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RESEARCH ARTICLE

Caught red-handed: behaviour of brood thieves in an Indian ant

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ABSTRACT

Theft of resources is ubiquitous in the animal kingdom. An evolutionary arms race between thieves and their victims is expected. Although several studies have documented inter- and intraspecific theft of resources in different taxa, studies that delve into the behaviour of thieves and the factors that influence their behaviour have not been undertaken. In the current study on the primitively eusocial ant *Diacamma indicum*, we caught brood thieves red-handed: we observed them in the act of stealing brood and examined their behaviour. Thieves were persistent in their attempts despite facing aggression in the victim colony. Experiencing aggression or failure to steal in the previous attempt negatively impacted a thief's drive to reattempt. To avoid the risks associated with theft, successful thieves exited from victim nests about three times faster than others who were procuring brood from unguarded nests. In a series of experiments examining factors that caused thieves to increase their exit speed, we found that indirect cues of a foreign colony's presence, such as odour or the presence of foreign ants, did not induce these changes in thieves. Thus, we conclude that these ant thieves only respond to the direct threat posed by aggressive foreign ants. In this comprehensive study using behavioural experiments, we reveal the simple rules of engagement between victims and brood thieves.

KEY WORDS: *Diacamma indicum*, Primitively eusocial, Ponerinae, Intraspecific theft

INTRODUCTION

Resources are important for the survival of every animal, and both time and energy is invested in the collection of these resources. One way to reduce this investment is to steal resources from those who have already procured or produced these resources. The most commonly stolen item across the animal kingdom is food, but theft of other resources such as nesting materials and brood have also been documented (Breed et al., 2012). Records of theft are present throughout the animal kingdom, from invertebrates to mammals (Iyengar, 2008). An evolutionary arms race between thieves and their victims would shape the behaviour and morphology of both thieves and victims as they go through cycles of adaptation to enhance their success. Thieves in different taxa employ many interesting strategies, which are found to be fitting to their circumstances and environment. Male satin bowerbirds (*Ptilonorhynchus violaceus*) keep an eye on their neighbouring males, and steal decorations from those that spend less time at their bowers (Wojcieszek et al., 2007). Ravens (*Corvus corax*) keep track of the location of other ravens' food caches; but while the owners are present they do not approach the caches. Instead, they search at places away from the caches in short bouts to hide their intention of pilfering (Bugnyar and Kotrschal, 2002; Bugnyar and Heinrich, 2005). The ant-eating spider *Zodarion rubidum* employs two different strategies depending on the situation. Thieves initially try to use aggression to monopolize the whole prey captured by a conspecific, but if unsuccessful they resort to becoming inconspicuous and steal part of the prey (Pekár, 2004).

Thievery is widespread in social insects, possibly because thieves can exploit the social mechanisms of the victim colonies (Breed et al., 2012). Thieves in social insects, as in other taxa, also employ various strategies to ensure success. The stingless bee *Lestrimellita limao* raids the nests of other stingless bees and honeybees, resulting in theft of stored honey, pollen, nesting materials and sometimes in the usurpation of the whole nest. Here, raids are initiated by a few scouts, and upon their successful return there is a rapid build-up of attackers at the victim colony to overturn the guards. These attackers also guard the entrance of the victim colony to prevent returning foragers of the victim colony from entering their nest (Sakagami et al., 1993; Grüter et al., 2016). The ant *Ectatomma ruidum* has specialized food thieves, which sneak in and wait inside a conspecific nest to steal food from returning foragers when they enter the nest. The thieves also modify their behaviour to avoid capture while returning to their own nest – taking a roundabout path through dense leaf litter, walking slowly and vigilantly – presumably to avoid encountering conspecifics (McGlynn et al., 2015; Jandt et al., 2015). Ants are a suitable system to study theft as the behaviour is particularly prevalent in these social insects. Observations in this taxa reveals that thieves are equipped to hijack the nestmate recognition system to their advantage. Thieves in many ant species deceive victim colony members by mimicking the colony's gestalt odour or by reducing the quantities of cuticular hydrocarbons they carry (Lenoir et al., 2001; Lhomme and Hines, 2018).

The first three stages of the life cycle of holometabolous insects – eggs, larvae and pupae – together are termed 'brood'. Theft of brood is mostly limited to ants. Brood theft has been observed in three different contexts: for consumption, for increasing workforce in incipient colonies and for rearing slave workers (Buschinger, 2009; Breed et al., 2012). Brood raids for consumption (Gotwald, 1995; LaPolla et al., 2002; Kaspari and O'Donnell, 2003) or for acquiring future slaves (Hölldobler and Wilson, 1990; D'Ettorre and Heinze, 2001) are mostly interspecific in nature. Intraspecific theft of brood for increasing workforce to ensure survival is seen in the incipient colonies of some species, and is mostly seen when colonies are founded in a spatially clumped manner (Pollock and Rissing, 1989; Tschinkel, 1992a,b). Brood theft has been previously recorded in about 50 species of ants, all of which reside in the temperate regions and are limited to the subfamilies Myrmicinae and Formicinae (Hölldobler and Wilson, 1990). Recently, however, one additional observation of intraspecific brood theft has been reported in a tropical ant *Diacamma indicum*, belonging to the subfamily Ponerinae (Paul et al., 2016; Paul and Annagiri, 2018).

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