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Flight initiation distance variation among streams in the field and between populations in a common garden in Sphyracephala detrahens (Diptera: Diopsidae)

Ayumi Kudo

ayu-kudo@yamaguchi-u.ac.jp

Yamaguchi University

Wataru Kojima

Yamaguchi University

Soyo Kawaguchi

Yamaguchi University

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Abstract

Flight initiation distance (FID) is widely used to measure escape responses to approaching predators. However, little is known about FID in small insects or population-level variation in insect escape behavior. We investigated FID in the stalk-eyed fly *Sphyracephala detrahens* in both field and common garden conditions. FID was measured in 523 adults from 10 wild populations on Ishigaki and Iriomote Islands, Japan, and significant variation were found among populations. We then reared flies from the two populations with contrasting field FIDs under common laboratory conditions. In both populations, fewer individuals showed a positive FID under common garden conditions than in the field. Among individuals with positive FID, the population difference remained under common garden conditions, but was substantially smaller than that in the field, resulting in a significant population × environment interaction. Under common garden conditions, FID among individuals with positive FID also showed a significant population × sex interaction: populations differed in females, but not in males. In contrast, neither body size nor residual eye span was significantly associated with the probability or magnitude of positive FID. These findings show substantial individual- and population-level variation in FID in small insects and suggest that both persistent population differences and factors associated with field versus laboratory conditions contribute to variations in escape behavior.

INTRODUCTION

Predation directly affects individual survival and is therefore expected to impose strong selection pressure favoring the ability to assess predation risk and escape predators (Wooster et al. 2026). One widely used measure of prey escape responses is flight initiation distance (FID; Cooper & Blumstein 2015). FID is defined as the distance between an approaching predator and its prey when the prey initiates escape (Ydenberg & Dill 1986). Escape theory predicts that escape timing depends on a trade-off between predation risk and fleeing costs, such as lost foraging opportunities (Cooper & Frederick 2007). Accordingly, higher predation risk is expected to induce earlier escape, and thus a longer FID, whereas higher fleeing costs are expected to delay escape initiation, resulting in a shorter FID. FID has been widely studied in vertebrates and is influenced by extrinsic factors (e.g., distance to refuge, predator approach speed, and group size) and intrinsic factors (e.g., body mass and physiological state) (Stankowich & Blumstein 2005, Atwell et al. 2012, Tätte et al. 2018). In contrast, studies of FID in insects have focused mainly on a limited range of taxa, including Orthoptera, Odonata, and Lepidoptera (Lagos 2017, Niemelä & Dingemanse 2017, Bell et al. 2019, Harbour et al. 2019, Kojima 2022, Kuga & Kasuya 2024, Mikula et al. 2025). To our knowledge, research on FID in relatively small insects remains scarce and has focused primarily on mayflies (Scrimgeour et al. 1997, Hoover & Richardson 2010).

Population-level variations in vertebrate FID have been associated with environmental differences, including predator density, food abundance, and vegetation cover (Diego-Rasilla 2003, Stankowich & Blumstein 2005, Grolle et al. 2014, Tätte et al. 2018). However, field observations alone cannot readily determine whether differences in FID among populations result from plastic responses to the local conditions at the time of measurement or reflect persistent differences between populations. Common

garden experiments can help distinguish these sources of variation by rearing and testing individuals from different populations under shared environmental conditions. As laboratory conditions differ substantially from natural environments, FID may vary between field and common garden conditions, even within the same population. Comparing these conditions help assess how strongly FID depends on the measurement environment and whether laboratory measurements reflect FID under natural conditions.

The focal species in this study, *Sphyracephala detrahens*, belongs to the family Diopsidae, whose members are characterized by laterally projecting eyestalks (Warren & Smith 2007). Eyestalk length varies greatly among species in this family, ranging from relatively short to markedly elongated (Zhou et al. 2026). Eyestalk length is associated with visual characteristics, including binocular visual fields and spatial resolution (Burkhardt & de la Motte 1983, Buschbeck & Hoy 1998). However, elongating the eye-stalk can also reduce flight maneuverability, although these costs may be offset by correlated changes in wing size, thorax size, and thoracic muscle development (Swallow et al. 2000, Ribak & Swallow 2007, Husak et al. 2011, Vance et al. 2023, Vance & Swallow 2024). Therefore, morphological variation may influence FID by affecting predator detection and escape performance. Sex may also contribute to variation in escape behavior. In the diopsid fly *Teleopsis dalmanni*, males and females respond differently to generalist arachnid predators (Worthington & Swallow 2010, 2011), suggesting that FID may also vary between sexes. Previous behavioral studies of diopsids have focused mainly on *T. dalmanni*, which has markedly elongated eye stalks and pronounced sexual dimorphism, and a few other species of the same genus (e.g., Rogers et al. 2006, Bubak et al. 2014, Cotton et al. 2015). In contrast, little is known about the behavior of diopsids with relatively short eyestalks and less pronounced sexual dimorphism, such as *S. detrahens* (Takeda et al. 2020, Kudo et al. 2022). Therefore, investigating the FID in *S. detrahens* may improve our understanding of escape behavior in Diopsidae and support future comparisons among species with different degrees of eye-stalk elongation.

We investigated population- and individual-level variation in FID in *S. detrahens* under both the field and common garden conditions. First, we measured FID in wild populations at 10 sites on the Ishigaki and Iriomote Islands, Japan, to determine whether it differed among populations. We then reared individuals from two populations that differed markedly in FID in the field under common laboratory conditions and tested whether the difference persisted in a common garden. We also compared the FID between field and common garden conditions to assess the differences associated with the measurement environment. We predicted that, if the population differences observed in the field primarily resulted from plastic responses to local environmental conditions, they would diminish or disappear under common garden conditions. Conversely, if persistent population differences contributed to the variation observed in the field, the differences between the two populations would persist under common garden conditions. Finally, we examined associations between FID and sex, body size, and eye span under laboratory conditions.

MATERIALS AND METHODS

Field experiments

We conducted field experiments at seven streams on Ishigaki Island and three streams on Iriomote Island in March and October 2020, November 2021, March and July 2022, and January 2024, during daytime, at air temperatures of 19–30°C, without rain (Table S1). Adult *S. detrahens* were observed on rocks, dead vegetation, or artificial objects (e.g., styrofoam and plastic pipes) in streams, as well as on vegetation overhanging streams. We estimated FID using a 1-m translucent rod with a black Styrofoam ball (65 mm in diameter) attached to its tip as a standardized predator model. The two observers walked slowly through the habitat while visually searching for adult flies. When a fly was detected, one observer moved the rod toward the focal fly at approximately 0.2 m/s. When the fly initiated flight, the observer stopped the rod, and the other observer measured the distance from the front of the styrofoam ball to the fly's initial position with a measuring tape. This distance was recorded as the FID. All trials began with the styrofoam ball positioned 120 cm from the focal fly because adult flies could not always be reliably detected with the unaided eye at distances greater than 150 cm. Therefore, we standardized the starting distance to 120 cm to minimize its effect on FID (Blumstein 2003).

Common garden experiment

We used two populations of *S. detrahens* from Ishi-4 and Ishi-6 on Ishigaki Island, Japan. Data from both populations were collected in 2019. Adults from each population were housed in 30 × 30 × 30 cm mesh cages and provided with banana and yeast on moistened cotton as food and oviposition substrates. Flies from both populations were kept at 25°C under a 14 h light:10 h dark photoperiod.

A mosquito net (2.8 × 1.9 × 2.1 m) was placed in a room with natural light. Newly emerged flies were transferred to the net within 48 h of eclosion at a density of fewer than 40 individuals and maintained for 3–4 days under a 14 h light:10 h dark cycle. Two plastic containers (23.5 × 16 × 8 cm), each containing two stones and 400 mL of water, were placed in the net as water sources. Flies were provided with banana slices and yeast placed on moistened cotton in disposable dishes, and fresh food was provided every 2 days. Two observers entered the net and measured FID using the same procedure as in the field experiments. Room temperature during FID measurements was 23–29°C. To prevent repeated measurements of the same fly, each individual was captured immediately after its FID was measured.

After FID measurements in the laboratory, the captured flies were stored in a freezer for at least 2 h. The sex of each fly was determined, and dorsal-view images of the head and thorax were taken using a Leica S8 APO stereomicroscope (Leica, Wetzlar, Germany) equipped with a Visualix STD2 digital camera (Visualix, Hyogo, Japan). Eye span and thorax width were measured from the respective images using ImageJ version 1.54d, with thorax width used as a proxy for body size.

Statistical analysis

All analyses were conducted in R (version 4.5.3) using RStudio (version 2026.04.0 + 526). The homogeneity of variances in FID among the 10 field populations was assessed using Levene's test. As

the assumption of homogeneity of variances was not met, differences in FID among populations were analyzed using Welch's one-way ANOVA, followed by Games-Howell post hoc comparisons.

To compare FID between field and common garden conditions, we analyzed individuals with positive FID from Ishi-4 and Ishi-6 using a Gamma generalized linear model (GLM) with a log link. Population, environment, and their interaction were included as explanatory variables. Simple effects were examined using estimated marginal means and pairwise comparisons with the *emmeans* package. In the common garden experiment, thorax width was used as a proxy for body size. Due to a strong correlation between thorax width and eye span, residual eye span was calculated as the residual from a linear regression of eye span on thorax width and used as a body-size-adjusted measure of eye span. We then examined the relationships between FID and population, sex, thorax width, and residual eye span. Because a substantial proportion of individuals in each population-sex group had an FID of 0, the FID was analyzed in two steps. First, we used a binomial GLM to analyze whether an individual showed a positive FID (FID > 0), with population, sex, thorax width, and residual eye span as explanatory variables. The population × sex interaction was tested but excluded from the final model because it was not significant. Second, among individuals with a positive FID, we analyzed FID using a Gamma GLM with a log link and the same explanatory variables. The population × sex interaction was tested, and because it was significant, simple effects were examined using estimated marginal means and pairwise comparisons with the *emmeans* package.

Sensitivity analyses using generalized linear mixed models (GLMMs) were also conducted to assess the potential effects of measurement temperature and date. Temperature was included as a fixed effect and measurement date as a random intercept. As accounting for these variables did not improve the main conclusions, simpler models without these variables were retained for primary analyses.

RESULTS

Field variation in FID among populations

We measured the FID of 523 adult *S. detrahens* flies at seven streams on Ishigaki Island and three streams on Iriomote Island (Fig. 1, Table S1). Overall, FID ranged from 0 to 101 cm and differed significantly among populations ($F(9, 166.31) = 7.43$, $P < 0.001$). Mean FID was highest in Ishi-4 (24.63 ± 2.77 cm, mean ± SE) and lowest in Ishi-6 (7.62 ± 1.04 cm).

Comparison of FID between field and common garden conditions

For both Ishi-4 and Ishi-6, a higher proportion of individuals had positive FID in the field than in the common garden (Ishi-4: 100% vs. 72.3%; Ishi-6: 90.5% vs. 67.1%). Among individuals with positive FID, the population × environment interaction was significant ($t = -3.08$, df = 229, $P = 0.0024$). Model-estimated FID was significantly greater in Ishi-4 than in Ishi-6 under both field (24.63 vs. 8.42 cm, ratio = 2.92, $P < 0.0001$) and common garden conditions (8.70 vs. 6.10 cm, ratio = 1.43, $P = 0.0366$). Within Ishi-4, model-estimated FID was significantly greater in the field than under common garden conditions

(24.63 vs. 8.70 cm, ratio = 2.83, $P < 0.0001$), whereas the difference between environments was not significant in Ishi-6 (8.42 vs. 6.10 cm, ratio = 1.38, $P = 0.0604$). Thus, population differences were substantially smaller under common garden conditions than under field conditions.

Common garden variation in FID

Sample sizes, the proportion of individuals with an FID of 0, and model-estimated FID among individuals with positive FID for each population × sex group are summarized in Table 1. The probability of having a positive FID was not significantly associated with population, sex, thorax width, or residual eye span (Table S3). However, among individuals with positive FID, the population × sex interaction was significant ($F(1, 105) = 6.24$, $P = 0.014$). In females, model-estimated FID was significantly greater in Ishi-4 than in Ishi-6 (9.54 vs. 4.92 cm, ratio = 1.94, $P = 0.0002$), whereas males showed no significant difference between populations (7.23 vs. 7.40 cm, ratio = 0.98, $P = 0.915$). Within each population, model-estimated FID did not differ significantly between sexes (Ishi-4: $P = 0.191$; Ishi-6: $P = 0.071$). Thorax width and residual eye span were not significantly associated with the magnitude of positive FID.

Table 1
Flight initiation distance under common garden conditions in two populations of *Sphyracephala detrahens*.

Population	**Sex**	***n***	**FID = 0, *n* (%)**	**Model-estimated FID (cm)**	**95% CI**
Ishi-4	Female	52	13 (25.0)	9.54	7.58–12.01
	Male	31	10 (32.3)	7.23	5.23–10.00
Ishi-6	Female	43	14 (32.6)	4.92	3.75–6.45
	Male	33	11 (33.3)	7.40	5.38–10.17

Model-estimated FID and 95% confidence intervals (CIs) were obtained from a Gamma GLM with a log link using individuals with FID > 0.

DISCUSSION

In the field, FID in *S. detrahens* varied substantially among individuals and significantly among populations. The differences between Ishi-4 and Ishi-6 observed in the field also persisted under common garden conditions, although they were smaller than those observed in the field. Under common garden conditions, among individuals with positive FID, a significant population × sex interaction was found; neither body size nor residual eye span was significantly associated with the probability of showing positive FID or the magnitude of positive FID.

At the population level, significant differences were detected among populations on southern Ishigaki Island (Ishi-4–7). Ishi-4 differed significantly from Ishi-5, Ishi-6, and Ishi-7 despite their relatively close geographic proximity. In contrast, no significant differences were detected among populations on

northern Ishigaki Island (Ishi-1–3) or on Iriomote Island (Iri-1–3). These patterns suggest that geographic proximity does not necessarily correspond to similarity in FID among populations. In vertebrates, population-level variation in FID has been associated with local environmental factors, such as vegetation and urbanization (Shuai et al. 2019, Katsis et al. 2024, Ye et al. 2025). Local environmental conditions may also vary among sites in southern Ishigaki. For example, Ishi-4 was located away from major roads, whereas Ishi-5–7 were near major roads. However, because we did not quantify local environmental factors such as vegetation, predator density, or the degree of human disturbance, further studies are needed to determine whether these differences are associated with population-level variation in FID in *S. detrahens*.

In both populations, positive FID was more common in the field than in the common garden. Among individuals with positive FID, a significant population × environment interaction was observed. In Ishi-4, which exhibited particularly high FID in the field, showed a substantial decrease in FID under common garden conditions, whereas Ishi-6 showed no significant difference between environments. Nevertheless, FID remained significantly greater in Ishi-4 than in Ishi-6 under both common garden and field conditions. The persistence of population differences under common garden conditions suggests that differences observed in the field cannot be explained solely by plastic responses to local environmental conditions at the time of measurement. Simultaneously, the substantial reduction in differences between populations under common garden conditions suggests that both persistent differences between populations and variation associated with the measurement environment may contribute to the population-level variation in FID observed in the field.

Under common garden conditions, the probability of a positive FID was not significantly associated with population, sex, body size, or residual eye span. However, among individuals with positive FID, a significant population × sex interaction was detected: the difference between Ishi-4 and Ishi-6 was significant in females but not in males. Because the sex of the individuals measured in the field was not determined, we could not assess how much differences in sex ratios between populations contributed to the population-level variation in FID observed in the field. Detecting population differences only in females under common garden conditions suggests that sex-dependent factors may contribute to population-level variations in FID. Sex differences in antipredator behavior have been reported in the stalk-eyed fly *T. dalmanni*; males show more aggressive responses toward predators and higher survival rates than females (Worthington & Swallow 2010, 2011). Males also tended to use flight as an escape response more frequently than females (Worthington & Swallow 2010). Sex differences in FID have also been reported in other insects, although their direction and presence vary across studies. Mikula et al. (2025) found that males initiated escape at greater distances than females, whereas Bell et al. (2019) detected no significant effect of sex on FID in odonates. Mukherjee et al. (2026) reported shorter FIDs in females than in males of a grasshopper species. Collectively, these findings suggest that sex-related variation in escape behavior may depend on species or ecological context, rather than reflecting a consistent difference between the sexes. However, the mechanism underlying the population × sex interaction remains unclear because FID did not differ significantly between sexes in either population.

In other diopsid flies, eye-stalk development has been associated with visual characteristics and flight performance (Burkhardt & de la Motte 1983, Buschbeck & Hoy 1998, Swallow et al. 2000, Ribak & Swallow 2007, Husak et al. 2011, Vance et al. 2023, Vance & Swallow 2024). However, within the range of intraspecific variation, we found no significant association between residual eye span and FID. Few studies have examined within-species associations between body size and FID in insects. In the mayfly *Baetis tricaudatus*, smaller larvae had greater FIDs than larger larvae (Scrimgeour et al. 1997). Previous studies reviewed by Gotanda et al. (2009) reported no association between body size and FID, or greater FIDs in larger, smaller, or intermediate-sized individuals, indicating that the relationship between body size and FID varies across species. Consistent with this lack of a general pattern, thorax width in *S. detrahens* was not significantly associated with the probability of showing a positive FID or the magnitude of a positive FID.

This study shows that FID can vary substantially among individuals and populations, even in small insects, a group that has received relatively little attention in FID research. It also shows that population difference observed in the field can persist, at least partly, under common garden conditions, whereas the magnitude of these differences can vary with the measurement environment. Future studies that quantify local environmental factors, such as predator density, vegetation, and human disturbance, and compare multiple populations under common garden conditions should help clarify the factors underlying population-level variation in FID.

Declarations

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AUTHOR CONTRIBUTIONS

A. K.: conceptualization, data curation, investigation, formal analysis, resources, visualization, writing-original draft, and writing-review and editing.; W. K.: investigation; S. K.: investigation.

Compliance with Ethical Standards

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Ethical Approval: Ethical approval was not required for this study because the experiments were conducted using insects and did not involve humans or vertebrate animals.

Informed Consent: Not applicable.

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Figures

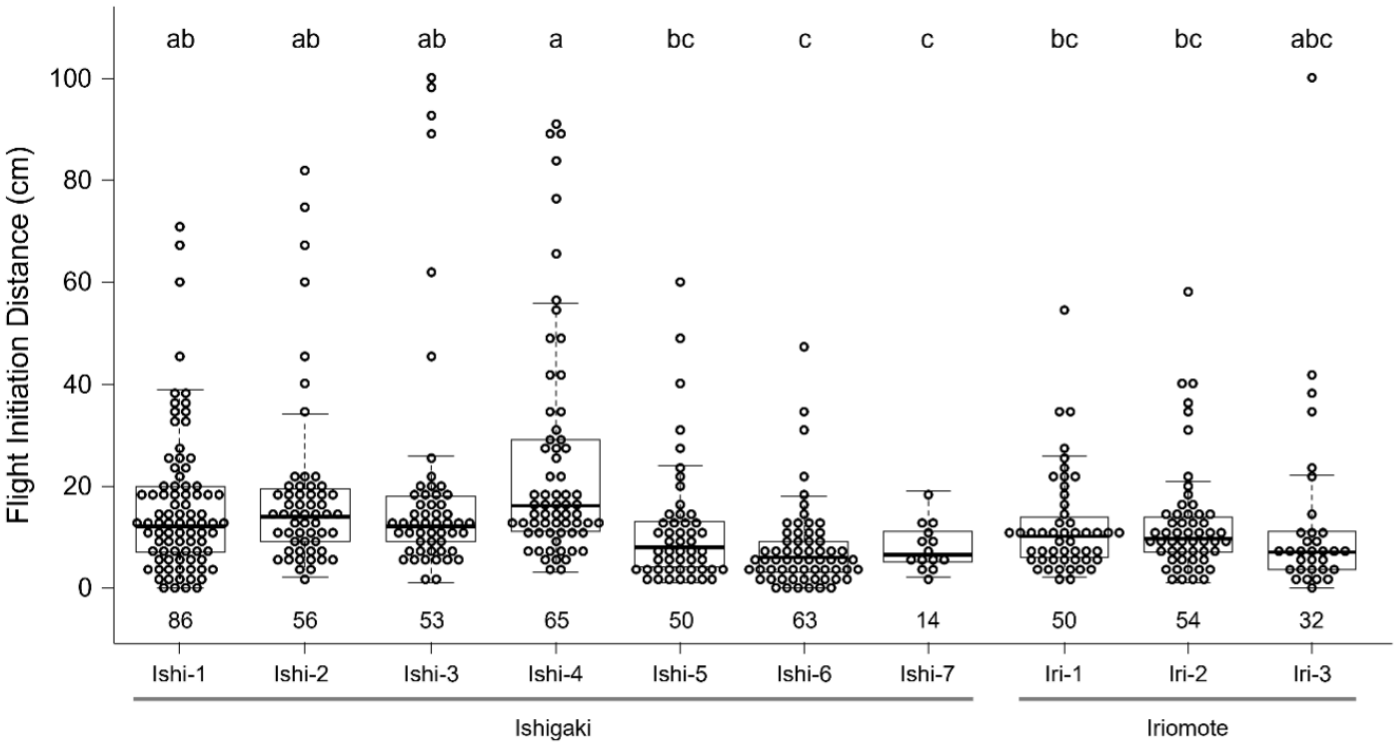

Figure 1

Flight initiation distance among ten field populations of *Sphyracephala detrahens*. Different letters indicate significant differences among populations based on Games–Howell post hoc comparisons ($P < 0.05$).

Supplementary Files

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