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Interpreting animal behaviors – A cautionary note about swaying in phasmids

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Diverse animals including snakes, spiders and phasmids sway in response to abiotic and biotic factors. Recent research on swaying in phasmids suggest they may adopt distinctive swaying to reduce detection from predators. This view was recently challenged, by interpreting swaying behavior as serving a balancing function related to postural sway and not a form of anti-predator behavior. We dispute this interpretation as the reanalysis of data for balance was based on an erroneous perception of the upright posture of the insects, contrary to the initial study and natural history observations. We present observations collected from four species of more than 300 phasmids over a three-day period and show that the insects seldom adopt an upright posture (4% of observations). While we appreciate that attempts to reinterpret data form a central role of the scientific method, we urge caution when inferring biological function without an accurate knowledge of the species' natural history. Investigations of signals in motion require great care to ensure they are interpreted in a natural environment and context.

KEYWORDS
swaying, phasmids, adaptive function, anti-predator, natural history

Introduction

Animals move for various purposes, such as to forage, find mates, deter rivals and predators and to seek shelter. This movement may draw unwanted attention from natural enemies. It is thus particularly surprising that many species sway, a non-perambulatory movement which involves the lateral rocking of the body, while the legs remain stationary and in contact with the substrate (Bian et al., 2016). This behavior is particularly prevalent in phasmids, but also occurs in diverse taxa, including spiders, mantids and snakes (Fleishman, 1985; Jackson, 1985; Watanabe and Yano, 2009; Tan and Elgar, 2021). Several lines of thought suggest that swaying behavior has a signaling function, providing offensive or defensive mechanisms to improve foraging success or the likelihood of attack from predators. For example, *Portia* spiders sway their palps, legs and bodies to evade detection when they approach their arachnid prey, as the movements give *Portia* the appearance unlike that of a spider or an animal that imposes a threat (Jackson, 1985). Vine snakes *Oxybelis aeneus* oscillate forward and backward, presumably to mimic vegetation movement (Fleishman, 1985). In mantids, swaying can reduce detection by predators, cannibalistic conspecifics and prey (Watanabe and Yano, 2009, 2012, 2013). Several species of phasmids are reported to sway (Rupprecht, 1971; Bian et al., 2016; Pohl et al., 2022), with recent research on phasmids consistent with the view that phasmids adopt swaying to reduce detection (Bian et al., 2016; Pohl et al., 2022). Thus, swaying provides phasmids with a form of concealment between revealing behaviors through motion masquerade, which is the matching of an animal's motion to environmental motion, such that the animal resembles an inanimate object and prevents detection by an observer (Fleishman, 1985). Through the interpretation of swaying behavior in phasmids, this article emphasizes the importance of inferring biological function with an accurate knowledge of the species' natural history.

Swaying, hanging and perching

Recently, swaying behavior has been interpreted as serving a balancing function (Kelty-Stephen, 2018; Cuthill et al., 2019), based on reanalysis by Kelty-Stephen (2018) using the data presented in Bian et al. (2016). Bian et al. (2016) examined the movement of the phasmid *Extatosoma tiartum* in response to wind cues. While the insects would sway in response to wind stimulus, the frequency of swaying declined over time. The number of sways was higher in variable wind conditions compared with constant wind conditions, suggesting that the insects react to environmental cues such as wind stimulus and modify their swaying behavior in response. In the presence of plants in the background, insect swaying was consistent with the movement of the wind-blown plants. Reanalyzing part of the same dataset, Kelty-Stephen (2018) proposed that the swaying behavior allows the insects to achieve stability in response to wind-like stimulation. Kelty-Stephen (2018) further proposes that these data provide evidence for multifractal complexity in postural stabilization under wind-like stimulation and point to similarities between phasmid and human postural sway. Kelty-Stephen (2018) proposed that the reduction in sway exhibited by phasmids can be explained by non-linear interactions across time consistent with tensegrity principles and dismissed Bian et al.'s (2016) suggestion of anti-predator behavior on the part of the insects. Such a balancing function could be more relevant to perching than hanging insects, with the latter relying on gravity to remain stable.

We do not seek to question Kelty-Stephen's (2018) analysis. However, we must point out that the author has foremost, incorrectly characterized the phasmids described in Bian et al. (2016) to 'perch upon a branch' (Kelty-Stephen, 2018, p. 8), when they were, in fact, hanging from a branch (Figures 1A,B). It is unclear why Kelty-Stephen (2018) took this perspective on phasmid swaying behavior and whether this inaccuracy influenced the author's interpretations. While phasmids can walk when perching, it is uncommon. *E. tiaratum* (Phasmatidae) typically hangs from perches, rarely spending time 'upright'. We found a similar pattern for four species of phasmids that we had collected from the field, maintained in the laboratory and observed over a three-day period (Figures 1C–F; Table 1). Hanging from the top or side of the enclosure, host plant or even another phasmid was the overwhelming position observed, while perching was relatively rare (60 out of 1,343 observations, 4%). Swaying behavior was not ubiquitous across these four species: swaying was common in *Lonchodes brevipes* (Diapheromeridae), occasionally observed in *Calvisia flavopennis* (Lonchodidae) and *Marmessoidea rosea* (Lonchodidae), and rarely observed in *Haaniella echinata* (Heteropterygidae). Indeed, our study (Pohl et al., 2022) indicate that even for the same species (*L. brevipes*), individuals at different life stages appear to sway to different extents. More nuanced studies in the future are crucial to understand the factors affecting swaying behavior, but the appropriate biological context to consider stabilizing mechanisms in such systems is of a hanging organism.

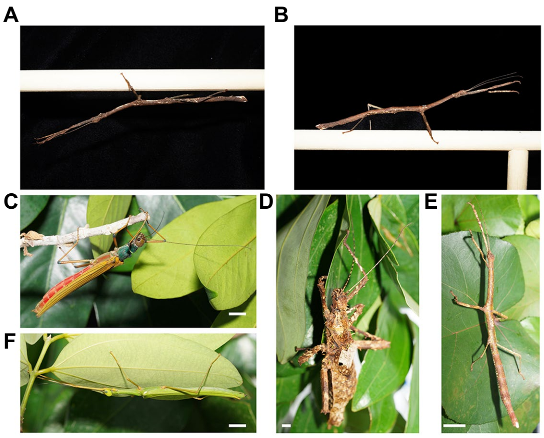

FIGURE 1
Phasmid *Lonchodes brevipes* **(A)** hanging and **(B)** perched from a dowel. Phasmids at rest: **(C)** *Calvisia flavopennis*; **(D)** *Haaniella echinata*; **(E)** *Lonchodes brevipes*; **(F)** *Marmessoidea rosea*. Only female adult insects are represented; white line represents 10mm in each panel. Images are presented as taken in real life without image rotation. Photos by Eunice J. Tan.

Interpreting behavior

We find it surprising that the author misrepresented the work in this way, particularly as the hanging phasmids considered in Bian et al. (2016) contrasts with upright focal organisms in references on postural sway (e.g., Straube et al., 1987; Clayton et al., 2003; Hutchinson et al., 2007; Munafo et al., 2016; Dewolf et al., 2021). Demonstrating tensegrity principles in a hanging organism seems novel and worthy of further attention; but evaluation of the significance and broader implications of these findings are relevant only when the behavior is placed in the correct context. Kelty-Stephen (2018) was, perhaps, too quick to dismiss the potential for sway to represent an adaptive behavior to avoid predators. We do not claim here that the data provides definitive evidence that it does, nor did Bian et al. (2016). However, we argue that Kelty-Stephen (2018) dismisses the possibility based on a limited consideration of the broader investigation, and we do not wish for this premature and inaccurate characterization to propagate (e.g., Cuthill et al., 2019).

In characterizing Bian et al.'s (2016) study, Kelty-Stephen (2018) correctly describes how phasmids decreased swaying over time and that these data were from trials in which no plants were present. It is from this account alone that Kelty-Stephen (2018) rejects the adaptation explanation, suggesting that decreasing sway could be regarded as "a morbid wish to stand out to predators" (p. 16). This is a flawed proposition because there were no plants present in the trial so continuing to sway would also offer no camouflage benefit. What Kelty-Stephen (2018) did not mention is that the aim of the initial experiment by Bian et al. (2016) was to determine whether wind initiates swaying in hanging insects; which was clearly demonstrated. A second experiment subsequently showed that insects swayed more under variable wind, which is a more natural wind stimulus, compared with constant wind as used in the first experiment. Together, these two experiments by Bian et al. (2016) showed that wind initiates swaying and that insects can control swaying. The presence of both wind and insect control of swaying are necessary for a putative motion camouflage explanation; however, neither were undertaken in the presence of plants and make no attempt to relate swaying behavior with plant movement.

TABLE 1 Observations of phasmids during daylight hours in captive, laboratory conditions.

Species	Age	Hang stationary	Hang and walk	Perch stationary	Perch and walk	Other behaviors	Total	Swaying observed?
Calvisia flavopennis	Nymphs	209	1	10	0	5	346	Sometimes
	Adults	105	4	7	0	5		Sometimes
Haaniella echinata	Nymphs	75	1	19	0	4	104	Rare
	Adults	3	0	2	0	0		Rare
Lonchodes brevipes	Nymphs	273	20	10	1	8	466	Common
	Adults	145	3	5	0	1		Common
Marmessoidea rosea	Nymphs	362	8	1	0	7	427	Sometimes
	Adults	43	0	5	0	1		Rare

Phasmids were observed over a three-day period in October 2020. Each individual was observed only once each day between the daylight hours of 1530 h–1800 h. Only the behaviors of animals with intact limbs and wings were recorded to ensure that the recorded behaviors were not influenced by morphological abnormalities. *Other behaviors* referred to relatively uncommon behaviors such as drinking, feeding and thanatosis. Instances of swaying in the absence of stimuli (e.g., during our observation of the captive insects in the laboratory) are rare. Swaying behaviour was recorded based on our observations of the species over the months of captivity.

Similarities between phasmid and plant movement was investigated in a third experiment. Here insects and plants were filmed in natural conditions and in many circumstance the movement of both matched in the frequency domain. There were some exceptions that serve to highlight the potential for non-moving objects to standout from moving ones, but also to prompt consideration of the circumstance that do and do not lead to swaying in natural environments. These are outlined in Bian et al. (2016) and highlight the complex factors that contribute to animal behavior, a point which seems to have alluded Kelty-Stephen (2018). Thus, contrary to Kelty-Stephen's (2018) assertion that Bian et al. (2016) "failed to find evidence that phasmids exploited the wind in the way they predicted" (p. 16), the complete dataset in Bian et al. (2016) showed that there most certainly is the potential for insects to benefit from swaying in wind and enough evidence was provided to take the next step, which is to confirm such behavior confers a survival advantage for the insects. Such investigations necessarily require an understanding of predator motion vision systems and behavior.

Conclusion

The range of taxa from phasmids to spiders and snakes that adopt swaying behavior suggests that this behavior may have an adaptive function. To uncover the adaptive function of swaying, further investigations are necessary to examine the circumstances in which individuals within species do and do not sway. We presented several offensive and defensive functions of swaying, which need not be mutually exclusive (Jackson, 1985; Watanabe and Yano, 2009, 2012, 2013; Bian et al., 2016; Tan and Elgar, 2021). We dispute Kelty-Stephen's (2018) conclusion following reanalysis of the data presented in Bian et al. (2016) and the following assertions, as the reanalysis was based on flawed assumptions – contrary to both the diagrams presented in Bian et al. (2016), and natural history observations, the species hangs rather than perches on the vegetation. A key challenge for studies of animal behavior is to understand the function of animal behaviors. We urge caution when inferring function without sufficient/accurate natural history knowledge, often best achieved by collaboration. Particularly for the investigation of signals in motion such as swaying, great care must be taken to interpret the signals in the natural environment and context.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

ET and ME conceptualized the project. ET collected the data. ET, ME, and RP wrote the draft. All authors contributed to the manuscript revision, read, and approved the final manuscript.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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