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Acknowledgments: We are grateful to J. Ahringer and E. Jorgensen for providing reagents. A.S. was supported by the Human Frontier Science Program and the Herchel-Smith Fund. N.J.L. was supported by a Ph.D. studentship from the Wellcome Trust (UK). E.-M.W. was supported by a Ph.D. studentship from the Herchel-Smith Fund. S.B. and M.J.S. were funded by the Canadian Institutes of Health Research (CIHR). M.J.S. is a New Investigator from CIHR. This work was supported by Cancer Research UK and the Wellcome Trust. Small RNA sequence data and Affymetrix gene expression data were submitted to the Gene Expression Omnibus under accession no. GSE37433. Detailed methods can be found in the supplementary materials.

Supplementary Materials

www.sciencemag.org/cgi/content/full/science.1220952/DC1
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23 February 2012; accepted 1 June 2012
Published online 14 June 2012;
10.1126/science.1220952

Cuckoos Combat Socially Transmitted Defenses of Reed Warbler Hosts with a Plumage Polymorphism

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In predator-prey and host-parasite interactions, an individual's ability to combat an opponent often improves with experience—for example, by learning to identify enemy signals. Although learning occurs through individual experience, individuals can also assess threats from social information. Such recognition could promote the evolution of polymorphisms if socially transmitted defenses depend on enemy morph frequency. This would allow rare variants to evade detection. Female brood parasitic common cuckoos, *Cuculus canorus*, are either gray or rufous. The gray morph is a Batesian mimic whose hawk-like appearance deters host attack. Hosts reject this disguise through social learning, increasing their own defenses when they witness neighbors mobbing a cuckoo. Our experiments reveal that social learning is specific to the cuckoo morph that neighbors mob. Therefore, while neighbors alert hosts to local cuckoo activity, frequency-dependent social information selects for a cuckoo plumage polymorphism to thwart host detection. Our results suggest that selection for mimicry and polymorphisms comes not only from personal experience but also from social learning.

The evolution of mimicry and polymorphisms depends on how receivers acquire information. In Batesian mimicry, where an undefended species mimics a defended (noxious or dangerous) model species, receivers first associate the model's defenses with a signal (aposematism) and then confuse the mimic with the model (1). If mimicry becomes less effective, then rare variants may have a frequency-dependent advantage, leading to the evolution of stable polymorphisms (2). These dynamics will depend on mixes of naïve and experienced receivers (3), but traditionally receivers have been assumed to gain information only from direct experience (1, 4). Naïve individuals can also learn from experienced individuals (5–7), however, which could lead to rapid social transmission of information about both dangerous models and mimetic disguises. Social learning is likely to be especially beneficial when personal learning is costly (5). Here, we tested whether social learning by receivers is frequency-dependent.

Cuckoos (Cuculidae) are unusually polymorphic [12% of species versus 3.5% of all birds (8)], and all polymorphic cuckoos are brood parasites (9). In the common cuckoo, all adult males are gray but females are either gray and ventrally barred, like males, or bright rufous with additional dorsal barring (10) (Fig. 1). The genetics underlying this polymorphism are unknown, but because females are the heterogametic sex, it is likely a sex-linked trait (10, 11). The gray morph mimics the sparrowhawk, *Accipiter nisus* (12, 13), a dangerous predator of small birds. This protective mimicry is “Batesian” in the sense that the adult cuckoo is otherwise defenseless, but the cuckoo is not harmless like typical Batesian mimics because although its mimicry deters host attacks (12), it facilitates parasitism of host nests (14). Hosts do not become less wary of gray cuckoos with increased direct experience [repeated encounters at their own nests (6, 7)]. However, if hosts observe neighbors mobbing a gray cuckoo, they take increased risks by closely approaching and mobbing gray cuckoos back at their own nest (6, 7), which reduces parasitism by a factor of 4 (14). Thus, the gray cuckoo's mimetic defenses become less effective when hosts are alerted to local cuckoo activity by social information. Although hosts

also recognize the rufous cuckoo morph as a threat (15), it is not known whether it is also a Batesian mimic [perhaps of a different model, e.g., kestrel, *Falco tinnunculus* (10)] or an imperfect “jack of all trades” mimic of more than one predator (1).

Why are polymorphisms common among parasitic cuckoos? Rufous and gray morphs of the common cuckoo co-occur across Europe, but their relative frequency varies. For example, at a site in Hungary 60% of females were rufous, whereas at a site in the Czech Republic only 10% were rufous. At both sites, there was no difference in host defenses toward females of the two morphs, and the proportion of host nests parasitized by the two morphs reflected their relative frequencies, which suggests that they gained equal success (15). During the past 20 years at our field site in Wicken Fen, Cambridgeshire, UK, there have been 2 to 14 gray females each year (14), but only one rufous female in two of the years. Habitat characteristics and/or Batesian model frequencies might mediate spatial variation in equilibrium frequencies, so detecting any frequency-dependent advantage to the cuckoo morphs will be difficult unless conditions change (1) or relative frequencies can be manipulated (16).

We took advantage of social learning in reed warbler (*Acrocephalus scirpaceus*) hosts to test the hypothesis that the female cuckoo's polymorphism thwarts recognition by receivers. We predicted that an increase in the apparent local frequency of one morph would alert host defenses specifically to that morph via social learning. This would reduce its success (14) and give a relative advantage to the alternate morph. Furthermore, when the local risk from sparrowhawks is increased, we predicted that gray cuckoos would be mobbed less because of the increased danger of a fatal mistake.

To test our hypothesis, we used balsam wood models of cuckoo morphs [gray (Cg) and rufous (Cr)] and a sparrowhawk (SH), similar to those used in previous experiments (6, 14, 17), to manipulate the public information received by 78 nesting reed warbler pairs. First, we placed each model in turn next to focal pairs' nests and recorded their baseline mobbing responses (mandible snaps and rasp calls) for 5 min. Models of the two cuckoo morphs were treated similarly [Cg, 39/78 pairs mobbed; Cr, 30/78 pairs mobbed; $\chi^2_{(1)} = 2.10$, $P = 0.15$; mean mobbing responses

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(±SE) per 5 min: Cg = 170.5 ± 41.4, Cr = 139.4 ± 30.0; P_{MCMC} (Markov chain Monte Carlo) = 0.84] and were mobbed more intensely than the sparrowhawk [SH = 88.4 ± 24.3; linear mixed model (LMM), model type: $\chi^2_{(2)} = 13.78, P = 0.001$] or a harmless control (figs. S1 and S2).

After recording these baseline responses, we presented one of the three models to the adjacent neighbor of our focal pairs. The model was placed next to the neighbor's nest for 10 min, with reed warbler mobbing calls broadcast close to the model to ensure that focal birds were attracted (6). In this way, we influenced public information about gray cuckoos, rufous cuckoos, or sparrowhawks, thus manipulating their relative local threat ($n = 26$ focal pairs for each treatment). Playbacks increased neighbor mobbing intensity relative to our focal birds' baseline, but their relative treatment of models was the same: The two cuckoo morphs were again mobbed more than the sparrowhawk (fig. S3). Although this meant that opportunities for social learning might have been fewer with the sparrowhawk, the neighbor's response never explained any variation in our next analyses of focal behavior. Furthermore, at a subset of our nests where vegetation did not obscure our view of bird activity, focal birds were just as attracted to neighbors presented with sparrowhawks as cuckoos (<2 m from models; Cg, 10/13; Cr, 8/12; SH, 11/12; Fisher's exact test, $P = 0.38$).

We then retested our focal birds with all three models. In support of our first prediction, after witnessing their neighbors mobbing a cuckoo,

reed warblers increased their mobbing response, and by an equal amount, but only toward the cuckoo morph seen at their neighbor's nest [Fig. 1; LMM, focal model type × neighbor model: $\chi^2_{(4)} = 23.06, P = 0.0001$]. By contrast, and against our second prediction, sparrowhawk presentation to neighbors had no effect on focal pair mobbing of gray cuckoos, or indeed any of the models (Fig. 1). Nonetheless, focal pairs did become more wary of approaching any model (Fig. 2). Conversely, seeing cuckoos at neighbors' nests tended to decrease approach times (Fig. 2). Cuckoos lay their eggs in seconds to facilitate parasitism (18), so even a small change in the host's latency to approach could affect parasitism success.

Generalized responses are advantageous when stimuli are highly dangerous (1, 19) but can lead to increased recognition errors (20, 21). If social learning led simply to a change in response thresholds, then any increased response should have been at the expense of more false alarms. The specificity of the increase in reaction to the cuckoo morph that neighbors mobbed (Fig. 1) suggests that in this case, social learning involved refining cues for recognition of local threats. Shy individuals, for example, could be encouraged by the mobbing of bolder neighbors to make a closer inspection of a cuckoo, learning that it lacks some salient hawk features (hooked bill, talons). By refining recognition through social experience, focal birds would then improve their own nest defense. The consequence of morph-specific learning is that the success of each cuckoo

morph is frequency-dependent. Any increase in one morph would result in local host populations becoming alerted to that morph, mobbing it more and hence reducing its parasitism success (14). This would give a relative advantage to the alternate morph, which would be more likely to slip past host defenses.

Our results suggest another step in complexity for the defense and offense portfolios of host and cuckoo (18). Because host defenses are costly, both mobbing (as a first line of defense) and egg rejection vary in relation to local parasitism risk (14, 18). In response, selection acts on cuckoos to be secretive and a Batesian mimic to reduce host detection. In counterdefense, hosts widen their sources of information about local cuckoo activity through social learning (6, 7). Our results show that cuckoos combat this by coming in different guises.

Not all reed warblers, however, mobbed cuckoos in response to their neighbor's information. Whereas 26 of 52 focal birds that observed neighbors mobbing cuckoos increased their mobbing response to that cuckoo morph, 21 pairs showed no change and 5 pairs decreased their mobbing (Fig. 3). We tested whether differences in costs and benefits of using social information, or the quality of this information, might explain why some birds did not respond. However, neither a pair's initial mobbing response, nor parasitism risk (14), nor reproductive

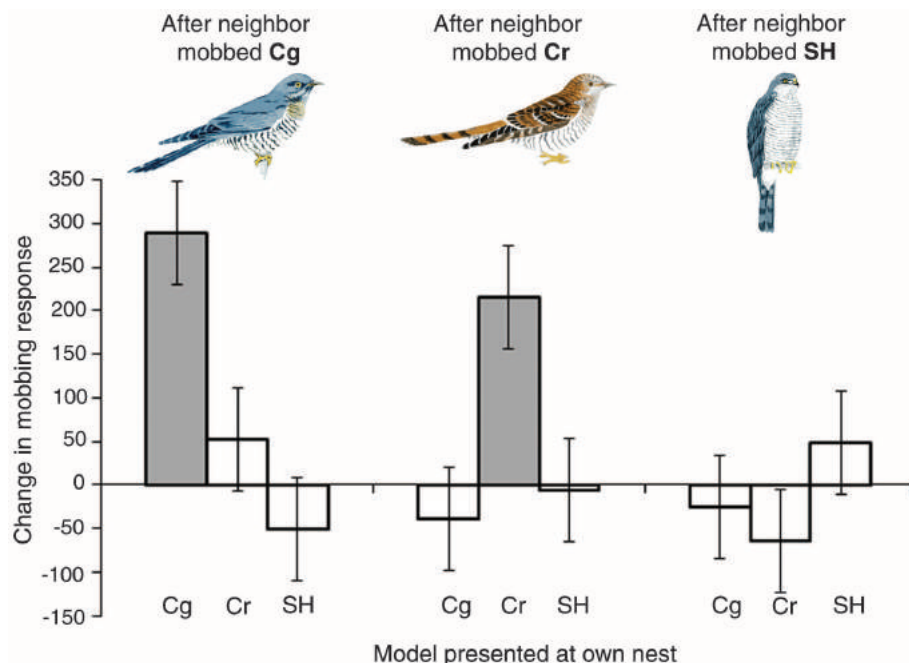


Fig. 1. Change (mean ± SE) in reed warblers' mobbing response (mandible snaps and rasp calls per 5 min) toward model cuckoos (Cg, gray morphs; Cr, rufous morphs) and the sparrowhawk (SH) after observing neighbors mobbing one of these models ($n = 26$ focal pairs for each neighbor-model treatment). Only mobbing responses in gray changed significantly from baseline responses (both $P_{MCMC} < 0.0004$). For baseline mobbing responses, see fig. S1.

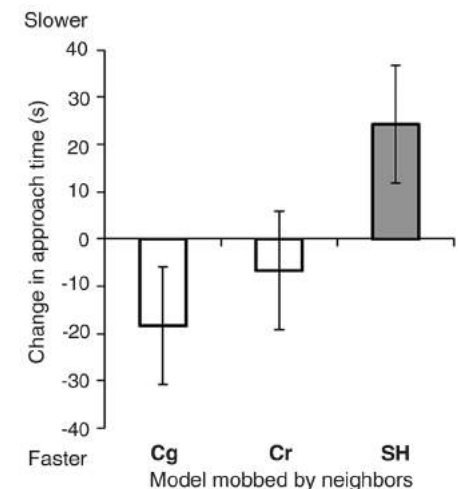


Fig. 2. Change (mean ± SE) in approach time of reed warbler pairs after observing their neighbors mobbing either of the cuckoo morphs or a sparrowhawk [LMM, neighbor × model type: $\chi^2_{(2)} = 6.32, P = 0.043$]. There was no difference in latency to approach the three models [focal model type, $\chi^2_{(2)} = 1.45, P = 0.48$; focal model × neighbor model, $\chi^2_{(4)} = 1.19, P = 0.88$], so we have plotted the mean approach time to all models for $n = 26$ pairs for each bar. Only neighbors mobbing sparrowhawks ($P_{MCMC} = 0.051$) led to a change in the focal birds' approach latency from their baseline measure (Cg, $P_{MCMC} = 0.13$; Cr, $P_{MCMC} = 0.58$). For baseline approach times, see fig. S2.

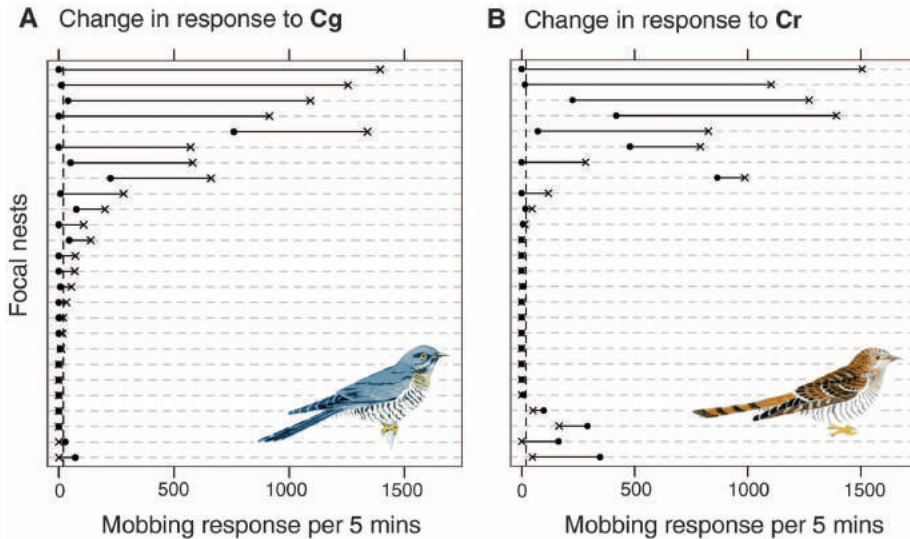


Fig. 3. Change in mobbing response (mandible snaps and rasp calls) of focal birds (one nest per horizontal line) from their baseline (black dot) until after they observed their neighbors (black X) mobbing either (A) gray cuckoo morph, Cg, or (B) rufous cuckoo morph, Cr. These data are only pairs' responses to the same cuckoo morph they observed their neighbor mobbing ($n = 26$ each). Our measure of mobbing was conservative; any mobbing response < 20 (vertical dashed line) was treated as no response (6).

investment (22) explained the variation in response to social information (table S2). Neither did variation in neighbor attributes such as age, clutch size, or nesting stage explain differences in focal response (table S2). When we considered only focal birds where we were certain whether they had observed their neighbor mobbing, there was also no relationship between attendance at the neighbor's nest and how likely they were to mob cuckoos back at their own nest (29 attended versus 8 not attended; generalized LMM, effect size = 0.43 ± 0.90 , $P_{MCMC} = 0.67$).

Although we cannot yet explain it, this variation in the host's response to social information has important consequences. Social learning can be effective as long as there are sufficient demonstrators, which allows a population to change rapidly as information spreads. But spatial heterogeneity in host propensity to respond or learn, and in the local frequency of cuckoos and sparrowhawks, will all influence host and cuckoo success. Recently, spatial heterogeneity of targets and searchers has been shown to influence selection (23) and to facilitate the evolution of polymorphisms (24, 25). However, the possible ways in which information might spread among searchers remains unexplored, as does its role in the evolution of polymorphisms and mimetic defenses. Our results show that the success of both cuckoo morphs will depend not only on their relative frequency, but also on the hosts' information landscape (26).

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Acknowledgments: We thank J. Davies for making the wooden models, illustrations, and help in the field; C. Lindstedt, J. Mappes, and attendees of the Coevolution Symposium at the University of Jyväskylä (October 2011) for helpful discussion; R. Kilner, M. Stevens, H. Rowland, and three anonymous referees for constructive comments on the manuscript; the National Trust, C. Thorne, and the Wicken Fen Group for facilitating our work at Wicken Fen; Natural England for a license for experimental work at reed warbler nests; and the Natural Environment Research Council for funding. Both authors contributed equally to the work, and data for all analyses are included within the supplementary materials.

Supplementary Materials

www.sciencemag.org/cgi/content/full/337/6094/578/DC1
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20 February 2012; accepted 18 June 2012
 10.1126/science.1220759

Unraveling the Life History of Successful Invaders

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Despite considerable current interest in biological invasions, the common life-history characteristics of successful invaders remain elusive. The widely held hypothesis that successful invaders have high reproductive rates has received little empirical support; however, alternative possibilities are seldom considered. Combining a global comparative analysis of avian introductions (>2700 events) with demographic models and phylogenetic comparative methods, we show that although rapid population growth may be advantageous during invasions under certain circumstances, more generally successful invaders are characterized by life-history strategies in which they give priority to future rather than current reproduction. High future breeding expectations reduce the costs of reproductive failure under uncertain conditions and increase opportunities to explore the environment and respond to novel ecological pressures.

Concern over the impact of invasive species on biodiversity and ecosystem functioning has generated interest in understanding what makes a successful invader (1). Although there is evidence that species differ in their invasion potential, controversy exists regarding the features that differentiate successful and un-

successful invaders (2–4). Life history—defined as the way organisms allocate time and energy to reproduction, growth and survival (5, 6)—has long been at the core of the controversy. It is generally agreed that extinction of introduced populations may result from either demographic stochasticity associated with small population