

Research Article

Unusual population attributes of invasive red-eared slider turtles (*Trachemys scripta elegans*) in Japan: do they have a performance advantage?

Mari Taniguchi^{1,2}, Jeffrey E. Lovich^{2,*}, Kanako Mine¹, Shintaro Ueno³ and Naoki Kamezaki^{4,5}

¹NatureRecoveryCo., Ltd., 1-1-5-504, Nishidaidori, Nagata, Kobe, 653-0844, Japan

²U.S. Geological Survey, Southwest Biological Science Center, 2255 N. Gemini Drive, MS-9394, Flagstaff, Arizona, 86001-1600 USA

³Department of Ecosystem Studies, Graduate School of Agricultural and Life Sciences, The University of Tokyo, 1-1-1 Yayoi, Bunkyo-ku, Tokyo, 113-8657, Japan

⁴Kobe-Suma Aquarium, 1-3-5, Wakamiya, Suma, Kobe, 654-0049, Japan

⁵Department of Biosphere-Geosphere Science, Okayama University of Science, 1-1 Ridai-cho, Kita-ku, Okayama, 700-0005, Japan

Author e-mails: m-taniguchi@shizenkaifuku.com (MT), jeffrey_lovich@usgs.gov (JEL), k-mine@shizenkaifuku.com (KM), shintaru-ueno@gmail.com (SU), n-kamezaki@sumasui.jp (NK)

*Corresponding author

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Abstract

The slider turtle (*Trachemys scripta* Thunberg in Schoepff, 1792) is native to the USA and Mexico. Due to the popularity of their colorful hatchlings as pets, they have been exported worldwide and are now present on all continents, except Antarctica. Slider turtles are well-established in Japan and occupy aquatic habitats in urban and agricultural areas, to the detriment of native turtles with which they compete. We asked the overall question, do slider turtles in Japan have a performance advantage because they are liberated from the numerous competing turtle species in their native range and released from many of their natural predators? Traits compared included various measures of adult body size (mean, maximum), female size at maturity as measured by size of gravid females, clutch size, population density and biomass, sex ratio, and sexual size dimorphism, the latter two a partial reflection of growth and maturity differences between the sexes. We sampled slider turtle populations in three habitats in Japan and compared population attributes with published data for the species from throughout its native range in the USA. Mean male body sizes were at the lower end of values from the USA suggesting that males in Japan may mature at smaller body sizes. The smallest gravid females in Japan mature at smaller body sizes but have mean clutch sizes larger than some populations in the USA. Compared to most populations in the USA, slider turtles achieve higher densities and biomasses in Japanese wetlands, especially the lotic system we sampled. Sex ratios were female-biased, the opposite of what is reported for many populations in protected areas of the USA. Sexual size dimorphism was enhanced relative to native populations with females as the larger sex. The enhanced dimorphism is likely a result of earlier size of maturity in Japanese males and the large size of mature (gravid) Japanese females. Slider turtles appear to have a performance advantage over native turtles in Japan, possibly as a result of being released from competition with numerous sympatric turtle species in their native range, and the absence of many co-evolved predators and parasites in Japan. This slight competitive edge, coupled with the catholic diet and broad tolerance of varying aquatic habitats of slider turtles, is reflected in their dominance over native and naturalized Japanese turtles in altered aquatic habitats.

Key words: body size, demography, size of maturity, sex-ratio, sexual size dimorphism, turtle

Introduction

Although the ecological consequences of invasive exotic species have long been recognized by scientists (Elton 1958), there is still uncertainty in the ability to predict which species have the capacity to become

invasive and under what circumstances (Kolar and Lodge 2001). However, for many years it was assumed that species that became invasive exhibited enhanced performance measures in their introduced habitats relative to their native range, even if the reasons for doing so were not always completely

understood. Potential responses of performance measures for invasive species in novel habitats include increased size (but see Thébaud and Simberloff 2001), fecundity, population density (see review in Parker et al. 2013), or phenotypic plasticity (Davidson et al. 2011). Enhanced performance measures are a possible response to “enemy release” in which invasive species are removed from natural predators (Keane and Crawley 2002) and parasites (Torchin et al. 2003). Enhanced performance may also result from lack of competition with other species in their native habitat once they are introduced elsewhere.

Parker et al. (2013) recently found limited support for the increased performance measure hypothesis after analyzing data from a variety of plants and animals. They concluded that while some species do indeed have higher performance measures in their introduced range, an equivalent number perform equally well in both native and introduced ranges. In this paper we compare demographical and morphological “performance measures” for the invasive red-eared slider turtle (*Trachemys scripta elegans* Wied-Neuwied, 1839) in Japan with published data from their native habitat in the United States of America (USA) as a qualitative test of the increased performance measure hypothesis advanced by Parker et al. (2013).

Slider turtles occur in sympatry with as many as five or more other turtle species in their native range in the USA (Congdon et al. 1986), but resources and habitat are generally partitioned among species (Lindeman 2000) due to their long history of interactions. However, the relative abundance of many turtle species was negatively correlated with the proportional abundance of *T. s. elegans*, even in their native range (Dreslik and Phillips 2005). Greater reproductive output and differences in nesting habitat of slider turtles may give them a competitive advantage over other turtle species without having to invoke additional direct forms of competition. As an opportunistic omnivore and habitat generalist, slider turtles are released from co-evolved competitive interactions with other turtles when introduced outside their natural range to the detriment of other native turtle species (Spinks et al. 2003; Cadi and Joly 2003, 2004; Polo-Cavia et al. 2010, 2011; Thomson et al. 2010; Pearson et al. 2015).

Among turtles worldwide, *T. s. elegans* is characterized by a number of superlatives, not all of which are positive from the standpoint of biodiversity conservation. First, the species is listed by the IUCN as one of the top 100 most invasive alien species (Lowe et al. 2000). From its native range in the lower Mississippi River Valley of the USA into northeastern Mexico (Ernst and Lovich 2009), the species has been introduced to all continents except

Antarctica and is widely distributed on temperate and tropical oceanic islands (Rödder et al. 2009; Kikillus et al. 2010). The near global spread of this species is due, in part, to the popularity of colorful hatchlings in the pet trade that continues to this day (Masin et al. 2014). Once released outside its native range, the traits of the species as an opportunistic omnivore and habitat generalist allow it to be successful as an invader (Masin et al. 2014). Their adaptive capabilities, coupled with other traits, make red-eared sliders significant competitors with other native turtles when they become established outside their natural range.

Second, turtles of the genus *Trachemys* are generally adaptable to a wide variety of habitats and environmental conditions. In its native distribution, the genus *Trachemys* occupies the greatest range of latitudes exhibited by any non-marine turtle (35° south–42° north), effectively covering the global latitudinal distribution of all turtle species combined (Buhlmann et al. 2009) and this is reflected in the distribution of *T. scripta* as an invasive species (Kikillus et al. 2010). Their natural ability to exploit new habitats is exemplified by their recent evolutionary history. The genus evolved in North America and entered Central and South America comparatively recently in geological time (Legler 1990). The diversity of habitats occupied by the genus over its wide native range contributed to taxonomic diversification and 28 species and subspecies of *Trachemys* are recognized (van Dijk et al. 2014). The red-eared slider turtle is the most-studied species of turtle that occurs in the USA based on number of peer-reviewed scientific papers per species (Lovich and Ennen 2013). Despite this large base of knowledge, comparatively little is known about the ecology and demography of *T. scripta* outside their native range.

Ongoing conservation-based efforts to remove slider turtles from ponds and rivers in Akashi City, Japan, provided an opportunity to collect data on adult body size (mean, maximum), female size of maturity as measured by size of gravid females, clutch size, population density and biomass, sex ratio, and sexual size dimorphism of invasive slider turtles. These data were then compared with data on these variables from native populations in the USA (Table 1), the presumed origin (Mali et al. 2014) of individuals introduced into Japan, in a largely qualitative attempt to answer the question of whether or not Japanese *T. s. scripta* populations exhibit increased performance over native populations. Our expectations were that adult Japanese *T. scripta* would exhibit potentially earlier maturity, have larger maximum adult body sizes and increased fecundity, and be more abundant per unit area than populations in the

Table 1. Representative body size estimates for adult slider turtles (*Trachemys scripta*) throughout much of their natural range in the United States. This list is by no means exhaustive given that this is the best-studied species of turtle in the United States (Gibbons 1990a; Lovich and Ennen 2013). Other citations are found in the text. All sizes are in mm. Not all sample sizes were given in each citation. For example, many citations focused on female reproduction so male data were not included.

| Location | Study # | Taxon | n | | Plastron length (PL) | | Citation | Comments |
|----------------|----------------------|----------------------|------|--------|----------------------|----------------------|---|--|
| | | | Male | Female | Male | Female | | |
| Central USA | 1 | <i>T. s. elegans</i> | | | 90–100 | 150–195 | (Cagle 1950) | Size of sexual maturity |
| Georgia | 2 | <i>T. s. scripta</i> | | 6 | | 194.4 | (Congdon and Gibbons 1983) | Mean size of reproductive females near the town of Moultrie |
| Illinois | 3 | <i>T. s. elegans</i> | | | 90–100 | | (Cagle 1948a) | Size of sexual maturity |
| | 4 | <i>T. s. elegans</i> | | | | 160–170 | (Cagle 1944) | Size of sexual maturity |
| | 5 | <i>T. s. elegans</i> | | | | 160 | (Cagle 1948b) | Size of sexual maturity |
| | 6 | <i>T. s. elegans</i> | | | | 185 | (Thornhill 1982) | Minimum size of sexual maturity in a heated reservoir |
| | 6 | <i>T. s. elegans</i> | | | | 173 | (Thornhill 1982) | Minimum size of sexual maturity in a normothermic wetland |
| | 7 | <i>T. s. elegans</i> | | | 94 | | (Readel et al. 2008) | Minimum or "benchmark" size at maturity for males |
| | 8 | <i>T. s. elegans</i> | | 9 | | 167 (mean 179) | (Tucker 2001) | Size of smallest nesting female with visible scute annuli |
| | 9 | <i>T. s. elegans</i> | | 53 | | 172 | (Tucker et al. 1998) | Size of smallest nesting female Stump Lake, 1994 |
| | 9 | <i>T. s. elegans</i> | | 11 | | 200 | (Tucker et al. 1998) | Size of smallest nesting female Pohlman Slough, 1994 |
| | 9 | <i>T. s. elegans</i> | | 53 | | 182 | (Tucker et al. 1998) | Size of smallest nesting female Swan Lake, 1994 |
| | 9 | <i>T. s. elegans</i> | | | | 167 | (Tucker et al. 1998) | Size of smallest nesting female Stump Lake, 1995 |
| | 9 | <i>T. s. elegans</i> | | 21 | | 191 | (Tucker et al. 1998) | Size of smallest nesting female Pohlman Slough, 1995 |
| | 9 | <i>T. s. elegans</i> | | 94 | | 181 | (Tucker et al. 1998) | Size of smallest nesting female Swan Lake, 1995 |
| | 9 | <i>T. s. elegans</i> | | | | 170 | (Tucker et al. 1998) | Size of smallest nesting female Stump Lake, 1996 |
| | 9 | <i>T. s. elegans</i> | | | | 187 | (Tucker et al. 1998) | Size of smallest nesting female Pohlman Slough, 1996 |
| 9 | <i>T. s. elegans</i> | | 91 | | 185 | (Tucker et al. 1998) | Size of smallest nesting female Swan Lake, 1996 | |
| Mississippi | 10 | <i>T. s. elegans</i> | 117 | 64 | 131.5 | 195.8 | (Parker 1984) | Greatest mean size of resident and immigrant turtles, 1977 |
| | 10 | <i>T. s. elegans</i> | 115 | 44 | 150.2 | 193.6 | (Parker 1984) | Greatest mean size of resident and immigrant turtles, 1978 |
| | 10 | <i>T. s. elegans</i> | 118 | 48 | 144.3 | 197.8 | (Parker 1984) | Greatest mean size of resident and immigrant turtles, 1979 |
| | 10 | <i>T. s. elegans</i> | 64 | 23 | 144.8 | 192.1 | (Parker 1984) | Greatest mean size of resident and immigrant turtles, 1980 |
| | 10 | <i>T. s. elegans</i> | 59 | 34 | 140 | 192.4 | (Parker 1984) | Greatest mean size of resident and immigrant turtles, 1981 |
| | 10 | <i>T. s. elegans</i> | 80 | 31 | 150.1 | 194.8 | (Parker 1984) | Greatest mean size of resident and immigrant turtles, 1982 |
| Oklahoma | 11 | <i>T. s. elegans</i> | | | 110 | 174 | (Webb 1961) | Size of sexual maturity |
| | 12 | <i>T. s. elegans</i> | 53 | 64 | 148.13 | 179.78 | (Hays and McBee 2010) | Mean size at Tar Creek Superfund Site |
| | 12 | <i>T. s. elegans</i> | 87 | 35 | 154.1 | 171.51 | (Hays and McBee 2010) | Mean size at the Sequoyah National Wildlife Refuge |
| | 12 | <i>T. s. elegans</i> | 25 | 29 | 167.96 | 164.45 | (Hays and McBee 2010) | Mean size at Lake Carl Blackwell |
| South Carolina | 13 | <i>T. s. scripta</i> | | | 90–110 | 160–175 | (Gibbons et al. 1981) | Size of sexual maturity in a normothermic wetland |
| | 13 | <i>T. s. scripta</i> | | | 100–120 | 195 | (Gibbons et al. 1981) | Size of sexual maturity in a heated reservoir |
| | 14 | <i>T. s. scripta</i> | | 5 | | 264 | (Congdon and Gibbons 1983) | Mean size of reproductive females at Kiawah and Capers Islands |
| | 14 | <i>T. s. scripta</i> | | 8 | | 242 | (Congdon and Gibbons 1983) | Mean size of reproductive females at Par Pond (heated reservoir) |
| | 14 | <i>T. s. scripta</i> | | 10 | | 230 | (Congdon and Gibbons 1983) | Mean size of reproductive females at Steel Creek (heated stream) |
| | 14 | <i>T. s. scripta</i> | | 11 | | 176.4 | (Congdon and Gibbons 1983) | Mean size of reproductive females at Ellenton Bay (normothermic) |

Table 1. (continued)

| Location | Study # | Taxon | n | | Plastron length (PL) | | Citation | Comments |
|----------|---------|----------------------|------|--------|----------------------|--------|-----------------------------|--|
| | | | Male | Female | Male | Female | | |
| | 14 | <i>T. s. scripta</i> | | 15 | | 193 | (Congdon and Gibbons 1983) | Mean size of reproductive females at Kearsse Bay (normothermic) |
| | 14 | <i>T. s. scripta</i> | | 10 | | 208.7 | (Congdon and Gibbons 1983) | Mean size of reproductive females at Lodge Lake (normothermic) |
| Texas | 15 | <i>T. s. elegans</i> | | | 105 | 145 | (Ingold and Patterson 1988) | Size of sexual maturity |
| Texas | 16 | <i>T. s. elegans</i> | 85 | 149 | | | (Rose and Manning 1996) | Poor conditions may have contributed to low numbers of adult males |
| Missouri | 17 | <i>T. s. elegans</i> | 387 | 392 | | | (Glorioso et al. 2010) | Missouri |

USA, as predicted under the increased performance measure hypothesis. Since *T. scripta* populations display substantial plasticity in growth rates, timing of maturity and adult body size in response to environmental conditions (Gibbons et al. 1979, 1981; Thornhill 1982), they are a model organism for evaluation of the enhanced performance hypothesis. We observed differences in several demographic attributes that are described in this paper.

Methods

Turtle collection was coordinated by staff of the Kobe Suma Aquarium who are leading conservation-based efforts to remove *T. scripta* from local aquatic habitats to aid in the recovery of declining Japanese turtles including *Mauremys japonica* (Temminck and Schlegel, 1835) and the Asian *Mauremys reevesii* (Gray, 1831) (Suzuki et al. 2011). The latter is a “naturalized” species that was likely introduced to Japan from the adjacent Asian mainland both before and after World War II (see review in Lovich et al. 2011). The study sites included two agricultural ponds in Akashi City (Kami Pond and Sara Pond) and the nearby Taniyagi River. Beyond the agricultural areas, there is little “natural habitat” as the area is highly urbanized. The river is channelized and lined with concrete at the site and the ponds serve as reservoirs in an agricultural area. The Taniyagi River samples were taken close to its mouth where it enters the marine environment.

Turtles were collected using traps baited with fish following techniques described by Gibbons (1988, 1990a). Two types of traps were used. Collapsible box-shaped traps measuring 100 cm × 50 cm × 60 cm were used in the ponds, and semicircular hoop traps, 70 cm × 38 cm × 47 cm, were set in the Taniyagi River. Both trap types were set to allow trapped turtles access to atmospheric air. Seven traps were set in Kami Pond from 17 July 2012 until 11 December 2012 and seven were set in Sara Pond from 18 July

2012 until 14 September 2012. From 49–109 traps were set along a 2 km stretch of the Taniyagi River during 11 trapping intervals (ranging from 2–6 days each) between 13 May 2013 and 16 November 2013.

All *T. scripta* were removed from the habitat and placed in temporary holding facilities at the Kobe Suma Aquarium. Turtle body size was measured as straightline plastron length (PL), a useful and commonly used metric for quantifying body size in this and other turtle species (Gibbons 1990a; Gibbons and Lovich 1990). Measurements were taken with calipers accurate to the nearest 0.1 mm and weight was recorded to the nearest gram. Reproductive data were taken from female turtles that were humanely euthanized with injections of pentobarbital sodium (see Saka et al. 2011; Suzuki et al. 2014) under guidelines recommended for unprotected invasive species by the Japanese Ministry of the Environment. Unfortunately, holding facilities and animal shelters in Japan and the USA are often overwhelmed by the sheer numbers of unwanted invasive slider turtles prompting advisories against their acceptance (e.g., the New York Turtle and Tortoise Society, <http://nytts.org/nytts/sliders.htm>). As a result, euthanasia is proposed as a way of dealing with invasive slider turtles, including by government agencies in the USA (<http://www.dgif.virginia.gov/wildlife/problems/turtles/>).

Surface areas of ponds and rivers were estimated by using Google Earth™. Biomass estimates were calculated as the sum of captured *T. scripta* body weights (including juveniles) divided by estimated surface area of the aquatic habitat sampled. Following Lovich and Gibbons (1992) and Lovich et al. (2014) we calculated ratios for sexual dimorphism indices (SDIs) and sex ratios of adults as follows. If females are larger or more numerous than males then SDI or sex ratio equals

$$\left(\frac{\text{adult female size or number}}{\text{adult male size or number}} \right) - 1$$

where the value for female size or numerical superiority is a positive number minus 1.

If males are larger or more numerous than females then SDI or sex ratio equals

$$- \left(\frac{\text{adult male size or number}}{\text{adult female size or number}} \right) + 1$$

where the value for male size or numerical superiority is a negative number plus 1. The values thus derived are symmetric around zero, the point of equal size or equal numbers of each sex, and properly scaled. The advantages of this approach are discussed in more detail by Lovich and Gibbons (1992) and Smith (1999).

To facilitate consistency in comparisons with data on adult SDI (Gibbons and Lovich 1990) and sex ratios (Gibbons 1990b) for *T. s. scripta* (Thunberg in Schoepff, 1792) and *T. s. elegans* (Tucker et al. 1998; Tucker 2001) from natural habitats in the USA, we assumed a minimum size of maturity for males and females in our calculations as 100 and 160 mm PL (Gibbons et al. 1981), respectively. We tested this assumption for females by determining the minimum and range of PL sizes for a subsample of gravid female Japanese *T. scripta*. Adult sex ratio was examined because it has important demographic and ecological consequences for turtle populations (Lovich and Gibbons 1990; Lovich 1996). Departures from a null hypothesis of 1:1 sex ratios of Japanese populations were tested with Chi-squared analyses. We also used least squares linear regression (and the associated Coefficient of Determination, R^2) to examine the relationship between the predictor variable (PL) and the response variable (clutch size) of Japanese turtles. Prior to conducting the linear regression analysis we examined normal probability plots of PL and clutch size and determined that the distributions did not deviate from expectations for parametric analysis and transformations were unnecessary. Statistical tests were considered to be significant at alpha levels ≤ 0.05 . Means are reported \pm one SD.

All comparisons and contrasts in our qualitative analyses were based on data for *T. scripta* populations from the USA (Table 1). More quantitative analyses are complicated by different measurements among studies as shown under the Comments column of Table 1 as well as different sample sizes and field techniques. The two subspecies, *T. s. elegans* and *T. s. scripta*, have very similar morphology and biology and readily interbreed (Ernst and Lovich 2009). For these reasons, our comparisons involve both taxa. Because of the plasticity of age and timing of maturity of *T. scripta* populations and their effects on adult body size, our comparisons and contrasts

are by necessity generalized. In addition, research on populations of slider turtles in thermally-impacted habitats (such as those receiving effluent from power plants or nuclear reactors; Gibbons et al. 1981; Thornhill 1982) and offshore subtropical barrier islands in the USA (Gibbons and Harrison 1981) show that these populations are comprised of very large individuals that vary in the timing and size of maturity relative to populations in normothermic habitats on the mainland. Most of our comparisons involve the latter for consistency.

Results

Body size, maturity and reproductive biology of red-eared slider turtles in Japan

A total of 2,111 *T. scripta* were captured at three locations in Japan and included in our analyses. The smallest turtle collected was a 24.4 mm hatchling and the largest was a 231.6 mm female. Mean and maximum size of adult males over 100 mm ranged from 129.3–133.3 mm and 173.4–207.0 mm, respectively. Mean and maximum size of adult females over 160 mm ranged from 184.8–188.7 mm and 215.3–231.6 mm (Table 2). Of the turtles collected in the Taniyagi River, 130 females were gravid with a mean PL of 182.4 ± 20.8 mm, and ranged from 134.9–231.6 mm PL. Mean clutch size of oviductal eggs was 8.3 ± 2.8 and ranged from 1–19 eggs. Clutch size increased with PL (Figure 1) and the relationship was statistically significant ($F_{1, 128} = 55.391$; $P < 0.001$). The slope of the relationship was 0.07, or an increase of about 1 egg/14.3 mm PL, and PL explained slightly more than 30% of the variation in clutch size ($R^2 = 0.302$).

Density and biomass of populations in Japan

Turtle densities ranged from 89.6–299.6 turtles/ha. Mean body mass of turtles from all study areas ranged from 533.5–622.5 g, with the largest mean weight in the Taniyagi River. Biomass estimates ranged from 47.8–186.5 kg/ha (Table 3).

Sex ratios and sexual size dimorphism in Japan

Adult sex ratios of turtles meeting our size criteria for sexual maturity were female-biased and ranged from 1.05 females:1 male (index of 0.05) to 1.69 females:1 male (index of 0.69). Sex ratio (Table 2) was not significantly different from 1:1 for Akashi Kami Pond (two-tailed $\chi^2 = 0.071$, $P = 0.79$, $df = 1$), but was significantly female-biased for Akashi Sara Pond (two-tailed $\chi^2 = 6.94$, $P = 0.008$, $df = 1$). The Taniyagi River sample was female-biased and almost

Table 2. Summary of sample sizes, mean plastron length (PL) in mm, standard deviation, and maximum PL of red-eared slider turtles (*Trachemys scripta elegans*) collected in various locations near Kobe, Japan. Data, including sex ratios and sexual dimorphism indices, are calculated using only adult males (PL \geq 100 mm) and adult females (PL \geq 160 mm) with the method of Lovich and Gibbons (1992) outlined in the text.

| | Sex/attribute | | | | | | | | Sex ratio | SDI |
|------------------|---------------|-----------|------|---------|---------|-----------|------|---------|-----------|------|
| | Males | | | | Females | | | | | |
| | n | \bar{x} | SD | maximum | n | \bar{x} | SD | maximum | | |
| Akashi Kami Pond | 62 | 131.0 | 21.1 | 192.5 | 65 | 184.8 | 15.9 | 215.3 | 0.05 | 0.41 |
| Akashi Sara Pond | 39 | 133.3 | 20.6 | 173.4 | 66 | 188.7 | 15.2 | 224.6 | 0.69 | 0.42 |
| Taniyagi River | 420 | 129.3 | 20.7 | 207.0 | 473 | 186.4 | 15.8 | 231.6 | 0.13 | 0.44 |

Table 3. Density and biomass of red-eared slider turtles (*Trachemys scripta elegans*) collected near Kobe, Japan. Refer to Table 1 for sample sizes of adults. Juveniles (Akashi Kami Pond: n = 111; Akashi Sara Pond: n = 133; Taniyagi River: n = 742) were included in these calculations.

| Location | Attribute | | | |
|------------------|---------------------------|--------------------|------------|-----------------|
| | Surface area sampled (ha) | Mean body mass (g) | Turtles/ha | Biomass (kg/ha) |
| Akashi Kami Pond | 1.9 | 585.7 | 123.8 | 72.5 |
| Akashi Sara Pond | 2.7 | 533.5 | 89.6 | 47.8 |
| Taniyagi River | 5.5 | 622.5 | 299.6 | 186.5 |

statistically different from 1:1 (two-tailed $\chi^2 = 3.146$, $P = 0.08$, $df = 1$). Sexual dimorphism indices (Table 2) based on mean PL of adult turtles were all female-biased with SDIs ranging from 0.41–0.44 (i.e. females were, on average, 1.41–1.44 times larger than males).

Body size of males in the USA

The size of male *T. s. elegans* in the USA ranges from 148.1–168.0 mm with a mean of 156.7 mm (Table 1, Study #12). If maximum mean size of males from Mississippi farm ponds are included (Table 1, Study #10) the range is 131.5–168.0 mm with a mean of 147.9 mm. Maximum mean size of females from the same Mississippi farm ponds ranged from 192.1–197.8 mm with a mean of 194.4. Lovich et al. (1990, Table 19.5) summarized mean and maximum male PL for eight populations of *T. s. scripta* in South Carolina based on whether males were melanistic (normally larger than nonmelanistic males) or not. Nonmelanistic males from normothermic, mainland populations had PL values ranging from 100–210 mm. Mean PL values for these populations ranged from 131–154 mm. Melanistic males from normothermic mainland populations had PL values ranging from 104–223 mm. Mean PL values ranged from 163–174 mm. Nonmelanistic males from thermally-altered or island habitats (Capers Island, Steel Creek, and Par Pond) had PL values ranging from 100–243 mm. Mean PL values for these populations ranged from 151–155 mm. Melanistic males from thermally-altered or island habitats had PL values ranging from 126–226 mm. Mean PL values ranged from 180–200 mm.

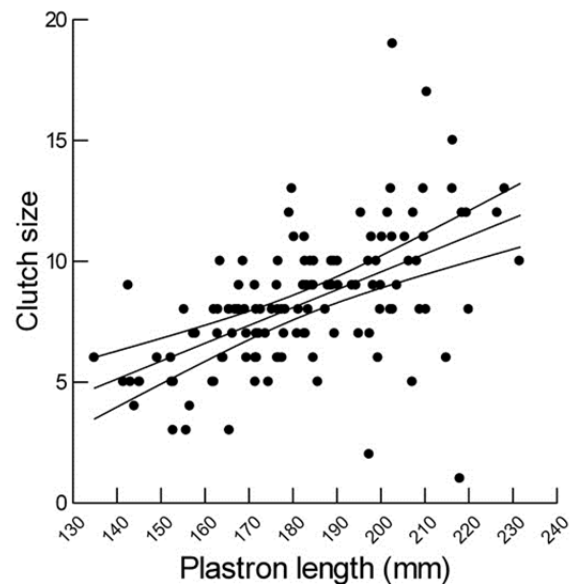


Figure 1. Relationship between plastron length and clutch size in a sample of 130 slider turtles (*Trachemys scripta elegans*) collected in Japan with 95% confidence interval. The relationship is statistically significant (F -ratio_{1,128} = 55.391; $P < 0.001$; $R^2 = 0.302$).

Size of maturity and reproductive biology of females in the USA

The minimum size of maturity of *T. s. elegans* females in the USA from normothermic, mainland habitats ranges from 150–200 mm with a mean of 175.6 mm (Table 1, Study # 1, 5, 6, 8, 9, 11). If *T. s. scripta* is included with the above stipulations, the range is 145–200 mm with a mean of 172.8 mm (Table 1, Study # 1, 5, 6, 8, 9, 11, 13, 15). The mean

size of known reproductive female *T. s. scripta* from normothermic mainland populations ranges from 176.4–208.7 mm with a mean of 193.1 mm (Table 1, Study # 2, 14). Populations of *T. s. scripta* from thermally-altered or island habitats exhibit much larger body sizes (Table 1, Study # 6, 13, 14). Clutch sizes in the USA range from 1–30 eggs (mean = 10.5) based on the literature reviewed by Ernst and Lovich (2009).

Density and biomass of populations in the USA

Densities and biomasses reported for *T. scripta* populations in the USA range from 41.8–61.5 turtles/ha and 33.6–37.1 kg/ha, respectively, in normothermic mainland populations (Congdon et al. 1986). Under exceptional circumstances, slider turtles can achieve densities of 983 turtles/ha (Rose and Manning 1996) and 877 kg/ha (Congdon et al. 1986), impressive figures for any vertebrate.

Sex ratios and sexual size dimorphism of populations in the USA

Using data tabulated in Table 1 and reported in other sources for *T. scripta* from the USA (e.g., Gibbons 1990b), adult sex ratios for *T. s. elegans* are predominantly male-biased and have indices ranging from -0.74 to -1.78 based on seven out of ten samples (Study # 10, 11, 12). Two samples (Study #12) were female-biased with indices of 0.16 and 0.21 and another (Study #17) was unbiased. It should be noted that sexual maturity was not confirmed in the latter three samples based on nesting observations, dissection, or radiography. In another study shown in Table 1 (#16), females greatly outnumbered males, but the authors suggested that low food availability may have disproportionately affected males due to their smaller body size relative to females perhaps resulting in their lower relative abundance. Sexual size dimorphism indices range from 0.09 to 0.55 throughout the range of the species, with mean adult female body size consistently greater than that of males (Gibbons and Lovich 1990), as reflected in Table 1.

Discussion

Slider turtles were introduced into Japan prior to 1972 (Lever 2003), probably in the 1950s (Kamezaki 2015, Lovich and Yamamoto *in press*). Since then, the species has become well-established, particularly in agricultural and urban areas where people are concentrated and opportunities for release of unwanted pets are high. Six non-marine species of Asian turtles are native to or naturalized in Japan (van Dijk et al. 2014) and the growth of slider turtle populations has

been implicated in the decline of indigenous species. For example, a survey of 802 sites in 46 prefectures in 2003 found that 90% of 5,966 turtles captured were invasive species with *T. scripta* making up 62% (3,708) of all captures (Ramsay et al. 2007). A more recent survey (2010–2014) from 518 ponds in western Japan found 4,347 turtles in the following proportions: *M. japonica* 15.4%, *M. reevesii* 45.6%, and *T. scripta* 36.9% (Taniguchi et al. 2015).

Body size

In terms of maximum body size, female *T. scripta* found in the three Japanese populations fit within the range of the largest females in five populations from South Carolina, USA in normothermic habitats reported by Gibbons and Lovich (1990). The largest Japanese male (207 mm) also fit within the range of values for males in the same USA populations. Growth rates and maximum body sizes in *T. scripta* vary in response to environmental conditions, even at a micro-geographic scale. For example, Gibbons et al. (1981) studied two *T. s. scripta* populations that occupied very different habitats. One population lived in a normothermic natural wetland (Ellenton Bay) and the other lived in a nearby thermally impacted reservoir (Par Pond) in South Carolina. Females in Ellenton Bay matured at about 160–175 mm PL in eight years, while faster growing females in Par Pond matured at about the same age, but at 195–210 mm PL. In contrast, males reached maturity at about the same size (90–120 mm PL) but at differing ages for Ellenton Bay and Par Pond of 4–5 years and 3–4 years, respectively. Gibbons et al. (1981) concluded that the differences were due to more optimal temperatures and food availability in Par Pond. Similar results were reported for *T. s. elegans* populations living in natural and thermally impacted lakes in Illinois, USA (Thornhill 1982).

Size of maturity in females and reproductive biology

Mean body sizes for female Japanese *T. scripta* were between the size ranges for maturity in the two populations discussed above, but closer to those for Ellenton Bay. Empirical data on maturity in female turtles requires the use of radiography (Gibbons and Greene 1979; Gibbons et al. 1981) or other means to determine egg production such as dissection, as used in our study. Our data on gravid females suggest that Japanese *T. scripta* can mature at a PL of only 134.9 mm, which is substantially smaller than females from Ellenton Bay, South Carolina, and the mean values of known age nesting female *T. s. elegans* in Illinois (Tucker et al. 1998; Tucker 2001).

Despite the smaller size at maturity, mean clutch size of Japanese *T. scripta* was 8.3 eggs, a value higher than the mean reported for Ellenton Bay ($\bar{x} = 6.1$ eggs) but lower than that for Par Pond ($\bar{x} = 10.2$ eggs) (Gibbons and Greene 1990). All are smaller than the mean clutch sizes reported by Tucker et al. (1998) for *T. s. elegans* in Illinois. The latter authors noted that once the effect of body size was removed in comparisons between Ellenton Bay and Par Pond, the mean clutch sizes were not significantly different. Thus, the increase in clutch size is no more than would be expected due to differences in body size between the two habitats in the USA. In support of this observation, we found that the slope of the least squares linear regression analysis between PL and clutch size was 0.07, exactly the same slope reported by Congdon and Gibbons (1983) for various populations of *T. s. scripta* in Georgia and South Carolina. However, our data for Japanese *T. scripta* suggest that mean clutch size is larger than Ellenton Bay even when the minimum size at maturity appears to be smaller in Japan. Collectively, our comparative data on maturity and reproduction suggest that *T. scripta* in Japan may mature at a smaller body size than females in the USA, with gravid females attaining slightly larger body sizes than natural populations (excluding those in thermally impacted environments) at similar latitudes in the USA.

Male body sizes

Mean body sizes for male Japanese *T. scripta* were on the lower end of the range of those in the USA implying earlier sizes at maturity in the former. Maturity in males is suspected to occur coincidentally with the expression of secondary sexual characteristics, presumably making determination of maturity more straightforward than it is in females (Lovich et al. 1990).

Density and biomass

Turtle populations make significant contributions to the biomass of their environment (Ernst and Lovich 2009). Biologists have been interested in turtle biomass since at least the late 1970s (Coe et al. 1979; Makeeb 1979). In the first critical review of the topic, Iverson (1982) noted that turtle biomass is generally very high in comparison to other vertebrates, surpassing that of all other reptiles. High biomasses are achieved by turtles for a variety of reasons including overlapping generations, individual longevity, and low energy requirements for most species. Some of the highest biomasses of turtles come from populations of turtles and tortoises living on islands.

The biomass and turtle density values we observed in Japan are within the range of most natural populations in the USA. However, the turtle density values are at the high end at 299.6 turtles/ha in the Taniyagi River. This is especially true if the exceptionally high densities reported from Capers Island, South Carolina (Congdon et al. 1986) and Texas cattle ponds (Rose and Manning 1996) are excluded. It is important to note that the highest density and biomass values in the USA are reported from populations living in ponds and lakes. Slider turtles prefer lentic aquatic habitats (Morreale and Gibbons 1986; Ernst and Lovich 2009). The high density and biomass values from the Taniyagi River may be the highest ever reported for *T. scripta* from a lotic habitat. The large number of *T. scripta* in the mouth of the Taniyagi River may be due to its proximity to marine and estuarine habitats with high prey diversity in the ecotone. Some of the *T. scripta* captured in the Taniyagi River contained the remains of sea urchins in their digestive tracts, a food item not previously noted for slider turtles (Ernst and Lovich 2009).

Sex ratios and sexual size dimorphism

Growth rates affect turtle sex ratios (Lovich and Gibbons 1990; Lovich 1996), including those for *T. s. scripta* (Gibbons 1990b). Similarly, growth rates affect the degree and direction of sexual size dimorphism in turtles like *T. scripta* (Gibbons and Lovich 1990; Lovich et al. 2014). The earlier maturing sex remains smaller, on average, throughout life and tends to predominate numerically in the adult population unless the sexes are strongly affected by differential mortality, differential emigration or immigration, or biased primary sex ratios (Lovich et al. 2014). Our raw data for Japanese *T. scripta* show female-biased sex ratios (Table 2). This result is the opposite of what has been demonstrated for most natural populations in protected areas of the USA (Gibbons 1990b) and what is predicted from data validated for other turtle species where, on average, adult males are smaller than adult females (Lovich and Gibbons 1990; Lovich et al. 2014). In keeping with our observations, a sample of 67 *T. s. scripta* captured in Kyoto Prefecture, Japan was also female-biased (41 males: 26 females based on Figure 3 in Haramura et al. 2008).

Perceived and actual adult turtle sex ratios vary due to five factors including sampling bias, differential mortality (see Takenaka and Hasegawa 2001 for an example from a turtle population in Japan), differential emigration or immigration, biased primary sex ratios, or sex-specific differences in the

size at maturity (i.e. bimaturation). All of these factors can affect turtle populations to some degree. We believe we can rule out sampling bias due to our large overall sample size and consistently female-biased sex ratios in our samples. However, an explanation is needed to explain the aberrant female-biased sex ratios observed in our data on Japanese *T. scripta* and we offer one that is a testable hypothesis.

Many turtles, including *T. scripta*, have environmental sex determination where incubation temperature determines hatchling sex. In *T. scripta*, eggs incubated at cool temperatures below 27 °C produce all males while those incubated at higher temperatures of 30 °C produce all females (Ewert and Nelson 1991). All the habitats we sampled are either in agricultural (Akashi Kami and Akashi Sara Ponds) or urban areas (Taniyagi River) virtually devoid of natural tree or shrub cover. It is likely that these areas receive high amounts of insolation resulting in warm female-producing soil temperatures. Turtle nests in open areas tend to produce more female hatchlings (Vogt and Bull 1982, 1984). Increasing temperature as little as 2 °C may dramatically alter sex ratios of hatchling turtles (Janzen 1994) toward a female bias. Research on another species of turtle (*Chelydra serpentina* Linnaeus, 1758) demonstrated that agricultural practices also affect sex ratio variation in hatchlings with open areas producing more females (Freedberg et al. 2011). Additional research is necessary to test our “high insolation hypothesis” and determine the cause of the adult female-biased sex ratios of *T. scripta* in Japan.

Our data on sexual size dimorphism show that Japanese *T. scripta* SDI values (Table 2) based on the mean PL of adult males and females are at the high end of the range of those for nine populations in South Carolina (Gibbons and Lovich 1990). The potentially early size of maturity in Japanese males and the large size of gravid Japanese females contributed to elevated SDI values. Ultimately, sexual size dimorphism in *T. scripta* is caused by the sometimes opposing forces of natural and sexual selection that drive growth and maturation patterns between the sexes (Gibbons and Lovich 1990).

Do Japanese slider turtles have a performance advantage?

Returning to our overall question, do *T. scripta* populations in Japan display enhanced performance measures (Parker et al. 2013) perhaps due to enemy release (Keane and Crawley 2002) or other factors that allow them to do better in their new habitat? Judging from the almost complete dominance of slider turtles relative to native Japanese turtles (Ramsay et

al. 2007), the answer would seem to be yes. Our data suggest that, compared to slider turtles in natural (not thermally-enhanced) habitats in the USA, gravid female *T. scripta* in Japan tend to be somewhat larger. Sexual maturity of male *T. scripta* is influenced by the need to mature early to enhance reproductive success, and to do so at a size that minimizes vulnerability to predation (Gibbons and Lovich 1990). It is possible that enemy release allows male Japanese *T. scripta* to mature at smaller sizes. However, a North American predator of slider turtles, the raccoon (*Procyon lotor* Linnaeus, 1758), is also well-established and widely distributed in Japan (Ikeda et al. 2004).

In turn, different growth rates in Japan affect both sex ratio and sexual size dimorphism in ways that differ from those observed in natural populations. In particular, sexual size dimorphism is at the high end of what is reported in the USA. The female-biased adult sex ratios we observed are unusual in comparison to native populations of *T. scripta*, but may be related to the lack of cover at nest sites that result in female-producing incubation temperatures. Given the conservation concerns associated with *T. scripta* in Japan, the dominance of females means that population recruitment may be enhanced, making control or eradication of slider populations even more difficult. This is especially true because in many turtle species, one male may inseminate multiple females (Pearse et al. 2002) and the latter are capable of storing viable sperm (Gist et al. 2001) for several years (Hildebrand 1929; Gist and Jones 1987; Palmer et al. 1998). Since Japanese *T. scripta* have larger clutch sizes than some native populations (e.g., Ellenton Bay, South Carolina, Gibbons and Greene 1990), their numerical dominance coupled with potentially smaller size of maturity may further complicate control efforts.

Finally, the high density and biomass of turtles in the Taniyagi River is exceptional since slider turtles prefer still water. The dominance of the “turtle niche” in the river by *T. scripta* is exemplified by the near absence of native and naturalized Japanese turtles in the study reach. Flood control efforts in Japanese rivers contribute to the deterioration of habitat quality for Japanese turtles (Usuda et al. 2012), but appear to have limited effects on *T. scripta* populations. To the best of our knowledge, the high density and biomass of turtles in the Taniyagi River is the highest value ever reported from a flowing water habitat. Slider turtles are well-established in Japan and will likely continue to dominate native turtle habitats until more effective control efforts are implemented.

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