Comments

Complex behavior can also emerge from simple linear interactions: comment on Bradbury and Vehrencamp

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We have read with great interest the Invited Anniversary Essay by Bradbury and Vehrencamp (2014). A general and explicit recognition of the benefits of a complex systems approach in behavioral ecology was long overdue and therefore this essay is more than welcome. However, we believe that it contains several imprecise statements and misconceptions about what emergent properties are and how they arise out of the interactions between parts of a system. The impact of this essay (causing readers to "stop and wonder whether [their] favorite system is actually nonlinear and complex") would be better served if the relationship between nonlinear interactions and emergent properties was explained more accurately, using some well-known examples that the authors have not used.

Our main concern is that readers of this essay may be left with the impression that the properties of a complex system can only emerge when there are nonlinear, complicated interactions between the system's components. In their Background section, the authors cite a sentence from Strogatz's (1994) book on nonlinear dynamics: "Whenever parts of a system interfere, cooperate, or compete, there are nonlinear interactions going on." (Strogatz 1994, p. 9). This sentence certainly applies to simple systems of low dimension and with nonlinear internal dynamics, which are the subject of Strogatz's book, but it must be nuanced if one deals with systems composed of several interacting elements.

Many complex systems can be viewed as a large number of individual entities connected to each other, where each entity is a low dimensional nonlinear dynamical system. By low dimensional, we mean that an entity is characterized by a small number of internal variables evolving with time. When an entity is completely isolated from others, it has an autonomous and relatively simple nonlinear dynamics (characterized, say, by limit cycles, stationary attractor points, or even chaotic behavior). We agree that the dynamics of each entity is the result of internal nonlinear interactions, in the sense meant by Strogatz (1994), among the internal variables. These variables characterize the state of the entity and can be, for instance, the activator and inhibitor concentrations in a well-mixed chemical reactor, the self-regulated electric potential of a piece of excitable biological tissue, the velocity of a mobile animal, etc. Since the entity is described as a low dimensional

dynamical system, it is not a complex system according to the above definition.

An important aim in the study of complex systems is to predict the patterns emerging from connecting many such entities. By connecting, we mean that, typically, the values of the internal variables of an entity at a given time will affect the evolution of the internal variables of its neighbors, and vice versa. Our main point here is to emphasize that complex phenomena can emerge at a global scale even if, locally, entities interact in extremely simple, additive, and linear terms. Many paradigmatic examples of complex systems follow this scheme.

For instance, in colonies of pigment cells, chemical reactants can diffuse from one part to the other by simple Brownian motion (which translates into the linear Fick's law of diffusion) and produce ordered, periodic color patterns in animal skins, or Turing patterns (Murray 1993). In the context of synchronization, another phenomenon of great relevance to biology, nonlinear oscillators that are coupled linearly (similarly to masses linked by harmonic springs) can explain the different gait regimes in animal locomotion (Collins and Stewart 1993). In very large populations of nonlinear oscillators, the same linear interactions are sufficient to lead to the emergence of globally synchronized states (with application to heart pacemaker cells or flashing fireflies, an example cited by the authors), as well as to other spatial patterns like nonlinear traveling waves or intricate turbulent states (Pikovsky et al. 2001).

In behavioral ecology, social insect colonies are paradigmatic examples of complex systems. Individual ants may behave and interact with others using very simple rules (trail laying using pheromones, trail following, bringing found food back to nest, etc.). Individual ants may respond linearly to a pheromone concentration gradient and still produce surprisingly elaborate collective patterns at the colony level, including optimal foraging behaviors attributed to the colony as a whole (Bonabeau et al. 1997). It is somewhat surprising that the authors left this classic example of self-organization in behavioral ecology out of their essay.

In their section on Networks, the authors of the essay "would not expect to see emergent properties" when relationships between network members are "essentially linear" but only when links are "largely nonlinear." The above examples clearly contradict this statement. In addition, unexpectedly rich network structures can be the outcome of minimal models of network formation, such as the classic Erdös-Renyi "random growth" model. This model has demonstrated that networks where nodes connect randomly to other nodes, and where each connection is independent of previous connections, can exhibit a percolation phase transition when a "giant cluster" of connected nodes appears at some critical value of the average connectivity. In this example, the number of links in the network is a linear function of the connection probability, but the

size of the giant cluster is a nonlinear function of that probability. Thus, even though the rules of network formation are strictly linear (a succession of independent events), we can see the emergence of a collective property that holds across different network types and sizes (Strogatz 2001).

Of course, there are also many complex systems where the interactions between elements are nonlinear, such as neural networks or discrete cellular automata, of relevance to avalanches in sand piles, a topic that is discussed in the essay. But this type of nonlinearity is by no means a necessary condition for complex behavior in general, in particular if the elements are themselves internally nonlinear. We hope that this clarification can serve to strengthen the essay's message and increase the awareness among behavioral ecologists that the properties of their study systems could be emerging not out of complicated rules, but out of linear interactions between their elements.

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Complex behavior can also emerge from simple linear interactions. A reply to Ramos-Fernández and Boyer

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We appreciate the thoughtful comments by Ramos-Fernández and Boyer (2014) on our article (Bradbury and Vehrencamp 2014). As we noted in the article, we do not pretend to be experts in complexity theory but feel that this perspective, so useful in other fields, deserves greater attention by behavioral ecologists.

That said, we would like to respond to some of the issues raised by Ramos-Fernández and Boyer. Their main point is that emergent properties can arise in large systems with linear interactions. All of the examples they cite involve interacting entities that are themselves nonlinear systems. We accept their point and acknowledge that we neglected this possibility in our article. Perhaps it helps to classify interacting systems into 1) linear entities interacting linearly, 2) linear entities interacting nonlinearly, 3) nonlinear entities interacting linearly, and 4) nonlinear entities interacting nonlinearly. By the definition of emergent properties used in our article (modeled after the discussion in Mitchell 2011), we would not expect the first category to produce emergent properties regardless of dimension beyond coupled oscillations (which can be fully described with linear equations). Our article focused on the second and last categories, whereas Ramos-Fernández and Boyer emphasize the third.

The question of which process trail-making ants fall into is unclear to us. Ramos-Fernández and Boyer imply that they fit the third option. We actually doubt that nonlinear entities, including ants and termites, are ever limited to linear interactions (although researchers studying them tend to linearize the observed patterns). The decision of an ant leaving the colony to follow a given trail may be linearly related to the amount of existing trail pheromone for intermediate pheromone intensities, but there is likely a minimal threshold below which the ant ignores the trail and a saturation point above which additional concentrations have no further effect on the ant's decisions. Similarly, although recruits at a dead prey may adjust their trail marking on their return quasi-linearly according to the quality and quantity of prey parts they can grab, there will again be likely threshold and saturation points that make the decision nonlinear.

It is often possible to linearize responses of nonlinear systems to varying contexts at least over a limited range of those contexts. But like the mammalian larynx discussed in our article, continued linear increases in some contextual parameter such as airflow can trigger sudden bifurcations and state transitions (Herzel et al. 1995; Riede et al. 2000; Fitch et al. 2002; Tokuda et al. 2002). Perhaps the pheromone levels in ant trails should be better considered contextual parameters (like air flow) affecting the behavior of the nonlinear ant entities. Although the behaviors and densities of recruits may change linearly with pheromone over a range of intensities, there could well be bifurcations outside that zone. Unless one considers this possibility, one might never look for such transitions.

We did not try to assign each of the behavioral systems we discuss in the latter part of our article to one of the four categories above. But we wonder whether any of them will turn out to consist of linear entities with linear interactions. Ramos-Fernández and Boyer did not mention which, if any of these systems, they think truly are just nonlinear entities with strictly linear interactions. Certainly those examples that have been examined with an eye to nonlinear processes (e.g., Hemelrijk 2002; Hemelrijk and Hildenbrandt 2008) appear to involve nonlinear interactions between nonlinear entities. We suspect that this is the more likely general case.

Ramos-Fernández and Boyer's mention of Erdös-Renyi network models is interesting. It is definitely the case that adding links to a sparse network randomly and at a steady rate initially produces a monotonic increase in the scope of propagation of any stimulus introduced into that network (see discussion in Chapter 15, Bradbury and Vehrencamp 2011). However, once every node is connected by some path to every other node, no further propagation scope is possible (although speeds might change). A graph of propagation scope (percolation) versus number of links added would show a monotonic rise that either asymptotes or hits a ceiling at high values. Any equation(s) for the entire graph would not be linear, and it is instructive that the point at which the state transition occurs is right when the graph shows a major kink. This raises the general question of whether bounded linear processes should be considered linear or nonlinear. We scientists have spent decades focusing on the former, but maybe it is time to look at the whole curve.

Finally, we note a minor correction. In our article's comparisons of linear and nonlinear oscillators, we imply that the two differ in how frequencies are determined. In fact, frequencies in both are determined