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Habitat Features Determine the Basking Distribution of Introduced Red-Eared Sliders and Native Western Pond Turtles

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ABSTRACT. – We quantified basking site usage by native western pond turtles (*Emys* [= *Actinemys*] *marmorata*) and introduced red-eared sliders (*Trachemys scripta elegans*) in an urbanized waterway. A lower frequency of human disturbance, steeper slopes, shallower water adjacent to basking sites, and a concrete substrate were all associated with a higher abundance of native threatened pond turtles relative to introduced sliders. These differences suggest new habitat management practices that could favor native pond turtles in the face of competition from invasive sliders.

Species declines are often driven by the impacts of exotic species (e.g., Wilcove et al. 1998). These introduced species may be a primary cause of decline in the native species or may act synergistically with ecosystem modification (Didham et al. 2005). Given the ubiquity of nonnative species in many landscapes, it is important to understand the effects that an introduced exotic may have on the abundance and distribution of native biota. When lacking such information, we cannot manage for the potential adverse effects of introduced populations (Didham et al. 2005; Shine 2010). Here, we provide field data on key interactions between the red-eared slider, *Trachemys scripta elegans*, the most widely introduced species of reptile on earth (Kraus 2009), and a native species, the western pond turtle, *Emys* (=*Actinemys*) *marmorata*.

Although *T. s. elegans* is a widely introduced species of global significance (e.g., Bury 2008; Ferri and Soccini 2008; Teillac-Deschamps et al. 2008; Kraus 2009), there have been few field studies that document their ecological consequences or habitat use differences between introduced *T. s. elegans* and native turtle populations (Bury 2008; Teillac-Deschamps et al. 2008). Furthermore, what information is available is largely limited to western Europe, where introduced *T. s. elegans* has been shown to outcompete native turtles (Cadi and Joly 2003; Polo-Cavia et al. 2011). A set of basking experiments showed reduced basking activity of Spanish terrapins (*Mauremys leprosa*) when *T. s. elegans* were present (Polo-Cavia et al. 2010). Another basking experiment with introduced red-eared sliders and native European pond turtles (*Emys orbicularis*) demonstrated that *T. s. elegans* again outcompetes the native species for preferred basking places, which causes *E. orbicularis* to shift to lower-quality basking locations (Cadi and Joly 2003). *Emys marmorata* is a close relative of *E. orbicularis* (Spinks and Shaffer 2009) and may be experiencing similar levels of basking site competition as a result of *T. s. elegans* introductions.

Emys marmorata occurs from Washington to Baja California (Ernst and Lovich 2009) and is declining in many parts of its range (Bury and Germano 2008; Ernst and Lovich 2009). It now is listed as endangered in Washington (Hays et al. 1999), sensitive in Oregon (Gray 1995), and a species of special concern in California (Jennings and Hayes 1994). *Emys marmorata* lives in a variety of habitats, from ponds to rivers (Reese and Welsh 1998), and can survive in highly altered habitat (Spinks et al. 2003; Germano 2010). Despite being a habitat generalist, *E. marmorata* numbers have declined precipitously in certain areas, mainly due to human activities (Hays et al. 1999; Bury and Germano 2008).

Native to the eastern United States, *T. s. elegans* is the most widely introduced reptile on earth, primarily as a result of the release of pet trade turtles (Kraus 2009). It is on the International Union for the Conservation of Nature Invasive Species Specialist Group's ''100 of the World's Worst Invasive Alien Species'' list (Global Invasive Species Database 2010). In California's Sacramento Valley, introduced *T. s. elegans* co-occur with *E. marmorata* in many areas, including modified and urban systems (Spinks et al. 2003; Patterson 2006). Generally, urbanized aquatic habitat tends to have reduced riparian vegetation, increased siltation, and a reduction in basking sites that are used by both species (Spinks et al. 2003). Aside from degraded habitat, turtles in urban areas can face higher risks of mortality due to increased encounters with humans, vehicles, and pets (Mitchell 1988; Garber and Burger 1995).

Because basking sites may be less common in an urbanized habitat, optimal basking sites may be a limiting resource and thus an important axis of competition among co-occurring turtle species in urbanized ecosystems. Alternatively, native and introduced species may favor different characteristics in basking sites, potentially reducing interspecific competition and allowing for coexistence. Given that the largest populations of introduced *T. s. elegans* are in or near relatively urbanized areas in California (Bury 2008; Thomson et al. 2010), this study examines the differences in basking site use between *E. marmorata* and *T. s. elegans* in an urbanized habitat. We conducted this research in the University of California (UC) Davis Arboretum waterway (hereafter Arboretum waterway). This waterway is typical of urbanized aquatic landscapes: it is highly modified for its primary purpose as a public exhibit and recreational space and experiences heavy traffic from people and their pets but also supports relatively large numbers of turtles. The majority of the turtle population in the Arboretum waterway consists of *E. marmorata* and the nonnative red-eared slider, *T. s. elegans.*

Whereas competition for basking sites is only one component of resource partitioning between these 2 species, it may provide more general insights into their ability to successfully exist in urbanized, human-dominated landscapes. *Emys marmorata* is typically considered easily alarmed and will readily abandon basking sites when approached by people (Bury and Germano 2008). Based on this cautious behavior generally and our own casual observations, we hypothesized that basking *E. marmorata* would generally avoid human activity more than *T. s. elegans* and, therefore, tend to be concentrated at those basking sites that experienced reduced exposure to people. If this is the case, then it follows that native *E. marmorata* may be excluded from prime basking sites through a combination of human activity patterns and competition with introduced *T. s. elegans*. To test this hypothesis, we measured several characteristics that describe both the levels of concealment as well as the level of human disturbance at each commonly used basking site in the Arboretum waterway, and we used generalized linear models to determine which of those characteristics best explains basking behavior. Our goal was to observe turtles under as wide a range of conditions as possible to maximize our ability to estimate the importance of each predictor variable. Ultimately, if certain basking-site characteristics tend to favor one turtle species over another, then modifying urban environments could lead to an increase in one species at the expense of the other.

METHODS

Study Site. — Our study took place at the Arboretum waterway, which runs along the southern border of the UC Davis campus in Yolo County, California. The waterway is formed by the historical north fork channel of Putah Creek, which was diverted into the current south fork in the early 1870s (Larkey 1980). The waterway is approximately 2.4 km in length, has an average width of 15 m, an average depth of 1 m, and a total surface area of roughly 4 ha (Spinks et al. 2003). The waterway is surrounded by extensively landscaped terrestrial habitat that comprise the UC Davis Arboretum, which varies between 10 and 30 m in width. The vegetation along the waterway is intensively irrigated in most areas, largely nonnative, and is primarily used for educational and recreational purposes. There is a 1.5- to 2.5-m-wide paved walking path that encircles the waterway and is generally within 5–10 m of its edge. The path is heavily used by joggers, walkers, bicyclists, and maintenance vehicles (Spinks et al. 2003). Within 1–2 m of the waterway, the shoreline is a combination of sloping concrete, exposed dirt, and exposed steel mesh.

Estimates of turtle population sizes based on repeated mark–recapture–release studies conducted by the 2009 UC Davis Field Herpetology course indicated nearly equal population sizes of *E. marmorata* ($n = 54$, 95% CI, 47–65) and *T. s. elegans* ($n = 50$, 95% CI, 41–65). The population estimate for *E. marmorata* is similar to that of Spinks et al. (2003), which reported a population size of 53 (95% CI, 48–66), which indicates a stable population size for this species, although these numbers remain lower than those reported from work conducted in the Arboretum waterway from 1991 to 1993 (Spinks et al. 2003). Spinks et al. (2003) did not provide a population estimate for *T. s. elegans* but reported that at least 125 individuals were removed from the Arboretum between 1994 and 2001.

Study Design. — We identified 24 basking sites that consisted of 1–2 m stretches of bank that were consistently used by turtles during a 2009 survey. The minimum distance that separated basking sites was 3 m. Although some of the environmental variables that we measured are similar among nearby locations (e.g., human disturbance), other variables (e.g., visibility) can vary greatly over 1 m or less. Given this, we consider basking sites to be statistically and biologically independent. The

position of each site was measured as a straight line distance from the west end of the Arboretum waterway. We observed turtles from these sites for a total of 94 d between November 2009 and May 2010. We conducted our surveys on days that could potentially show a wide range of turtle basking habits but focused most of our surveys during late winter and spring. We added one of the basking sites to the study in January 2010 and added 2 additional sites in March 2010. We conducted turtle surveys opportunistically between 1000 and 1500 hrs, to coincide with the period of greatest basking activity during the winter and spring. All basking sites were surveyed once per day in rapid succession to avoid observing the same turtle at more than one basking site. The range of sites surveyed represents the full range of available basking habitats between the far west end and 1510 m east. During each survey, the numbers of *E. marmorata* and *T. s. elegans* at each site were counted by using ×8 binoculars. Nine other turtle species have previously been documented in the Arboretum at low abundance (Spinks et al. 2003) and we occasionally observed a few introduced cooters (*Pseudemys* spp.) basking in one of our sites. Because these taxa were rarely seen basking with our 2 focal species, they were excluded from our analyses.

Basking Site Characteristics. — We chose variables that we suspected were important in explaining basking and habitat use by focusing particularly on factors that quantify the exposure of basking sites to human disturbance. In addition to water and air temperature, we measured 9 basking-site characteristics: water depth, distance to the opposite bank, distance to the path, slope at the water's edge, the midslope between the basking site and the path, substrate, degree of shading, visibility of basking sites from the path, and frequency of human disturbance. We measured water and air temperatures when turtle surveys were conducted. Surface water temperature (approximately 10 cm deep) was measured at a single central location, whereas air temperature was recorded as the highest value for that day at the Russell Ranch Weather Station approximately 1.3 km from the study site. We did not measure temperatures at each basking site because this would have caused turtles to abandon basking activity. Water depth was measured 33 cm from the water's edge. In the case of steel mesh substrate, the water's edge was defined by the edge of the mesh rather than the edge of the bank; the two may be up to a meter apart, but the mesh always defines the basking area–water interface. The distance to the opposing bank was measured by using Google Maps (www.google.com/maps). With a tape measure, we measured the distance to the path along a perpendicular line from the water's edge at the center of each basking site. We used a clinometer to measure the slope at the water's edge where turtles bask and at midslope, defined as a point halfway between the water's edge and the path. Shading was measured for each basking site on each observation day as shaded, partially shaded, or unshaded.

To determine how protected basking sites were from view, we developed an index to quantify the amount of cover at each site. We created a ''visualization board'' by painting a grid of 300 4-cm-diameter dots on a 33 × 200-cm board. With the board positioned parallel to the water's edge, we computed a visibility score as the number of dots visible when viewed from the path on the same side of the water at a standardized height of 1.3 m (roughly the height of an average person's field of view). The visibility score is primarily a function of vegetation cover but is also influenced by slope and distance to the path. Visibility was measured from 3 vantage points (directly facing the site and at 45° angles to either side) during fall, winter, and spring, and averaged to yield a mean annual visibility.

The frequency of human disturbance (hereafter disturbance) was quantified at each basking site on 4 different days during spring 2010. We chose the UC Davis Picnic Day, an annual public festival characterized by tens of thousands of visitors to the UC Davis campus, to capture an atypically high level of human-associated disturbance, one day during the university's spring recess as an unusually low level of disturbance and 2 more typical days during the academic year. We considered a disturbance event to be any time a person or a group of people passed on the path on the same side as the basking site. We counted the number of disturbance events that occurred in a 10-min period and defined disturbance as the average number of events per hour for each basking site.

Statistical Analyses. — Our general approach was to model turtle counts as a function of the different predictors by using generalized linear models and generalized linear mixed models. With these approaches, we asked 2 questions: 1) which factors determine the relative abundance of *E. marmorata* at a basking site, and 2) which factors determine the overall abundance of each species at a basking site?

Relative Abundance of E. marmorata. — To test which factors predict the relative abundance of *E. marmorata* at a basking site we defined relative abundance as:

$$\frac{N_{E.\ marmorata}}{N_{E.\ marmorata} + N_{T.\ s.\ elegans}}$$

We used a generalized linear model with a logit link function and quasi-binomial distribution because the response varied from 0 to 1 (Venables and Ripley 2002). We limited our analysis to the 41 d when all 24 sites were observed from March to May 2010. This approach allowed us to use the most informative data from the greatest number of sites, because little basking activity occurred between November and February (Fig. 1). During this period, we recorded 5 sites that had turtles basking at most 1 d, so these sites were excluded from the analysis (data from 19 sites were used). The following 9 basking site predictors were used in the model: disturbance, midslope, slope at water, water depth,

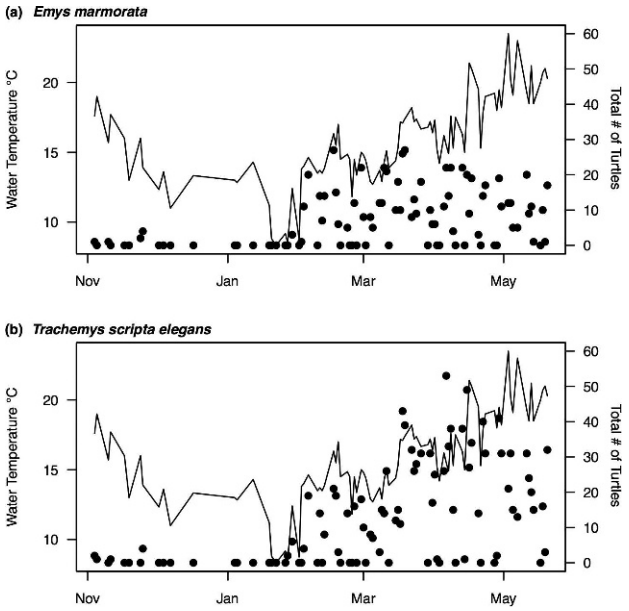

Figure 1. Total number of turtles observed each day for (a) native *Emys marmorata* and (b) introduced *Trachemys scripta elegans*. The black lines show water temperatures.

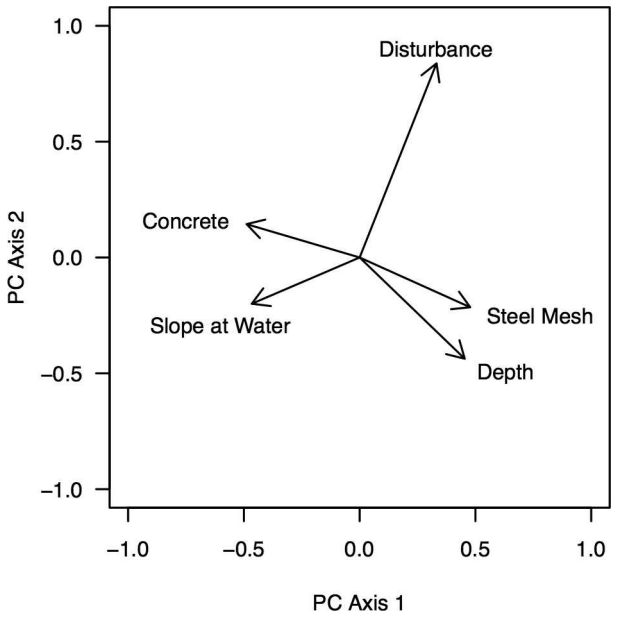

Figure 2. Principal components (PC) analysis on 4 collinear basking site variables: slope at water's edge, frequency of human disturbance, water depth, and substrate (split into concrete and steel mesh). Vectors represent loadings of each variable on the first 2 PC axes. PC axis 1 accounts for 79% of the variation among the variables.

substrate, visibility, degree of shading, distance to the path, and distance across water. Visibility was log transformed; no other transformations were necessary. The degree of shading was averaged across the 41 d for each site. Thus, each site had a single value for the 9 variables and a single value for relative abundance of *E. marmorata* (relative abundance averaged across days).

Several of these variables were strongly collinear. A principal components (PC) analysis on the slope at water, disturbance, depth, and substrate found that the first PC axis explained 79% of the variation, with the loadings on PC 1 as follows: slope at water −0.466, disturbance 0.332, depth 0.454, concrete −0.488, substrate 0.478 (Fig. 2). Substrate was analyzed as 2 separate binary variables for concrete and steel mesh, with dirt excluded because only a single site had this relatively rare substrate type. The collinear variables were then replaced with a single PC score from the first axis in the analysis, because the other PC axes accounted for very little variation among the variables.

Absolute Abundance. — To determine which factors predict the total abundance of each species at a basking site, we used a generalized linear mixed model with a log link function and Poisson distribution because the responses in this case are count data (Venables and Ripley 2002). The same predictor variables were used as in the previous analysis, plus water and air temperature. Date and basking site were treated as random effects to account for repeated measurements of basking sites over time. To account for overdispersion, an observation-level random effect was also included (Maindonald and Braun 2010). All 94 d of turtle observations as well as all sites, including those added later in the study, were used in this analysis.

RESULTS

The minimum number of observation days for a given month was 4 (in December) and the maximum was 22 (in April). The maximum number of turtles observed at a single basking site in a single day was 29 and the average number of turtles observed at a site in a single day was 0.92 (± 0.06 SE). The maximum number of *E. marmorata* observed at a single basking site in a single day was 14, with an average of 0.34 (± 0.03 SE). For *T. s. elegans*, the maximum number of turtles observed in a single day was 18 with an average number of 0.58 (± 0.04 SE). Turtle activity showed a strong seasonal pattern (Fig. 1), with few individuals of either species observed basking during the fall and early winter (November through January). Basking-site use started increasing in February, remained high for the duration of the study, and was qualitatively similar for both species.

The relative abundance of *E. marmorata* at a basking site was strongly predicted by the first PC axis ($F_{1,12} = 12.36$, $p = 0.004$). *Emys marmorata* made up a greater proportion of turtles at basking sites that had steeper midslopes, steeper slopes at the water's edge, shallower water depths near the edge, less disturbance, and concrete substrates. No other factors were significant in the model.

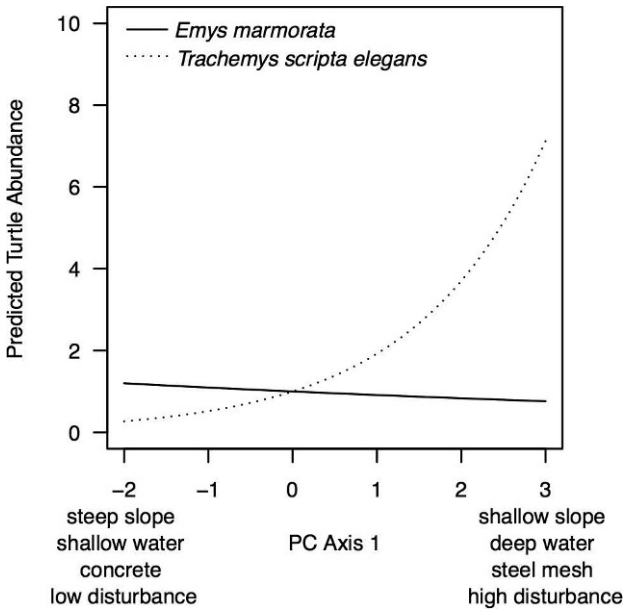

Figure 3. Model fit of predicted turtle abundance by principal components axis 1 for native *Emys marmorata* and introduced *Trachemys scripta elegans*. The predicted values are from the model fit with all other predictors held constant.

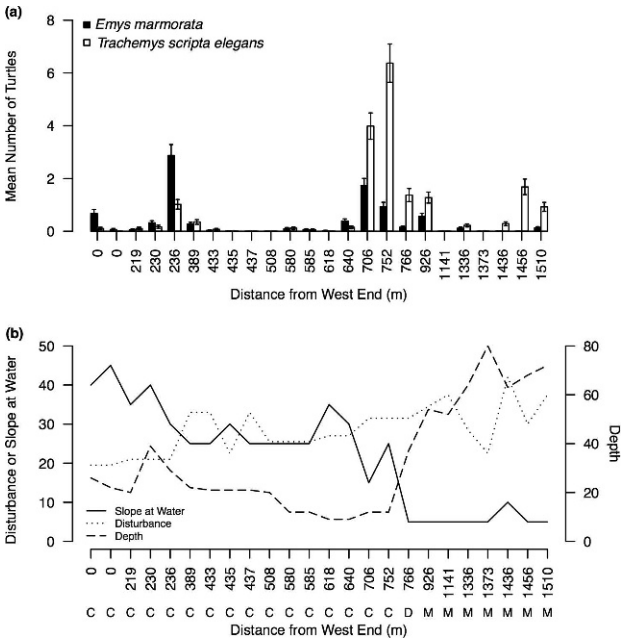

Figure 4. Average turtle abundance (a) and collinear basking site characteristics (b) by distance from the western end of the study site. Note that the *x*-axes are not to scale. Each tick mark represents a different basking site. Average turtle abundance is the average number of each species observed per day at each basking site over the entire course of the study; error bars are standard errors. Letters in (b) indicate substrate type: C = concrete, D = dirt, and M = steel mesh. Units for (b) are as follows: disturbance in number of events per hour (see ″Methods″), slope at water in degrees, depth in cm.

In likelihood ratio tests, both turtle species were more abundant at basking sites when water temperatures were warm and the area was less shaded (water temperature and degree of shading, both $p < 0.001$) and at sites that were farther from the path ($p < 0.001$). No other factors were important for determining the abundance of *E. marmorata*, but the overall abundance of *T. s. elegans* was higher at sites with shallower slopes at the water's edge, deeper water depths near the edge, more disturbance, and steel mesh substrates (Fig. 3) (likelihood ratio tests, all $p < 0.005$). The average abundance of each turtle species varied spatially in a west–east gradient, as did the slope at the water's edge, depth, and disturbance (Fig. 4). *Emys marmorata* and *T. s. elegans* primarily basked in the western and eastern ends of the waterway, respectively. From the west (relatively native occupied) to the east (relatively nonnative) side of the waterway, the slope at water edge decreases dramatically, and both water depth and the level of human disturbance increase (Fig. 4).

DISCUSSION

Analysis of our data indicates that *E. marmorata* habitat use is relatively constant across most of the factors that we measured (Fig. 3), but habitat use by introduced *T. s. elegans* is much more selective. All 4 of the collinear variables (slope, depth, substrate, and disturbance) varied in a west–east gradient and were closely matched by shifts in average *T. s. elegans* abundance (Fig. 4). Although we cannot determine if turtles are directly responding to all or only some of these variables, the result that higher levels of human disturbance predict a greater abundance of introduced *T. s. elegans* at basking sites is of particular interest.

There are several possible explanations for the patterns in basking-site use observed here. First, *T. s. elegans* may be relatively more abundant in areas with greater human disturbance because they respond less negatively to anthropogenic activity than *E. marmorata*. Greater tolerance for disturbance by introduced relative to indigenous species (*sensu* Byers 2002) is a pattern often seen among successful invasive species and is plausible for *T. s. elegans* given that it is widespread in the pet industry (Kraus 2009). In the Arboretum, *T. s. elegans* may preferentially occupy highly disturbed basking sites because they flee from those sites less frequently than *E. marmorata*. Alternatively, it may be that both species prefer low disturbance conditions and do not differ in their tolerance of human activities. Under this hypothesis, the greater relative abundance of *E. marmorata* at low-disturbance sites suggests that they may be excluding *T. s. elegans* from those preferred, less-disturbed sites. We find this scenario unlikely given the greater flight distance (Shaffer et al., unpubl. data) of *E. marmorata* and because *T. s. elegans* has been shown to be competitively dominant to European turtle species (Cadi and Joly 2003; Polo-Cavia et al. 2008, 2011). Second, *T. s. elegans* may avoid potential costs, such as the interruption of basking, of unnecessary repeated escape responses to water, when the numbers of predators are reduced in modified environments (Polo-Cavia et al. 2008). In urban

habitats, such behavioral changes may give *T. s. elegans* a greater competitive advantage. Finally, each species may differ in innate preferences for structural basking-site characteristics (e.g., substrate, slope, or depth) and the distribution of both species may be determined by the availability of these different suites of physical characteristics. We could not assess structural habitat preferences for each species in the absence of the other and, therefore, cannot distinguish the degree to which structural habitat preferences vs. tolerance of human disturbance is driving the observed patterns. Differentiating among these 3 hypotheses (which are not mutually exclusive) is an important next step to inform restoration projects seeking to enhance habitat for native turtles.

Although visibility did not have a direct, measurable effect on the total abundance of either species in our study, lower visibility was correlated with increased distance to the path. A greater distance from the path was a strong predictor of abundance for both species, and decreased visibility may be a key component of distance's overall role in basking-site selection. Visibility may also be an underlying element of midslope, another significant predictor of relative turtle abundance. A metric that captures visibility of people from the perspective of a basking turtle, as opposed to our metric taken from a human's perspective on the path, would be much more difficult to measure but may better capture this effect. Variations in slope and substrate may also reflect behavioral differences associated with antipredator responses. For example, if *E. marmorata* is more cautious and thus more likely to abandon basking sites relative to *T. s. elegans* (and our unpublished observations suggest that this is the case for human approach distance), then steeper slopes and a concrete substrate may be chosen because they facilitate more rapid, frequent escapes.

It is important to recognize that basking-site use is only one of the many potential arenas for interactions between *E. marmorata* and introduced *T. s. elegans*. If basking sites are limited, as they appear to be in many urbanized waterways, they could be a key resource for which turtles compete, given the critical need for thermoregulation by these ectotherms. However, our results are observational, and experimental manipulations of turtle densities and basking-site characteristics are necessary before causal interpretations of species interactions can be made with confidence. Further, research on other axes of their biology (e.g., diet, chemosensory responses, heat exchange rates, or use of underwater refugia) is important to better understand interactions between *T. s. elegans* and native *E. marmorata*.

Conservation and Management. — Our data indicate that native *E. marmorata* and introduced *T. s. elegans* are using basking habitat differently in this urbanized habitat. Our results suggest that providing basking sites that are in some way protected from human activities may provide increased basking opportunities for native turtles. Such management efforts could include providing basking sites (e.g., natural logs/snags or artificial platforms) in the center of the largest pools, increasing the terrestrial or aquatic vegetated area around the waterway, and erecting barriers that act as visual screens for turtles. Environmental manipulations may minimize competition among species by increasing availability of basking sites. This is the case even for basking sites that are exploited mainly by introduced turtles, because such sites may encourage sliders away from areas preferred by native pond turtles.

We acknowledge that our data are observational and do not indicate whether the presence of *T. s. elegans* is directly responsible for the differences in basking distribution reported here. However, to our knowledge, our study is the first to provide solid field evidence that there are important differences in basking behavior between exotic sliders and native turtles. Although exotic *T. s. elegans* may have no effect on the native population, our field data, along with experimental results (e.g., Cadi and Joly 2003; Polo-Cavia et al. 2010, 2011), support the contention that *T. s. elegans* have negative impacts on native turtles. Even though turtles in general lack the typical ''weedy'' life-history attributes that often characterize successful invaders, including rapid maturation, high reproductive rates, and high dispersal capability (Sakai et al. 2001), *T. s. elegans* exhibits larger body sizes, a broader diet, and earlier sexual maturity than most other turtles (Gibbons 1990). These features, combined with artificially high levels of recruitment and dispersal as people release pet turtles, presumably contribute to their success as an invasive species.

Our data, complemented by these life-history traits and experimental work from Europe, indicate that curtailing the spread of *T. s. elegans* would undoubtedly be beneficial to native turtle populations. In 2010, the California Game and Fish Commission took a step in this direction when they considered but did not fully enact a policy to stop the importation and sale of nonnative frogs and turtles for food (http://www.fgc.ca.gov/public/reports/nonnativefrogsandturtlesstaffrecommendation091610.pdf). Analysis of our data indicates that curtailing the importation of red-eared sliders (and their inevitable subsequent release) would benefit native turtles. In addition, the experimental removal of exotic *T. s. elegans* from populations where they coexist with native turtles, like the Arboretum waterway, is a logical next step to determine their impact on native populations.

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