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Research Article

Non-native pond sliders cause long-term decline of native Sonora mud turtles: a 33-year before-after study in an undisturbed natural environment

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Abstract

Using a before-after study design in a stable, largely undisturbed pond habitat and a dataset spanning 33 years, we document and describe the decline of native Sonora mud turtles (*Kinosternon sonoriense*) after the introduction of non-native pond sliders (*Trachemys scripta*). The Sonora mud turtle population in Montezuma Well in central Arizona, USA, declined to less than 25% of previous numbers, from 372 ± 64 in 1983 to 80 ± 21 in 2011. We trapped and removed the non-native turtles between 2007 and 2013 and after removal of the non-natives, the Sonora mud turtle population increased to 139 ± 34 in 2015. The native turtles also significantly increased basking activity after removal of the non-natives, paralleling results of small-scale mesocosm studies showing that pond sliders negatively affect basking rates of native turtle species. Reproductive rates of female Sonora mud turtles (numbers of females with eggs) were lower during the period of peak non-native turtle abundance, and increased after removal of the non-native turtles. We hypothesize that the reduction in effective reproductive rate links interference competition (reflected in reduced basking rates) to the long-term decline of the native mud turtles. Results from the undisturbed natural system of Montezuma Well provide new insights on the overall occurrence, magnitude, and mechanisms of negative effects of introduced pond sliders on native turtle species. Sonora mud turtles are very different in their morphology, behavior, and ecology from pond sliders and from native turtles in other studies, suggesting that impacts of non-native pond sliders are more pervasive than previously thought.

Key words: impacts, interference competition, *Kinosternon sonoriense*, long-term studies, non-native reptiles, Red-eared Slider, *Trachemys scripta*

Introduction

Clearly identifying and quantifying negative effects remains difficult for many introduced, non-native species in natural systems that are almost invariably altered and affected by other changes and stressors. Extensive human-caused habitat degradation and loss, altered food webs, pollution, and direct and indirect human-caused losses to natural populations are now the rule rather than the exception in most ecosystems. Hence, unambiguously attributing negative effects to non-native species and quantifying "impacts" is often problematic (e.g., Carlton 2002; Gurevitch and Padilla 2004; Gherardi 2007a; Jeschke et al. 2014). Simple correlation of higher numbers of non-native species and lower numbers of native species provides only weak inference, as a non-native species may be the "passenger" rather than the "driver" of ecosystem change—taking advantage of and prospering due to the same habitat alterations that are causing the decline of a native population (Didham et al. 2005; MacDougall and Turkington 2005). Freshwater ecosystems, particularly in more developed areas of the world, are among the most extensively disturbed, modified, and degraded natural systems in the world (National Research Council 1992; Dudgeon et al. 2006; Gozlan et al. 2019; Reid et al. 2019). Analyses for North America, for example, estimate a recent and mean future extinction rate for freshwater fauna five times greater than that for terrestrial fauna (Ricciardi and Rasmussen 1998). Given the burgeoning increases of non-native species introductions in nearly all natural systems, robust assessment of negative effects of invasive species on native populations and communities is increasingly important, but also more difficult (Gherardi 2007b). Such assessments, clearly differentiating among different potential stressors and quantifying impacts, are critical for making management decisions and allocating limited resources for protection and restoration of natural systems (Parker et al. 1999).

The nature and extent of impacts from non-native reptiles on native communities are generally poorly known compared to invasive plants, invertebrates, mammals, and other taxa (Lever 2003; Kraus 2009), but there are a few high-profile examples of non-native reptile predators having severe negative effects on native populations, including the brown tree snake (*Boiga irregularis* (Merrem *in* Bechstein, 1802)) on the island of Guam (Savidge 1987; Rodda et al. 1997; Mortensen et al. 2008), and Burmese pythons (*Python bivittatus* (Kuhl, 1820)) in Florida, USA (Dove et al. 2011; Dorcas et al. 2012; Hoyer et al. 2017). The pond slider (*Trachemys scripta* (Thunberg *in* Schoepff, 1792)) is one turtle species that has received substantial attention as a non-native invader. Several million pond sliders per year are exported from the species' native range in eastern North America to all parts of the world, primarily for the pet trade (Ficetola et al. 2012; Mali et al. 2014; García-Díaz et al. 2015). Through intentional release or escape, wild individuals and populations of non-native pond sliders have been documented in at least 90 countries, on all continents except Antarctica, in 34 USA states outside of the species' native range, and on at least 48 offshore islands (compilations from Lever 2003; Kraus 2009; Ficetola et al. 2012; Global Invasive Species Database 2020). Introduced pond sliders are particularly widespread and common in parts of Europe, eastern Asia, and western North America and may reach unusually high numbers. In Japan, non-native pond sliders comprised over 60% of turtle numbers in surveys of 800 ponds (Ramsay et al. 2007), and pond slider numbers and biomass at some sites were five times greater than in the slider's native range (Taniguchi et al. 2017). In observations at Bukit Timah Nature Preserve, MacRitchie Reservoir, and other freshwater ponds in urban and suburban areas throughout Singapore, most or all of the turtles seen were pond sliders (SDG, *unpublished data*, 2015).

Particularly where they occur in high numbers, introduced pond sliders have the potential to adversely affect a variety of native animal species and communities (Ficetola et al. 2012; Cuthbert et al. 2019), but our focus here is on impacts on native turtle species. Particular concern has been expressed for related species in the families Emydidae and Geoemydidae, including the European pond turtle (*Emys orbicularis* (Linnaeus, 1758)) and Mediterranean pond turtle (also known as Spanish terrapin, *Mauremys leprosa* (Schweigger, 1812)) in several countries in Europe (e.g., Cadi and Joly 2004; Ficetola et al. 2012; Polo-Cavia et al. 2014); the Japanese pond turtle (*Mauremys japonica* (Temminck and Schlegel, 1838)) in Japan (Taniguchi et al. 2015); and the western pond turtle (*Actinemys marmorata* (Baird and Girard, 1852)) in western North America (Spinks et al. 2003; Thomson et al. 2010). Research on potential negative effects of pond sliders has focused on competition for basking sites with native turtle species (Cadi and Joly 2003; Macchi et al. 2008; Polo-Cavia et al. 2010; Thomson et al. 2010). Other studies have investigated relative foraging success and competition for food (Cadi and Joly 2004; Polo-Cavia et al. 2011; Pearson et al. 2015), and changes in survival rates of native turtles in the presence of pond sliders (Cadi and Joly 2004). Where pond sliders have been introduced into areas with congeneric turtle species, hybridization with local species may occur (e.g., Powell et al. 2000; McCranie 2018) and has been documented for species on Caribbean islands (Parham et al. 2013) and in the Rio Grande drainage of the southwestern United States (with the native Big Bend Slider, *T. gaigeae* (Hartweg, 1939); Lovich et al. 2016; Parham et al. 2020). Such hybridization results in the loss of genetic integrity in relatively rare local species. Introduced pond sliders may also bring in novel parasites and pathogens (e.g., Spinks et al. 2003; Soccini and Ferri 2004; Oi et al. 2012; Silbernagel et al. 2013; Meyer et al. 2015), and non-native blood flukes (*Spirorchis elegans* Stunkard, 1923) hosted by pond sliders have been documented causing severe pathology and mortality in European pond turtles at a natural wetland site in northwestern Spain (Iglesias et al. 2015).

There is clearly the potential for introduced pond sliders to have negative effects on native freshwater turtle populations, and many published reports include seemingly definitive statements on such impacts, e.g.: "*T. s. elegans*...is silently replacing the few remnant populations of the European pond turtle, *E. orbicularis*" (Scalera 2007a); "In the Iberian Peninsula, this American turtle is competing and displacing the Iberian turtles, *Emys orbicularis* and *Mauremys leprosa*" (Polo-Cavia et al. 2014);

and "…the negative impact of pond sliders is out of question for native European turtle species…" (Standfuss et al. 2016). Database compilations of non-native species echo these ideas: "…Sliders compete with indigenous species for food and basking sites" (Somma et al. 2020, repeated in Global Invasive Species Database 2020). Such beliefs are presumably part of the reason that pond sliders were included on the International Union for Conservation of Nature list of "100 of the world's worst invasive alien species" (Lowe et al. 2004). In spite of such assertions, there is little rigorous data on population-level effects of non-native pond sliders on native turtle species in natural habitats. For the European pond turtle, for example, Kraus (2009, p. 72) notes "Impacts on wild populations of *E. orbicularis* have not been demonstrated but may be feasible…". Most field studies (e.g., Arvy and Servan 1998; Spinks et al. 2003; Kamezaki 2015) provide only weak correlational evidence, such as low numbers of natives in association with introduced pond sliders (cf. Kraus 2009), and speculation about potential mechanisms of negative effects. The studies investigating competition for basking sites between pond sliders and native turtle species (e.g., Cadi and Joly 2003; Macchi et al. 2008; Polo-Cavia et al. 2010) have nearly all been small scale experiments under artificial conditions, and it is not clear how such studies relate to large, complex environments in nature (cf. Lambert et al. 2019). The only experimental field study to date of potential basking competition yielded equivocal results: removing pond sliders from a site in central California, USA, did not result in predicted changes in basking behavior of native western pond turtles, but was associated with an increase in body condition (mass relative to linear measurement) of the native species (Lambert et al. 2019).

Pond sliders are not native to Arizona, USA, but have been introduced in several areas of the state, including our protected study area at Montezuma Well in central Arizona. The only native turtle at Montezuma Well is the Sonora mud turtle (*Kinosternon sonoriense* Le Conte, 1854), and preliminary studies (Malone 1999) suggested a substantial decline in native turtle numbers after pond sliders were introduced. From 2007–2015, we trapped and removed all non-native turtles at Montezuma Well, with the last non-natives trapped in 2013. Throughout this period, we recorded mark-recapture data on Sonora mud turtles to analyze changes in their population size in relation to non-native turtle removal, and we recorded behavioral and ecological data to assess species interactions. Trapping during 2015, after the last non-native turtles were removed, was undertaken to determine if the Sonora mud turtle population showed signs of recovery, and to evaluate existing hypotheses of negative effects of introduced pond sliders on native turtle species. We specifically tested the hypothesis that presence of the large pond sliders negatively affected basking of the Sonora mud turtles. We also assessed potential effects of the non-native turtles on reproduction in the Sonora mud turtles in Montezuma Well.

Figure 1. Montezuma Well in central Arizona, USA, site of a long-term study on the effects of introduced pond sliders (*Trachemys scripta*) on native Sonora mud turtles (*Kinosternon sonoriense*). The light tan-colored object in the water in the left foreground and the square white rings near the far shoreline are hoop nets and basking traps, respectively, for capturing turtles. U.S. Geological Survey (USGS) photo by C. Drost.

Materials and methods

Study site

Montezuma Well is a spring-fed sinkhole pond formed from a collapsed travertine spring mound in northeastern Yavapai County in central Arizona, USA. This area and its associated prehistoric Native American dwelling sites and cultural remains are protected as part of Montezuma Castle National Monument, administered by the U.S. National Park Service (NPS). The Montezuma Well portion of the National Monument has an area of 112 ha, with an elevation range of 1,060–1,110 m. The spring that feeds Montezuma Well has a mean output of 3,720 L/min and forms a pond that is roughly circular in outline and approximately 100 m in diameter, with a surface area of 0.76 ha (Figure 1). The deepest part of the pond, where the spring issues forth, is over 15 m deep (Konieczki and Leake 1997). The aquifer supplying the spring flows through calcareous rock strata, so that the water of the pond is highly carbonated from dissolution of the limestone. The high volume of the spring inflow results in a highly stable seasonal and inter-annual thermal regime, with water temperatures ranging from 18 °C in the winter to 26 °C in late summer (Konieczki and Leake 1997; Blinn 2008; authors *unpublished data*). The waters of Montezuma Well are also strongly isolated from surrounding aquatic habitats by the encircling cliffs, which rise an average of 20 m above the water surface. Water drains through underground caves and fissures to adjacent Wet Beaver Creek, and the level of the cave outlet maintains a near-constant water level in the pond.

Due to the high and consistent spring flow and high carbonate and resultant high carbon dioxide levels, Montezuma Well has a unique and stable aquatic ecosystem that is low in overall invertebrate diversity but is highly productive (Boucher et al. 1984; Blinn and Sanderson 1989; Blinn 2008). A dense growth of aquatic vegetation (primarily the endemic pondweed *Potamogeton montezumawellensis* Ricketson, G. Ricketson, & Greenawalt, 2018) and exceptionally high populations of aquatic invertebrates vary primarily in response to the annual cycle of solar insolation (Blinn 2008). The endemic amphipod *Hyalella montezuma* Cole and Watkins, 1977 forms the base of the aquatic food web. There are no fish or amphibians in Montezuma Well due to the very high CO_2 concentrations (Cole and Barry 1973). Except for a few Muskrats (*Ondatra zibethicus* (Linnaeus, 1766)), and several species of winter-visiting ducks and other water birds, the lone native aquatic vertebrate in Montezuma Well is the Sonora mud turtle. Extensive inventory studies of the site have recorded no other non-native plants or animals, except the pond sliders (Boucher et al. 1984; Blinn and Sanderson 1989; Drost 2005; Schmidt et al. 2006; Blinn 2008).

Previous population and ecological studies of the Sonora mud turtle at Montezuma Well include Rosen (1987), Malone (1999), Lovich et al. (2010, 2012), and Drost et al. (2011). The Sonora mud turtle is a small species, with a carapace length of 110–145 mm (maximum 175 mm – Rosen 1987; Ernst and Lovich 2009). They feed primarily on aquatic invertebrates and other animal matter (Hulse 1974) and have a maximum adult lifespan of over 40 years (Ernst and Lovich 2009). Over much of their southwestern USA–northern Mexico range, they occur in highly-variable desert streams and pools, where they are subject to extremes of water temperature, flash floods, and drying of pools during desert droughts (Stone 2001; Hensley et al. 2010). Activity levels in Montezuma Well are greatest between May and September, and highest levels of reproduction (females with eggs) are from June through August (Drost et al. 2011).

Field methods

Fieldwork for this study occurred over three discrete time periods, spanning 33 years. Concurrent with fieldwork, we reviewed and synthesized unpublished notes and records on observations of turtles at Montezuma Well. In particular, this included review of observation logs maintained by NPS and discussions with long-term NPS staff and volunteers. Author Rosen (PCR) conducted live-trapping sessions for turtles in Montezuma Well in June, July, and August 1983. In 1999, authors MM and SDG conducted similar trapping sessions in July, August, and October. Fieldwork for the third period extended from May 2007 through September 2015. We conducted trapping in all years during this third period, with intensive trapping throughout the active season of the turtles in 2007, 2008, 2010, 2011, and in August and September 2015. Throughout all periods of the study, we used hoop traps (76 cm in diameter by 132 cm long, with a funnel opening on one end) as the primary method of capturing turtles (e.g., Sterrett et al. 2010). We baited traps with canned sardines or canned cat food (Rosen 1987; Drost et al. 2011). Hoop traps were set in shallow water around the margins of the pond for one to three nights per trapping session and checked daily. Twenty traps were set each trapping day in 1983 (140 total trap-days, where trap-days = number of traps * number of days traps were open), 12 were set on most trapping days in 1999 (70 trap-days), and from seven to ten traps were set during sessions in 2007, 2008, 2010, 2011, and 2015 (range 55–240 trap-days per year).

In 2007–2015, we also set out basking traps (MacCulloch and Gordon 1978) that were 100 cm long by 60 cm wide, with a ring-like floating platform attached above an open-topped cage submerged in the water. Basking traps were primarily intended to target pond sliders, because of the propensity of that species to bask on logs and similar elevated perches out of the water. One to five basking traps were set out in 2007–2015 and left for the duration of the active season. When basking traps were in place, they were checked every one to three days, depending on time of year and amount of turtle activity.

Fieldwork used the same methods during all periods from 1983 through 2015, including live-trapping of turtles, permanent marking of Sonora mud turtles, collection of morphological measurements and ecological data (Rosen 1987; Malone 1999; Drost et al. 2011). No mortality or injuries of captured turtles occurred during any of the trapping sessions. In 2007, we began capture and removal of non-native turtles. At the direction of NPS, we used only non-lethal capture methods for the non-native turtles, and we removed them to a reptile sanctuary (Phoenix Herpetological Society, Phoenix, Arizona). All turtles were measured and examined for health and overall condition. We determined turtle sex based on plastron shape and tail size. Measurements included straight-line (midline) carapace length, carapace width and height, plastron length and width, and mass (Gibbons 1990). Sonora mud turtles were individually marked by filing a unique combination of triangular notches in the marginal scutes around the edge of the carapace (Cagle 1939); these marks remained throughout the entire study, as evidenced by recapture of turtles marked in 1983 and 1999 during the 2007–2015 period. We assessed reproduction by palpating female turtles for the presence of shelled eggs. Beginning in 2007, we radiographed adult female turtles during the nesting season with a portable X-ray machine to determine if shelled eggs were present (Lovich et al. 2012). In 1983, PCR radiographed a sub-sample of the females he captured, to verify assessment of reproductive condition by palpation (Rosen 1987; cf. Keller 1998). We counted number of eggs present in the radiograph images and measured maximum width of all eggs with digital calipers. Reproductive data were not collected in 1999.

We made systematic observations of turtle activity and basking behavior in 2007–2015 to compare basking patterns of Sonora mud turtles in relation to presence or absence of non-native turtles. All observations were made from observation stations along the rim of Montezuma Well, which provided unobstructed views of nearly the entire water surface and shoreline of the site. We used binoculars to scan shoreline areas and confirm species identifications, and recorded time, species, numbers, location, and behavior of all turtles seen (e.g., basking on emergent rocks or logs, swimming, basking at the water surface), and watched specifically for behavioral interactions between individuals. For comparisons of the period of peak non-native turtle abundance (2007–2008), low numbers (2010–2011), and non-native turtle absence (2014–2015), we compared numbers of turtles observed per 20-minute time period, using one 20-minute period per observation day. For all periods, observations spanned the active season of the turtles in Montezuma Well (March through October) and the diurnal period from 0800–1700, when most basking behavior occurs.

We used weather data for Montezuma Well from the Western Regional Climate Center (2019) to summarize and evaluate conditions over the study period. In particular, we assessed annual precipitation, for its potential effects on runoff and nutrient input into Montezuma Well, or successful hatching of turtle eggs.

Data analysis

Because we removed all non-native turtles from May 2007 onward, we simply used total counts of turtles removed to determine initial population size of the non-natives, and subsequent decrease in numbers over the course of removal. We found shell remains of a single pond slider during searches of the shore and slopes of Montezuma Well at the start of 2007 fieldwork, but otherwise found no evidence of non-native turtle mortality. We recorded no immigration or emigration of non-native turtles at Montezuma Well, and we assume the cliffs surrounding the site prevented any such movement. Beginning in 2007, NPS personnel at Montezuma Well highlighted non-native species concerns in discussions with visitors, focusing on non-native turtles, and were alert for any further introduction of non-native turtles. For this reason (and because we did not observe any evidently new non-native turtles), we believe there were no additional turtle introductions after the start of fieldwork in 2007.

For the Sonora mud turtle population in Montezuma Well, we used the closed-population mark-recapture models in the program *Rcapture* (Baillargeon and Rivest 2007; Rivest and Baillargeon 2014) to estimate population size over the course of pond slider introduction, peak numbers, and removal. Population closure is a key assumption for these population estimation methods (Otis et al. 1978) and the Montezuma Well turtle population is effectively closed geographically because of the surrounding slopes and cliffs. Over the short time period of our population estimates (three–four months during individual activity seasons), we also assumed that populations of the long-lived turtles were effectively closed demographically in terms of recruitment and mortality. *Rcapture* fits loglinear models that account for variation in capture probabilities among individuals (heterogeneity), variation over the course of the trapping period (time), changes in capture probability because of being trapped (behavioral response), and combinations of these sources of variation. *Rcapture* also computes values for model deviance, AIC, and goodness of fit, allowing assessment of the best-fit model and population estimate. To allow comparisons with other turtle populations, we calculated density estimates for both native and non-native turtles, based on the total surface area of Montezuma Well (0.76 ha), as well as on the area of the shallower, vegetated area of the pond (0.4 ha), which provided most or all of the primary habitat for both non-native turtles and Sonora mud turtles (see Hensley et al. 2010 for discussion of area effects on density estimates).

The basking data consisted of counts and were strongly non-normally distributed, so we used a non-parametric Kruskal-Wallis test for overall comparison among years. We tested hypotheses on basking of Sonora mud turtles by modelling counts of basking individuals across time periods of peak non-native turtle numbers, low numbers, and no non-natives (i.e., after removal of the non-natives was complete). We used generalized linear models (GLM) with a negative binomial error distribution and a log link function (package *MASS* in R; R Core Team 2018) to test the hypotheses that the number of basking Sonora mud turtles was negatively related to either presence/absence of non-native turtles, P_{trsc}, or the abundance of non-native turtles, N_{trsc}. We compared against various null hypotheses, including: 1) that number of basking Sonora mud turtles was simply proportional to their population size, by including the offset of the log of the Sonora mud turtle population estimates, $\log(N_{kiso})$, as a covariate; 2) that basking varied randomly by year, which we tested by estimating year-specific basking rates; and 3) a null hypothesis that included only a single intercept for all years. We based the analysis on counts of basking Sonora mud turtles on independent days (10–22 counts per period) and we compared models using AIC scores (Burnham and Anderson 2002). The models included all study years for which we had population estimates for both Sonora mud turtles and non-native turtles, as well as basking counts for Sonora mud turtles. We used parameter estimates from the top-ranked model to calculate predicted values for numbers of basking Sonora mud turtles.

We also used a model comparison approach for analyzing reproductive status of female Sonora mud turtles (number of adult females gravid, vs. not gravid), before, during, and after peak non-native turtle numbers. Female reproduction was compared by logistic regression using data from the peak breeding period of the turtles at Montezuma Well (June–August), for which we had consistent data across all time periods compared: 1983 (low numbers of non-native turtles); 2007 and 2008 (peak numbers of non-natives); and 2013–2015 (no non-natives). Models included a null model (intercept only, M_0), variation across time periods (M_1), and low numbers or no non-native turtles vs. high numbers of non-natives (1983+2013–15 vs. 2007–2008; M_2). Models were compared using AIC scores, as for the basking analyses. Statistical analyses were conducted using R version 3.5.1 (R Core Team 2018).

Results

Introduction of non-native turtles to Montezuma Well

The earliest date that we found for pond sliders in Montezuma Well was 1 May 1971, when NPS staff noted in natural history observation records that two red-eared sliders (*Trachemys scripta elegans* (Wied-Neuwied, 1839)) were seen in the pond. The written entry specifically noted "red stripes behind the eyes", and this character is diagnostic for *T. scripta elegans* (Ernst and Lovich 2009). A total of 42 NPS observation records of turtles in Montezuma Well prior to this (from 1947 to 1971) did not record non-native turtles of any kind. During his work in summer 1983, Rosen (1987) noted that pond sliders were "rare" in Montezuma Well, and he captured and removed only one. During a single, 2-hour period of careful observation on 24 June 1983, he saw a total of three pond sliders (PCR *unpublished notes*). Observations by NPS staff from 1985 through 1993 continued to record pond sliders, and MM (*unpublished data*) caught two pond sliders during fieldwork in October 1999 (these were released at the site); he noted that there were "many more" non-native turtles in Montezuma Well at that time (Malone 1999, p. 24).

Slider removal, and population estimates

In 2007, we removed seven pond sliders and one western pond turtle (also non-native, and the first observation of a non-native turtle other than pond sliders in Montezuma Well). In 2008, we caught and removed five additional pond sliders, including one yellow-bellied slider (*T. scripta scripta* (Thunberg in Schoepff, 1792)); all other pond sliders removed from Montezuma Well were red-eared sliders). Additional single pond sliders were caught in May 2011 and May 2012. In March 2013, a river cooter (*Pseudemys concinna* (LeConte, 1830)), also non-native) was captured in a basking trap, and in July 2013, one additional pond slider was captured. Based on intensive observations of the non-native turtles in 2012 and 2013, we believed that the two turtles captured in 2013 were the last non-natives present, and this was confirmed by continued trapping and observations in 2014 and 2015. Overall, we removed 15 pond sliders, one western pond turtle, and one river

Table 1. Estimated population size (± S.E.) and density of Sonora mud turtles (*Kinosternon sonoriense*) and non-native turtles (primarily pond sliders, *Trachemys scripta*) at Montezuma Well, Arizona, USA, from 1983 through 2015. Trapping to remove the non-native turtles began in 2007, and the last two non-natives were removed in 2013. Densities (per ha) are for the entire pond area ("Density 1", 0.76 ha), and the shallower, vegetated area ("Density 2", 0.4 ha), where most turtle activity was concentrated.

	Sonora mud turtles			Non-native turtles		
	Population size	Density 1	Density 2	Number	Density 1	Density 2
1983	372 ± 64	489	930	5	6.6	12.5
1999	158 ± 43	208	395	18	23.7	45
2007	134 ± 17	176	335	17	22.4	42.5
2008	99 ± 29	130	248	9	11.8	22.5
2011	80 ± 21	105	200	4	5.3	10
2015	139 ± 34	183	348	0	0	0

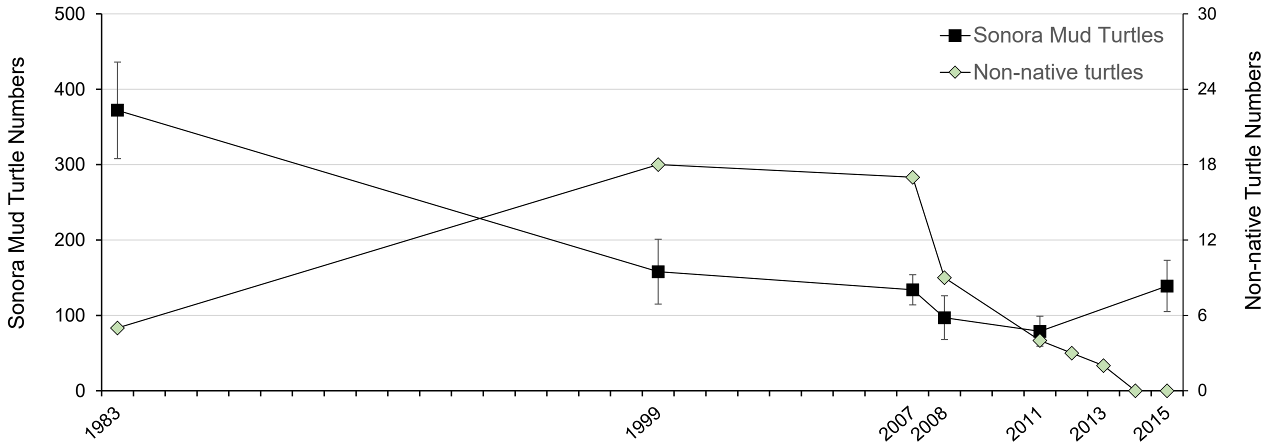

Figure 2. Population estimates of Sonora mud turtles (*Kinosternon sonoriense*; mean ± S.E., left axis) and non-native turtles (primarily pond sliders, *Trachemys scripta*; right axis) at Montezuma Well, Arizona, USA, from 1983–2015. Non-native turtle counts are at the beginning of each year. Removal of non-native turtles began in 2007, with the last two captured in 2013.

cooter from 2007–2013. The shell remains of one additional pond slider were found during surveys of the shore and slopes of Montezuma Well at the start of 2007 fieldwork, bringing the total number of non-native turtles accounted for to 18. All of the non-native turtles were adult individuals. Among pond sliders, this included seven males (carapace lengths ranging from 176 to 221 mm) and eight females (carapace lengths 186–237 mm).

Non-native turtle numbers are summarized in Table 1 and Figure 2, as the number of non-native turtles at the beginning of each year (prior to any removal that year). As noted, a total of three red-eared sliders were counted during an intensive, 2-hour observation period in 1983 (PCR *unpublished field notes*). During our basking observations from 2007–2013, we typically saw from 45–75% of the total non-native turtles that were known to be present (based on retrospective calculation of non-native turtle numbers; Table 1). Using the average of these detection probabilities (60%), we estimate five non-native turtles present in 1983. Although MM and SDG noted that non-native turtles were present in higher numbers in 1999 (Malone 1999), they did not attempt to estimate population size. The number of non-native turtles shown for 1999 is thus simply the number of non-native turtles that we accounted for at the beginning of 2007 (18, as described above).

Both our own observations and NPS reports document that the non-native turtles were producing eggs, and at least some of these were viable. Six of the eight female pond sliders that we removed from Montezuma Well were radiographed for eggs, and four were gravid. One female was induced to lay eggs after capture, and these eggs were artificially incubated and hatched successfully. In addition, the female river cooter removed from Montezuma Well laid 14 eggs in the summer after her capture (despite being the lone member of her species in the system); the eggs were incubated, but did not hatch and showed no signs of development when opened. The pond sliders also excavated nests and laid eggs at Montezuma Well: a female was observed laying 14 eggs on the south side of the Well (1999 or 2000, NPS records); and a female captured on land on 25 May 2008 laid one egg after her capture (this study). Despite the production of viable eggs, we did not observe nor find records of any hatchling or juvenile non-native turtles over the 43-year span of observations at Montezuma Well (1971–2013).

Sonora mud turtle populations

Over the span of the study, we had 818 captures of Sonora mud turtles in Montezuma Well, and we marked a total of 403 different individuals. There were only two recaptures during the 2010 trapping sessions, and the model estimators did not yield population estimates. Most of the best-fit mark-recapture models for population estimates for all other years were models including time variation in capture probabilities over each annual trapping period. Time variation may reflect a late-summer lull in Sonora mud turtle activity that we observed during basking observations each year (Drost et al. 2011). Estimated population size of Sonora mud turtles in Montezuma Well was highest in 1983, when numbers of non-native turtles were low; numbers had declined to less than half by the time of the 1999 study and reached their lowest point during non-native turtle removal in 2011, at 22% of the population size in 1983. Sonora mud turtle population size in 2015, after removal of all non-natives, had increased by over 70% from the population's low point in 2011 (Table 1, Figure 2).

Basking

Basking sites in Montezuma Well are limited. They include a single emergent log that was present throughout the 2007–2015 period, several small emergent boulders near the shore, and occasional floating sticks and small logs that did not persist through the observation period (Drost et al. 2011). Counts of basking Sonora mud turtles increased during observations from 2007 through 2015. Counts in 2007 and 2008 ranged from 0–5 individuals per 20-minute time period, with a median of 0 each year (Figure 3). Counts of basking non-native turtles ranged from 0–8 in 2007, and 0–3 in 2008, reflecting ongoing capture and removal of the non-natives.

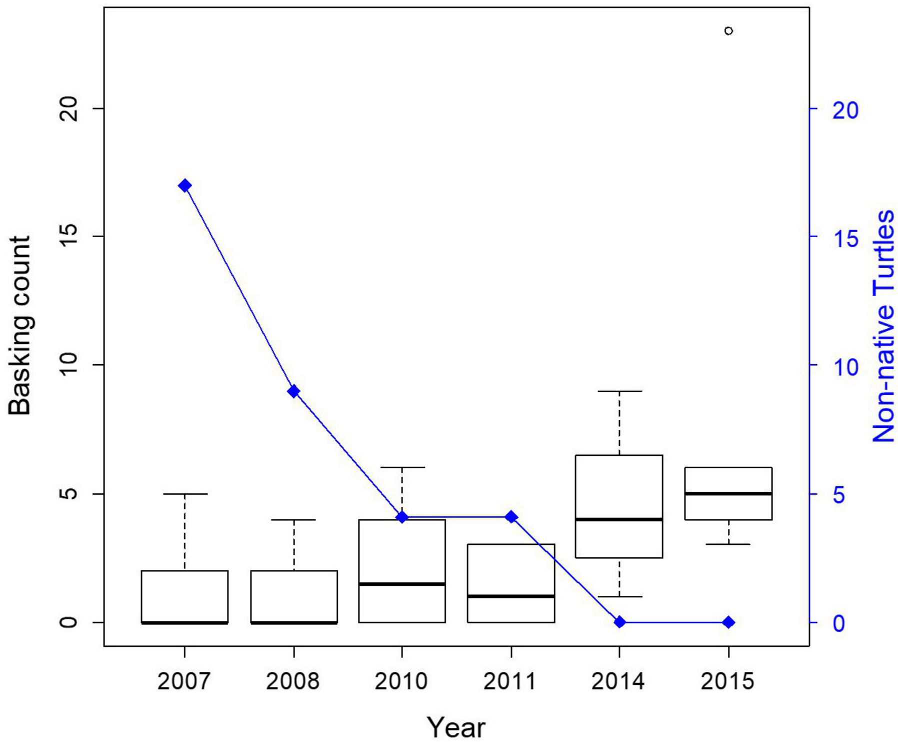

Figure 3. Boxplot of numbers of basking Sonora mud turtles (*Kinosternon sonoriense*) seen per 20-minute observation period at Montezuma Well, Arizona (left axis), in relation to numbers of non-native turtles (line graph and right axis, in blue). In the boxplots, the dark horizontal bar is the median count, the box encloses upper and lower quartiles, and the upper and lower bars denote minimum and maximum counts. One outlier—a high count of 23 in 2015—is denoted by a hollow circle. 2007 and 2008 had median counts of 0.

Figure 4. Sonora mud turtles (*Kinosternon sonoriense*) basking at Montezuma Well, Arizona, in May 2015, after removal of non-native turtles from the site. The number of turtles seen in this one view nearly equals the total high count seen for all of Montezuma Well when non-native turtles were most abundant, in 2007 and 2008. USGS photo by C. Drost.

Following the removal of the last non-native turtles, counts of basking Sonora mud turtles ranged from 2–9 in 2014 (median 4), and from 3–23 in 2015 (median 5; Figures 3, 4). There was a significant difference in counts across years (Kruskal-Wallis chi-square = 27.716, 5 df, $p < 0.0001$).

Table 2. Model results for effects of non-native turtles on basking rates of Sonora mud turtles (*Kinosternon sonoriense*) at Montezuma Well in central Arizona, USA. Models are: 1) intercept only (M_0); 2) population size of Sonora mud turtles (N_{kiso}); 3) numbers of non-native turtles (primarily pond sliders, *Trachemys scripta*; N_{trsc}); 4) observation year (M_{year}); 5) population size of Sonora mud turtles, along with presence/absence of non-native turtles ($M_{kiso,pres}$); and 6) presence/absence of non-native turtles, alone (P_{trsc}).

Model	df	AIC	ΔAIC	AIC weight
M_0	46	192.10	15.75	< 0.001
N_{kiso}	46	189.85	13.5	< 0.001
N_{trsc}	45	186.1	9.75	0.005
M_{year}	43	180.17	3.82	0.092
$M_{kiso,pres}$	45	177.93	1.58	0.282
P_{trsc}	45	176.35	0.0	0.621

Table 3. Reproductive condition of Sonora mud turtles (*Kinosternon sonoriense*) at Montezuma Well, Arizona, USA, in relation to non-native pond sliders (*Trachemys scripta*): summary data (top) and logistic regression model results for effects of non-native turtles on reproductive condition (bottom). Periods are: 1983 – low numbers of non-native turtles; 2007–2008 – high numbers of non-native turtles; and 2013–2015 – after removal of all non-natives. Models are: 1) null (intercept only, M_0); 2) variation by year (M_1); and 3) peak non-native turtle numbers vs. low numbers, or no non-natives (M_2).

Year(s)	Condition		
	Gravid	Not Gravid	% Gravid
1983	36	7	84
2007–2008	13	9	59
2013–2015	16	4	80

Model	Df	AIC	ΔAIC	AIC weight
M_0	84	94.75	2.63	0.162
M_1	82	93.99	1.87	0.236
M_2	83	92.12	0.0	0.602

The best model identified by AIC included presence/absence of non-native turtles as a covariate (Table 2; AIC weight 0.62). Numbers of basking Sonora mud turtles were significantly higher following complete removal (i.e., absence) of non-native turtles from the Well (cf. Figure 3). The model based on actual numbers of non-native turtles (not simple presence/absence) had much less support (ΔAIC 9.75, AIC weight < 0.01), as did an intercept-only model (ΔAIC 15.75, AIC weight < 0.001), and a model that assumed basking counts were proportional to estimated Sonora mud turtle population size (ΔAIC 13.5, AIC weight < 0.001). Predicted values of the highest-ranked model for mean numbers of basking Sonora mud turtles per 20 minutes were 1.14 ± 1.24 S.E. in the presence of non-native turtles and 6.37 ± 1.33 S.E. in the absence of non-natives.

Reproduction

Reproductive status of female Sonora mud turtles also varied across time periods in relation to presence of non-native turtles in Montezuma Well. Eighty-four percent of adult females had eggs in 1983 (low numbers of non-natives), and 80% had eggs in 2013–2015 (after removal of non-natives). This compares to 59% of adult females with eggs in 2007–2008 (high numbers of non-natives; Table 3). Comparison of logistic regression models testing

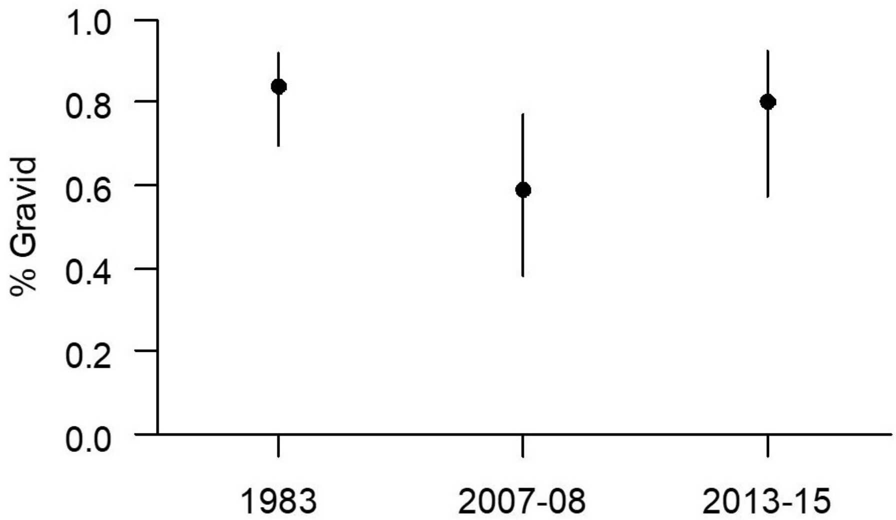

Figure 5. Reproductive status of female Sonora mud turtles (*Kinosternon sonoriense*) at Montezuma Well, central Arizona, USA: model-predicted values (mean ± 95% confidence interval) for proportion of adult females that were gravid, in relation to presence (2007–2008) or absence (low numbers/early invasion, 1983; post-removal, 2013–2015) of non-native pond sliders (*Trachemys scripta*).

non-native turtle effects on reproductive status of female Sonora mud turtles (gravid vs. not gravid) indicated that the best model was one contrasting peak numbers of non-native turtles (2007 and 2008) with before (early invasion, 1983) and after (post-removal, 2013–2015). AIC weight for this model was 0.60, compared to models of variation among all time periods (AIC = 0.24) and the null/intercept-only model (0.16; Table 3, Figure 5).

Capture rates of juvenile Sonora mud turtles (≤ 80 mm carapace length as used here – three years old or less) also suggest differences in successful reproduction associated with non-native turtles. Among trap captures, 12 of 180 Sonora mud turtles in 1983 were juveniles (6.7%), compared to five of 130 captures in 1999 (3.9%) and five of 201 in 2007–2008 (2.5%). Captures of juveniles remained low in 2013–2015, as only five of 205 captures were juveniles (2.4%). However, during basking observations in 2007 and 2008, two juveniles were seen out of a total of 106 Sonora mud turtles observed (1.9%, 139 hours observation time), while in 2014 and 2015, nine juveniles were seen, out of 132 total (6.8%, 32 hours observation time).

Discussion

The combination of strongly uniform hydrological conditions, lack of disturbance, and isolation from outside influence, makes Montezuma Well a compelling natural experimental setting for assessing the effects of introduced pond sliders on a native turtle population. Isolation from surrounding environments facilitates accurate population estimates with little or no immigration or emigration, and also limits outside, uncontrolled influences on the Montezuma Well ecosystem. The only observable change in the system over the course of this study was the introduction of pond sliders and other non-native turtles, and their subsequent removal. Controlled studies in small artificial pond and terrarium environments have shown that native turtles may be excluded from favored basking sites by non-native pond sliders (e.g., Cadi and Joly 2003; Macchi et al. 2008; Polo-Cavia et al. 2010), and other laboratory and mesocosm studies have demonstrated pond slider effects on vitality of native turtle species, up to and including increased mortality rates in the presence of pond sliders (Cadi and Joly 2004). However, results from simple, artificial settings cannot be assumed to translate to natural environments with much greater complexity (cf. Lambert et al. 2019). The natural setting of Montezuma Well can be seen as intermediate between the simplicity and strict controls of a lab or mesocosm experiment, and the complexity of a large, open, uncontrolled aquatic system – the latter with the potential for multiple confounding influences. Results from the Montezuma Well system thus provide essential corroboration for hypotheses and further insights into the occurrence, magnitude, and mechanisms of negative effects of introduced pond sliders on native turtle populations.

Population trends of native and non-native turtles

We focus on pond sliders throughout this discussion, as they comprised 90% of the non-native turtles in Montezuma Well, and they are known to be aggressive toward other turtle species (Lindeman 1999; Polo-Cavia et al. 2011). Pond sliders were present in Montezuma Well for over 40 years, dating back at least to the first report of their presence in 1971, but only a few individuals were present through the early 1980's (Rosen 1987). Although we do not know the detailed history of non-native turtle introduction to Montezuma Well, the increasing numbers of non-natives probably resulted from repeated human releases over a number of years. The variety of turtle species and subspecies that were present (none of them native to Arizona) provides evidence of this, as does the absence of any captures or observations of hatchling or juvenile individuals. If introductions continued beyond 1999, then peak numbers of non-native turtles may have occurred sometime between 1999 and 2007. Annual counts are lacking, but NPS observations suggest that the period between 1999 and 2007 had consistently high numbers of non-native turtles. Density and biomass of pond sliders in Montezuma Well in 2007 were within the average range of the species in its native distribution in the eastern United States (biomass 52.1 kg/ha at Montezuma Well, vs. a mean of 37.1 kg/ha in native range; cf. Congdon et al. 1986 for native range), but were much lower than the high levels reported for some introduced populations (e.g., density up to 300/ha and biomass up to 187 kg/ha; Taniguchi et al. 2017).

The absence of juvenile pond sliders, despite recorded egg-laying, suggests possible failure at the incubation / egg-hatching stage in the dry conditions of the southwestern United States, consistent with reports from other arid areas outside the native range of the species (Tucker and Paukstis 2000; Bringsøe 2001, in Ficetola et al. 2009, 2012). In other areas, failure of reproduction by non-native pond sliders has also been attributed to little or no egg production, or low over-winter survival of neonate sliders in colder regions (Luiselli et al. 1997). Regardless of limitations on reproduction, turtles are generally long-lived, and pond sliders may live 30–40 years or more (Ernst and Lovich 2009). Field research and modeling studies in different parts of the world have sought to determine climatic and environmental limits for successful reproduction of pond sliders, allowing establishment of self-sustaining non-native populations (Luiselli et al. 1997; Ficetola et al. 2009; Rödder et al. 2009; Kikillus et al. 2010; Cerasoli et al. 2019), as a condition for negative impacts on local native species. However, widespread international trade and subsequent release to the wild of pond sliders and other non-native turtles continues in many parts of the world, with or without regulations and restrictions (e.g., Mali et al. 2014; Nori et al. 2017). Our results indicate that continued introductions, coupled with the long lifespan of the adult turtles, may result in non-native turtle populations large enough to cause substantial harm to local native turtle populations – even in the absence of local recruitment.

Although anecdotal, written NPS observation notes suggest that Sonora mud turtles had been present in consistently high numbers prior to the introduction of pond sliders, with records dating back to 1948 describing Sonora mud turtles as "common" in Montezuma Well. Counts of Sonora mud turtles reported in the notes include 23 on 30 June 1952 and "15–20 at a time", recorded on 1 May 1971. Sonora mud turtles are small, spend much of their time underwater, and are generally inconspicuous, particularly at typical observing distances at Montezuma Well, so these counts are suggestive of a large population. PCR (*unpublished notes*) counted 13 Sonora mud turtles in his single observation period, in June 1983. The numbers reported in the NPS notes are three to four times higher than we counted in most of our systematic surveys when non-native turtles were present, and the high historic count of 23 by NPS staff equals our highest count during our much more intensive observations following non-native turtle removal.

After introduction of pond sliders, the Sonora mud turtle population in Montezuma Well declined by nearly 80%, from an estimated 372 in 1983, when the introduced turtle population was small, to 80 during the non-native turtle removal period, in 2007–2013. Neither our study, nor any other study of pond slider effects on native turtles, suggests negative effects due to direct, acute mortality. Instead, the pattern of decline seen at Montezuma Well—a slow, near-monotonic decrease through the period when non-native turtles were present—is the pattern that is expected in long-lived, slowly reproducing species like turtles (Bury 1979; Wilbur and Morin 1988; Hensley et al. 2010), due to the gradual loss of older adults without replacement by sufficient numbers of young individuals. This pattern of slow, nearly imperceptible loss in long-lived populations has been highlighted previously for declines in turtles and other species with similar life history characteristics (Congdon et al. 1993; Klemens 2000; Lovich et al. 2018; Howell et al. 2019). The population estimate of 139 individuals in 2015—two years after the removal of the last non-native turtles—is a significant, but relatively modest, increase, and the recovery of the population is also expected to be gradual and to require a decade or more.

Ecological effects of pond sliders

Our basking data indicate a behavioral response by the Sonora mud turtles in Montezuma Well to the presence of the large pond sliders. Model-predicted mean basking rate of Sonora mud turtles was 5.6 times higher after the removal of non-native turtles, compared to the period when non-native turtles were present. AIC-based model comparison identified simple presence/absence of non-native turtles as having the strongest effect on basking rate (as opposed to a direct quantitative relationship with numbers of non-native turtles), suggesting that even relatively small numbers of pond sliders negatively affected Sonora mud turtle activity (Table 2). Nonetheless, our observations suggest that basking rates had begun to increase in 2010 and 2011, in the latter stages of removal when only four non-native turtles remained (Figure 3). Documentation of significantly reduced basking rates by Sonora mud turtles in the presence of pond sliders in a natural environment parallels results under controlled, experimental conditions for European pond turtles and Mediterranean pond turtles (Cadi and Joly 2003; Polo-Cavia et al. 2010) and suggests that this interaction may lead to substantial long-term population declines.

Competition for basking sites is a form of interference competition, in which access to a resource is limited by aggressive behavior of the competitor (Schoener 1986; Polo-Cavia et al. 2014; Zhang et al. 2015). In some cases, overt aggressive interactions are seen between turtle species, both in the wild (Lindeman 1999) and in controlled, experimental studies of pond sliders and other basking turtles (Polo-Cavia et al. 2011). However, patterns of behavioral avoidance appear to represent more typical behavior in response to pond sliders, as in experimental studies of European pond turtles and pond sliders in small artificial ponds (Cadi and Joly 2003). Relatively small individuals frequently show such avoidance behavior (Lindeman 1999), and Sonora mud turtles average about 25% of the mass of pond sliders at Montezuma Well. During our observations, we did not record any overt aggressive interactions (cf. Lovich 1988) between Sonora mud turtles and non-native turtles, and in fact we rarely saw the two species in close proximity. Rather, our observations suggest avoidance of the large pond sliders by the Sonora mud turtles. In particular, during the period when pond sliders were present in Montezuma Well, Sonora mud turtles rarely occupied basking sites used by sliders. In 2014 and 2015, after removal of the non-natives, Sonora mud turtles began to regularly use conspicuous log and boulder basking sites they had not used before, and that were previously favored basking sites of the pond sliders. During 139 hours of systematic observations of turtle activity in 2007 and 2008, the few close encounters of Sonora mud turtles and non-native turtles included: 1) a Sonora mud turtle that was basking on top of an emergent branch in the water backed up and dropped into the water when a pond slider surfaced by the branch; and 2) a Sonora mud turtle that surfaced about one meter away from a pond slider, faced the other turtle briefly, then abruptly turned and submerged. We do not have data to evaluate the possibility, but it may also be the case that behavioral avoidance of non-native turtles by Sonora mud turtles also resulted in decreased access to prime foraging areas and food resources, in addition to reduced opportunities for basking and thermoregulation.

Basking in turtles (and in reptiles generally) is important for a variety of physiological functions, including maintaining body temperature in an optimum range (e.g., Boyer 1965; Regal 1966). Lowered physiological condition may result from inability to maintain body temperatures high enough for efficient digestion of food (e.g., Congdon 1989), and a link between reduced basking due to competition with introduced pond sliders, and lowered metabolic efficiency, has specifically been suggested in studies of Mediterranean pond turtles (Polo-Cavia et al. 2012). Alternatively (or in addition), reproduction may be directly affected because of the need for females to bask to elevate their body temperatures during the development of eggs (Bulté and Blouin-Demers 2010; Millar et al. 2012). Limitation of basking has also been shown to reduce growth in juvenile turtles, even in the presence of abundant food (Koper and Brooks 2000); this may further reduce recruitment to the adult population, or result in stunted growth (e.g., Ylikarjula et al. 1999). In this manner, reduced basking by Sonora mud turtles at Montezuma Well, leading to lowered body condition and reduced reproduction, have presumably been critical links in the long-term decline in the population.

Reproductive rates of Sonora mud turtles (as measured by proportion of adult females that were gravid) were lower when non-native turtles were present in the highest numbers (2007–2008, vs. 1983 and 2014–2015; Table 3, Figure 5). An extended period of reduced reproductive success over a span of 24 years (1983–2007), with normal population loss rates, reasonably accounts for the population decline documented in Sonora mud turtles at Montezuma Well (cf. Heppell 1998 and Howell et al. 2019). After removal of all non-native turtles, the proportion of gravid females returned to near levels in 1983. Although young turtles are generally under-sampled by standard methods for trapping turtles (e.g., first-year Sonora mud turtles can fit through the mesh size of the hoop traps that we used), the numbers of juvenile Sonora mud turtles generally paralleled changes in female reproductive rate over the time periods of non-native turtle presence, and removal. The proportion of juveniles captured in traps remained low in 2014–2015, but the relative numbers seen during basking observations in 2014 and 2015 were 3.5 times higher than numbers seen in 2007 and 2008.

Alternative hypotheses and explanations

Rainfall varied within historic bounds over the 33-year study period, with relatively lower levels from 2007–2015 (mean 30.6 cm, vs. long-term mean of 32.5 cm). This pattern shows no evident relationship to the population trend of the Sonora mud turtle population during this period. More importantly, the strongly uniform hydrologic conditions of Montezuma Well ameliorate any minor variation in annual precipitation. Compared to the extreme environmental variation that Sonora mud turtles experience across much of their range (cf. Hensley et al. 2010), Montezuma Well may represent the most favorable conditions that the species inhabits anywhere in its natural distribution.

Predation on adult turtles is limited to terrestrial carnivores such as raccoons (*Procyon lotor* (Linnaeus, 1758)) and gray foxes (*Urocyon cinereoargenteus* (Schreber, 1775)) during infrequent occasions when the turtles are on land (e.g., when females lay eggs during the summer). As with most turtles, there is heavy predation on eggs (e.g., Wilbur and Morin 1988), but there is no evidence that predation on adults or on eggs or hatchlings has changed in a systematic manner over the course of this study.

Competition for food resources has been suggested between pond sliders and ecologically similar European pond turtles (Balzani et al. 2016). However, Sonora mud turtles are largely or entirely carnivorous (Hulse 1974), while adult pond sliders and the other non-native turtles at Montezuma Well feed more heavily on plant food, both in their native range (60–90% or more of dietary volume; Parmenter and Avery 1990), and where they are introduced (Chen and Lue 1998; Prévot-Julliard et al. 2007). Considered together with the abundant aquatic invertebrate populations in Montezuma Well (e.g., Blinn 2008) that form the prey base of the Sonora mud turtles, over-exploitation of food resources in Montezuma Well is unlikely.

Transmission of novel disease-causing organisms from introduced pond sliders is likely for native turtles in the same family (Emydidae; e.g., Meyer et al. 2015; Héritier et al. 2017). However, such parasite transfer has not been reported for more distantly-related turtles such as Sonora mud turtles. Of over 700 Sonora mud turtles examined during this study, a single leech was the only ectoparasite found, and we did not note poor health except in one very old individual. Turtle leeches (*Placobdella* sp.) have not been found at Montezuma Well, where the leech fauna is comprised of endemic or narrowly-distributed local species (*Helobdella* and *Motobdella* spp. – Govedich et al. 1999; Beresic-Perrins et al. 2017).

Necropsies of two Sonora mud turtles that we found dead did not reveal internal parasites or evident pathological bacterial infection. Further, pathogens and parasites are not reported to have the kinds of effects on reproduction and basking behavior that we documented in the Sonora mud turtles at Montezuma Well. Nonetheless, novel pathogens from introduced pond sliders should continue to be evaluated for negative effects on native turtles.

Pond slider effects in other areas, and on other turtle species

Some other areas in the southwestern USA appear to show similar effects of introduced pond sliders on Sonora mud turtles. In the Tucson, Arizona, area, Sonora mud turtles formerly occurred in and around ponds and streams at Agua Caliente Spring. During draining and renovation of the main pond at this site in 2019, only non-native turtles were found—including approximately 35 pond sliders, two spiny softshells (*Apalone spinifera* (LeSueur, 1827)), and four snapping turtles (*Chelydra serpentina* (Linnaeus, 1758)); Brian Powell, Pima County Natural Resources Department, *pers. comm.*). The Agua Caliente pond is approximately 1 ha in surface area, a little larger than Montezuma Well. In an extensive series of ponds in Papago Park, Phoenix, Arizona annual surveys have found only two Sonora mud turtles among over 1400 non-native turtles of 18 species captured and removed (updated from Wang 2014) and no Sonora mud turtles have been observed in ponds at Reid Park in Tucson, where large populations of pond sliders and other non-native turtles appear to have excluded native mud turtles (PCR *unpublished data*).

The most significant threat of non-native pond sliders to Sonora mud turtles and other native southwestern species is probably for small, genetically isolated populations restricted to desert ponds and spring pools. In addition to the Montezuma Well population, this includes restricted populations at Quitobaquito Springs, Organ Pipe Cactus National Monument, in southern Arizona—where pond sliders and other non-native turtles have been found and removed (Rosen and Lowe 1996)—and also parts of the Rio Sonoyta in adjacent northern Sonora, Mexico. These sites represent the only known habitats for *K. sonoriense longifemorale* Iverson, 1981, listed as an endangered subspecies by the U.S. Fish and Wildlife Service (Riedle et al. 2012).

Sonora mud turtles are widely separated from pond sliders taxonomically (superfamily Kinosternoidea, vs. superfamily Testudinoidea; Rhodin et al. 2017) and differ markedly from that group in aspects of morphology, ecology, and behavior. Sonora mud turtles are much smaller (ca. one-half the carapace length, and one-quarter the mass), with a more domed, elongate carapace. As noted, Sonora mud turtles are largely carnivorous, feeding on aquatic invertebrates and other animal matter; they have nocturnal as well as diurnal activity, much of their activity and foraging is on the bottom of ponds and streams, and basking activity is less pronounced than in other aquatic turtles. Pond sliders are omnivorous, with adult diet composed largely of plant material; they are diurnal in their activity pattern, feed at the surface or in the water column in areas of aquatic vegetation, and basking behavior is strongly developed (Mahmoud 1960; Hulse 1974; van Loben Sels et al. 1997 and Ernst and Lovich 2009 for Sonora mud turtle; Gibbons 1990 and Ernst and Lovich 2009 for pond slider). In light of this wide range of differences, the strong effects of pond sliders on Sonora mud turtle behavior, reproduction, and population numbers documented here are striking and unprecedented.

The majority of research on potential negative effects of non-native pond sliders has focused on native turtles that are more closely related taxonomically, and that are more similar in their morphology, ecology, and behavior – particularly the European pond turtle in parts of Europe and the western pond turtle in western North America (family Emydidae, like the pond slider) and the Mediterranean pond turtle in Spain and southern Europe (in the related family Geoemydidae; e.g., Cadi and Joly 2003; Spinks et al. 2003; Polo-Cavia et al. 2010, 2014; Lambert et al. 2019). Substantial negative population-level effects of introduced pond sliders on a dissimilar species like the Sonora mud turtle lend support to concerns about negative impacts of pond sliders on native turtles more broadly. Many of the research studies on pond slider interactions with European pond turtles, western pond turtles, and Mediterranean pond turtles highlight similar effects to those documented for Sonora mud turtles at Montezuma Well. In other parts of the non-native distribution of pond sliders, large populations of that species now outnumber native species in some countries in eastern Asia, such as the Japanese pond turtle (*Mauremys japonica*, Geoemydidae; Taniguchi et al. 2015). However, research on ecological effects of pond sliders in this part of the world is limited (Ramsay et al. 2007). Pond sliders may also compete for basking sites and food with other species such as the helmeted turtle (*Pelomedusa subrufa*) in South Africa, which are divergent taxonomically but have similar habitat preferences (Newbery 1984; Lever 2003).

Adverse effects of introduced pond sliders on native turtles in other areas may also be slow, cumulative over a period of years, and difficult to evaluate in the absence of intensive, long-term studies. More immediate assessments of impacts on native populations may come from repeat surveys of sites that have data from historic inventories. Modeling studies may provide valuable insights in this regard, by measuring population parameters of native populations at sites across a region, with time since introduction of pond sliders as a covariate (e.g., Gherardi 2007b). Accurate estimates of population size are time-intensive (requiring multiple capture occasions for mark-recapture analyses, for example), and may be prohibitive in extensive studies of natural populations. Our results from

Montezuma Well suggest that other parameters that may be evaluated in addition to (or instead of) population numbers, include size and age structure (which may be biased toward larger, older individuals in the presence of pond sliders), basking and other behaviors (cf. Lambert et al. 2019), and measures of reproductive condition and body condition (e.g., mass relative to a linear measurement, such as carapace length in turtles; e.g., Cadi and Joly 2004; Peig and Green 2009; Lambert et al. 2019). A variety of measures should be testable between native turtle populations with, and without, introduced pond sliders.

Finally, we note the calls of many other authors for increased regulation and control of trade and export of pond sliders and other turtle species. Invariably, many of these turtles are released into natural aquatic systems where they are not native. Worldwide, turtle species have suffered greater population losses than most other vertebrate groups, with 61% of turtle species threatened with extinction, or recently extinct (Lovich et al. 2018). Pond sliders and other non-native species add to the weight of habitat loss and habitat degradation, high levels of human exploitation, and other impacts that have caused major population declines and driven many turtle species to the brink of extinction. For invasive non-native species of all kinds, the most effective and least expensive management strategy is to prevent such introductions at the outset—and species like pond sliders and other turtle species that are purposefully traded through legal channels, should be the most straightforward to control, both at the point of export (Mali et al. 2014) and points of import (e.g., Scalera 2007b).

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Finally, we note that co-author Phil Rosen passed away during final revisions of this manuscript, and we honor his many contributions and generous collaborative spirit. Phil was a consummate naturalist and scientist who will be missed by his many friends and colleagues.

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Conflict of interest

The authors declare that they have no conflicts of interest. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the United States Government.

Ethics and permits

All capture and handling of turtles followed the recommendations for field studies of the American Society of Ichthyologists and Herpetologists (ASIH 2004), and was conducted under permits SP574796, SP643562, and SP684131 from the Arizona Game and Fish Department. Fieldwork starting in 2007 followed Animal Care and Use (IACUC) Protocol Number 07-004 (and renewals) through Northern Arizona University (earlier fieldwork did not require IACUC approval).

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Supplementary material

Capture data for Sonora Mud Turtles over the span of the study are available at Drost et al. 2021 (U.S. Geological Survey data release, https://doi.org/10.5066/P9EL65UI).