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Population Dynamics of Japanese Pond Turtles (*Mauremys japonica*) in a Ramsar Wetland Conserved from Primary Anthropogenic Negative Disturbances in Japan

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Abstract: When determining the most effective conservation measures for endangered species, it is critical to understand their population dynamics, the primary drivers influencing their populations, and their life history strategies. Long-term monitoring is essential to obtain this information, and a lack of adequate data exists for numerous native species experiencing substantial population declines in recent years due to various anthropogenic factors. In the present study, we investigated the population dynamics and demographic characteristics of the Japanese pond turtle, *Mauremys japonica*, an endemic species native to Japan. Accordingly, we conducted an eight-year mark-recapture study in a Ramsar wetland that has remained relatively unaffected by numerous primary anthropogenic disturbances in Japan. The population size estimation of this study demonstrated that the wetland was inhabited by approximately 200 individuals, comprising both males and females. Both sexes exhibited a high annual survival rate (0.87), indicating that the wetland population was stable or slightly increasing. These findings provide baseline data regarding *M. japonica*, a species for which information on demographic parameters and population dynamics in healthy populations is lacking.

Key words: Capture-recapture study; Conservation; Freshwater turtle; Nakaikemi wetland; Population size estimation

Introduction

When planning and developing appropriate conservation and management measures for wildlife species, it is imperative to understand

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their population dynamics, the primary drivers influencing their populations, and their life history strategies (Crouse et al., 1987; Gaillard et al., 1998; Jonsson and Ebenman, 2001; Sánchez-Bayoa and Wyckhuys, 2019). To acquire this information, it is necessary to undertake long-term field surveys for wildlife, particularly in the case of long-lived species, across various populations (Roe et al., 2021). In recent years, a significant decline has been observed in the populations of several native species because of various adverse anthropogenic disturbances (Wilcove et al., 1998; Gurevitch and Padilla, 2004; Doherty et al., 2015; Sánchez-Bayoa and Wyckhuys, 2019). Consequently, the acquisition of novel data on population dynamics and demographic parameters (e.g., survival rate, fecundity, and longevity) for species in their natural habitats has become increasingly challenging as these species strive to evade the impacts of anthropogenic activities.

For turtles, long-term monitoring provides valuable insights into the population dynamics and life history strategies of many species. Turtles exhibit distinct ecological characteristics, including high mortality rates in young individuals (e.g., eggs, hatchlings, and juveniles), late maturation, high survival rates in adults, and a long lifespan (Wilbur, 1975; Gibbons, 1987; Iverson, 1991; Shine and Iverson, 1995). Therefore, the annual population size of turtles under natural conditions would typically exhibit moderate fluctuations unless catastrophic mortality events or major anthropogenic disturbances have occurred (Litzgus and Mousseau, 2004; Keevil et al., 2018; Mullin et al., 2020). These ecological characteristics imply that the maintenance of high adult survival rates in turtles is important for the conservation of this species (Congdon et al., 1993, 1994; Heppell, 1998).

However, many turtle species experienced declines in various regions due to various anthropogenic factors in recent years (Stanford et al., 2020). The Japanese pond turtle, *Mauremys japonica*, an endemic species that inhabits a large portion of Japan (including Honshu, Shikoku, Kyushu, and adjacent small islands) (Yasukawa et al., 2008), is one of the freshwater turtles for which conservation measures have made limited progress due to lack of information regarding its current status and life history. Although some information regarding the population structure and growth of *M. japonica* have been reported (Yabe, 1989; Kagayama, 2020), limited knowledge exists regarding their population dynamics, the primary drivers of these populations (Kosuge and Kobayashi, 2015; Kagayama et al., 2021), and their demographic parameters (e.g., Kagayama, 2022). In recent years, *M. japonica* has experienced declines in various parts of its distribution range due to multiple anthropogenic factors, including river alterations (Yabe, 2014; Ogano et al., 2015), interspecific competition (Yabe, 2014; Ogano et al., 2015; Kagayama et al., 2020) with the introduced red-eared slider, *Trachemys scripta elegans*, native to the United States of America and Mexico (Ernst and Lovich, 2009) and the introduced Reeves' pond turtles, *Mauremys reevesii*, introduced from Korea since the late 18th century and from China since the 1970s (Hikida and Suzuki, 2010; Suzuki et al., 2011); reproductive interference and gene pollution resulting from hybridization with *M. reevesii* (Yabe, 2014; Suzuki et al., 2014; Ogano et al., 2015; Kagayama et al., 2020); predation by alien raccoons, *Procyon lotor* (Yabe, 2014; Kosuge and Kobayashi, 2015; Ogano et al., 2015), and overexploitation for commercial purposes (Yasukawa et al., 2008; Yabe, 2014; Ogano et al., 2015). Therefore, it has become increasingly challenging to clarify the population dynamics and demographic parameters of various turtle populations within their natural habitats where the adverse impacts of anthropogenic disturbances are minimal. To collect this fundamental information amidst these conditions, it is necessary to identify populations that were spared from the primary causes of decline and conduct long-term monitoring of these populations.

Fortunately, a breeding population of *M. japonica* has been discovered in recent years that has remained relatively unaffected by a range of negative anthropogenic disturbances (Kagayama and Nishibori, 2021). The Nakaikemi wetland, which was designated as a Ramsar wetland in 2012, serves as a thriving ecosystem that has not experienced the primary factors leading to declines in *M. japonica* populations; however, a small number of alien *M. reevesii* have invaded this habitat and caused hybridization with *M. japonica* (Nishibori et al., 2020).

In this study, we elucidate the current status and demographic characteristics of *M. japonica* via an eight-year capture-recapture study of turtle populations inhabiting a Ramsar wetland in Japan. The data derived from these surveys were used to determine the demographic parameters and interannual variations in population size. Finally, we investigated the future directions of conservation efforts pertaining to *M. japonica*.

Materials and Methods

Study site

Fieldwork study was conducted in channels and ponds within the Nakaikemi wetland (35°39' N, 136°05' E), a designated Ramsar wetland located in Tsuruga City, Fukui Prefecture, Japan (Fig. 1). The wetland constitutes an inland swamp covering an area of approximately 25 ha (Watanabe and Kawano, 2003). It is situated at an elevation of approximately 48 m (Kihara et al., 2015) and surrounded by low hills covered with natural deciduous forest and planted *Cryptomeria* forest (Kato and Miura, 1996). Within these ranges, the wetland comprises several ponds, paddy fields, and irrigation channels (for more information, consult Nakaikemi Net, Online). The water from the wetland flows into a tributary of the Kinome River (Fig. 1).

In the Nakaikemi wetland, the channels and ponds are not equipped with extensive concrete bank revetments. Additionally, the presence of alien predators such as raccoons, *Procyon lotor*, or alien competitors such as red-eared sliders, *Trachemys scripta elegans*, were not reported earlier in this habitat (Kohmatsu et al., 2000; Kawamichi et al., 2003; Nishibori et al., 2020). Finally, the prohibition on the collection of wildlife in the Nakaikemi wetland prevents instances of overexploitation for commercial purposes (e.g., pet trade). Unfortunately, although the occurrence of the invasion of alien *M. reevesii* and its subsequent hybridization with *M. japonica* has been reported since 2016 (Nishibori et al., 2020), the number of captured individuals of these aliens and hybrids was found to be relatively low. Therefore, because *M. japonica* in the Nakaikemi wetland was largely unaffected by multiple primary anthropogenic factors, it is expected that it will be possible to evaluate the demographic parameters and population dynamics of *M. japonica* populations experiencing little adverse disturbances caused by human activities.

Study species

The Nakaikemi wetland was exclusively inhabited by *M. japonica* until 1996 (Kohmatsu et al., 2000). However, a survey conducted in 2016 reported the invasion of *M. reevesii* and the subsequent occurrence of hybridization between *M. japonica* and *M. reevesii* (Nishibori et al., 2020). The precise timing and specific circumstances (e.g., escape or release of captive individuals) surrounding the invasion of alien *M. reevesii* into the Nakaikemi wetland remain unclear.

We identified *M. japonica* and *M. reevesii* based on their morphological characteristics (e.g., head color, head and neck pattern, carapace and plastron color, number of carapace keels, the existence of a line pattern on the four limbs, serrated carapace, and iris color) in accordance with the methodology outlined by Yabe (1994), Yasukawa et al. (2008), and Lovich et al. (2011). Individuals that displayed morphological characteristics of both *M. japonica* and *M. reevesii* or exhibited at least one intermediate characteristic were classified as putative hybrids, as per the methodology described by Kosuge et al. (2003), Kato et al. (2010), and Suzuki et al. (2014).

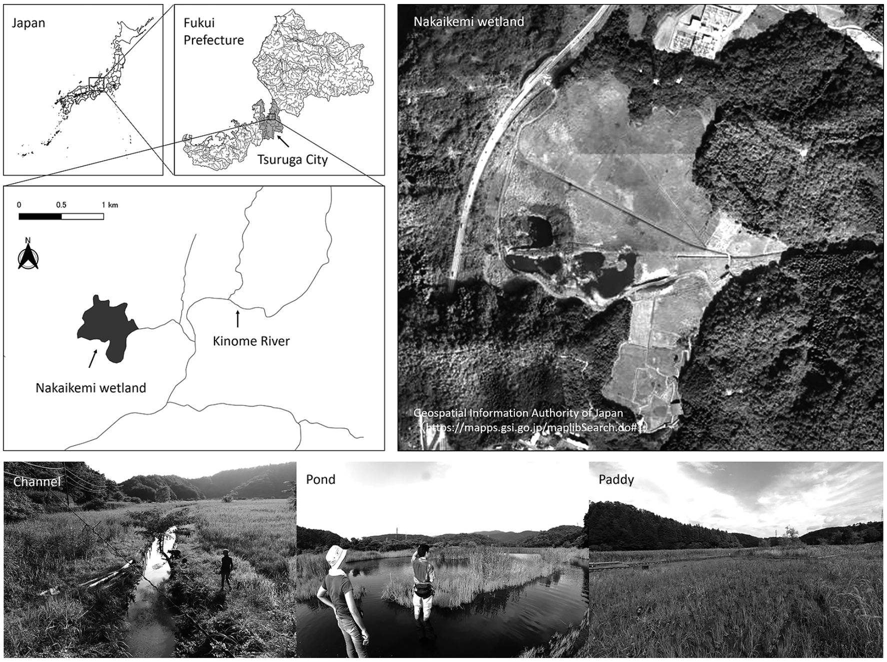

FIG. 1. Study site and surrounding environment.
In the upper left figures, the grey lines and the shape indicate rivers and the outline of the Nakaikemi wetland, respectively. Within the range of the Nakaikemi wetland (grey shape), a few ponds, paddy fields, and irrigation channels exist (bottom figures). The river line and wetland shape data were acquired from the National Land Information Division, the National Spatial Planning and Regional Policy Bureau, MLIT of Japan (https://nlftp.mlit.go.jp/ksj/), and the Ministry of the Environment, Biodiversity Center of Japan (http://gis.biodic.go.jp/webgis/sc-023.html), respectively.

Capture-recapture procedures

Turtles were captured in ponds and channels of the Nakaikemi wetland between August and October each year over an eight-year period (2016–2023) using three types of fish-baited traps (Trap 1: 55 cm×22 cm×45 cm; Trap 2: 72 cm×39 cm×55 cm; Trap 3: 72 cm×44 cm×55 cm, which incorporated a 1.7 m-long bag-like passage enabling the trapped turtles to breathe; see details in Nishibori et al., 2020). The use of several different types of traps in this study was driven by the objective to reduce the likelihood of turtles drowning at deep trap sites where the entire trap would be completely submerged. The traps were prepared in the afternoon and inspected the following morning. We conducted two to four capture-recapture sessions annually, employing 10–20 traps (Table 1).

Captured turtles were marked to distinguish and identify individuals as outlined in the methodology of Kobayashi (2008). Sex and carapace length (CL) were recorded for each of the captured turtles. Sex was categorized as female, male, or unsexed (i.e., young individuals of undetermined sex based on morphological characteristics) using the relative position of the cloaca as a basis (Yabe, 1989). 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, 2020). This categorization was employed to determine trends in the population dynamics of adult male and female turtles. The reason for this was that the smallest

TABLE 1. Survey efforts and the number of captured *Mauremys japonica.*
(Trapping effort=the number of traps set×the number of trips and catch per unit effort=captured turtles/trapping effort). The symbol "+1" means a hatchling captured by hand in a paddy. Because this specimen was captured by methods other than trapping, it was not used in the calculation of CPUE.

Year	Number of traps set	Number of trips	Trapping effort	Captured turtles	Catch per Unit Effort
2016	10	2	20	36	1.8
2017	16	2	32	31	0.97
2018	16	2	32	55	1.72
2019	16	3	48	26	0.54
2020	20	4	80	72	0.9
2021	20	4	80	42	0.53
2022	20	4	80	26 (+1)	0.33
2023	20	4	80	60 (+1)	0.75

females capable of producing eggs had a CL>150 mm, whereas the smallest males that exhibited signs of maturity had a CL>80 mm (Yasukawa et al., 2008).

All individuals of *M. japonica* captured in this study were released subsequent to body condition measurements during the study period. Additionally, all captured *M. reevesii* and all but 13 hybrids were removed to eliminate potential negative effects (e.g., reproductive interference, gene pollution) on *M. japonica*. However, only 13 hybrids captured during the first survey in 2016 were reintroduced to the wetland because no decision was made on the treatment of captured individuals (e.g., kept in isolation, culling, see detail Nishibori et al., 2020).

Population size estimation

To estimate the population size of males and females of *M. japonica*, we applied the Jolly–Seber (JS) model (Jolly, 1965; Seber, 1965), which is based on the state-space formulation of Bayesian hierarchical models described by Kéry and Schaub (2012a, b). We conducted analyses using two models: one with only adults (Model 1) and the other with adults and immature individuals (Model 2).

We made extensive use of parameter-expanded data augmentation (Royle et al., 2007; Kéry and Schaub, 2012a; Royle and Dorazio, 2012), which involved augmenting the dataset by introducing numerous potentially unobserved individuals, all with zero-only encounter histories. The main idea was to fix the dimension of the parameter space in the analysis by augmenting the observed data with a large number of all-zero capture histories, resulting in a larger dataset with a fixed dimension (M). Subsequently, this augmented dataset was analyzed using a reparametrized (zero-inflated) iteration of the model, which could be applied if the superpopulation size (the number of individuals that survived during the study) was known (Kéry and Schaub, 2012a). Furthermore, we adopted the restricted dynamic occupancy model parameterization approach for the JS model (refer to Kéry and Schaub, 2012a). This model can be used to estimate various statistical measures: superpopulation size of both sexes ($Nsuper_{male}$, $Nsuper_{female}$), population size in each year (t) of both sexes (N_{male} [t], N_{female} [t]), detection probability of both sex (P_{male}, P_{female}), survival rate of both sexes (φ_{male}, φ_{female}), number of entries of both sexes (B_{male} [t], B_{female} [t]), entry probability (b [t]), and inclusion probability (ψ). ψ represented the probability that a member from the augmented dataset, M (M individuals), was included in the Nsuper.

Here, we used the capture histories of 74 and 78 adult males and females, respectively, in Model 1. The datasets were augmented with 1,000 individuals with all-zero capture histories. Additionally, we used the capture histories of 80 males and 119 females in Model 2. The datasets were augmented with 1,000 individuals with all-zero capture histories.

We employed a similar model to that of Kagayama et al. (2021), who estimated the population dynamics of male and female individuals of *M. japonica* based on the model described by Kéry and Schaub (2012b). They assumed that the entry probability of adults was time-dependent, the survival rate of adults was sex-dependent because larger-bodiesd females were expected to have higher survival rates, and the capture probability was constant. However, given that the summer activity of *M. japonica* differs between males and females (Yabe, 1992), it was assumed that both the detection probability and survival rate were sex-dependent, as modeled by Kéry and Schaub (2012b). Additionally, the sex ratio (Sr [t], representing the proportion of males to the total number of males and females) for each year was added to the derived parameters to be estimated. Sr [t] were defined as the values calculated by dividing the estimated number of males in each year by the estimated number of total individuals of males and females ($N_{male}[t]/N_{male}[t]+N_{female}[t]$).

We estimated the parameters (such as N [t], P, φ, ψ, and Sr [t]) of the JS model using Markov chain Monte Carlo (MCMC) methods in Just another Gibbs sampler (JAGS) ver. 3.4.0 (Plummer, 2003) via the R2jags package (Su and Yajima, 2015) in R ver. 3.6.1 (R Core Team, 2019). We discarded the initial 50,000 MCMC samples as burn-in and proceeded with an additional 50,000 MCMC iterations, with a saving implemented every 100th iteration to minimize serial autocorrelation among the samples. We confirmed convergence by assessing whether the $\widehat{R}$ value<1.1 for all estimates. We summarized the posterior distributions of all parameters using the median 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).

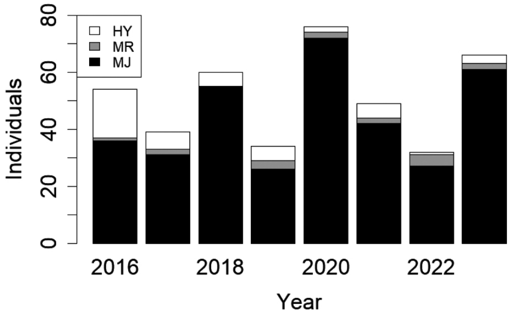

FIG. 2. Changes in the species composition from 2016 to 2023.
Abbreviations are as follows: HY, hybrids; MR, *Mauremys reevesii*; MJ, *Mauremys japonica*.

RESULTS

Changes in the species composition and population structure of Mauremys japonica

While the species composition was consistently dominated by *M. japonica* throughout the study period, the proportion of *M. japonica* increased from 66.7% (2016) to 94.7% (2020) over the 2016–2023 period (Fig. 2). Additionally, no *T. scripta elegans* were captured during the study period.

The number of captured *M. japonica* individuals changed from 26 to 72 during the 2016–2023 period (Table 1; Fig. 2). A limited number of juvenile individuals of undetermined sex were captured throughout the study period (13 individuals were marked), whereas numerous individuals of both sexes were captured (80 males and 119 females were marked) (Fig. 3). Additionally, the catch per unit effort (CPUE) as a density index of *M. japonica* changed from 1.8 to 0.33 during the 2016–2023 period (Table 1). Table 2 shows the number of turtles recaptured per recapture times; about half of the males and females were never recaptured, and all juveniles were never recaptured. No carcasses or injured individuals of *M. japonica*, considered a sign of predation by raccoons, were observed during the study period.

Figure 3 illustrates the size composition of *M. japonica* in each year. The mean CL of

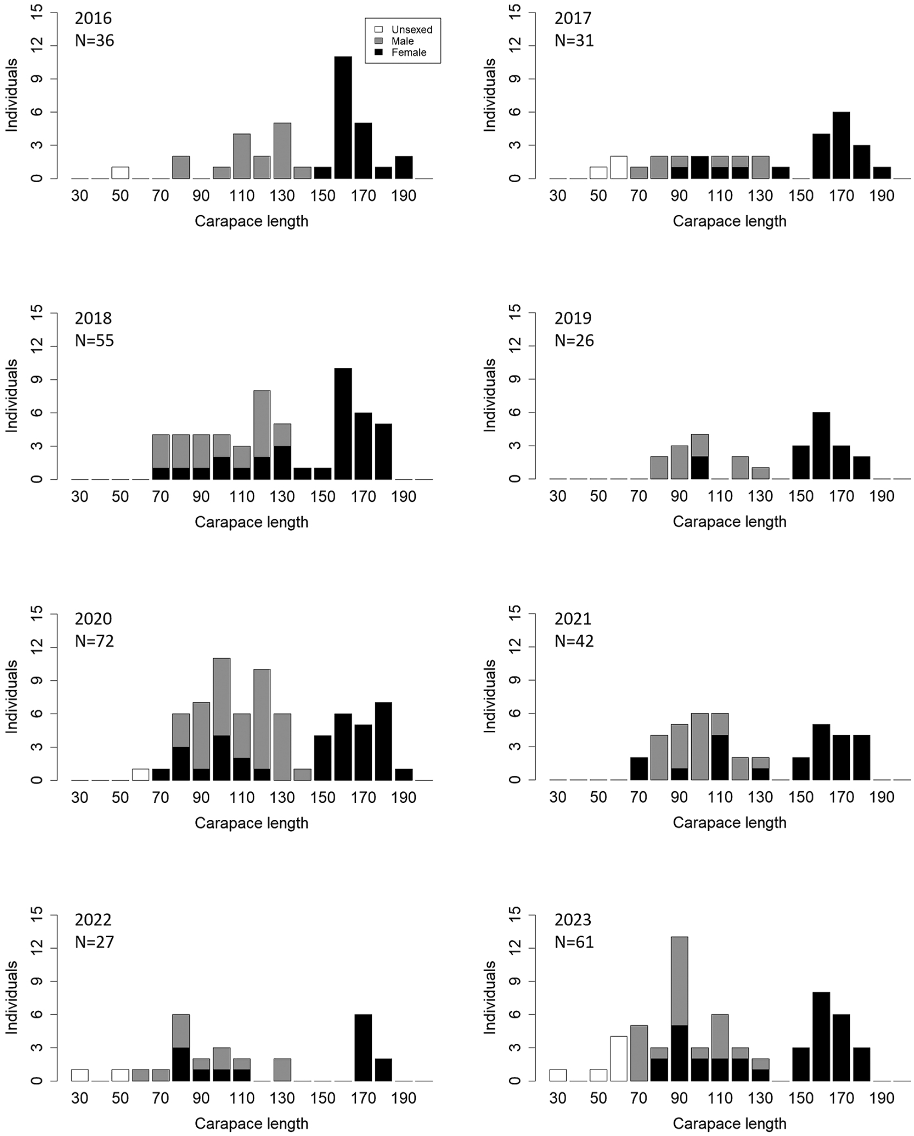

FIG. 3. The size composition of *Mauremys japonica* from 2016 to 2023.

males changed from 120.64±16.66 to 98.36±16.29 during 2016–2023, and that of females changed from 169.88±10.93 to 141.05±41.50 for the same period (Table 3). However, the results of the Tukey HSD test revealed no significant annual change in mean CL for males (except for the differences between 2023 and 2016) or females. According to the Tukey HSD test, the mean CL of males in 2023 was significantly lower than that of males in 2016 (diff=–22.28, 95% confidence interval=–41.01 to 3.54, p-value<0.01).

Population size estimation for Mauremys japonica

All model parameters are presented in Table S1 (Model 1) and Table S2 (Model 2). In Model 1 (adults only), the population size of

TABLE 2. Number of recaptured turtles and recapture times.
Adults and juveniles (immature individuals) were combined for both sexes as some individuals developed from juveniles to adults during the study period. Unsexed refers to juveniles for which sex discrimination was not possible.

Sex	Number of captured turtles	Number of recaptured turtles				
		Once	Twice	Three times	Four times	None
Male	80	23	10	5	1	41
Female	119	34	8	6	2	69
Unsexed	13	0	0	0	0	13

TABLE 3. Mean carapace length and standard deviations of males and females of *Mauremys japonica* from 2016 to 2023.

Year	Males	Females
2016	120.64±16.66 (N=15, range=87.22–146.53)	169.88±10.93 (N=20, range=153.79–196.86)
2017	105.61±21.71 (N=8, range=79.26–136.46)	157.56±31.72 (N=20, range=93.42–196.42)
2018	106.28±19.87 (N=21, range=71.5–136.55)	152.26±31.10 (N=34, range=70.05–187.90)
2019	103.78±16.60 (N=10, range=84.41–130.94)	160.25±22.38 (N=16, range=105.79–185.61)
2020	113.62±17.06 (N=36, range=85.55–147.83)	146.62±36.23 (N=35, range=77.16–187.65)
2021	104.27±13.74 (N=19, range=81.59–136.45)	147.50±36.78 (N=23, range=71.69–196.46)
2022	99.26±20.33 (N=11, range=69.34–134.54)	141.05±41.50 (N=14, range=81.61–184.48)
2023	98.36±16.29 (N=21, range=75.04–133.82)	143.61±34.25 (N=34, range=83.74–188.61)

males changed from 50.00 (95% credible interval: 35.00–73.00) to 72.50 (59.00–92.00) individuals during 2016–2023 (Fig. 4). Additionally, that of females changed from 59.00 (44.00–81.52) to 74.00 (59.00–93.00) individuals during 2016–2023 (Fig. 4). The detection probability, apparent annual survival rate, and super population size were 0.26 (0.19–0.35) and 0.26 (0.19–0.33), 0.87 (0.77–0.96) and 0.87 (0.79–0.95), and 125.00 (105.00–150.00) individuals and 130.00 (110.00–157.00) individuals in males and females, respectively. The sex ratio (proportion of males to the total number of males and females), focusing on the estimated population size of the turtles, changed from 0.46 (95% CI: 0.38–0.53) to 0.50 (0.43–0.57) during the 2016–2023 period (Fig. 4; Table S1). The sex ratio tended to be biased toward females from 2016 to 2019, whereas the 95% credible interval overlapped the value of 0.5 in all study years (Fig. 4).

In Model 2 (adults and immatures), the population size of males changed from 52.00 (36.00–75.00) to 84.00 (57.00–121.00) individuals during the 2016–2023 period (Fig. 4). Similarly, the population size of females changed from 70.00 (52.00–94.00) to 112.00 (83.47–152.00) individuals during the 2016–2023 period (Fig. 4). The detection probability, apparent annual survival rate, and super population size were 0.27 (0.20–0.35) and 0.27 (0.21–0.33), 0.83 (0.75–0.92) and 0.87 (0.80–0.94), and 157.00 (131.00–192.00) individuals and 191.00 (167.00–225.00) individuals in males and females, respectively. The sex ratio remained almost unchanged from 0.42 (0.31–0.52) to 0.43 (0.37–0.50) during the 2016–2023 period (Fig. 4; Table S2). The sex ratio tended to be biased toward females throughout the study period; however, the 95% credible interval overlapped the value of 0.5 slightly except from 2017 to 2019 (Fig. 4).

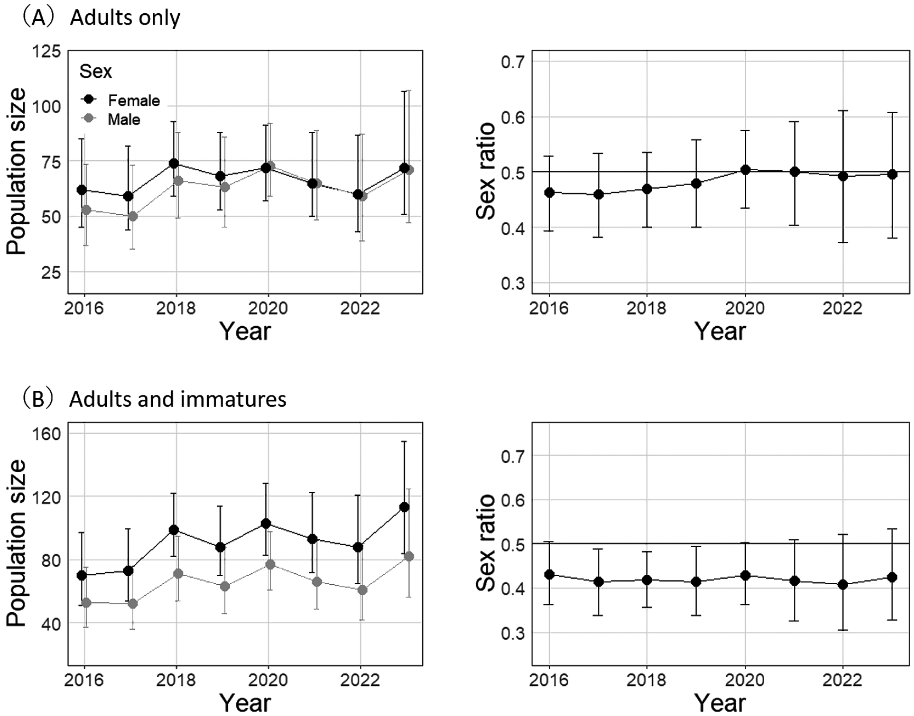

FIG. 4. Annual changes in the estimated population size of males and females and the sex ratio (proportion of males) of *Mauremys japonica* from 2016 to 2023.
(A) adults only model (Model 1); (B) adults and immatures model (Model 2). Plot and var refer to the median value and 95% credible interval of the posterior distribution, respectively.

DISCUSSION

An eight-year capture-recapture study revealed that the population size estimates (median values) of *M. japonica* (adults and immatures) increased from its minimum and maximum years by 1.62 and 1.60 times in males and females, respectively. Additionally, the population size of adults changed marginally by 1.45 times in males and 1.25 times in females. Therefore, the findings of this study suggested that the wetland population was either stable or slightly increasing. To the best of our knowledge, the present study represents the first case to quantitatively evaluate the annual changes in the population size of an *M. japonica* population that has managed to evade the adverse impacts caused by primary anthropogenic disturbances in Japan. The findings of the present study provide baseline data on *M. japonica*, a species for which information on demographic parameters and population dynamics in healthy populations has been lacking (Kagayama, 2022). In the remainder of this section, we elaborate on the following topics: 1) the current status, 2) demographic characteristics, and 3) future direction for the conservation of *M. japonica* in the Nakaikemi wetland.

Current status

Although invasive *M. reevesii* and hybrids between *M. reevesii* and *M. japonica* were observed (Nishibori et al., 2020; present study), the species composition revealed that *M. japonica* remained dominant (approximately 67–95%) over the long term. Additionally, the wetland accommodated an estimated population of 200 turtles (approximately 84 males and 112 females) in 2023. These turtles displayed a range of body sizes within the wetland ecosystem. Particularly, several immature-sized individuals of both sexes were captured, in addition to a few juveniles of undetermined sex (unsexed). These findings suggest that the wetland has a healthy turtle population exhibiting normal reproductive patterns. The survival rate of young life stages in turtles (e.g., eggs, hatchlings, juveniles) is very low in general (Iverson, 1991), therefore, juveniles (unsexed individuals) would not be found in large numbers as seen in present study. In contrast, because young turtles (particularly hatchlings) of *M. japonica* tend to be found in shallow waters where traps cannot be set (e.g., Kagayama, 2020), it is possible that juveniles inhabit in the study area were simply not captured.

The decline and disappearance of turtle populations can be attributed to overexploitation for commercial purposes (Moll and Moll, 2004; Stanford et al., 2020), competition and hybridization with invasive turtle species (Cadi and Joly, 2003, 2004; Lee et al., 2019; Kagayama et al., 2020), predation by invasive predators (Fordham et al., 2006; Kosuge and Kobayashi, 2015), and river alteration (Chen and Lue, 2009; Usuda et al., 2012). However, the findings of the present study suggest that the lack of a gradual or sharp decline in the turtle population indicates that this population was not affected by the adverse impacts associated with the abovementioned anthropogenic negative disturbances. The prohibition on collecting *M. japonica* individuals, dearth of *T. scripta elegans* observations, low number of *M. reevesii* and hybrids, absence of injured individuals of *M. japonica* attacked by invasive predators, and lack of widespread habitat destruction collectively provide evidence that the wetland population of *M. japonica* has successfully evaded various major anthropogenic factors.

Demographic characteristics

The total number of individuals (adults and immatures) of both sexes and the number of adult males changed about 1.5 times. Whereas, the number of adult females was stable in comparison (Fig. 4). The little change observed in the adult female population can be attributed to two primary factors: the delayed age at which adult females reach maturity (typically 8–10 years) compared to that of adult males (typically over three years) (Kagayama, 2020; Kagayama and Nishibori, 2021); and the substantially higher annual survival rate of adult females (Kagayama, 2022). Therefore, the life history traits (e.g., life history stage-specific survival rate) of *M. japonica* (Kagayama, 2022) and the findings of the present study, indicate that the annual population size of the turtles (in particular adults) generally fluctuates moderately over a brief time period, barring major human disturbances and catastrophic mortality events.

Generally, male *M. japonica* with smaller body sizes have lower survival rates and shorter life spans than those observed in females (Yabe, 1989; Kagayama, 2020, 2022). However, the survival rate of adult males (0.87) in this wetland was approximately similar to that of adult females (0.87). An alternative method of estimating survival rates (Cormack–Jolly–Seber Model) demonstrated that adult males in a river located in hilly terrain, which was relatively unaffected by major anthropogenic disturbances, had lower survival rates (0.79, Kagayama, 2022) than adult females (0.94, Kagayama, 2022). This implies that males in the Nakaikemi wetland may possess comparatively higher survival rates than males in other populations. This may be explained by the limited presence of major predators (such as Carnivora, Pelicaniformes, and Squamata; Kagayama and Ogano, 2021) in the wetland. Additionally, although the wetland is connected to a river tributary via a channel, the primarily lentic nature of the ecosystem suggests that emigration induced by rising water levels during heavy rainfall is minimal.

The adult sex ratio was approximately 0.5. However, although no significant bias was observed (95% credible interval overlapping at 0.5, except for 2017–2019) throughout the study period, the sex ratio of total adults and immatures was slightly skewed toward females (sex ratio: 0.42–0.43). To date, interpopulation variation in the sex ratio of *M. japonica* has been reported in various studies (Yabe, 1989; Okada et al., 2011; present study), which may be influenced by differences in temperature in nesting sites and predator fauna. For example, Kagayama et al. (2021) estimated the annual changes in the population size of *M. japonica* in two adjacent rivers in an area where raccoons had invaded. The adult sex ratios (calculated based on the mean values of the posterior distribution reported by Kagayama et al., 2021) were 0.28–0.37 in the Sunomiyagawa River (indicating a bias toward females) and 0.47–0.58 in the Sanogawa River. In the Sunomiyagawa River, adult males had much lower survival rates (0.31) than adult females (0.76). In the Sanogawa River, adult males had slightly higher survival rates (0.68) than adult females (0.58) (Kagayama et al., 2021). Additionally, Okada et al. (2011) reported that the sex ratio (based on the number of captured individuals) of *M. japonica*, a species that exhibits temperature-dependent sex determination (males are exclusively produced at low temperatures of 22.0 to 28.0°C) (Okada et al., 2010), tends to be biased toward females in environments with open nesting sites and toward males in environments with sheltered nesting sites.

Although no significant differences were observed, a decreasing trend in mean CL was observed in both sexes. This may be due to an increase in the number of young individuals captured of undetermined sex (Fig. 3). However, since the detection probability of *M. japonica* in the Nakaikemi wetland was low (about 0.25) and many surviving individuals were not captured each year, the study period was insufficient to evaluate the main factors (e.g., increase in young individuals) of the negative trend of mean CL estimated in the present study.

Future direction

This study could not identify the primary drivers that contributed to the population dynamics of *M. japonica*. Generally, turtles have very low survival rates for their immature stages (e.g., eggs, hatchlings, and juveniles) and very high survival rates and long lifespans for their adult stage (Gibbons, 1987; Iverson, 1991; Shine and Iverson, 1995). Therefore, unless subjected to major adverse anthropogenic disturbances (e.g., predation by invasive predators and overexploitation for commercial uses), the population size would not fluctuate significantly over the short term (Brooks et al., 1991; Mullin et al., 2020; present study). To identify the primary drivers influencing *M. japonica* population dynamics, it is imperative to undertake long-term investigations encompassing various turtle populations in future studies.

The population of *M. japonica* in the Nakaikemi wetland represents a healthy breeding population with marginal annual fluctuations in population size. However, because *M. reevesii* has invaded the area and subsequently hybridized with *M. japonica*, it is essential to strengthen *M. reevesii* eradication measures in the future. The reproductive capabilities of hybrids (Suzuki et al., 2014; Ueno et al., 2021) raises the concern that pure *M. japonica* species will disappear. Furthermore, reproductive interference (e.g., courtship, chasing, mating, and hybrid production) from *M. reevesii* and hybrid males is expected to reduce the fitness (e.g., survival rate and the number of offspring) of adult *M. japonica* females.

No *M. reevesii* were found in the survey of the Nakaikemi wetland conducted prior to 2000 (Kohmatsu et al., 2000). Additionally, the number of captured *M. reevesii* in present study is low, suggesting a relatively recent introduction of this species into the study area. Therefore, it is highly likely that the impact of *M. reevesii* and its hybrids on *M. japonica* is still minor. Consequently, we aim to quantify the effects of early control measures for this species in future studies.

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Data Availability

All model parameter estimates (Table S1 and Table S2) and the JAGS code for the population size estimation models (supplementary materials) are available via figshare at https://doi.org/10.6084/m9.figshare.25382485.

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