

Factors related to sound production by the Chinese grasshopper *Acrida cinerea* during escape

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Abstract

Many grasshopper species produce conspicuous sounds while escaping from approaching predators; however, they occasionally escape without producing sounds. The Chinese grasshopper, *Acrida cinerea*, often exhibits noisy escape behavior. Therefore, a field experiment was conducted using *A. cinerea* to identify factors related to the production of sound during escape. This study utilized a predator model with an investigator approaching *A. cinerea* three times. We examined the relationship between the production of sound during escape and the following factors: ambient temperature and relative humidity as environmental factors; sex, body length, body weight, and limb autotomy as prey traits; and the repeated approach as a predator trait. The relationships between noisy escape and flight initiation distance (i.e., predator-prey distance when the prey initiates the escape), distance fled (i.e., distance the prey covered during the escape), and the mode of locomotion during escape (i.e., flying or jumping) were also examined. Noisy escape was observed only in males that escaped by flying, whereas the females and males that escaped by jumping invariably escaped silently. Among males that flew, noisy escape was related to ambient temperature, limb autotomy, and distance fled. The proportion that produced sound increased in parallel with the ambient temperature and distance fled. This proportion was lower among individuals that had autotomized one of their hind legs. These results indicate that noisy escape behavior is most frequent in healthy male *A. cinerea* under warm conditions.

Keywords

antipredator tactics, crepitation, distance fled, flight initiation distance, fly, jump, predator-prey interaction

Introduction

Many animals exhibit conspicuous behavior when they escape from approaching predators (Edmunds 1974, Ruxton et al. 2018). For example, Thomson's gazelle *Eudorcas thomsonii* (Günther, 1884) leaps vertically (Caro 1986), the skylark *Alauda arvensis*

Linnaeus, 1758 sings (Cresswell 1994), and the mountain katydid *Acripeza reticulata* Guérin-Ménéville, 1832 reveals its bright body color (Umbers et al. 2019) when escaping from predators. Intuition suggests that such conspicuous behaviors may attract predators' attention and lead to failure of the escape, unless performed by unpalatable prey as aposematic signals (e.g., Kang et al. 2016). Contrary to this notion, such conspicuous behaviors increase the survival rate of some prey animals (Ruxton et al. 2018). However, due to the lack of experimental evidence, the function of conspicuous escape in most prey animals remains to be determined.

Many species of grasshoppers produce sounds when they escape by flying (Otte 1970). These sounds are considered an antipredator defensive strategy (Edmunds 1974, Low et al. 2021). Nevertheless, silent escape is occasionally observed in species that are capable of producing sound in flight (e.g., *Acrida cinerea* (Thunberg, 1815), Kuga, personal observation). Clarification of the factors related to the production of sounds during escape is necessary to reveal the function of this phenomenon (herein termed noisy escape) in grasshoppers. Previous studies have revealed factors related to some types of grasshopper escape strategies, particularly the predator-prey distance where the prey initiates the escape, termed flight initiation distance (FID), or the distance that the prey covered during the escape, termed distance fled (DF) (Lagos 2017). However, factors related to the noisy escape of grasshoppers remain unknown.

This study examined the environmental factors as well as prey and predator traits that may be related to the noisy escape of the Chinese grasshopper *A. cinerea* (Fig. 1A). In Japan, this grasshopper often produces conspicuous sounds while escaping from an approaching human by flying (Takaie 1998). We focused on environmental factors (i.e., ambient temperature and relative humidity), prey traits (i.e., sex, autotomy of hind limb, body length, and body weight), and a predator trait (i.e., repeated approaches). It has been shown that temperature, sex, limb autotomy, and

repeated approaches affect the escape behavior of orthopteran insects (Lagos 2017). Moreover, the body size of invertebrates can affect their escape behaviors (Bateman and Fleming 2015). Thus, we included body length and weight in the prey traits. Humidity was included as an environmental factor because it affects the flight behavior of some insects (Belton 1986, Parmezan et al. 2021).

As a function of conspicuous escape, the sudden disappearance of conspicuous behavior during the escape may confuse predators about the location of the prey and deter predators from searching for it (Edmunds 1974, Loeffler-Henry et al. 2018). Such conspicuous behavior is termed flash behavior. Loeffler-Henry et al. (2021) hypothesized that flash behavior is effective for prey with longer FID because an approaching predator located far away will be unaware of the prey's appearance at rest when it does not behave conspicuously. Evidence obtained from an experiment using computer-generated prey and a human predator model supported this hypothesis (Loeffler-Henry et al. 2021). If the noisy escape of *A. cinerea* is a flash behavior, it may be observed more frequently in individuals with longer FID. Thus, the relationship between sound production and FID was investigated to see if noisy escape is consistent with flash behavior.

Another function of conspicuous escape is to send a signal to predators that the prey has a good ability for escape and deter them from approaching the prey (Vega-Redondo and Hasson 1993). This signal is termed a pursuit-deterrent signal. The lizard *Psammotromus algirus* (Linnaeus, 1758) escapes farther away when it produces sounds during escape attempts (Martín and López 2001). If the noisy escape of *A. cinerea* is a pursuit-deterrent signal, it may be observed more frequently in individuals with longer DF, similar to *P. algirus*. Therefore, the relationship between noisy escape and DF of *A. cinerea* was examined.

Many grasshopper species, including *A. cinerea*, escape via two locomotion modes: flying and jumping (Forsman 1999, Maeno et al. 2019). The relationship between locomotion modes and sound production was also examined.

Materials and methods

Study animals and study sites.—*Acrida cinerea* is commonly found in Japan and characteristically produces sound during flight (Orthopterological Society of Japan 2006). The grasshoppers produce this sound (crepitation) by clapping their hindwings (Kuga and Kasuya 2021). We conducted field experiments with adult *A. cinerea* at three grassland sites at Kyushu University, Fukuoka, Japan (33°35'42"N, 130°13'08"E; 33°35'33"N, 130°13'10"E; and 33°35'33"N, 130°13'07"E, Fig. 1B). Many adults were observed at the sites during the experimental period (August 1–September 25, 2017). Grasshoppers were identified following the taxonomic key of the Orthopterological Society of Japan (2006).

Experimental procedure.—The escape behavior of grasshoppers is often induced by the approach of an investigator (Cooper Jr. 2006, Butler 2013, Bateman and Fleming 2014, Collier and Hodgson 2017, Maeno et al. 2019). In the present study, utilizing a predator model, an investigator approached *A. cinerea* to provoke escape. A high-speed digital camera (Casio EX-ZR1700, Tokyo, Japan, frame rate: 120 frames/s) and non-high-speed digital camera (PENTAX WG-1, Tokyo, Japan, frame rate: 30 frames/s [August 1–8, 2017]; Sony DSC-WX170, Tokyo, Japan, frame rate: 60 interlaced-fields/s [August 9–September 25, 2017]) were attached to the waist of the investigator during experiments to record the escape behavior of

A. cinerea. The high-speed digital camera was placed next to the non-high-speed digital camera. The appearance of the investigator remained unchanged during the approaches to avoid potential effects on escape behavior.

At each site, the investigator recorded the behavior of an individual grasshopper during three consecutive escapes. The experiments took place from 10:00 to 15:00 each day. An interval between experiments in the same sites was 1 h or longer to minimize potential effects of the previous experiment that could influence the results of the next experiment (e.g., disturbance of the grass). Experiments were not conducted during periods of rain.

The experimental procedure that was followed at each site included the three steps below: identification of an individual, three consecutive approaches to the target, and capture of the target. The investigator searched for an individual *A. cinerea* while walking at one step per second (walking speed, mean $\pm$ standard deviation [SD] = 36.6 ± 1.0 cm/s, $n = 20$). The walking speed was maintained using the metronome sound from an audio player (MD720J/A, Apple, California, USA; METRONOME STAR app v.2.0.0, 60 beats/min). The same area in the site was never searched more than once during the experimental procedure. Following the identification of an individual *A. cinerea*, the investigator approached the target at the same walking speed. The first encounter with a target often occurred while the grasshopper was escaping, and this escape was regarded as the first attempt. The first approach was terminated when the target initiated the escape. Then, markers (wire rings with a diameter of 5 cm) were quickly placed on the investigator's position and the initial location of the target grasshopper at the start of the first escape. The second and third approaches were conducted in the same manner immediately after the markers were placed. Following the three consecutive approaches, the investigator captured the grasshopper and placed a marker on the position of the grasshopper at the end of the third escape.

When the investigator failed in either the approach step or the capture step, the step of identification was restarted at the same site. The three steps were repeated at that site until the investigator accomplished all three steps or searched the whole area of the site for the target grasshopper. All captured grasshoppers were maintained in a laboratory (temperature: 22–26°C; food: mostly *Paspalum urvillei* Steudel) until the end of the study.

Measurements.—The sound produced by *A. cinerea* is detectable by the human ear. The investigator recorded whether sounds were produced by *A. cinerea* during the escape attempts. This data recording was confirmed using videos captured by the non-high-speed digital camera. Video analyses were conducted using the BORIS v.4.1.11 software (Friard and Gamba 2016).

Locomotion modes during escape attempts were classified according to the video recorded by the high-speed digital camera. Wing flapping after takeoff indicated flying, while lack of wing flapping after takeoff denoted jumping. A preliminary experiment showed that target grasshoppers often escaped outside the camera frame. To confirm the locomotion modes of targets outside the camera frame, the investigator observed the locomotion modes visually while approaching the target in the field. When wing flapping of the target was not recorded in the video but was observed in the field, the locomotion mode of that target was classified as flying.

FID and DF were recorded by measuring the distances between markers using a steel tape measure to the nearest 1 cm. FID was measured as the distance between two markers placed on the positions of the grasshopper and the investigator at the initial

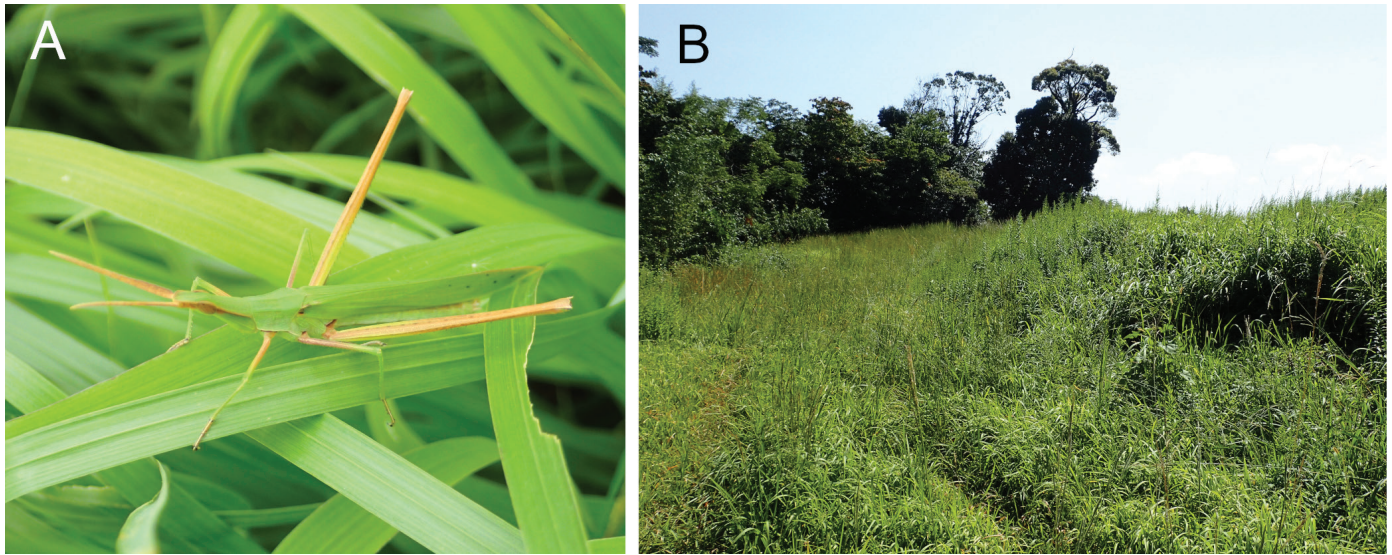


Fig. 1. Photos of male *A. cinerea* (A) and its habitat where field experiments were conducted (B).

tion of each escape attempt. DF was measured as the distance between the two markers placed at the positions of the grasshopper at the initiation and end of each escape attempt. The second and third escape attempts were induced immediately after the previous escape. Hence, the markers placed at the positions of the grasshopper at the initiation of the second and third escape attempts were considered to be placed at the positions of the grasshopper at the end of the first and second escape attempts, respectively. These measurements were conducted after capturing the target grasshopper.

The ambient temperature (to the nearest 0.01 °C) and relative humidity (to the nearest 0.01%) were recorded after the capture of the target. We used a temperature and humidity data logger (Sato-shoji LITE5032P-RH, Kanagawa, Japan) for the recording. During each experiment, the data logger was hung on a tree branch at a height of 140–200 cm.

The morphological traits of the individuals were measured in a single day after the end of the final experiment. Body weight to the nearest 0.01 g was measured using an electronic balance device (Sartorius 1416MP8, Göttingen, Germany). The grasshoppers defecated frass, thereby reducing their body weight between the time of collection and that of the measurement. Measurement of body weight at the time of escape was important to examine the relationship with noisy escape. Thus, the total weight of the grasshopper and its frass, rather than the grasshopper's weight alone, was measured. Using a digital caliper, body length was measured to the nearest 0.01 mm as the distance from the tip of the head to the end of the forewings (Mitutoyo CD-20C, Kanagawa, Japan).

Statistical analyses.—The following statistical tests were conducted with R v.4.1.1 (R Core Team 2021) in RStudio v.2021.9.0.351 (RStudio Team 2021). The significance level was set at 0.05.

We examined the relationship between noisy escape, sex, and locomotion modes. The frequency of noisy escape was compared between males and females in each of the three consecutive escape attempts using Fisher's exact test. This test was also used to examine sex differences in the frequency of each locomotion mode.

Factors related to sound production in the first escape attempt were examined using generalized linear models (GLMs)

with a quasi-binomial error structure and logit link. The models were fitted to the data of males that flew in the first escape attempt because females and males that escaped by jumping did not produce sounds (see Results). The objective variable was sound production (no = 0; yes = 1) in the first escape attempt. The explanatory variables were ambient temperature, humidity, body length, body weight, limb autotomy (no = 0; yes = 1), FID, and DF in the first escape attempt. We also fitted models that contained a quadratic term of temperature or humidity as another explanatory variable to the data and examined the possibility that these parameters affect sound production quadratically. There were no significant effects found in these quadratic terms of temperature (coefficient $\pm$ standard error [SE] = -0.06 ± 0.03 , $t = -1.795$, degree of freedom [df] = 125, $p = 0.075$) and humidity (coefficient $\pm$ SE = -0.002 ± 0.006 , $t = -0.323$, $df = 125$, $p = 0.747$). Similarly, there were no significant effects of the quadratic terms of temperature and humidity when the model contained both these terms at the same time (temperature: $t = -1.755$, $df = 124$, $p = 0.082$; humidity: $t = -0.182$, $df = 124$, $p = 0.856$). Thus, these quadratic terms were removed from the model.

Changes in the frequency of noisy escape through repeated escape attempts were tested using the exact McNemar test. Changes in frequency were examined for each of the first and second escape attempts and for the second and third escape attempts. We used only the data of males that escaped by flying in the three escape attempts for this and the subsequent statistical tests on repeated escapes.

Factors that affect sound production during repeated escape attempts were examined using GLMs with quasi-binomial error structure and logit link. The objective variable was sound production in the second or third escape attempt. In the model for sound production during the second escape attempt, the explanatory variables were FID, DF, and sound production in the first escape attempt, as well as FID and DF in the second escape attempt. In the model for sound production during the third escape attempt, the explanatory variables were FID, DF, and sound production in the second escape attempt, as well as FID and DF in the third escape attempt.

Results

We collected data on three consecutive escape attempts of 136 males and 13 females (Table 1). Sound was produced by approximately 70% of male *A. cinerea* (first escape: 75%, second escape: 76%, third escape: 71%); most males escaped by flying (first escape: 99%, second escape: 96%, third escape: 96%) (Table 1). Although some males escaped by jumping in each of the three escape attempts, they did not produce sounds (Table 1).

Female *A. cinerea* did not produce conspicuous sounds regardless of the locomotion mode (Table 1). Significant sex differences in sound production were detected in each of the three consecutive escape attempts (Fisher's exact test: $p < 0.001$ for all escape attempts). Females escaped by jumping more frequently than males (Fisher's exact test: $p < 0.001$ for all the escape attempts).

For males that flew in the first escape attempt, temperature, limb autotomy, and DF were significantly related to sound production (Table 2). More males produced sounds under high temperatures (temperature when sounds were produced, mean $\pm$ SD = $30.73 \pm 2.48^\circ\text{C}$; $n = 102$; temperature when sounds were not produced, mean $\pm$ SD = $29.06 \pm 3.35^\circ\text{C}$; $n = 32$). Autotomized

males exhibited noisy escape less frequently than intact males (53%, $n = 17$ vs. 79%, $n = 117$, respectively). Sound was produced more frequently by males with longer DF (Fig. 2A). No significant relationships were observed between sound production and body length, body weight, humidity, or FID (Table 2; Fig. 2B for FID).

Some of the males that escaped by flying in all three consecutive escape attempts showed both noisy and silent flight (Fig. 3). There was no significant change in the frequency of noisy escape between the first and second escape attempts (exact McNemar test: $p = 0.392$) and between the second and third escape attempts (exact McNemar test: $p = 0.327$).

In the second escape attempt, sound production was significantly related to DF (Table 3). Similar to the first escape attempt, in the second attempt, males that produced sounds flew further than those that did not produce sounds (Fig. 2C). In the second attempt, FID was not significantly related to sound production (Table 3; Fig. 2D). FID, DF, and sound production in the first attempt also showed no significant relationship to sound production in the second attempt (Table 3).

Sound production in the third escape attempt was significantly related to DF in the third escape attempt and sound production in the second escape attempt (Table 3). In the third attempt, males that produced sound during their escape showed longer DF than those that escaped without sound (Fig. 2E). The frequency of noisy escape in the third attempt was higher in males that produced sound in the second attempt than in those that escaped silently in the second attempt. There were no significant relationships between sound production in the third attempt and the third FID (Fig. 2F), second FID, or second DF (Table 3).

Table 1. Numbers of individuals in the locomotion modes and sound production in three escape attempts.

Sex	Attempt	Locomotion mode	Sound production	
			No	Yes
Male	First	Fly	32	102
		Jump	2	0
	Second	Fly	27	103
		Jump	6	0
	Third	Fly	35	96
		Jump	5	0
Female	First	Fly	6	0
		Jump	7	0
	Second	Fly	5	0
		Jump	8	0
	Third	Fly	3	0
		Jump	10	0

Table 2. Result of GLM on sound production (no = 0; yes = 1) in the first escape attempt. The error structure was quasi-likelihood ("quasibinomial" in GLM function of R), and the link function was logit. The model contained all the explanatory variables at the same time. Only data of males that escaped by flying in the first escape attempt were included in the analysis. Definitions/Abbreviations: Autotomy, the occurrence of autotomy of the hind leg (no = 0; yes = 1); Coefficient, estimated value of the coefficient; p , p -value of the statistical test on the coefficient; SE, standard error of the estimate of the coefficient; t , value of t -statistics ($df = 126$).

Explanatory variable	Coefficient	SE	t	p
(Intercept)	-4.919	8.952	-0.550	0.584
Temperature	0.266	0.121	2.196	0.030
Humidity	-0.059	0.049	-1.216	0.226
Body length	0.130	0.177	0.735	0.464
Weight	-17.453	9.323	-1.872	0.064
Autotomy	-1.865	0.818	-2.281	0.024
FID	-0.006	0.008	-0.757	0.450
DF	0.012	0.004	3.527	<0.001

Table 3. Result of GLM on sound production (no = 0; yes = 1) in repeated escape attempts. The error structure was quasi-likelihood ("quasibinomial" in GLM function of R), and the link function was logit. The model contained all the explanatory variables at the same time. Only data of males that escaped by flying in all three consecutive escape attempts were included in the analyses. Definitions/Abbreviations: Coefficient, estimated values of the coefficient; DF1, DF2, and DF3, DF in the first, second, and third escape attempts, respectively; FID1, FID2, and FID3, FID in the first, second, and third escape attempts, respectively; SE, standard error of the estimate of the coefficient; Sound1, Sound2, and Sound3, sound production (no = 0; yes = 1) in the first, second, and third escape attempts, respectively; p , p -value of the statistical test on the coefficient; t : value of t -statistics ($df = 120$).

Objective variable	Explanatory variable	Coefficient	SE	t	p
Sound2	(Intercept)	-1.180	0.695	-1.698	0.092
	Sound1	1.014	0.584	1.737	0.085
	FID1	0.020	0.010	1.928	0.056
	FID2	-0.014	0.010	-1.332	0.185
	DF1	-0.002	0.003	-0.545	0.587
	DF2	0.009	0.004	2.602	0.010
Sound3	(Intercept)	-0.985	0.634	-1.554	0.123
	Sound2	2.081	0.552	3.774	<0.001
	FID2	-0.005	0.008	-0.601	0.549
	FID3	-0.002	0.009	-0.167	0.867
	DF2	-0.002	0.003	-0.527	0.599
	DF3	0.006	0.003	1.990	0.049

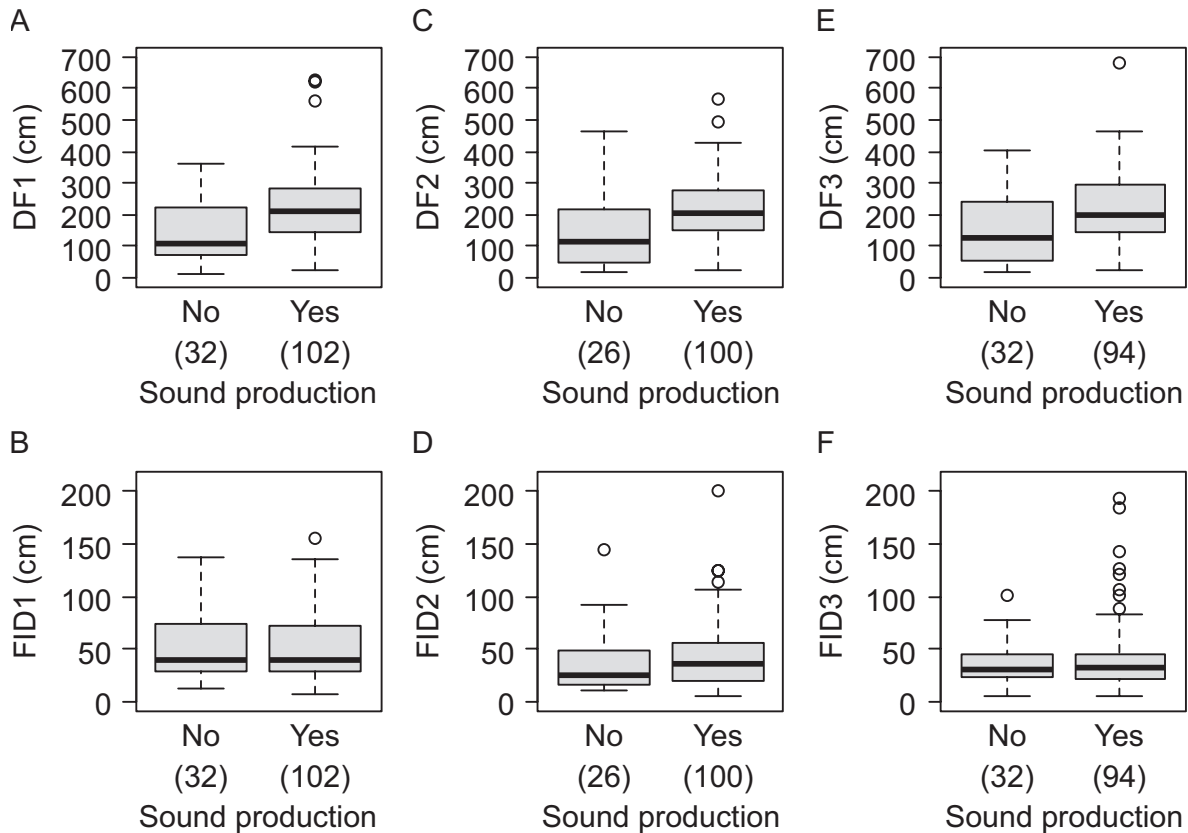


Fig. 2. Relationships between sound production and DF or FID in the first (A, B), second (C, D), and third (E, F) escape attempts. Data on the first attempt (A, B) were obtained from males that flew in the first attempt. Data for the second (C, D) and third (E, F) attempts were obtained from males that flew in all three consecutive escape attempts. The number of observed individuals is shown in parentheses. The centerline, lower edge, and upper edge of the box indicate the median, first quartile, and third quartile, respectively. The bottom of the lower whisker is the minimum value that is not lower than the first quartile minus 1.5 times the interquartile range. The top of the upper whisker is the maximum value that is not higher than the third quartile plus 1.5 times the interquartile range. The data points that are not contained in the box-and-whisker plot are represented as open circles.

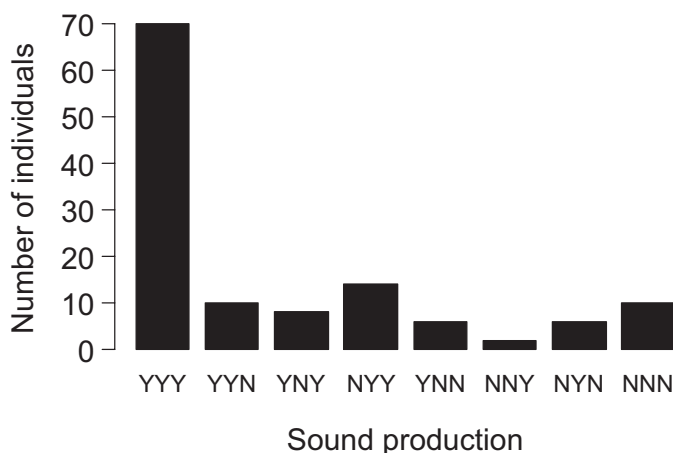


Fig. 3. Observed number of male *A. cinerea* that escaped by flying in all three consecutive escape attempts. The horizontal axis shows the production of sound (N = No; Y = Yes) in three consecutive escape attempts in the order they took place. For example, YYN indicates that the grasshopper produced sounds in the first and second escape attempts but did not produce sound in the third attempt.

Discussion

Sound was produced only by male *A. cinerea* that escaped by flying. Most of the males escaped by flying, whereas some escaped by jumping and did not produce sound. Even when the males escaped by flying, they did not always produce sound. Sound production by these males was related to ambient temperature, limb autotomy, and DF.

Ambient temperature was the only environmental factor found to be related to noisy escape. High ambient temperature results in a higher wingbeat frequency in many kinds of insects (Oertli 1989, Foster and Robertson 1992, Parmezan et al. 2021). Male *A. cinerea* produce sound more frequently when the duration of upstroke before clapping their hindwings is short (Kuga and Kasuya 2021). High ambient temperature allowed male *A. cinerea* to elevate their upstroke speed, thus increasing the frequency of noisy escape. Relative humidity was not related to the noisy flight of male *A. cinerea*, although it affects wingbeat frequency in some insects (Belton 1986, Parmezan et al. 2021).

Limb autotomy was the only morphological trait of male *A. cinerea* found to be related to their noisy escape. Males that autotomized one of their hind legs produced sound less frequently than intact males. Many grasshoppers and locusts can autotomize

their hind legs for survival (Fleming et al. 2007), thereby decreasing their leaping power (Norman 1995, Bateman and Fleming 2011). In autotomized *A. cinerea*, this reduction in leaping power may prevent stability during takeoff and fast wing clapping, which is necessary for sound production after takeoff. Alternatively, males that often escape silently may be less effective at avoiding predators and therefore have a higher likelihood of having an autotomized leg. Body length and weight were not related to the noisy escape of male *A. cinerea*. This result suggests that males have sufficient energy for wing clapping, which is necessary for noisy flight, regardless of their size.

Repeated approaches, as a predator trait, were not related to the frequency of noisy escape by male *A. cinerea*. The lizard *Callisaurus draconoides* Blainville, 1835, which escapes conspicuously by waving its tail, decreases the frequency of conspicuous escape through repeated escape attempts (Cooper Jr. 2010). Possible causes of the decrease in frequency of conspicuous escape include a high risk of predation associated with repeated escape attempts or ineffectiveness of the conspicuous escape against a persistent predator (Cooper Jr. 2010). Unlike this lizard, male *A. cinerea* did not show significant changes in the frequency of conspicuous escape. Rather, they showed individual consistency in the use of noisy escape from the second to the third escape attempts. The absence of individual consistency in noisy escape from the first to the second escape attempts may be caused by a short preparation time for escape against the first predatory approach. The escape tactics against repeated predatory approaches vary depending on the species of the prey (Bateman and Fleming 2014). Therefore, further studies of other prey animals are required to understand the use of conspicuous escape against a persistent predator.

DF was related to the noisy escape of *A. cinerea*. Conspicuous escape was observed more frequently in males with longer DF. Three non-mutually exclusive hypotheses may explain this relationship. First, conspicuous behaviors by males with a longer DF might act as an honest signal of good ability for escape to deter predatory attacks, as suggested for the lizard *P. algirus* (Martín and López 2001). Second, a long escape distance may provide males with more opportunities for hindwing clapping and the production of sound during flight. Third, males might clap their hindwings to increase aerodynamic forces (Kuga and Kasuya 2021). This clapping motion may result in both sound production and a long DF. These hypotheses should be examined to understand the relationship between noisy escape and DF.

Contrary to DF, FID did not differ significantly between males that escaped noisily and those that escaped silently. A computer-based experiment showed that long FID was necessary for the antipredator benefit of flash behavior (Loeffler-Henry et al. 2021). The absence of difference in the FID of male *A. cinerea* suggests that their conspicuous escape may not be a flash behavior. Notably, unlike our study, which investigated sound production, an experiment conducted by Loeffler-Henry and colleagues focused on the visual conspicuousness of prey. Hence, the relationship between FID and flash noise should be explored further.

All females of *A. cinerea* examined in this study escaped silently. In a previous study by Kuga and Kasuya (2021), females under experimental conditions produced pulse sounds while flying through the same mechanism observed in males (i.e., via wing clapping). In the present field study, females under natural conditions escaped by jumping more frequently than males and thus had little opportunity for noisy flight. Although some females escaped by flying, they did not produce a conspicuous sound during

the flight. In the locust *Schistocerca gregaria*, wingbeat frequency is lower in females than in males (Fischer and Kutsch 2000). The wingbeat frequency of *A. cinerea* may also be lower in females than in males, and the slow upstroke of females may reduce sound production at the time of wing clapping.

This study identified factors related to the noisy escape of male *A. cinerea*. High ambient temperature, long DF, and intact hind legs were found to be important for the production of sound by males during their escape. These conditions indicate that the ability to escape is higher in males that produce sound than in males that do not produce sounds. Hence, the sound may act as an antipredator signal, indicating this escape ability and deterring predators from approaching the prey (Vega-Redondo and Hasson 1993). However, there is still the possibility that the sound does not act as an antipredator signal. Males produce sounds during flight by clapping their hindwings (Kuga and Kasuya 2021). Wing clapping during flight increases aerodynamic forces in insects (Chin and Lentink 2016). Thus, male *A. cinerea* may clap their hindwings to improve flight performance, and pulse sounds may be produced by this clapping motion; that is, the sound may be a byproduct of wing clapping. The reaction of predators should be studied in the future to determine the antipredator function of this phenomenon. We found that the noisy escape of *A. cinerea* was related to ambient temperature, limb autotomy, and DF. Future studies on the noisy flight of grasshoppers should record these parameters as potential confounding factors.

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