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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

Batesian mimicry emerges from the dynamics among predator, chemically defended prey (model) and prey that phenotypically resemble the model but are not chemically defended (mimic; Bates 1862, Van-Wright 1980, Mallet and Joron 1999, Ruxton *et al*. 2004). Mimics evolve phenotypic similarity to a model as predators evolve avoidance of the phenotype of the toxic species (or is learned; e.g. Sena and Ruane 2022). Batesian mimicry is generally thought to be parasitic (because the toxic model should not benefit from the relationship, e.g. Bates 1862, Fisher 1930, Wickler 1968, Brower and Brower 1972, Lea and Turner 1972, Turner *et al*. 1984, Huheey 1988, Speed 1993, Ohsaki 1995, Turner 1995, Joron and Mallet 1998, Edmunds and Golding 1999, Mallet and Joron 1999, Speed and Turner 1999, Lindstrom *et al*. 2004, Rowland *et al*. 2010, Pfennig and Kikuchi 2012, Aubier *et al*. 2017b, Akcali *et al*. 2018, Hassall *et al*. 2018, Anderson and de Jager 2020, Kikuchi *et al*. 2021, Loeffler-Henry and Sherratt 2021); however, some have suggested Batesian mimetic systems cohere primarily through mutualistic processes (e.g. Aubier *et al*. 2017a, b, Fredrickson 2017)—a fundamental element of the model presented here.

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

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Turner 1998, Iserbyt *et al*. 2011, Kikuchi *et al*. 2021, Prusa and Hill 2021). For example, Joron and Mallet (1998: 463) argued: 'this very powerful frequency-dependent effect will typically influence the outcome of the mimetic association much more strongly than merely the frequency-independent effect of relative palatability.' Empirical studies (e.g. Dunn 1954, Sheppard 1959, Brower and Brower 1962, Pfennig *et al*. 2001, Harper and Pfennig 2007, Kikuchi and Pfennig 2010, Kikuchi *et al*. 2021) and simulations (e.g. Charlesworth and Charlesworth 1975, Turner *et al*. 1984, Speed and Ruxton 2010) have found support for the frequency effect while others have questioned it (e.g. Brower 1960, Springer and Smith-Vaniz 1972, Otte 1974, Greene and McDiarmid 1981, Randall 2005, Pfennig 2016, Rabosky *et al*. 2016, Prusa and Hill 2021). Notably, Fisher (1930) argued a Batesian mimic might be more numerous if the model is extremely noxious (Otte 1974) or if the mimic is a relatively unimportant prey item. Here, we argue feedback dynamics might be at least as important as frequency in shaping mimetic trophic systems; more important, because of feedback, rewarding predation 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.

Intraspecific variation has been documented in many aspects of mimetic systems including colour pattern, predatory behaviour, prey behaviour, toxicity and physiological drive (e.g. hunger in the predator), but such variation has not always been understood (e.g. Marshall 1908, Dixey 1909, Brown *et al*. 1974, Papageorgis 1975, Fink and Brower 1981, Turner 1984, Brower and Calvert 1985, Dittrich *et al*. 1993, Speed 1993, Turner and Mallet 1996, Joron and Mallet 1998, Mallet and Joron 1999, Turner and Speed 1999, Edmunds 2000, Sherratt 2002, Ruxton *et al*. 2004, Mappes *et al*. 2005, Rowland *et al*. 2010, Nokelainen *et al*. 2012, Speed *et al*. 2012, Kikuchi and Pfennig 2013, Aubier *et al*. 2017b, Akcali and Pfennig 2017, Akcali *et al*. 2018, Bosque *et al*. 2018, Hegedus *et al*. 2018, Rönkä *et al*. 2018, Briolat *et al*. 2019, Anderson and de Jager 2020, de Solan *et al*. 2020, Moore *et al*. 2020, Burdfield-Steel and Kemp 2021, Curlis *et al*. 2021, Kikuchi *et al*. 2021, Kunte *et al*. 2021, Liu *et al*. 2022). Long-standing enigmas include cases where models and mimics do not closely resemble each other (e.g. Huheey 1988, Dittrich *et al*. 1993, Lindstrom *et al*. 1997, Sherratt 2002, Ruxton *et al*. 2004, Gilbert 2005, Speed and Ruxton 2010, Penney *et al*. 2012, Kikuchi *et al*. 2016, Pfennig and Kikuchi 2012, Kikuchi and Pfennig 2013, Iserbyt *et al*. 2011, Dalziell and Welbergen 2016, Rönkä *et al*. 2018, de Solan *et al*. 2020, Katoh *et al*. 2020), including cases where 'imperfect mimics appear more numerous than more perfect mimics' (Edmunds, 2000). Some of the observed variation in mimetic systems is argued to be the result of the model escaping parasitism by evolving away from the mimic (e.g. Sheppard *et al*. 1985, Huheey 1984, 1988, Joron and Mallet 1998, Ruxton *et al*. 2004, Pfennig and Kikuchi 2012, Aubier *et al*. 2017b, Akcali *et al*. 2018). In addition, some have argued in the context of generalized feedback models that mimetic systems exhibit accelerated rates of evolution (Dunn 1954, Van Valen 1973, Dawkins and Krebs 1979, Darlington 1980, DeAngelis *et al*. 1986, Turner 1995, Gavrilets and Hastings 1998, Joron and Mallet 1998, Seaborg 1999, 2021, Thompson 2013, Kizirian and Donnelly 2017, Anderson and de Jager 2020, Cazzolla Gatti *et al*. 2020, Kikuchi *et al*. 2021). Here, we more intensively consider how feedback may produce the observed unexpected variation in mimetic systems such as polymorphism, imperfect mimicry and accelerated evolution.

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 mimetic 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, Bailer-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.

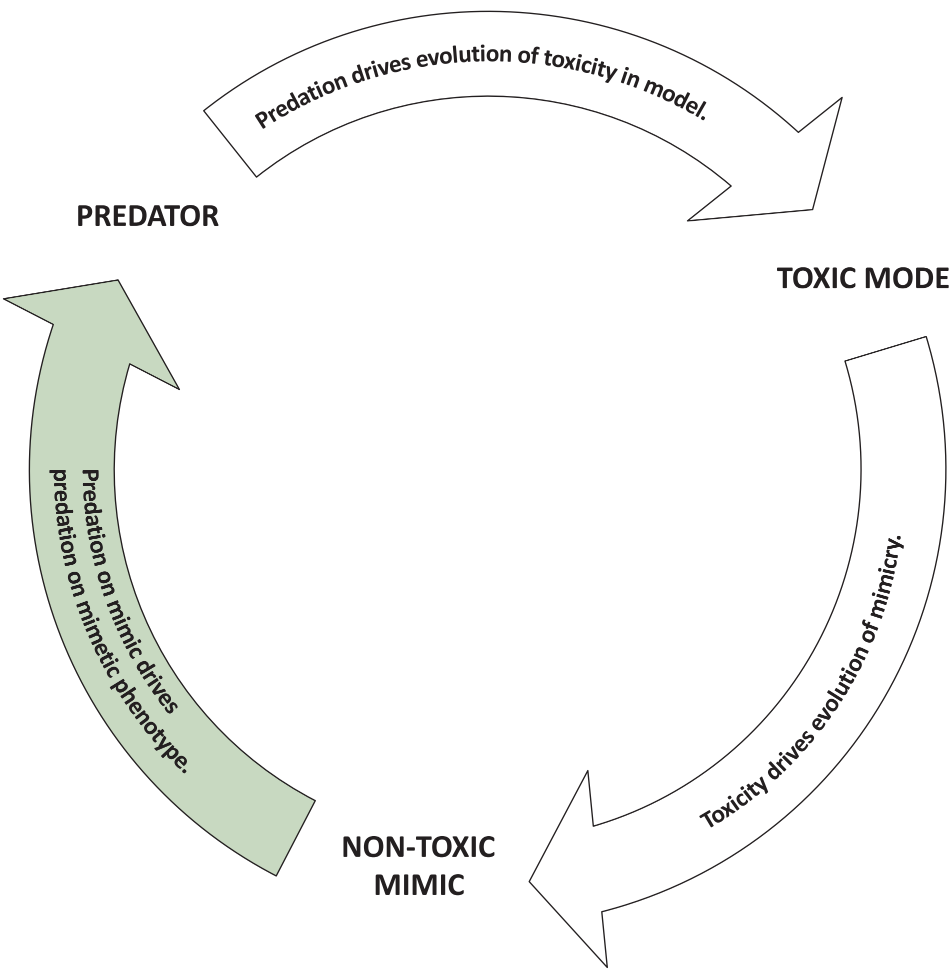

Figure 1. Feedback in a hypothetical Batesian mimetic trophic system. The previously overlooked link (shaded) between the non-toxic mimic and the predator completes the feedback circuit, specifically, selection for predation on the mimetic phenotype, which drives subsequent processes that drive mimicry.

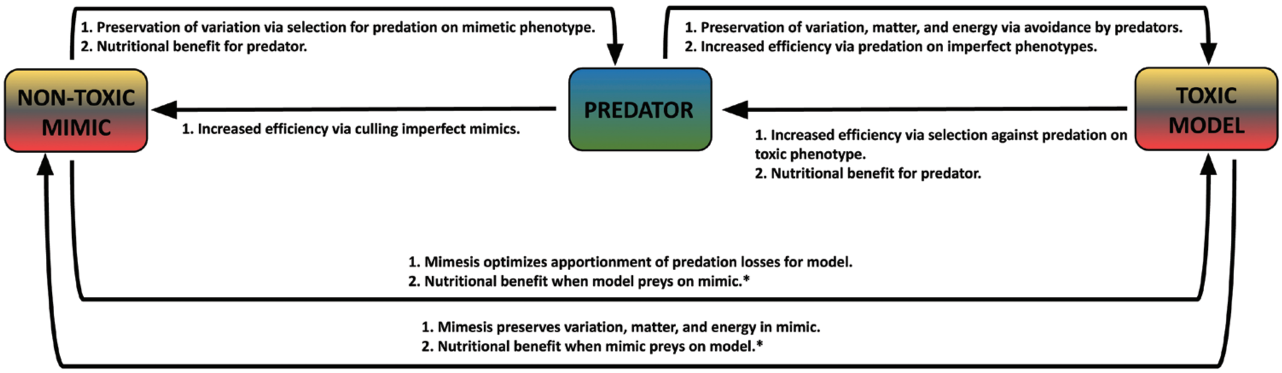

Figure 2. A more inclusive feedback model of a hypothetical mimetic trophic system. This model includes two countercurrent feedback circuits that account for processes directly related to mimesis and some indirect benefits. Asterisks denote benefits in cases where model and/or mimic prey on each other (e.g., coral snakes and their mimics), which increases the number of links and further optimizes the stability of the system.

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 1998, Guimaraes *et al*. 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 sympatrically with a model, and similar situations that are challenging to explain (e.g. Gadow 1911, Huheey 1976, Yamauchi 1993, Ruxton *et al*. 2004, Przeczek *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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