± 0.24 SE) than in 2012 (15.4 C ± 0.36 SE). However, maximum daily air temperatures (averaged across all days of each survey period) were not different between years (two-tailed t-test, $p = 0.74$; 2010, 19.2 C ± 0.69 SE; 2012, 18.8 C ± 0.88 SE). Furthermore, in the two weeks prior to our surveys, maximum daily air temperatures were warmer in 2012 (18.8 C ± 1.08 SE) than in

2010 (15.2 C ± 0.65 SE); two-tailed t-test, $p < 0.001$). Air temperatures were also warmer in the winter (beginning of December to end of February) preceding the post-removal survey than the winter preceding the pre-removal survey (two-tailed t-test, $p < 0.0001$; 2009-2010, 13.4 C ± 0.36 SE; 2011-2012, 15.5 C ± 0.30 SE). Colder water temperatures may thus have contributed to the lower overall turtle basking we observed in 2012, but this effect might have been modulated by warmer air temperatures prior to our 2012 surveys.

Effects of RES Removal on Turtle Basking

The interaction between removal treatment and distance from the west end of the UCD Arboretum was not significant ($p = 0.18$) and was removed from the model. Both treatment ($p < 0.0001$) and distance from the west end ($p < 0.0001$) were retained ($cR^2 = 0.31$, $mR^2 = 0.31$).

The non-significant interaction indicates the removal did not change the ratio of WPT:RES basking distributions across the UCD Arboretum. Both pre- and post-removal, the basking distribution of turtles was WPT-biased in the west end and RES-biased in the east end (Fig 4). However, the proportion of basking individuals that were WPT increased from 30.5% pre-removal to 41.3% post-removal ($p < 0.0001$; Tukey's post-hoc test, function 'glht', package "multcomp"). Individual binomial GLMMs for each basking site showed removal treatment effects on the WPT:RES basking ratio for site Q ($p = 0.002$, 9% WPT to 55% WPT) and a marginal effect for site O ($p = 0.09$, 30% WPT to 75% WPT). All other individual basking sites showed no differences (all $p > 0.1$).

Pre-removal, the WPT basking distribution declined from west to east, and post-removal WPT basking had a relatively flat distribution (Fig 5). We detected a shift in the absolute basking distribution of WPT with a significant interaction between removal treatment and distance from the west end (Poisson GLMM, $p = 0.012$, $cR^2 = 0.23$, $mR^2 = 0.06$). Individual GLMMs for each year indicated that distance from the west end was significantly associated with WPT basking abundance in the pre-removal year ($p < 0.012$, $cR^2 = 0.27$, $mR^2 = 0.03$) but not in the post-removal year ($p = 0.55$).

WPT predominantly used the same basking sites post-removal but showed a more even distribution across basking sites, with more basking activity at two center-east sites (Q and X) compared to before the RES removal (Fig 3A, B). Contingency table analyses showed that sites Q ($p = 0.01$) and X ($p = 0.001$) encompassed larger proportions of total WPT basking observations post-removal than pre-removal (Fig 3A, B). All other sites made up similar proportions pre- and post-removal (all $p > 0.1$), though some sites had generally low basking activity (Fig 3A, B), possibly limiting our power to detect shifts.

Our experimental removal of RES was associated with flatter observed distribution of WPT. Even so, if more eastern sites that were dominated by RES pre-removal (e.g., sites O, P, Q, and R) are also preferred WPT basking locations, then WPT should have increased basking at these sites post-removal. We did not see this shift. While our experiment suggests that WPT basking is influenced by RES densities, we did not observe a dramatic shift toward previously RES-dominated sites; thus, we did not find evidence of strong interspecific competition for those sites. Interspecific competition is greatest at higher densities and the effects of an introduced competitor can similarly manifest or become most pronounced when the introduced species is at high densities (Gurnell et al. 2004). Therefore, competition is presumably greatest at high densities of RES (or turtles generally) and perhaps influenced by the relative densities of both species.

After removal, remaining RES were sparse throughout much of the UCD Arboretum and concentrated in the east end (Fig 3B, 5). For RES, a Poisson GLMM indicated a significant interaction between treatment and distance to the west end ($p < 0.0001$, $cR^2 = 0.30$, $mR^2 = 0.16$). Individual GLMMs for each year showed a positive relationship between RES basking and the distance to the west end pre-removal ($p < 0.0001$, $cR^2 = 0.27$, $mR^2 = 0.02$) and post-removal ($p < 0.0001$, $cR^2 = 0.14$, $mR^2 = 0.14$). The distance of each basking site from the west end explained substantially more of the variation in RES basking abundance post-removal than pre-removal, indicating that remaining RES concentrated in the east end more strongly after we removed most of the RES population (Fig 3B, 5). Contingency table analyses indicated that sites E, O, P, and R comprised lower proportions of total RES basking observations after the removal and site X comprised a higher proportion (all $p < 0.05$). Site Q made up similar proportions of total RES observations in both years ($p = 0.14$).

The RES remaining post-removal abandoned several basking sites that they previously used heavily (particularly sites O and P) and shifted towards the east end of the UCD Arboretum (e.g., site X). This result suggests that RES prefer habitat at this end of the waterway and that, prior to our experiment, RES densities were high enough for intraspecific competition to force many RES into less preferred areas of the waterway. Our previous work showed that RES basking activity was highest at sites with shallow slopes, deeper water adjacent to the site, a steel mesh (rather than concrete or dirt) substrate, and high human activity (Lambert et al. 2013). Post-removal, RES basking activity was highest at the two sites (V and X) that maximized this combination of variables based on 2010 surveys (Fig 4B from Lambert et al. 2013).

Discussion

Our experimental removal dramatically altered both RES and total turtle density in the UCD Arboretum by eliminating over half of the turtles in the waterway, and offers new insights into competition for basking habitats and food between introduced RES and native WPT. Our removal experiment produced three important results.

First, the prevalence of basking turtles at our survey sites post-removal was about 15% of that pre-removal, and this reduction in basking observations was measured in both species. We have no evidence that the removal of RES negatively affected the WPT population size, and a follow-up trapping survey confirmed that the number of WPT present remained roughly constant. Rather, it appears that the overall lower density of turtles in the UCD Arboretum allowed many WPT to either shift their basking activity patterns, redistribute themselves to sites that we were not monitoring, or both. Environmental differences, including cooler water temperatures during our post-removal monitoring, may also explain the lower WPT basking numbers, although our previous results from the same site suggest that the water was warm enough for maximal basking activity in WPT (Lambert et al. 2013).

Second, after removing RES, we found that WPT basking activity at our monitoring sites shifted but did not increase at sites previously dominated by RES. Remaining RES concentrated their basking at sites (V and X) consistent with their previously identified preferred habitat characteristics (Lambert et al. 2013), suggesting that high RES densities prior to our experimental removal produced strong intraspecific competition, forcing many RES to use less-preferred basking habitat. While earlier laboratory and mesocosm experiments suggest introduced RES outcompete native turtles for basking sites and other resources, (Cadi and Joly 2003; Polo-Cavia et al. 2010; Pearson et al. 2015), our results suggest more subtle effects found in complex, natural communities that are not predicted by simplified mesocosm experiments (Skelly 2002, Winkler and Van Buskirk 2012).

Third, we found that removing RES led to an increase in WPT body condition, suggesting that these turtle species compete for food. Whether this reflects interference competition (direct interactions between the two species), exploitation competition (both species indirectly competing for overlapping food resources), or a combination of the two is unclear. Experimental work on RES and other native turtles suggests RES may behaviorally prevent native turtles from obtaining sufficient food (Cadi and Joly 2004, Polo-Cavia et al. 2011, Pearson et al. 2015), and our experimental removal may have reduced such interference if it does exist in this population. However, we also removed a substantial portion of the overall turtle community thereby reducing the overall pressure on food resources in the system. Regardless of the mechanism, the ~40 g average increase in body condition we detected is substantial given that all WPT in our analysis pre-removal weighed under 1,100 g. To our knowledge, this result represents the first evidence from wild populations that introduced RES might compete with native turtles for food and that RES removal might improve the body condition of native turtles.

Should We Remove RES to Benefit Declining Native Turtles?

A recent summary of research goals for effective conservation of WPT (Thomson et al. 2016) identified the need for a clearer quantitative understanding of the impact of introduced RES. Controlling invasive species is a substantial commitment that rarely eliminates the entire population, particularly in situations with continual introductions (Kikillus et al. 2012, Gaeta et al. 2015, Garcia-Diaz et al. 2017), and removing 177 RES from the UCD Arboretum was an intensive effort requiring hundreds of person-hours of field work across 40 days. While our study suggests that removing RES does influence native turtle basking ecology and feeding, the potential benefits with respect to short-term basking-site usage appear to be quantitatively modest. However, the substantial increase in WPT body condition during the year following the RES removal suggests that removing RES meaningfully increased resource availability for WPT. Whether these returns justify the effort may well depend on several variables, including RES abundance / density, attitudes of local human residents to introduced RES, disease risk (Héritier et al. 2017), other potential axes of competition (e.g., nesting sites), and other aspects of ecosystem health.

Our results also provide evidence that RES introductions may affect native turtles simply by inflating turtle densities in general (regardless of species identity). Therefore, removing RES may not necessarily relieve native turtles from a dominant competitor but, rather, may relieve ecological or behavioral pressures associated with high turtle densities and could conceivably result in unexpected responses by native species. The very low number of WPT basking observations post-removal here points to the unexpected consequence of removing over half of the turtle community, leading to changes in WPT behavior and habitat use that our experimental design, with fixed monitoring sites, failed to capture. Unlike many other freshwater turtles, WPT are aggressive baskers and prefer to bask alone or in low numbers (Bury and Wolfheim 1973). As such, reducing turtle densities may have allowed WPT to occupy other basking habitats in lower numbers as is their preference. Additionally, higher WPT body condition post-removal was likely influenced by there simply being fewer turtles overall competing for food in the UCD Arboretum. Improved body condition may also be the result of WPT adopting preferred basking behaviors, thereby improving digestive efficiency and mass gain. Future studies that include unmanipulated control sites, pre-removal surveys that span multiple years and account for year-to-year variation, as well as a design that tracks the behavior of native turtles pre- and post-RES removal (e.g., using GPS-enabled radio transmitters) may better elucidate these unexpected outcomes on native turtles. Overall, our analyses suggest WPT responded to removing RES in a manner consistent with interspecific competition for food but inconsistent with strong interspecific competition for basking habitats, implying that removing RES may well be an important management strategy in some situations.

Directly managing basking habitat may be a tractable conservation activity for WPT in addition to non-native RES removal (Spinks et al. 2003, Thomson et al. 2016). In human-modified waterways, removal of floating basking sites for flood control and aesthetics (Spinks et al., 2003) could exacerbate competition for basking sites. Emerging research suggests that experimentally-added floating logs are preferred by WPT compared to bank-side basking sites and are more heavily used by WPT than RES, especially when they are isolated from human activities (Cossman et al. unpubl.). Adding artificial basking sites that favor WPT, alone or in combination with RES population reduction, is a simple, comparatively inexpensive manipulation that should be explored in future field experiments.

Study Limitations

The primary limitations of our study center on interpreting our basking results. We expected to observe fewer basking RES in the second year of study due to our intense removal effort but did not expect a concomitant decline in WPT observations. It is possible that water temperature, other environmental variation, or unforeseen consequences of our manipulation resulted in reduced overall turtle basking activity, or (more likely to us) radical shifts in basking to new and unmonitored locations, after the RES removal. Unfortunately, we cannot confidently identify which factor(s) resulted in fewer WPT basking observations. Although we studied both basking and feeding, we also recognize that our experiment did not address other potentially important axes of competition that are important for the continued recruitment and persistence of WPT populations. While we employed a before-after comparative design, the use of unmanipulated control sites would have improved our ability to make stronger inferences in this study. We do not believe that the lower number of WPT basking observations confounds our results because our analyses of relative basking distribution differences between species and years across the waterway can accommodate sample size differences. Additionally, our analyses found that residual RES shifted their basking in intuitive ways (i.e., towards sites with preferred characteristics), increasing confidence in our results. While field experiments offer more biological realism than experiments in captivity, that added complexity may also yield unexpected results, such as changing a focal species' behaviors or habitat use.

Conclusions

We present the first large-scale field manipulation testing for basking site and food competition between non-native RES and native turtles. Consistent with expectations based on laboratory and mesocosm studies, RES removal increased WPT body condition and altered WPT basking activity. However, contrary to expectations, this change in basking was not consistent with intense competition between RES and WPT for individual basking sites in the UCD Arboretum. Our results offer evidence for intraspecific competition for food and basking sites at high RES densities, and suggest that reducing introduced RES densities allows WPT to access more food and occupy a broader range and distribution of basking sites. We encourage other researchers to replicate our field-based experiment, perhaps using control sites or multiple years of pre-removal observations. These modifications to our protocol would improve the ability to interpret competition between RES and native turtles and the magnitude of behavioral shifts that occur when removals lead to changes in both relative and absolute turtle densities.

Data Availability: Basking and body size data are available in the electronic supplementary material.

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References

Bury, R. B. and J. H. Wolfheim. 1973. Aggression in free-living pond turtles (*Clemmys marmorata*). BioScience 23: 659–662.

Cadi, A. and P. Joly. 2003. Competition for basking places between the endangered European pond turtle (*Emys orbicularis galloitalica*) and the introduced red-eared slider (*Trachemys scripta elegans*). Canadian Journal of Zoology 81: 1392–1398.

Cadi, A. and P. Joly. 2004. Impact of the introduction of the red-eared slider (*Trachemys scripta elegans*) on survival rates of the European pond turtle (*Emys orbicularis*). Biodiversity and Conservation 13: 2511–2518.

Ernst, C. H. and J. E. Lovich. 2009. Turtles of the United States and Canada. Johns Hopkins University Press, 2nd Ed. 840 pages.

Gaeta, J. W., Hrabik, T. R., Sass, G. G., Roth, B. M., Gilber, S. J., and M. J. Vander Zanden. 2015. A whole-lake experiment to control invasive rainbow smelt (Actinopterygii, Osmeridae) via overharvest and a food web manipulation. Hydrobiologia 746: 433–444.

García-Díaz, P., Ramsey, D. S. L., Woolnough, A. P., Franch, M., Llorente, G. A., Montori, A., Buenetxea, X., Larrinaga, A. R., Lasceve, M., Álvarez, A., Traverso, J. M., Valdeón, A., Crespo, A., Rada, V., Ayllón, E., Sancho, V., Lacomba, J. I., Bataller, J. V., and M. Lizana. 2017. Challenges in confirming eradication success of invasive red-eared sliders. Biological Invasions 19: 2739–2750.

Gurnell, J., Wauters, L. A., Lurz, P. W. W., and G. Tosi. 2004. Alien species and interspecific competition: effects of introduced eastern grey squirrels on red squirrel population dynamics. Journal of Animal Ecology 73: 26–35.

Héritier, L., A. Valdeón, A. Sadaoui, T. Gendre, S. Ficheux, S. Bouamer, N. Kechemir-Issad, L. Du Preez, C. Palacios, and O. Verneau. 2017. Introduction and invasion of the red-eared slider and its parasites in freshwater ecosystems of southern Europe: Risk assessment for the European pond turtle in wild environments. Biodiversity and Conservation 26: 1817–1843.

Holland, D. C. 1991. A Synopsis of the Ecology and Status of the Western Pond Turtle *Clemmys marmorata* in 1991. Report to National Ecological Research Center. United States Fish and Wildlife Service, San Simeon, CA.

Iverson, J. B. and E. L. Lewis. 2018. How to measure a turtle. Herpetological Review 49: 453-460.

Kikillus, K. H., Hare, K. M., and S. Hartley. 2012. Online trading tools as a method of estimating propagule pressure via the pet-release pathway. Biological Invasions 14: 2657–2664.

Kraus, F. 2009. Alien Reptiles and Amphibians, a Scientific Compendium and Analysis. Springer, Netherland. 563 pp.

Lambert, M. R., Nielsen, S. N., Wright, A. N., Thomson, R. C., and H. B. Shaffer. 2013. Habitat features determine the basking distribution of introduced red-eared sliders and native western pond turtles. Chelonian Conservation and Biology 12: 192–199.

Litzgus, J. D., Bolton, F., and A. I. Schulte-Hostedde. 2008. Reproductive output depends on body composition in spotted turtles (*Clemmys guttata*), Copeia 2008: 86–92.

Lowe, S., Browne, M., Boudjelas, S., and M. De Poorter. 2000. 100 of the World's Worst Invasive Alien Species. A Selection from the Global Invasive Species Database. The Invasive Species Specialist Group (ISSG) of the Species Survival Commission (SSC) of the World Conservation Union (IUCN), 12 pp.

Pearson, S. H., Avery, H. W., and J. R. Spotila. 2015. Juvenile invasive red-eared slider turtles negatively impact the growth of native turtles: implications for global freshwater turtle populations. Biological Conservation 186: 115–121.

Polo-Cavia, N., Lopez, P., and J. Martin. 2008. Interspecific differences in responses to predation risk may confer competitive advantages to invasive freshwater turtle species. Ethology 114: 115–123.

Polo-Cavia, N., Lopez, P., and J. Martin. 2010. Competitive interactions during basking between native and invasive freshwater turtle species. Biological Invasions 12: 2141–2152.

Polo-Cavia, N., Lopez, P., and J. Martin. 2011. Aggressive interactions during feeding between native and invasive freshwater turtles. Biological Invasions 13: 1387–1396.

Rhodin, A. G. J., Iverson, J. B., Bour, R., Fritz, U., Georges, A., Shaffer, H. B., and P. P. van Dijk. 2017. Turtles of the World. Annotated checklist and atlas of taxonomy, synonymy, distribution, and conservation status (8^{th} Ed.). Chelonian Research Monographs 7: 1–292.

Schulte-Hostedde, A. I., Zinner, B., Millar, J. S., and G. J. Hickling. 2005. Restitution of mass-size residuals: validating body condition indices. Ecology 86: 155–163.

Skelly, D. K. 2002. Experimental venue and estimation of interaction strength. Ecology 83: 2097–2101.

Spinks, P. Q., Pauly, G. B., Crayon, J. J., and H. B. Shaffer. 2003. Survival of the western pond turtle (*Emys marmorata*) in an urban California environment. Biological Conservation 113: 257–267.

Thomson, R. C., Spinks, P. Q., and H. B. Shaffer. 2010. Distribution and abundance of invasive red-eared sliders (*Trachemys scripta elegans*) in California's Sacramento River basin and possible impacts on native western pond turtles (*Emys marmorata*). Chelonian Conservation and Biology 9: 297–302.

Thomson, R. C., Wright, A. N., and H. B. Shaffer. 2016. California Amphibian and Reptile Species of Special Concern. University of California Press, Oakland, CA. 408 pp.

United States Fish & Wildlife Service. 2015. Endangered and threatened wildlife and plants; 90-day findings on 10 petitions. Federal Register 80: 19259–19263.

Winkler, J. D. and J. Van Buskirk. 2012. Influence of experimental venue on phenotype: multiple traits reveal multiple answers. Functional Ecology 26: 513–521.

Figure 1

The UC Davis Arboretum waterway, turtle basking sites, and basking turtles.

The UC Davis Arboretum waterway is in blue and turtle basking sites are displayed as red circles. Inset shows a native western pond turtle (left) and an introduced red-eared slider (right) basking side-by-side in the Arboretum. Map data © 2019 Bing. Photo credit Max Lambert.

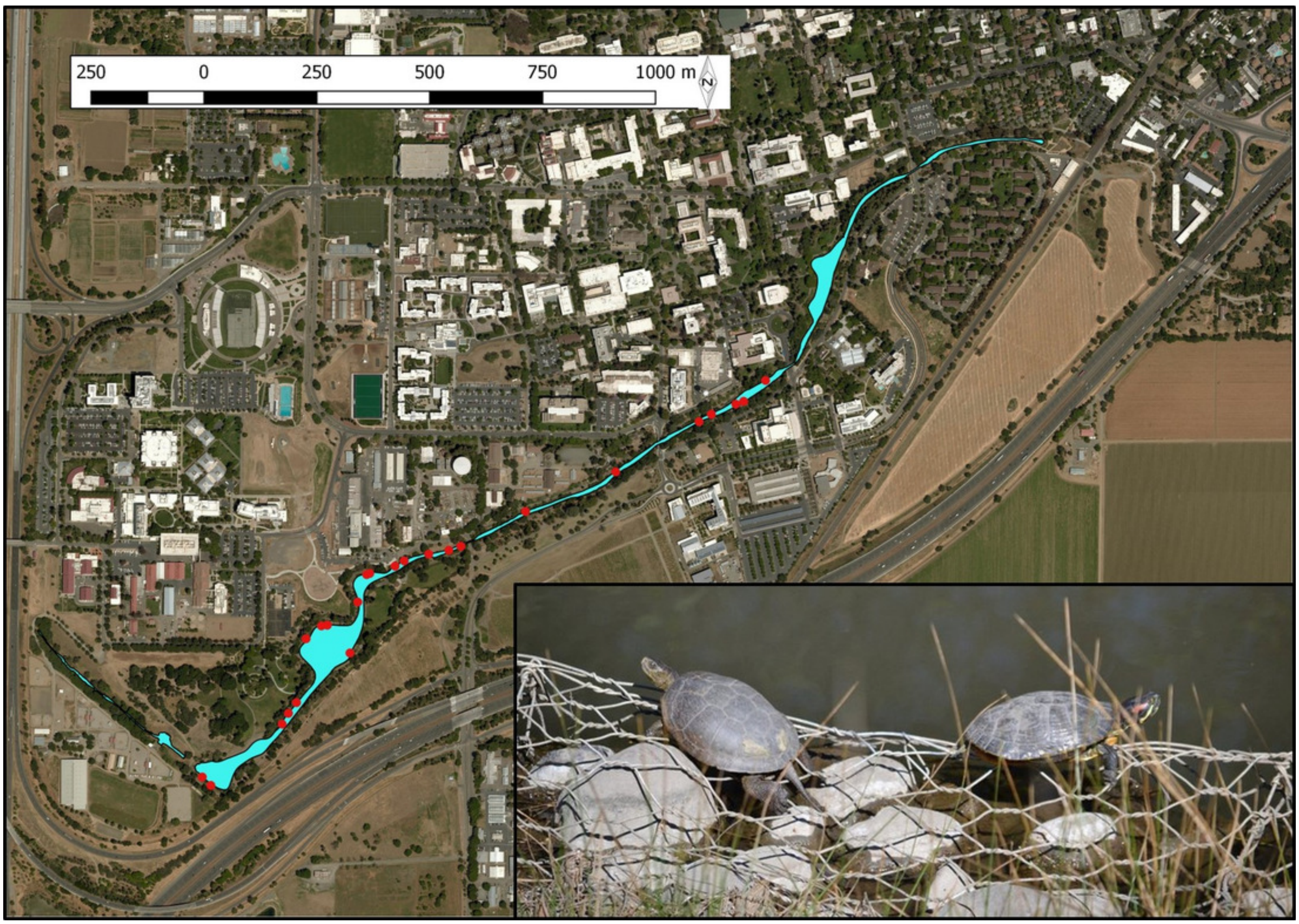

Figure 2

Native western pond turtle (WPT) body condition before and after introduced red-eared slider (RES) removal.

Body condition is shown as the residuals of body mass regressed against plastron length. Individual WPT varied in their body condition response to introduced RES removal (A) but body condition generally improved. On average (B) WPT are 39.80 g heavier after RES removal. Boxplot hinges show the 25th and 75th body condition percentiles, whiskers show the extent of data within 1.5 times the interquartile range, and the center line is the median for each treatment year pre- and post-removal.

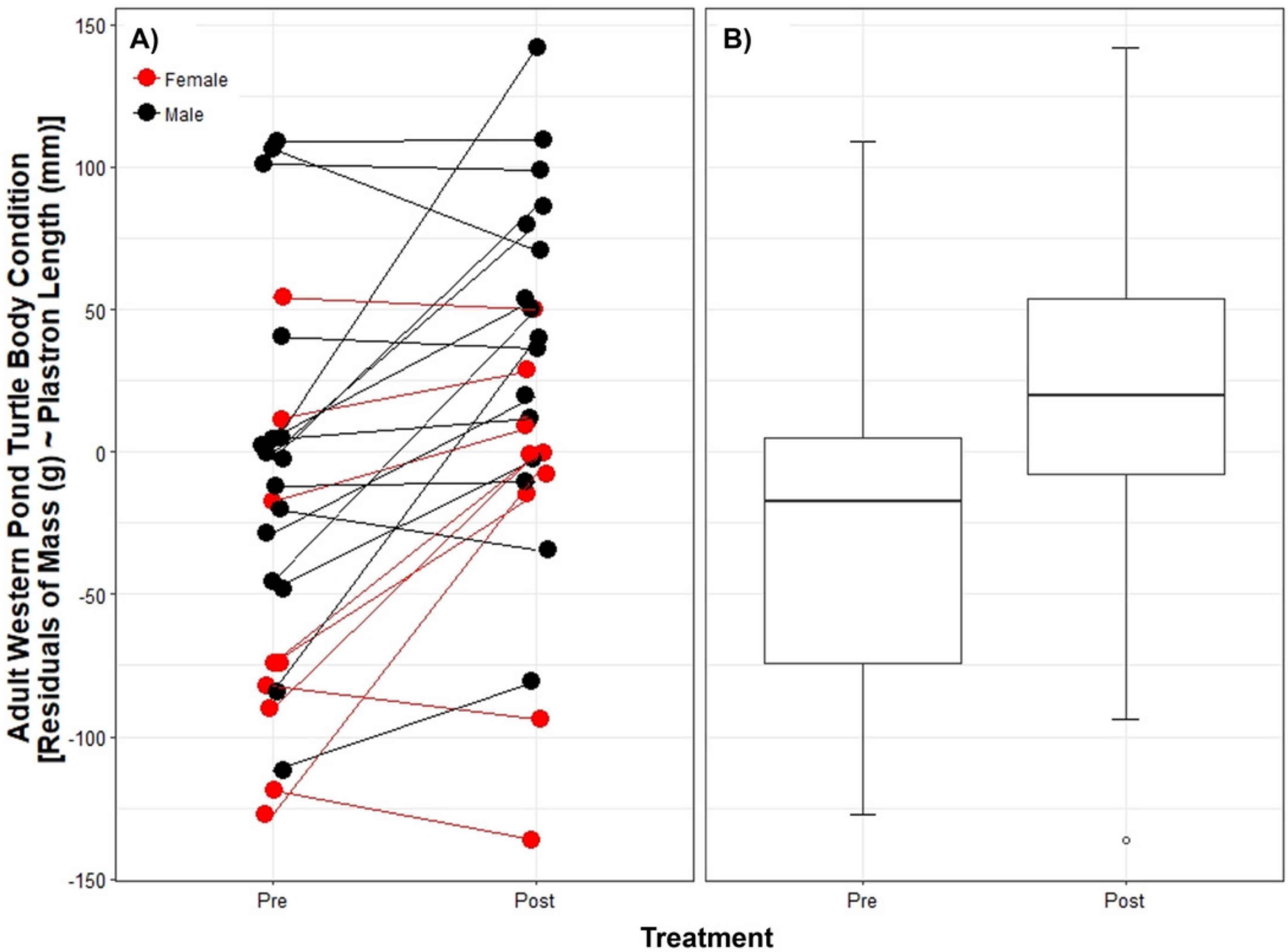
A)
B)
Female
Male
Adult Western Pond Turtle Body Condition
[Residuals of Mass (g) ~ Plastron Length (mm)]
150
100
50
0
-50
-100
-150
Pre
Post
Treatment

Figure 3

Cumulative basking observations of native WPT (Emys) and introduced (RES).

Basking observations before (A) and after (B) the RES removal are arrayed along a west-east gradient in the UCD Arboretum. Letters under the x-axis are basking site identifiers.

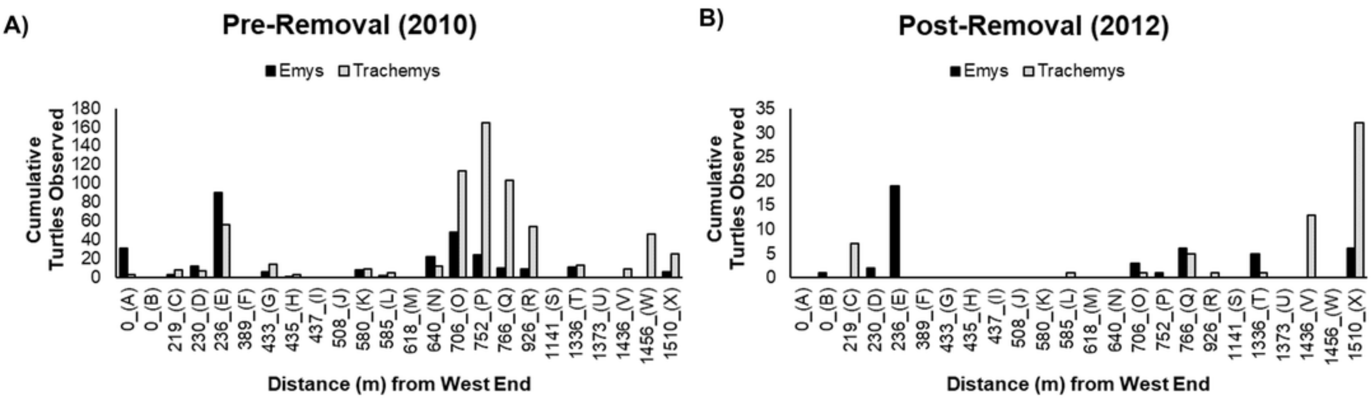

Figure 4

The proportion of native WPT (Emys) to introduced RES (Trachemys) basking across the UCD Arboretum waterway pre- and post-removal.

Curves are modeled proportions of the WPT to RES basking along a west-east gradient in the UCD Arboretum pre- and post-removal (black and red curves, respectively). The proportion of WPT to RES basking along the waterway was similarly WPT-biased in the west and RES-biased in the east in both years. WPT basking observations were higher after the RES removal.

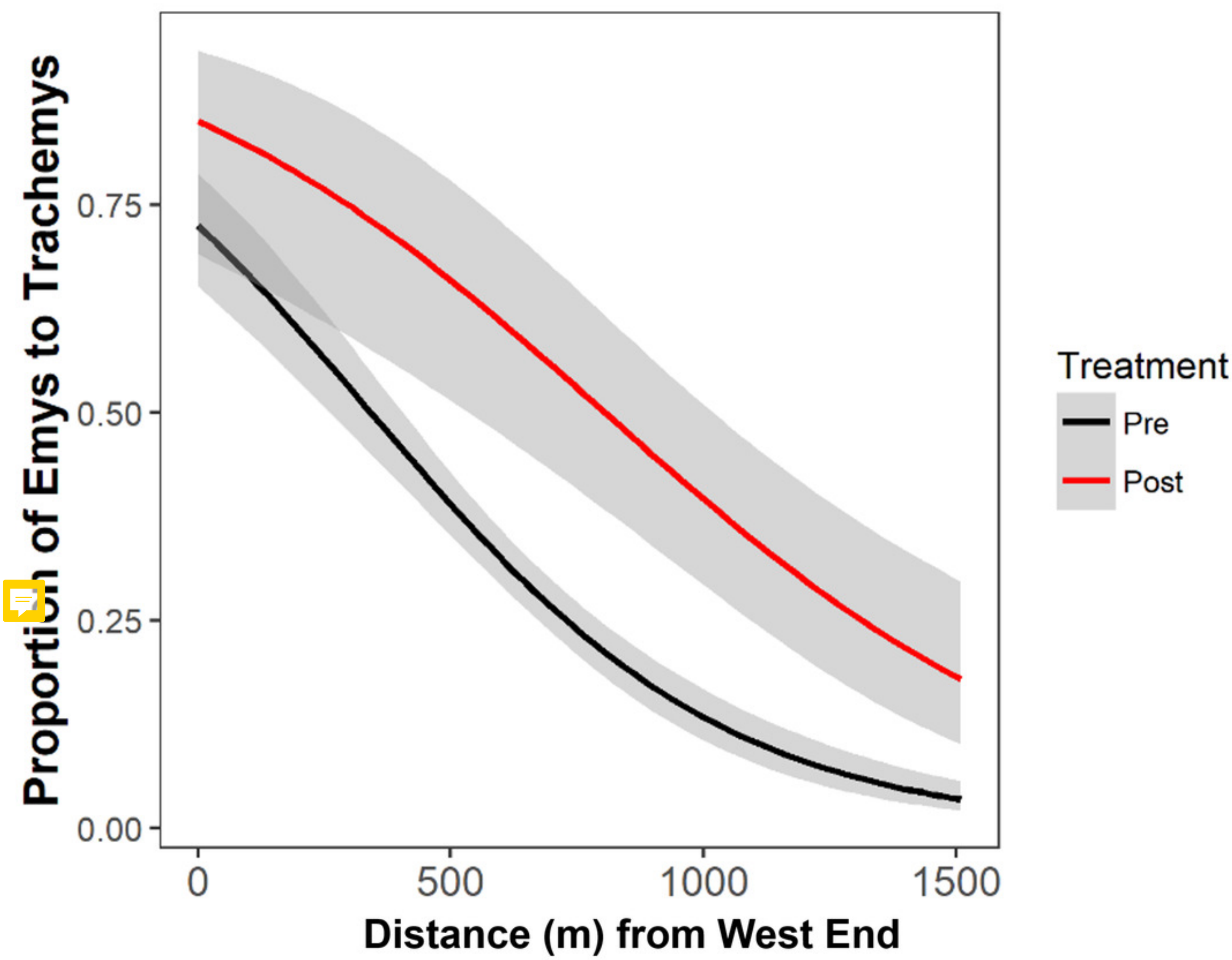

Figure 5

The total number of native WPT (*Emys*) and introduced RES (*Trachemys*) basking along the UCD Arboretum.

Curves are the modeled daily number of WPT and RES along a west-east gradient in the UCD Arboretum pre- and post-removal (black and red curves, respectively). WPT displayed a more even basking distribution after the RES removal and RES concentrated basking activity towards the east end of the Arboretum after most of their population was removed.