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Research Article

Trophic plasticity of the endemic Japanese weasel in a lowland agricultural landscape

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Abstract

The conversion of natural ecosystems into human-modified landscapes (HMLs) is the main driver of biodiversity loss in terrestrial ecosystems, particularly the loss of large predators. Their demise can alter food webs substantially, sometimes releasing smaller carnivores, such as members of the Mustelidae. Nevertheless, even small carnivores must adapt to anthropogenic impacts on food availability, altering their resource use. In this context, the crops grown in agrarian habitats can profoundly affect community assembly. Here, we conducted dietary analysis on 75 Japanese weasel (*Mustela itatsi*) scats, collected between July 2017 and August 2018, to determine their seasonal food habits in a landscape dominated by rice paddy fields in Saitama prefecture, eastern Japan. From spring to autumn, Japanese weasels consumed predominantly (semi-)aquatic and terrestrial animal taxa, specifically invasive crayfish (*Procambarus clarkii*), insects (e.g., Coleoptera and Odonata) as well as adult anurans, which are all readily available prey species. In winter, Japanese weasels consumed predominantly fruit (e.g., figs, *Ficus carica*), with a relative decrease in combined animal content in scats, due to the scarcity of animal prey in dried-out paddy fields and irrigation ditches. Although frugivory is unusual in *Mustela* species diets, our findings demonstrate that Japanese weasels are capable of adaptive trophic plasticity, enabling them to survive atypical resource conditions in paddy field habitats. To enhance broad efforts to conserve *Mustela itatsi* in Japan, we recommend the diversification of rice paddy monocultures and encourage winter flooding to increase the availability of aquatic and semi-aquatic animal prey.

Introduction

The conversion of natural ecosystems into human-modified landscapes (HMLs) is the main driver of biodiversity loss in terrestrial ecosystems (Foley et al., 2005; Tucker et al., 2018). However, the consequences of habitat degradation arising from agricultural land conversion remain poorly understood (Magioli et al., 2019). Apex predators are often the first to be lost from HMLs because their extensive home ranges are sensitive to habitat loss and fragmentation (Dirzo et al., 2014; Tucker et al., 2018). When apex predators are lost, the ecological release (Ritchie and Johnson, 2009) of subordinate predators results in 'winner and loser' replacements (Filgueiras et al., 2021) causing the alteration or loss of trophic interactions that disrupt local ecological networks (Hanski, 2005; Valiente-Banuet et al., 2015; Galiana et al., 2022). Those predators that can persist in or colonize HMLs are usually more generalist and often omnivorous, opportunistic species with broader ecological niches (Fleming and Bateman, 2018; Magioli et al., 2019). In this context, the crops grown in agrarian habitats can profoundly determine community assembly according to a trade-off between productivity and disturbance (Gorczynski et al., 2021).

In the absence of large mammalian predators (Order Carnivora) from HMLs (Ordiz et al., 2021), small-medium sized carnivores (generally defined as ≥ 21.5 kg; Do Linh et al., 2022) are elevated to the highest remaining trophic level in depauperate food webs (Gehrt et al., 2010; Marneweck et al., 2021, 2022). Nevertheless, their population dynamics and life history traits remain fundamentally different to those of larger carnivores (Wallach et al., 2015). Due to energy lost in trophic level transitions (Shurin and Seabloom, 2005), small carnivores predate toward the broad base of trophic pyramids (Norrdahl and Korpimäki, 2000; Barbier and Loreau, 2019), and typically affect primary consumers, such as rodents (Lambin, 2017) and invertebrates. In turn, this can affect primary producer communities (e.g., plant biomass, regeneration, pollination, and seed dispersal) through trophic cascade effects (Hamback et al., 2004). Ultimately, however, pyramids topped by smaller carnivores are less steep and diverse than unperturbed systems (Duffy , 2003; Marneweck et al., 2022), with lower ecosystem functionality (Duffy et al., 2007). Furthermore, even smaller carnivores must adapt their resource use (i.e., food choice and habitat use), spatial organization, and life-histories to continue to persist in habitats altered substantially by human activities (Gehrt et al., 2010; Fischer et al., 2012; Rosalino et al., 2014). A better understanding of small carnivore adaptability, especially their trophic plasticity, is therefore vital for maintaining residual ecosystem functionality in HMLs and for planning future conservation management (Macdonald et al., 2017; Marneweck et al., 2021, 2022).

Rice (*Oryza sativa*) crops are gown extensively across Asia (Bandumula, 2018), often as a monoculture that structurally alters former natural habitats and ecological communities (Katayama et al., 2015). Rice cultivation in Japan dates back over 2000 years (Verschuer and Cobcroft, 2016), with rice paddy fields now covering c. 2,335,000 hectares (Ministry of Agriculture, Forestry and Fisheries, 2024a), producing approximately 7,165,000 tons of rice per year (Ministry of Agriculture, Forestry and Fisheries, 2024b). Across Japan, these extensively modified farmland areas lack large predators, but do support a guild of medium-sized generalist carnivores, including raccoon dogs (*Nyctereutes procyonoides*), invasive raccoons (*Procyon lotor*) and introduced masked palm civets (*Paguma larvata*), although they are less

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suitable for Japanese martens (*Martes melampus*) and Japanese badgers (*Meles anakuma*) (Ohdachi et al., 2015).

The much smaller (110–600 g, with male-biased sexual size dimorphism; Masuda and Watanabe, 2015) Japanese weasel, *Mustela itatsi*, an endemic mustelid, is also distributed broadly over agricultural lowlands and urbanized areas across Honshu, Shikoku, and Kyusyu Islands of Japan (Masuda and Watanabe, 2015). The Japanese weasel population has gradually declined across Japan, especially in lowlands (Sasaki et al., 2014), resulting in their 'Near Threatened' IUCN Red List status (under A2, A3 and A4), equivalent to a decline of c. 25 % over the last three generations (Kaneko et al., 2016). Furthermore, populations in western Japan face competition with the invasive Siberian weasel (*M. sibirica*) (Sasaki et al., 2014). The Japanese weasel is thus a species of urgent conservation concern in lowland HMLs (Kaneko et al., 2016; Suzuki, 2018b).

Typically, weasel species, such as *Mustela nivalis, M. erminea*, and *M. frenata* (now *Neogale frenata*), rely mostly on predating rodent prey in wooded habitat (McDonald et al., 2000; Zub et al., 2008; Vaca-León et al., 2019). In its natural hilly or mountain habitats, however, the Japanese weasel exhibits wider trophic plasticity than other weasel species, hunting in terrestrial and riverine habitats and consuming not only small mammals (i.e., mice, voles, shrews, and moles) but also aquatic or semi-aquatic prey (e.g., herptiles, fish, insects, crustaceans and anurans: Fujii et al., 1998; Suda et al., 2014). Furthermore, they occasionally supplement their diet with seeds, fruits, and berries (Kaneko et al., 2009, 2013; Okawara et al., 2014). This diet is similar to that of the larger (500–1500 g) western polecat (*M. putorius*) that also predates both terrestrial and aquatic prey (e.g., Hammershoj et al., 2004; Lode, 1997; Sainsbury et al., 2020), as well as occasionally eating fruits (Santos et al., 2009).

In this study, we conducted faecal analysis to investigate how trophic plasticity enables Japanese weasels to survive in rice paddy monoculture farmland in Saitama prefecture, eastern Japan. Here, intense agricultural activities, habitat modifications, water pollution, and the introduction of invasive species (Fujioka and Lane, 1997; Takeuchi, 2010; Tsunoda et al., 2010) affect food web structure and integrity, and rodents are uncommon due to being controlled (Lorica et al., 2020; Singleton et al., 2021) and limited by summer flooding (Aplin et al., 2006). We hypothesize that Japanese weasels may (i) consume substantial quantities of (semi-)aquatic prey (e.g., anurans and fish as well as introduced red-swamp crayfish, *Procambarus clarkii*), and (ii) sustain themselves by consuming eclectic food sources in winter, when other prey are less available due to the drainage of rice paddy fields. Finally, we use our findings to make recommendations for improving the conservation value of rice paddy fields in Japan for weasels and broader biodiversity.

Materials and methods

Study area

The study area, located in Kazo-shi, Saitama, Japan, was approximately 1.2 km^2 of agricultural land entirely covered by paddy fields, with a few small buildings but no forest cover (36°4′ N, 139°32′ E; Fig. 1 and Fig. S1 in Supporting information, SI). In addition, a few fig trees (*Ficus carica*) were cultivated along the side of a local floriculture farm (Figs. S1 and S2 in SI).

There was one paved road (Prefectural route 38) through this area, with a traffic volume of av. 12,466 cars per day (Saitama prefecture, 2017). This region has a humid-temperate climate (Köppen climate classification: Cfa) with hot, humid summers and cold, dry winters. Average monthly temperature and total precipitation during the study period (July 2017 to August 2018) ranged from 2.5 °C in January to 28.2 °C in August and from 11.0 mm in February to 453.0 mm in October (Automated Meteorological Data Acquisition System at Kuki station; data obtained from Japan Meteorological Agency, http://www.jma.go.jp/jma/menu/menureport.html, accessed 27 May 2020). Rice was planted in mid-May, with harvesting completed by mid-November (see Figs. S4 and S5 in SI). There were many small irrigation ditches between paddy fields, which dried up during the fallow season (i.e., between December to April), making aquatic prey scarce (see Fig. S5 in SI). In this area, raccoon dogs and introduced masked palm civets, as well as invasive raccoons also occurred at low densities (author's unpublished camera-trapping data) and potentially competed with Japanese weasels in the predatory guild; however, the Japanese marten and Japanese badger were absent (Saitama prefecture, 2018).

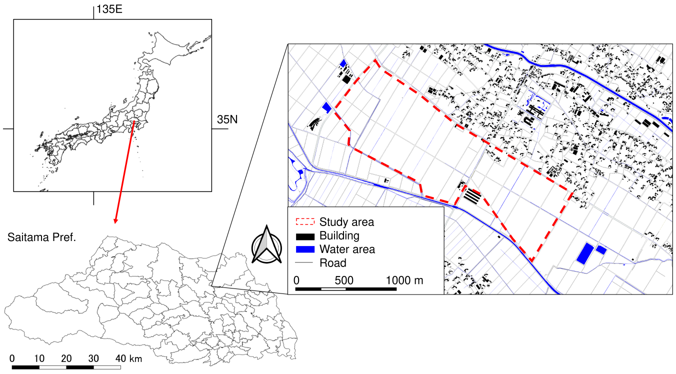

Figure 1 – Location of the study area, depicting the use of roads and adjacent road margins (shown as thin lines in the dashed-line polygon) as the transect route..

Field survey protocol

To collect Japanese weasel scats, we used all farmland roads and tracks (i.e., c. 60 % paved and 40 % gravel roads, c. 5 m wide) between paddy fields, as well as an adjacent margin of c. 2 m, as our survey transect, following the general scat detection protocol (Martinoli et al., 2001; Zhou et al., 2013; Lei et al., 2023). This amounted to a total tortuous transect distance of ca. 5.4 km (represented as thin lines in the polygon depicted in Fig. 1). We repeated these surveys three to four times a month from July 2017 to August 2018. Japanese weasel scats were easy to differentiate from other candidate sympatric carnivore species (mentioned above) based on their diminutive size (mean diameter of scats sampled = 5.6 (S.D. 1.2) mm: standardized size $\geq$ 8.7 mm from Tsuji et al., 2011) and appearance. Japanese weasel scats were collected and sealed in plastic bags, then taken to the laboratory and frozen at −20 °C.

Faecal analysis

Scat samples were rinsed through a sieve (0.5 mm mesh) with water and sorted under a ×10 magnifying lens. All food items were dried in an incubator at 80 °C and then weighed (to 0.01 g). We also collected the rinse water into a glass flask, which we left undisturbed for ca. 15 min to settle. We then collected 10 mL of bottom sediment with a pipette, which we plated on a petri dish and examined at × 20 magnification for earthworm chaetae, according to methodology used by Kaneko et al. (2009). We divided scat contents into ten categories, after excluding non-food materials (e.g., sand and gravel): rodents; herptiles (i.e., reptiles and amphibians); fish; insects; crayfish (the only crayfish species observed in our study area); earthworms; other animals (e.g., myriapods, land and aquatic snails); seeds (implying they consumed fruits); other plant parts (i.e., leaves and stems); and unidentified items.

For dietary analyses, we estimated the frequency of occurrence (FO; %) for all food categories and average proportion of dry weight (PDW; %) values for the nine categories (excluding earthworms) using the following equations (see Kaneko et al., 2009; Hisano et al., 2016):

FO (%) = (the number of occurrences of a food category present in sampled scats/ the total number of sampled scats) × 100

PDW (%) = (dry weight of a food category in a scat / total dry weight of all food items in that scat) × 100.

To assess seasonal dietary changes empirically, we compared PDW of all food categories within each season using Kruskal-Wallis tests. When statistical significances were identified using Kruskal-Wallis tests, we performed post hoc *t*-test with Bonferroni corrections for multiple comparisons. Finally, to determine seasonal dietary breadth, we estimated Shannon-Wiener indices using the PDWs of all food categories in each season. All analyses were performed using the R ver. 4.1.3 (R Core Team, 2022).

Results

In total, we sampled 75 scats, including 11 from spring, 20 from summer, 23 from autumn and 21 from winter. Overall, crayfish were the dominant food category (FO = 44.0 %; PDW = 26.1 %), followed by the insect (mainly Coleoptera and Odonata larvae, FO = 41.3 %; PDW = 16.4 %), herptile (FO = 36.0 %; PDW = 15.8 %), and seed (FO = 26.7 %; PDW = 15.8 %) categories (Table 1 and Table S3 in SI). The FO and PDW of the rodent and earthworm categories comprised a relatively small proportion (<10 %) of the overall diet (Table 1 and Table S3 in SI).

In spring, the insect and herptile categories predominated, and were found in 90.9 % and 72.7 % of the weasel scats sampled, respectively. Crayfish dominated weasel diet through summer (FO = 45.0 %) and autumn (FO =73.9 %), followed by the insect, herptile, and other animal categories (Table 1). In winter, vegetable matter, i.e., seed (FO = 66.7 %) and other plant part categories (FO =61.9 %), occurred more frequently than combined animal remains (FO = 4.8–23.8 %; Table 1).

The PDWs of food categories differed significantly across all four seasons (Kruskal-Wallis tests, $P < 0.01$; Fig. 2). In spring, the PDW of the insect category was predominant, occurring at significantly higher proportions ($P < 0.01$) than five of the other food categories (Fig. 2a). In summer and autumn, the PDW of the crayfish category was predominant, followed by the insect and herptile categories (Fig. 2b and 2c). Multiple pairwise comparison tests between all food categories revealed that the PDW of crayfish was significantly higher than that of either the rodent or fish category in summer ($P < 0.05$) and significantly higher than seven of the other food categories (excluding comparison with herptiles, $P = 0.08$) in autumn ($P < 0.05$). Furthermore, in autumn, the PDWs of the herptile and insect categories were significantly higher than that of the fish category ($P < 0.05$). In winter, the PDW of the seed category (indicating Rosales fruits, e.g., fig; Fig. S2 in SI) predominated, followed by the other plant part category, while combined animal remains comprised a relatively small percentage dry weight of each scat (Fig. 2-d and Table S3 in SI). Multiple comparison tests indicated the PDW of the seed category was significantly higher than for any single animal category ($P < 0.01$; Fig. 2), while there was no statistical significance between the seed category and the other plant part category ($P = 0.30$).

Shannon-Wiener indices for seasonal dietary breadth of the Japanese weasel (estimated using PDW) were 2.5 in spring, 2.6 in summer, 2.3 in autumn and 2.4 in winter.

Discussion

From spring to autumn, Japanese weasels ate prey species that were readily available in our study area. In support of our first hypothesis, weasels predominantly consumed (semi-) aquatic and terrestrial animal taxa (specifically crayfish, insects, and herptiles), but with only a modest FO for the rodent category in spring (18.2 %), with no rodent consumption in summer. Among prey species, the consumption of the insect category decreased gradually from spring to autumn, while the consumption of crayfish increased (Tab. 1 and Fig. 2). The consumption of the herptile category decreased from spring to summer and then increased to autumn. These seasonal patterns reflect the phenological cycles of prey taxa as they reproduce and proliferate in paddy fields from spring to autumn, benefitting from warm temperatures and water supplied by irrigation for rice cultivation (Washitani, 2007; Takeuchi, 2010). In spring when rice cultivation and irrigation commences, aquatic insect larvae (e.g., Coleoptera and Odonata) and a diverse abundance of adult anurans (e.g., *Pelophylax porosus porosus* and *Fejervarya kawamurai*) are available, due to immigration, emergence and/or reproduction (specifically for anurans) (Ban and Kiritani, 1980; Fujioka and Lane, 1997); similarly, around mid-May, red swamp crayfish emerge from underground hibernation in paddy field irrigation ditches, where they over-winter. From summer to autumn, the availability of insects gradually decreases as temperatures cool (e.g., Nezu et al., 2011), while juvenile anurans and crayfish mature. Importantly, water depth in paddy fields is around 5 cm when rice crops start to grow in spring (typically in mid-May; Fig. S4 in SI), but levels drop and irrigation ditches become shallower from summer to autumn (Fig. S5 in SI), allowing weasels greater predatory access to aquatic animals.

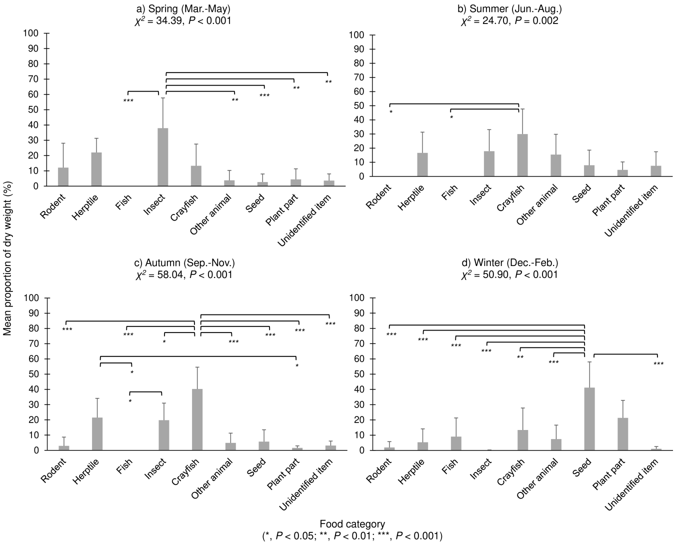

Figure 2 – Seasonal scat content for Japanese weasels in a paddy area in Saitama, Japan, divided into food categories and then expressed as mean proportions of dry weight (PDW; %) with 95% confidence intervals (represented by vertical bars). Kruskal-Wallis tests comparing PDWs among food categories in each season are shown at the top of each panel. Horizontal bars with star(s) represent statistically significant pairwise comparisons of food categories, using post hoc multi-comparison t tests with Bonferroni correction..

In winter, paddy fields and irrigation ditches dry up entirely, causing (semi-)aquatic animal prey to become scarce. In support of our second hypothesis, this resulted in Japanese weasels switching to a more frugivorous diet composed of plant food categories (i.e., seeds, especially fig fruits, as well as other plant material). Although rodents are common in the winter diets of Japanese weasels in other parts of their range (Otsu, 1971; Fujii et al., 1998; our Tab. 2), in our study, the rodent category FO was just 4.8% in winter (Tab. 1). This is likely because the homogeneous paddy field monoculture in our study area did not include any scrub or wooded habitats that support terrestrial rodent populations over winter. We did, however, find that Japanese weasels continued to consume red swamp crayfish in winter (FO = 14.3 %; Tab. 1). These were likely either dug out of dry irrigation ditch beds where they over-winter (Gherardi et al., 2002; Sato et al., 2023) or taken from small pools (typically less than 20 cm water depth) that persist at intersections between ditches in during winter (Fig. S6 in SI) and likely provide an important feeding site for Japanese weasels through the winter months.

Although our study area was relatively small (i.e., 1.2 km^2), home range sizes of male weasels typically range from 0.1 km^2 (in an agricultural landscape) to 0.35 km^2 (in suburban riverine habitats) with range overlap between several individuals (Masuda and Watanabe, 2015; Watanabe, 2005). This suggests that our study area likely supported several individuals. Carnivore home range sizes are determined by the dispersion of food resources (Macdonald and Johnson, 2015), and thus it is possible that not all resident weasels had access to fig trees in their territories or chose to eat fruit. Whether only a few weasels eat fruit could be determined by future studies that track which foraging sites individuals use.

Consistent with our findings, previous studies on Japanese weasel diet in HMLs have also reported a high FO value for red swamp cray-

Table 1 – Seasonal frequency of occurrence (FO; %) of 10 food categories (including unidentified items) in the diet of Japanese weasels in a paddy area in Saitama, Japan (*N*, number of items occurred)..

Season	Spring		Summer		Autumn		Winter		Whole period	
	Mar.-May		Jun.-Aug.		Sep.-Nov.		Dec.-Feb.			
Number of scats	11		20		23		21		75	
Food category	*N*	FO (%)	*N*	FO (%)	*N*	FO (%)	*N*	FO (%)	*N*	FO (%)
Rodent	2	18.2	0	0.0	1	4.3	1	4.8	4	5.3
Herptile	8	72.7	5	25.0	11	47.8	3	14.3	27	36.0
Fish	0	0.0	0	0.0	0	0.0	2	9.5	2	2.7
Insect	10	90.9	7	35.0	12	52.2	2	9.5	31	41.3
Crayfish	4	36.4	9	45.0	17	73.9	3	14.3	33	44.0
Earthworm	0	0.0	0	0.0	2	8.7	2	9.5	4	5.3
Other animal	2	18.2	7	35.0	6	26.1	5	23.8	20	26.7
Seed	1	9.1	2	10.0	3	13.0	14	66.7	20	26.7
Other plant part	5	45.5	3	15.0	10	43.5	13	61.9	31	41.3
Unidentified item	5	45.5	4	20.0	5	21.7	3	14.3	17	22.7

fish (> 20 %) and seeds (19.0–63.1 %) (Fujii et al., 1998) with one report of the high rates of frugivory in a mountainous habitat (Furuya et al., 1979; see Tab. 2). In contrast to our study site, weasels in natural habitats typically consume terrestrial insects (e.g., Coleoptera and Orthoptera) and/or reptiles (e.g., Furuya et al., 1979; Sekiguchi et al., 2002), as well as rodents in winter (Otsu, 1971). In HMLs, specifically in urban and suburban areas where the land is covered by buildings and paved roads, riverine habitats are important for weasels, providing both foraging and resting sites (Fujii et al., 1998; Suda et al., 2014; Suzuki, 2018a; Watanabe, 2005). This can also cause weasels to rely more heavily on aquatic prey, such as red swamp crayfish (Fujii et al., 1998). Furthermore, urbanized HMLs may have fruit available from cultivated trees and bushes planted in parks, gardens, and orchards (Fujii et al., 1998; Kaneko et al., 2009).

In conclusion, our findings broadly corroborate previous reports that the Japanese weasel is far less specialized on mammalian (especially rodent) prey than other small *Mustela* species (e.g., McDonald et al., 2000; Zub et al., 2008; Vaca-León et al., 2019), due to its adaptable and plastic trophic niche (Tab. 2). The consumption of red swamp crayfish and other (semi-)aquatic animals by Japanese weasels reveals the species' capacity for opportunism and efficient dietary switching to exploit environmental prey availability; a trait also seen in the western polecat (Lode, 1997) that can adapt to various environments (Lode, 1994) as well as in larger mustelids (e.g., Zhou et al., 2011, 2015). Simultaneously, this predation effect may provide some degree of biological control on invasive red swamp crayfish, which are a pest species in Japan (Nakata et al., 2005), although likely not sufficient to substantially reduce numbers. The high frequency of seed category (FO = 67.7 %; Tab. 1) in Japanese weasel scats further exemplifies their trophic plasticity, where, among related mustelids, switching to seasonal fruits is rare among *Mustela* species (McDonald et al., 2000; Martinoli et al., 2001; Zub et al., 2008; Vaca-León et al., 2019) and a trait more typically seen in martens (*Martes* spp., Zhou et al., 2011). This winter frugivory is important because Japanese weasels are too small and slender to hibernate (Newman et al., 2011; Wereszczuk and Zalewski, 2015; Macdonald and Newman, 2017).

A broader guild of mesocarnivores were present in this study area, especially raccoons and raccoon dogs (author's unpublished camera trapping data and footprint track observations in mud), and these may exert intra-guild competitive pressures on smaller Japanese weasels, also affecting their access to food resources. Certainly, raccoons are known to predate crayfish (Boncompagni et al., 2021) and to consume seasonal fruit, with raccoon dogs also eating a significant proportion of available fruit and crustaceans (Xu et al., 2023), including crayfish (Takatsuki and Kobayashi, 2023). Masked palm civets are similarly adaptive opportunists that consume various fruits and invertebrates in Japan (Iwama et al., 2017).

While the versatile feeding habits of Japanese weasels enable them to exploit alternative food resources, and thus to survive in HMLs, their population has been in steady decline across Japan, especially in lowland areas (Sasaki et al., 2014; Kaneko et al., 2016). Consequently, the Japanese government has banned the hunting of female Japanese weasels (Kaneko et al., 2016). In addition to the difficult resource conditions that agricultural and urbanized habitats present (Sasaki et al., 2014; Masuda and Watanabe, 2015), this decline is exacerbated by competitive exclusion resulting from the spread of the invasive alien

Table 2 – Frequency of occurrence (%) of nine food categories in the diet of Japanese weasels observed in previous studies from different habitat types across Japan in comparison to our study (*N*, number of faeces or stomachs analyzed). Seasons are abbreviated as 'Su', summer; 'Au', autumn; 'Wi', winter; and 'Whole', all year round.

Site	Zamami Island, Okinawa	Nishikuma valley, Kochi	Hiwa, Hiroshima	Asahi & Iide Mts, Yamagata	Hamura, Tokyo	Tachikawa, Tokyo	Hamura, Tokyo	Mito, Ibaraki	Kazo, Saitama
Habitat type	Hilly forest	Montane forests	Montane forests	Montane foothill	Riverine, suburban	Riverine, suburban	Riverine, suburban	Suburban	Paddy fields
Season	Su–Au	Whole	Au	Wi	Whole	Whole	Whole	Wi	Whole
N	141	317	46	75	285	65	33	237	75
Food category									
Mammal	17.0	21.8	13.0	50.7	26.5	32.3	6.1	21.5	5.3
Bird	1.4	8.8	6.5	13.3	8.1	4.6	3.0	2.5	0.0
Herptile	34.0	10.4	54.3	5.3	6.7	1.5	9.1	0.0	36.0
Fish	0.0	0.0	17.4	6.7	20.5	7.7	21.2	18.1	2.7
Insect	85.8	63.1	8.3	0.0	32.3	44.6	75.8	39.2	41.3
Crustacean	14.9	2.2	8.7	5.3	43.9	27.7	21.2	20.3	44.0
Earthworm	0.0	0.0	15.2	0.0	0.0	0.0	0.0	8.3	5.3
Other animal	3.5	0.0	2.2	0.0	6.7	7.7	12.1	12.5	26.7
Seed (fruits)	7.1	83.9	0.0	0.0	63.1	60.0	33.3	19.0	26.7
Reference	Sekiguchi et al. (2002)	Furuya et al. (1979)	Yukawa (1968)*	Otsu (1971)	Fujii et al. (1998)	Fujii et al. (1998)	Okawara et al. (2014)	Kaneko et al. (2009)	This study

* Data cited from the Tab. 3 in Sekiguchi et al. (2002).

Siberian weasel through western Honshu, Shikoku and Kyushu Islands of Japan (Sasaki et al., 2014) — although not detected in our study site.

To further conserve weasel populations in agricultural lowlands and especially in paddy field monocultures, we recommend that habitat management strategies aimed specifically at enhancing winter food availability are implemented (Korpimäki et al., 2004). For example, at a microhabitat scale, allowing winter flooding of paddy fields would result in the year-round availability of more aquatic and semi-aquatic animal prey (Washitani, 2007) and waterfowl (Katayama et al., 2020), especially in the south of the Japanese archipelago. At landscape scale, breaking rice monoculture with a mosaic of habitats through reforestation and managing abandoned fields as a biotope or ecological park could also be advantageous. This could result in greater year-round prey diversity, particularly enhancing the availability of rodents (Alain et al., 2006; Panazacchi et al., 2010; Rey Benayas and Bullock, 2015), invertebrates, and fruits (Haggar et al., 2019; Katayama et al., 2020). Furthermore, Japanese weasels use small burrows on river banks or fallow paddy fields as reproductive nests (Watanabe, 2005). Therefore, natural embankments of rivers and irrigation ditches are important to maintain their viable populations. However, any intervention must be monitored carefully to ensure this does not disadvantage Japanese weasels by favouring other small carnivore species to a greater extent, and thus promoting intra-guild competition (Linnell and Strand, 2000).

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Figure S1 Aerial photograph of the study area.
Figure S2 Seeds of fig fruits and a cultivated fig tree planted in a small farm.
Table S3 Seasonal mean proportions of dry weight of 10 food categories.
Figure S4 View of paddy fields in late spring and mid summer.
Figure S5 View of paddy fields, ditch and pool dried up during fallow season.
Figure S6 Examples of temporary pools at an intersection of irrigation ditches.