CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

COMPETITIVE MIMICRY: SYNTHESIS OF A NEGLECTED CLASS OF MIMETIC RELATIONSHIPS

MEREDITH M. RAINEY AND GREGORY F. GRETHER[1]

Department of Ecology and Evolutionary Biology, University of California, Los Angeles, California 90095-1606 USA

Abstract. Protective mimicry has been studied extensively for over a century. Mimicry in a competitive context, however, has remained largely neglected. It has been overlooked in mimicry classification schemes, and few systems have been rigorously studied. We define "competitive mimicry" as mimicry that enables access to a defended resource or aids in defense of a resource. We explain how competitive mimicry fits with existing mimicry classification schemes and outline criteria for identifying competitive mimicry systems. For each form of competitive mimicry, we describe the effects of the mimic on the model and receiver, predict the evolutionary dynamics of the system, and present examples. We then identify key directions for the study of competitive mimicry.

Key words: adaptive resemblance; Batesian mimicry; contest competition; evolutionary dynamics; interference competition; Mullerian mimicry; resource defense.

INTRODUCTION

The best-studied forms of mimicry are those in which a mimic gains protection from predators by resembling an unpalatable or otherwise protected model. Batesian mimics are palatable and otherwise unprotected, avoiding predation by deceiving predators as to their identity (Bates 1862). Mullerian mimics are, like their models, protected, and both mimic and model (or co-mimics) gain by sharing the cost of predators' avoidance education (Muller 1879). These two forms of mimicry, which fall under the functional category of protective mimicry, have been investigated extensively for decades (reviewed in Ruxton et al. 2005). Many protective mimicry systems have been studied rigorously in the field, and the evolutionary dynamics of these systems have been modeled under a wide variety of conditions. Although our understanding of protective mimicry remains incomplete, other categories of mimicry have been neglected by comparison.

Perhaps the most overlooked class of mimicry systems are those in which mimicry plays a role in interference competition. Many such examples are known, but the common ecological basis of these mimicry systems has not been recognized and they have never been expressly included in mimicry classification schemes. Studies of such systems have rarely extended beyond determining the advantage of mimicry; the underlying theory and evolutionary dynamics have been almost entirely ignored. We propose that the term "competitive mimicry" be used to encompass all forms of mimicry that enable access to a defended resource or aid in defense of a resource. This term has previously been used to describe two different phenomena, both of which fall within our definition. Willis (1976) offered this term as an alternative to Cody's (1969) "character convergence" for cases in which competing species converge in display traits (e.g., song, coloration) because of the mutual benefits of recognizing competitors and advertising competitor status. Payne (1982, 1983) later used the term to describe cases in which dominant competitors are mimicked to intimidate other competitors. Our broader definition includes these forms of mimicry as well as many other cases in which mimicry plays a role in competitive interactions.

We begin this paper by briefly explaining how competitive mimicry fits with existing mimicry classification schemes and then outline criteria for identifying competitive mimicry. In the body of the paper, we describe the various forms of competitive mimicry in terms of the relationship between mimic, model, and receiver and the expected evolutionary dynamics of the system, with examples where known. We conclude by setting priorities for future research.

Species composition		Synergic				Antergic			
		I Warning	II Aggressive	III Defensive	IV Inviting	V Inviting	VI Defensive	VII Aggressive	VIII Warning
Disjunct		Type C†		Type F (Burrowing Owls)			Type A (*Acanthurus pyroferus*) Type D†		
Bipolar	$S_1 + R$	Type C (*Pomacanthus*) Type E (Mockingbirds)					Type D (Song Sparrows)		
Bipolar	$S_1 + S_2$								
Bipolar	$S_2 + R$	Type C (*Pomacanthus*)		Type F†			Type A† Type B (*Pomacanthus*) Type D†		
Intraspecific		Type E (song sharing)					Type A (sexual mimicry) Type D (Indigo Buntings)		

FIG. 1. Vane-Wright's (1976) unified classification matrix for mimetic resemblances. Column categories describe the relationship between model, mimic, and receiver. Mimicry is synergic if the existence of the mimic is beneficial to the model and antergic if the existence of the mimic is detrimental to the model. Mimicry is "warning" when the receiver would benefit from responding negatively to (e.g., avoiding) both model and mimic and "inviting" when the receiver would benefit from responding positively to (e.g., approaching) both model and mimic. Mimicry is "aggressive" if the receiver would benefit from responding positively to the model but negatively to the mimic and "defensive" if the receiver would benefit from responding negatively to the model but positively to the mimic. Row categories describe the species composition of the system, where S_1 is the model, S_2 is the mimic, and R is the receiver. Disjunct means that model, mimic, and receiver are all different species; bipolar means that two species are involved. For example, $S_1 + S_2$ indicates that model and mimic are conspecifics and the receiver is a different species. Shaded boxes are forms of mimicry for which Vane-Wright (1976) presented examples. The forms of competitive mimicry are designated by the letter labels given to each in Table 1, and some examples from the text are given; daggers mark other plausible forms of competitive mimicry.

CLASSIFICATION OF COMPETITIVE MIMICRY

Several mimicry classification schemes have been proposed, but some are orthogonal and no one scheme is universally accepted over others. Vane-Wright (1976) identified the eight possible interactions between model, mimic, and receiver and crossed these with the five possible states of species composition to create 40 distinct classes of interactions that encompass every possible mimetic relationship (Fig. 1). Vane-Wright's paper was also intended to provide a comprehensive review of how the known forms of mimicry fit into the 40 theoretical classes, but no examples of competitive mimicry were included. The various forms of competitive mimicry (see *Forms of competitive mimicry*) fall into 10 of the 40 classes, including seven classes that Vane-Wright (1976) had left empty for lack of examples (Fig. 1). Endler (1981) proposed an alternative classification scheme, in part to distinguish between mimicry and crypsis. He identified two criteria based on whether mimicry affects the population dynamics of the model(s) and a third criterion based on the importance of the mimic's signal background. All forms of competitive mimicry fall within two of Endler's three mimicry categories (Batesism and Mullerism). Pasteur (1982) followed the older tradition

of classifying mimicry systems based on the functional/ecological relationships between the players and came up with seven overlapping categories: aggressive, aggressive/reproductive, reproductive, reproductive/mutualistic, mutualistic, commensalist, and protective. Other authors have condensed this into three functional categories: aggressive (or foraging), reproductive, and protective (Zabka and Tembrock 1986, Starrett 1993). Competitive mimicry does not overlap with any of these functional categories (except where mates are considered resources, which may result in overlap with reproductive mimicry) and thus would be a logical addition to such classification schemes. (Note that we refer here to overlap in category definitions; a given case of mimicry may provide multiple advantages and therefore fall under multiple categories.)

CRITERIA FOR COMPETITIVE MIMICRY

For a phenotypic resemblance to qualify as competitive mimicry, two primary criteria must be satisfied. First, the mimic must gain greater access to a defended resource than closely related non-mimics that also compete for the resource. Reduced aggression by a receiver toward the mimic relative to non-mimics can provide indirect evidence that this criterion is met (Eagle

TABLE 1. Forms of competitive mimicry, with classical forms of protective mimicry included for comparison.

Type†	Category	Receiver's relationship to mimic	Mimic's relationship to receiver	Model's relationship to receiver
	Batesian mimicry	predator	undefended	defended
	Mullerian mimicry	predator	defended	defended
A	Deceptive mimicry of non-competitor (unidirectional)	competitor	competitor	non-competitor
B	Deceptive mimicry of non-competitor (reciprocal)‡	competitor	competitor	non-competitor
C	Honest mimicry of non-competitor	non-competitor	non-competitor	non-competitor
D	Mimicry of dominant competitor	dominant competitor	subordinate competitor	dominant competitor/ identical
E	Mimicry of equal competitor	equal competitor	equal competitor	equal competitor/ identical
F	Mimicry of competitor's predator	competitor	competitor	predator

Notes: The evolutionary dynamics described (frequency of mimic relative to model, evolution of model, and accuracy of mimic) are general predictions based on the effects of mimicry on the model and receiver. Positive and negative effects are indicated by − and +, respectively.

† Letter designations referenced in the text. Batesian and Mullerian mimicry are shown for comparison only and have not been assigned letters.

‡ Mimic and model switch roles depending on the identity of the receiver.

§ Co-mimics should maintain proportional population sizes.

¶ Model phenotype does not evolve in response when the mimicked trait is not genetic.

Model phenotype does not evolve in response when the model does not return the mimic's warning.

and Jones 2004). Second, as in all mimicry systems, the mimic and model must share at least one receiver (Bates 1862, Muller 1879). This usually means that the mimic and model occur in sympatry for at least part of the year and overlap in habitat use, but this may not be necessary if, for example, the receiver is migratory (reviewed in Ruxton et al. 2005). Other criteria apply to specific forms of competitive mimicry. If the mimicry is deceptive, the mimic usually must be less abundant than the model (Bates 1862, Ruxton et al. 2005: Section 10.3.4 and references therein). With vision-based mimicry, the mimic must be similar to the model in size and behavior (Randall and Randall 1960, Moyer 1977, Baylis 1982, Snyder 1999, Eagle and Jones 2004). In most forms of competitive mimicry, the mimic should gain greater access to defended resources when it is closely associated with the model than when alone (Eagle and Jones 2004).

Some of the examples presented below may represent retention of an ancestral phenotype rather than evolutionary convergence and thus may be more accurately described as cases of adaptive resemblance (Starrett 1993) than mimicry. Nevertheless, resemblance to a model can provide the same benefit to "mimics" as it does in comparable cases that fit strict mimicry definitions, and the predictions we make concerning the evolutionary dynamics of competitive mimicry also apply to the maintenance of such resemblances.

FORMS OF COMPETITIVE MIMICRY

We divide competitive mimicry into three subcategories for ease of presentation and discussion: mimicry of a non-competitor, mimicry of a competitor, and mimicry of a competitor's predator. Each form of mimicry is examined in terms of the effect of the mimic on the

model and receiver. We then offer predictions regarding the evolutionary dynamics of the mimicry system, including (1) the form of frequency-dependence in the mimic population; (2) the direction of evolution of the model in response to the mimic; and (3) the strength of selection on the mimic to accurately match the model. These "verbal" predictions need to be tested with formal modeling (see *Conclusions and future directions*).

Mimicry of a non-competitor (interspecific)

When a competitor mimics a non-competitor to gain access to a defended resource, the system is directly analogous to Batesian mimicry: resource defenders (receivers) are analogous to predators in that they must choose whether or not to attack intruders; competitor intruders (mimics) are analogous to palatable prey in that they are profitable to attack; and non-competitor intruders (models) are analogous to unpalatable prey (Table 1, type A). As in Batesian mimicry, this form of mimicry is negatively frequency dependent. As the frequency of mimics relative to models increases, resource defenders are expected to switch from tolerating intruders of both types to attacking both types (because of trial-and-error learning or selection on response thresholds). Models would benefit if resource defenders could distinguish between model and mimic, and thus the model phenotype is predicted to be under selection to diverge from that of the mimic. However, selection on the mimic to accurately resemble the model is expected to be strong because the mimic needs to deceive the resource defender to gain access to the defended resource.

In Papua New Guinea, juveniles of the surgeonfish *Acanthurus pyroferus* closely resemble the angelfish

TABLE 1. Extended.

Effect on receiver	Effect on model	Direction of model evolution	Mimic frequency dependence	Selection on mimic accuracy
−	−	divergent	negative	strong
+	+	convergent	positive	weak
−	−	divergent/static	negative	strong
−	+	convergent	weakly negative§	moderate
+	+	convergent	positive	weak
−	−	divergent/static¶	negative	strong
+	+	convergent/static#	positive	weak
−	+	convergent	negative	strong/moderate

Centropyge vrolikii in both behavior and coloration (see photographs in the Appendix). This apparently enables *A. pyroferus* juveniles to forage freely in the territories of a damselfish (*Plectroglyphidodon lacrymatus*) that tolerates angelfishes but vigorously repels non-mimetic surgeonfishes (Eagle and Jones 2004). The diet of *C. vrolikii* overlaps with that of *P. lacrymatus* less than does the diet of *A. pyroferus*, which suggests that this system involves mimicry of a non-competitor (*C. vrolikii*) by a competitor (*A. pyroferus*) (Eagle and Jones 2004, but see Randall 2005). This form of competitive mimicry may be widespread among juvenile Indo-Pacific surgeonfishes. *A. pyroferus* juveniles resemble one of three different *Centropyge* species depending on which model is present at a given location (see photographs in the Appendix; Randall and Randall 1960, Myers 1989, Kuiter 1996), and juvenile coloration resembling *Centropyge* species is exhibited by six other species in the *Acanthurus, Ctenochaetus,* and *Zebrasoma* surgeonfish genera (Kuiter and Debelius 1994, Guiasu and Winterbottom 1998, Moland et al. 2005; FishBase [*available online*]).[2]

When two or more non-competitors of a resource defender resemble each other to reduce the probability that a resource defender will (unprofitably) attack them, the relationship is analogous to Mullerian mimicry (Table 1, type C). Co-mimics benefit from sharing the cost of educating the resource defender about their unprofitability, and the resource defender benefits from receiving a dependable signal that prevents waste of time and energy attacking non-competitors. These positive effects of mimicry on all players in the interaction suggest that the predicted evolutionary dynamics of Mullerian mimicry should apply. Co-mimics are expected to experience positive frequency dependence because frequent encounters with co-mimics should remind the resource defender of the lack of profit in attack. All co-mimics are expected to converge on the same phenotype

because of the mutual benefit of being recognized as a member of a group that is unprofitable to attack. However, selection for highly accurate resemblance is predicted to be relatively weak; the resource defender need not be deceived, therefore mimics must only resemble each other strongly enough to remind the receiver of their common unprofitability. Further selection for convergence is expected to be weak or absent.

A possible example is provided by angelfish in the genus *Pomacanthus*. All Indo-Pacific *Pomacanthus* species display a common juvenile pattern that differs strikingly from all species' adult patterns. Fricke (1980) found that juvenile coloration provides protection from territorial conspecifics in *Pomacanthus imperator*. First- and second-stage juvenile *P. imperator* were always ignored by adults, while third and fourth (subadult) stages, which look increasingly like adults, were attacked with increasing intensity (Fricke 1980). One explanation for this behavior is that *Pomacanthus* juveniles do not pose much of a competitive threat to adult conspecifics. If *Pomacanthus* juveniles experience high mortality and are unlikely to survive to establish a territory, as is the case in many coral reef fishes (Shulman 1985), then attacks on juveniles may be wasteful until their mortality risk decreases. Thus, shared juvenile coloration in *Pomacanthus* may be an honest signal of non-competitor status that reduces the probability of being attacked by conspecific and congeneric adult territory holders.

Alternatively, it might be profitable for adult *Pomacanthus* to repel conspecific but not heterospecific juvenile intruders (if little or no interspecific interference competition occurs). If so, the shared juvenile coloration of *Pomacanthus* spp. may be adaptive because it conceals a juvenile's species identity. We refer to this as reciprocal mimicry of a non-competitor (Table 1, type B), because mimic and model switch roles depending on the species identity of the receiver. That is, juveniles play the role of model in interactions with heterospecific adults and the role of mimic in interactions with conspecific adults. This form of mimicry may only be effective where multiple (more than two) co-mimetic species occur in sympatry at similar densities. Otherwise, resource defenders of the numerically dominant species would be likely to encounter mimics (conspecific juveniles) more frequently than models (heterospecific juveniles), and consequently would be selected to treat all juveniles in the mimicry complex as potential resource competitors. So long as the probability of any given resource defender encountering a conspecific mimic is less than that of encountering a heterospecific model, the benefits of being a mimic are expected to outweigh the costs of being a model, and convergence of subordinates on a common phenotype is predicted. Selection on the quality of imitation may be relaxed; if co-mimics are not identical, then the phenotype of a subordinate playing the role of mimic may be easily confused with those of its models if it falls anywhere within the range of model phenotypes.

[2] ⟨www.fishbase.org⟩

Mimicry of a non-competitor (intraspecific)

Mimicry of conspecific juveniles, females, or males may help subordinates contend with dominant same-sex competitors for defended mates and/or territory space (Table 1, type A). This well-known form of mimicry is detrimental to dominant resource defenders. Mimicry would be detrimental to the model if frequent encounters with mimics led dominant individuals to attack models, but this seems unlikely to occur in sexual mimicry (i.e., mimicry of the opposite sex) because of the high cost of attacking a potential mate. For this reason, the frequency of sexual mimics may not be strongly limited, while juvenile mimics probably must be rare. In sexual mimicry, the model phenotype is expected to evolve away from that of the mimic while retaining characteristics that are important in attracting mates, although selection to diverge from the mimic is predicted to be weak because of the high cost of attacking models. In juvenile mimicry, continuous evolution of the mimic and model is not expected to occur because the juvenile phenotype is simply retained into adulthood. Strong selection on mimic accuracy is predicted.

Female mimicry is exhibited by subordinate males in a diverse range of taxa (insects [Thornhill 1979, Steiner et al. 2005], fishes [Dominey 1980, Norman et al. 1999], amphibians [Arnold 1976, Sparreboom 1996], reptiles [Shine et al. 2000], birds [Rohwer 1978, Hakkarainen et al. 1993], and mammals [Leboeuf 1974]) and may function to distract dominant males from true females, to fool dominant males into allowing close approach to females, to gain access to territories, to reduce aggression from dominant males, or to control the timing of aggressive interactions with dominant males. Mimicry of males by females seems to be rare but may occur in some species in which females compete for access to mates or other resources.

In the Capuchinbird (*Perissocephalus tricolor*), sexual mimicry appears to be bidirectional; both sexes of this sexually monochromatic lekking species exhibit intra-sexual competition and have been observed to mimic the behavior of the opposite sex at the lek (Trail 1990). Subordinate males may benefit from mimicking female behavior because it enables them to get closer to alpha males and sneak copulations with approaching females. Females may benefit from mimicking male behavior because it enables them to avoid being harassed by subordinate males while en route to the alpha male's perch and also because it helps them supplant other females from the alpha perch (Trail 1990).

Sexual mimicry can operate interspecifically as well as intraspecifically. Female Pied and Collared Flycatchers are nearly indistinguishable, and the dull male Pied Flycatchers that occur where the species are in sympatry effectively mimic both species' females; dull males are able to gain access to territories and escape aggression from dominant males of both species (Saetre et al. 1993, Saetre and Slagsvold 1996). The predominance of female-like male Pied Flycatchers in areas of sympatry has also been interpreted as a product of reinforcement (Saetre et al. 1997), but these ideas are not mutually exclusive.

We are not aware of any verified examples of intra-specific juvenile mimicry; nearly all potential juvenile mimics have proven to be young males honestly signaling their subordinate status (e.g., McDonald 1993, Cucco and Malacarne 1999, VanderWerf and Freed 2003).

Mimicry of a competitor

Mimicry of a competitor may be advantageous when aggressive displays (e.g., territorial songs) typically precede physical fights. The interactions between the players and the resulting dynamics vary depending on the receiver's chances of winning a physical confrontation. If the receiver is a dominant competitor that is likely to win a physical fight (Table 1, type D), then mimicry is deceptive and detrimental to the receiver because excess time and energy may be wasted defending resources from an inferior competitor, and in some cases, defensible resources may be relinquished to the mimic. This form of mimicry is also detrimental to models because frequent encounters with mimics may lead receivers to physically confront models rather than exhibit a return display, resulting in a costly fight. Thus, mimics are expected to experience negative frequency dependence. The model phenotype is predicted to diverge from that of the mimic in a way that is costly for the mimic to simulate, and the mimic is expected to experience strong selection for accurate resemblance to the model.

A problem with confirming examples of deceptive mimicry of a competitor is showing that the receiver is truly deceived. The hypothesis that some songbirds mimic song components of heterospecific competitors to aid in territory acquisition and defense amidst these competitors has been tested and supported several times. Most playback experiments, however, have used artifi-cially repeated segments of mimicked song (e.g., Lemaire 1975 [in Catchpole and Baptista 1988], Breno-witz 1982), while in nature these mimics typically embed heterospecific song components within their own song or the songs of other species, making deception unlikely. Catchpole and Baptista (1988) overcame this issue by testing the hypothesis on Song Sparrows, which naturally mimic the songs of White-crowned Sparrows in repetitive bouts. Territorial White-crowned males responded strongly to both mimic and model White-crowned songs, but most showed no response to control Song Sparrow songs, suggesting that they were in fact deceived by the mimicry. Payne (1983) reported that young Indigo Buntings successfully intimidate other young males by imitating the songs of older males.

If the mimic and receiver are equal competitors, then mimicry serves as an honest warning of a costly fight (Table 1, type E). This form of mimicry is beneficial to all players. Mimics are expected to experience positive

frequency dependence, and the mimicry probably need only be accurate enough to be recognized as a warning by the receiver. If the warning is bidirectional (e.g., two species mimic each other's warning signals), the situation is analogous to Mullerian mimicry and convergence of mimic and model phenotypes should occur. Cody (1969) used the term "character convergence" to describe numerous possible examples of interspecific resemblance in song components and plumage among interspecifically territorial birds (Cody 1969, 1973, Cody and Brown 1970, Cody and Walter 1976; see also Grant 1966, Hagen et al. 1972, Emlen et al. 1975). These examples, however, have since been contradicted by experimental evidence, criticized for a lack of experimental evidence, or found to be complicated by other factors (Grant 1972, Murray 1976, Brown 1977, Martin and Thibault 1996, Baker and Boylan 1999, Scott and Foster 2000). Song sharing between territory neighbors (Wilson and Vehrencamp 2001) may be the only currently accepted example of mimicry among equal competitors. This is an example of intraspecific competitor mimicry, but interspecific cases are also plausible. Note that in many of the examples discussed here, mimetic resemblances are acquired through song learning, and thus coevolution of mimic and model phenotypes need not occur.

When mimicry of an equal competitor is unidirectional, the situation is analogous to aposematism (which advertises a prey species' defenses to predators). In this case, the model phenotype is not expected to change in response to convergence of the mimic phenotype. This form of mimicry is illustrated by Northern Mockingbirds, which mimic the territorial songs of a wide array of potential competitor species. In one study, Northern Mockingbirds were observed to counter-sing against and attack 14 other species of birds (Baylis 1982). Intruder species are not likely to be deceived by mimetic mockingbird song because their own territorial songs are embedded amongst those of other species. Thus, mockingbirds appear to broadcast an honest warning of a costly fight.

Mimicry of a competitor's predator

Mimicry of a competitor's predator may allow a subordinate individual to gain access to resources defended by a dominant competitor (Table 1, type F). This form of mimicry is deceptive and detrimental to the receiver because it causes the receiver to leave resources undefended while fleeing the perceived danger. The predator may benefit from being mimicked because receivers are faced with distinguishing between true predators and mimics; tests of an intruder's identity may make the receiver easier for the predator to catch. In this situation, convergent evolution between predators and their mimics would be favored. The mimic probably must be infrequent compared to its model unless receivers that test the mimic's identity are very likely to be killed by the predator; this high risk may lead to

avoidance of any potential predator regardless of the proportion of "predators" that are mimics. When the mimic is exposed to sustained scrutiny from the receiver, mimetic quality must be high because selection on the receiver to distinguish predators from competitors is strong. Selection on imitation quality may be relaxed for predator mimics that simply startle the receiver from its territory.

Acoustic mimicry of rattlesnake rattles by Burrowing Owl hisses (Garman 1882, Rowe et al. 1986) provides a possible example of predator mimicry. Both rattlesnakes (Crotalus viridis) and Burrowing Owls (Athene cunicularia) frequently use the burrows of rodents for thermoregulation and shelter. While rattlesnakes are predators of these rodents, Burrowing Owls compete with the rodents for shelter. Rowe et al. (1986) tested the effectiveness of the mimicry by presenting California ground squirrels (Spermophilus beecheyi) from two different populations with playbacks of rattlesnake rattles, Burrowing Owl hisses, Burrowing Owl scream chatters, and white noise. Ground squirrels from a population where rattlesnakes are rare responded weakly to the playbacks and failed to discriminate among the sounds, while those from a population where rattlesnakes are abundant responded strongly to rattlesnake rattles and Burrowing Owl hisses but not to the other two sounds. These results support the competitive predator mimicry hypothesis. If the owls scare off predators by mimicking rattlesnakes, however, then this would also qualify as classic Batesian mimicry (Owings et al. 2002). Note that rattlesnakes probably do not benefit from being mimicked by owls because they prey on juvenile squirrels, not adults (Owings and Coss 1977). Thus, in this case, we would not expect the predator phenotype to converge on that of the mimic. A second example may be that of Skuas resembling the outline of falcons in flight (Wickler 1968). Mimetic resemblance to falcons may aid in stealing prey from gulls and terns, which generally drop their prey and flee when a falcon approaches for an attack. In other systems, it may be possible to frighten a competitor away from defended resources by mimicking scents produced by the competitor's predator.

Flash coloration resembling eyes or other features of a top predator that is used to startle predators may frighten away competitors, as well. Examples of such flash coloration include hind wing eyespots in butterflies (Vallin et al. 2005) and moths (Sargent 1973) and the dorsal fin eyespots of the crab-eye goby (Signigobius biocellatus) (Hudson 1977). Most studies (reviewed in Ruxton et al. 2005: Chapter 13) suggest that eyespots are not actually cases of mimicry of eyes, but instead simply trigger a hardwired startle response to the sudden appearance of conspicuous markings. We include these examples here, however, because these markings may have the same utility as true cases of mimicry of a competitor's predator and therefore help to illustrate this mimicry category. We also wish to encourage

investigation of whether eyespots may function in competition for defended resources.

CONCLUSIONS AND FUTURE DIRECTIONS

Our definition of competitive mimicry encompasses a wide variety of intriguing mimetic relationships. This entire group of mimicry systems has not only been excluded from classification schemes for decades but has also been neglected in terms of the research devoted to understanding it. In the examples presented here, we have identified or at least hypothesized the advantage that the mimic gains from resemblance to its model. There are likely to be many competitive mimicry systems, however, for which a hypothesis based on competition has never been considered. These may be cases of mimetic resemblances that have never been formally examined (e.g., Randall and Randall 1960, Russell et al. 1976, Bunkley-Williams and Williams 2000, Gorissen and Eens 2005) or known mimicry relationships in other functional categories that also provide an advantage in competition for resources (e.g., acoustic mimicry of rattlesnakes).

Studies of protective mimicry have extended far beyond explaining why mimicry is advantageous in a given system to address the evolutionary dynamics among the players in mimicry systems, the accuracy of our assumptions about the receiver's perception, the implications of mimics with intermediate defense levels, the processes through which mimicry can evolve in the first place, and many other details of the mimic–model–receiver interaction. These issues must now be addressed in competitive mimicry systems. Much of our understanding of protective mimicry dynamics has been obtained through mathematical models and simulations (reviewed in Ruxton et al. 2005). These techniques are expected to be equally useful when applied to competitive mimicry.

In our review of the various forms of competitive mimicry, we have generally predicted that when the effects of the mimic on the model and receiver are the same as in Batesian or Mullerian mimicry, the evolutionary dynamics of the system will also be the same. These predictions, however, rely on many untested assumptions. One aspect of competitive mimicry relationships that may differ greatly from protective mimicry is the perception and learning process of the receiver. Unpalatable (or otherwise protected) models in Batesian and Mullerian mimicry systems provide immediate, unpleasant, educating feedback to potential predators, but this sort of feedback may be absent from most competitive mimicry systems. For example, if a resource defender attacks a non-competitor model by mistake, the result is some wasted energy and perhaps a neglected territory border elsewhere rather than a bad taste, pain, or illness. More importantly, this result does not differ from the result of attacking a competitor mimic in the perception of the attacker. The response functions of resource defenders to mimetic intruders may therefore be shaped by natural selection across generations as opposed to being shaped by associative learning.

An additional difference between protective and competitive mimicry systems is that selection on deceptive competitive mimics is likely to be weaker than on deceptive protective mimics because they risk only reduced access to resources rather than death in encounters with receivers. This means that deceptive competitive mimics are likely to converge on the model phenotype more slowly than their protective mimic counterparts, and other selection pressures (such as sexual selection) may constrain convergence to a greater extent. The stability of these systems therefore cannot be assumed to be comparable to protective mimicry systems and should be formally investigated. Competitive mimicry relationships that are beneficial to all players are expected to be as stable as Mullerian protective mimicry.

Several forms of competitive mimicry are expected to differ greatly from protective mimicry systems in their dynamics due to the unique combination of negative effects on the receiver and positive effects on the model (Table 1, types B, F). Our predictions about the evolutionary dynamics of these systems will require formal testing. For example, we predict that when a competitor's predator is mimicked, the predator's phenotype may actually converge on that of the mimic. This "ganging up" of the mimic and model would probably make life extremely difficult for the receiver, given the potentially prohibitive cost of testing the identity of the predator. Such mimicry systems may exhibit instability when the mimic and model become indistinguishable. Interestingly, we know of no actual or theoretically plausible competitive mimetic relationships in which mimicry benefits the receiver but not the model. Perhaps relationships of this form have simply not yet been recognized, or perhaps their absence from the literature suggests the existence of constraints on the evolution of this interaction.

Our main goal in presenting this synthesis is to stimulate empirical and theoretical research on this long-overlooked class of mimetic relationships. Closing this large gap in our knowledge of mimicry will broaden our capacity to identify equivalent forms of mimicry across ecological contexts and improve our understanding of the underlying evolutionary processes.

LITERATURE CITED

Arnold, S. J. 1976. Sexual behavior, sexual interference and sexual defense in salamanders *Ambystoma maculatum*, *Ambystoma tigrinum* and *Plethodon jordani*. Zeitschrift für Tierpsychologie 42:247–300.

Baker, M. C., and J. T. Boylan. 1999. Singing behavior, mating associations and reproductive success in a population of hybridizing lazuli and indigo buntings. Condor 101:493–504.

Bates, H. W. 1862. Contributions to an insect fauna of the Amazon Valley. Lepidoptera: Heliconidae. Transactions of the Linnean Society of London 23:495–566.

Baylis, J. R. 1982. Avian vocal mimicry: its function and evolution. Pages 51–83 in D. E. Kroodsma and E. H. Miller, editors. Acoustic communication in birds. Academic Press, New York, New York, USA.

Brenowitz, E. A. 1982. Aggressive responses of Red-winged Blackbirds to Mockingbird song imitation. Auk 99:584–586.

Brown, R. N. 1977. Character convergence in bird song. Canadian Journal of Zoology 55:1523–1529.

Bunkley-Williams, L., and E. H. Williams. 2000. Juvenile black snapper, *Apsilus dentatus* (Lutjanidae), mimic blue chromis, *Chromis cyanea* (Pomacentridae). Copeia 2000:579–581.

Catchpole, C. K., and L. F. Baptista. 1988. A test of the competition hypothesis of vocal mimicry, using song sparrow imitation of white-crowned sparrow song. Behaviour 106:119–128.

Cody, M. L. 1969. Convergent characteristics in sympatric species: a possible relation to interspecific competition and aggression. Condor 71:223–239.

Cody, M. L. 1973. Character convergence. Annual Review of Ecology and Systematics 4:189–211.

Cody, M. L., and J. H. Brown. 1970. Character convergence in Mexican finches. Evolution 24:304–310.

Cody, M. L., and H. Walter. 1976. Habitat selection and interspecific interactions among Mediterranean Sylviid Warblers. Oikos 27:210–238.

Cucco, M., and G. Malacarne. 1999. Is the song of black redstart males an honest signal of status? Condor 101:689–694.

Dominey, W. J. 1980. Female mimicry in male bluegill sunfish: a genetic-polymorphism. Nature 284:546–548.

Eagle, J. V., and G. P. Jones. 2004. Mimicry in coral reef fishes: ecological and behavioural responses of a mimic to its model. Journal of Zoology 264:33–43.

Emlen, S. T., J. D. Rising, and W. L. Thompson. 1975. Behavioral and morphological study of sympatry in Indigo and Lazuli Buntings of Great Plains. Wilson Bulletin 87:145–179.

Endler, J. A. 1981. An overview of the relationships between mimicry and crypsis. Biological Journal of the Linnean Society 16:25–31.

Fricke, H. W. 1980. Juvenile–adult colour patterns and coexistence in the territorial coral reef fish *Pomacanthus imperator*. Marine Ecology (Naples) 1:133–141.

Garman, S. 1882. The scream of the young Burrowing Owl sounds like the warning of the rattlesnake. Nature 27:174.

Gorissen, L., and M. Eens. 2005. Complex female vocal behaviour of Great and Blue Tits inside the nesting cavity. Behaviour 142:489–506.

Grant, P. R. 1966. Coexistence of two wren species of genus *Thryothorus*. Wilson Bulletin 78:266.

Grant, P. R. 1972. Convergent and divergent character displacement. Biological Journal of the Linnean Society 4:39–68.

Guiasu, R. C., and R. Winterbottom. 1998. Yellow juvenile color pattern, diet switching and the phylogeny of the surgeonfish genus *Zebrasoma* (Percomorpha, Acanthuridae). Bulletin of Marine Science 63:277–294.

Hagen, D. W., G. E. E. Moodie, and P. F. Moodie. 1972. Territoriality and courtship in Olympic mudminnow (*Novumbra hubbsi*). Canadian Journal of Zoology 50:1111–1115.

Hakkarainen, H., E. Korpimaki, E. Huhta, and P. Palokangas. 1993. Delayed maturation in plumage color: evidence for the female-mimicry hypothesis in the kestrel. Behavioral Ecology and Sociobiology 33:247–251.

Hudson, R. C. L. 1977. Preliminary observations on behavior of Gobiid fish *Signigobius biocellatus* Hoese and Allen, with particular reference to its burrowing behavior. Zeitschrift für Tierpsychologie 43:214–220.

Kuiter, R. H. 1996. Guide to sea fishes of Australia. New Holland, Sydney, Australia.

Kuiter, R. H., and H. Debelius. 1994. Southeast Asia: tropical fish guide. IKAN-Unterwasserarchiv, Frankfurt, Germany.

Leboeuf, B. J. 1974. Male–male competition and reproductive success in elephant seals. American Zoologist 14:163–176.

Lemaire, F. 1975. Le chant de la rousserolle verderole (*Acrocephalus palustris*): fidélité des imitations et relations avec les espèces imitées et avec les congénères. Gerfaut 65:3–28.

Martin, J. L., and J. C. Thibault. 1996. Coexistence in Mediterranean Warblers: ecological differences or interspecific territoriality? Journal of Biogeography 23:169–178.

McDonald, D. B. 1993. Delayed plumage maturation and orderly queues for status: a manakin mannequin experiment. Ethology 94:31–45.

Moland, E., J. V. Eagle, and G. P. Jones. 2005. Ecology and evolution of mimicry in coral reef fishes. Oceanography and Marine Biology: An Annual Review 43:455–482.

Moyer, J. T. 1977. Aggressive mimicry between juveniles of snapper *Lutjanus bohar* and species of damselfish genus *Chromis* from Japan. Japanese Journal of Ichthyology 24:218–222.

Muller, F. 1879. *Ituna* and *Thyridia*; a remarkable case of mimicry in butterflies. [Translated by R. Meldona.] Proceedings of the Entomological Society of London 1879:xx–xxix.

Murray, B. G. 1976. Critique of interspecific territoriality and character convergence. Condor 78:518–525.

Myers, R. F. 1989. Micronesian reef fishes: a practical guide for the identification of the coral reef fishes of the tropical central and western Pacific. Coral Graphics, Guam.

Norman, M. D., J. Finn, and T. Tregenza. 1999. Female impersonation as an alternative reproductive strategy in giant cuttlefish. Proceedings of the Royal Society of London B 266:1347–1349.

Owings, D. H., and R. G. Coss. 1977. Snake mobbing by California ground squirrels: adaptive variation and ontogeny. Behaviour 62:50–69.

Owings, D. H., M. P. Rowe, and A. S. Rundus. 2002. The rattling sound of rattlesnakes (*Crotalus viridis*) as a communicative resource for ground squirrels (*Spermophilus beecheyi*) and burrowing owls (*Athene cunicularia*). Journal of Comparative Psychology 116:197–205.

Pasteur, G. 1982. A classificatory review of mimicry systems. Annual Review of Ecology and Systematics 13:169–199.

Payne, R. B. 1982. Ecological consequences of song matching: breeding success and intraspecific song mimicry in Indigo Buntings. Ecology 63:401–411.

Payne, R. B. 1983. The social context of song mimicry song matching dialects in Indigo Buntings *Passerina cyanea*. Animal Behaviour 31:788–805.

Randall, J. E. 2005. A review of mimicry in marine fishes. Zoological Studies 44:299–328.

Randall, J. E., and H. A. Randall. 1960. Examples of mimicry and protective resemblance in tropical marine fishes. Bulletin of Marine Science of the Gulf and Caribbean 10:445–480.

Rohwer, S. 1978. Passerine sub-adult plumages and deceptive acquisition of resources: test of a critical assumption. Condor 80:173–179.

Rowe, M. P., R. G. Coss, and D. H. Owings. 1986. Rattlesnake rattles and Burrowing Owl hisses: a case of acoustic Batesian mimicry. Ethology 72:53–71.

Russell, B. C., G. R. Allen, and H. R. Lubbock. 1976. New cases of mimicry in marine fishes. Journal of Zoology 180:407–423.

Ruxton, G. D., T. N. Sherratt, and M. P. Speed. 2005. Avoiding attack: the evolutionary ecology of crypsis, warning signals and mimicry. Oxford University Press, New York, New York, USA.

CONCEPTS & SYNTHESIS

Saetre, G. P., M. Kral, and V. Bicik. 1993. Experimental evidence for interspecific female mimicry in sympatric *Ficedula* Flycatchers. Evolution 47:939–945.

Saetre, G. P., T. Moum, S. Bures, M. Kral, M. Adamjan, and J. Moreno. 1997. A sexually selected character displacement in Flycatchers reinforces premating isolation. Nature 387:589–592.

Saetre, G. P., and T. Slagsvold. 1996. The significance of female mimicry in male contests. American Naturalist 147:981–995.

Sargent. 1973. Studies on the *Catocala* (Noctuidae) of Southern New England. IV. A preliminary analysis of beak-damaged specimens with discussion of anomaly as a potential anti-predator function of hindwing diversity. Journal of the Lepidopterists Society 27:175–192.

Scott, R. J., and S. A. Foster. 2000. Field data do not support a textbook example of convergent character displacement. Proceedings of the Royal Society B 267:607–612.

Shine, R., P. Harlow, M. P. Lemaster, I. T. Moore, and R. T. Mason. 2000. The transvestite serpent: why do male garter snakes court (some) other males? Animal Behaviour 59:349–359.

Shulman, M. J. 1985. Recruitment of coral-reef fishes: effects of distribution of predators and shelter. Ecology 66:1056–1066.

Snyder, D. B. 1999. Mimicry of initial phase blue-head wrasse, *Thalassoma bifasciatum* (Labridae) by a juvenile tiger grouper, *Mycteroperca tigris* (Serranidae). Cybium 25:227–232.

Sparreboom, M. 1996. Sexual interference in the sword-tailed newt, *Cynops ensicauda popei* (Amphibia: Salamandridae). Ethology 102:672–685.

Starrett, A. 1993. Adaptive resemblance: a unifying concept for mimicry and crypsis. Biological Journal of the Linnean Society 48:299–317.

Steiner, S., J. L. M. Steidle, and J. Ruther. 2005. Female sex pheromone in immature insect males: a case of pre-emergence chemical mimicry? Behavioral Ecology and Sociobiology 58:111–120.

Thornhill, R. 1979. Adaptive female-mimicking behavior in a scorpionfly. Science 205:412–414.

Trail, P. W. 1990. Why should lek-breeders be monomorphic. Evolution 44:1837–1852.

Vallin, A., S. Jakobsson, J. Lind, and C. Wiklund. 2005. Prey survival by predator intimidation: an experimental study of peacock butterfly defence against Blue Tits. Proceedings of the Royal Society of London B 272:1203–1207.

VanderWerf, E. A., and L. A. Freed. 2003. Elepaio subadult plumages reduce aggression through graded status-signaling, not mimicry. Journal of Field Ornithology 74:406–415.

Vane-Wright, R. I. 1976. A unified classification of mimetic resemblances. Biological Journal of the Linnean Society 8:25–56.

Wickler, W. 1968. Mimicry in plants and animals. McGraw-Hill Book Company, New York, New York, USA.

Willis, E. O. 1976. Similarity of a Tyrant Flycatcher and a Silky Flycatcher: not all character convergence is competitive mimicry. Condor 78:553–553.

Wilson, P. L., and S. L. Vehrencamp. 2001. A test of the deceptive mimicry hypothesis in song-sharing Song Sparrows. Animal Behaviour 62:1197–1205.

Zabka, H., and G. Tembrock. 1986. Mimicry and crypsis: a behavioral approach to classification. Behavioural Processes 13:159–176.

APPENDIX

Photos showing mimicry of pygmy angelfishes (*Ecological Archives* E088-146-A1).

CONCEPTS & SYNTHESIS