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REVIEW ARTICLE

Warfare in stingless bees

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Abstract Bees are well known for being industrious pollinators. Some species, however, have taken to invading the nests of other colonies to steal food, nest material or the nest site itself. Despite the potential mortality costs due to fighting with an aggressive opponent, the prospects of a large bounty can be worth the risk. In this review, we aim to bring together current knowledge on intercolony fighting with a view to better understand the evolution of warfare in bees and identify avenues for future research. A review of literature reveals that at least 60 species of stingless bees are involved in heterospecific conflicts, either as attacking or victim colonies. The threat of invasion has led to the evolution of architectural, behavioural and morphological adaptations, such as narrow entrance tunnels, mud balls to block the entrance, decoy nests that direct invaders away from the brood chamber, fighting swarms, and soldiers that are skilled at immobilising attackers. Little is known about how victim colonies are selected, but a phylogenetically controlled analysis suggests that the notorious robber bee *Lestrimelitta* preferentially attacks colonies of species with more concentrated honey. Warfare among bees poses many interesting questions, including why species differ so greatly in their response to attacks and how these alternative strategies of obtaining food or new nest sites have evolved.

Keywords Stingless bees · Warfare · Alternative foraging strategies · Cleptoparasitism · *Lestrimelitta* · Meliponini

Introduction

The nest is the all-important centre of the bee's universe, providing food and shelter for the entire colony, together with the necessary architecture for rearing subsequent generations of workers and reproductive individuals (Schwarz 1948; Michener 1974; Roubik 1983, 1989, 2006). Finding and acquiring the resources to maintain the colony is often a time consuming and laborious activity. A honeybee forager, for example, may visit several hundred flowers during a single foraging trip to fill its crop (Ribbands 1949). Stealing the stored resources of another colony therefore has substantial benefits in terms of time and energy, and we would expect that collective attacks evolve when the overall payoff for both individual and colony is higher than from independent acquisition (Iyengar 2008). Since these resources (e.g. honey or pollen) have similar chemosensory features (e.g. sugars and floral volatiles) as flowers, a switch from foraging to stealing might not have required a major change in sensory adaptations (Breed et al. 2012). This behaviour, also called cleptobiosis (sensu Breed et al. 2012) or cleptoparasitism (sensu Iyengar 2008), is

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known to occur in several stingless bee species, with the nature of these intercolony attacks varying considerably in terms of mortality (from none to thousands) and duration (hours to weeks). Attacks occur in two different contexts, foraging (raiding of supplies) and swarming (usurpation of the entire nest to establish a new colony). When attacks eventuate in hive usurpation, the attacking colony not only gains the entire provisions of the hive (e.g. supplies of food, wax and resin), but also the nest cavity itself. Thus, the attacking colony does not lose a substantial amount of its resources as a result of swarming, which could be particularly advantageous when competition for food is intense (Quezada-Euán and González-Acereto 2002). Usurpation might also be favoured in an environment where nest-sites are scarce (Foitzik and Heinze 1998; Rangel et al. 2010). However, attempts to gain resources by force can have considerable mortality costs if attacked colonies mount a strong defence (see Cunningham et al. 2014; Johnson 1987) and invaders risk acquiring diseases and pathogens from the resident colony (Breed et al. 2012; Lindström et al. 2008). In this review, we aim to explore the range of collective attacks and defensive behaviours in social bees to improve our understanding of how bee warfare has evolved. We focus on stingless bees (Meliponini) because of the sheer number of species and diversity of lifestyles (> 500 described and many undescribed species, Rasmussen and Cameron 2010), including species with an exclusively cleptobiotic foraging strategy. For a recent review on robbing in other social insects we recommend Breed et al. (2012).

Diversity in warring behaviour

Stingless bees are highly eusocial, honey producing bees (Michener 2007) and several species have evolved robbing and usurping life-styles, with considerable diversity in the form that this takes. The genera *Lestrimelitta* (c. 21 species) (Gonzalez and Griswold 2012) and *Cleptotrigona* (1 species) (Eardley 2004) are obligate cleptoparasites with no flower foraging behaviour, stealing resources by invading other stingless bee (and occasionally honey bee) nests (Michener 1946; Müller 1874; Roubik 1989; Sakagami and Laroca 1963) (Fig. 1a). Workers of these robber species are equipped with powerful mandibles that allow them to kill workers of defending colonies with ease (Nogueira-Neto 1970). Other stingless bee species, such as *Melipona fuliginosa*, are known to raid nests but are not exclusive robbers (Nogueira-Neto 1970): this facultative raiding may occur under particular environmental conditions, such as food shortages (Downs and Ratnieks 2000), or may represent a transitional state from facultative to obligatory robbing (Nogueira-Neto 1970). In other species, such as *Trichotrigonaextranea* robbing behaviour has not yet been observed, but the lack of food stored in the colony's nest suggests a cleptobiotic foraging strategy (Camargo and Pedro 2007). Nest usurpation, where the attacking colony takes up residence in the hive, also shows variation among species. In *Tetragonula hockingsi*, for example, nest usurpation appears to be the primary goal of the attacks, with no evidence of food raiding behaviour (Cunningham et al. 2014), whereas *Tetragonisca angustula* may usurp other nests only occasionally (Sakagami et al. 1993).

Mortality in both attacking and defending colonies varies widely among species. In many instances (e.g. attacks by *Lestrimelitta*), raids do not involve fights and mortality of adult workers in both parties is close to zero (Nogueira-Neto 1970; Sakagami et al. 1993). Some species might simply be incapable of an adequate defensive response and conserve energy by not fighting (Iyengar 2008). At an intermediate level of aggression, attacks cause some degree of fighting, generally at the beginning of an attack, but worker mortality overall is relatively low (Nogueira-Neto 1970; Sakagami et al. 1993; video 1 in Table 2). Finally, there are large-scale battles that lead to the death of hundreds to thousands of workers (Fig. 1b; video 2 in Table 2) (Cunningham et al. 2014; Johnson 1987; Sakagami et al. 1993). Perhaps the most striking of these is the collective attacks in the Australian stingless bees, *Tetragonula carbonaria* and *Tetragonula hockingsi* (Cunningham et al. 2014). These two species engage in large-scale intraspecific and interspecific battles in which thousands of workers from both attacking and defending colonies die. This severe level of mortality undoubtedly comes at a high cost to both colonies, which are fighting over possession of the hive: in a successful attack, the invading colony brings a daughter of their own queen to the usurped hive (Cunningham et al. 2014).

The organisation of attacks

A central question in bee warfare is how collective attacks are instigated and coordinated. Studies on *Lestrimelitta* robber bee species have shown that raids, which involve dozens to hundreds of bees, usually start with one or a few scouting workers (Wittmann 1985; Sakagami et al. 1993). This is followed by a small group of workers invading the targeted nest, and shortly afterwards a larger group of several dozens of robber bees (Sakagami et al. 1993; LvZ, pers. obs.). The rapid build-up of workers may be necessary to overcome the entrance guards of the attacked colony, and during the raid, *Lestrimelitta* workers guard the entrance of the attacked nest (video 3 in Table 2) and often start building a new entrance (Nogueira-Neto 1970; Sakagami and Laroca 1963). The communication signals underlying these initial phases of attack remain poorly

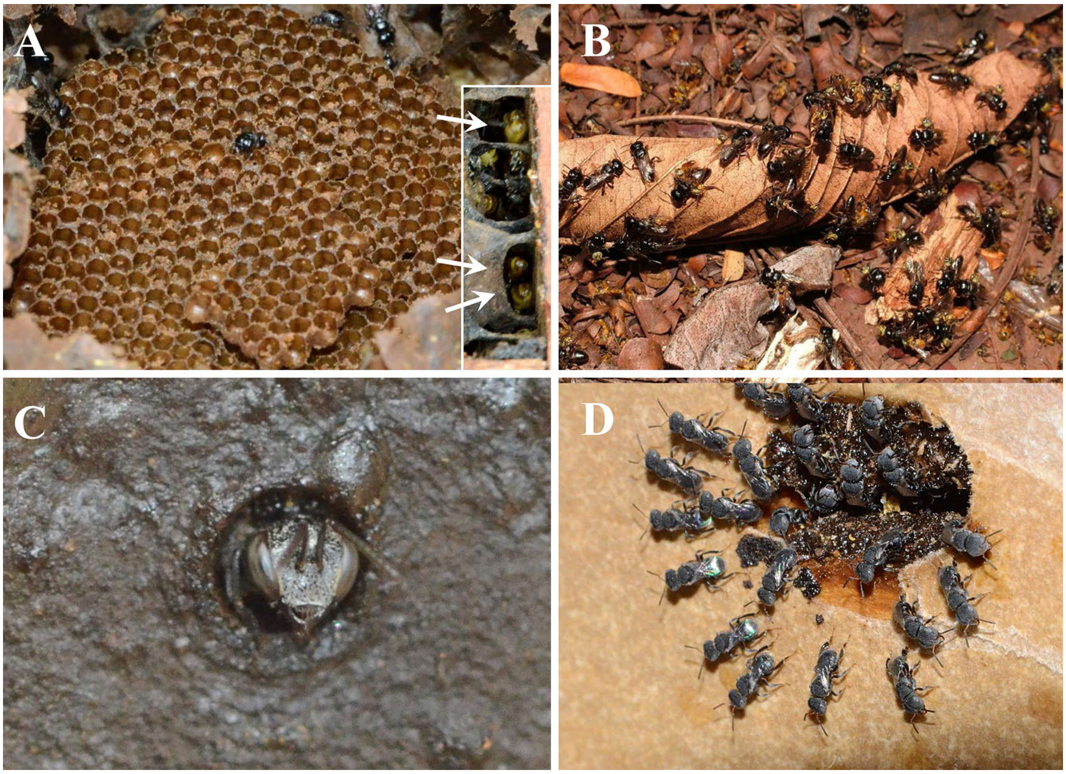

Fig. 1 **a***Aparatrigona* sp. brood nest during an attack of *Lestrimelitta maracaia*. The robber bees have removed the larval food from the brood cells. Workers of the attacked colony are hiding in the corners of the nest box (*white arrows*). Many workers have full abdomen (Photo: C. Grüter). **b** Fighting and dead workers of *Lestrimelitta limao* (*black*) and *Tetragonisca angustula* (*light brown*) on the ground near an attacked *T. angustula* colony (Photo: C. Menezes, with permission). **c** A *Frieseomelitta languida* guard in the entrance of its nest (Photo: C. Grüter). **d***Trigonisca nataliae* guards around their nest entrance (Photo: C. Grüter)

understood, but pheromones are likely to play an important role (see Lenoir et al. 2001 for a discussion of chemical strategies in parasitic ants). Sakagami et al. (1993) proposed that the lemon-like odour, citral, plays an important role in the chemical coordination of attacks. Citral is produced in the mandibular glands of robber bees and recent research suggests that volatiles emitted from the labial gland (mainly the esters hexadecyl acetate and 9-hexadecenyl acetate) also play an important role (von Zuben et al., in press). Labial gland compounds are used by other stingless bees to recruit to food sources (Jarau et al. 2004, 2006, 2010; Schorkopf et al. 2007, 2009; Stangler et al. 2009), and *Lestrimelitta* may have co-opted these pheromones to coordinate raids.

During robber bee attacks, foragers from the invaded colonies that are returning to the hive often remain hovering in front of the entrance or land in the nearby vegetation (Michener 1946; Kerr 1951; Nogueira-Neto 1970; Sakagami et al. 1993). This response to the presence of *Lestrimelitta* has led to the hypothesis that robbers use chemical compounds to disrupt defensive behaviours (Kerr 1951; Moure et al. 1958). In particular, Kerr (1951) proposed that robbers release a chemical signal that supersedes the colony or alarm odours produced by defenders, repelling attacked workers and attracting other attackers (“superseding odour” hypothesis; see D’Ettorre et al. 2000; Zimma et al. 2003; Tsuneoka and Akino 2009 for repellent pheromones in other parasitic social insects). Citral has been regarded as the main compound responsible for this reaction (Blum et al. 1970).

The “retreat message” hypothesis proposed by Nogueira-Neto (1970) argues that workers of an attacked colony release a pheromone that triggers a retreat. Thereby, a colony could avoid larger losses (Nogueira-Neto 1970). Alternatively, attacked colonies could respond to *Lestrimelitta* signals directly to avoid a costly loss of workers. Foragers of *Frieseomelitta varia* stop entering their colony in response to the extracts of labial glands of *L. limao*, but not mandibular glands (including citral), suggesting that labial gland compounds are responsible for the host response during raids (von Zuben et al., in press). This might explain why robber presence seems to have a dose-dependent effect: attacked bees gradually become more active inside the nest as the number of robbers (and thus the concentration of the attack signal) decreases towards the end of an attack (Sakagami et al. 1993). The use of heterospecific signals to avoid costly encounters with other species has also been observed during stingless bee foraging (Lichtenberg et al. 2011, 2014).

Collective attacks vary considerably in their duration. In *Lestrimelitta*, raids last from a few hours to several days or weeks, until most or all pollen, honey and larval food have been removed. Chemical signals might then trigger the gradual departure of robber bees (Sakagami et al. 1993). In the nest usurping stingless bees, *T. carbonaria* and *T. hockingsi*, fighting swarms vary in duration and intensity, from small skirmishes that last hours or a few days and have relatively small numbers of casualties (50 or less fighting pairs of bees per day) to escalated attacks that continue for several weeks and result in hundreds or even thousands of casualties each day (Heard 1996; Cunningham et al. 2014). It is these latter attacks that can eventuate in usurpation. The reason why some fights escalate whilst others are aborted remains elusive. Given the huge fitness costs (in terms of worker mortality) to the attacking *Tetragonula* colony, some form of assessment of the relative size of the target colony would be expected to be under selection prior to engaging in a full scale attack. In territorial tournaments of the honey ant *Myrmecocystus mimicus*, for example, "reconnaissance ants" gather information about the number of ants on the opposite side (Hölldobler and Wilson 2009). In *Tetragonula* (and other warring species), this assessment could include behavioural cues (e.g. activity of returning scouts), chemical cues (e.g. defence pheromone concentration), or visual cues (e.g. defending swarm size).

Selection of nests for invasion

Analysis of the literature reveals that at least 60 bee species belonging to 20 genera are involved in heterospecific conflicts: 22 species are known to attack other nests, whereas 48 species are victims of attacks (some species are both attackers and victims) (Table 1). These numbers are likely to greatly underestimate the occurrence of warfare in stingless bees: for example, 12 *Lestrimelitta* species are not recorded in Table 1 because no description of their raiding behaviour was found. Obligate robbers (*Cleptotrigona* and *Lestrimelitta*) represent 45 % of the attacking species and were involved in 74 % of the reported conflicts (Table 1). Certain species appear to be the victims of heterospecific raids more often than others (Nogueira-Neto 1970; Sakagami et al. 1993; Roubik 1989; Quezada-Euán and González-Acereto 2002). For example, the African bee *Cleptotrigona cubiceps* frequently attacks *Hypotrigona braunsi*, whereas attacks on the sympatric *H. araujoi* are very rare (Portugal-Araújo 1958). Furthermore, species that may frequently be attacked in one area, may not be attacked in another: *Scaptotrigona pectoralis* is a popular target of *Lestrimelitta danuncia* in Panama (Sakagami et al. 1993), whereas in Mexico it shows a strong defensive reaction towards *Lestrimelitta niitkib* and colonies are not normally attacked (Quezada-Euán and González-Acereto 2002). Even within a population, some colonies are targeted repeatedly by *Lestrimelitta*, while other colonies from the same species remain undisturbed (e.g. *Plebeia droryana*; Nogueira-Neto 1970; Sakagami et al. 1993). This also appears to be the case in Australian *Tetragonula* species, where hives often coexist in close proximity without any observed fighting, whilst particular hives are prone to frequent attacks (T. Heard, personal communication). Choosing the right colony to attack would be expected to be under strong selection, particularly if a poor choice leads to high mortality in attacking workers. Selection could therefore favour choosing nests that provide the highest rewards (maximising gains), or the recognition of weaker species and weaker colonies within species (decreasing losses). There are several hypotheses regarding factors that might influence selection of victims.

Preferred victims harbour high quality rewards

Both quality and quantity of stored resources should play a role in obligate and facultative robbing as this strongly determines the overall fitness benefits of an invasion (Roubik 1989). In *L. niitkib*, evidence suggests that colonies prefer to attack species that produce honey with a higher sugar content (Quezada-Euán and González-Acereto 2002). To explore this further, we have combined the data of Quezada-Euán and González-Acereto (2002) and Sakagami et al. (1993) to test whether the total sugar content of the honey (see Table S1) predicts whether a species is a victim of *Lestrimelitta* in a given area. A phylogenetically controlled analysis showed that the honey of known victim species had significantly higher sugar content, whereas the abundance of a species in a given population does not predict the likelihood for being attacked (Fig. 2, details in legend). Sugar content is known to affect resource exploitation in other bees. In honey bees (*Apis mellifera*), for example, foragers are more likely to communicate about and return to food sources of higher sugar content (von Frisch 1967; Al Toufailia et al. 2013). The amount of resources stored in colonies might also be important, but more natural history information about food stores is needed to test this. Stored food would also be expected to play a role in attacks where usurpation occurs, but since the attacking colony takes up residence in the nest of their victims, species-specific features of hives (e.g. cavity size and location) are likely to determine suitability for (and thus likelihood of) usurpation.

Victims have smaller colonies

Attacking small colonies might be beneficial because a smaller number of defenders must be overcome (Hölldobler

Table 1 Stingless bee species involved in aggressive inter-specific interactions

Attacking species	Attacked species	Context	Attacks successful?	Aggressive defense?	Colony size attacker	Colony size defender	Colony size a–d	Body size attacker	Refs
Apis mellifera	*Melipona scutellaris*	?	Occasionally	Yes	10,000–60,000^{a,h}	400–2000^{d,h}	+	Similar	Schwarz (1948)
Cleptotrigona cubiceps	*Hypotrigona araujoi***	Raid	Quite resistant	Yes		2500 ^{h}		Larger	Portugal-Araújo (1958)
Cleptotrigona cubiceps	*Hypotrigona braunsi*	Raid	Yes	Low		100–750 ^{h}		Larger	Portugal-Araújo (1958)
*Lestrimelitta danuncia**	*Frieseomelitta nigra*	Raid	Yes	?	900^{b}	400–1500^{a,b,d}	~	Larger	Sakagami et al. (1993)
*Lestrimelitta danuncia**	*Melipona eburnea*	Raid	Yes	No	900^{b}			Smaller	Sakagami et al. (1993)
*Lestrimelitta danuncia**	*Melipona favosa*	Raid	Yes, based on 1 raid	?	900^{b}	60–700^{b,d,e}	+	Smaller	Sakagami et al. (1993)
*Lestrimelitta danuncia**	*Nanno. perilampoides*	?	Yes	No	900^{b}	700–2000^{a,c}	~		Sakagami et al. (1993), Michener (1946)
*Lestrimelitta danuncia**	*Paratrigona ornaticeps*	Raid	Yes	?	900^{b}	1100–2400^{b}	–	Larger	Sakagami et al. (1993)
*Lestrimelitta danuncia**	*Paratrigona* sp.	?	?	?	900^{b}				Roubik (1989)
*Lestrimelitta danuncia**	*Partamona aff. cupira*	Raid	Yes, based on 1 raid	Yes	900^{b}	2000–2900^{b,h}	–	Similar	Sakagami et al. (1993)
*Lestrimelitta danuncia**	*Scaptotrigona barrocoloradensis*	Raid	Yes	Occasionally	900^{b}	3000–7827^{b,d}	–	Similar	Sakagami et al. (1993)
*Lestrimelitta danuncia**	*Scaptotrigona luteipennis*	Raid	Yes	Probably not	900^{b}				Sakagami et al. (1993)
*Lestrimelitta danuncia**	*Scaptotrigona pectoralis*	Raid	Yes	No	900^{b}	2000–5200^{a,b}	–		Sakagami et al. (1993)
*Lestrimelitta danuncia**	*Scaura latitarsis*	Raid	Yes	No	900^{b}	387–450^{b}	+	Larger	Sakagami et al. (1993)
*Lestrimelitta danuncia**	*Tetragonisca angustula*	Raid	Occasionally	Yes	900^{b}	2000–8000^{d,h}	–	Larger	Sakagami et al. (1993)
*Lestrimelitta danuncia**	*Trigona muzoensis*	Raid	Yes, based on 1 raid	Yes	900^{b}				Sakagami et al. (1993)
*Lestrimelitta ehrhardti**	*Melipona quadrifasciata*	Usurpation/ raid	Yes	Yes		300–1500^{d,h}		Smaller	Sakagami et al. (1993), Sakagami and Laroca (1963)
Lestrimelitta guyanensis	*Melipona* sp.	Raid	Yes	?	2890^{e}			Smaller	e
Lestrimelitta limao	*Apis mellifera*	Raid	Often	Yes	2000–7000^{f,j}	20,000–60,000^{a,h}	–	Smaller	Schwarz (1948), Sakagami et al. (1993), Nogueira-Neto (1997), Rech et al. 2013
Lestrimelitta limao	*Friesella schrottkyi*	Raid	Yes	?	2000–7000^{f,j}	300–2500^{d,h}	+	Larger	Sakagami et al. (1993)
Lestrimelitta limao	*Frieseomelitta silvestrii*	Raid	?	?	2000–7000^{f,j}	400–600 ^{h}	+	Larger	Nogueira-Neto (1997)

Table 1 continued

Attacking species	Attacked species	Context	Attacks successful?	Aggressive defense?	Colony size attacker	Colony size defender	Colony size a–d	Body size attacker	Refs
Lestrimelitta limao	*Frieseomelitta varia*	Raid	Quite resistant	Yes	2000–7000^{f,j}	800–1600^{d}	+	Larger	Sakagami et al. (1993), Nogueira-Neto (1997)
Lestrimelitta limao	*Melipona bicolor****	?	No, strong defense	Yes	2000–7000^{f,j}	150–800^{d}	+	Smaller	Sakagami et al. (1993), Sakagami and Laroca (1963)
Lestrimelitta limao	*Melipona fasciata*	?	Yes	No	2000–7000^{f,j}	200–2500^{b,d}	+	Smaller	Roubik (1989)
Lestrimelitta limao	*Melipona quadrifasciata*	Raid	Yes	Occasionally	2000–7000^{f,j}	300–1500^{d,h}	+	Smaller	Sakagami et al. (1993), Sakagami and Laroca (1963), Nogueira-Neto (1997)
Lestrimelitta limao	*Melipona rufiventris*	Raid	Relatively resistant	Yes	2000–7000^{f,j}	500–700 ^{g}	+	Smaller	Pompeu and Silveira (2005)
Lestrimelitta limao	*Nanno. testaceicornis*	Raid	Yes	Low	2000–7000^{f,j}	2000–3000 ^{h}	~	Larger	Sakagami et al. (1993), Bego et al. (1991), Nogueira-Neto (1970)
Lestrimelitta limao	*Plebeia catamarcensis*	Raid	Yes	No	2000–7000^{f,j}				Laroca and Orth (1984)
Lestrimelitta limao	*Plebeia droryana*	Raid	Yes	Rarely	2000–7000^{f,j}	3000^{d}	~	Larger	Sakagami et al. (1993), Nogueira-Neto 1997, Bego et al. (1991), Nogueira-Neto (1970)
Lestrimelitta limao	*Plebeia emerina*	Raid	Yes	Low	2000–7000^{f,j}				Sakagami and Laroca (1963), Bego et al. (1991)
Lestrimelitta limao	*Plebeia franki*	Raid	Yes	?	2000–7000^{f,j}				Sakagami et al. (1993)
Lestrimelitta limao	*Plebeia remota*	Raid	No, small entrance		2000–7000^{f,j}	800–5000^{d}	~		Sakagami and Laroca (1963), Nogueira-Neto (1970)
Lestrimelitta limao	*Scaptotrigona bipunctata*	Raid	Yes	?	2000–7000^{f,j}			Smaller	Laroca and Orth (1984)
Lestrimelitta limao	*Scaptotrigona postica*	Raid	Yes	Occasionally	2000–7000^{f,j}	2000–50,000^{d,h}	~	Smaller	Sakagami et al. (1993)
Lestrimelitta limao	*Scaptotrigona* sp.	?	?	?	2000–7000^{f,j}				Roubik (1989)
Lestrimelitta limao	*Scaptotrigona tubida*	Raid	Yes	?	2000–7000^{f,j}	1764^{e}	+	Larger	Laroca and Orth (1984)
Lestrimelitta limao	*Scaura* sp.	?	?	?	2000–7000^{f,j}				Roubik (1989)
Lestrimelitta limao	*Tetragonisca angustula*	Raid	Occasionally	Yes	2000–7000^{f,j}	2000–8000^{d,h}	~	Larger	Bego et al. (1991), Sakagami et al. (1993)
Lestrimelitta limao	*Trigonisca* sp.	Raid	Yes	?	2000–7000^{f,j}			Larger	Sakagami et al. (1993)
Lestrimelitta maracaia	*Aparatrigona* sp.	Raid	Yes, based on 1 raid	?					pers. obs. FS and CG

Table 1 continued

Attacking species	Attacked species	Context	Attacks successful?	Aggressive defense?	Colony size attacker	Colony size defender	Colony size a–d	Body size attacker	Refs
*Lestrimelitta mourei**	*Plebeia frontalis*	Raid	Yes	No	>1100^{i}	100^{b}	+		Johnson (1987)
*Lestrimelitta mourei**	*Trigona dorsalis*	Raid	Yes	?	>1100^{i}	1500–2000^{b}	~		Hubbell and Johnson (1977)
*Lestrimelitta mourei**	*Trigona fulviventris*	Raid	Yes, based on 1 raid	Yes	>1100^{i}	2000– >10,000^{b}	~	Smaller	Johnson (1987)
Lestrimelitta niitkib	*Apis mellifera*	Raid	Yes	Yes	3000–5000^{a}	20,000–60,000^{a,h}	–	Smaller	Quezada-Euán and González-Acereto (2002)
Lestrimelitta niitkib	*Frieseomelitta nigra*	Raid	Yes	No	3000–5000^{a}	400–1500^{a,b,d}	+	Larger	Quezada-Euán and González-Acereto (2002)
Lestrimelitta niitkib	*Melipona beechi*	Raid	Yes	Yes	3000–5000^{a}	500–3000^{d}	+	Smaller	Quezada-Euán and González-Acereto (2002)
Lestrimelitta niitkib	*Nanno. perilampoides*	Raid	Yes	No	3000–5000^{a}	700–2000^{a,c}	+		Quezada-Euán and González-Acereto (2002)
Lestrimelitta niitkib	*Plebeia frontalis*	Raid	Yes	No	3000–5000^{a}	100^{b}	+		Quezada-Euán et al. (2013)
Lestrimelitta rufa	*Partamona vicina*	?	No	?					Camargo and Pedro (2003)
Lestrimelitta rufipes	*Duckeola ghiliani*	?	?	Yes		10,000^{d}		Smaller	Rech et al. (2013)
Lestrimelitta rufipes	*Scaptotrigona* sp.	?	Yes	No					Rech et al. (2013)
Lestrimelitta rufipes	*Scaptotrigona tricolorata*	?	Yes	Yes					Gonzalez et al. (2010)
Melipona fuliginosa	*Apis mellifera*	Raid	Yes	Yes	250–600^{b}	20,000–60,000^{a,h}	–	Similar	Roubik (1989)
Melipona fuliginosa	*Melipona flavolineata*	Raid	Yes	?	250–600^{b}	1000–3000^{f}	–	Similar	Camargo and Pedro (2008)
Melipona fuliginosa	*Melipona seminigra*	Raid	Yes	Yes	250–600^{b}	1000–3000^{f}	–	Similar	Nogueira-Neto (1997)
Melipona quadrifasciata	*Melipona rufiventris*	Raid	Yes	Yes	300–1500^{d,h}	500–700 ^{g}	~	Similar	Video 1
Melipona rufiventris	*Melipona quadrifasciata*	?	No	Yes	500–700 ^{g}	300–1500^{d,h}	~	Similar	Schwarz (1948)
Melipona scutellaris	*Melipona marginata*	?	?	?	400–2000^{d,h}	50–2500^{d}	~	Larger	Schwarz (1948)
Melipona scutellaris	*Scaptotrigona postica*	?	?	?	400–2000^{d,h}	2000–50,000^{d,h}	–	Smaller	Schwarz (1948)
Oxitrigona mellicolor	*Apis mellifera*	Raid	Yes	No	5442^{b}	20,000–60,000^{a,h}	–	Smaller	Rinderer et al. (1988)
Oxitrigona tataira	*Apis mellifera*	Raid	Yes	Yes	1900^{b}	20,000–60,000^{a,h}	–	Smaller	Roubik (1989), Nogueira-Neto (1997)
Scaptotrigona pectoralis	*Lestrimelitta* sp.	?	Yes	Yes	2000–5200^{a,b}			Similar	Nogueira-Neto (1997)
Scaptotrigona postica	*Oxitrigona* sp.	?	Yes	Yes	2000–50,000^{d,h}			Similar	Schwarz (1948)
Tetragonisca angustula	*Apis mellifera*	Usurpation	Yes	Yes	2000–8000^{d,h}	20,000–60,000^{a,h}	–	Smaller	Kerr (1951)
Tetragonisca angustula	*Lestrimelitta limao*	Usurpation	Yes	Yes	2000–8000^{d,h}	2000–7000^{f,j}	~	Smaller	Schwarz (1948)
Tetragonisca angustula	*Melipona eburnea*	Usurpation	Yes	Yes	2000–8000^{d,h}			Smaller	Sakagami et al. (1993)
Tetragonisca angustula	*Melipona favosa*	Usurpation	Yes	Yes	2000–8000^{d,h}	60–700^{b,d,e}	+	Smaller	Sakagami et al. (1993)

Table 1 continued

Attacking species	Attacked species	Context	Attacks successful?	Aggressive defense?	Colony size attacker	Colony size defender	Colony size a–d	Body size attacker	Refs
Tetragonisca angustula	*Nanno. perilampoides*	Usurpation	Yes	Yes	2000–8000^{d,h}	700–2000^{a,c}	+		Sakagami et al. (1993)
Tetragonisca angustula	*Plebeia emerina*	Raid	Yes	Occasionally	2000–8000^{d,h}				Sakagami and Laroca (1963)
Tetragonisca angustula	*Scaptotrigona barrocoloradensis*	Usurpation	Yes	Yes	2000–8000^{d,h}	3000–7827^{b,d}	~	Smaller	Sakagami et al. (1993)
Tetragonisca angustula	*Scaptotrigona postica*	?	?	?	2000–8000^{d,h}	2000–50,000^{d,h}	~	Smaller	Schwarz (1948)
Tetragonula hockingsi	*Tetragonula carbonaria*	Usurpation	Yes	Yes	3000–10,000^{d}	2500–8000^{d}	~	Similar	Cunningham et al. (2014)
Trigona hyalinata	*Melipona rufiventris*	Raid	Yes	Yes	43,758^{e}	500–700 ^{g}	+	Smaller	Nogueira-Neto (1997)

Information about relative body sizes are from unpublished observations (CG, LvZ, FS). + indicates that the attacking species (a) has larger average colony sizes than the defending species (d), whereas – indicates that defending colonies are expected to have larger colonies. The context (raid vs. usurpation) refers to the observations reported in the cited studies

* *L. limao* before Camargo and Pedro (2013), ** *H. braunsi* before Eardley (2004), *** *M. nigra* before Camargo and Pedro (2013)

[a] Quezada-Euán and González-Acereto 2002, [b] Roubik 1983, [c] Quezada-Euán et al. 2011, [d] Tóth et al. 2004, [e] Roubik 1979, [f] C. Menezes, unpublished estimates, [g] Nieh et al. 2005, [h] Michener 1974, [i] Johnson 1987, [j] von Zuben, L. and Grüter, C. unpublished estimates

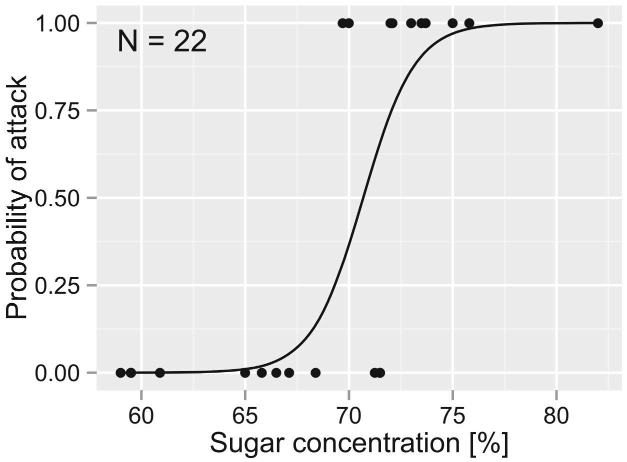

Fig. 2 Sugar content of honey of both victim and non-victim species inhabiting the same areas. The plot shows the raw data (see Table S1). The average sugar concentration (data predominantly from Roubik 1983; Quezada-Euán and González-Acereto 2002; see Table S1) of the species that were attacked by *Lestrimelitta* was 73.7 ± 3.5 % (mean ± SD; $N = 10$) *versus* 65.5 ± 4.8 % in the species that were not attacked ($N = 12$) (Fig. 2). There was a tendency for sugar content to affect the probability that a species was a victim of *Lestrimelitta* (logistic regression, $z = 1.9$, $p = 0.06$). The prevalence of a species (number of colonies in the study areas) had no effect ($z = 0.4$, $p = 0.66$). To explore this further, we used a generalised least squares model that controlled for phylogenetic relationships (Paradis 2011). The phylogenetic tree was based on Ramírez et al. (2010) and Rasmussen and Cameron (2010). Branch length was set equal and a Brownian motion model was used (Paradis 2011). The GLS showed that the sugar content of attacked species was significantly higher than of non-attacked species (Brownian motion model: $t = 4.2$, $p < 0.001$; excluding the honeybee: $p = 0.0084$)

1976), reducing the overall mortality costs for the attacking colony. Relative colony size is particularly important if the outcome of battles follows the “square law” of combats (in ants: Whitehouse and Jaffe 1996; McGlynn 2000). In this scenario, individuals are killed at a rate proportional to the number of opponents (i.e. individual worker strength has little benefit) and the side with the greatest number of opponents will win. Nest usurpation in *T. hockingsi* and *T. carbonaria* fits well with this hypothesis (Cunningham et al. 2014). Thus we would expect colony size to be a good predictor of vulnerability. However, if colony size is small because of a disease, then attackers risk acquiring pathogens (Breed et al. 2012; Lindström et al. 2008). Furthermore, smaller colonies are likely to have fewer resources, which can favour a preference for larger colonies through increased rewards and the necessity for fewer attacks per year (Pohl and Foitzik 2011).

In *Lestrimelitta*, evidence suggests that weaker colonies are better targets: *L. limao* has been observed killing smaller *Melipona rufiventris* colonies, whereas strong *M. rufiventris* colonies aggressively repel attacks (Pompeu and Silveira 2005). Similarly, in attacks on *Apis mellifera* colonies, *L.*

limao appears to be more successful when attacking weaker colonies (Nogueira-Neto 1997). However, it is not clear whether attackers preferentially target weaker or smaller colonies. To investigate this further we explored the effect of colony size on *Lestrimelitta* attacks from Sakagami et al. (1993) and Quezada-Euán and González-Acereto (2002) (Table S1). Attacked species did not have significantly different colony sizes (6170 ± 10,953 workers) than non-attacked species (4111 ± 10,143 workers) (phylogenetically controlled Brownian motion model: $t = 1.73$, $p = 0.09$, see legend of Fig. 2 for more details). An examination of the colony size data provided in Table 1, shows that in 19 instances (58 %) attacking species have larger estimated colonies sizes than victim species, whereas in 14 cases (42 %) aggressor species have smaller estimated colony sizes (Chi square test: $\chi^2 = 0.76, df = 1, p = 0.38$).

Victims are chosen based on defensive abilities

Aggressors might be expected to have superior fighting abilities (Hamilton 2002), with victims being weaker, less aggressive or having a poor defence. In support of this, raids often occur with no or only slight mortality among attackers (Nogueira-Neto 1970; Sakagami et al. 1993). *L. niitkib*, for example, seems to prefer species that show less defensive behaviours towards robbers (Quezada-Euán and González-Acereto 2002). On the other hand, the aggressively defending *T. angustula* is frequently attacked by *L. limao* (Bego et al. 1991; Nogueira-Neto 1970) and attacking colonies often loose many workers in these attacks (Nogueira-Neto 1970; Sakagami et al. 1993; Fig. 1b). Raids leading to high mortality on the attacker side could result from an inability to recognise an aggressively defending species (Johnson 1987).

According to the data summarised in Table 1, attackers had a larger body size than victims in 16 instances, while in 26 instances victim workers were larger. Both *Lestrimelitta* sp. and *Cleptotrigona cubiceps* workers are relatively small (Friese 1931). For example, *L. limao* weighs approx. 13 mg (Grüter et al. 2012) but attacks species that are considerably larger, e.g. *Melipona* (c. 50–100 mg). Overall, worker size does not seem to be an important factor in host colony selection (also noted by Kerr 1951).

Victims are chosen based on chemical similarity of recognition cues

The ability of entrance guards to detect intruders depends on the visual and chemical similarity of nestmates and non-nestmate intruders (Bowden et al. 1994; D'Ettorre et al. 2006; Jones et al. 2012; Martin et al. 2012; Nunes et al. 2008) and it might be easier to infiltrate a colony and initiate an attack if the first scouts remain undetected. Accordingly, Quezada-Euán et al. (2013) showed that the cuticular hydrocarbon profile of *Lestrimelitta niitkib* is more similar to the chemical profile of preferred host species compared to non-preferred species (see Guillem et al. 2014 for an ant example). On the other hand, guards of many species strongly alter their behaviour in the presence of *Lestrimelitta* workers (or chemical and visual cues resembling *Lestrimelitta*) suggesting they are aware of the presence of invaders (e.g. Nogueira-Neto 1970; van Zweden et al. 2011; Nunes et al. 2014). Frequently attacked species should be under strong selection to evolve the ability to recognise when they are being attacked and show an adaptive response.

Additional intrinsic and extrinsic factors

A number of other factors could affect the likelihood of warfare. For example, most *Lestrimelitta* attacks occur during the wet season when raided colonies did not have large amounts of stored food (Sakagami et al. 1993). In these conditions, *Lestrimelitta* colonies would have to raid more colonies to acquire a given amount of food. On the other hand, colony and/or worker sizes of victims might be reduced when food stores are lower (Ramalho et al. 1998; Veiga et al. 2013), which might facility invasions during the wet season. *Tetragonula* battles, on the other hand, do not seem to depend on the season (Cunningham et al. 2014). Intrinsic factors favouring swarming, e.g. large colony size and food stores, are likely to increase the occurrences of nest usurpation.

Defending the nest

The constant threat of invasion has led to many defensive adaptations in behaviour, morphology and nest architecture.

Structural defence: small entrance holes, intranidal mazes and false nests

The main access to a nest is the entrance tunnel, for which relative sizes vary greatly among species (Biesmeijer et al. 2007; Couvillon et al. 2008; Lima et al. 2013). A narrow entrance is easier to defend at the cost of restricting foraging traffic (Fig. 1c) (Biesmeijer et al. 2007; Couvillon et al. 2008). Comparative studies show that species with relatively larger entrances may solve the challenge of a well-defended nest by having a larger number of entrance guards (Biesmeijer et al. 2007; Couvillon et al. 2008). Guards in species with larger entrances may also be more aggressive (Biesmeijer et al. 2007); whilst smaller, more easily defendable entrances have been shown to be associated with a small colony size (Biesmeijer et al. 2007).

Defence chambers and false nests are remarkable structural features that have evolved in *Partamona* spp. (Camargo and Pedro 2003; Michener 1974; Roubik 1989). Workers build intricate structures made from mud and resin in chambers adjacent to the nest entrance (Fig. 3). These defence chambers may function to distract and delay attackers, or provide space for guards. So-called false nests can contain empty cells, food pots and wax sheets, and Camargo and Pedro (2003) argue that these structures play a significant role in defence against insect attackers, in particular *Lestrimelitta*. During a *L. rufa* attack on a *Partamona vicina* colony, robbers only occupied the false nest, while the actual brood chamber remained unharmed. *Partamona ferreirai* workers block the access tunnel to the brood and food chambers with a sticky resinous substance within minutes after disturbance (Camargo and Pedro 2003). Thus, false nests may distract attackers and thereby give attacked colonies time to seal the vital parts of the nest.

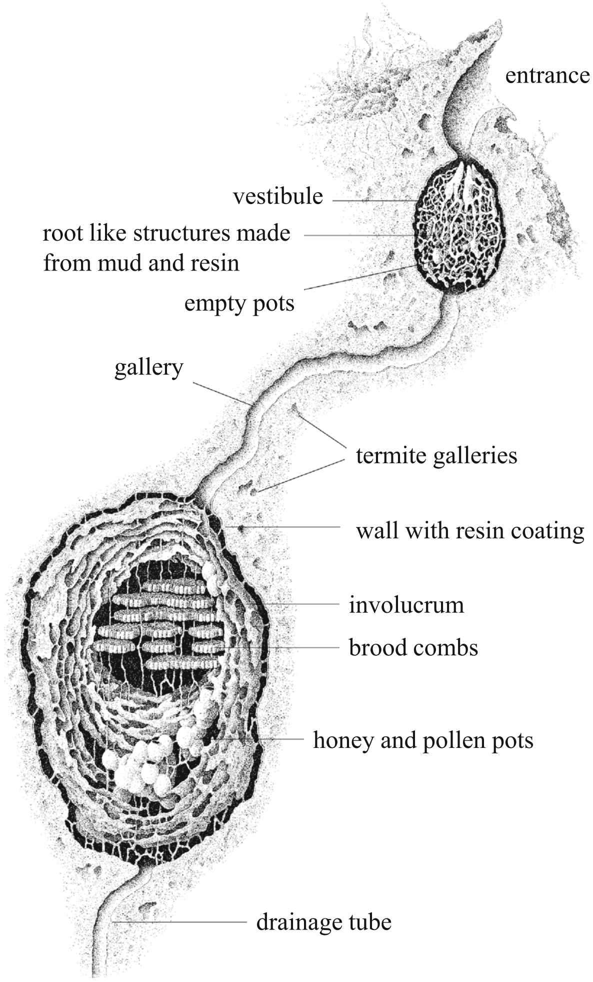

Fig. 3 *Partamona testacea* nest in an active termite nest, *Syntermes* sp., Amazonas state, Brazil (from Camargo and Pedro 2003, with permission)

Behavioural defence: entrance blocking, resin use and guarding

The blocking of the entrance or tunnels leading to the brood and food pots are potentially efficient ways to prevent severe damage during attacks. Unfortunately, despite numerous anecdotal accounts and descriptions of different types of blocking behaviours, systematic studies about this phenomenon are rare (but see Nunes et al. 2014). Virgilio de Portugal-Araujo (reported in Kerr 1984), for example, observed that *Melipona seminigra* makes small balls of mud, which workers use to block the entrance during attacks of *Lestrimelitta*. Other *Melipona* species use balls of batumen (a mix of mainly wax and resin) for entrance blocking during *Lestrimelitta* attacks (Nunes et al. 2014). *Hypotrigona braunsi* workers reportedly block the entrance by pouring honey from the inside into the tube during attacks of *Cleptotrigona cubiceps* (Portugal-Araújo 1958). This would appear to be a costly way of stopping an attack as it kills all bees in the entrance tube, including defenders, and the honey is subsequently collected by the attackers (Portugal-Araújo 1958). In species with small entrance holes, guards can block the entrance with their heads (Sakagami et al. 1993; Fig. 1c). Another commonly observed phenomenon is that nest guards (e.g. *Frieseomelitta* and *Tetragonisca*) carry sticky resinous substances in their corbiculae or in their mandibles, which they attach onto attackers during fights, presumably to immobilise them (Sakagami 1982; Nunes et al. 2014).

Stingless bee entrances are defended by nest-entrance guards that prevent intruders from entering (Fig. 1d; video 4 in Table 2) (Biesmeijer et al. 2007; Couvillon et al. 2008;

Table 2 Some of the behaviours we describe can be seen on videos provided by the authors

Description	Address
Video 1: A *Melipona quadrifasciata* colony attacking a *M. rufiventris* colony	http://youtu.be/-yFsJPYggMk
Video 2: Large scale warfare between *Tetragonulacarbonaria* and *T. hockingsi*	http://youtu.be/FOX_CGqP0vE
Video 3: *L. limao* workers at the entrance of a *P. droryana* nest during a raid	http://youtu.be/3oJBGfMLfF4
Video 4: Two types of guards in *Tetragonisca angustula*	http://youtu.be/P6Q4LGVDgh8
Video 5: *Lestrimelitta limao* bee immobilised by a *T. angustula* guard attached to a wing	https://youtu.be/3o_QoTlkgKo

Below is a description and the corresponding internet address van Zweden et al. 2011; Wittmann 1985). The recognition of con- and heterospecific intruders in stingless bees can be based on either visual or chemical recognition or both (Bowden et al. 1994; Nunes et al. 2008; van Zweden et al. 2011; Jones et al. 2012; Couvillon et al. 2013; Quezada-Euán et al. 2013). The most common behavioural response of guards under attack is biting of the opponent (Michener 1974; Shorter and Rueppell 2012; Shackleton et al. 2015). Additionally, guards often release alarm pheromones when under threat (Cruz-López et al. 2007; Schorkopf et al. 2009; Nunes et al. 2014), which in turn can mobilise more guards (Gloag et al. 2008; Nunes et al. 2014). More specific responses are the use of caustic chemical secretions in *Oxitrigona* sp. (Michener 1974; Rinderer et al. 1988).

In usurping *Tetragonula* bees, colonies exhibit defensive swarming in response to the presence of non-nestmates at the nest entrance (Gloag et al. 2008). This defensive behaviour, in which hundreds of workers swarm in close proximity to the hive entrance, can be triggered by a small number of non-nestmate workers (Gloag et al. 2008; see Wittmann et al. 1990 for a similar behaviour in the Neotropical *T. angustula*), suggesting that such swarming is an evolutionary adaptation to what may be a serious threat to the hive. Defensive swarms may be in preparation for an attack, or may function to prevent invading scouts from entering the hive or returning to their colony. Given the high mortality costs in these *Tetragonula* battles, combined with the outcome being dependent on colony size, defensive swarms could also function as a show of strength to warn would be invaders of the size of the targeted colony.

Morphological adaptations: soldiers

At least one stingless bee has evolved a morphologically specialised soldier caste. *Tetragonisca angustula* is a common and widespread Neotropical stingless bee that is frequently involved in battles with *Lestrimelitta* species (Nogueira-Neto 1970; Bego et al. 1991; Sakagami et al. 1993) (Fig. 1b). It responds aggressively to objects that visually or chemically resemble *Lestrimelitta* workers (Wittmann 1985; Bowden et al. 1994; van Zweden et al. 2011). *T. angustula* colonies are defended by two groups of soldiers: hovering soldiers, and soldiers that stand around the entrance tube (video 4 in Table 2) (Wittmann 1985; Kärcher and Ratnieks 2009; Grüter et al. 2011; van Zweden et al. 2011). Soldiers are morphologically different from foragers (Grüter et al. 2012; Segers et al. 2015; Hammel et al. 2016): they are larger and some body parts differ in their relative size. It has been suggested that the unusual defence in *T. angustula* has evolved as a response to *Lestrimelitta* attacks (Wittmann 1985; Bowden et al. 1994; Grüter et al. 2012; Segers et al. 2016) and the size of soldiers is positively correlated with fighting ability against *L. limao* workers (Grüter et al. 2012). Furthermore, in areas where *Lestrimelittalimao* is more common, *T. angustula* colonies have more soldiers defending the entrance (Segers et al. 2016). Even though guards often die during fights against the larger *L. limao* workers, they are highly effective in immobilizing *L. limao* workers by biting the wings (Grüter et al. 2012) (video 5 in Table 2).

Colony mortality

Colony mortality caused by interspecific wars has been reported in several species (Müller 1874; Michener 1946; Schwarz 1948; Portugal-Araújo 1958; Sakagami and Laroca 1963; Nogueira-Neto 1970; Johnson 1987; Bego et al. 1991; Sakagami et al. 1993; Quezada-Euán and González-Acereto 2002; Pompeu and Silveira 2005; Cunningham et al. 2014). However, the damage caused by attacks is often difficult to quantify because even raids with minor adult mortality can potentially be lethal. *Lestrimelitta* workers often empty food stores and remove brood food, thereby killing all eggs and young larvae (Fig. 1a). This could lead to the slow death of colonies weeks after the attack. Death of the invaded colony is inevitable after a successful usurpation by Australian *Tetragonula* species and the introduction of a daughter queen, though the fate of the emerging workers from the defeated hive is unknown (Cunningham et al. 2014). Some species have evolved ways to avoid a complete removal of resources: during raids, *Aparatrigona*, *Nannotrigona* or *Plebeia* workers can be seen hiding in corners with their abdomen completely filled with liquid food (Nogueira-Neto 1970; Fig. 1a).

Fight or flight?

Iyengar (2008) suggested that the response to cleptoparasitism is largely dichotomous across animal taxa: while some species actively fight robbers, others seem to relinquish their resources without a fight (‘retaliation’ vs. ‘toleration’). Most reports of attacks in stingless bees are consistent with this dichotomy (Table 1). Fleeing has the advantage that most adult workers and some of the food stores are spared during an attack. Eggs, young larvae and large amounts of the food stores, however, are lost. Overall, the costs are relatively predictable for a colony. In the case of an aggressive defence, costs are more complex and variable among different attacks. If an aggressive defence, e.g. by the soldiers at the nest entrance of a *T. angustula* colony can prevent an attack in an early stage by killing the *Lestrimelitta* scouts, then costs might be close to zero. If, however, a large scale *Lestrimelitta* attack cannot be prevented, costs can be very high as colonies risk losing eggs, larvae, many adult workers and their food stores. The existence of a ‘retaliation’ response in several species suggests that *Lestrimelitta* attacks are often successfully prevented at an early stage, but more observations are needed to quantify the occurrence of unsuccessful *Lestrimelitta* attacks.

Conclusions and open questions

Given that warfare is relatively widespread and often has dramatic consequences for colonies, surprisingly little is known about aggressive strategies of resource acquisition in stingless bees. In particular, more information is needed about species with non-obligate robbing or usurping behaviour. One important obstacle to research is that it is often difficult to follow the flying invaders and locate the attacking colony in order to study it. Nests might be located in remote locations or high up in trees. However, the literature clearly shows that warring stingless bees show considerable variation in the nature of attacking and defending strategies and we are beginning to understand how ecological, chemical or life-history traits might explain this variation. Some questions are of particular interest for further research. For example, how are attacks organised and coordinated? Why do *Lestrimelitta* or *Tetragonula hockingsi* occasionally attack aggressively defending species? Under what circumstances does warfare provide higher payoffs than more conventional methods of acquiring resources? Why do some species retaliate, while others tolerate? Does learning play a role in host selection? Empirical studies performed in semi-natural bee yards can circumvent some of the methodological problems mentioned above and improve our understanding of the costs and benefits of different strategies for both parties and, thereby, help us understand the evolution of this strategy.

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