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Rarely Parasitized and Unparasitized Species Mob and Alarm Call to Cuckoos: Implications For Sparrowhawk Mimicry By Brood Parasitic Cuckoos

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ABSTRACT.—Recent experiments support the long-standing hypothesis that Common Cuckoos (*Cuculus canorus*) are mimics of Eurasian Sparrowhawks (*Accipiter nisus*). Additional experiments further suggest that mimicry benefits the cuckoos by reducing the intensity of mobbing they suffer near host nests, at least in some host populations, potentially increasing their access to the hosts' nests. We observed two species of birds—one very rarely parasitized and the other never parasitized by cuckoos—responding to a cuckoo as they would a bird of prey. On the island of Öland, Sweden, we observed two instances of a gray phase cuckoo being mobbed by a group of Barn Swallows (*Hirundo rustica*) during the non-breeding season. These mobbing observations cannot be explained as a consequence of selection in the context of brood parasitism, because swallows are extremely rare cuckoo hosts and should not show co-evolutionary responses to parasitism. Instead, the swallows appear to have mistaken the cuckoos for Eurasian Sparrowhawks and responded as they would to true hawks. Similar observations were made in California, where a vagrant Common Cuckoo repeatedly elicited alarm calls from Bushtits (*Psaltriparus minimus*), a species completely allopatric with cuckoos and thus with no evolutionary history of brood parasitism. Because Eurasian Sparrowhawks visually resemble related North American bird-eating *Accipiter* hawks in plumage and flight characteristics, the cuckoo likely triggered a general *Accipiter* response in the Bushtits. Together, these observations provide additional evidence that cuckoos successfully mimic Eurasian Sparrowhawks and that such mimicry comes not only with benefits to the cuckoos, but costs as well. Received 2 October 2012. Accepted 2 March 2013.

Key words: Barn Swallow, brood parasitism, Bushtit, Common Cuckoo, Eurasian Sparrowhawk, hawk mimicry, mobbing.

The costs avian brood parasites impose on their hosts has led to co-evolutionary arms races in a variety of taxa (Rothstein 1990, Davies 2000). Hosts evolve defenses to reduce the risks or costs

of parasitism, which in turn favor selection for counter adaptations in the parasites to thwart the host defenses, and vice versa. Many studies of this antagonistic co-evolution have focused on adaptations related to egg recognition and rejection, but there is also growing evidence that host-parasite behavioral interactions before or during the act of parasitism are important as well (Neudorf and Sealy 1992, Feeney et al. 2012). For example, hosts of the Common Cuckoo (*Cuculus canorus*) aggressively defend their nests by mobbing cuckoos (Moksnes et al. 1991, Røskaft et al. 2002, Grim 2005, Honza et al. 2006), and at sites where parasitism is common, hosts that mobbed more intensively were also less likely to be parasitized (Welbergen and Davies 2009).

Intense mobbing is potentially costly to the brood parasites (Welbergen and Davies 2008), and cuckoos appear to have reduced some of these costs by the evolution of plumage traits that mimic a bird predator, the Eurasian Sparrowhawk (*Accipiter nisus*). The strongest evidence for mimicry comes from experimental presentations of cuckoo and sparrowhawk models to two species of titmice not parasitized by cuckoos, and therefore not under selection to recognize cuckoos in the context of parasitism. In both titmouse species, individuals showed similar heightened responses to a hawk and a cuckoo relative to a control mount, implying that the cuckoo successfully mimics the hawk (Davies and Welbergen 2008). Experimental presentations of similar mounts at nests of Eurasian Reed Warblers (*Acrocephalus scirpaceus*), a species parasitized by cuckoos, showed that the hosts are particularly aggressive to cuckoos. However, experimental alteration of the presence or absence of the barred breast pattern on the cuckoo—a plumage trait shared with the hawks—affected the intensity of aggression shown by hosts (Welbergen and Davies 2011). Taken together, these studies provide convincing evidence that specific aspects of cuckoo plumage mimic features of sparrow-

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hawks, and that the mimicry benefits the cuckoos. Here, we describe observations that provide additional evidence that cuckoos are sometimes mistaken for sparrowhawks or other similar *Accipiter* hawks by two bird species that should not be under selection from brood parasitism, a very rarely parasitized species and an unparasitized species. These observations also suggest that by mimicking hawks, cuckoos may incur costs not directly connected to brood parasitism.

OBSERVATIONS

We observed two instances of a flock of Barn Swallows (*Hirundo rustica*) mobbing a lone cuckoo in Sweden during the non-breeding season (BEL, pers. obs.) and one instance of a cuckoo repeatedly eliciting alarm calls from a flock of Bushtits (*Psaltriparus minimus*; GSG, pers. obs.) in California, USA. We observed the swallows 2.4 km north of the Ottenby Bird Observatory at the southern tip of the island of Öland, southeastern Sweden, an area known to be a migratory hotspot for many birds. This area is mostly open heath with scattered short trees and bushes, but there is also a large patch of woodland adjacent to where we made the observations. The observation of the Bushtits was made in Watsonville, California, in riparian habitat with a mixture of dense patches of willows (*Salix* sp.) and open areas.

On 10 August 2012, at approximately 0800, we were observing migrant birds at the edge of a small patch of woodland surrounded by heath. A group of 30–40 Barn Swallows was intermittently switching between perching on a tree and foraging in the air nearby (we therefore, had a sense of the maximum number of swallows in the area). Our attention was caught by a sudden burst of alarm calls and we looked up to see some of the swallows aggressively mobbing a larger bird that was flying towards us. The swallows were calling excitedly and several individuals dive-bombed the larger bird. The vocalizations and dive-bombing behavior were similar to the mobbing behavior we observed several times in North American populations of Barn Swallows in the presence of a raptor. The mobbed bird eventually flew close enough (30 m) that we could see clearly that it was a gray phase Common Cuckoo. The swallows continued to mob the cuckoo aggressively until it looped around and returned to the trees, in what appeared to be an evasive maneuver. The entire

interaction lasted approximately 10 secs. Thirty minutes later we observed another mobbing event at the same place, but this time the swallows mobbed a real Eurasian Sparrowhawk. Their behavior towards the real hawk seemed identical to their treatment of the cuckoo.

The next day (11 Aug 2012, at ~0830) we observed another mobbing incident between swallows and a cuckoo, at the same location. As before, our attention was initially drawn to mobbing vocalizations and we noticed a group of approximately 15–30 Barn Swallows mobbing a gray bird in flight. We were initially convinced that the bird was a sparrowhawk, but when it flew sufficiently close (again ~30 m) we could see that it was a gray phase cuckoo. The bird appeared to take evasive action to avoid the swallows by suddenly changing direction and flying rapidly about 150 m across an open area before disappearing into a large tree (distance estimated from the locations of individual trees on Google Earth). It remained hidden in the tree for 5 mins but flushed when we approached the tree, and it then flew across an open area towards a large patch of forest.

On 29 September 2012 in the early afternoon, a hepatic plumage cuckoo was observed in wetlands near Watsonville, California. Common Cuckoos are very rare vagrants to North America, so there were a couple of dozen birdwatchers at the site observing the bird's every movement. The cuckoo was generally hidden from view in the willows. However, it came into view three times over a period of 15 mins when it briefly flew out into the open before disappearing into the willows again. Each time the cuckoo flew into the open, a flock with at least 10 Bushtits erupted in their loud and distinctive alarm calls. Bushtits frequently give these calls in the presence of avian predators (Sloane 2001), and we have frequently observed flocks of Bushtits in central California giving these alarm calls when Cooper's Hawks (*Accipiter cooperii*) fly by. Some of the birdwatchers in the group also commented that they found the Bushtits' response to the cuckoo similar to the manner in which Bushtits may respond to Cooper's Hawks.

DISCUSSION

These observations add to the very limited published evidence that birds respond aggressively to cuckoos as hawk mimics, and not just as brood parasites. They also highlight the need to consider that hawk mimicry may come with fitness costs as well as benefits. Naturalists have

long noted a resemblance between Common Cuckoos and Eurasian Sparrowhawks, both in terms of plumage features and flight characteristics. Ash (1965), for example, described several instances where the flight characteristics of Common Cuckoos were very similar to those of sparrowhawks, including the characteristic flap-gliding flight pattern typical of *Accipiter* hawks in general. Ash also noted that the hawk-like flights often seemed to be associated with visits to potential host nests, and in some cases they were specifically associated with parasitic egg-laying. However, he concluded that the resemblance to raptor flight was 'fortuitous'—because of the aerodynamic aspects of flight—rather than because of mimicry. The recent studies of hawk mimicry by cuckoos, however, suggest that this resemblance to raptor flight might make sense in terms of cuckoo mimicry of the raptors.

In a series of elegant experiments Welbergen and Davies (Welbergen and Davies 2008, 2009, 2011, 2012; Davies and Welbergen 2008, 2009) provide clear evidence that cuckoos mimic Eurasian Sparrowhawks, at least in some plumage features, and that such mimicry affects the way that cuckoos are treated by some hosts. Enemy recognition, in general, is typically assessed by how victims respond to a putative enemy. Davies and Welbergen (2008) assessed the responses of Great Tits (*Parus major*) and Eurasian Blue Tits (*Cyanistes caeruleus*)—both species are unsuitable as hosts and not parasitized by cuckoos—to cuckoo and hawk mounts placed at feeders during the winter, when cuckoos were absent. Individuals in both species showed similar responses to cuckoo and sparrowhawk mounts—high rates of alarm calls and avoidance of the feeder—but very little response to a dove mount (the control). Moreover, experimentally altering aspects of the cuckoo plumage revealed that the barred breast pattern in particular caused a similar response to both the cuckoo and hawk models, and hence is a critical component of the mimicry. The observation that these two titmice respond similarly to cuckoo and hawk mounts, coupled with the fact that they are unsuitable cuckoo hosts (they nest in small holes inaccessible to cuckoos) so their responses to cuckoos cannot be explained by selection from brood parasitism, provides powerful evidence for hawk mimicry by cuckoos.

Our observations of two other species showing classic anti-predator responses to cuckoos—mobbing a cuckoo in flight (swallows) or alarm calling

when a cuckoo flew (Bushtits)—provides additional, independent support for the hypothesis that cuckoos mimic hawks. Swallows have traditionally been considered as unsuitable hosts for cuckoos, but there are a few dozen records of cuckoo chicks in swallow nests (T. Grim, pers. comm.). Nonetheless, the scarcity of such records compared to those for more typical hosts suggests that parasitism of swallows is so rare that their response is very unlikely to be a selected anti-parasite response. Moreover, our observations were made during the non-breeding season. Bushtits provide a more striking example, because they are fully allopatric with Common Cuckoos, including breeding and wintering. We do not know what cues triggered the responses in the swallows and Bushtits. Although the observations in both species involved cuckoos in flight, in neither case were the cuckoos adopting an *Accipiter*-like flap and glide flight profile. However, *Accipiter* hawks themselves do not always adopt flap and glide flight, so it is not a prerequisite for effective mimicry.

Given that many birds mob hawks, it is somewhat counterintuitive that cuckoos that mimic hawks can benefit in the context of brood parasitism. Cuckoo hosts will aggressively mob cuckoos—particularly when they have learned through social transmission to distinguish cuckoos from hawks. However, inexperienced hosts seem to be more wary of hawks, and it is in this context that mimicry of sparrowhawks appears to reduce the intensity of mobbing by hosts (Welbergen and Davies 2009). Welbergen and Davies (2009) also suggest that this reduction in mobbing may make it easier for the cuckoos to successfully access host nests.

Our observations suggest that the traits that benefit cuckoos by reducing their mobbing intensity at host nests may also bring costs in terms of higher mobbing rates or intensities outside the context of brood parasitism. Moreover, these costs are to be expected anywhere (including wintering areas) that cuckoos are sympatric with Eurasian Sparrowhawks or other similar *Accipiter* hawk species. The fitness costs of being mobbed are not known for birds in general, but studies of mobbing in hawks and owls show that mobbing can have dramatic effects on the behavior of the mobbed individuals, including where they choose to roost to reduce the risk of being mobbed (Hendrichsen et al. 2006) and moving away from foraging areas after being mobbed (Pettifor 1990).

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