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Coordinated misdirection: a probable anti-nest predation behavior widespread in Neotropical birds

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ABSTRACT—Nest predation has driven the evolution of specialized behaviors that decrease the probability that a predator encounters a nest. We collected descriptions from the literature of a behavior wherein male and female adults fly to their nest as a pair, with one bird flying onward or veering off while the other enters the nest. We suggest that the most likely function of this behavior is to decrease the risk of nest predation from visual nest predators. In this hypothesis, visual nest predators are distracted by the flying bird and thus fail to observe the bird arriving to the nest entrance (and the nest itself), although the putative adaptive value of this behavior remains to be confirmed. While this behavior has been sporadically noted in the natural history literature, few ornithologists are aware it is found across multiple taxa, especially in the Neotropics. We show that this behavior occurs in at least 28 species across 5 distinct families (and 11 genera) of passerines. We propose a classification scheme for this and similar behaviors and discuss factors hypothesized to promote the evolution of this behavior (e.g., mate guarding, building enclosed nests). We call this behavior "coordinated misdirection" (or "desvío coordinado" in Spanish) because it depends on the cooperation of at least 2 birds, and its presumed function is a visual misdirection—a ruse to draw the observers' attention away from the nest. Finally, we encourage future research so that the evolutionary history of the behavior can be explored and the behavior can be analyzed under a life history framework. *Received 24 March 2017. Accepted 18 March 2018.*

Key words: antipredator behavior, breeding biology, distraction display, dynamic nest-crypsis behavior, natural history, nest defense.

Desvío coordinado: un probable comportamiento anti-depredadores de nidos que es común en aves neotropicales

RESUMEN (Spanish)—La depredación de nidos ha impulsado la evolución de comportamientos especializados que disminuyen la probabilidad de que un depredador encuentre a un nido. Recolectamos descripciones de la literatura sobre un comportamiento donde los adultos macho y hembra vuelan al nido en pareja, con un pájaro siguiéndose de largo o desviándose mientras que el otro entra al nido. Sugerimos que la función más probable de este comportamiento es disminuir el riesgo de depredación del nido de parte de depredadores de nidos que usan señales visuales. Según esta hipótesis, depredadores de nidos visuales son distraídos por el ave que sigue en vuelo y no llegan a observar al ave que llega a la entrada del nido (o al mismo nido), aunque el supuesto valor adaptivo del comportamiento aún debe ser confirmado. Mientras que este comportamiento ha sido notado esporádicamente en la literatura de historia natural, pocos ornitólogos se han percatado de que se encuentra en varios taxones, especialmente en los neotrópicos. Demostramos que este comportamiento ocurre en un mínimo de 28 especies en cinco familias diferentes (y 11 géneros) de Passeriformes. Proponemos un sistema de clasificación para este y comportamientos parecidos y discutimos factores que hipotéticamente promueven la evolución de este comportamiento (por ejemplo, la vigilancia de la pareja, la construcción de nidos encerrados). Llamamos a este comportamiento "desvío coordinado" porque depende de la cooperación de al menos dos aves y su supuesto función es un truco visual – una táctica para llamar la atención del observador lejos del nido. Finalmente, esperamos que futuras investigaciones puedan explorar la historia evolutiva de este comportamiento y que puedan analizarlo dentro de la estructura de la teoría de la historia de vida.

Palabras clave: biología de la reproducción, comportamiento anti-depredadores, comportamiento de ocultamiento de nidos dinámico, defensa del nido, distracción anti-depredadores, historia natural.

Nest predation is a ubiquitous pressure facing breeding birds (Skutch 1985). A variety of organisms consume bird eggs and nestlings, including other birds, snakes, and mammals. This selective pressure has driven the evolution of many behaviors that minimize nest predation. Life history theory predicts that nest defense behaviors represent a tradeoff between balancing the fitness benefits of protecting a nest against the potential costs of exposure to a nest predator (Montgomerie and Weatherhead 1988). Given the large fitness consequences of nest predation, it is not surprising that birds exhibit an extensive array of antipredator behaviors. One set of behaviors, termed distraction or diversionary displays, are performed to lure predators away from active nests, including broken-wing displays, rodent running, tail flagging, erratic fluttering with calls, vibrating wings from the ground, and boldly displaying bright color patches (Greig-Smith 1980, Gochfeld 1984, Gelis et al. 2006). In addition, adult birds may reduce nest visitation rate and increase vigilance when they perceive an increased risk of predation

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(Ghalambor and Martin 2001, Eggers et al. 2008, Morosinotto et al. 2013).

When predators are not present, or at least unperceived, adult birds must still visit the nest to incubate, brood, or feed their young. In these situations, some species employ behaviors that may serve to "camouflage" the presence of the nest. These behaviors can either occur when arriving to (nest entry behaviors) or departing from (nest exit behaviors) the nest and are not necessarily associated with the presence of predators or elevated perceived predation risk. Examples of nest exit behaviors have been previously documented. Canopy nesting birds dive straight down from their nests before changing direction and leaving the nest's vicinity, presumably to avoid betraying the nest's precise location (Skutch 1954a, 1954b). Both fairy hummingbirds (*Heliothryx* spp.), the Fiery-throated Fruiteater (*Pipreola chlorolepidota*), and the Long-wattled Umbrellabird (*Cephalopterus penduliger*) tumble out of their nests in the manner and speed of a falling leaf (Cintra 1990, Schuchmann 1990, Gelis et al. 2006, Greeney et al. 2006), and White-necked Jacobin hummingbirds (*Florisuga mellivora*) depart their nests using a moth-like flight (Stiles pers. comm. as cited in Cintra 1990). Examples of nest entry behaviors that may be adaptive responses to nest predation are generally poorly described but may be widespread. For example, the Purple-crowned Fairy (*Heliothryx barroti*) and Spotted Pardalote (*Pardalotus punctatus*) have been observed to fly back and forth in the air or between branches rapidly before visiting the nest (Schuchmann 1990; ERGC, pers. obs.).

We describe and summarize reports of a largely overlooked nest entry behavior that is plausibly an adaptation to decrease the probability of nest detection by visual predators. This behavior involves both parents flying in synchrony until they have reached the nest, whereupon one continues flying away from the nest while the other discreetly stays at the nest. This behavior has been largely neglected in the ornithological literature, although it is occasionally noted in natural history accounts (e.g., Skutch 1954a). We present an overview of this behavior and use data from the literature and our own field experience to preliminarily document the phylogenetic distribution of this behavior among multiple families of mostly Neotropical passerines. We then suggest profitable avenues for future research to better understand this behavior's effectiveness in distracting predators (its presumed function), the frequency with which it is performed, and factors that may facilitate the evolution of the behavior. We propose calling this behavior "coordinated misdirection" because it involves the cooperation of at least 2 birds, and its presumed function is a visual misdirection, a term borrowed from the magic industry (Fleischman 1949). We additionally suggest classifying it under the larger umbrella category of "dynamic nest-crypsis behaviors."

Methods

We collected observations from 3 sources: the literature, our personal observations, and personal communication with other scientists. Our review of the literature initially focused on the writings of A. Skutch, who was familiar with coordinated misdirection and clearly described this behavior in several of his species accounts (Skutch 1954a, 1960, 1972). We further compiled evidence after searching for additional information of these and related species or by finding it by chance while reading literature on breeding biology.

Personal observations by ERGC and BGF were collected haphazardly when watching nests while bird watching or doing unrelated field work between 2007 and 2015. Observations by HFG were collected in Central and South America by video-taping the nest or making periodic visits to the nest. For the most part, only presence or absence of the behavior was noted.

We assume that many observations of this behavior have not yet appeared in the published literature. To survey fieldworkers active in the Neotropics, BGF sent an email to the NEOORN listserv in April 2015 asking if members had observed behaviors similar to coordinated misdirection. Observations obtained through responses to this query were included and properly acknowledged (Supplemental Table S1).

Observations

How coordinated misdirection works

Coordinated misdirection requires synchronization within a pair and therefore occurs only in species in which both sexes provide parental care.

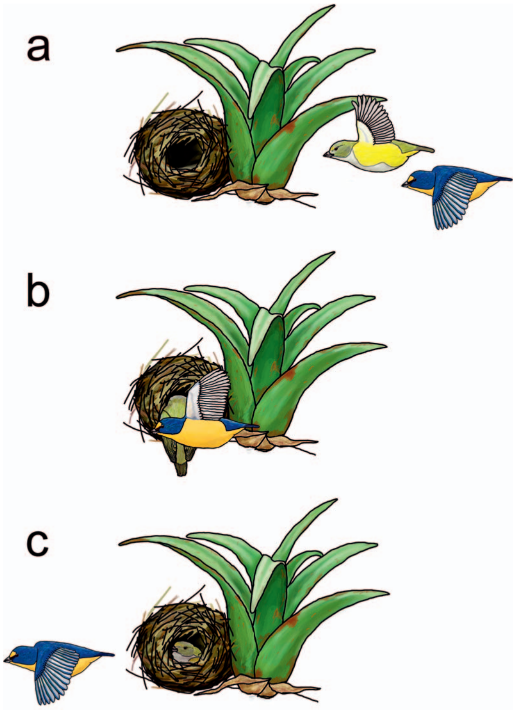

Figure 1. A typical sequence of a mated pair performing coordinated misdirection behavior. (a) Male and female Yellow-throated Euphonias (*Euphonia hirundinacea*) fly together toward their nest. (b) As one (here, the female) flies into the nest, the other (here, the male) obscures her from view and flies onward, often changing direction in flight. (c) One bird enters the nest to incubate, provision nestlings, or brood while the other bird continues in flight. Human observers tend to visually follow the male in this scenario, decreasing the probability that they observe the female entering the nest; if visual nest predators are similarly deceived, coordinated misdirection may decrease nest predation. Figure credit: ERGC and M. M. Ferraro.

Skutch (1954a, 1972) memorably described this behavior as a ritualistic race to the nest between the female and the male in which the female was always victorious. A typical example begins with both adults perched together in the general vicinity of the nest. They then fly parallel to each other in close proximity until they reach the nest. At this point, one bird discreetly enters the nest while the other flies onward, sometimes looping in flight to return to the original perch (Fig. 1; Skutch 1972, Sargent 1993, Gelis et al. 2006). This theme has several variations: for example, another pattern occurs when one bird perches above or near the nest (e.g., the male) and swoops toward the nest as the other (e.g., female) flies to the nest entrance such that their paths coincide in front of the nest before the swooping bird changes direction, sometimes taking an elliptical path back to its perch or making a Y-shaped intersection by flying onward (e.g., Cisneros-Heredia 2006, Greeney 2006; see video in hbw.com/ibc/1428531 as cited in Wright et al. 2017), and a third variant occurs when the bird visiting the nest never changes course while its accompanying mate abruptly changes course halfway to the nest instead of in front of the nest (e.g., *Chorophonia* spp; Skutch 1954a, Freeman et al. 2012). In Black-faced Grosbeak (*Caryothraustes poliogaster*), the sole cooperatively breeding species for which we found reports of the display, the member of the pair flying by the nest may be accompanied by a helper, thus sometimes involving more than 2 birds (Skutch 1972). This behavior is typically a nest entry behavior but also occurs as a nest exit behavior in some species, when the bird at the nest departs its nest and its mate immediately joins it in flight, as seen regularly in Blue-naped Chlorophonia (*Chlorophonia cyanea*; Freeman et al. 2012) and on occasion in the Olive-backed Euphonia (*Euphonia gouldi*; ERGC, pers. obs.) and Fiery-throated Fruiteater; Gelis et al. 2006). In some birds (e.g., *Pachyramphus* becards) the behavior may not be as stylized or consistently synchronized as in other birds (e.g., euphonias and attilas; HFG, pers. obs.).

The phylogenetic distribution of coordinated misdirection

Coordinated misdirection occurs in many species of Neotropical oscine and suboscine passerines and has also been observed in a Polynesian passerine (Supplemental Table S1). To date, the behavior has been documented in 5 families: Fringillidae, Cardinalidae, Tyrannidae, Tityridae, and Cotingidae (Supplemental Table S1). The degree to which coordinated misdirection is phylogenetically conserved remains uncertain; in some lineages most species exhibit this behavior (e.g., *Euphonia* spp., possibly *Attila* and *Pachyramphus* becards; see Supplemental Table S1) and also in cases where closely related species differ; for example, the Black-headed Tody-Flycatcher (*Todirostrum nigriceps*) does not perform the behavior while the closely related Common Tody-Flycatcher (*T. cinereum*) does (Skutch 1960).

Discussion

What is the function of coordinated misdirection?

The hypothesis most often suggested to explain coordinated misdirection is that it is an adaptation to prevent nest depredation. This hypothesis posits that the eyes of a predator follow the bird that continues flying rather than the bird that visits the nest (Sargent 1993, Cisneros-Heredia 2006, Gelis et al. 2006, Greeney 2006), derived from the observation that this often is the experience of humans watching the nest (Sargent 1993). An alternate hypothesis is that the behavior may be a byproduct of mate guarding behavior (Sargent 1993). Coordinated misdirection occurs beyond the laying phase when mate guarding is no longer as necessary, such as while nestlings are being provisioned (Sargent 1993; Supplemental Table S1). Although this explanation may seem inconsistent with the hypothesis that mate guarding is the principal selective force for the behavior, mate guarding could still possibly be important for future nesting attempts and interactions with neighboring nesting pairs.

Coordinated misdirection could have additional functions, such as monitoring the parental investment of a mate as feedback for the appropriate investment an individual should make (similar to how blue eggs might indicate female investment in a clutch to her mate; Moreno et al. 2004) and avoiding brood parasites. Brood parasitism, however, is unlikely to affect the subset of birds that predominantly feed their nestlings fruit, such as euphonias (Morton 1973, Sargent 1993) and fruiteaters (Gelis et al. 2006), because nestling diets of plant material are known to cause malnourishment in brood parasites (Rothstein 1976, Middleton 1991, Kozlovic et al. 1996). Oddly, Common Tody-Flycatchers and Black-faced Grosbeaks have been reported to call from the nest immediately following the procedure (Skutch 1960, 1972), which would decrease the presumed antipredatory benefits, perhaps indicating that additional factors influence this behavior.

Coordinated misdirection differs in 2 meaningful ways from traditional distraction displays, the behaviors commonly associated with preventing nest depredation. First, coordinated misdirection is most often observed in the absence of nest predators and without being followed by a predation attempt. For example, this behavior occurs even with no human observers present (e.g., video recordings in Greeney 2006). Meanwhile, all reported distraction displays are elicited by the presence of a nest predator or a human that the bird perceives as a threat to the nest (Armstrong 1949a, Gochfeld 1984). Second, parental cooperation and synchronization is critical for the success of coordinated misdirection, whereas most distraction displays can be employed with one individual.

Coordinated misdirection and "dynamic nest-crypsis behaviors"

We suggest that the behavior we describe as coordinated misdirection does not fit well into existing categorizations of nest defense behaviors. For example, it may seem appropriate to think of it as a diversionary display, defined as "those various types of behaviour, apart from actual attack, which have the effect of deflecting the attention or attack of a potential predator or other potentially dangerous intruder from the nest, eggs or young to the adult" (Armstrong 1949a: p. 89). Unlike coordinated misdirection, however, diversionary displays involve the obligatory presence of a predator or intruder. When considering nest defense itself, we see that nest defense is defined as: "[a] behavior that decreases the probability that a predator will harm the contents of the nest (eggs or chicks) while simultaneously increasing the probability of injury or death to the parent" (Montgomerie and Weatherhead 1988: p. 170). Montgomerie and Weatherhead (1988) explicitly excluded any behaviors that did not threaten the survival of the parent (i.e., incur a high cost to the parent) from their "nest defense" category, a caveat that seemingly excludes the behavior we describe. In line with this, Montgomerie and Weatherhead (1988: p. 170) exclude behaviors that result in "changes to the physical features of the nest that might render it cryptic (e.g. such as how or where it is constructed)." Indeed, coordinated misdirection can be interpreted as a means to making the nest more cryptic, although the nest's physical features are unaltered, and the behavior likely has higher costs than altering the nest's structure. In many ways, the energetic costs of coordinated misdirection seem to share features of distraction displays, nest defense, and physical alterations to the nest but differ from these categories in the fitness costs incurred by adult birds.

We propose classifying coordinated misdirection and similar ruses in a new category called "dynamic nest-crypsis behaviors": those that disguise the location of the nest through coordinated or elaborately directed flight not necessarily or usually performed in the presence of a predator. This definition includes coordinated misdirection and other nest entry and exit behaviors (Skutch 1954a, 1954b; Cintra 1990; Schuchmann 1990; Greeney et al. 2006) but excludes less specialized behaviors, such as a general hesitation when approaching or departing the nest. Dynamic nest-crypsis behaviors can be considered either a category of "diversionary displays" independent of those previously described by Armstrong (1949a) or its own grouping of nesting behaviors in which affinity with nest defense remains a topic for future discussion.

Dynamic nest-crypsis behaviors may also help categorize a behavior historically problematic to understand, known as the "fly-away trick." Some shorebirds, after a potential predator has backed off, conspicuously fly away while calling only to return soon using local topography to hide their path back to their nests (Meltofte 1977). Meltofte (1977) suggests this behavior is likely performed to misdirect the predator in case it is still attentive to the bird. The fitness costs of this display are different from those of distraction displays because the predator is now distant and the bird is flying even farther away. As a sort of dynamic nest-crypsis behavior, however, we can interpret the fly-away trick as a means to keep the nest hidden through purposeful flight patterns, even as the bird visits the nest.

Outstanding research questions

We hope that drawing attention to coordinated misdirection will encourage researchers to document this behavior in greater detail and use observational and experimental methods to better understand it. We briefly describe several questions that are potentially answerable with additional data.

Has coordinated misdirection evolved repeatedly or independently among avian taxa?

Unfortunately, the nesting biology of a vast number of Neotropical passerines is understudied or entirely undocumented (Supplemental Table S1). This lack of information limits our understanding of the distribution of coordinated misdirection within and across bird families and places answering this question beyond our current reach. This behavior likely evolved independently between the 2 major groups in which the behavior has been documented (New World suboscines and 9-primaried oscines) because these clades are separated by numerous taxa that include well-studied species that do not display coordinated misdirection, a logic used previously when discussing the potentially repeated appearances of distraction displays (Skutch 1955). Alternatively, it possibly evolved independently in each reported family (especially because most of these families include well-studied temperate species that do not seem to perform the behavior) or even multiple times within each family (e.g., the behavior has been observed in a small number of species from various large Tyrannidae subfamilies; Ohlson et al. 2008, Tello et al. 2009). More complete surveys of breeding biology in Neotropical birds will eventually allow analyses such as ancestral state reconstruction to more confidently determine the number of times coordinated misdirection has evolved independently.

Coordinated misdirection seems to have repeatedly evolved independently within Neotropical birds, suggesting there may be a common mechanism that explains why a variety of morphologically and evolutionarily distinct passerine lineages have evolved this behavior. We note that all birds in our sample are tropical or subtropical birds and none from the temperate zone, possibly due to factors that vary with latitude, but additional data would be necessary to detect whether this observation is a pattern or random. Most of our samples are Neotropical birds and not from other tropical regions, which may simply reflect our greater familiarity with the breeding biology of the former, and we predict this behavior is probably more widespread throughout the world.

Is coordinated misdirection related to nest structure?

Skutch (1972) noticed that nearly all of the birds he observed performing coordinated misdirection built enclosed nests, suggesting that the ability of the bird visiting the nest to "disappear" into the nest as its mate flies by may increase the effectiveness of this behavior. Enclosed nests have been suggested to generally have lower predation rates than open-cup nests (e.g., Nice 1957; but see Martin et al. 2017). Our survey demonstrates that some cup-nesting species, including tyrant-flycatchers and the Black-faced Grosbeak, perform coordinated misdirection at least on occasion. Closer inspection, however, reveals that most of the cup nests are built in somewhat enclosed spaces, such as crevices and behind tree knobs or epiphytes (Skutch 1972; HFG, pers. obs.). Whether enclosed nest environments may favor this behavior is unclear. For example, in hiding the visiting adult, the nest environment may favor coordinated misdirection as a means for the mate to be sure of the former's location.

What are the parental roles in coordinated misdirection?

The roles of each sex in coordinated misdirection seem to vary among species. In some cases, only the female visited the nest while the male (and helpers, if present) performed the behavior (e.g., Black-throated Grosbeak [$n = 1$ nest] and Orange-bellied Euphonia [*Euphonia xanthogaster*, $n > 15$ visits]; Skutch 1972, Cisneros-Heredia 2006). By contrast, both sexes perform the behavior in other species (e.g., in the Blue-naped [$n = 1$ nest] and Golden-browed [*Chlorophonia callophrys*, $n = 1$ nest] chlorophonias, and Yellow-throated Euphonia [*Euphonia hirundinacea*, $n = 10$ nests]; Skutch 1954a, Sargent 1993, Freeman et al. 2012), sometimes in a stereotyped order with the male visiting the nest first and the female second. Skutch (1954a, 1960, 1972) noted that only the female incubates in all species he witnessed performing this behavior (see references in Supplemental Table S1; Skutch 1960).

Is coordinated misdirection facultative or obligate?

Preliminary observations suggest that the frequency of coordinated misdirection performed by birds may vary between species, with some appearing to perform every visit (e.g., at least for some euphonias and chlorophonias) while others employ this display facultatively. In the latter case, some birds only display the behavior in a subset of nest visits (e.g., Ochracious Attilas [*Attila torridus*] performed it in 8 of 32 nest visits; Greeney 2006) or in particular periods of the nesting cycle (e.g., Black-faced Grosbeaks performed it until early in the nestling stage but stopped by the late nestling stage; Skutch 1972, Moermond 1981). Whether the frequency of coordinated misdirection performed by birds is correlated with temporal patterns in parental investment (as in distraction displays; Barash 1975), or whether it may be inversely correlated with the effort birds expend on activities away from the nest (such as defending a territory), remains to be learned.

Is coordinated misdirection related to mate guarding?

Previous studies have suggested that distraction displays are most easily co-opted from other behaviors closely associated with nesting (Armstrong 1949a, 1949b, 1956). Coordinated misdirection could have evolved from mate guarding because the latter involves the proximity of both parents to facilitate the coordination necessary to perform the former. Previous studies suggest, however, that mate guarding strengthens as a response to the threat of extra-pair copulations rather than an increase of parental investment (Møller and Birkhead 1993a, 1993b; Mumme et al. 1983), which is required of both parents performing coordinated misdirection throughout the length of the breeding attempt. Further research is needed to understand if a relationship exists between coordinated misdirection and mate guarding, and whether birds that perform the behavior show stronger mate guarding than congeners or other neighboring birds that do not display coordinated misdirection.

Conclusions

Coordinated misdirection is a widespread behavior that requires coordination between at least 2 birds, likely has an antipredatory function, and may be associated with other behavioral aspects of a bird's life history, such as building enclosed nests and mate guarding. The extent of this behavioral display in birds is likely underestimated here and will become clearer as more observations on the nesting biology of birds are documented. A more complete analysis of the number of independent evolutions, as well as the selective pressures driving those processes, will then become possible.

We recommend that future studies address the fitness benefits and costs of this behavior to facilitate analysis within a life-history framework. In particular, the various hypotheses for its function require testing, such as examining whether an increase of perceived predator presence around the nest drives the frequency of coordinated misdirection, or whether potential predators watching the display on a screen follow the bird flying to the nest or flying by. We also invite further discussion on the classification of dynamic nest-crypsis behaviors and their relationship with diversionary displays and nest defense. Further studies should evaluate whether coordinated misdirection occurs more broadly in additional avian lineages (i.e., families not included in Supplemental Table S1) and in regions beyond the Neotropics. Species that live in places with high rates of nest predation, that have biparental care, and where both sexes forage in close proximity to one another may be especially likely candidates to have evolved coordinated misdirection behavior. Finally, our survey describing the prevalence of coordinated misdirection demonstrates the value of observing the many behaviors, some of which are quite intricate, that occur around the nest but are overlooked by simple surveys of clutch size or nest fate.

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