Feedback in Batesian mimetic systems

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We propose a feedback model for Batesian mimetic trophic system dynamics that integrates evolutionary and ecological processes including those not directly related to mimicry such as nutrient transfer. The proposed feedback circuit includes a previously overlooked link, specifically: selection for predation on the mimetic phenotype, which results when predators consume palatable mimics, and which perpetuates predation on the mimetic phenotype that drives mimicry. Preservation of variation throughout the feedback loop may also explain polymorphism, suboptimal mimicry, and other aspects of mimetic trophic system evolution.

ADDITIONAL KEYWORDS: autocatalysis – mimicry – mutualism – systems.

INTRODUCTION


Mueller (1879) argued that Batesian mimics must exist in lower numbers than models (i.e. frequency-dependent evolution), otherwise predation on mimics would be rewarded and fail to deter predation on the model. For more than 100 years, Mueller's constraint has been a cornerstone of mimicry dynamics (e.g. Cott 1940, Dunn 1954, Brattstrom 1955, Gilbert 1983, Huheey 1976, 1984, Turner et al. 1984, Mallet and
Feeding on mimics could drive mimicry rather than thwart it (contra Mueller 1879). More generally, systems characterized by feedback may generate indirect benefits for constituents (e.g. Bondavalli and Ulanowicz 1999), hence, predation may present benefits, in addition to costs, for prey species.


Sena and Ruane (2022) argued for increased rigor in mimicry studies, including improved diligence regarding consideration of alternative hypotheses (easy) and increased effort to obtain empirical data (challenging). We add that greater rigor could also be sought in the theoretical models used to explain mimesis. We present a more integrative and explicit feedback model for Batesian mimic systems, bringing additional ecological dynamics into what has traditionally been treated as primarily an evolutionary topic (Johnson and Stinchcombe 2007), with an eye towards explaining long-standing questions related to unexpected variation and other aspects of mimicry. In addition to salient processes (e.g. mimicry between toxic and non-toxic prey species; predation on models), we consider indirect benefits (e.g. Patten 1982, Bondavalli and Ulanowicz 1999, Fath 2007) and processes not generally addressed in studies of mimesis such as nutrient transfer, ‘to avoid missing important non-trivial dynamics of the coupled system’ (Henderson and Loreau 2018). We also submit that additional rigor may be realized by integration of thought across scientific disciplines, and hence we craft our model in a broad theoretical context including systems ecology and thermodynamics, and we employ their respective lexicons where appropriate (e.g. Ulanowicz 1997, Fath and Patten 1998, Toussaint and Schneider 1998, Pross and Khodorkovsky 2004, Fath 2007, Bailier-Jones 2009, Ulanowicz 2009b, Ho 2013, Pascal and Pross 2015, Cazzolla Gatti et al. 2020, Seaborg 2021; see Glossary). We will pay particular attention to published data for mimetic snakes because unique complexity of those systems is relevant to the theoretical model.
Feedback dynamics in Batesian trophic systems

We argue that mimicry is best understood through integration of ecological and evolutionary processes (e.g. Johnson and Stinchcombe 2007, Basu et al. 2023), which may be mutualistic rather than agonistic overall, even if some relationships are ostensibly one-sided (e.g. Boucher et al. 1982, Fath and Patton 1998, Fath 2007, Ulanowicz 2009b, Borrett et al. 2016, Aubier et al. 2017a, b, Fredrickson 2017, Henderson and Loreau 2018). Modelling Batesian mimicry in this context reveals a previously overlooked key link (e.g. Borrett et al. 2016) between predators and mimics that drives the evolution of mimesis, specifically, ‘selection for predation on the mimetic phenotype results when predators consume mimics’, which drives continued predation on the model and perpetuates mimicry (Fig. 1). That critical link in the feedback loop preserves variation in the predator, which allows a mimetic trophic system to evolve and persist, even if high toxicity evolves in the model. In addition, a dualistic (Ulanowicz 2009a, 2009b; Glossary) dynamic between predator and mimic is evident under the proposed feedback model: predation on the Batesian mimic (i) preserves variation (in the predator and the trophic system as a whole) by rewarding predation on the mimetic phenotype and, at the same time, (ii) culls variation (in the mimic and the trophic system as a whole) by selecting against imprecise mimics, which may further optimize mimesis. Rather than expecting mimicry to evolve towards a perfect endpoint, we expect ecological and evolutionary dynamics to perpetually optimize multiple variables through overlapping feedback circuits, resulting in both preservation and culling of variation (and other processes) in mimetic systems (e.g. Wignall and Soley 2021; Fig. 2). Hence, ‘imperfect mimicry’ is not an anomaly but an expectation of mimetic system dynamics.

Figure 1. Feedback in a hypothetical Batesian mimetic trophic system. The previously overlooked link (shaded) between the non-toxic mimic and the predator completes the feedback circuit, specifically, selection for predation on the mimetic phenotype, which drives subsequent processes that drive mimicry.
Feedback circuits may engender autocatalysis, a type of positive feedback that results in self-sustaining accelerated rates of change (e.g. Ostwald 1890, Edelstein 1971, Eigen 1971, Kauffman 1971, Ulanowicz 2004, 2009b, Plasson et al. 2011, Hordijk et al. 2012, Szostak et al. 2016, Seaborg 2021; Glossary), which may underlie hypothesized accelerated evolution for some mimetic trophic systems (e.g. Marshall 1908, Nicholson 1927, Dunn 1954, Van Valen 1973, Turner 1976, 1984, 1995, Dawkins and Krebs 1979, Darlington 1980, DeAngelis et al. 1986, Gavrilets and Hastings 1998, Joron and Mallet 2011, Thompson 2013, Santos et al. 2014, Arbuckle and Speed 2015, Rabosky et al. 2016, Anderson and de Jager 2020, Cazzolla Gatti et al. 2020, Kikuchi et al. 2021, Cabral et al. 2022). Further, countercurrent feedback (or bidirectional feedback; Henderson and Loreau 2018) circuits, which tend to increase system efficiency (Hartigay and Kuhn 1951), are evident in the more inclusive model (Fig. 2). For example, benefit streams that increase efficiency (e.g. culling imprecise mimics) flow counter to more conspicuous pathways associated with mimesis (e.g. those directly involving predation and mimicry), such that a mimetic trophic system might be composed of multiple countercurrent feedback pathways, possibly inducing countercurrent autocatalysis (Fig. 2) which, may contribute to the accelerated evolution of those systems.

Feedback probably optimizes multiple processes in mimetic systems including underlying ecological processes overlooked in evolutionary studies of mimicry. Nutrient transfer, for example, is a core element of trophic systems that is key to understanding mimetic system dynamics. For example, when a predator consumes a mimic, it might simultaneously (i) optimize prey signalling in the mimic, (ii) select for predation on the mimetic phenotype and drive mimicry, (iii) apportion predation risks among model and mimic, as well as (iv) provide a nutritional benefit for the predator (Fig. 2). Nutrient transfer pathways should, therefore, increase complexity in mimetic systems where model and mimic prey on each other (Spawls and Branch 2020), such as those including coral snakes and mimics (e.g. Beebe 1946, Campbell et al. 2004), which, in addition to apportioning costs exacted by the non-ophidian predator that drives mimicry (Mueller 1878), would result in nutritional benefits for model, or mimic, or both. Nutrient transfer on a global scale (e.g. Swap et al. 1992) may also partially explain the high diversity (and other patterns including latitudinal and longitudinal gradients) of Neotropical mimetic systems (e.g. butterflies, snakes). Namely, airborne nutrients originating in the Sahara, captured by the Amazonian slopes of the Andes, and accumulated in the deltaic floodplain of the Amazon, might provision the increased diversity and complexity of ecosystems, including mimetic systems, in far eastern (Rabosky et al. 2016: fig. 1) and far western (Rabosky et al. 2016: fig. 1; Doré et al. 2022) Amazonia.

Biological systems in general (e.g. cells, organisms, species, ecosystems, corporations, cities) tend to optimally evolve greater autonomy, agency, complexity, efficiency, emergence, robustness and stability as they mature (e.g. Rosnay 1979, Toussaint and Schneider 1998, Ulanowicz 2009b, Cazzolla Gatti et al. 2020, Zisopoulos et al. 2022a, b). Mimicry emerges via an entanglement of myriad processes that should be considered when modelling them (e.g. Gavrilets and Hastings 1998, Henderson and Loreau 2018). For example, mimicry co-evolves with numerous other emergent phenomena including those not directly related to mimicry such as crypsis, competition, feeding efficiency, geographical variation, learning, sexual dimorphism, prey availability, physiological drive...
(e.g. hunger) and ontogeny (e.g. Sweet 1985, Yanosky and Chani 1988, Ruxton et al. 2004, Nokelainen et al. 2012, Rönkä et al. 2018, Anzaldo et al. 2020, Pizzigalli et al. 2020, Yamazaki et al. 2020, Lev-Yadun 2021, Loeffler-Henry and Sherratt 2021, Rabosky et al. 2021, Cabral et al. 2022), at the same time that Mullerian and Batesian evolution jointly shape trophic systems (Bosque et al. 2022). Such a multiplication of links and layered complexity within a trophic system is expected to increase overall system efficiency and stability (Pross and Khodorkovsky 2004. Ho 2013. Pascal and Pross 2015. Panyam et al. 2019. Cazzolla Gatti et al. 2020. Zisopoulos et al. 2020a, b), and may explain, for example, the high diversity of mimetic systems involving snakes in the New World and Africa (e.g. Campbell et al. 2004, Spawls and Branch 2020). Further, autocatalysis underlying the diversity and complexity of biological systems drives the evolution of yet more diversity and complexity; in short, complexity begets more complexity (Cazzolla Gatti et al. 2020). Such organized complexity, as ascendency, (e.g. Ulanowicz et al. 2006, Huang and Ulanowicz 2014), is potentially quantifiable (e.g. Ulanowicz 1997, Henderson and Loreau 2018, Panyam et al. 2019, Zisopoulos et al. 2020a) and may provide a metric for comparison of mimetic systems.

Highly evolved systems may become frangible if efficiency results in loss of adaptability in response to perturbation (Conrad 1983, Holling 1986, Ulanowicz 2009b, Ulanowicz et al. 2009). In other words, biological systems tend to optimize robustness as they evolve but at the same time tend to be inherently brittle (Damiani et al. 2013, Zisopoulos et al. 2022a, b). For example, highly efficient aerobic respiration probably partly explains the high diversity and functional capacity of homeotherms; however, the fragility of that physiological strategy can be readily demonstrated in a few anaerobic minutes (e.g. blockage of cervical blood vessels and trachea in prey by canine teeth of predators). Perhaps cases wherein mimics do not occur sympathetically with a model, and similar situations that are challenging to explain (e.g. Gadow 1911, Huheey 1976, Yamauchi 1993, Ruxton et al. 2004, Przecz et al. 2008, Pfennig and Mullen 2010, Rabosky et al. 2016, Sena and Ruane 2022), represent mimetic systems in the process of collapse caused by the loss of order in an autocatalytic system (Kauffman 1986, Filisetti et al. 2011, Panyam et al. 2019), as is the ultimate fate of all biological systems (e.g. Toussaint and Schneider 1998). Ascendency values might provide a means of evaluating the robustness of such systems (Panyam et al. 2019, Zisopoulos et al. 2022a).

CONCLUSIONS

Our consideration of mimicry in the context of feedback systems offers new insights. One of the pathways hypothesized herein regarding Batesian mimicry, i.e. predation drives the evolution of toxicity, which drives mimicry, which in turn drives selection for predation on the mimetic phenotype, constitutes a feedback cycle that, in part, preserves variation essential for the evolution and persistence of mimetic trophic systems (Figs 1, 2). The preservation of variation via feedback in mimetic systems may explain polymorphism within species, suboptimal mimicry and other deviations from frequency-dependent evolution. Feedback cycles may engender autocatalysis, which may explain disproportionate rates of evolution previously hypothesized for some mimetic systems.

GLOSSARY

Ascendency: The capacity for a system to order itself, or organized complexity, including size. For example, eukaryote cells, with their extensive internal membranes and myriad coordinated metabolic processes, tend to exhibit greater ascendency than prokaryotic cells.

Autocatalysis: Self-accelerating positive feedback or the tendency for change to propagate in a feedback loop; evident at multiple levels of organization, sometimes as exponential growth; in citric acid cycle, some aquatic bladderwort (Utricularia) oligotrophic ecosystems, human population growth since the Industrial Revolution.

Autonomy: The independence and persistence of systems beyond that of their constituent subunits. For example, an individual organism remains a unitary independent system despite replacement of all its atoms and cells.

Countercurrent autocatalysis: Bidirectional feedback; opposing pathways of self-accelerating positive-feedback.

Duality: Opposing tendencies; for example, predation is both good (e.g. imperfect mimics culled) and bad (e.g. loss of matter, energy, information) for prey species in mimetic systems.

Emergence: Novel processes that manifest with new system organization; for example, development is change over time at the organism level, natural selection is change over time at the species level.
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