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Complex floral behavior of an angiosperm family

Commentary on **Segundo-Ortin & Calvo** on *Plant Sentience*

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Abstract: Segundo-Ortin & Calvo provide a comprehensive overview of the many aspects of plant behavior examined to date. In our view, multiple lines of evidence make it difficult to deny plant sentience. We add further evidence to support the conclusion that plants are sentient organisms. As in animals, the behavior of plants can be seen and studied as an evolutionary trait, subject to and a consequence of increasing complexity in the interactions of plants with their environment. Our example is the evolution of floral behavior in Loasaceae, where complex patterns of stamen movement have co-evolved in interaction with specialized pollinators.

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The evidence nicely summarized in the target article by Segundo-Ortin & Calvo, (2023) is sufficient for us. Plants are anything but passive organisms functioning apathetically, steered by automatisms. We need to set aside the human exceptionalism and the zoocentrism of current research on sentience and acknowledge that plants make complex decisions, interact with many different organisms and move at their own speed.

Shouldn't sentience be the null hypothesis with all living organisms? About fungi, Hathaway (2022) puts it thus: "Various measures of the world, accepted as scientific standards, are shaped by the specific anatomy of the human body and, in particular, our species-specific senses."

The target article cites one of our studies as evidence of anticipatory behavior in the context of pollination in flowering plants (Mittelbach et al., 2019). This can be interpreted as an expression of underlying sentient capabilities. The mostly Andean Loasaceae have developed a complex reward- and pollen-partitioning system that is actively adjusted to a principle pollinator taxon and its visit intervals. We were able to show that these plants learn from previous visits to alter their pollen presentation by adjusting stamen movement to the learned visit frequency. As Mallatt et al. 2023, p. 6) note in their commentary, this "system offers promise as a model for investigating plant learning" and can be considered anticipatory learning which is "thought to indicate sentience."

An earlier study of the same plant family sheds light on the evolution of plant behavior (Henning et al., 2018). In many animal groups *behavioral diversity* is used to distinguish and describe animal species and to explain how taxa are derived in certain lineages. In contrast, in plants, only abiotic traits (such as distribution and soil preference) are typically used to support and refine taxon delimitation and to determine the systematics of certain groups. For the Loasaceae, we have shown how the diversity in floral behavior observed across about 50 different species is expressed in a complex interaction between the plants and their pollinators that reflects the evolutionary history of this plant family. This behavior takes the form of staggered, active presentation of pollen through "thigmonastic" movements of the stamen. The complexity of this floral behavior gradually increases in the derivation of single lineages.

In animal evolution, the gradual refinement and expansion of behavioral repertoire is frequently used as a basis for deriving taxa. Our study shows that the earliest lineages of Loasaceae cannot yet adjust the way they present their pollen in response to the behavior of pollinators. This capacity seems to be a novel trait in the family´s evolutionary history. The patterns of movement show a gradual increase in complexity and accuracy in the younger lineages. It is difficult, just as it is in the evolution of animals, to pinpoint where this behavior can be considered sentient. There is, however, no principled distinction between the two realms with respect to this difficulty.

Segundo-Ortin & Calvo state that: "Plants have evolved their own means of behaving adaptively, through phenotypic plasticity instead of locomotion, as in the case of animals." Our study reveals that there is not only phenotypic plasticity in plants, but also behavioral plasticity. The behavior consists of controlled stamen movement. Hence Loasaceae have evolved a way to behave adaptively through (loco-)motion with parts of their body.

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