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Factors influencing the duration of death feigning in *Eucryptorrhynchus scrobiculatus* and *E. brandti* (Coleoptera: Curculionidae)

Huijuan Li[1] · Junbao Wen[1]

Abstract

Death feigning is an adaptive defence strategy that improves survival rates, often by decreasing predation risk. Although death-feigning behavior has been documented in many animals, the study on insects has gradually attracted more focus. Previous study reported two weevil species—*Eucryptorrhynchus scrobiculatus* (ESCR) and *E. brandti* (EBRA)—considered forestry pests, and exhibited death-feigning behavior. To examine the trade-off between the particular anti-predator behaviors and prey fitness, we endeavoured to experimentally determine how temporal (age), activity, and diurnal rhythm may affect death-feigning duration. We found that the death-feigning duration was gradually increased and then decreased with the increased age, and the variation appeared on 5 days. The death-feigning duration during the day (the zeitgeber time, ZT12) was shorter than during the night (the zeitgeber time, ZT5 and ZT24) for both species. However, ESCR weevils with lower locomotor activity displayed longer death-feigning durations. The significant correlations between age, activity, diurnal rhythm, and death feigning would provide the timescale when death-feigning pests were likely to be caught by natural enemies, which help us fully understand the behavioral rhythm to develop novel methods of biological pest control.

Keywords Death feigning · Tonic immobility · Thanatosis · Defence behavior · Anti-predator adaptation

Introduction

Death feigning, also known as tonic immobility and thanatosis, is a state of arousal characterized by severe and prolonged immobility that serves as an adaptive strategy exhibited by prey against predators (Miyatake et al. 2019; Ruxton et al. 2018). This behavior may cause predators to misclassify live prey as unpalatable dead prey (Ruxton et al. 2018; Giannico et al. 2014) and thus increase the survival probability of the death-feigning prey.

Although death-feigning behavior has been directly studied since the beginning of the twenty-first century, the mechanisms underlying this behavior remain unknown. This gap in knowledge makes it a fascinating area of research that is rapidly gaining attention in the field of animal behavior.

Death feigning has been documented in mammals (e.g., *Oryctolagus cuniculus*; Giannico et al. 2014), reptiles (e.g., *Tropidurus itambere*; Nunes et al. 2012), fish (e.g., *Astronotus ocellatus*; Richardson et al. 1977), but studies on death-feigning insects are particularly abundant. Previous research subjects have included *Tribolium castaneum* (Coleoptera: Tenebrionidae; Matsumura et al. 2016; Miyatake et al. 2008), *T. confusum* (Coleoptera: Tenebrionidae; Nakayama et al. 2010), *Callosobruchus chinensis* (Coleoptera: Bruchidae; Nakayama and Miyatake 2010), *Hieroglyphus banian* (Orthoptera: Acrididae; Miriyala et al. 2013), *Timema cristinae* (Phasmida; Farkas 2016), *Gryllus bimaculatus* (Orthoptera: Gryllidae; Nishino and Sakai 1996), *Perreyia flavipes* (Hymenoptera: Pergidae; Neves and Pie 2017), *Hylobius abietis* (Coleoptera: Curculionidae; Sibul et al. 2013), *Agriotes subrittatus* (Coleoptera: Elateridae; Ritter et al. 2016), and *Leptinotarsa decemlineata* (Coleoptera: Chrysomeloidea; Metspalu et al. 2002).

Li et al. (2019) reported that two *Eucryptorrhynchu* species, *E. scrobiculatus* (ESCR) and *E. brandti* (EBRA) (Coleoptera: Curculionidae) exhibited death-feigning behavior when their metaventrite (the metathorax

✉ Junbao Wen
  wenjb@bjfu.edu.cn

1 Beijing Key Laboratory for Forest Pests Control, Beijing Forestry University College of Forestry, No. 35, Tsinghua East Rd., Haidian district, Beijing 100083, People's Republic of China

between the midleg and hindleg) was disturbed. ESCR and EBRA are most destructive to the tree of heaven, *Ailanthus altissima* (Mill.) Swingle, and are highly host-specific (Herrick et al. 2012). However, both species have been found to feed on corkwood, *Leitneria floridana*. *A. altissima* is not common throughout the range of corkwood in the United States (Herrick et al. 1938). Additionally, the duration of death feigning, but not the frequency, was affected by external (e.g., light) and internal factors (e.g., starvation condition) (Li et al. 2019; Li and Wen 2021). Because the duration of death feigning decreased as the duration of starvation increased, we suspected that death feigning was associated with the temporal rhythm. At present, the only effective control technology for the two weevil species is trunk trap nets (Yang et al. 2019a, b). We supposed that the behavioral rhythm of death feigning of ESCR and EBRA under different environmental factors would provide a timescale of the biological control for natural enemies, and research was required.

Previous studies reported that there is a negative genetic correlation between temporal rhythm (e.g., age) and death feigning, and younger individuals feigned death more frequently than older individuals in *T. cristinae* (Farkas 2016). Moreover, the diurnal and activity rhythm also had a relationship with death feigning. For example, *C. formicarius*, a nocturnal species, had the lowest frequency and the shortest duration of death feigning at night (Miyatake 2001); in *T. castaneum* (Matsumura et al. 2016; Miyatake et al. 2008), *T. confusum* (Nakayama et al. 2010; Konishi et al. 2020), and *C. chinensis* (Nakayama and Miyatake 2010), individuals with greater locomotor activity had shorter death-feigning durations because more energy were invested in activity than in defense. Few studies have focused on the trade-off between age, diurnal rhythm, and locomotor activity with the duration of death feigning; thus, we supposed that the influence of interactions among three factors should be worthy of more detailed investigation.

Our primary goals in this study were two-fold. First, to present ESCR and EBRA as novel research models for the comparison of anti-predator behaviors (death feigning) among forestry insect species. Second, because there is often a trade-off between the particular anti-predator behaviors and prey fitness, we endeavored to experimentally determine how temporal (age), activity, and diurnal rhythm may affect death feigning. Because previous experiments showed that the duration, but not the frequency, was significantly variable (Li et al. 2019; Li and Wen 2021), all experiments were conducted in the laboratory condition to observe the duration of death feigning to compare and evaluate the influence of the three factors, that is, insect age, locomotor activity, and diurnal rhythm, on the two Curculionidae weevils.

Materials and methods

Study site and weevil collection

We conducted this study from June–July 2020, in and around the village of Haizi, Ningxia, China (N 38° 51.241′, E 106° 31.301′). The study area had an average daily temperature of 15–32 °C, with a light:dark cycle ranging from 14:10 to 15:9 h. We established one plot (100 m × 2 m), located along a canal lined with the tree of heaven. There were no other trees to confound the experimental insect source. ESCR and EBRA adults were abundant in the plot and heavily infested the trees of heaven.

ESCR and EBRA have one generation per year and primarily occur from May to August in Ningxia, China (Zhao and Chen 1980). To standardize age, newly emerged, unpaired female and male weevils were identified and collected. Because both species have mounting behavior in the wild, once a new male found a virgin female, the female will cling to the male closely to complete the mating process (Zhang et al. 2017). For this reason, we collected single new weevils using forceps and placed each individual in its own incubator box (20 mm diameter × 25 mm depth) to prevent mating and cannibalism.

All experimental weevils were collected from the sample plot. Because both ESCR and EBRA have only one generation per year, it is difficult to collect large numbers of adults from all age classes in the field. Furthermore, rearing methods are not satisfactory for obtaining large numbers of adults from eggs in laboratory conditions. The method used to obtain weevils of similar age was the same as that used by Li et al. (2019). Briefly, we collected and discarded as many weevils as possible every three days for nine days. After that, all newly emerged weevils in the same plot were of a similar age of 1–3 days.

We observed death-feigning behaviors using the same method as Li et al. (2019). One ESCR or EBRA was placed in a stock culture container (20 × 35 mm) with no feeding to observe the duration of death feigning. Specifically, for each behavior assay (age, locomotor activity, circadian rhythm), light stimulus was applied to the metaventrite using forceps, and the duration of death feigning was recorded. The duration was the time from when movement ceased until the first visible movement. If the weevil did not respond, the same stimulus was applied a second time, or at most a third time. If the weevil still did not respond, the duration was recorded as zero.

Age

Because the life span of adult ESCR or EBRA ranged from 23 to 34 days (Li et al. 2019), the 15-day continuous test

for age was performed as follows. On June 18, we first assayed ESCR and EBRA for death-feigning behavior as described above (1–3 days old and virgins, $n = 3 \times 3$ ESCR, $n = 3 \times 10$ EBRA, three replicates). All weevils were fed fresh tree of heaven branches every two days until July 2, at which point duration of death feigning was recorded at 17:00 every day for a total of 15 days.

Because we were concerned that the 15-day continuous test might have death-feigning adaptation to interfere the duration, the 10-day interval test (control group) was assessed as follows. The control weevils were tested once for death-feigning behavior on June 23 and again on July 3 (1–3 days old virgin weevils, $n = 3 \times 8$ ESCR, $n = 3 \times 8$ EBRA, three replicates). Because weevils in the control group began to die after the 10th d, our observations lasted only 10 days, not 15 days.

Locomotor activity

Locomotor activity was measured for each weevil (2–5 days old and virgins, $n = 37$ ESCR, $n = 57$ EBRA) by placing a weevil into a plastic tube (15×150 mm) that only allowed one weevil to pass through at a time. Food was not provided to interfere activity. We captured one hindleg of the weevil with the forceps so as not to induce death feigning and transferred it to the opening of the experimental tube and blocked. We recorded the moving duration it took for each weevil to move from the opening of the horizontally tube to the bottom and measured movement for no more than 6 min. If a weevil did not walk 150 mm within 6 min, it was considered infinite (600 s) and discarded. Weevils with lower moving duration determined the higher locomotor activity.

Age, locomotor activity and duration of death feigning

On July 6, ESCR and EBRA adults (1–3 days old and virgins, $n = 3 \times 4$ ESCR, $n = 3 \times 4$ EBRA, three replicates) were randomly selected to test the relationship between locomotor activity and duration of death feigning. First, as described above, we assayed the duration of death feigning, and after 10 min, locomotor activity was measured. After 5 days, on July 11, activity and death feigning were tested again as described above. During the test periods, one weevil was held alone in a box and fed fresh tree of heaven branches daily.

Diurnal rhythm

After collection, experimental weevils were cultured in the laboratory under normal ambient indoor light for 48 h to adapt to the laboratory environment. Two days later, the weevils (3–5 days old and virgins, $n = 3 \times 8$ ESCR, $n = 3 \times 8$ EBRA, three replicates) were used to measure the duration of death feigning at four times (zeitgeber time, ZT), including ZT5, ZT12, ZT17, and ZT24. The photoperiod at the study site in July is 15:9 h, light:dark, and the daytime coverage is 5:30–20:30. Therefore, ZT5 and ZT24 correspond to nighttime and ZT12 and ZT17 correspond to daytime. When tests were conducted in the dark (ZT5 and ZT24), we turned on the red led light (660 nm, 3 W) to observe the duration of death feigning. We triggered death feigning using the method described above.

Statistical analyses

All statistical analyses were performed using SPSS Statistics V 17.0. We conducted an analysis of variance (ANOVA) separately for both ESCR and EBRA for evaluating the effects of age and diurnal rhythms on the duration of death feigning. To test the interaction between age and diurnal rhythms with species, we used a generalized linear model (GLM) and multiple comparisons. The relationship between the two continuous variables—locomotor activity and duration—was analyzed using a linear regression. Assumptions of data the normality homogeneity of variances were verified to guarantee the reliability of the results, and all results in the text were reported as mean values and standard errors (mean ± SE).
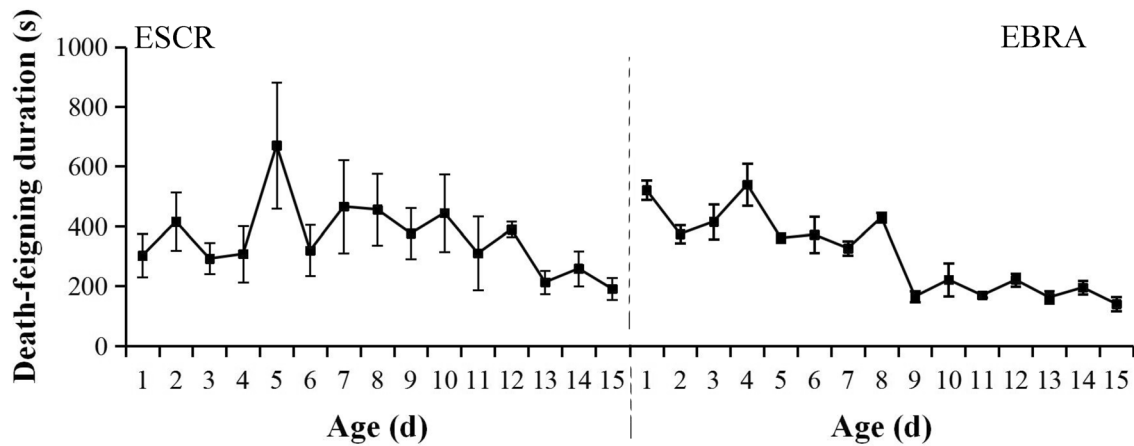
Results

Age

The relationships between age and duration of death feigning for ESCR and EBRA are shown in Fig. 1, and the GLM results for each group are shown in Table 1. For the 15-day continuous test, the duration of death feigning of EBRA was significantly affected by age, with older (15 days) weevils having a shorter duration. For the 10-day interval test (control group), age was a significant effect for both ESCR and EBRA. Older ESCR and EBRA (10 days) weevil feigned death for shorter duration (Fig. 2). Given the sample size of ESCR weevils was too small to determine a clear age pattern, the 15-day continuous experiment showed no age differences in duration of death feigning, and therefore results were inconclusive.

Locomotor activity

Results of the linear regression between locomotor activity and duration of death feigning showed that the locomotor
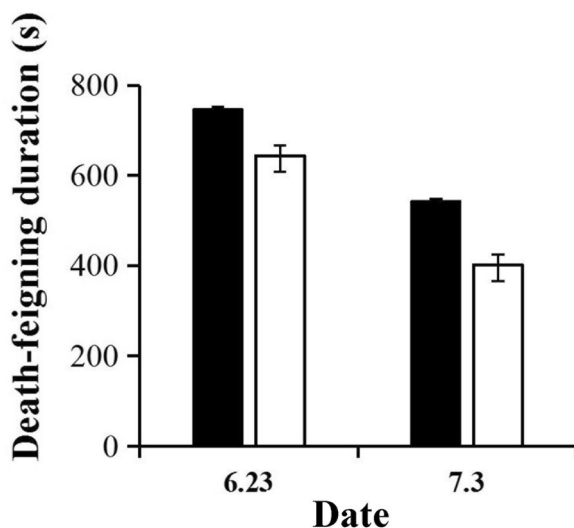
Fig. 1 The effects of age on the duration of death feigning in the 15-day continuous test. Error bars show standard error

Table 1 Results of ANOVA the effects of age on the duration of death feigning and locomotor activity

Factor	Species	Variable	d.f.	F	P
Duration	ESCR	Age 15 days	–	–	–
	EBRA	Age 15 days	14.30	8.849	**< 0.001**
	ESCR	Age 5 days	1.22	8.994	0.04
	EBRA	Age 5 days	1.22	21.553	**< 0.001**
	ESCR	Age 10 days	1.4	73.860	0.001
	EBRA	Age 10 days	1.4	22.364	0.009
Locomotor activity	ESCR	Age 5 days	1.4	7.329	0.013
	EBRA	Age 5 days	1.4	5.911	0.072

Significant differences are shown in bold. $P < 0.001$

Fig. 2 The effects of age on the duration of death feigning in the 10-day interval test. Black bar: ESCR, white bar: EBRA. Error bars show standard error

activity elicited different responses for ESCR and EBRA. As shown in Fig. 3, the duration of death feigning in ESCR was positively correlated with moving duration ($F = 41.016$, $P < 0.001$; $r = 0.735$, $P < 0.001$; $n = 37$). Because the locomotor activity was determined by moving duration, specifically, ESCR weevils with lower moving duration indicated to have shorter duration of death feigning and higher locomotor activity. In contrast, the duration of death feigning of EBRA was not correlated with locomotor activity (Table 2).

Results of the GLM for locomotor activity and duration of death feigning showed significant effects (Fig. 4, Table 1). ESCR and EBRA showed longer duration, indicating that older weevils (5 days) were less defensive than younger weevils.

Diurnal rhythm

The ANOVA and GLM showed that duration of death feigning was correlated with diurnal rhythms as well as species (Fig. 5, Table 3), although the interaction between diurnal rhythms and species was non-significant. The duration of death feigning at daytime ZT12 was shorter than during the nighttime (ZT5 and ZT24) for both ESCR and EBRA, and the duration at daytime ZT17 was shorter than nighttime ZT24 for EBRA (Table 4).

Discussion

We used ESCR and EBRA weevils as research model to describe interspecific variation in death-feigning behavior as it relates to age, locomotor activity, and diurnal rhythms. We found that age and diurnal rhythms had significant effects on the duration of death feigning in ESCR and EBRA. Compared with previous studies in *T. castaneum*, *C. formicarius*, and other species (Miyatake 2001; Uchiyama et al. 2019;
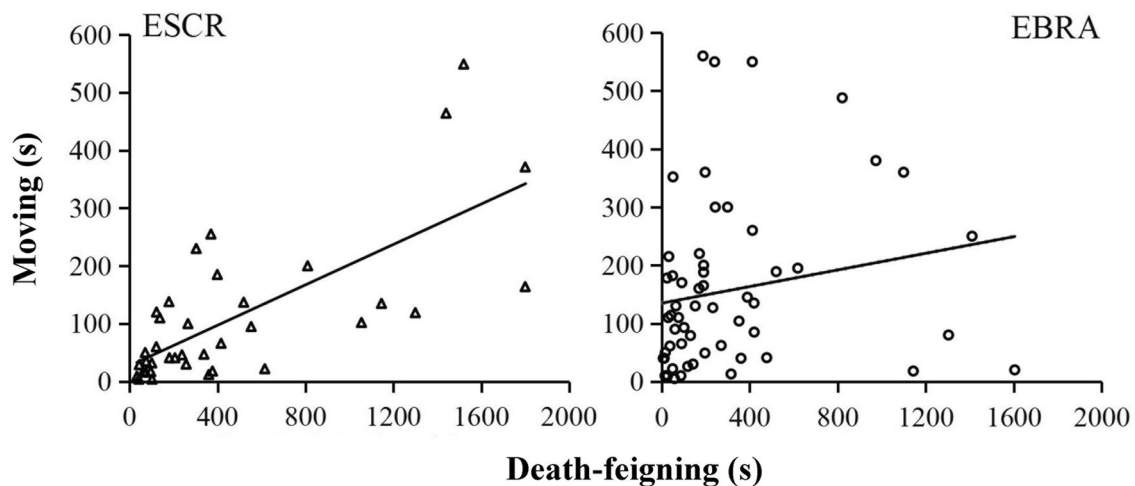
Fig. 3 The relationship between locomotor activity and death-feigning behavior. The *y*-axis shows the moving duration (s), and the *x*-axis shows the duration of death feigning (s). The moving duration means the locomotor activity that moving through the tube. Weevils with lower moving duration indicate to have a shorter duration of death feigning and higher locomotor activity

Table 2 Results of a linear regression between locomotor activity and duration of death feigning

Species	Source	Locomotor activity × duration
ESCR	*F*	41.016
	P	**< 0.001**
	r	0.735
	P	**< 0.001**
EBRA	*F*	1.939
	P	0.169
	r	0.185
	P	0.085

Significant differences are shown in bold. *P* < 0.001

Konishi et al. 2020), our results indicate that the death-feigning behavior of ESCR and EBRA provide a tractable system for further research into factors influencing death feigning.

Age

We found a significant relationship between weevil age and duration of death feigning. This relationship has also been observed in stick insects (*T. cristinae*); younger individuals feign death more frequently than older individuals (Farkas 2016). However, the relationship was confounded by inconsistent stick insect ages and laboratory habituation. In our study, we standardized age by using a single sample plot and a scheduled collection time. Weevils were also held separately to prevent mating, cannibalism, and laboratory habituation. Furthermore, three age treatments—15-day continuous test, 10-day interval test, and 5-day interval test—were performed in this study.

Our results showed younger weevils (ESCR: 746.54 ± 5.10 s; EBRA: 643.38 ± 23.03 s) had a longer duration of death feigning than older (ESCR: 543.67 ± 18.59 s; EBRA: 401.78 ± 34.78 s) in the 10-day interval test. However, older weevils (ESCR: 1148.43 ± 163.55 s; EBRA: 459.54 ± 134.03 s) had a longer duration than younger (ESCR: 146.96 ± 22.38 s; EBRA: 210.83 ± 31.50 s) in the 5-day interval test. Previous study showed older weevils may tend to have higher residual reproductive value (e.g., increased opportunities for mating and egg-laying; Guo et al. 2019). Kuriwada et al. (2011) also suggested the life-history theory that states that the increased body size, mating, and foraging with age could decrease the death-feigning behavior. If this is the case, older weevils might tend to flee and younger weevils might tend to feign death rather than facing risks, but whether the reason for the variation of the duration of wild-caught weevils in 5 days was adaptation in the laboratory condition needed further study.

Locomotor activity

Negative relationships between locomotor activity and duration of death feigning have been reported in *T. castaneum* (Matsumura et al. 2016; Miyatake et al. 2008), *T. freemani* (Konishi et al. 2020), and *C. chinensis* (Nakayama and Miyatake 2010). In these species, individuals with greater locomotor abilities had a shorter duration of death feigning. Alternatively, Miyatake (2001) observed the frequency and duration of death feigning in *C. formicarius* and found that resting individuals tended to feign
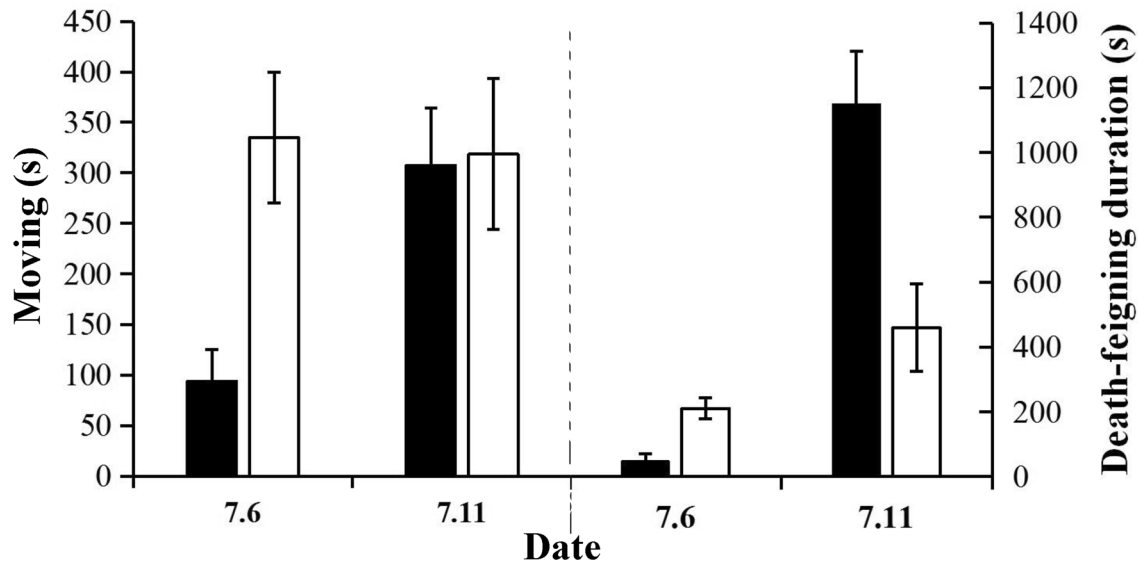
Fig. 4 The effects of age on locomotor activity and duration of death feigning. The *y*-axis shows the moving duration indicating the locomotor activity that moving through the tube. Weevils with lower moving duration indicate to have a shorter duration of death feigning and higher locomotor activity. Black bar: ESCR, white bar: EBRA. Error bars show standard error

Fig. 5 The effects of diurnal rhythms on the duration of death feigning. Black bar: night-time, white bar: daytime. ZT: zeitgeber time. Error bars show standard error
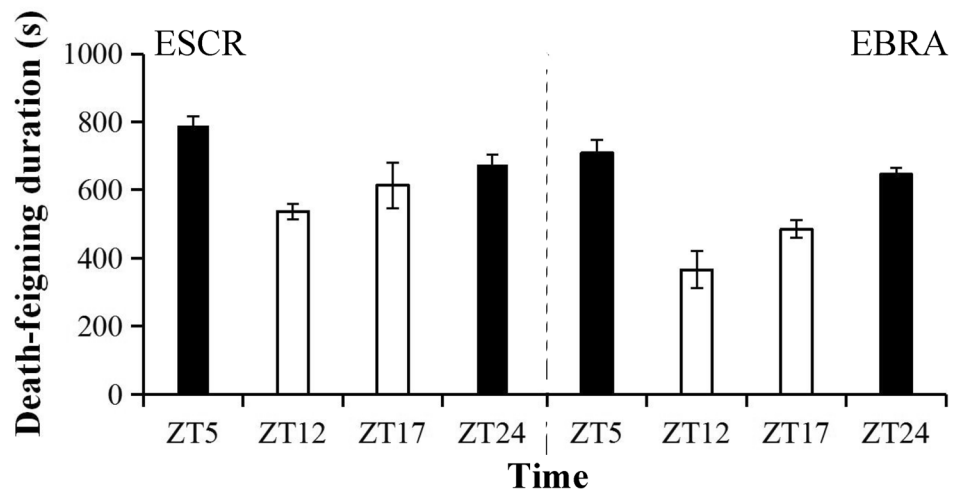
Table 3 Results of GLM of the effects of diurnal rhythms on the duration of death feigning

Species	Source	*df*	*P*
ESCR×EBRA	Diurnal rhythms	3	**< 0.001**
	Species	1	0.04*
	Diurnal rhythms × Species	3	0.404

Significant differences are shown in bold. *P* < 0.001

*The mean difference is significant at the *P* = 0.05 level

death but walking individuals seldom feigned death, suggesting that individuals with higher activity levels tend to flee rather than feign death as a result of the trade-off between locomotor activity and duration of death feigning. Similar negative relationship was also observed in ESCR but not in EBRA and locomotor activity of older ESCR (5 days) decreased with increased age. Our results showed the duration of death feigning was related to age and locomotor activity, but we did not further confirm this relationship due to the limitations of the experimental weevils.

Table 4 Results of ANOVA the effects of diurnal rhythms on the duration of death feigning

Species	Zeitgeber time	Duration (s; mean ± SE, $N=8$)
ESRC	ZT5	788.75 ± 27.21 a
	ZT12	536.92 ± 22.78 b
	ZT17	613.79 ± 67.05 bc
	ZT24	673.79 ± 30.11 cd
EBRA	ZT5	708.63 ± 47.75 a
	ZT12	366.29 ± 66.52 b
	ZT17	484.48 ± 31.49 bc
	ZT24	646.09 ± 22.97 cd

Significant differences are indicated using different lowercase letters

The mean difference is significant at the $P=0.05$ level

Konishi et al. (2020) suggested that negative genetic correlations between activity and death feigning in *T. freemani* could result in the constrain of genetic evolution. Two strains were artificially selected to have the shortest duration (short regimes) and the longest duration (long regimes) to compare the locomotor activity, and the selection of *T. freemani* showed that long regimes had significantly lower locomotor activity than short regimes. Similar studies conducted in *T. confusum* and *C. chinensis* also found that death feigning is genetic inheritance and evolvable antipredator strategy (Nakayama et al. 2010; Nakayama and Miyatake 2010).

Diurnal rhythm

We also compared the relationship between diurnal rhythms and death-feigning behavior in ESCR and EBRA. Ji et al. (2017) described both weevils as diurnal animals because they started to climb up the trunks of trees of heaven for feeding from 9:00 to 12:00 and were actively feeding from 12:00 to 17:00. In the present study, the duration of death feigning during the day ZT12 was shorter than during the night (ZT5 and ZT24) for both species, which was related to feeding activity. Similar results have reported (Rovee et al. 1976, 1977) that chicks in the nighttime had a longer duration of death feigning than in the daytime due to a high risk of nocturnal predation (Rovee et al. 1976). However, nocturnal *C. formicarius* decreased the frequency and duration of death feigning at night (Miyatake 2001).

Diurnal insects have an increased risk of predation at night and increased activities such as feeding during the day, while nocturnal insects have an increased risk of predation during the day and increased night activity. Our results showed that the duration of death feigning in diurnal or nocturnal animals was variable, which suggested that the diurnal rhythm would be an important factor to evaluate the behavioral traits of death feigning across more species.

To the best of our knowledge, behavioral rhythms in insects are endogenously controlled by circadian clock (Saunders et al. 2002). For example, in *Drosophila melanogaster*, there are more than 100 circadian clock genes involved in olfaction, vision, and feeding (Zhou et al. 2005; Tomioka and Matsumoto 2009). Expression of the circadian clock genes *per1*, *crz*, *cry1* and *cry2* in the nocturnal species *Spodoptera liturais* are higher in nighttime, consistent with its period of activity. Elevated expression of circadian clock genes in the nighttime is beneficial to increase related enzyme activity and promote nocturnal behavior (Lin et al. 2017). In the present study, the duration of death feigning of ESCR and EBRA was influenced by a diurnal rhythm may be regulated by circadian clock genes. The influences of circadian clock genes on the regulation of death feigning are a promising area for further investigation.

Conclusions

When comparing two results of the temporal (age) and diurnal rhythm, we found that the variations in the duration of death feigning showed similar regulations for both ESCR and EBRA. The duration of death feigning was gradually increased and then decreased with the increased age, and the variation appeared on 5 days. Moreover, the results of the diurnal rhythm experiment demonstrated ESCR and EBRA decreased the duration of death feigning due to the feeding activity during the day. However, research methods of locomotor activity were similar to those of Miyatake (2001), and the results showed that only ESCR had a significant negative correlation between activity and death feigning, which suggested ESCR deserving more detail investigation.

In the present study, we considered the behavioral rhythm that both weevils had shorter death-feigning duration in older age and daytime as the death-feigning timescale when pests were in the activity phase so that they were likely to be caught by natural enemies. Ultimately, further studies are needed to fully understand the behavioral rhythm among more pests with death-feigning behavior, which would benefit the development of novel methods of biological pest control.

Author contributions All authors have read and agreed to the published version of the manuscript.

Declarations

Conflict of interest The authors declare no conflict of interest.

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