ECOLOGY LETTERS

Ecology Letters, (2020) **23**: 1421–1422 doi: 10.1111/ele.13403

TECHNICAL COMMENT

Changes in floral nectar are unlikely adaptive responses to pollinator flight sound

Graham H. Pyke,[1,2]* Zong-Xin Ren,[1]* Judith Trunschke,[1] Klaus Lunau[3] and Hong Wang[1]

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13403.

Abstract

Under noiseless experimental conditions, sugar concentration of secreted floral nectar may increase after flower exposure to nearby sounds of pollinator flight (Veits et al. *2019*). *However, we reject the argument that this represents adaptive plant behaviour, and consider that the appealing analogy between a flower and human ear is unjustified.*

Keywords

Evolution, floral nectar production, nectar sugar concentration, plant adaptation, pollinator behaviour, pollinator flight sound.

Ecology Letters (2020) **23**: 1421–1422

Veits *et al*. (2019) obtained a novel result that, under noiseless experimental conditions and following nectar removal from flowers, sugar concentration of nectar secreted by flowers of *Oenothera drummondii* increased through petal vibration arising from sounds of nearby pollinator flight (i.e. about 19% vs. 16% wt/wt). Nectar volume was not significantly affected by such sounds.

In retrospect, such effects of sound-induced petal vibration on nectar production are unsurprising, but without expectations regarding direction and magnitude of such effects. Nectar production is a physico-chemical process and plant vibration affects such processes (De Luca & Vallejo-Marin 2013; Appel & Cocroft 2014; Body *et al*. 2019). However, lacking relevant information, changes, in any direction, to volume production, sugar concentration and sugar composition seem equally likely. That sugar concentration increase is expected (Veits *et al*. 2019), is without basis.

Whether the experimental results are relevant to natural situations is unclear because:

- The experiments involved flower exposure to maximum natural sound amplitudes (Kirchner & Roschard 1999; Lapshin & Vorontsov 2007), while neglecting negative effects of background noise (Bolin & Abom 2010);
- Pollinators may approach flowers without visiting them and removing nectar;
- Any effects of petal vibration on nectar production could vary with the level of nectar in a flower, just as may occur in the absence of sound induced vibration (Luo *et al*. 2014).

However, to consider the presented arguments, we ignore these issues.

We also had to assume that:

- Observed relatively high sugar concentration of secreted nectar, following flower visitation with associated pollinator flight noise, will continue indefinitely, but with no decline and no further enhancement through successive visits to a flower;
- All plants, in experiments and nature, have a single flower; and nectar production occurs continuously between dusk and dawn, with little nectar available during daytime.

For example, flowers will normally receive multiple pollinator visits with varying temporal gaps between visits, but experimental results provide no relevant information (Veits *et al*. 2019). In the experiments, there was a single flower per plant (Veits *et al*. 2019), but natural plants usually have several flowers (Eisikowitch & Lazar 1987; Veits *et al*. 2019). Since flowers open shortly before sunset, and are visited by hawk moths at night and by honeybees around dusk and dawn (Eisikowitch & Lazar 1987; Veits *et al*. 2019), nectar production probably occurs continuously between dusk and dawn, with little nectar available during the day.

In order to apply the experimental results to the relatively natural situation, observed by the authors at Tel Aviv beach, we also assumed that:

- Both hawk moths and honeybees obtain nectar from flowers of *Oenothera drummondii* and are equally effective pollinators;
- These plants and pollinators have co-evolved.

However, hawk moths are likely the major pollinators, as only they can reach nectar at the ends of spurs about 34 mm in length, while honeybees forage for pollen and are at most minor pollinators (Gregory 1964). Here, *Oenothera drummondii* is an introduced species.

[1]*Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, CN-650201,Kunming, China*
[2]*Department of Biological Sciences, Macquarie University, Ryde, NSW 2109, Australia*
[3]*Institute of Sensory Ecology, Heinrich-Heine-University, Dusseldorf, Germany*
**Correspondence: E-mail: graham.pyke@mq.edu.au (or) renzongxin@-mail.kib.ac.cn*

We also assume the overall visitation rate per flower is high and average nectar standing crop per flower is correspondingly low. Judging from the high average rates of approaches (Veits *et al.* 2019) (assumed visits with nectar removal) to individual flowers following previous pollinator visits to those flowers, and moderate rates of visitation following gaps between visits, overall average rate of visitation per flower must be high.

We deduce that:

- All plants should quickly become statistically similar with no patchiness in nectar standing crop, and hence no reason for a pollinator to behave differently at a flower/plant that has higher nectar concentration through exposure to pollinator flight noise (e.g. Hodges & Wolf 1981);
- Such enhanced nectar concentration should negligibly affect the time a pollinator requires to visit and remove nectar from a flower (Kim *et al.* 2011);
- Since average time spent removing nectar from a flower would be a minor component of total time involved, pollinator time spent accessing and removing nectar from flowers should be independent of nectar sugar concentration, and depend only on volume which is unaffected by exposure to pollinator flight noise.

The reported enhancement of nectar concentration through exposure to pollinator flight noise should therefore have no effect on pollinator behaviour, and consequently there is no basis to claim (Veits *et al.* 2019) that this consequence of pollinator flight noise represents a plant adaptation to exploit pollinator behaviour. If there is no effect on pollinator behaviour, then there can be no effect on subsequent pollen transfer and ultimately plant reproductive fitness (Pyke 2016a,b). If a plant trait does not affect plant fitness, then it cannot be considered a plant adaptation (Pyke 2016a,b).

Consequently, as appealing as it is, the analogy between a flower and the human ear is unjustified. Not surprisingly, however, this analogy has been enthusiastically adopted by segments of the media and venues outside scientific publications (e.g. Donahue 2019).

ACKNOWLEDGEMENTS

This comment is a result of discussion and thinking during pollination field work supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB31020000) at Lijiang Forest Ecosystem Research Station on Yulong Snow Mountain, SW China. Visits by GP and KL to China were funded by the Chinese Academy of Sciences President's International Fellowship Initiative (Grant No. 2020VBA0004 to GP; Grant No. 2019VBA0037 to KL). Helpful comments on an earlier draft of this article were provided by Rob Raguso and Peter Raven.

AUTHORSHIP

GP, Z-X R, JT, KL & HW participated in discussions about subject article; GP led the writing and co-ordinated contributions from the others.

DATA ACCESSIBILITY STATEMENT

No new data were used in the study.

REFERENCES

Appel, H.M. & Cocroft, R.B. (2014). Plants respond to leaf vibrations caused by insect herbivore chewing. *Oecol.*, 175, 1257–1266.

Body, M.J.A., Neer, W.C., Vore, C., Lin, C.-H., Vu, D.C., Schultz, J.C., et al. (2019). Caterpillar chewing vibrations cause changes in plant hormones and volatile emissions in *Arabidopsis thaliana*. *Frontiers. Plant Sci.*, 10, 810.

Bolin, K. & Abom, M. (2010). Air-borne sound generated by sea waves. *J. Acoust. Soc. Am.*, 127, 2771–2779.

De Luca, P.A. & Vallejo-Marin, M. (2013). What's the 'buzz' about? The ecology and evolutionary significance of buzz-pollination. *Curr. Opin. Plant Biol.*, 16, 429–435.

Donahue, M.Z. (2019). Flowers can hear buzzing bees – and it makes their nectar sweeter. *National Geographic*.

Eisikowitch, D. & Lazar, Z. (1987). Flower change in *Oenothera drummondii* hooker as a response to pollinators visits. *Bot. J. Linn. Soc.*, 95, 101–111.

Gregory, D.P. (1964). Hawkmoth pollination in the genus oenothera. *Aliso: A J. Syst. Evol. Botany*. 5, 357–384.

Hodges, C.M. & Wolf, L.L. (1981). Optimal foraging in bumblebees - Why is nectar left behind in flowers? *Behav. Ecol. Sociobiol.*, 9, 41–44.

Kim, W., Gilet, T. & Bush, J.W.M. (2011). Optimal concentrations in nectar feeding. *Proc. Natl Acad. Sci. USA*, 108, 16618–16621.

Kirchner, W.H. & Roschard, J. (1999). Hissing in bumblebees: an interspecific defence signal. *Insectes Soc.*, 46, 239–243.

Lapshin, D.N. & Vorontsov, D.D. (2007). The sound production of flying moths (Lepidoptera, Noctuidae). *Zoologichesky Zhurnal*, 86, 1452–1463.

Luo, E.Y., Ogilvie, J.E. & Thomson, J.D. (2014). Stimulation of flower nectar replenishment by removal: A survey of eleven animal-pollinated plant species. *J. Pollin. Ecol.*, 12, 52–62.

Pyke, G.H. (2016a). Floral nectar: pollinator attraction or manipulation? *Trends Ecol. Evol.*, 31, 339–341.

Pyke, G.H. (2016b). Plant–pollinator co-evolution: It's time to reconnect with optimal foraging theory and evolutionarily stable strategies. *Persp. Plant Ecol. Evol. Syst.*, 19, 70–76.

Veits, M., Khait, I., Obolski, U., Zinger, E., Boonman, A., Goldshtein, A., et al. (2019). Flowers respond to pollinator sound within minutes by increasing nectar sugar concentration. *Ecol. Lett.* 22, 1483–1492

Editor, Christoph Scherber
Manuscript received 5 August 2019
First decision made 4 September 2019
Manuscript accepted 16 September 2019