Erschienen in: Science ; 380 (2023), 6644. - S. 454-455
https://doi.org/10.1126/science.adh5264

PHOTO: CHANG *ET AL*. (5)

The chemical ecology of locust cannibalism

An anticannibalistic signaling pathway offers a new understanding of locust swarm formation

By **Iain D. Couzin**[1,2,3] *and* **Einat Couzin-Fuchs**[2,3]

Locust plagues threaten food security across the globe, with infestations estimated to affect the livelihood of 1 in 10 people (*1*). Cannibalistic interactions have been implicated in the formation and maintenance of these swarms (*2 4*). The threat of consumption by others is thought to have resulted in selection pressure for flightless juvenile locusts to use both visual and tactile information to move away from those approaching and to move toward those moving away (*4*). The outcome is large-scale, coordinated motion out of nutrient-poor areas, with the benefit of conspecifics being a source of essential, yet often scarce, nutrients along the way (*2*, *3*). On page 537 of this issue, Chang *et al*. (*5*) report that chemical communication plays a central role in regulating cannibalistic interactions in the migratory locust (*Locusta migratoria*). This discovery contributes new understanding about the role of cannibalism in locust ecology and suggests possible targets for their control.

Cannibalistic behavior is ubiquitous in the natural world (*6*) and may once have been common among human ancestors (*7*). Cannibalism has the potential to act as a key modulator in population growth and dispersal (*8*), an ecological role that may be especially profound for certain swarm-forming insects. In Mormon crickets (*Anabrus simplex*), for example, cannibalism is rife, with insects marching in unison not through some cooperative tendency, but rather with individuals being on what is effectively a "forced march" to avoid the threat of attack (*9*).

Even when cannibalism is less prevalent, such as among the two principal locust pest species the migratory locust and desert locust (*Schistocerca gregaria*) it has the potential to exert strong selection pressure on behavior. Thus, the proximate mechanisms that regulate social interactions among locusts, such as visually mediated attraction and avoidance, likely reflect this cannibalistic aspect of their evolutionary ecology (*4*). If food supplies are abundant, individuals will tend to persist as shy and cryptic "solitarious" grasshoppers. Population upsurges start with atypical rainfall that provides temporarily good breeding conditions, followed by food limitation. The increase in local density experienced by individuals, which ever closely aggregate on limited food resources, causes them to become actively "gregarious" (*10*). Moving in the same direction as others minimizes contact, and thus cannibalism (*4*), while facilitating collective motion out of areas of low food availability.

It is this extreme phenotypic plasticity, which involves rapid and substantial changes in physiology and behavior, that allows locusts to be so well suited to highly variable and unpredictable environments. Yet despite behavioral similarities, the differences in the molecular mechanisms by which the phylogenetically distant *S. gregaria* and *L. migratoria* regulate density-dependent plasticity could provide valuable insights into the evolutionary ecology of swarm formation (*10*, *11*). Both species exhibit a striking density-dependent color change when gregarious. This acts as a warning signal to predators (*12*). However, it is only the gregarious migratory locust that is known to synthesize a potent toxin hydrogen cyanide. Doing so is likely to be costly, owing to energetic costs and the risk of self-poisoning, and only occurs under conditions of stress (*13*). However, by emitting a precursor in the hydrogen cyanide biosynthesis pathway, phenylacetoni-

---

[1]Department of Collective Behavior, Max Planck Institute of Animal Behavior, Konstanz, Germany. [2]Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Konstanz, Germany. [3]Department of Biology, University of Konstanz, Konstanz, Germany.
Email: icouzin@ab.mpg.de

A migratory locust (*Locusta migratoria*) consumes a conspecific. Juveniles deter cannibalism by emitting the chemical phenylacetonitrile (PAN).

trile (PAN), they provide an "honest" (i.e., truthful) olfactory signal of their toxicity to potential predators (*13*). Gregarious desert locusts, by contrast, bias their diet toward toxic plants, and so their gut contents confer protection. This difference may imply that desert locusts are incapable of producing PAN, but this is not the case. Gregarious sexually mature adult male *S. gregaria* emit PAN as an aversive volatile to rival males during courtship (*14*, *15*). Thus, the emission of PAN has evolved, likely independently, as an aversive signal in both species. Neither species produces PAN when solitarious, using instead both cryptic coloration and behavior to avoid predation.

Chang *et al.* identified a PAN-sensitive olfactory receptor (LmOR70a) and edited mutations in the encoding gene that make this receptor nonfunctional, thereby creating a means to test how the reception of PAN affects behavior. They also engineered insects that are unable to produce PAN by introducing a loss-of-function mutation in *CYP305M2*, a crucial gene for PAN biosynthesis (*13*). Behavioral experiments with these gene-edited insects demonstrated not only that PAN is a generally aversive compound associated with crowding but also that it plays a specific role in suppressing cannibalism among juvenile migratory locusts. (It is notable that cannibalism is expected to play a greater role in the swarms of flightless juveniles that inevitably precede the adult flying swarms.) Juveniles that were unable to produce PAN were both more frequently attacked and preferentially consumed compared with wild-type nymphs. Conversely, *LmOR70a*-edited locusts, which are unable to detect PAN, readily consumed PAN-releasing individuals. Together, this suggests that PAN may be an honest signal to deter cannibalism (warning of the locusts' capability to produce hydrogen cyanide if attacked), but whether this results from direct toxicity or an association with another physiological and/or behavioral mechanism remains to be determined.

The finding that PAN mediates within-species communication in *L. migratoria* narrows the disparities between its role in the two locust species, which is thus-far associated with male-male antiharassment in *S. gregaria* and antipredation in *L. migratoria*. It could be that migratory locusts, which are adapted to grassland biomes in which plant toxins are less prevalent, cannot use gut contents as a chemical deterrent. Why juvenile *S. gregaria* do not use the PAN pathway to suppress cannibalism is less clear.

The work of Chang *et al.* serves as an important step in understanding the mechanisms that mediate the intricate balance between aggregation and competition in locusts. Because the PAN pathway regulates cannibalistic interactions, which in turn can drive mass migration, it may also prove to be a promising target for the future development of locust control agents. ■

REFERENCES AND NOTES

1. A. Steedman, *Locust Handbook* (Natural Resources Institute, ed. 3, 1990).
2. S. Bazazi *et al.*, *Curr. Biol.* **18**, 735 (2008).
3. S. Bazazi *et al.*, *Proc. R. Soc. London Ser. B* **278**, 356 (2011).
4. V. Guttal, P. Romanczuk, S. J. Simpson, G. A. Sword, I. D. Couzin, *Ecol. Lett.* **15**, 1158 (2012).
5. H. Chang *et al.*, *Science* **380**, 537 (2023).
6. M. A. Elgar, B. J. Crespi, *Cannibalism: Ecology and Evolution Among Diverse Taxa* (Oxford Univ. Press, 1992).
7. T. D. White, *Sci. Am.* **285**, 58 (2001).
8. L. R. Fox, *Annu. Rev. Ecol. Syst.* **6**, 87 (1975).
9. S. J. Simpson, G. A. Sword, P. D. Lorch, I. D. Couzin, *Proc. Natl. Acad. Sci. U.S.A.* **103**, 4152 (2006).
10. M. P. Pener, S. J. Simpson, *Adv. Insect Physiol.* **36**, 1 (2009).
11. H. Song, *J. Orthoptera Res.* **14**, 235 (2005).
12. G. A. Sword, S. J. Simpson, O. T. M. El Hadi, H. Wilps, *Proc. Biol. Sci.* **267**, 63 (2000).
13. J. Wei *et al.*, *Sci. Adv.* **5**, eaav5495 (2019).
14. K. Seidelmann, H. J. Ferenz, *J. Insect Physiol.* **48**, 991 (2002).
15. D. A. Cullen *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **119**, e2200759119 (2022).

ACKNOWLEDGMENTS

The authors thank G. Sword for discussions and the Deutsche Forschungsgemeinschaft (DFG) (grant 2117 422037984) for support.