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Spatial Distribution Pattern of Free-ranging Miyako Grass Lizards (*Takydromus toyamai*) and Its Causal Factors

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Abstract.—**Free-ranging animals often form aggregations, which may bring various benefits. Clarifying the spatial distribution patterns and their implications can be beneficial for understanding the potential causes of population decline in endangered species. The Miyako Grass Lizard (*Takydromus toyamai*) is an endangered grass lizard endemic to the Miyako Islands, Japan, and has experienced a significant population decline. If found, they often occur in small groups, not spread out across a habitat. This observation implies that this species tends to aggregate, which may be beneficial for population maintenance. To confirm this, we investigated the spatial distribution patterns of free-ranging *T. toyamai* within high-density habitats by monthly surveys over a 3-y period. We also examined spatial variation in habitat quality and its relation to lizard aggregation. We found that *T. toyamai* exhibited a significantly aggregated distribution on numerous survey days across various seasons. We found lizards more frequently in habitats dominated by grasses than non-grassy sites, and were aggregated within these grass-dominated areas. There was no clear correlation between lizard aggregation and vegetation amount, which indicates that the aggregation of lizards is not a coincidence due to spatial heterogeneity of the habitat. Further analyses for temporal consistency of aggregated lizards and the sex ratios within these groups revealed that the aggregations were dynamic and formed randomly in sex ratio. These findings suggest that the aggregated distribution of *T. toyamai* is likely driven by intrinsic factors, with individuals being drawn to one another for reasons unrelated to sexual behavior. This implies that the lizards may derive some benefits from aggregations.**

Key Words.—aggregation; Allee effect; capture-mark-recapture; Lacertidae; moving pattern; vegetation

Introduction

Free-ranging animals frequently form aggregations at certain periods or under specific environmental conditions to gain some benefits, such as increase of breeding success, reducing predation risk, better hibernation success, and effective thermoregulation (Allee 1927). The formation of aggregations may also have various costs, however, such as excessive competition among individuals for food and other resources, inbreeding depression, higher risk of disease infection, and heightened vulnerability to predators (Rubenstein 1978; Chapman and Valenta 2015). Based on natural selection considerations, animals would only aggregate when the advantages outweigh the associated costs (Ward and Webster 2016). Because these benefits may affect the fitness of animals and the dynamics of their populations, understanding the factors leading to aggregation can be important for effective population conservation and habitat management, particularly for endangered species.

Both extrinsic and intrinsic pressures may drive aggregations. Aggregations driven by extrinsic factors occur incidentally when available resources, such as food, shelters, thermoregulation sites, or spawning areas, are concentrated in some places within the habitat and many individuals congregate to access these resources (Graves and Duvall 1995; Mouton 2011; Gardner et al. 2016; Vasconcelos et al. 2017). In contrast, intrinsic aggregations are formed when individuals are drawn to one another at close distances, being independent of surrounding environmental conditions. The aggregations that are formed by intrinsic factors would provide certain benefits to the aggregated members, such as increased vigilance against predators, improved thermoregulation efficiency, and/or enhanced mating opportunities (Chapple 2003; While et al. 2015; Gardner et al. 2016).

Figure 1. A Miyako Grass Lizard (*Takydromus toyamai*) from Miyakojima Island in the southern part of the Ryukyu Archipelago, Japan. (Photographed by Mamoru Toda).

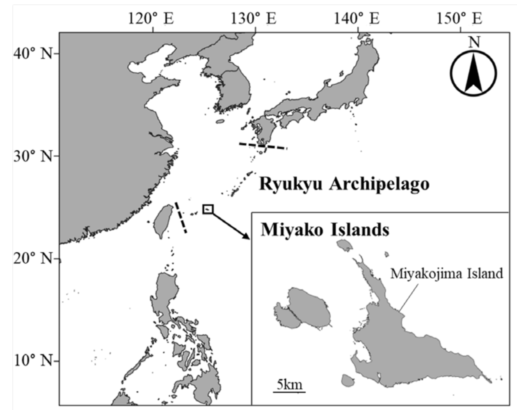

Figure 2. Location of the Miyako Islands in the southern part of the Ryukyu Archipelago, Japan.

The Miyako Grass Lizard (*Takydromus toyamai*) is a striking, green-colored grass lizard (Fig. 1) endemic to the Miyako Islands of the Ryukyu Archipelago, Japan (Takenaka 2021). *Takydromus toyamai* is a small to medium-sized grass lizard from the family Lacertidae, with an average snout-vent lengths (SVL) of 55.1 ± 5.4 mm (standard deviation) for males and 54.3 ± 5.6 mm for females (Asato and Toda 2025). The species inhabits herbaceous environments nearby forests, farmlands, and villages (Saiki et al. 2018; Toda and Takahashi 2018) and has a prolonged breeding season from March to September (Asato and Toda 2025). They reach sexual maturity in < 3 mo after hatching, allowing some females hatched in the spring to lay eggs in the late summer of the same year. In addition, *T. toyamai* is short-lived, with most individuals not surviving beyond a year (Asato and Toda 2025).

In recent years, this species has undergone severe population declines and is now listed as an Endangered and Critically Endangered species in the International Union for Conservation of Nature and Natural Resources and Japanese Red Lists, respectively (Kidera and Ota 2017; Ministry of the Environment of Japan. 2020. The Japanese Red List 2020. Available from https://www.env.go.jp/content/900515981.pdf [Accessed 30 August 2024]). Based on field surveys on 160 localities across the Miyako Islands for the occurrence of *T. toyamai*, Toda and Takahashi (2018) reported that these lizards were absent from many seemingly suitable habitats, and very few habitats were found with numerous individuals. The putatively patchy distribution of free-ranging *T. toyamai* was also implied from our observations in the life-history surveys we conducted in high population density areas (Asato and Toda 2025). Frequently, several *T. toyamai* were found in close proximity within small areas of the study sites. If aggregation within habitats indeed supports population stability for this species, understanding the factors driving such behavior could provide valuable insights for restoring populations in many other areas. The extent to which *T. toyamai* forms aggregations, however, as well as the factors inducing these aggregations, remains unclear.

We first examined the distribution pattern of free-ranging *T. toyamai* using exact location data of individual lizards in high-density populations to verify the hypothesis that this species predominately forms aggregations in nature. We explored contributions by three possible factors shaping the distribution pattern of this lizard: (1) we examined spatial heterogeneity of vegetation quality as a possible extrinsic factor; (2) we analyzed movement pattern of the lizards and consistency of the individual lizards forming aggregations over time to test contribution of site fidelity and synchronous movement of individuals; and (3) we examined sex ratios within aggregations observed in the study sites to see whether these aggregations were related to reproductive behavior. We discuss the possible major factor shaping the distribution pattern of this grass lizard and its implications in accordance with results of these analyses.

Materials and Methods

Study sites.—Miyakojima Island covers an area of 204.5 km^2 and is located in the southern part of the Ryukyu Archipelago, Japan (Fig. 2). The island has a humid subtropical climate, with average air temperatures ranging from 28.9° C in July (the hottest month) to 18.3° C in January (the coldest month) with monthly precipitation of 119.8–259.3 mm (https://www.data.jma.go.jp/obd/stats/etrn/view/nml_sfc_ym.php?prec_no=91&block_no=47927&year=&month=&day=&view=). The study site, located in the western part of Miyakojima Island, is surrounded by a secondary forest, sugarcane fields, and a meadow with a cowshed. This is the same site designated as Site B in Asato and Toda (2025). At this site, three routes were established for transect surveys: (1) Route A, 138 m long; (2) Route B, 136 m long; and (3) Route C, 88 m long. Routes A and Route B run through herbaceous zone along the forest edge, while Route C is a trail through the forest with herbaceous zone on both sides. Local people occasionally cut the grasses and other herbaceous plants along these routes, with the vegetation recovery occurring within a few months. Sometimes due to high rates of growth in the warm season, the herbaceous zone along both sides of Route C merge with each other across the trail. We regarded the herbaceous zone of both sides of Route C as single transect and pooled location data for lizards recorded along both sides of the route, as most animals inhabiting the herbaceous zone, including *T. toyamai*, were expected to shuttle between both sides of the trail.

Field surveys.—We conducted the transect survey on basically two nights nearly every month from June 2019 to December 2021, although not in August 2019, April-May 2020, January, April, and August 2021. These transect surveys overlap with those reported by Asato and Toda (2025). *Takydromus toyamai* is diurnal but is much more easily detected and caught at night because they sleep on vegetation (Asato et al. 2021). During each transect survey, we carefully searched for sleeping grass lizards on the plants by walking slowly along the designated routes we mentioned above. We captured all individuals encountered by hand whenever possible and temporarily placed them in plastic bags with small air holes and pieces of paper. We marked the locations of all lizards (whether successfully captured or not) on the plants using clothespins, each with a unique number.

We measured the captured lizards for SVL to the nearest 1 mm. We determined sex by the presence or absence of a hemipenial bulge in the base of the tail, and treated individuals < 46 mm in SVL as juveniles, following Asato and Toda (2025). We assigned a unique identification number to each captured lizard through toe clipping and then subsequently released them at the exact point of capture. Passive Integrated Transponder (PIT) tags are too large for *T. toyamai* and toe clipping has been commonly used for small lizards, which has been shown to have little effect on survival or stress of individuals (Langkilde and Shine 2006; Perry et al. 2011).

When we released the captured lizards, we measured the precise locations of the original sighting points on the basis of the clothespins that we have left on the plants. To minimize measurement errors, we used a tape measure or a walking tape measure instead of a GPS. We determined the sighting locations by measuring the distance from the starting point along the respective survey route (following the physical path rather than a straight line) to the nearest 1 cm.

Distribution pattern analysis.—To analyze the distribution pattern of *T. toyamai*, we used the number of lizards we found along transects in 4 m intervals. Based on the location data obtained from the field surveys, we evaluated the distribution pattern using the Iδ index (Morishita 1959):

$$I\delta = n\frac{\sum_{i=1}^{n} x_i\,(x_i - 1)}{N(N-1)}$$

where n represents the number of 4 m intervals along the route, xi is the number of individuals in the i-th interval, and *N* is the total number of individuals recorded along the route. The Iδ index ranges from 0 to infinity, with Iδ = 1 indicating a random distribution, Iδ > 1 indicating an aggregated distribution, and Iδ < 1 indicating a uniform distribution (Morishita 1959). We tested the significance of deviation from Iδ = 1 (random distribution) following a method proposed by Morishita (1959). We calculated F-value for a given Iδ index score for each survey day by using the following formula and compared it with the value of significant level based on F-distribution of F (n-1, ∞).

$$F = \frac{\mathrm{I\delta(N-1) + n - N}}{n-1}$$

We judged an Iδ index score to be significantly deviated from 1 when the former was greater than the latter (Morishita, 1959). We counted the number of lizards within each 4 m section along each survey route based on the location data from the field survey. We calculated the Iδ index for each survey day and tested statistical significance of those values when at least 10 individuals were found to assess the seasonality of the distribution pattern. A sample size of fewer than 10 lizards were unsuitable for the statistical analysis.

Vegetation survey.—From September 2019 to September 2021, we conducted monthly vegetation surveys to examine the relationship between the spatial distribution of *T. toyamai* and the condition of vegetation along the study routes. The herbaceous environments inhabited by *T. toyamai* are highly variable both spatially and temporally. For instance, vegetation height can often be heterogeneous along a single survey route and may change dramatically within a few months due to rapid growth in the humid subtropical climate, as well as by mowing by humans. In some cases, sections of the herbaceous environment disappeared nearly entirely due to over-mowing or natural disturbances, such as typhoons. Therefore, we performed vegetation surveys concurrently with the lizard distribution surveys to monitor these environmental fluctuations as precisely as possible.

We placed 2 × 2 m quadrats back-to-back along the survey routes from the starting point to the end points and recorded the gross averaged height of vegetation and percentage cover in each quadrat. We determined the averaged height of vegetation in each quadrat by visual inspection, measured to the nearest 0.1 m. To do this, we visually smoothed the height of all plants in the quadrat and determined its height using a measuring rod. We defined vegetation cover as the percentage of ground covered by plants in the quadrat by visual assessment to the nearest 10%. We determined the dominant species through visual inspection in each quadrat based on the percentage cover of each plant species. We obtained a vegetation amount score of each quadrat as a rough indicator of vegetation biomass by the formula; gross averaged height of vegetation × percentage cover of that quadrat.

Vegetation quality and aggregated lizards.—To assess the relationship between vegetation parameters and the occurrence of lizards, we first counted the number of *T. toyamai* individuals found in each 2-m section, which corresponded to the vegetation quadrats, on a monthly basis. We categorized the 2-m sections into two vegetation types: grasses dominant sections and non-grass dominant sections. We used Fisher's Exact Probability Test to determine whether there was a significant difference in the number of sections with and without lizards between these two vegetation types. In addition, we examined the correlation between the vegetation amount score and the number of lizards found in each section using Kendall's Rank Correlation for each survey route and monthly dataset.

As our analyses indicated that *T. toyamai* was more frequently found in grass-dominated sections (see Results), we further examined whether lizards displayed aggregated distribution within the grass-dominated area. We selected the areas comprised of at least 13 spatially continuous grass-dominant sections (i.e., sections spanning more than 26 m) and which contained a minimum of 10 lizards. We evaluated the spatial distribution pattern of the lizards in these areas using the $I\delta$ index to assess whether aggregation occurred even within the grass-dominated areas.

Movement pattern of lizards.—To assess the influence of site fidelity to the aggregated distribution, we investigated the movement patterns of *T. toyamai*. We used two indices, the monthly distance moved and the range of distances moved for individual lizards. The monthly distance moved was defined as the distance between two sighting points from consecutive monthly surveys for a given recaptured lizard. If an individual was captured more than once during the same monthly survey, we used the location data from the first capture/recapture record within that month. We allowed multiple observations of the same lizard across different months. For instance, if a lizard was captured in three successive months, we calculated two monthly scores of distances moved for that individual.

The second index, the range of distances moved, was defined as the distance between the two most distant sighting points for a given lizard over the entire survey period. We used only individuals that were recaptured with two months intervals or more for this index. We measured these distances along the survey routes rather than as straight-line geographic distances. Given that the herbaceous zones along the routes were narrow and *T. toyamai* was predominantly found within these zones, we assumed that the calculated values approximated the actual minimum distances moved and their ranges.

Dynamics and sex ratio in the aggregated lizards.—To investigate how lizard aggregations formed and changed over time, we analyzed the temporal dynamics or consistency of individuals within each aggregation. First, we selected the daily survey data in which the distribution pattern was identified as significantly aggregated. We then defined an aggregation of lizards as a group of four or more lizards found within two adjacent 2-m sections (i.e., a 4-m section) along a survey route. We tracked the movements of the lizards within these aggregations throughout the study period to determine how the aggregations were formed, persisted, or disbanded. These analyses were performed for Route A, where we recorded the highest number of lizards.

To assess whether the lizard aggregations were related to reproductive behavior, we analyzed the sex ratios within the aggregations. Specifically, we used 4-m sections that contained three or more adult lizards and counted the number of males and females in each aggregation using data from all three survey routes across all daily surveys. If reproductive behavior influenced the aggregated distribution, we expect that all aggregations include both male and female, with no aggregations comprised solely of one sex. We used the Binomial Test to evaluate whether the observed number of single-sex aggregations significantly deviated from the number expected under a random assumption based on the overall population sex ratio. To account for potential differences in capture rates between males and females, we calculated the sex ratio of the entire population as the total number of adult males divided by the total number of adult lizards (both sexes) captured, yielding the operational sex ratio.

Results

Spatial distribution pattern.—We collected 1,860 records of *T. toyamai* between June 2019 and December 2021, with 847 records from Route A, 531 from Route B, and 468 from Route C. Of these, 174 records lacked individual data due to the inability to capture the lizards. As a result, we used 796 records from Route A, 462 from Route B, and 428 from Route C for analyses of movement patterns and sex ratios. The number of 4-m sections with at least one lizard was 352 for Route A, 262 for Route B, and 176 for Route C. Of these, 178 sections (50.6%) in Route A, 93 sections (35.0%) in Route B, and 82 sections (46.0%) in Route C contained multiple individuals. The maximum number of lizards found in a single section was nine, which occurred on Route C in July 2021.

On Route A, the $I\delta$ index scores exceeded 1 in all 31 daily surveys that recorded 10 or more individuals. In 19 of these 31 daily surveys (61%), the $I\delta$ index scores were significantly > 1, indicating an aggregated distribution (Appendix Table). On Route B, the $I\delta$ index scores were significantly > 1 in 10 of 17 daily surveys with 10 or more lizards, and on Route C, 5 of 12 daily surveys with 10 or more lizards also showed significantly higher scores (Appendix Table). Although the $I\delta$ index scores were < 1 in two survey days on Route B and four survey days on Route C, these results were not significant (Appendix Table).

Spatiotemporal variations in vegetation parameters.—In the vegetation surveys conducted along the three routes, we recorded 17 plant species, including two unidentified species, as dominant in some 2 m quadrats. During the vegetation survey period, some parts of the herbaceous zones experienced moderate to large-scale mowing, leaving certain quadrats temporarily exposed to bare soil without vegetation. The most frequently recorded dominant plant species in the quadrats across the three routes was a broad-leaved type of Guineagrass (*Panicum maximum*), which occupied 66.9% of total number of quadrats with some vegetation. The second most frequent species was Romerillio (*Bidens pilosa* var. *radiata*), which accounted for 12.3% of the quadrats. Grass species were overwhelmingly abundant and were recorded as the dominant species in more than 80% of the total number of quadrats with some vegetation.

On Route A, the proportion of the grasses dominant sections varied seasonally. The grasses dominant sections constituted over half of the vegetated sections in summer, but this proportion declined in winter, with *B. pilosa* var. *radiata* becoming more prevalent (Appendix Figure). The dominant grass species along this route were primarily the broad-leaved type of *P. maximum*, normal type of *P. maximum*, and Paragrass (*Urochloa mutica*). Large-scale mowing in December 2020 significantly reduced the vegetation amount in many quadrats along Route A; however, the vegetation amount gradually increased and returned to pre-mowing levels by the following summer (Appendix Figure).

On Route B and Route C, grass species, predominantly the broad-leaved type of *P. maximum*, remained the dominant plant species throughout the study period (Appendix Figure). Vegetation amount on Route B experienced a sharp decline due to extensive mowing in September 2020 and recovered slowly over the subsequent months; however, most quadrats on Route B did not regain the pre-mowing levels until the next summer. Grasses along Route C were mowed extensively three times, leading to significant reductions in vegetation amounts in December 2019, and again in June and September 2020.

Spatiotemporal variations in distribution pattern of lizards.—Based on comparisons of 2-m sections dominated by grasses to non-grass dominant sections, *T. toyamai* were found significantly more often in the grassy sections along Route A (Fisher's Exact Test; $P < 0.05$; Fig. 3). There were no significant differences in the number of lizards found between grass and non-grass sections on Route B and Route C (Fisher's Exact Test; $P > 0.05$ for each). Lizards displayed aggregated distributions in five of seven cases within areas spanning more than 26 m that contained only grass-dominant sections on Route A (Ps < 0.05). Similarly, we observed significant aggregation on Route B and Route C, where grass species predominated throughout the entire lengths of the routes (Appendix Table). With the exception of a weak positive correlation in September 2019 on Route B ($\tau = 0.21$, $P < 0.05$), there was no significant correlation between the vegetation amount scores and the numbers of lizards ($P > 0.05$).

Movement patterns and instability of aggregation members.—Throughout the study period, 31 of 246 recaptured lizards (12.6%) relocated between different survey routes. Of these, 26 relocations occurred between Route A and Route B, which are continuous herbaceous zones connected at a right angle. We observed the remaining five relocations in four males and one female, who moved between Route C and the other two routes. For these relocations, the lizards had to travel at least 200 m through sugarcane fields or unstable herbaceous zones along forest edges and across an unpaved road. Notably, we initially captured one female (No. 2432) as a juvenile with a 45 mm SVL on Route A on 27 February 2020, we recaptured it on Route C on 13 July 2020, and we found it again on Route A on 13 August 2020, representing the shortest period of relocation across routes among the five cases. Of the remaining four cases, three were juveniles and one was a young adult male with a 48 mm SVL at the time of the first capture, and we found these lizards again on another route at the time of the second capture. None of these lizards relocated again after the initial route change.

We calculated the monthly distance moved and the range of movement distances for individual lizards after excluding the 26 cases of movements across different routes. The monthly moving distances within each route did not show any significant seasonal variation ($q = 4.67$, $P > 0.05$). The mean monthly distances moved were 9.09 ± 9.81 m (standard deviation; n = 114; range of values, 0.05–55.44 m) for males, 7.59 ± 12.36 m (n = 84; range of values, 0.02–83.68 m) for females, and 7.50 ± 16.32 m (n = 33; range of values, 0.11–94.46 m) for juveniles. These differences were not statistically significant ($q = 3.34$, $P > 0.05$). The range of movement distances for 205 lizards recaptured over intervals exceeding 2 mo varied from 0.06 to 126.64 m (Fig. 4). More than half of the lizards (44.4%, n = 91) had a range of movement distances of < 10 m, but 80% of these individuals were tracked for < 6 mo. There was a significant positive correlation between range of movement distances and the time period between the first capture and the last recapture ($\tau = 0.26$, $P < 0.05$).

On Route A, where lizard density was high, lizards exhibited a significantly aggregated distribution on 19 survey days (Appendix Table). During these 19 survey days, we detected 23 aggregations of lizards (each with more than four lizards in a 4-m section), and illustrated the movement paths of the aggregation members (Fig. 5). The locations where lizard aggregations were formed varied between months and included areas dominated by grasses as well as areas where *B. pilosa* var. *radiata*, a non-grass species, dominated. Although some aggregations were formed repeatedly in the same parts of Route A over the survey period, these aggregations were unstable. While a few lizards remained in the same location for certain periods, there were frequent influxes of new lizards from nearby areas and the withdrawal of others. Occasionally, lizards traveled from more distant locations to join an aggregation. For instance, the aggregations we observed on 13 September 2020 were formed by lizards arriving from various locations (Fig. 5).

Sex ratio in aggregated lizards.—The operational sex ratio of the population, based on the total number of captured adult individuals, was 1F:1.41M (382 females and 540 males), which significantly deviated from an equal 1:1 ratio (Binomial Test; $P < 0.05$). We found three or more adults within a single 4-m section in 59 cases. Of these, 46 aggregations contained both males and females, while the remaining 13 aggregations were composed solely of males or females. This proportion did not significantly deviate from what would be expected

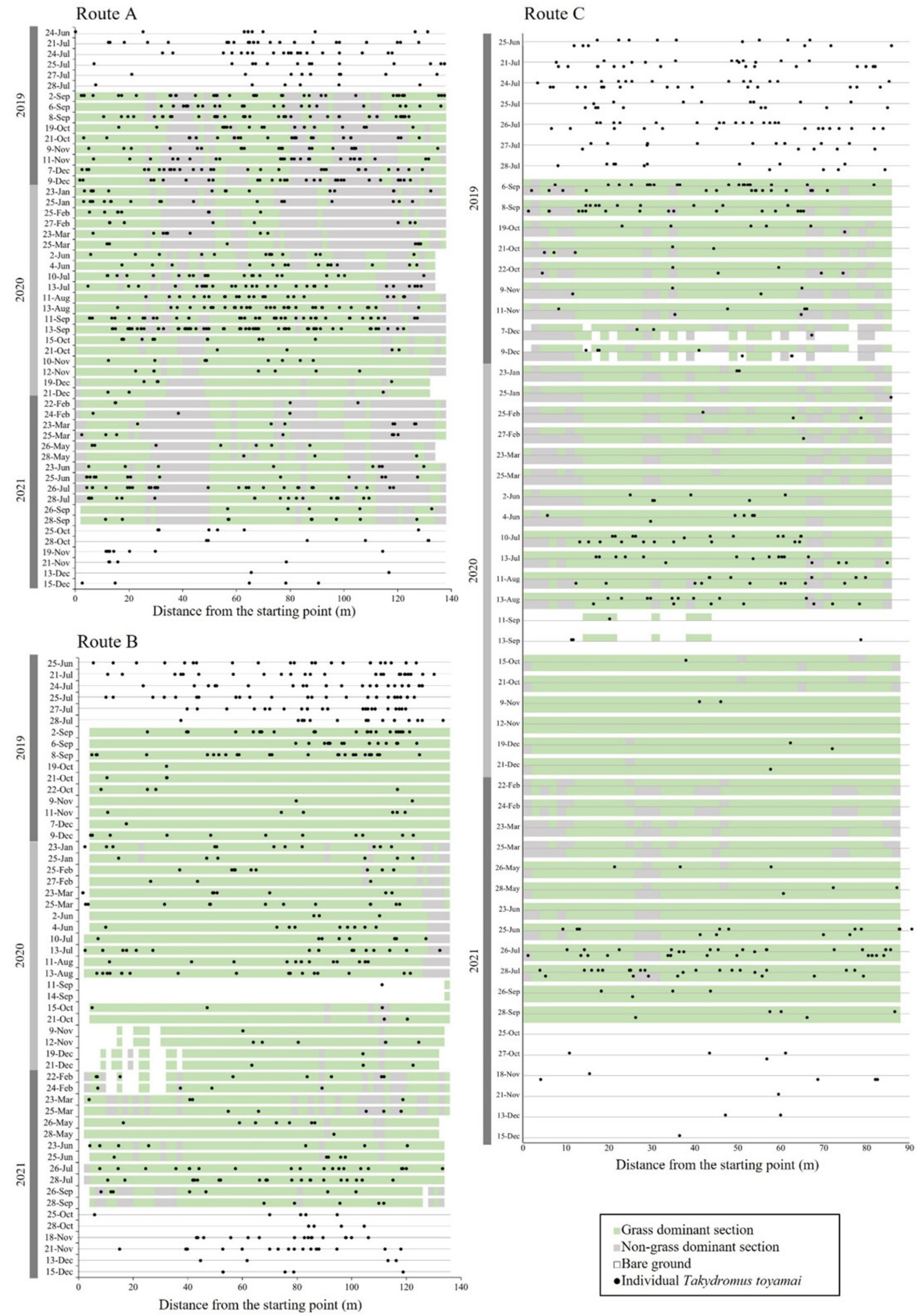

FIGURE 3. Diagrams showing the spatial distributions of individual Miyako Grass Lizards (*Takydromus toyamai*) along the survey routes with 2-m sections of vegetation types over entire survey periods on Miyakojima Island, Japan. Horizontal bars indicate each survey day. Note that vegetation data for survey days in the same month are represented by the results of the single monthly vegetation survey. Months outside the vegetation survey period are shown only with lines. The vegetation zones on the left and right sides of Route C are shown above and below the line for each survey day.

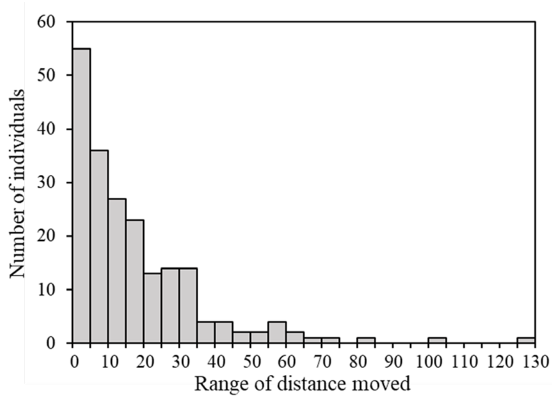

Figure 4. The range of distances moved by 205 individual Miyako Grass Lizards (*Takydromus toyamai*) on Miyakojima Island, Japan, recaptured over intervals exceeding two months. See text for definition of the range of distances moved.

under a random assumption based on the sex ratio of the entire population (Binomial Test; $P > 0.05$).

Discussion

The results of our study suggest that *Takydromus toyamai* exhibits an aggregated distribution commonly, as reflected by the significantly higher Iδ index scores in many cases. To our knowledge, this is the first study to demonstrate such an aggregated distribution pattern in free-ranging lizards of the genus *Takydromus* based on substantial field data. Many previous authors investigated the spatial distribution pattern in many lizard species and discussed the contributions of both intrinsic and extrinsic causal factors, such as the interaction of environmental heterogeneity, mating, and increased vigilance for predators (e.g., Fischer et al. 2005; Lanham and Bull 2004; Vasconcelos et al. 2017).

Among the extrinsic factors potentially influencing the spatial distribution of *T. toyamai*, vegetation heterogeneity seems the most likely, given the strong dependence of the species on herbaceous environments. Our findings partially supported this hypothesis, because *T. toyamai* is more frequently found in grass-dominated sections, particularly on Route A, where various plant species were unevenly distributed. This result aligns with previous reports that *T. toyamai* often uses grasses for daytime activities as well as for nighttime sleeping substrates (Mochida et al. 2013; Asato et al. 2021).

We observed the significantly aggregated distribution on Routes B and C, however, where the broad-leaved type of *P. maximum* was the dominant vegetation throughout the routes, and in specific areas of Route A dominated exclusively by

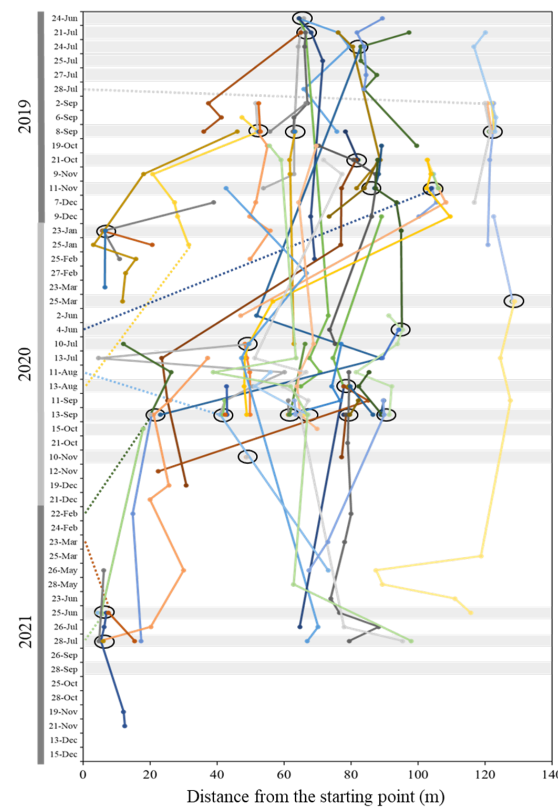

Figure 5. Locations of aggregations of Miyako Grass Lizards (*Takydromus toyamai*) on Miyakojima Island, Japan, and relocations of the aggregation members within Route A. Circles represent aggregations of four or more lizards observed within a 4-m section on a given survey day when the total distribution was judged as significantly aggregated (the grey horizontal bar). Solid lines indicate movements of the relocated lizards, and dotted lines represent migrations to different routes. Note that the intervals between the survey days (vertical axis) are not even.

grasses. These results suggest that the aggregated distribution of *T. toyamai* is not solely a result of vegetation heterogeneity. In addition, the lack of a clear correlation between the vegetation amount score and the number of lizards further suggests that this extrinsic factor is not the primary driver of the aggregation behavior of the species.

The aggregated distribution of *T. toyamai* might be influenced by its site fidelity. Some species in the genus *Egernia*, which are known as the social lizards, exhibit strong site fidelity, with newly matured young lizards often staying in their natal areas and sharing shelters with their parents for extended periods (Masters and Shine 2003; Langkilde et al. 2007). The Gidgee Spiny-tailed Skink (*Egernia stokesii*), another species of same genus, displays high site fidelity, such as monogamous pairs that remain in one location for long periods (Gardner et al. 2002). In the case of *T. toyamai*, the small average monthly distances moved (approximately 8 m) suggest a tendency for site fidelity; however, when examined over longer periods, individual lizards demonstrated longer distances moved. In addition, the dynamic nature of aggregation membership and the instability of aggregation locations suggest that lizard aggregations were transient, at least on the monthly survey timescale. These findings indicate that the aggregated distribution is not a result of high site fidelity or synchronous movement of a group of individuals.

Given the process of elimination as above, it is possible that the observed aggregated distribution is driven by intrinsic factors where individuals are attracted to each other. The potential benefits of these aggregations are likely because of increased reproduction or higher survival rates than individual distribution (Courchamp et al. 2008). To explore the reproductive hypothesis, we examined the sex ratio within adult aggregations in *T. toyamai*. We found that many aggregations were composed solely of males or females, and the proportion of these single-sex aggregations did not significantly differ from what would be expected by random chance. The adult aggregations were also observed outside of the breeding season (March-September; Asato and Toda 2025). These results indicate that the aggregated distribution of *T. toyamai* is not due primarily to mating behavior. Therefore, other intrinsic factors, such as increased vigilance against predators, may be responsible for the observed aggregation behavior. Because we conducted field surveys at night, when lizard sightings are more efficient, we lack data on their spatial distribution during the day. We cannot fully rule out the possibility that the aggregated distribution of the lizards is formed only at night, although small monthly distances moved imply that their spatial distribution pattern in daytime is not very different from that at night. Future studies focusing on the daytime behavior and spatial distribution of *T. toyamai* are necessary to clarify this issue and to understand the underlying factors contributing to their aggregation.

We found an overall aggregated distribution of *T. toyamai* at our study site, but many individuals did not join aggregations even when the overall population showed a significantly aggregated pattern. These findings suggest that the aggregations of *T. toyamai* are relatively loose and weak compared to the more cohesive structures seen in typical herds of animals or schools of fish. Nevertheless, this tendency to aggregate might provide certain benefits to both juvenile and adult lizards. The positive effects of increased population density on individual fitness are referred to as the Allee effects (Stephens et al. 1999). According to this theory, when population density falls below a certain threshold (the Allee threshold), individuals experience further reduced survival and/or reproductive success, leading to a decrease in the per capita population growth rate (Courchamp et al. 2008). The absence of *T. toyamai* from many seemingly suitable grassy environments, despite its historical ubiquity, can be interpreted as a consequence of such a negative feedback loop affecting many local populations. In recent years, the Allee effect has gained attention in the conservation of endangered species, particularly in the context of recovery and reintroduction programs for low-density populations (Dennis 1989; Boukal and Berec 2002). While the specific proximate and ultimate causes of the observed aggregation in *T. toyamai* remain unclear, further research on the potential Allee effects in this species is essential for informing effective conservation strategies for this critically endangered lizard.

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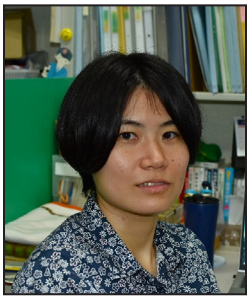

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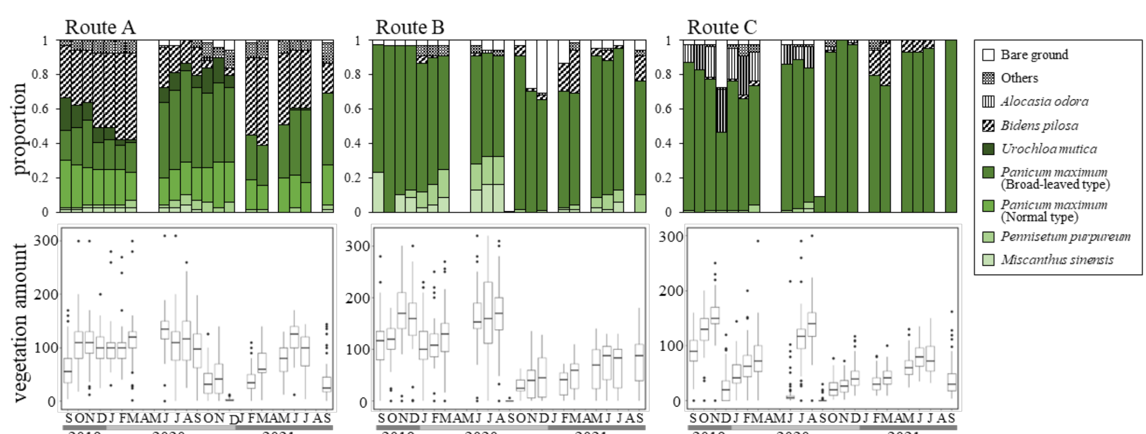
Appendices



Appendix Figure. Proportions of quadrats with each dominant plant species (upper graphs) and variations of the vegetation amount among quadrats (lower box plots) in the three survey routes at each survey day. In the upper graphs, the colored portions of the bars indicate the five dominant grass species, and the colorless hatched portions indicate non-grass plants species except for Bermuda Grass (*Cynodon dactylon*), which is included in Others. Others includes *Cynodon dactylon*, Chinese Elderberry (*Sambucus chinensis* var. *formosana*), Lead Tree (*Leucaena leucocephala*), Shell Ginger (*Alpinia zerumbet*), Blue Morning Glory (*Ipomoea indica*), Giant Swordfern (*Nephrolepis biserrate*), Alim (*Melanolepis multiglandulosa*), and two unidentified non-grass species.

Appendix Table. Number of lizards observed and the Iδ index score on each survey day. Asterisks (*) indicate Iδ index scores significantly > 1, indicating significant aggregated distribution.

Route A			Route B			Route C		
Date of survey	n	Iδ	Date of survey	n	Iδ	Date of survey	n	Iδ
24 June 2019	16	6.71*	25 June 2019	24	0.99	25 June 2019	18	0.86
21 July 2019	28	1.94*	21 July 2019	30	2.74*	21 July 2019	32	1.33
24 July 2019	22	1.97*	24 July 2019	29	1.67*	24 July 2019	28	1.28
25 July 2019	16	2.04*	25 July 2019	33	1.61*	25 July 2019	18	1.01
27 July 2019	10	3.11*	27 July 2019	25	2.27*	26 July 2019	35	0.96
28 July 2019	8	-	28 July 2019	16	2.55*	27 July 2019	17	1.78*
2 September 2019	35	1.18	2 September 2019	25	2.38*	28 July 2019	13	1.69
6 September 2019	21	1.33	6 September 2019	15	3.89*	6 September 2019	35	1.18
8 September 2019	43	2.21*	8 September 2019	26	1.78*	8 September 2019	25	1.54*
19 October 2019	17	1.29	19 October 2019	1	-	19 October 2019	6	-
21 October 2019	24	1.78*	21 October 2019	3	-	21 October 2019	5	-
9 November 2019	21	1.50	22 October 2019	4	-	22 October 2019	6	-
11 November 2019	29	2.93*	9 November 2019	2	-	9 November 2019	4	-
7 December 2019	29	1.03	11 November 2019	6	-	11 November 2019	6	-
9 December 2019	28	1.48	7 December 2019	1	-	7 December 2019	3	-
23 January 2020	16	2.63*	9 December 2019	12	2.06	9 December 2019	7	-
25 January 2020	20	1.66	23 January 2020	11	1.24	23 January 2020	2	-
25 February 2020	8	-	25 January 2020	6	-	25 January 2020	1	-
27 February 2020	9	-	25 February 2020	9	-	25 February 2020	3	-
23 March 2020	8	-	27 February 2020	3	-	27 February 2020	1	-
25 March 2020	11	7.64*	23 March 2020	8	-	23 March 2020	0	-
2 June 2020	14	1.92	25 March 2020	12	2.06	25 March 2020	0	-
4 June 2020	16	2.33*	2 June 2020	3	-	2 June 2020	6	-
10 July 2020	24	1.90*	4 June 2020	9	-	4 June 2020	6	-
13 July 2020	29	1.12	10 July 2020	8	-	10 July 2020	22	1.62*
11 August 2020	21	1.17	13 July 2020	15	1.30	13 July 2020	17	0.81
13 August 2020	35	1.53*	11 August 2020	15	2.91*	11 August 2020	15	1.89*
11 September 2020	44	1.15	13 August 2020	17	1.50	13 August 2020	16	0.73
13 September 2020	62	1.52*	11 September 2020	1	-	11 September 2020	1	-
15 October 2020	10	3.11*	11 September 2020	0	-	13 September 2020	3	-
21 October 2020	4	-	15 October 2020	3	-	15 October 2020	1	-
10 November 2020	10	4.67*	21 October 2020	2	-	21 October 2020	0	-
12 November 2020	7	-	9 November 2020	1	-	9 November 2020	2	-
19 December 2020	4	-	12 November 2020	6	-	12 November 2020	0	-

Appendix Table, Continued.

Route A			Route B			Route C		
Date of survey	n	Iδ	Date of survey	n	Iδ	Date of survey	n	Iδ
21 December 2020	3	-	19 December 2020	1	-	19 December 2020	2	-
22 February 2021	4	-	21 December 2020	3	-	21 December 2020	1	-
24 February 2021	3	-	22 February 2021	9	-	22 February 2021	0	-
23 March 2021	7	-	24 February 2021	4	-	24 February 2021	0	-
25 March 2021	8	-	23 March 2021	4	-	23 March 2021	0	-
26 May 2021	7	-	25 March 2021	5	-	25 March 2021	3	-
28 May 2021	3	-	26 May 2021	7	-	26 May 2021	3	-
23 June 2021	8	-	28 May 2021	1	-	28 May 2021	3	-
25 June 2021	13	4.94*	23 June 2021	7	-	23 June 2021	5	-
26 July 2021	26	1.51	25 June 2021	6	-	25 June 2021	15	1.47
28 July 2021	19	2.25*	26 July 2021	20	0.89	26 July 2021	32	2.13*
26 September 2021	5	-	28 July 2021	20	1.25	28 July 2021	27	1.00
28 September 2021	10	3.11*	26 September 2021	7	-	26 September 2021	5	-
25 October 2021	6	-	28 September 2021	5	-	28 September 2021	5	-
28 October 2021	6	-	25 October 2021	5	-	25 October 2021	0	-
19 November 2021	8	-	28 October 2021	4	-	27 October 2021	4	-
21 November 2021	4	-	18 November 2021	16	1.70	18 November 2021	5	-
13 December 2021	2	-	21 November 2021	17	2.00*	21 November 2021	1	-
15 December 2021	5	-	13 December 2021	4	-	13 December 2021	2	-
			15 December 2021	5	-	15 December 2021	1	-