Volume 36 (January 2026), 1–8

Herpetological Journal

FULL PAPER

https://doi.org/10.33256/36.1.18

Published by the British Herpetological Society

What do foot shakes of grass lizards *Takydromus tachydromoides* inform predators?

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Several animals advertise their escape performance toward potential predators and convey their unprofitability as prey by exhibiting pursuit-deterrent displays. Foot shakes, which are exhibited by lizards in response to potential predators, are considered as a pursuit-deterrent signal. This pursuit-deterrent signal is thought to be either perception advertisement, indicating the detection of a predator, or quality advertisement, informing the individual's condition. However, it remains unclear what foot shakes advertise to predators. To address this, we conducted a field experiment using the Japanese grass lizard *Takydromus tachydromoides*, which is known to perform foot shakes. To simulate a predator, we approached the lizards, and measured our distance from the lizards when first spotted (starting distance) as well as the distance between the lizards and us when they fled (flight initiation distance). We also recorded the presence or absence of foot shakes and their distance from us when they initiated the display (display distance). Tested lizards were captured whenever possible and snout-vent length (SVL), sex and body temperature (Tb) were recorded. In 151 approaches, 43 lizards exhibited foot shakes. Approximately half of the lizards displayed foot shakes with display distance between 1 m and 2 m, but none at closer distance. These results align with those observed in foot shakes of other lizards, which are considered as a pursuit-deterrent signal, and are consistent with pursuit-deterrent theory. SVL and Tb had a positive correlation with the probability of foot shakes, and males performed foot shakes more frequently than females. Because SVL and Tb are well known to influence the escape performance of lizards, and sex potentially influences the performance, our results suggest that foot shakes of *T. tachydromoides* advertises the quality of the lizard rather than the perception of predators.

Keywords: predator-prey interaction, pursuit-deterrence, antipredator signal, visual display, Lacertidae

INTRODUCTION

Several animals use signals toward their predators as a protective defence mechanism. Pursuit-deterrence is one of possible functions of such signals, defined by Caro (1995) as a signal emitted by a prey animal informing that it has detected the predator, and thus lower the probability of a successful predation attempt (Huang & Caro, 2023). Additionally, the predator can also benefit, saving its energy and time stalking unprofitable prey (Hasson, 1991). Such signals generally occur at a specific distance between prey and predator; when a predator approaches closer than that distance, the prey ceases signalling and initiates flight (Hasson, 1991).

Pursuit-deterrent signals can be divided into three types by the content they convey: vigilance advertisement, perception advertisement and quality advertisement (Caro, 2005; Huang & Caro, 2023). Vigilance advertisement is a signal that indicates to potential predators that the prey is vigilant, and it can be exhibited even in situations where the predator has not yet been detected by the prey (Huang & Caro, 2023). For example, tail wagging of white wagtails *Motacilla alba* is considered as a vigilance advertisement, due to the negative correlation between tail wagging and pecking behaviour, as the latter reflects non-vigilant motivation (Randler, 2006). Perception advertisement indicates that a predator has been detected and is aimed at predators relying on stalking or ambushing (Caro, 2005; Ruxton et al., 2018). The upright stance of hares *Lepus europaeus*, which is an example of perception advertisement, is performed when an ambushing predator, a fox *Vulpes vulpes*, is within a range of 20–50 metres. Furthermore, hares that perform the signal are less likely to be attacked (Holley, 1993). Finally, quality advertisement indicates a particularly fleet individual that is difficult to approach or that is challenging to subdue (Caro, 2005; Ruxton et al., 2018). Quality advertisement is exemplified by the singing of a skylark *Alauda arvensis*. The singing occurs only when pursued by the predator, merlins *Falco columbarius*, and skylarks that do not sing are pursued for a longer time and are more likely to be caught compared to those that sing (Cresswell, 1994).

Lizards also exhibit pursuit-deterrent signals. Tail displays (Hasson et al., 1989; Cooper, 2001), push-up displays (Leal & Rodríguez-Robles, 1997; Leal, 1999) and dewlapping (Leal & Rodríguez-Robles, 1997) have been considered as pursuit-deterrent signals in some species.

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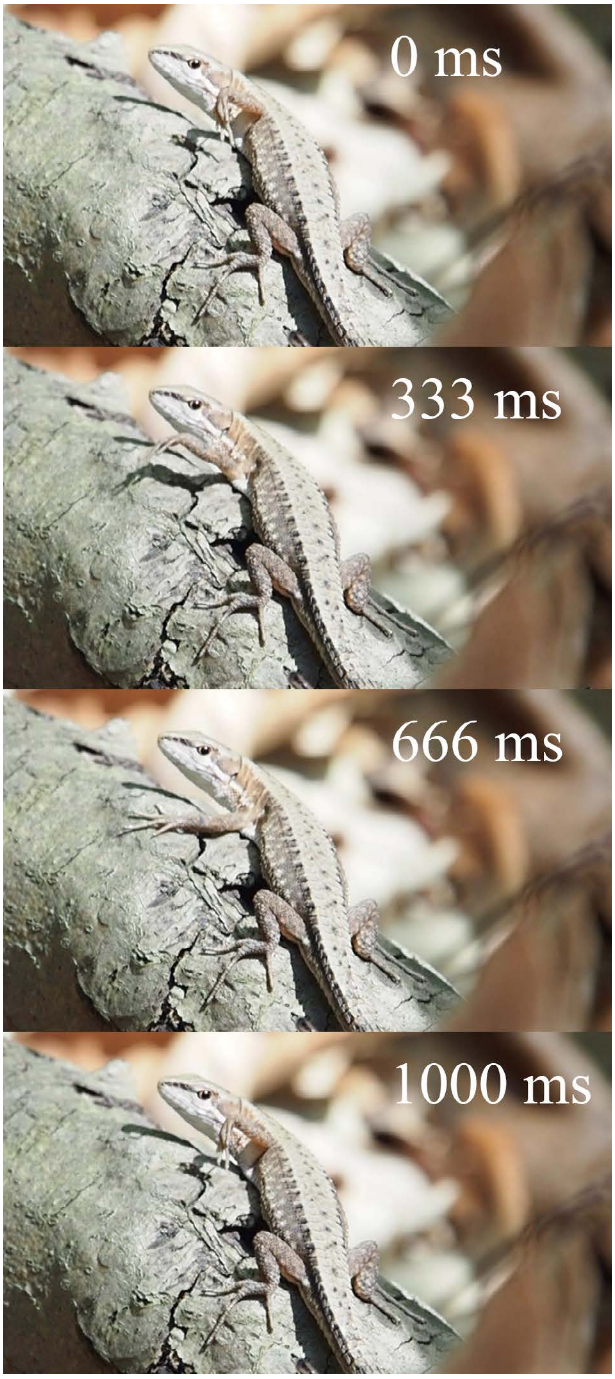

Figure 1. *Takydromus tachydromoides* performing foot shakes (extracted from a video). The number in the top right corner of each photograph indicates the time (milliseconds) from the beginning of the display.

Leal (1999) showed a positive correlation between the number of push-up displays and running endurance in the Puerto Rican anole *Anolis cristatellus*. A study of the zebra-tailed lizard *Callisaurus draconoides* demonstrated a correlation between the lizard's state of alertness, escape ability and tail displays (Hasson et al., 1989). These two examples showed that those displays are related to the individual's condition, such as running endurance and escape ability, and thus Huang & Caro (2023) considered them as quality advertisement signals.

Foot shakes are another potential pursuit-deterrent signal in lizards (Cooper et al., 2004; Font et al., 2012b). Foot shakes are displays where the forearm is rotated or moved up and down (Fig. 1). Font et al. (2012b) described that in a lacertid lizard *Podarcis muralis*, the foreleg follows a roughly elliptical trajectory, first moving toward the head and then toward the tail. Foot shakes are behaviourally similar to other displays of lizards such as arm-waving, hand-waves and circumduction. These displays have been reported in a wide range of lizard families, including Agamidae (e.g. Brattstrom, 1971; Ord et al., 2002; Van Dyk & Evans, 2008), Iguanidae (Distel & Veazey, 1982), Scincidae (Whitter, 1994), Teiidae (e.g. Cooper et al., 2004; Senter, 2024), Gymnophthalmidae (Poma-Soto et al., 2021), Phrynosomatidae (Carpenter, 1967), Liolaemidae (Halloy & Castillo, 2006) and Lacertidae (e.g. Font et al., 2012b). Foot shakes are considered to have various functions, including antipredator signals as pursuit-deterrence (Cooper et al., 2004; Font et al., 2012b), social signals (e.g. Brattstrom, 1971; Ord et al., 2002) and response to a hot substrate (Cooper et al., 2004). In a lacertid species *P. muralis*, foot shakes are classified into the following three types (Font et al., 2012b; de la Cruz et al., 2023). Type I occurs spontaneously and is not directed to any specific receiver. Type II is directed to conspecifics and is considered as a social signal conveying appeasement (Font et al., 2012a; Abalos et al., 2024). Type III is an antipredator signal. In Font et al. (2012b), the lizards fled without performing foot shakes when the observer approached within a close distance, and this result aligns with the characteristics of pursuit-deterrent signals. Therefore, Type III is considered as a pursuit-deterrent signal.

This pursuit-deterrent display of *P. muralis* is considered to be perception advertisement or quality advertisement (Font et al., 2012b). However, no study has measured the escape performance of any lizard species that performs foot shakes in the context of an antipredator signal, and what the display advertises is still unclear. Caro (2005) stated that perception advertisement should not be linked to an individual's condition, and thus, the information that foot shakes advertise can be determined by examining the occurrence of correlation between the condition of the lizard and the probability of performing the display (Font et al., 2012b).

The escape performance of lizards varies depending on conditions of the individual. Snout-vent length (SVL) is considered a major factor influencing escape performance because SVL affects sprint speed (e.g. Lowie et al., 2019) and running endurance (e.g. Huyghe et al., 2005). Body temperature (Tb) also affects the escape performance, since being ectotherms, lizard escape performance strongly depends on the Tb (Angilletta, 2006). Sex may also affect escape performance because it has been considered that females, when engaging in escape, incur costs associated with reproduction, particularly costs related to clutch mass (e.g. Tinkle & Hadley, 1975; Vitt & Congdon, 1978). Therefore, by measuring these individual states, we could predict their escape performance.

The Japanese grass lizard *Takydromus tachydromoides*, which is a small diurnal lizard endemic to Japan, performs foot shakes (Kubo et al., 2023). Kubo et al. (2023) reported that foot shakes were directed to both conspecifics and an observer, suggesting it functions as a social signal as well as a pursuit-deterrent signal. This lizard tends to escape by running along the ground rather than seeking shelter, making it easy to capture and measure the state of individuals. The purpose of this study is to determine whether foot shakes of *T. tachydromoides* convey a pursuit-deterrent signal, and if true, do foot shakes function as perception advertisement or quality advertisement? To achieve this purpose, we examined the following two issues:

1) Does *T. tachydromoides* stop performing foot shakes and flee when a predator approaches within a certain distance, as predicted by the pursuit-deterrent signalling theory?
2) Is the occurrence of foot shakes of *T. tachydromoides* associated with SVL, Tb or sex, which are correlated with escape performance?

MATERIALS & METHODS

Study site

We collected data from July to September 2023 at Mt. Uryu, Kyoto, Japan (35.04° N, 135.80° E, 100–301 metres above sea level), where *T. tachydromoides* is abundant. We set a survey route along a trail in this mountain, which extends approximately 2 km and is seldom used by other people. In this field site, the Japanese striped snake *Elaphe quadrivirgata*, a diurnal and active predator known to prey on *T. tachydromoides* (Mori & Moriguchi, 1988; Hamanaka et al., 2014), has been observed. Other known predators of the lizard, such as snakes, *E. climacophora, Gloydius blomhoffii* and *Lycodon orientalis* (Mori & Moriguchi, 1988; Hamanaka et al., 2014), and avian species, *Lanius bucephalus* (e.g. Karasawa, 1976), *Pernis ptilorhynchus* (Inoue et al., 2014) and *Parus cinereus* (Kurokawa & Akiyama, 2016), are also likely to inhabit this study site.

Field survey

Following Font et al. (2012b), we walked slowly along the trail to search for lizards. We conducted the survey on sunny or cloudy days, and the survey was limited to once per day. The survey began around 08:00 h and lasted for approximately 3 hours. If two or more people conducted the survey, differences in the ability to find lizards and walking pace could arise. To prevent this observer bias, this field survey was conducted by only GK. GK also conducted a pilot training to maintain a consistent walking speed of approximately 16–20 m/min.

When GK found a lizard, he stopped walking immediately and measured the distance between the observer and the lizard (i.e. starting distance) with a laser rangefinder (Zamo3; BOSCH Co., Inc.). Then, he observed the lizard's behaviour for one minute without moving. After one minute, he slowly approached the lizard. Several previous studies have shown that the probability of a pursuit-deterrent display is high when the lizard is slowly approached (e.g. Dial, 1986; Cooper et al., 2004). Following Font et al. (2012b), he approached at a speed of 10 m/min, and approach continued until the lizard fled. The distance between the observer and the lizard at the time of its fleeing was the flight initiation distance. He recorded the presence/absence of foot shakes during the approach. If foot shakes occurred, the distance between the observer and the lizard when the lizard began performing foot shakes was measured as display distance. Because this experimental design involved a human approaching the lizards as a surrogate predator, it is extremely unlikely that the foot shakes are social signals (Type II) rather than antipredator signals (Type III).

In previous studies, it has been pointed out that using humans as surrogate predators has several issues, and some studies reported the differences of responses between humans and natural predators (e.g. Stuart-Fox et al., 2008). However, another study found no such difference in the responses (Cooper, 2008), and using humans as surrogate predators is still considered useful (Samia et al., 2016). Therefore, we considered humans as appropriate surrogate predators.

After the lizard fled, GK attempted to capture the lizard by hand. If captured, he measured their cloacal body temperature (Tb) using a digital thermometer (SN-350 II; Netsuken Co., Inc.). Then their SVL was recorded using a ruler and the sex was determined observing the presence/absence of hemipenal bulges. For lizards with SVL under 35 mm he did not determine their sex because lizards less than 39 mm in SVL are hatchlings (Takenaka, 1980; 1989), and are immature. After measurements, the lizards were promptly released at the point of capture.

Statistical analysis

Capturing the same individual multiple times can cause the violation of the statistical assumption of the independence of the data. Because this study was conducted repeatedly along the same trail, it is possible that the same lizards were captured multiple times. However, in this study site, 117 lizards had been previously marked using the visible implant elastomer for another research project, and among the lizards captured in the present study, only 11.1% of them had already been marked. Therefore, we considered the percentage of observing the same individuals in this study as quite low and thus the effects of possible repeated use of the same individuals in the statistical analysis are limited.

To verify whether lizards stop performing foot shakes and flee when they are approached closer than a certain distance, we examined the distribution of starting distance, display distance and flight initiation distance. To examine the effects of SVL, Tb and sex on foot shakes, we employed a generalised linear model (GLM) with a logit link function. All data analyses were conducted using RStudio ver. 3.5.0 (R Core Team, 2024). We analysed the presence or absence of foot shakes as response variable, using a GLM with a binomial distribution. Explanatory variables included SVL, sex and Tb, which may influence escape performance. We excluded the data of hatchlings from the analysis of GLM because their sex was not determined.

Table 1. Number of captures, SVL (snout-vent length) and Tb (body temperature) by growth stage and sex. All values in SVL and Tb are given as mean ± SD with range in parentheses.

Age-sex class	Captures	SVL (mm)	Tb (°C)
Adult males	50	51.70 ± 5.03 (41.00–61.00)	32.38 ± 3.18 (24.00–36.70)
Adult females	42	51.69 ± 3.00 (46.00–59.00)	30.64 ± 2.56 (25.40–35.60)
Hatchlings	35	30.06 ± 2.42 (25.00–34.00)	30.83 ± 2.79 (25.00–34.00)
Total	127	45.73 ± 10.42 (25.00–61.00)	31.42 ± 2.98 (24.00–36.70)

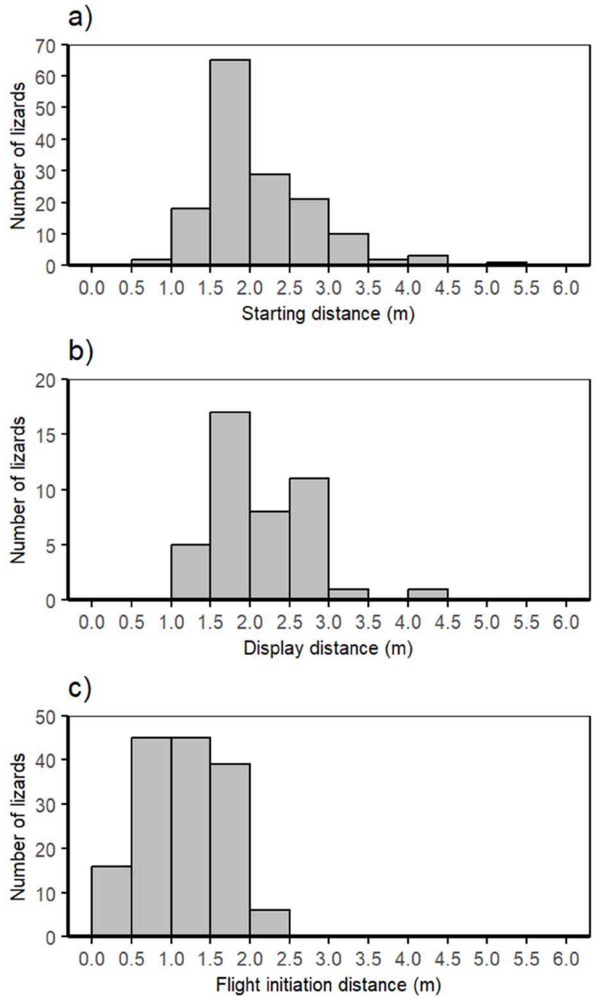

Figure 2. Frequency distribution of **a)** starting distance, **b)** display distance and **c)** flight initiation distance.

RESULTS

We conducted 151 approaches to lizards, and foot shakes were observed in 43 cases (28.5%). We successfully captured lizards in 127 (84.1%) approaches, obtaining data of 50 males, 42 females and 35 hatchlings (Table 1). Three females were apparently gravid, but due to the difficulty in definitely determining whether females were gravid, we did not examine the effects of reproductive condition on foot shakes.

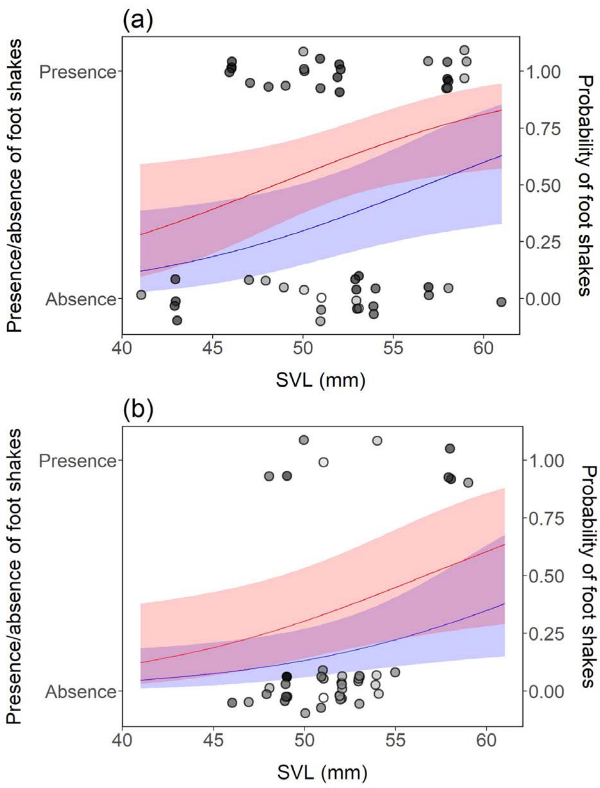

Figure 3. Relationship between snout-vent length (SVL) and presence/absence of foot shakes, along with a regression curve indicating the probability of foot shakes by **a)** male and **b)** female. Each point indicates the presence/absence of foot shakes of an individual. The colour of each point indicates body temperature (Tb), with darker colours indicating higher temperature from white (25 °C) to black (35 °C). The points are adjusted with jitter to prevent overlap. The regression curves show the estimated probability of foot shakes as the response variables, with SVL, sex and Tb as explanatory variables in the GLM model. The blue curve represents the regression curve when Tb is fixed at the first quartile (29.0 °C) of the entire lizards. The red curve represents the regression curve when Tb is fixed at the third quartile (34.7 °C). The ribbon graphs indicate the range of the regression curves within the 95% confidence interval.

Starting distance ranged from 0.84 to 5.10 m (mean ± SD: 2.13 ± 0.72 m), display distance ranged from 1.28 to 4.30 m (mean ± SD: 2.16 ± 0.62 m) and flight initiation distance ranged from 0.15 to 2.24 m (mean ± SD: 1.16 ± 0.48 m) (Fig. 2). Due to the mechanical limitation of the laser rangefinder the minimum flight initiation distance was recorded as 0.15 m, but several individuals actually had a shorter flight initiation distance than 0.15 m. No individuals had a display distance shorter than 1.28 m, and approximately 50% of the displays occurred at a distance of 1–2 m. Among the 43 individuals that displayed, starting distance of 13 (30%) individuals were equal to display distance; i.e. these 13 lizards were already displaying when we found them. The mean ± SD of the distance from the display to flight initiation (display distance-flight initiation distance) was 0.75 ±

0.56 m. In the individuals that did not display (n = 108), the mean ± SD of the distance between starting and flight initiation (starting distance-flight initiation distance) was 0.99 ± 0.71 m.

The results of GLM showed that SVL and Tb have significantly positive effects on the probability of foot shakes (SVL: estimate = 0.126, SE = 0.0559, z = 2.25, p = 0.0246; Tb: estimate = 0.186, SE = 0.0857, z = 2.18, p = 0.0294) (Fig. 3). Male lizards had a significantly higher probability of foot shakes than female lizards (estimate = 1.03, SE = 0.508, z = 2.03, p = 0.0427).

DISCUSSION

Generally, pursuit-deterrent signals are exhibited most frequently at a certain distance (Hasson, 1991). This is assumed to be the result of the optimisation of the distance-dependent relationship between the cost of predation and the benefit of deterrence. Type III foot shakes of *P. muralis*, which are considered to be pursuit-deterrent signals, are performed most frequently at the distance of 1–2 m and decrease below 1 m (Font et al., 2012b). These results are similar to those obtained in *T. tachydromoides*. Therefore, our results suggest that foot shakes of *T. tachydromoides* function as a pursuit-deterrent signal. Regarding display distance obtained in this study, it may be underestimated, because 30% of individuals (n = 13) had starting distance equal to display distance, and thus in some cases the display would have been already performed and terminated by the time the observer found the lizards. In that case, the display distance is larger than the starting distance that we recorded. Nonetheless, the average distance from start to flight initiation in individuals that did not display was greater than the average distance from display to flight initiation in those that did. This implies that if the lizards had ceased displaying by the time they were first observed, they remained in the position an unusually long time until they started to flee. We believe that only a few individuals took an unusually long time to initiate flights from display. Therefore, it can be said that only a few individuals, if any, had already finished foot shakes when we found them and that underestimation of display distance would be limited.

The GLM results revealed that SVL, Tb and sex influence the probability of the occurrence of foot shakes. SVL in lizards generally affects escape performance (e.g. Foster et al., 2015) and is believed to be a major factor that affects the performance. In *T. tachydromoides*, an experimental study demonstrated a positive correlation between SVL and sprint speed (Mochida et al., 2018). Thus, the positive relation between SVL and the foot shakes supports the quality advertisement function of this display. The higher foot shakes frequency with higher Tb may be attributed to the relationship between Tb and escape performance. In general, ectotherms improved performance with rising Tb, reaching maximum sprint speed at optimal body temperature (Angilletta, 2006). *Takydromus tachydromoides* also shows increased sprint speed with rising Tb, and the optimal body temperature is approximately 31.6 °C (Mochida et al., 2018). Therefore, the positive correlation between Tb and the probability of foot shakes in our results supports the idea that foot shakes function as quality advertisement. Cooper (2011) also supports the idea demonstrating a positive correlation between substrate temperatures and frequency of tail display, which is considered as quality advertisement (Huang & Caro, 2023). The higher probability of foot shakes in males may be due to sexual differences in escape performance because gravid females of the western fence lizard *Sceloporus occidentalis* decrease their sprint speed (Sinervo et al., 1991). On the other hand, in studies on *P. muralis* and *T. tachydromoides* that excluded gravid females, no sexual differences in sprint speed were detected (Zajitschek et al., 2012; Mochida et al., 2018). Therefore, a comparison of gravid and non gravid females would be important in understanding sexual differences in escape performance. However, because we did not record the reproductive conditions of females, we cannot discuss this issue at present. Overall our results generally support the idea of quality advertisement rather than perception advertisement as a function of foot shakes of *T. tachydromoides* although further verification is necessary.

Quality advertisement is directed to active predators, whereas perception advertisement is primarily directed to stalking or ambush predators (Huang & Caro, 2023). As visually oriented predators, several diurnal avian species and a diurnally active snake, *E. quadrivirgata*, are likely to be the primary receivers of quality advertisement by foot shakes display of *T. tachydromoides*. On the other hand, *T. sexlineatus*, a congeneric species of *T. tachydromoides*, exhibits foot shakes in response to the scent of the ambush predator snake, *Ahaetulla prasina* (Van Moorleghem & Van Damme, 2020), which implies the perception advertisement function of the display. Thus, differences in foraging mode of predators may lead to the variation in the content conveyed by foot shakes. Furthermore, because *E. quadrivirgata* adopts foraging tactics other than active search according to environmental conditions (Mori, 1989; Mori et al., 1992), the content conveyed by foot shakes of *T. tachydromoides* would vary even within the same predator. In fact, Huang & Caro (2023) suggested that perception and quality advertisement are not mutually exclusive but rather continuous. Thus, even if a correlation between individual conditions and display frequency is found, the pursuit-deterrent signals may function as perception advertisement.

If foot shakes of *T. tachydromoides* have the function of quality advertisement, this display would be considered as honest signalling that accurately reflects the individual’s condition. Theoretical models predict that pursuit-deterrent signals that incur costs lead individuals in poor conditions to be unable to signal, and thereby the signal is evolutionarily stable (Vega-Redondo & Hasson, 1993; Bergstrom & Lachmann, 2001). The cost is especially paid for quality advertisement and can include not only energy expenditure but also increased visibility of the prey and the loss of opportunities to escape due to the display (Huang & Caro, 2023). Font et al. (2012b) noted that foot shakes do not seem to incur significant energy costs and thus the increased visibility may be the primary cost. Further study is necessary to discuss the costs of foot shakes.

In summary, our study suggests that foot shakes of *T. tachydromoides* in the context of antipredator signal align with pursuit-deterrent theory, similar to Type III foot shakes of *P. muralis*. Furthermore, the correlation between foot shakes and the condition of the lizard partially supports the idea that the display is an honest signal that advertises quality. To the best of our knowledge, this is the first empirical study to investigate what foot shakes advertise. Although many theoretical studies have been conducted on the mechanisms of evolutionary stability of honest antipredator signalling, empirical research is limited. *Takydromus tachydromoides* is common and easy to capture, and thus well-suited for future studies on foot shakes that require measuring individual conditions. This study could serve as a significant starting point for such research.

ACKNOWLEDGEMENTS

We are grateful to Teppei Jono for his comments on this manuscript and the overall research. We thank Shouta Iyoda for his assistance with the analysis and Ryotaro Yanagihara for sharing his insight on antipredator displays. We would also like to thank all the members of our laboratory for their helpful comments and support.

Author contributions

Gumma Kubo: conceptualisation; methodology; software; formal analysis; investigation; data curation; writing-original draft; visualisation. Akira Mori: writing-review and editing; supervision; resources.

Data accessibility

The data in this study are included in the supplementary material.

Ethical statement

This submission adheres to the British Herpetological Society's Ethical Policy and Guidelines. All experimental procedures in the present study were approved by the Regulation on Animal Experimentation at Kyoto University (No. 202324).

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Accepted: 12 May 2025

Please note that the Supplementary Material for this article is available online via the Herpetological Journal website: https://thebhs.org/publications/the-herpetological-journal/volume-36-number-1-january-2026