

(15). Research is limited by the difficulty of examining interactions in the field and the possibility that mismatches may be uncommon or quickly corrected by evolutionary processes (15), and many interactions are hidden or would take too much time to observe. In cases of mimicry, like those studied by Hassall et al. (3), identifying model-mimic pairs can require complex measurements and comparisons of morphology. As a result, testing the influence of shifts in phenology on the fitness of organisms is rare (but see refs. 16 and 17). In the case of model species, mimics, and predators, measuring the fitness consequences of phenological change can require experiments to test predator preference or behavior, but such experiments are difficult to carry out and might have unexpected artifacts depending on their design.

New Approaches to Investigating Interactions

In recent decades, new technologies have paved the way for more indirect approaches—for example, environmental DNA, satellite tracking, and time-lapse videos or camera traps—to investigate interactions among species. These techniques enhance our ability to assess which species are in the same locations at the same times and to document occurrences of specific interactions that might get captured on camera. But they leave open questions about the nature of interactions and the consequences of phenological shifts on interacting species. The approach of Hassall et al. (3) shows one way to fill these gaps; their unusual methodology allowed them to investigate dozens of interactions across complex trophic relationships. Each step of their approach demonstrates a unique value of citizen science that other researchers might find useful in their own work.

First, rather than observing model-mimic relationships directly in the field or using feeding tests with birds, Hassall et al. (3) created an online game in which citizen scientists could rate the visual similarities of co-occurring pairs of syrphids and hymenopterans based on size, shape, color, hairiness, and other characters (Fig. 1). Over the course of a year, volunteers (recruited via Twitter) submitted 30,300 ratings and identified 237 high-fidelity model-mimic pairs out of 2,352 potential combinations, with results that correlated strongly with pigeon experiments. This technique demonstrates the value of citizen science to allow researchers to assess pairwise combinations faster and in greater numbers than can be achieved using traditional methods. Variations on this method could be appropriate for other studies involving morphological comparisons, such as in other model-mimic or camouflage studies, or studies of specimens collected during bioblitzes or biodiversity inventories.

Second, Hassall et al. (3) analyzed over a million records of syrphid fly, bee, and wasp abundance from two long-term citizen science monitoring projects in the United Kingdom. This extensive dataset showed that hymenoptera emerge earlier, on average, than syrphid flies, and that the spring emergence of hymenopterans is advancing faster than that of syrphids in response to warming temperatures. This study adds to the growing body of research using citizen science data to document shifts in species phenology and interactions, including community-level interactions at single locations (18), possible interactions across trophic levels (1), and known interactions (2).

Third, Hassall et al. (3) developed a virtual reality game to simulate model-mimic-predator interactions in different phenological scenarios. Instead of offering live hymenopterans and syrphids to birds in complicated feeding experiments, or using data-intensive and highly parameterized computational algorithms, 45 humans took on the role of bird predators in a game. Participants were

recruited from the University of Leeds and surrounding areas and were compensated £5 for their time. They gained points by feeding on benign mimic syrphids and lost points when they ate stinging model hymenopterans. Participants had to identify mimics against complex backgrounds, a simulation of the challenges that bird predators face in deciding whether or not to feed on an insect. The results of the game showed that model species (i.e., bees and wasps) perform best (i.e., had highest survival rates) when they are active before the syrphid mimics. Mimics, on the other hand, perform best when the phenology of model species and mimics overlaps and occurs randomly from the perspective of predators.

In PNAS, Hassall et al. use a combination of citizen science techniques to investigate the effects of climate change on dozens of specific interactions.

And predators do best when either the model bees and wasps emerge first or when the syrphid mimics emerge first, with consistency. This creative game-based approach worked because researchers could be fairly confident that decisions made by humans in simulations were similar to those previously observed in animal-based experiments and results from algorithms and neural nets. This technique could be promising in other ecological systems in which human behavior and decision making provides an added value, such as in other predator-prey, competition, or mutualism interactions.

Fourth, in the final phase of their study, Hassall et al. (3) returned to the long-term citizen science data to analyze changes in the phenology of the interacting species as the climate warms in light of what they discovered about the fitness benefits and costs of different phenological scenarios. They found that the phenology of many model bee and wasp species is shifting so that they appear before mimic syrphid species. These shifts create new situations that benefit bees and wasps and bird predators, while reducing the circumstances during which syrphids do best (overlapping phenology) and worst (mimics emerge first). These conclusions result from the synthesis of three citizen science tools, each of which benefitted from different styles and values of participant contributions, and each of which provided a different piece of this complex story.

What Next?

The approaches of Hassall et al. (3) avoid labor-intensive field research and sometimes impossible-to-get direct observations of interactions in nature. We are confident that researchers will find many more applications for these techniques. Most obviously, similar methods might be applied to other Batesian mimicry systems such as those occurring in butterflies, in which there are models, mimics, and bird predators (e.g., 19). This approach might also be applied to other complex species interactions such as some predator-prey interactions, or to human activities such as bushmeat hunting or fishing strategies.

Moreover, the results of Hassall et al. (3) have intriguing implications and raise questions about their generality and how they play out in nature. Is selection driving these changes in phenology or are the hymenopteran model species just more phenotypically plastic than the mimic syrphids? The predictions generated from this study (and other such studies) should also be tested with field studies of the target species. Do syrphid mimics really do worse

