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ORIGINAL ARTICLE

Nestmate killing by obligate brood parasitic chicks: is this linked to obligate siblicidal behavior?

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Abstract The remarkable phenomenon of nestmate killing behavior among some birds that are obligate brood parasites (OBP) has fascinated scientific researchers for hundreds of years. This "nestmate-cide" behavior has been found in two clades of OBP birds (most OBP cuckoos and all the parasitic honeyguides), though it is absent in parasitic *Clamator* cuckoos, viduid finches, cowbirds, and the single parasitic duck. Several hypotheses have been developed to explain the existence of nestmate toleraters, including recent acquisition of OBP and insufficient time to evolve nestmate killing behavior, parasitizing a host with a brood reducers strategy, or the occurrence of high costs for killing nestmates. However, none of these hypotheses have provided a complete explanation for the origin of chick killing behavior in OBP birds and its "fixed" distribution pattern within certain clades. There are similarities in the process and consequences of nestmate killing behavior in obligate brood parasites with that of obligate siblicidal behavior. After mapping these two behaviors on recent avian phylogenies, we found that the two clades of brood parasites that exhibit nestmate killing behavior are both within larger clades that contain species with obligate siblicidal behavior. Since no previous studies have considered the potential linkage between obligate siblicidal behavior and parasitic chick killing behavior, we proposed that the evolution of the potential for siblicide may also result in the potential for parasitic chicks to kill nestmates, and that siblicidal behavior may even promote the origin of this "killing-type" OBP.

Keywords Obligate brood parasitism · Nestmate killing behavior · Nestmate tolerance · Obligate siblicidal behavior

Zusammenfassung

Das Töten von Mitnestlingen obligat brutparasitischer Vögel: Besteht ein Zusammenhang mit obligatem Geschwistermordverhalten?

Für Jahrhunderte hat Wissenschaftler das bemerkenswerte Phänomen fasziniert, dass manche, obligat brutparasitische (OBP) Vogelarten ihre Mitnestlinge töten. Dieses „Mitnestlingszid"-Verhalten wurde für zwei Zweige OBP Vögel nachgewiesen (die meisten OBP Kuckucke und alle parasitischen Honiganzeiger), findet sich allerdings nicht in parasitischen Kuckucken der Gattung Clamator, Finken aus der Familie Viduidae, Kuhstärlingen und der einzigen parasitischen Entenart. Zur Erklärung der Existenz von Brutparasiten, die ihre Mitnestlinge tolerieren, wurden mehrere Hypothesen aufgestellt, unter anderem die kürzliche Entstehung von OBP und die damit fehlende Zeit Mitnestlingsrmord zu evolvieren, einen Wirt mit Brutreduziererstrategie zu parasitieren, oder hohe Kosten für den Geschwistermord. Dennoch konnte keine dieser Hypothesen eine vollständige Erklärung für die Entstehung des Verhaltens von OBP Vögeln Mit-Nestlinge zu töten und dessen „fixierten" Verteilungsmusters innerhalb bestimmter Zweige liefern. Es gibt allerdings Ähnlichkeiten

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im Vorgang und in den Konsequenzen des Tötungsverhaltens von Mitnestlingen obligater Brutparasiten mit dem von obligatem Geschwistermordverhalten. Nach Kartierung beider Verhaltensweisen auf einer modernen phylogenetischen Vogelsystematik fanden wir heraus, dass sich beide brutparasitischen Zweige, die Mit-Nestlingsmordverhalten zeigen, innerhalb größerer Zweige befinden, die Arten mit obligatem Geschwistermordverhalten beinhalten. Da keine frühere Studie diesen potentiellen Zusammenhang zwischen obligatem Geschwistermord- und parasitischem Nestlingsmordverhalten in Betracht gezogen hat, schlagen wir vor, dass die Evolution einer Veranlagung zu Geschwistermord gleichzeitig ein Potential für parasitische Nestlinge darstellt, ihre Mitnestlinge zu töten, und dass Geschwistermordverhalten sogar die Entstehung des „Mord-Typus“ unter OBP begünstigt.

Introduction

Post-hatching parental care is costly for altricial birds and can significantly influence the total fitness of reproducing parents. Brood parasitism, in which females lay eggs in a nest that is not their own, releases individuals from parental care and can allow them greater reproductive potential than non-parasitic relatives (Davies 2000). Although some brood parasitic species are facultative, and also lay eggs in their own nest, other species exhibit obligate brood parasitism (OBP), in which the parasitic species never construct nests and instead lay eggs in the nests of other species. OBP is found in approximately 90 species of birds among four orders (Passeriformes, Piciformes, Cuculiformes, and Anseriformes) and is thought to have evolved independently seven times (Sorenson and Payne 2002, 2005). Among them, six gains of OBP are in altricial birds and only one in a precocial bird (Black-headed Duck, *Heteronetta atricapilla*; Sorenson and Payne 2002). Since altricial birds incur greater costs in post-hatching parental care, this distribution of OBP is expected; altricial birds should gain greater benefits from brood parasitism than precocial birds (Dearborn et al. 2009).

Chicks of some OBP species kill host nestmates in various ways (Kilner 2005). In most Old World cuckoos, parasitic chicks evict eggs (and occasionally young) from the nest (Payne 1997; Honza et al. 2007), while honeyguide (Indicatoridae spp.) and Striped Cuckoo (*Tapera naevia*, a parasitic New World cuckoo) chicks inflict lethal injuries on nestmates by using sharp bill hooks (Davies 2000). However, other OBP species such as the *Clamator* cuckoos, viduid finches, parasitic cowbirds, and the Black-headed Duck typically share the nest with host chicks (e.g., Rothstein 1990; Soler et al. 2001; Sorenson et al. 2003; Kilner 2005). The evolution of OBP chick killing behavior has been an active area of research (reviewed by Kilner 2005). In this paper, we briefly review the major hypotheses to explain the variation of nestmate virulence among OBP chicks. However, none of them can fully explain the distribution of nestmate killing versus tolerance among OBP species. Thus, we present a novel idea to understand the origin of “nestmate-cide” behavior in OBP chicks based on its distribution on recent avian trees of life (Ericson et al. 2006; Hackett et al. 2008).

Why kill?

Parasitic chicks can directly or indirectly enhance their survival by eliminating their nestmates. First, a single parasitic chick can monopolize all host parental care with no need to increase begging vigor to outcompete host nestmates (e.g., Kilner 2001). Second, elimination of nestmates is expected to reduce the chance that host parents will discriminate parasites from their own chicks (e.g., Lawes and Marthews 2003), although some hosts are still able to recognize parasites even after eviction has occurred (Kilner 2005; Grim 2006a, 2007; Anderson and Harber 2007). Finally, elimination can reduce space competition and displacement risk from mixed broods (Moskát and Hauber 2010). Given the above, it is not surprising that the failure to evict nestmates has a negative effect on the fitness of cuckoo chicks (e.g., Hauber and Moskát 2008; Grim et al. 2009a): in nests where host offspring remain, cuckoo chicks received considerably less food than when there is a single parasitic chick (Martín-Gálvez et al. 2005; Grim et al. 2009a), and it appears that this may be due to the inability of cuckoo chicks to stimulate foster parents to feed them preferentially in a mixed brood (Hauber and Moskát 2008). However, there appears to be strong selection on parasitic chick killers to evolve strategies to “trick” their host parents into providing resources to them, including imitating the begging signals of a complete host brood (Davies et al. 1998), exaggerated call rates (Kilner and Davies 1999), and special skin patches to compensate the subnormal visual stimuli of a single gape (Tanaka and Ueda 2005). Collectively, these phenomena demonstrate the strength of selection on parasitic chicks to monopolize host resources and emphasize the strength of selection for mechanisms to eliminate nestmates.

To better understand the evolution of nestmate killing behavior, Soler (2002) presented a model based upon the breeding strategies of the host (either brood reducers that preferentially feed larger chicks or brood adjusters that prefer to feed smaller chicks). Specifically, for parasitic chicks that are larger than host chicks (which is typical; e.g., Hauber 2003), OBP birds that parasitize brood reducers would be expected to survive better even when host chicks are present. In contrast, parasites of brood adjusters might be less likely to survive due to preferential parental provisioning of the smaller host chicks. Therefore, nestmate killing would be more likely to be selected for in species that parasitize brood adjusters. Although results consistent with this have been found in some studies (e.g., Martín-Gálvez et al. 2005; Grim 2006b), since host generalists are likely to parasitize both brood adjusters and brood reducers, this hypothesis is insufficient to explain the complete distribution of nestmate killing behavior in OBP birds.

Why not kill?

Considering the great benefits gained through killing nestmates and the potential costs for not killing, why do some species tolerate the presence of host young in the nest? Although Soler's (2002) hypothesis (see above) provides one explanation (i.e., birds parasitize brood reducers are more likely to be nestmate toleraters), there is no evidence that the hosts of cowbirds (nestmate toleraters) and Common Cuckoos (*Cuculus canorus*, nestmate evictors) differ in their feeding stratigies (Soler 2001; Martín-Gálvez et al. 2005). It has also been suggested that limitations such as host nest structure and larger host species may constrain the parasitic chicks from evicting or destroying host nestmates (Grim 2006c; Grim et al. 2011). Although nest structure may restrict evicting behavior of parasitic young, it is unlikely to prevent the evolution of killing nestmates by other means (such as the bill hook found in parasitic honeyguides; Kilner 2006). Physical strength alone also seems an unlikely barrier to killing host young (Kilner 2006; but see interactions of different constraints: Grim et al. 2011), since many parasitic chicks (such as Common Cuckoo and Horsfield's Bronze Cuckoo *Chrysococcyx basalis*) can handle host chicks or eggs more than twice their body weight (Davies 2000).

Recently, it has been suggested that the costs of killing may lead to nestmate tolerance (Kilner 2005; Grim et al. 2009b; Anderson et al. 2009). Inspired by similar variation in the virulence behavior of parasitic pathogens, Kilner (2005) developed a general model explaining the situations when chick killing or chick tolerance could be favored, which involved both costs and benefits of nestmate killing behavior to brood parasitic chicks (for details, see Kilner 2005). In essence, selection should favor tolerance of host chicks whenever the overall costs of killing exceeded its benefits and vice versa.

There are three major costs that can occur after the destruction of nestmates. First, the killer might lose kin if individual host nests have been multiply parasitized (Davies 2000). This is unlikely to be a major factor because parasitic siblings typically are not raised in the same nest (Alderson et al. 1999). Second, parasitic nestlings may be unable to solicit parental care if they are alone in nests (e.g., Kilner et al. 2004), though there are mechanisms to stimulate parental care with only a single chick (see above). If host parents adjust food provisioning to the combined intensity of their brood's begging behavior (Ottoson et al. 1997), eviction of host chicks could immediately reduce the potency of the begging display to hosts. This has been observed in Brown-headed Cowbirds *Molothrus ater* where parasitic chicks had greater survival and growth rate in the presence of a medium number of companion host chicks (1–2) than when reared alone (Kilner et al. 2004). More than just tolerating host chicks, parasitic cowbirds have been suggested to effectively exploit host chicks to solicit a higher provisioning rate from host parents (Kilner et al. 2004). Finally, eviction behavior may increase the risk of desertion by host parents (e.g., Langmore et al. 2003; Grim 2007). Since OBP greatly reduces host fitness (Hoover 2003), hosts have developed multiple desertion strategies against parasitic eggs or chicks. These include recognition-based mechanisms (e.g., recognize own eggs or chicks through imprinting or adjusting clutch variation; Lotem et al. 1995; Stokke et al. 2002; Moskát et al. 2008), and recognition-free mechanisms (e.g., parents might desert nestlings that require high food provisioning levels, parents might desert when parasitic nestlings take too long to fledge, or desert when there is only a single chick in the nest; e.g., Grim et al. 2003; Langmore et al. 2003; Grim 2007; Anderson and Harber 2007). For this last hypothesis, concerning chick killing, game theory has shown that the parasitic chick always kills host young if the host never abandons depleted broods, while the parasite never kills host offspring if the risk of being deserted is very high (Broom et al. 2008). Although single chick desertion has been observed to occur regularly in Superb Fairy-wrens (*Malurus cyaneus*), few studies have tested whether hosts of nestmate toleraters are more likely to desert single chick nests, as predicted by Broom et al. (2008).

While the previous hypotheses seek to understand under what situations nestmate killing or tolerance is adaptive, the evolutionary lag hypothesis is different. Under this hypothesis, even if nestmate killing is adaptive, nestmate tolerance may be present as nestmate killing may not have had sufficient time to evolve. Thus, parasitic species that have more recently acquired OBP would not be expected to exhibit nestmate killing (Davies 2000; Sorenson and Payne 2002). This hypothesis is not an alternative to the other hypotheses (e.g., it does not seek to explain why nestmate killing evolved), but instead may explain the absence of nestmate killing in some cases. Evidence in support of this comes from the viduid finches and cowbirds, both of which are nestmate toleraters and have been suggested to have acquired OBP relatively recently (Sorenson and Payne 2002).

A novel insight on the origin of nestmate killing behavior in OBP birds

Once nestmate killing behavior has arisen, it remains largely fixed within a clade (Fig. 1). However, with the exception of the evolutionary lag hypothesis, other proposed hypotheses to explain the evolution of killing behavior by parasitic chicks (Soler 2002; Kilner 2005; Broom et al. 2008) do not predict this fixation. In contrast, more interspecific variation should be expected within clades given that even closely related parasitic species vary in the type(s) of hosts that are parasitized. Additionally, several brood parasitic species are host generalists (e.g., Winfree 1999; Davies 2000) and often have broad geographic distributions. In spite of the potential for local adaptation in these species, there is very little intraspecific variation in killing behavior among OBP chicks (e.g., Common Cuckoos are known to have more than 100 hosts but always exhibit nestmate killing behavior). To better explain the fixed distribution pattern of this behavior, we turn to a brood reduction behavior—obligate siblicide.

Siblicide is one of many mechanisms that can lead to brood reduction (Zieliński 2002), and may be either facultative or obligate (Edwards and Collopy 1983; Simmons 1988). Unlike facultative siblicide, which is largely driven by food scarcity and occurs in many species (e.g., Gargett 1993), obligate siblicide occurs in nearly all nest attempts (independent of food resources) and has only been identified for 26 species in eight families and seven orders (Fig. 1; Layne 1982; Anderson 1990; Gerhardt et al. 1997; Tarlow et al. 2001). The occurrence of obligate siblicide appears largely innate (Gerhardt et al. 1997), similar to nestmate killing behavior in OBP parasitic chicks. Moreover, the typical phenomenon of obligate siblicidal behavior is that the first-hatched chicks will kill younger siblings and monopolize parental care, again similar to what is observed in OBP nestmate killers. Given the extraordinary similarity between obligate siblicide and nestmate killing in OBP, we extend our idea to look for an

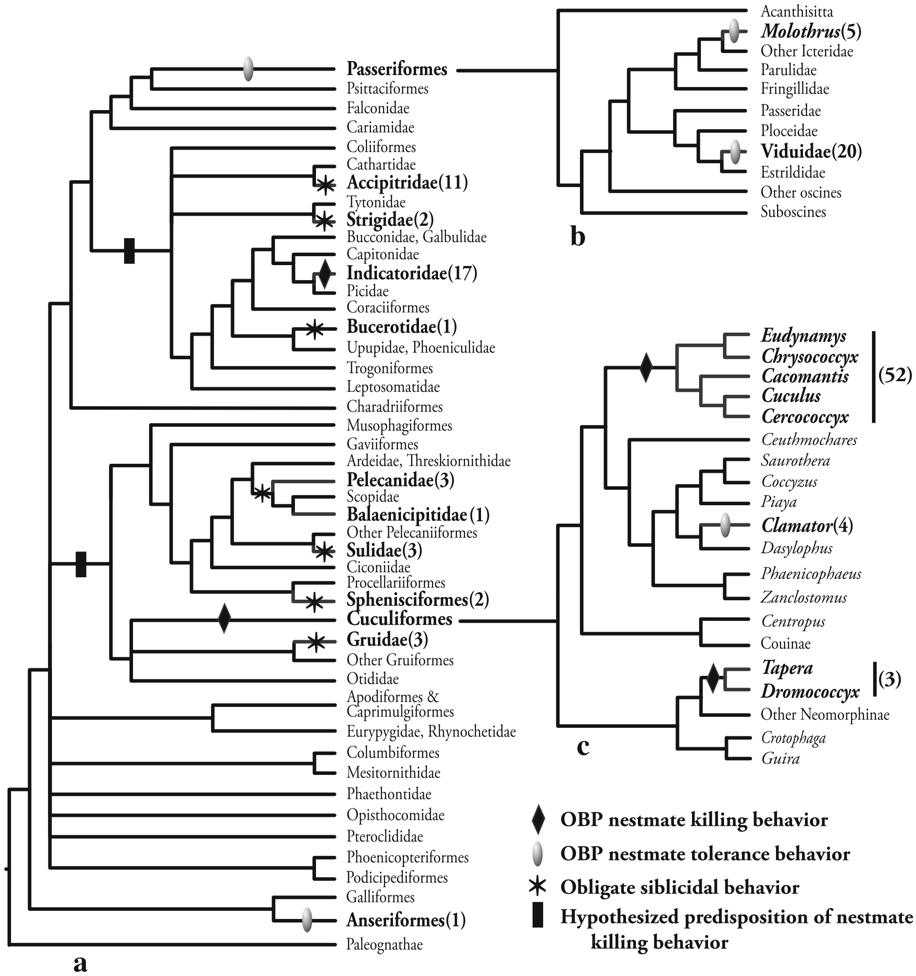

Fig. 1 Distribution of OBP and obligate siblicide across birds. The *vertical bold bars* show the hypothesized gain of a predisposition to virulent behavior (obligate siblicide or OBP killing), while other *marks* indicate taxa that exhibit specific behaviors by MacClade 4.08. A phylogeny of **a** all birds modified from Fig. 4 of Hackett et al. (2008), with **b** an expanded Passeriformes modified from Barker et al. (2002), and **c** an expanded Cuculiformes from Sorenson and Payne (2002). *Numbers in parentheses* following taxon names indicate the total number of species that exhibit certain behavior in that clade

evolutionary link between obligate siblicide and OBP nestmate killing.

To examine this, we mapped these behaviors on recent avian phylogenies in MacClade 4.08 (Maddison and Maddison 2005; Fig. 1). We used two recent estimates of avian phylogenetic relationships (Ericson et al. 2006; Hackett et al. 2008) as our backbone trees, collapsing all clades that were not well supported. To explore intra-clade variation, we combined these trees with expanded Passeriformes (Barker et al. 2002) and Cuculiformes (Sorenson and Payne 2002) phylogenies. We primarily focused on a relatively consistent taxonomic level (Fig. 1a) to make a better comparative analysis, then expanded critical clades to show more details about OBP behavior (Fig. 1b, c). After examining both phylogenies, we noticed that parasitic species that exhibit nestmate killing behavior are in larger clades with species that show obligate siblicidal behavior (Fig. 1; only Hackett et al. 2008 is shown, as both trees yielded similar conclusions, but Ericson et al. 2006 was based on fewer taxa and loci). For example, obligate siblicide occurs within Pelecaniiformes (both pelicans and boobies), Sphenisciformes (penguins) and Gruiformes (cranes), that form a larger clade that includes Cuculiformes. Similarly, the obligate siblicidal raptors, owls and Southern Ground-hornbill *Bucorvus leadbeateri* group with the honeyguides (Fig. 1). On the other hand, parasitic cowbirds, viduid finches, and the Black-headed Duck are not members of clades that include obligate siblicidal birds (Fig. 1). The observation that parasitic birds with nestmate killing behavior are found within larger "siblicidal groups" suggests that the evolution of the potential for obligate siblicide may also result in the potential for obligate parasitic chicks to kill nestmates (i.e., a predisposition of nestmate killing in specific clades). Although the small number of existing events (obligate nestmate killing or siblicide) means that a parsimony reconstruction did not indicate the ancestral condition of these large clades as having obligate chick killing behavior, it is still possible that a predisposition towards such behavior may be ancestral.

Although it is impossible to recreate evolutionary history, certain aspects of our hypothesis could be further explored with additional data coming from a better understanding of the distribution of obligate siblicidal behavior. For many species, there is only limited reproductive data, and while obligate siblicidal behavior may be present, it may not have been identified at this time. Moreover, our hypothesis predicts that there should be more OBP birds with nestmate killing behavior in the "obligate siblicidal" groups. Taken as a whole, there are several approaches that might provide some additional insight into the link between OBP chick killing behavior and obligate siblicidal behavior.

It is noteworthy that not all data are consistent with our suggested hypothesis. Members of the genus *Clamator* do not evict nestmates and two other genera (*Scythrops* and *Eudynamis*) also appear to be relatively "benign", since they tolerate nestmates to some degree (not shown in Fig. 1). For example, the Channel-billed Cuckoo *Scythrops novaehollandiae* tends to crowd and starve host nestlings without evicting them, and Common Koels do not evict host young in India but they do in Australia (Davies 2000; Grim 2006c). However, our hypothesis, like the evolutionary lag hypothesis, can work in concert with the other hypotheses discussed above. Thus, these species could have evolved from aggressive killers but lost or reduced nestmate killing behavior under some circumstances (e.g., for the reasons detailed above). Alternatively, the potential for nestmate killing may be present but nestmate killing may never have evolved in cuckoos that tolerate nestmates (e.g., *Clamator*). So the distribution of nestmate killing behavior may involve a predisposition to the behavior, combined with both selection for the behavior and time for the behavior to evolve.

There is also an observation of a Brown-headed Cowbird with eviction behavior. However, although this species is well studied, this phenomenon has been reported only once (Dearborn 1996), which suggests that it is not innate in this species as it is in the parasitic cuckoos and honeyguides. Instead, the existence of rare cases of eviction in nestmate-tolerant species may be caused by special circumstances (such as the scarcity of food), and thus unlikely to provide strong evidence contradicting this predisposition idea (analogous to facultative siblicide which also may be driven by the scarcity of food; Gargett 1993).

In addition to siblicidal behavior predisposing species with OBP to exhibit nestmate killing behavior, obligate siblicide may also promote the evolution of OBP itself. Under our predisposition hypothesis, parents could be selected to deposit eggs in other nests to guarantee their fitness given the potential fitness reduction incurred by obligate siblicide. Since intraspecific brood parasitism (Robert and Sorci 2001) would not be advantageous when chicks commit siblicide, such a system would primarily select for interspecific brood parasitism. However, given the relatively broad taxonomic distribution of siblicide, why has OBP arisen so rarely in these clades? This question may be answered by the numerous constraints already suggested to prevent the evolution of OBP (e.g., Grim et al. 2011), such as different prey types that are hard for parasites to ingest (Turtumoygard and Slagsvold 2010; but see Martín-Gálvez et al. 2005; Grim 2006b), competition from host nestlings (Slagsvold 1998; Hauber and Moskát 2008), asynchronous egg laying and incubation periods between parasite and host (Slagsvold 1998; Davies 2000), and preexisting rejection behavior of host to clean unfamiliar objects from the nest (Moskát et al. 2003). Since OBP has also evolved in clades that lack obligate siblicide, other factors and evolutionary routes (e.g., Yamauchi 1995; Dearborn et al. 2009) may also be important for the evolution of OBP, particularly in clades that lack nestmate killing behavior.

In conclusion, although nestmate killing behavior in parasitic chicks has been intensively studied during the last decades, the existing hypotheses largely focus on the existence of nestmate killing or tolerance, but lack the ability to explain the relatively homogenous distribution of these behaviors among OBP birds. In this paper, we have suggested a linkage between the nestmate killing behavior in OBP birds and obligate siblicidal behavior, which may help better explain the distribution of lethal virulent behavior among OBP species. The novel insight hinges on the idea that specific clades may be characterized by predispositions toward specific behaviors, though the exact distribution of the behavior may then depend upon other factors (e.g., other hypotheses are necessary to explain why some OBP cuckoo chicks exhibit killing behavior while others do not). In fact, that some taxa may be predisposed to certain behaviors has been suggested for many types of behaviors that are clustered phylogenetically but not “fixed” in all members of a clade (e.g., Ligon 1993). Although the absence of a tight linkage with evolutionary history or ecological factors can make testing such hypothesis difficult, it is important to recognize that such “predispositions” may help explain the evolution of many traits. In this light, the link we have identified between siblicidal behavior and OBP nestmate killing, where OBP may even be selected for in siblicidal clades, should not be overlooked.

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