

COMMENTARY

Why we have been unable to generalize about bird nest predation

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Nest predation is such an important determinant of the reproductive success of many birds, particularly passerines, that its dynamics are of great interest to ecologists and wildlife managers. The large body of literature devoted to assessing these dynamics, however, has not succeeded in producing much consensus as to what makes a nest more or less likely to be depredated. The idea that nest predation increases at habitat edges, for instance, was very popular for a time, but in fact most studies do not find such an 'edge effect', and in a few sites nest predation actually decreases towards the edge (Lahti, 2001). Perhaps the nearest we have come to a definitive statement about nest predation is that it is exacerbated by habitat fragmentation at the landscape scale (Donovan *et al.*, 1995). This hypothesis has strong intuitive appeal: the nesting success of forest birds, for instance, seemingly must decline if their habitat is broken up into small pieces surrounded by a matrix known to harbor an abundance of generalist predators.

Apparently, we cannot maintain even this moderate and unsurprising generalization. Spanhove *et al.* (2009) found, among several Afrotropical forest fragments, that the lower the edge-to-area ratio (in other words, the larger a patch and less convoluted its shape), the more likely a forest-dwelling passerine nest will be ravaged by predators. Thus, their focal bird, the white-starred robin *Pogonochla stellata*, might actually benefit from a fragmented forest habitat, with more edge and lower habitat patch sizes. To some extent, at least in the largest patch in the study site, predation rates were highest in the less disturbed interior of the patch, where nesting tended to occur later in the season and under denser canopy and sparse herbaceous cover.

Can landscape fragmentation really benefit some bird species? I believe that the answer is yes, but that conservationists and managers ought to regard this point as trivial, and that more productive questions in avian reproductive success lie elsewhere. The reality of our ecological situation, in Kenya's Taita Hills as elsewhere, is that distinctive habitats for wildlife have been and often continue to be

greatly shrunk and subdivided. Species like the white-starred robin, which are common, have a broad range and inhabit a variety of forest types as well as shrublands, are not the species of concern in this situation. Many species might benefit from fragmentation, in which case we are in the serendipitous situation of having inadvertently managed a landscape in their favor. Managers should, of course, consider the nesting and other habitat requirements of a threatened species before drafting a plan; this goes without saying. The point here is that very few of these plans will ever need to be drawn up for birds that benefit from fragmentation.

Nevertheless, studies that buck the general trends in ecological correlates of nest predation are valuable red flags for those who wish to understand the factors underlying the reproductive success of birds. From Spanhove *et al.* (2009), one can gather four candidate explanations for their surprising result and its apparent inconsistency with other studies: the use of artificial nests in many studies, different life histories or habitat requirements of the prey species, the scarcity of Afrotropical studies, and different nest predator assemblages. Dozens of studies of nest predation, including assessments of edge and other fragmentation effects, have used natural as well as artificial nests, with no clear distinction overall in their findings (Lahti, 2001), and so this factor is unlikely to be key. Nest site and other behavioral and life-history traits will certainly be important determinants of reproductive success, but studies during the last 40 years in the temperate zone have already assessed nest predation for a broad array of species with a range of nesting habits and life histories. This brings us to the scarcity of studies of tropical birds, and birds of the Afrotropics in particular. In recent years, nest predation studies on African birds have become more common (e.g. Schaefer *et al.*, 2005; Hanson, Newmark & Stanley, 2007; Kotze & Lawes, 2007; Lloyd, 2007; Boukhriss, Selmi & Nourira 2009), but a tentative conclusion that one might draw from them as a whole is that general ecological correlates of nest predation are not

emerging for Africa any more clearly than they are for the temperate zone. Another common thread in these studies, and in nest predation studies in general, is that different patterns of nest predation are widely thought to result from variation in the predator species present and the ways in which they respond to the relevant habitats. At first this conclusion seems like a truism, but this simple point might be the one we have been missing.

The nest predation literature is largely a series of unfinished whodunits. Each 'Introduction' or 'Methods' section provides a cast of potential culprits, and the 'Results' section portrays crime scenes and assorted clues. The 'Discussion' sections, however, generally lack the satisfying part of a detective story, the 'a-ha' moment where reasoning and observation contribute to a clear conclusion and the villain is unmasked. (There are exceptions, of course; for instance, studies where nest predators have been captured on camera are reviewed in Richardson, Gardali & Jenkins, 2009). Rather, most studies end with a 'lead' – a suspicion of some subset of nest predators, along with a postulated *modus operandi* for how they produced the observed pattern. Neither Spanhove *et al.* (2009) nor any of the African studies cited above reliably identify the predators of their study nests, but all of the studies include lists of presumed predators and important suggestions of predator behavior in the explanation of their results. If ecological phenomena like edge and patch size effects were universal, conservation efforts could proceed despite a lack of knowledge of the nest predators. Researchers would be spared the arduous work of determining what organisms are preying on bird nests and how they are ranging across the landscape. Unfortunately, studies with titles like 'Forest fragmentation relaxes natural nest predation . . .' show that the effects of fragmentation are not universally applicable and indicate that a more predator-focused research strategy may be necessary.

Thus, perhaps the main reason why nest predation has eluded generalization is because researchers continue to focus on factors that are easier to measure (landscape, habitat, nest site and nest characteristics), while casting just a passing glance at factors that are more directly related to the process of nest predation (predator identity and behavior). The dynamics that influence nest predation are not really a particular kind of landscape or habitat or nest site per se, but rather an interaction between these things and the behavior of the particular nest predators that are active in a certain area. Wherever an interaction is driving a system, one term of the interaction commonly does not achieve significance by itself. Therefore, we should not expect to see universal edge or other fragmentation effects on nest predation, even if habitat fragmentation generally plays an important role.

Spanhove *et al.* (2009) and other studies have provided interesting possibilities as to how nest predators might be interacting with ecological features in particular cases involving habitat fragmentation in Africa. Generalizable hypotheses can be derived from these suggestions and tested. I provide three here. First, a single predator or guild of predators with similar habits might dominate an area and

determine the dynamics of nest predation. For instance, rodents have been suggested to be the dominant nest predators in fragmented Afromontane forest habitats, and they might range indiscriminately across habitat edges (Hanson *et al.*, 2007; Spanhove *et al.*, 2009). A similar phenomenon may be occurring in the edge versus interior of desert oases (Boukhriss *et al.*, 2009). Second, ecological effects on nest survival might be predominantly indirect, via the cumulative effects at different trophic levels. A commonly cited example is that habitat fragmentation could reduce populations of top predators and stimulate a 'mesopredator release,' increasing predation on nests in fragmented habitat (Crooks & Soulé, 1999; Lloyd, 2007). Spanhove *et al.* (2009) suggest a route to an indirect effect of the opposite sign: fragmentation might adversely affect the nest predators more than it does the nesting birds, resulting in a net positive effect of fragmentation on the survival of bird nests. A third general hypothesis is that the reproductive success of nesting birds might depend on the relative degree to which the bird and its predator are adapted to the nesting habitat. For instance, Kotze & Lawes (2007) suggest that the biota of Afromontane forests may be resilient to fragmentation effects because they evolved throughout the Pleistocene in a fragmented landscape. The relative extent to which this is true of the nesting birds and their predators will influence the dynamics of nest predation on such a landscape.

Given our failure to explain nest predation dynamics in terms of general ecological phenomena at the nest site, habitat or landscape scale with limited reference to predators, we may wish to adopt a different strategy. One promising possibility is that future nest predation research use the 'inverted detective story' format. In contrast to a whodunit, this approach would begin rather than end with the crime and the identity of the perpetrator. Then the goal would be to see how they did it. We will be in a better position to understand the ecological factors that govern nest predation if we focus more on the predators.

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