Changes in Population Structure of the Freshwater Turtle Mauremys japonica Following the Invasion of Feral Raccoon Procyon lotor in the Southern Tip of the Boso Peninsula, Japan

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Abstract: The raccoon (*Procyon lotor*) was introduced to Japan from North America, and has been implicated in the population declines or local extinctions of native freshwater turtles. We conducted a capture–recapture study of the Japanese pond turtle (*Mauremys japonica*) at two sites in the Boso Peninsula, Japan, to investigate the effects of *P. lotor* predation on the demography of native turtle populations, during the period from 2014 to 2017, shortly after an invasion of *P. lotor*. The study revealed a steady decline in turtle population size, along with changes in age structure, characterized by a skew toward older age classes. We also found a number of living individuals with amputated limbs, which we suspect to be evidence of *P. lotor* predation. Such injuries highlight the importance of the early detection of population declines and identification of related warning signals or demographic characteristics, which in turn will enable the timely implementation of appropriate conservation measures to prevent local extinctions of freshwater turtles.

Key words: Adult and juvenile survival rate; Capture-recapture; *Mauremys japonica*; Non-native raccoon predation; Population decline

INTRODUCTION

The Japanese pond turtle (*Mauremys japonica*) is endemic to Japan, where it is distributed in the islands of Honshu, Shikoku, Kyushu, and the adjacent small Japanese islands (Yasukawa et al., 2008). Although the eggs, hatchlings, and juveniles of *M. japonica* are preyed upon by native predators, such as Japanese striped snake (*Elaphe quadrivirgata*), Japanese giant salamander (*Andrias japonicus*), weasel (*Mustela itatsi*), crows (*Corvus* spp.), and raccoon dog (*Nyctereutes procyonoides*) (Yabe, 2002; Matsukubo, 2005; Kosuge and Kobayashi, 2015), mature and large adult turtles are generally at little

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risk from predation by native predators (Yabe, 2002; Yasukawa et al., 2008). Consequently, *Ma. japonica* used to be a common and sometimes abundant freshwater turtle in Japan (Yasukawa et al., 2008).

However, anthropogenic threats including habitat loss, river alteration, resource competition (e.g., for food and basking sites) with the red-eared slider (*Trachemys scripta elegans*), hybridization with Reeves' pond turtle (*Ma. reevesii*), and overexploitation for the pet trade (Yasukawa et al., 2008; Usuda et al., 2012; Yabe, 2014) all threaten this species. In recent predation by the feral raccoon *Procyon lotor* native to North America, has also been recognized as a novel threat to *Ma. japonica* populations (Kosuge and Kobayashi, 2015; Ogano et al., 2015a). Although there is circumstantial evidence that *Ma. japonica* underwent rapid declines in local and restricted areas where *P. lotor* has appeared (Kosuge and Kobayashi, 2015; Ogano et al., 2015a), the processes and mechanisms underlying these population declines have yet to be established. In Japan naturalists and herpetologists suspect that the recent spread of *P. lotor* is a prominent causal factor in the recorded population declines and local extinctions of *Ma. japonica* in formerly *P. lotor*-free freshwater habitats (Kosuge and Kobayashi, 2015; Ogano et al., 2015a).

Procyon lotor preys not only on the eggs and juveniles of freshwater turtles but also on adults (Seigel, 1980; Tucker et al., 1999; Feinberg and Burke, 2003; Karson et al., 2019). The findings of previous studies (e.g., Congdon et al., 1993, 1994; Enneson and Litzgus, 2008) have indicated that populations of freshwater turtles with slow life-history strategies are vulnerable to even small reductions in adult survivorship, with as little as a 2–3% reduction in survivorship resulting in severe population declines (Keevil et al., 2018). Therefore, *P. lotor* may cause substantial reductions in native turtle populations in countries such as Japan where it has been introduced (Kosuge and Kobayashi, 2015; Ogano et al., 2015a).

To obtain basic information on the demographic risk posed by *P. lotor* to native freshwater turtles, we conducted a capture–recapture study of *Ma. japonica* during the initial period when feral *P. lotor* invaded the study area, in order to identify the warning signals of *P. lotor* predation. We detected a steady population decline, characterized by an age structure skewing toward older age classes and an increasing number of living individuals with amputated limbs, which we considered to be evidence of *P. lotor* predation (Kosuge and Kobayashi, 2015; Ogano et al., 2015b; Suzuki et al., 2015). On the basis of these findings, we discuss strategies for the early detection of serious declines in the populations of freshwater turtles, thereby enabling the implementation of timely and appropriate conservation measures to prevent local extinctions.

MATERIALS AND METHODS

Study sites

During the period between late July and late September in the years from 2014 to 2017, we conducted a capture–recapture study of *Ma. japonica* along approximately 3 and 1.5 km reaches of two small rivers in Tateyama City (the Sunomiyagawa and Sanogawa rivers, respectively) at the southern tip of the Boso Peninsula, Chiba Prefecture, Japan (Fig. 1). The study area is located within a region of Chiba Prefecture containing habitats favorable to *Ma. japonica* (Ogano et al., 2015a), owing to an absence of anthropogenic disturbance, such as extensive river alteration practices. Moreover, though hybridization between *Ma. japonica* and the non-native *Ma. reevesii* has occurred (Kagayama et al., 2017), there is an absence of potentially detrimental biotic impacts associated with the presence of the non-native competitor *T. s. elegans*. Although the study area is inhabited by potential native and non-native predators of the eggs, hatchlings, and juveniles of *Ma. japonica* (e.g., Japanese striped snakes, raccoon dogs, weasels, crows, and feral cats), there are no major predators
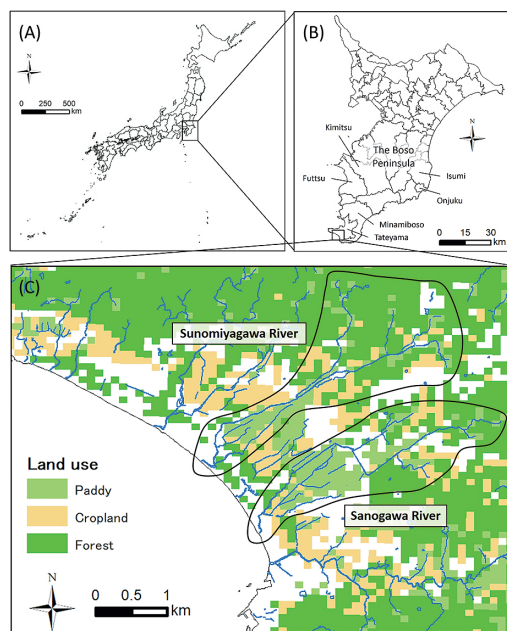
Fig. 1. Study area, (A) Japan, (B) Chiba Prefecture, and (C) study rivers. Blue lines indicate the shoreline of rivers and ponds (Suigaisen). The data were provided by the Geospatial Information Authority of Japan (2019). Land use data (100×100 m grids) were provided by the Ministry of Land, Infrastructure, Transport, and Tourism of Japan (2014). To prevent potential over-exploitation of turtles for the pet trade, we have not included details of the survey sites.

of adult female *Ma. japonica*.

Given these aforementioned characteristics, the study area could be regarded as an important area in which to study the temporal dynamics of the detrimental effects of *P. lotor* on native turtle populations. In the area around Tateyama City, no *P. lotor* individuals were captured prior to 2009 (Asada and Shinohara, 2009; Asada, 2011), and the number of captures remained low until 2012 (Asada, 2014). In the Boso Peninsula, *P. lotor* initially established breeding populations in the late 1990s in the cities of Isumi and Onjuku on the southeastern side of the peninsula, which are assumed to have originated from individuals that were either accidentally or intentionally released (Ochiai et al., 2002).

Further founding populations of *P. lotor* were detected in the cities of Kimitsu and Futtsu, located in the northwestern part of Boso mountain (Yoshida et al., 2020). The time-lag in the appearance of *P. lotor* in Tateyama could be ascribed to the time required for individuals to disperse from one or both of these locations.

In each of the administrative units in Chiba Prefecture, the programs to control and reduce the agricultural damage caused by *P. lotor* have been implemented in each fiscal year by capturing individual using baited traps, and catch per unit effort (CPUE: the number of removed individuals/100 trap-days) data have been compiled by Chiba Prefecture since 1999. For the purposes of the present study, we used CPUE data for Tateyama City collected during the period from 2013 to 2017 (fiscal years) to examine causal relationships between trends in the local populations of *Ma. japonica* and *P. lotor* in the study area.

Capture–recapture procedures

Turtles were captured using traps (72 cm× 44 cm×55 cm) baited with fish, which incorporated a 1.7-m-long bag-like passage for the trapped turtles to breath air (Fig. 2). The traps were prepared in the afternoon of the day prior to deployment and inspected the following morning. Each year, we conducted four to seven capture–recapture sessions using 14 or 18 traps in the Sunomiyagawa River and three to five capture–recapture sessions using 12 or 14 traps in the Sanogawa River (Table 1). Furthermore, during the day, we walked along a channel (approximately 20 m in length) connected to the Sunomiyagawa River and captured all observed turtles by hand. These turtles were marked to identify individuals following the method described by Kobayashi (2008). For each of the captured turtles, we recorded sex, age, carapace length (CL), and limb amputation status. Sex was categorized as female, male, or undetermined (unsexed), based on the relative position of the cloaca (Yabe, 1989). Turtle age was esti-

TABLE 1. Number of sampling sessions and traps used per year.

Year	Sunomiyagawa River		Sanogawa River	
	Number of sampling sessions	Number of traps	Number of sampling sessions	Number of traps
2014	7	18	3	14
2015	6	14	5	12
2016	5	14	3	12
2017	5	14	4	12

mated by counting the annuli on the plastron scutes (Sexton, 1959). All individuals with effaced carapaces and uncountable plastron scutes and/or estimated to be over 11 years of age were classified as old individuals. To determine trends in the population dynamics of male, female, and juvenile turtles, males with a CL>80 mm (approximately >three years old) and females with a CL>150 mm (approximately >eight years old) were defined as adult turtles (Yabe, 1989, 1992; Yasukawa et al., 2008; Kagayama, 2020a). In contrast, zero- (hatchlings) to four-year-old turtles (including unsexed individuals and females, but excluding males; see the following section) were defined as juveniles. Turtles that had at least one amputated limb were recorded as limb-amputated individuals.

Population size estimation

To estimate the population size of *Ma. japonica* in the Sunomiyagawa and Sanogawa rivers from 2014 to 2017, we applied the Jolly–Seber (JS) model (Jolly, 1965; Seber, 1965), based on the state-space formulation of Bayesian hierarchical models and the Just Another Gibbs Sampler (JAGS) code described by Kéry and Schaub (2012a, b). We made extensive use of parameter-expanded data augmentation (Royle et al., 2007; Kéry and Schaub, 2012a; Royle and Dorazio, 2012), which entails augmenting a dataset by adding a large number of potentially unobserved individuals, all with zero-only encounter histories. The key idea is to fix the dimension of the parameter space in the analysis by augmenting the observed data with a large

FIG. 2. Method used to capture freshwater turtles. (A) A trap baited with fish (mesh size: 11 mm), (B) an installed trap in a river pool. The photographs were taken in an area that is not located at the study site (Isumigawa River system in Chiba Prefecture, Japan).

number of all-zero capture histories, resulting in a larger dataset with a fixed dimension M. This augmented dataset is then analyzed using a reparameterized (zero-inflated) version of the model that could be applied if the superpopulation size (the number of individuals that survived during the study) is known (Kéry and Schaub, 2012a). Moreover, we adopted the superpopulation parameterization approach for the JS model (see details in Kéry

and Schaub, 2012a). This model can be used to estimate the superpopulation size (Nsuper), population size in each year (N), capture probability (P), survival rate (Phi), number of entries (B), entry probability (b), and inclusion probability (Psi). Psi is the probability that a member of the augmented dataset, M (M individuals), is included in Nsuper.

Given that the survival rate of turtles is highly dependent on their body size and life-history stage (Iverson, 1991), we used separate models for adults and juveniles to estimate their respective population sizes from 2014 to 2017. Furthermore, as the survival rates of males and females of different body sizes can potentially differ, we assumed that survival rate of adults is sex-dependent. We also assumed a constant capture probability (P) and time-dependent entry probabilities (b). In this model, we used the capture histories of 34 adult males (Sunomiyagawa River: 19 individuals; Sanogawa River: 15 individuals) and 47 adult females (Sunomiyagawa River: 33 individuals, Sanogawa River: 14 individuals). For both males and females, the datasets were augmented with 500 individuals with all-zero capture histories. The JS model for the adults was constructed based on the JAGS code described by Kéry and Schaub (2012b) (Appendix I).

In contrast, those individuals marked (identified) when they were between zero (hatchlings) and four years old were defined as juveniles (including unsexed individuals and females). Given that males attain adulthood at approximately three years of age, we excluded male turtles from our estimations of juvenile population sizes. In this model, we assumed constant survival (Phi), capture probabilities (P), and time-dependent entry probabilities (b). We used the capture history of 80 juveniles, and augmented the model with 1000 individuals with all-zero capture histories. The JS model for juveniles was constructed based on the JAGS code described by Kéry and Schaub (2012a) (Appendix II). However, given the small number of samples obtained for the Sanogawa River, we did not estimate the population size of juveniles in this river.

We estimated the parameters of the JS model using Markov Chain Monte Carlo (MCMC) methods in JAGS ver. 3.4.0 (Plummer, 2003) via the R2jags package (Su and Yajima, 2015) in R ver. 3.5.0 (R Core Team, 2018). We discarded the initial 50,000 MCMC samples as burn-in, and performed an additional 50,000 MCMC iterations, saving every 100th iteration to reduce serial autocorrelation among the adult turtle samples. In contrast, for juvenile turtle samples, we discarded the initial 100,000 MCMC samples as burn-in and performed an additional 100,000 MCMC iterations, saving every 200th iteration to reduce serial autocorrelation. We confirmed convergence by assessing whether the $\hat{R}$ value was smaller than 1.1 for all estimates. We summarized the posterior distributions of all parameters using the mean of all MCMC samples as a point estimate and used the 2.5 and 97.5 percentiles of the MCMC samples as a 95% credible interval (95% CI).

RESULTS

Current status of Ma. japonica *in a* P. lotor *invasion area*

We marked 181 *Ma. japonica* individuals (identified individuals: 144 and 37 in the Sunomiyagawa and Sanogawa rivers, respectively). Turtles of all life-history stages, from hatchlings and juveniles to adults, were captured from both rivers. However, during the study period the age structure of females in the Sunomiyagawa River tended to be skewed toward older adults (Fig. 3). During the survey period from 2014 to 2017, the number of captured turtles declined from 57 to 35 in the Sunomiyagawa River, and from 18 to 11 in the Sanogawa River, as the proxy for *P. lotor* abundance (CPUE) increased (Fig. 4A). Correspondingly, the number of turtles recorded with amputated limbs
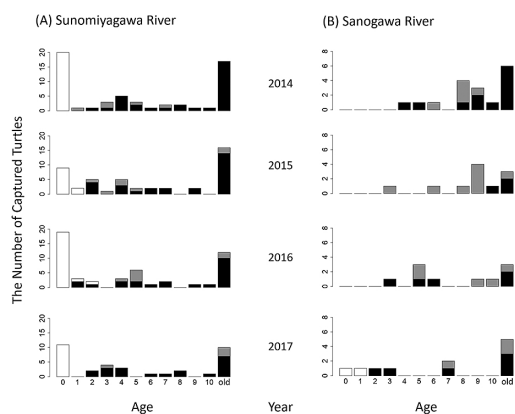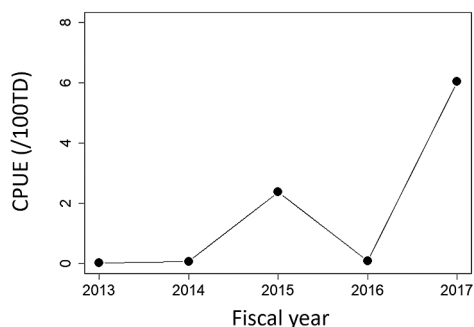
FIG. 3. Temporal changes in the age structure of *Mauremys japonica* in the (A) Sunomiyagawa River and (B) Sanogawa River during the period from 2014 and 2017. Black, gray, and white squares indicate females, males, and individuals of undetermined sex, respectively.

FIG. 4. Increases in the number of injured *Mauremys japonica* following *Procyon lotor* invasion.
(A) Catch per unit effort (CPUE; the number of exterminated *P. lotor*/100 trap days) of non-native *P. lotor* in Tateyama City during the period from 2013 to 2017 (fiscal years). TD means trap days, (B) The number of limb-amputated turtles in the Sunomiyagawa and Sanogawa rivers (black circles and white squares represent Sunomiyagawa River and Sanogawa River, respectively) during the period from 2014 to 2017.

increased from two in 2014 to six in 2017 in the Sunomiyagawa River, and from one in 2014 to four in 2017 in the Sanogawa River (Fig. 4B). Of a total of 232 turtles examined, limb amputation was recorded in 29 individuals (Table 2). The incidence of limb amputation tended to increase with age (Table 2).

Population dynamics of adult and juvenile turtles

All parameters estimated in the adult population dynamics model are shown in Appendix III. For the Sunomiyagawa River, the estimated mean population size of adult female and male turtles decreased from 35.28 (95% CI: 25.00–50.00) to 26.65 (14.00–47.00) and 20.46 (9.00–37.00) to 10.12 (5.00–21.00), respectively, during the period from 2014 to 2017 (Fig. 5). Similarly, the estimated mean population size of adult female and male turtles in the Sanogawa River decreased from 22.65 (95% CI: 13.00–43.00) to 10.42 (5.00–25.00) and 19.93 (9.00–38.53) to 13.77 (5.00–29.53), respectively (Fig. 5). The rate of population decline for the past three years was calculated to be 0.66 ([26.65+10.12]/[35.28+20.46]) for the Sunomiyagawa River

and 0.57 ([10.42+13.77]/[22.65+19.93]) for the Sanogawa River. These rates of decline corresponded to the annual changes of population size (R) of 0.87 (a product of $R^3=0.66$) and 0.83 (a product of $R^3=0.57$), respectively. The detection probabilities of adult turtles were estimated to be 0.44 (0.27–0.62) and 0.36 (0.17–0.58), for the Sunomiyagawa and Sanogawa River populations, respectively.

TABLE 2.   Summary of the number of *Mauremys japonica* individuals with amputated limbs recorded during the period 2014–2017. The same individuals that were recaptured in different years were counted as different individuals to account for differences in age.

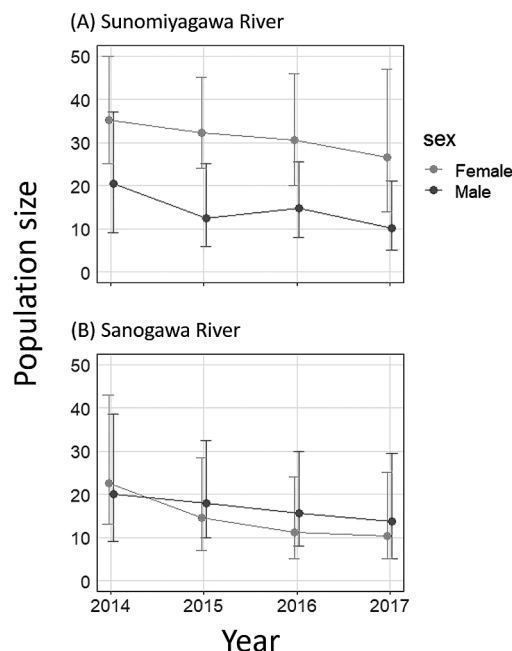| River	Sex	Age	Captured turtles	Limb-amputated individuals	Limb amputation rates (%)
Sunomiyagawa River	Unsexed	0	59	0	0
		1	3	0	0
		2	1	0	0
	Male	1	1	0	0
		2	1	0	0
		3	4	0	0
		4	3	0	0
		5	6	1	16.7
		6	0	0	—
		7	1	0	0
		8	0	0	—
		9	0	0	—
		10	0	0	—
		Old	7	2	28.6
	Female	1	2	0	0
		2	8	1	12.5
		3	4	0	0
		4	13	3	23.1
		5	5	0	0
		6	5	1	20.0
		7	6	2	33.3
		8	4	1	25.0
		9	4	0	0
		10	3	0	0
		Old	42	6	12.5
Sanogawa River	Unsexed	0	1	1	100
		1	1	0	0
	Male	1	0	0	—
		2	0	0	—
		3	1	0	0
		4	0	0	—
		5	2	1	50.0
		6	2	0	0
		7	1	1	100
		8	4	1	25.0
		9	6	1	16.7
		10	1	1	100
		Old	4	1	25.0
	Female	1	0	0	—
		2	1	0	0
		3	2	0	0
		4	1	0	0
		5	2	0	0
		6	1	1	100
		7	1	0	0
		8	1	1	100
		9	2	0	0
		10	2	1	50.0
		Old	14	2	14.3

(A) Sunomiyagawa River

(B) Sanogawa River

Fig. 5. Estimated population sizes of male and female adults of *Mauremys japonica* during the period from 2014 to 2017. The point and error bar represent the mean and 95% credible interval of the estimated population size, respectively.
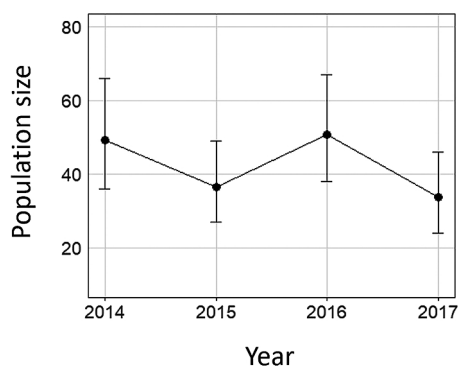

Fig. 6. Estimated population size of juvenile of *Mauremys japonica* during the period from 2014 to 2017. The point and error bar represent the mean and 95% credible interval of the estimated population size, respectively.

The annual adult survival rates of females and males were estimated to be 0.76 (0.59–0.93) and 0.31 (0.06–0.69) in the Sunomiyagawa River, and 0.58 (0.34–0.82) and 0.68 (0.37–0.94) in the Sanogawa River.

All parameters estimated for the juvenile population dynamics model are shown in Appendix IV. Although the estimated size of the juvenile turtle population was higher in 2016 than in other years of the study period, it showed an overall slight reduction [from 49.31 (36.00–66.00) to 33.67 (24.00–46.00)] from 2014 to 2017 (Fig. 6). The juvenile detection probability and survival rate were 0.23 (0.01–0.75) and 0.30 (0.18–0.44), respectively. All parameters converged as the $\hat{R}$ value did not exceed 1.1.

Discussion

Our study revealed a steady decline in turtle population sizes (0.66 and 0.57 for the three years) at the southern tip of the Boso peninsula, where the feral raccoons recently appeared. The annual rates of population change estimated for adult turtles were 0.87 and 0.83, which were lower than 1.0 of the assumed stable population sizes. If the sizes of *Ma. japonica* populations continue to decline at this rate, the populations are likely to undergo severe declines (to approximately 10% of the current population sizes) within 15 years. Similarly, Kosuge and Kobayashi (2015) reported mass mortalities and declines in the populations of *Ma. japonica* and *Ma. reevesii* in 2008 in a river in Kimitsu City. Kosuge and Kobayashi (2015) suspected that the mass mortalities (the finding of dead turtles), living turtles with amputated limbs, and rapid population declines recorded in Kimitsu were attributable to *P. lotor* predation. Therefore, the steady decline in the population of *Ma. japonica* in Tateyama City concomitant with the appearance and increase in CPUE of *P. lotor* in Tateyama since 2009 (Ochiai et al., 2002; Asada and Shinohara, 2009; Asada, 2011, 2014) is compatible with the hypothesis that *P. lotor* can be a source of marked declines in the populations of *Ma. japonica*. In this regard, however, it should be acknowledged that we

obtained no direct evidence of *P. lotor* preda-tion, such as *P. lotor* gut contents or photo-graphic records of predation events. In the following paragraphs, we discuss the causal factors and mechanisms associated with limb amputation (Kosuge and Kobayashi, 2015; Ogano et al., 2015b; Suzuki et al., 2015; Tagami et al., 2019) and the skewed popula-tion age-size structure, as proxies of predation impacts by *P. lotor* on native freshwater turtle populations.

Reduced recruitment of newly matured adults from juveniles would potentially skew the population structure toward older-aged individuals. Low reproductive output through low egg production, high egg mortality, or the high mortality of juveniles (including hatch-lings) due to predation would all contribute to reducing the recruitment of newly matured individuals (Gibbons, 1968; Wilbur, 1975; Tinkle et al., 1981; Browne and Hecnar, 2007; Dorcas et al., 2007; Chen and Lue, 2009). However, even though we annually recorded reasonable numbers of adult females capable of producing large clutches and numerous newly hatched turtles, the higher survivorship of adult turtles in general (Wilbur, 1975; Iverson, 1991; Congdon et al., 1993, 1994) would not compensate for the low annual survival of hatchlings and reduced recruit-ment of newly matured adults to sustain a stable population size.

In the present study, we found that those turtles characterized by amputated limbs were generally adult males and females rather than juveniles (Table 2). However, a low incidence of juvenile turtles with injured limbs is not necessarily indicative of a low rate of preda-tion, as it is more likely to reflect the high mortality rate of predated individual, and that predators tend to leave no traces of dead indi-viduals (Ogano et al., 2015b). The turtles could also lose limbs because of lawnmower activities. When the turtles were injured by lawnmower operation, severe scars were left on turtle carapaces (Kagayama, 2020b). The fact that no such scarring was detected in the limb-amputated turtles identified in the present study would thus tend to indicate that limb amputation was caused by predation rather than by human disturbance. Further-more, although further confirmatory data are required, we did find some evidence of skewed limb amputation rates in the turtle popula-tion, indicating size-specific predation on smaller turtles. This could reflect the fact that large and heavy turtles may escape *P. lotor* predation, as these *P. lotor* generally consume smaller prey items that they can conveniently grasp with their forefeet (Kosuge and Kobayashi, 2015), and it is assumed that *P. lotor* would experience difficulties in handling larger prey items (particularly adult female *Ma. japonica*).

Ogano et al. (2015a) noted that although feral *P. lotor* population management in Japan has been conducted mostly from the perspective of agricultural damage control, measures should also be taken to eradicate feral *P. lotor* for the purposes of biodiversity conservation. Even in its native range in North America, *P. lotor* has purposely been removed from certain areas for the conserva-tion of freshwater and marine turtles (e.g., diamondback terrapins and loggerhead turtles), in order to reduce predation pressure at vulnerable lifestages for native turtles (Garmestani and Percival, 2005; Barton and Roth, 2007; Munscher et al., 2012). However, whether it be for agricultural control or biodi-versity conservation, early detection of *P. lotor* predation is pivotal to the planning and implementation of conservation programs for native turtle populations in Japan.

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APPENDIX I

The JAGS code used for an adult population size estimation model (JS model)
The model was constructed based on Kéry and Schaub (2012b).

```
model {
# Priors and constraints
for (i in 1:M){
  for (t in 1:(n.occasions-1)){
    phi[i,t] <- beta[group[i]]
    } # t
  for (t in 1:n.occasions){
    p[i,t] <- mean.p
    } #t
  } #i
for (i in 1:2){
  beta[i] ~ dunif(0, 1)
  }
mean.p ~ dunif(0, 1)
for (t in 1:n.occasions){
  gamma[t] ~ dunif(0, 1)
  } #t
# Define the likelihoods
for (i in 1:M){
  # First occasion
  # State process
  z[i,1] ~ dbern(gamma[1])
  mu1[i] <- z[i,1] * p[i,1]
  # Observation process
  y[i,1] ~ dbern(mu1[i])
  # Subsequent occasions
  for (t in 2:n.occasions){
    # State process
    q[i,t-1] <- 1.00000001-z[i,t-1]
    mu2[i,t] <- phi[i,t-1]*z[i,t-1] + gamma[t]*prod(q[i,1:(t-1)])
    z[i,t] ~ dbern(mu2[i,t])
    # Observation process
    mu3[i,t] <- z[i,t] * p[i,t]
    y[i,t] ~ dbern(mu3[i,t])
    } # t
  } # i
# Calculate derived population parameters
for (t in 1:n.occasions){
  qgamma[t] <- 1.00000001-gamma[t]
  }
cprob[1] <- gamma[1]
for (t in 2:n.occasions){
  cprob[t] <- gamma[t] * prod(qgamma[1:(t-1)])
```

```
  } # t
psi <- sum(cprob[])          # Inclusion probability
for (t in 1:n.occasions){
  b[t] <- cprob[t] / psi     # Entry probability
  } # t
for (i in 1:M){
  recruit[i,1] <- z[i,1]
  for (t in 2:n.occasions){
    recruit[i,t] <- (1.00000001-z[i,t-1]) * z[i,t]
    } # t
  } # i
for (t in 1:n.occasions){
  Nm[t] <- sum(z[1:mm,t])          # Actual population size of males
  Nf[t] <- sum(z[(mm+1):M,t])        # Actual population size of females
  Bm[t] <- sum(recruit[1:mm,t])      # Number of entries of males
  Bf[t] <- sum(recruit[(mm+1):M,t])  # Number of entries of females
  } # t
for (i in 1:M){
  Nind[i] <- sum(z[i,1:n.occasions])
  Nalive[i] <- 1.00000001-equals(Nind[i], 0)
  } # i
Nsuperm <- sum(Nalive[1:mm])          # Size of superpopulation of males
Nsuperf < sum(Nalive[(mm+1):M])       # Size of superpopulation of females
}
```

APPENDIX II

The JAGS code used for a juvenile population size estimation model
We used the code described by Kéry and Schaub (2012a).

```
model {
# Priors and constraints
for (i in 1:M){
  for (t in 1:(n.occasions-1)){
    phi[i,t] <- mean.phi
    } #t
  for (t in 1:n.occasions){
    p[i,t] <- mean.p
    } #t
  } #i
mean.phi ~ dunif(0, 1)          # Prior to mean survival
mean.p ~ dunif(0, 1)            # Prior to mean capture
psi ~ dunif(0, 1)              # Prior to inclusion probability
# Dirichlet prior for entry probabilities
for (t in 1:n.occasions){
  beta[t] ~ dgamma(1, 1)
  b[t] <- beta[t] / sum(beta[1:n.occasions])
  }
# Convert entry probs to conditional entry probs
nu[1] <- b[1]
for (t in 2:n.occasions){
  nu[t] <- b[t] / (1-sum(b[1:(t-1)]))
  } #t
# Likelihood
for (i in 1:M){
  # First occasion
  # State process
  w[i] ~ dbern(psi)           # Draw latent inclusion
  z[i,1] ~ dbern(nu[1])
  # Observation process
  mu1[i] <- z[i,1] * p[i,1] * w[i]
  y[i,1] ~ dbern(mu1[i])
  # Subsequent occasions
  for (t in 2:n.occasions){
    # State process
    q[i,t-1] <- 1-z[i,t-1]
    mu2[i,t] <- phi[i,t-1] * z[i,t-1] + nu[t] * prod(q[i,1:(t-1)])
    z[i,t] ~ dbern(mu2[i,t])
    # Observation process
    mu3[i,t] <- z[i,t] * p[i,t] * w[i]
    y[i,t] ~ dbern(mu3[i,t])
    } #t
  } #i
```

```
# Calculate derived population parameters
for (i in 1:M){
  for (t in 1:n.occasions){
    u[i,t] <- z[i,t]*w[i]    # defined latent state (u)
    }
  }
for (i in 1:M){
  recruit[i,1] <- u[i,1]
  for (t in 2:n.occasions){
    recruit[i,t] <- (1-u[i,t-1]) * u[i,t],
    } #t
  } #i
for (t in 1:n.occasions){
  N[t] <- sum(u[1:M,t])       # Actual population size
  B[t] <- sum(recruit[1:M,t])  # Number of entries
  } #t
for (i in 1:M){
  Nind[i] <- sum(u[i,1:n.occasions])
  Nalive[i] <- 1-equals(Nind[i], 0)
  } #i
Nsuper <- sum(Nalive[])       # Superpopulation size
}
```

APPENDIX III

Posterior distribution of the estimated parameters of the Jolly-Seber model for adult turtles in (A) the Sunomiyagawa River and (B) the Sanogawa River.

Nm: actual male population size, Nf: actual female population size, Nsuperm: size of the male superpopulation, Nsuperf: size of the female superpopulation, Bm: number of male entries, Bf: number of female entries, b: entry probability, Phim: annual survival rate of males, Phif: annual survival rate of females, P: mean detection probability, and Psi: inclusion probability.

(A) Sunomiyagawa River				(B) Sanogawa River			
Parameter	Mean	SD	95% CI	Parameter	Mean	SD	95% CI
Nm [2014]	20.46	7.48	9.00–37.00	Nm [2014]	19.93	7.43	9.00–38.53
Nm [2015]	12.47	5.10	6.00–25.00	Nm [2015]	17.90	6.02	10.00–32.53
Nm [2016]	14.74	4.78	8.00–25.53	Nm [2016]	15.62	6.11	8.00–30.00
Nm [2017]	10.12	4.22	5.00–21.00	Nm [2017]	13.77	6.81	5.00–29.53
Nf [2014]	35.28	6.26	25.00–50.00	Nf [2014]	22.65	7.53	13.00–43.00
Nf [2015]	32.19	5.74	24.00–45.00	Nf [2015]	14.63	5.71	7.00–28.53
Nf [2016]	30.47	7.02	20.00–46.00	Nf [2016]	11.25	5.27	5.00–24.00
Nf [2017]	26.65	8.67	14.00–47.00	Nf [2017]	10.42	5.49	5.00–25.00
Nsuperm	41.94	9.43	27.00–62.53	Nsuperm	29.63	9.02	18.00–51.00
Nsuperf	48.94	8.21	37.00–69.00	Nsuperf	30.21	9.68	18.00–55.00
Bm [2014]	20.46	7.48	9.00–37.00	Bm [2014]	19.93	7.47	9.00–38.53
Bm [2015]	5.17	3.48	0.00–13.00	Bm [2015]	3.51	3.12	0.00–11.00
Bm [2016]	10.53	4.02	3.00–19.00	Bm [2016]	3.12	2.93	0.00–10.00
Bm [2017]	5.78	3.06	1.00–13.00	Bm [2017]	3.07	2.87	0.00–11.00
Bf [2014]	35.28	6.26	25.00–50.00	Bf [2014]	22.65	7.53	13.00–43.00
Bf [2015]	4.23	3.14	0.00–11.00	Bf [2015]	2.43	2.42	0.00–8.00
Bf [2016]	5.53	3.16	1.00–13.00	Bf [2016]	2.32	2.46	0.00–8.00
Bf [2017]	3.91	2.98	0.00–11.00	Bf [2017]	2.81	2.96	0.00–11.00
b [2014]	0.60	0.09	0.41–0.78	b [2014]	0.68	0.12	0.45–0.89
b [2015]	0.11	0.07	0.01–0.26	b [2015]	0.11	0.09	0.00–0.33
b [2016]	0.18	0.07	0.05–0.33	b [2016]	0.10	0.08	0.00–0.28
b [2017]	0.11	0.06	0.02–0.24	b [2017]	0.11	0.08	0.01–0.29
Phim	0.31	0.17	0.06–0.69	Phim	0.68	0.15	0.37–0.94
Phif	0.76	0.09	0.59–0.93	Phif	0.58	0.13	0.34–0.82
P	0.44	0.09	0.27–0.62	P	0.36	0.11	0.17–0.58
Psi	0.09	0.02	0.06–0.13	Psi	0.06	0.02	0.04–0.11

APPENDIX IV

Posterior distribution of the estimated parameters of the Jolly Seber model for juvenile turtles in the Sunomiyagawa River. N: actual population size of juvenile turtles, Nsuper: size of the juvenile superpopulation, B: number of juvenile turtle entries, b: entry probability of juveniles, Phi: annual survival rate of juvenile turtles, P: mean detection probability, and Psi: inclusion probability.

Parameter	Mean	SD	95% CI
N [2014]	49.31	7.60	36.00–66.00
N [2015]	36.59	5.88	27.00–49.00
N [2016]	50.85	7.44	38.00–67.00
N [2017]	33.67	5.80	24.00–46.00
Nsuper	129.19	12.48	106.00–155.00
B [2014]	49.31	7.60	36.00–66.00
B [2015]	23.28	5.96	12.00–36.00
B [2016]	38.33	7.08	27.00–54.00
B [2017]	18.28	5.50	8.00–30.00
b [2014]	0.37	0.06	0.27–0.51
b [2015]	0.18	0.05	0.08–0.29
b [2016]	0.30	0.06	0.19–0.43
b [2017]	0.15	0.05	0.06–0.25
Phi	0.30	0.07	0.18–0.44
P	0.23	0.20	0.01–0.75
Psi	0.12	0.02	0.09–0.15