

Why do honeybee foragers follow waggle dances?

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In our recent article [1], we discussed the ways in which the honeybee waggle dance provides followers with different kinds of information about food sources, such as their presence, odour or location [1]. However, the traditional interpretation of dance following, the decoding of spatial information ('dance language'), seems to explain only a small proportion of following events [2,3]. Therefore, we argued that to understand the means by which the waggle dance modulates honeybee-colony foraging, researchers need to take into account a range of different decision-making strategies of dance followers [1].

In response to our article, Brockmann and Sen Sarma [4] contend that, even though only a small proportion of dance followers attempts to decode the spatial information, this does not mean that the functional significance of the 'dance language' is questionable. This assertion is in agreement with our interpretation of the existing data that the 'dance language' does provide benefits under certain ecological conditions [1], such as those highlighted by the authors [4].

In addition, Brockmann and Sen Sarma [4] state that we used an unjustified metric of efficiency. Although various researchers have argued that recruitment to food sources by means of waggle dances seems to be less efficient than the degree stated by von Frisch (e.g. Refs. [5,6]), we pointed out in many of the cases where bees follow a dance but do not locate the advertised food source, it is not known whether the dance followers attempted to find the food source [1]. Therefore, two possible interpretations of these data (and the ones reported by Seeley [7]) are that, either only a small proportion of dance followers attempts to decode the 'dance language' or that the 'dance language' is not very efficient [1]. The notion that we need to consider recruitment events and not single waggle runs to estimate recruitment efficiency [4] is true, but does not elucidate why some foragers follow dozens of waggle runs whereas others do not [1].

Furthermore, Brockmann and Sen Sarma [4] imply that social information such as 'dance language' is more reliable than is private location information because foragers of social insect colonies collect food for the colony rather than for themselves. Although honeybee foragers do collect food for their colony, this does not tell us whether: (i) they should rely mostly on social information; (ii) follow purely solitary hunting strategies, as the desert ant *Cataglyphis* sp. does [8]; or (iii) follow mixed strategies such as switching

from a strategy of using social information to using private information with increasing foraging experience, as seen in wood ants [8]. The quality of both social and private location information is not fixed, but depends on factors that we discussed [1]. However, there is good evidence that honeybee foragers prefer private information about food locations if the information is recent and associated with profitable food [2,3].

Private information has some important advantages. Brockmann and Sen Sarma [4] speculate that the reception of abstract 'dance language' information is likely to be prone to failed transmission. Indeed, factors such as the crowding on the dance floor, imprecision of the dancers themselves and imperfect interpretation of the signal makes the dance a noisy information channel. This was illustrated by Riley *et al.* [9], who analysed the flight paths of bees recruited by dancing. Nevertheless, the existence of such a signal makes sense if its benefits to the colony are bigger than the costs.

Moreover, whereas foragers with field experience usually quickly discover the previously visited food source [3,10], recruits with only 'dance language' information approach the advertised food source slowly and often return unsuccessfully if not assisted by further information sources, such as the sight of other bees [1,6]. While the 'dance language' provides only vector information, experienced foragers additionally store information about landmarks en route and about the visual appearance of the food patch itself [11]. This visual information facilitates the localisation of a food source. It is probable, however, that the superiority of updated private information over 'dance language' information decreases with increasing food patch size.

Finally, we agree with Brockmann and Sen Sarma's [4] statement that the nest site selection hypothesis [12] is not the only possible scenario for the evolution of the dance language. However, Beekman *et al.* [12] are, to our knowledge, the only researchers so far to test predictions deduced from one of the possible hypotheses.

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Letters

Invasive species can also be native...

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In a recent review in TREE, Wilson *et al.* [1] aim to link success of biological invasions and the dispersal pathways of species. The authors emphasize the characteristics of human-mediated extra-range dispersal pathways (i.e. rapidity, high propagule pressure and high genetic diversity of the introduced population) in order to argue that biological invasions are, above all, a biogeographical phenomenon of unprecedented magnitude and, thus, that it would be better to separate biological invasions from 'considerations of ecological dominance' [1]. In other words, their approach automatically leads them to reserve 'the term and concept "biological invasions"' for allochthonous species. We disagree with this conclusion because, in our view, invasive species can also be native [2].

Two main findings show that dispersal and invasion are two distinct phenomena. (i) At least in the short term (cf. lag time), species introduction or dispersal by humans does not necessarily result in the activation of the invasion process. This fact leads to the 'tens rule' [3], which is widely cited and is notably acknowledged by at least one of the authors [4]. (ii) While the great increase in the number of biological invasions is undoubtedly linked to the development of human activities [5], it would be particularly restrictive to limit the influence of the humans solely to 'extra-range species dispersal'. While it is true that some allochthonous species have become invasive because they have moved to a different environment, it is also true that some native species, like some introduced species after a lag time [6–8], have undergone demographic explosions and rapidly conquered new areas as a result of a change in their environment owing to human activities (e.g. eutrophication, habitat and land use changes, global warming) [9,10, see ref. in 11]. Thus, we should retain the nature of the invasion phenomenon itself (i.e. as an ecological, and not biogeographical, phenomenon), which is what we proposed in our definition [2]. Species dispersal is a separate phenomenon that is neither a sufficient condition (cf. tens rule) nor a necessary condition (cf.

native species) in conferring the status of invasive species. Otherwise, we could reach absurd conclusions, as we can illustrate using the case of the European starling *Sturnus vulgaris* L., which would be considered invasive only in North America and not in Europe, where it is native, even though its populations have increased and spread in a similar way on both sides of the Atlantic [see ref. in 2].

The analysis of a concept consists of determining what features necessarily belong to it [12]. Taking into account the essence of the phenomenon itself thus constitutes an indispensable prerequisite to defining, understanding and managing it.

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