Abstract

Cognitive Models of Defense Behaviors in Hosts of Brood Parasites

By

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An avian brood parasite is a bird who lays its eggs in another individual's nest, forgoing the effort of nest building and chick rearing by passing it along to its host. As hosts incur a significant fitness cost by investing resources rearing unrelated offspring (especially since some species of parasite chicks are known to employ strategies to outcompete or even kill their unrelated nestmates), they are under evolutionary pressure to detect and mitigate or prevent their parasitization. In this dissertation, I examine some of the defense behaviors of hosts targeted by brood parasites, in particular the detection by visual cues and subsequent ejection of foreign eggs from the nest. In chapter 1, I review an extensive history of research aiming to isolate the cognitive mechanism that a host assessing eggs in the nest uses to identify and reject parasite eggs. The two most commonly evoked candidate heuristics are the discordancy mechanism, wherein the host would choose to reject the egg most dissimilar in appearance to other eggs in the nest after on-site comparison, and the template mechanism, wherein the host would compare an egg it is assessing to a known internal template of its own eggs' appearance, and assess dissimilarity that way. Most experimentation specifically pitting these competing mechanisms against one another concludes in support of the template explanation for egg discrimination. However, recent, more careful attempts to tease these mechanisms apart has suggested that, far from

mutually exclusive, these strategies may in many cases be simultaneously activated and work in tandem to come to a rejection decision. Further, chapter 1 reviews a growing body of work demonstrating, on the individual level, plasticity in the degree-of-difference threshold of rejection in hosts. In order to examine egg rejection behavior effectively, the host species investigated must meet certain requirements. That they are rejecters in the first place is of utmost importance to test the limits and plasticity of rejection behavior. The globally ubiquitous house sparrow *Passer domesticus* is known to engage in conspecific brood parasitism, and its invasive proliferation across many continents and biomes represents a potentially attractive system to study anti-parasite behavior across ecological contexts. Chapter 2 assesses the generalizability of previous work by one research group exhibiting egg rejection in house sparrows in Spain and South Africa, especially after data out of China suggested that they are not rejecters. We robustly examined house sparrow responses to artificial parasitism in distinct areas of North America, Israel, and New Zealand, and found negligible rejection rates in all three areas, suggesting that the house sparrow is not a suitable model for egg rejection behavior. In chapter 3, the cognitive mechanisms of rejection laid out in chapter 1 were examined in the context of multiple datasets focused on the great reed warbler *Acrocephalus arundinaceus*, a well-established model host of the common cuckoo *Cuculus canorus*. Specifically, the "simultaneous activation" of the discordancy and template models suggested in chapter 1 was considered, as if multiple methods were employed at the same time, they may interfere with one another (especially if the heuristics would yield different targets for rejection) and ultimately result in reduced rejection accuracy. Host individuals were artificially parasitized with painted eggs of varying color, quantity, and uniformity. Hosts were found to be more permissive of foreign eggs, or "error prone," as both the proportion of foreign eggs the nest increased and when the eggs in the nest became more perceptually distinct from one another. This indicates that host defenses could be compromised by causing recognition mechanisms to yield differing rejection targets, and that multiple parasitism (more than one parasitic egg laid in the host nest) may be one way to accomplish this. No matter which mechanism(s) are employed, most studies agree that the primary visual cue used by hosts to distinguish foreign eggs is the overall degree of distance in color between the egg being assessed and the host's own egg(s). Until recently, rejection decisions were attributed to only the absolute (regardless of direction) perceptual distance between the eggs. Chapter 4 is a parallel study to Hanley et al. 2017 and 2019's discovery that directional difference on a continuous color gradient of avian eggshell colors may be the true salient cue. In particular, they found that their hosts preferentially rejected eggs browner than their own, but not eggs more blue/green than their own, suggesting a single threshold of rejection only in one direction on the color gradient, rather than multiple symmetrical thresholds of absolute distance. We examined this phenomenon using the European redstart *Phoenicurus phoenicurus*, which in contrast to the house sparrow observed in chapter 2, has consistently demonstrated rejection of non-mimetic eggs and acceptance of mimetic eggs, providing an attractive variable rejection model to investigate the limits of color-based rejection thresholds. In addition, this study provides support for Hanley's hypothesis in the context of a host parasitized by a mimetic parasite, which none of their own host species were. We examined redstarts in Finland, where they were simultaneously under parasitic pressure from the common cuckoo, and in the Czech Republic, where no parasitic pressure was present. Using 3D printed eggs painted on a continuous color gradient of brown to blue/green, we artificially parasitized redstart nests and recorded rejection behavior. In keeping with the findings of Hanley et al., we found the redstarts regardless of locality to preferentially reject noticeably browner eggs but not noticeable more blue/green eggs, in full support of the single threshold hypothesis. Finally, in chapter 5, I shift the lens to the insect kingdom to examine highly analogous brood parasitic systems in place. Though the exact mechanisms differ, the evolutionary arms race of mimicry and recognition as parasites attempt to exploit unrelated individuals for offspring care is remarkably similar, and the relative advantages of examining host-parasite interactions from this new perspective are laid out. In particular, the more straightforward life histories and behavioral repertoires of social insects allows for uncomplicated interpretation of the results of experimental manipulation. Relative to avian brood parasitism, the study of social parasitism in insects is largely incomplete, even when there are strong analogies (such as parasitic larvae manipulating caretakers to receive disproportionate attention, just as many avian brood parasite chicks do, the mechanisms of the larval manipulation are entirely unknown). Making use of these multiple perspectives on host-parasite dynamics across taxa can inspire more cohesive research on both sides of the divide. Such advancement could be critically important, with such impending crisis as the increasing collapse of honeybee colonies in Africa due to the recent surge of virulence of a brood parasite.