

S

Social Parasitism



Christian Rabeling
School of Life Sciences, Arizona State University,
Tempe, AZ, USA

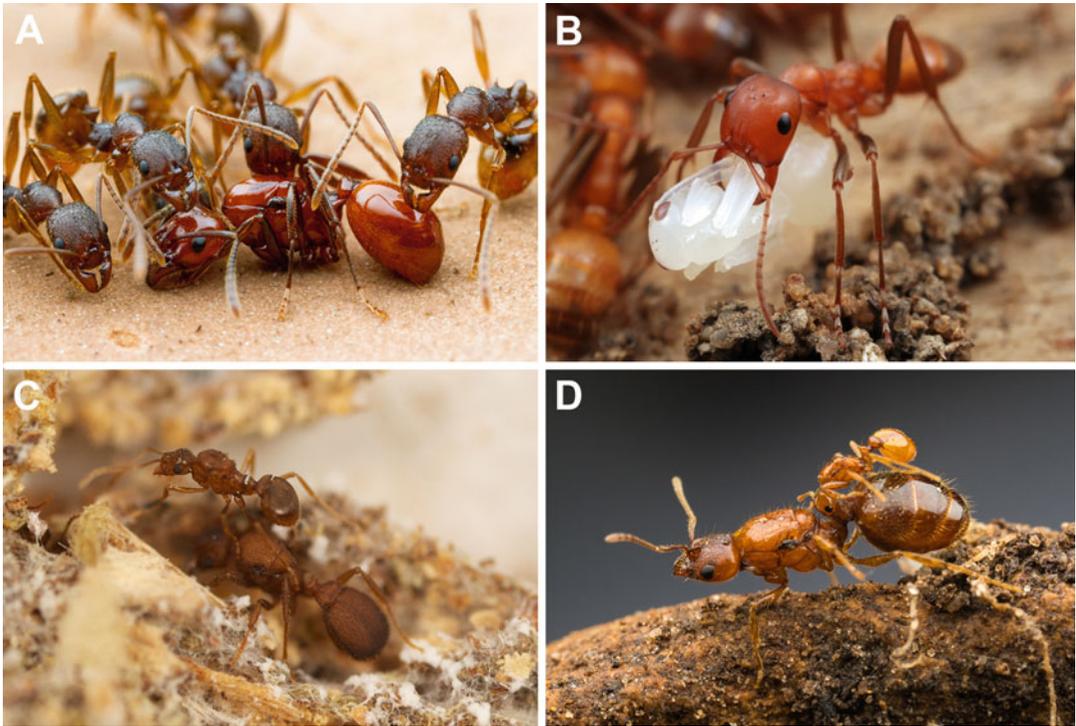
In the broadest sense, social parasitism is a form of brood parasitism, where the social parasite depends on the social behavior of the host for survival and reproduction. Brood parasitism is known from a variety of vertebrate species, such as mammals, birds, and fishes, where the host's brood care behavior is exploited by the parasite. Brood parasitism has been studied in great detail in some bird species, including cuckoos, cow birds, and honeyguides, where parasites lay their eggs into the nests of the host, deceiving the host into providing parental care for their offspring.

In social insects, social parasites also exploit the brood care behavior of their hosts and can therefore be regarded as brood parasites. However, and in addition to exploiting the brood care behavior, the hosts of social parasites also provide added benefits associated with a social colony life, augmenting the social parasite's survival and reproductive fitness. Social services provided by the host include nest construction and defense, foraging and feeding of the adult parasite and its brood, as well as grooming and other hygiene-related behaviors. Some social parasite species are facultatively dependent on their host and require the host's assistance for only part of their

life cycle, such as colony founding, but are otherwise able to live independently without the host's help. Alternatively, social parasites can be obligately dependent on their hosts' social behavior.

Among the Hymenoptera, social parasitism is commonly found in ants, social bees, and social wasps [25] (Figs. 1–4). However, it is not always easy to recognize a true social parasite because insect societies are readily exploited by scavengers, parasites, and predators, and consequently, nests of social insects are riddled with “guests” [10, 25]. Although highly intriguing and directly relevant to understanding the rich biology of social parasites, this overview primarily focuses on interspecific social parasitism among eusocial Hymenoptera. Other symbiotic interactions between social insects and other organisms, such as intraspecific parasitism (which is probably a widespread but often overlooked form of social parasitism occurring in polygynous colonies of a single species), myrmecophily, interactions between social insects and vertebrates, or other symbioses of social insects with other arthropods, are only mentioned in passing or not at all.

In ants, myrmecologists have been teasing apart the many interactions between ants and other organisms that live in their nests, and these relationships occupy the full breadth of the species interaction spectrum from parasitism and predation, over commensalism to mutualism. Organisms interacting with ants in their nests can be roughly characterized as (a) ► **myrmecophiles**, which are chiefly arthropods living in ant nests



Social Parasitism, Fig. 1 Diversity of socially parasitic life histories in ants. (a) The queen of the temporary social parasite *Aphaenogaster tennesseensis* is groomed by workers of the host *A. rudis*; (b) a worker of the dulotic ant *Polyergus mexicanus* carries a stolen *Formica* pupa; (c) the inquiline social parasite *Mycocepurus castrator* stands on top of the *M. goeldii* host queen; (d) the parasitic

relationship of the tiny *Solenopsis phoretica* queen clinging to the petiole of the *Pheidole* host queen is still a mystery, but the ectoparasitic habit is reminiscent of the enigmatic *Tetramorium inquilinum* inhabiting the European Alps. (Photos A, B and D © Alex Wild. Photo C by Scott Solomon)

scavenging on food scraps or preying on ant brood; (b) ants living in compound nests, which refers to two ant species sharing a nest space and interacting occasionally, but keeping and rearing their brood separately; species interactions are mostly commensalistic in compound nests; and (c) ants living in mixed colonies, where two ant species share a nest space, interact frequently, and store brood in a common area where they are cared for by one species, which is usually referred to as the host [3, 10]. All forms of true interspecific social parasitism in ants are examples of mixed colonies.

In bees, the life history of social parasites is distinct from the very speciose group of brood parasites which are also referred to as kleptoparasites or cuckoo bees. The brood- or kleptoparasites neither build a nest nor do they

collect pollen to provide food for their larvae [6, 15]. Instead they lay an egg into the cell of a solitary, free-living, pollen-collecting bee where either the parasitic queen or its larva kills the host larva and consumes the pollen and nectar provided by the host. In contrast, socially parasitic bees are specialists usurping eusocial host species where parasitic queens replace the host queens as the primary reproductive individuals in the colony. The queens of the workerless, socially parasitic ► **cuckoo bumble bee** *Psithyrus*, for example, are highly integrated into the host societies and are well-adapted to their socially parasitic lifestyles [13]. *Psithyrus* queens emerge late in the spring from hibernation and search for a ► *Bombus* host colony where the first worker generation has already been raised. Following successful nest invasion, the parasite queen

eliminates the egg laying host queen and the resident host workers are coopted to raise the social parasite's sexual offspring. The cuckoo bumble bee queens invest only in the production of reproductive offspring, instead of workers. Once the sexual offspring emerges from the host nest, the abbreviated cuckoo bumble bee life cycle is concluded and newly emerged queens mate before winter hibernation. Despite the differences in the life cycles of brood and social parasites, distinguishing between the two forms of parasitism can sometimes be ambiguous because a considerable amount of variation of parasitic behaviors exists in bees [6, 15]. In general, socially parasitic bees assume the reproductive role in the host colony and exploit eusocial hosts, but some brood parasites attack both solitary and social host species.

In wasps, brood parasitism is relatively rare and only a few species have lost the ability to construct nests and found their own colonies independently. Social parasites of ► *Polistes paper wasps*, for example, are workerless social parasites where the parasitic queen recognizes a new host colony via chemical cues, infiltrates a nest, and devours the host brood [4]. Host brood eating provides both a nutritious meal for the egg-laying parasite queen and empty cells for depositing the social parasite's eggs. After the host workers raised the parasite's offspring, young foundress queens first mate and then hibernate before they start the parasitic life cycle during the next growth season.

One of the most striking life history differences between social parasites of ants versus parasites of bees and wasps is that ant social parasites are perennial and form intimate relationships with their hosts over multiple years. Host-parasite relationships in most bees and wasps are annual and foundress queens have to infiltrate new host colonies each spring [4, 13], although some social parasites of ► *allodapine bees* can also form perennial relationships [21]. The annual versus perennial life cycles have a profound influence on the evolutionary origins of social parasitism in ants versus bees and wasps.

Integrating, true social parasites remain unknown in termites. Instead, some termite

species share the same nest mound but keep their brood strictly separate, a situation analogous to the compound nests of ants. The absence of true social parasitism begs the question whether social parasites of termites have simply not been discovered, or whether fundamental biological differences between the societies of termites and those of eusocial Hymenoptera precluded the evolution of social parasitism? One compelling hypothesis suggests that in contrast to the holometabolous Hymenoptera, termites are hemimetabolous insects and after a nymph hatches from the egg, the larva can provide for itself instead of depending on the brood care behavior of nestmates, as is the case in the holometabolous Hymenoptera. As a consequence, socially parasitic behavior is simply not expected in the absence of elaborate brood care behavior. Despite the plausibility of the hypothesis, it remains somewhat puzzling that other forms of social parasitism, such as intraspecific cheating, seems to be entirely absent from termites. With more than 3000 described species, termites are diverse and their colonies provide predictable resources to parasites. Hence, it remains enticing to ponder whether reproductive cheaters simply remained unnoticed in the societies of termites?

Despite the diverse life history traits and idiosyncrasies related to eusociality and social parasitism in ants, bees, and wasps, for the purpose of studying social parasitism in a comparative framework, interspecific social parasitism is defined here as a life history syndrome where the queen of a social insect species enters the colony of a different, free-living, eusocial insect species, replaces the host queen as the primary egg-laying individual, and exploits the social behavior and colony resources of the host for parts or the entirety of its life cycle to initiate a new colony, survive, and/or realize its individual reproductive fitness.

Diversity of Social Parasites in Social Insects

Worldwide at least 492 social parasite species have been discovered in 58 genera across four

families of eusocial Hymenoptera including the ants (Formicidae), two families of bees (Apidae and Halictidae), and the social wasps (Vespidae) (Table 1). Considering the current level of taxonomic and phylogenetic resolution, socially parasitic lineages evolved at least 88 times independently. The highest diversity of social parasite species and socially parasitic life histories as well as the highest number of independent evolutionary origins and phylogenetic diversity can be found in the ants. At first, a brief overview over the diverse social parasite lineages is provided for each family, before the fascinating diversity of socially parasitic life histories, their morphological and behavioral adaptations, as well as their evolutionary biology and biogeography are introduced.

Ant Social Parasites

Among the approximately 13,700 described extant ant species, at least 401 social parasite species have been recognized in six subfamilies of the formicoid clade, including the Dolichoderinae (with $n = 51$ social parasite species), Ectatomminae ($n = 1$ sp.), Formicinae ($n = 156$ spp.), ► *Myrmeciinae* ($n = 1$ sp.), Myrmicinae ($n = 185$ spp.), and ► *Pseudomyrmecinae* ($n = 7$ spp.) (Table 1). Ant social parasites are known from at least 42 ant genera and the current resolution of the ant tree of life allows for estimating at least 61 independent evolutionary origins of social parasitism in ants (Table 1). The estimate for the evolutionary origins of social parasitism is expected to increase with increasing phylogenetic resolution. Social parasites are notably absent from the army ant subfamily Dorylinae within the formicoid clade, as well as from the poneroid and leptanilloid clades of the ant tree of life. Historically, ant social parasite species have been divided into three main life history categories: the (i) temporary, (ii) dulotic, and (iii) inquiline social parasites [3, 10] (Fig. 1). These life history categories remain useful for classifying socially parasitic species and for comparatively studying myrmecosymbioses, or the interactions between ant species.

When employing these life history categories, it is important to keep in mind that social parasites evolved at least 61 times convergently across the ant tree of life. Therefore, individual social parasite species constitute mosaics of morphological, behavioral, and life history traits that are characteristic of social parasitism, and because of their independent evolutionary origins, they are also expected to vary individually. However, and despite the high number of independent evolutionary origins of social parasites among ants, it is remarkable that distinctly diagnosable social parasite syndromes evolved repeatedly via convergent evolution.

Temporary Social Parasitism

Temporary social parasites lost the ability to establish new colonies independently (i.e., claustrally) and depend on already established colonies of their hosts for colony foundation. The temporary social parasite queen invades the host nest, at times kills the resident host queen(s), and once established the host workers raise the parasite's offspring [3, 10, 24]. In the absence of an egg-laying host queen, the host workers are gradually replaced with parasite workers until the colony is composed solely of the temporary social parasite species. As mature colonies, the social parasites are independent of their hosts, and if one were to observe a mature colony of a temporary social parasite species in nature, there would be no way of knowing that this species dependent on a host for colony foundation.

Temporary social parasitism is practiced by more 200 species, which is about half of the known ant social parasite species (Table 1). Temporary social parasitism is particularly widespread in the Dolichoderinae, Formicinae, and Pseudomyrmecinae, but it also evolved repeatedly in the Myrmicinae. Approximately, one third of all temporary social parasite species can be attributed to a single origin and subsequent radiation in the genus *Formica*. Other clades harboring a significant diversity of temporary social parasites include the formicine genus *Lasius*, the myrmecine genus *Crematogaster*, and a

Social Parasitism, Table 1 The diversity, life histories, evolutionary origins, and biogeography of socially parasitic Hymenoptera. Total species diversity refers to the sum of free-living and socially parasitic species per genus, subfamily, or family. Social parasite diversity refers to the number of socially parasitic species per taxon.

Family/Subfamily	Genus including social parasite species	Socially parasitic life history syndrome	Total species diversity	Social parasite diversity	Independent evolutionary origins of social parasitism	Biogeography of socially parasitic species	References
1. FORMICIDAE							
Dolichoderinae							
	<i>Arnoldius</i>	Temporary social parasitism	3	3	Single origin of <i>Arnoldius</i> , <i>Bothriomyrmex</i> and <i>Chronoxenus</i>	Australasia	21,74
	<i>Azteca</i>	Temporary social parasitism, inquilinism	84	11	1	Neotropic	28,43
	<i>Bothriomyrmex</i>	Temporary social parasitism	25	25	Single origin of <i>Arnoldius</i> , <i>Bothriomyrmex</i> and <i>Chronoxenus</i>	Neotropic, Palearctic	32,74
	<i>Chronoxenus</i>	Temporary social parasitism	6	6	Single origin of <i>Arnoldius</i> , <i>Bothriomyrmex</i> and <i>Chronoxenus</i>	Australasia	32,74
	<i>Dorymyrmex</i>	Temporary social parasitism, inquilinism	60	3	At least 1	Nearctic, Neotropic	71, Johnson, Cover & Rabeling unpubl. data
	<i>Tapinoma</i>	Inquilinism	71	3	At least 1	Nearctic	Cover & Rabeling unpubl. data
Subtotal	6 genera	Temporary social parasitism, inquilinism	711	51 (7.2%)	At least 4	Australasia, Nearctic, Neotropic, Palearctic	
Ectatomminae	<i>Ectatomma</i>	Inquilinism	15	1	1	Neotropic	26,50
Subtotal	1 genus	Inquilinism	269	1 (0.4%)	1	Neotropic	
Formicinae	<i>Anoplolepis</i>	Inquilinism	9	1	1	Afrotropic	63
	<i>Camponotus</i>	Inquilinism (putative)	1043	2	At least 1	Palearctic	36,70

(continued)

Social Parasitism, Table 1 (continued)

Family/Subfamily	Genus including social parasite species	Socially parasitic life history syndrome	Total species diversity	Social parasite diversity	Independent evolutionary origins of social parasitism	Biogeography of socially parasitic species	References
	<i>Cataglyphis</i>	Inquilinism (putative)	93	2	At least 1	Palaearctic	1,58
	<i>Formica</i>	Temporary social parasitism, dulosis, inquilinism	178	90	1	Nearctic, Palaearctic	10,60
	<i>Lasius</i>	Temporary social parasitism	116	33	2	Nearctic, Neotropic, Palaearctic	34,45
	<i>Myrmelachista</i>	Temporary social parasitism (putative)	56	2	At least 1	Neotropic	42
	<i>Nyländeria</i>	Inquilinism	123	3	At least 1	Nearctic	46,47
	<i>Plagiotlepis</i>	Inquilinism	60	5	At least 1	Nearctic	3,13
	<i>Polyergus</i>	Dulosis	14	14	1	Nearctic, Palaearctic	29,72
	<i>Rossomyrmex</i>	Dulosis	4	4	1	Palaearctic	29,62
Subtotal	10 genera	Temporary social parasitism, dulosis, inquilinism	3177	156 (4.9%)	At least 11	Afrotropic, Nearctic, Neotropic, Palaearctic	
Myrmecinae	<i>Myrmecia</i>	Inquilinism	93	1	1	Australasia	20
Subtotal	1 genus	Inquilinism	94	1 (1.1%)	1	Australasia	
Myrmicinae	<i>Acromyrmex</i> and <i>Pseudoatta</i>	Inquilinism	35	5	At least 2	Neotropic	55,56,57,68
	<i>Aphaenogaster</i>	Temporary social parasitism	205	1	1	Nearctic	32
	<i>Cardiocondyla</i>	Inquilinism (putative)	72	1	1	Afrotropic	9
	<i>Chimaeridris</i>	Social parasitism (putative)	2	2	1	Indomalaya	78
	<i>Crematogaster</i>	Temporary social parasitism (putative)	504	28	At least 2	Afrotropic, Australasia, Indomalaya, Malagasy, Nearctic, Neotropic	8,33,41
	<i>Harpagoxenus</i>	Dulosis	3	3	1	Nearctic, Palaearctic	32

<i>Leptothorax</i>	Inquilinism	20	6	At least 2	Nearctic, Palearctic	52, Prebus & Rabeling unpubl. data
<i>Manica</i>	Temporary social parasitism (putative)	6	1	1	Nearctic	17
<i>Monomorium</i>	Inquilinism	307	7	At least 1	Indomalaya, Nearctic, Neotropic, Palearctic	32
<i>Mycocetopus</i>	Inquilinism	6	1	1	Neotropic	53,54
<i>Myrmecina</i>	Social parasitism (putative)	56	1	1	Nearctic	Cover pers. comm.
<i>Myrmica</i>	Temporary social parasitism, inquilinism	189	19	At least 9	Indomalaya, Nearctic, Palearctic	5,6,35,59,64
<i>Oxyepoecus</i>	Social parasitism (putative)	21	3	At least 1	Neotropic	2,37
<i>Pheidole</i>	Temporary social parasitism, inquilinism	1095	26	At least 3	Afrotropic, Australasia, Indomalaya, Malagasy, Nearctic, Neotropic	22,49,77,79
<i>Pogonomyrmex</i>	Inquilinism	68	2	1	Nearctic	51,67
<i>Solenopsis</i>	Temporary social parasitism, inquilinism	196	6	At least 1	Neotropic	65
<i>Strongylognathus</i>	Dulosis	25	25	1	Palearctic	61,75
<i>Strumigenys</i>	Inquilinism	850	5	At least 1	Afrotropic, Australasia, Nearctic	19,32
<i>Temnothorax</i>	Dulosis, inquilinism	413	24	At least 4	Nearctic, Palearctic	4,30,52
<i>Tetramorium</i>	Temporary social parasitism, inquilinism	583	18	At least 1	Afrotropic, Australasia, Indomalaya, Palearctic	61,75
<i>Vollenhovia</i>	Inquilinism	59	1	1	Palearctic	39,67
Subtotal	Temporary social parasitism, dulosis, inquilinism	6838	185 (2.7%)	At least 37	Afrotropic, Australasia, Indomalaya, Malagasy, Nearctic, Neotropic, Palearctic	
<i>Pseudomyrmecinae</i>	Temporary social parasitism, inquilinism	137	5	5	Nearctic, Neotropic	15,73, Ward pers. comm.
<i>Tetraponera</i>	Temporary social parasitism	93	2	2	Afrotropic	15,73, Ward pers. comm.

(continued)

Social Parasitism, Table 1 (continued)

Family/Subfamily	Genus including social parasite species	Socially parasitic life history syndrome	Total species diversity	Social parasite diversity	Independent evolutionary origins of social parasitism	Biogeography of socially parasitic species	References
Subtotal	2 genera	Temporary social parasitism, inquilinism	231	7 (3%)	7	Afrotropic, Nearctic, Neotropical	
Total FORMICIDAE	42 genera	Temporary social parasitism, dulosis, inquilinism	~13,700	401 (2.9%)	At least 61	Afrotropic, Australasia, Indomalaya, Malagasy, Nearctic, Neotropical, Palearctic	
2. APIDAE							
Apinae	<i>Bombus</i> (subgenera <i>Alpinobombus</i> , <i>Psithyrus</i> and <i>Thoracobombus</i>)	Obligate social parasitism (inquilinism)	239	31	3	Nearctic, Palearctic	11,31,40
Subtotal	1 genus	Obligate social parasitism (inquilinism)	1284	31 (2.4%)	3	Nearctic, Palearctic	
Xylocopinae	<i>Allodape</i>	Social parasitism (putative)	30	1	1	Afrotropic	48
	<i>Allodapula</i>	Social parasitism (putative)	15	1	1	Afrotropic	48
	<i>Braunsapis</i>	Facultative social parasitism, inquilinism	87	9	7	Afrotropic, Australasia, Indomalaya	48,66,69
	<i>Eucondylops</i>	Inquilinism	2	2	1	Afrotropic	48,66
	<i>Effractapis</i>	Social parasitism (putative)	1	1	1	Malagasy	48,66
	<i>Inquilina</i>	Inquilinism	7	7	1	Australasia	48,66,69
	<i>Macrogalea</i>	Facultative social parasitism, inquilinism	11	2	1	Afrotropic, Malagasy	48,66,69
	<i>Nasutapis</i>	Inquilinism	2	2	1	Afrotropic	48,66
Subtotal	8 genera	Facultative social parasitism, inquilinism	1044	25 (2.4%)	14	Afrotropic, Australasia, Indomalaya, Malagasy	

Total APIDAE	9 genera	Facultative social parasitism, inquilinism	5829	56 (1%)	17	Afrotropic, Australasia, Indomalaya, Malagasy, Nearctic, Palearctic	
3. HALICTIDAE							
Halictinae	<i>Lasioglossum</i> <i>Megalopta</i> <i>Microsphecodes</i>	Social parasitism Social parasitism (putative) Social parasitism	~1800 1 9	15 1 9	At least 4 1 1	Nearctic Neotropic Neotropic	18,27,76 7 23,25
Total HALICTIDAE	3 genera	Social parasitism	3426	25 (0.7%)	At least 6	Nearctic, Neotropic	
4. VESPIDAE							
Polistinae	<i>Polistes</i>	Obligate social parasitism (inquilinism)	218	3	1	Palearctic	14,16
Subtotal	1 genus	Obligate social parasitism (inquilinism)	~1100	3 (0.3%)	1	Palearctic	
Vespinae	<i>Dolichovespula</i> <i>Vespula</i> <i>Vespa</i>	Obligate social parasitism (inquilinism) Facultative social parasitism, inquilinism Facultative social parasitism	23 28 22	3 3 1	1 At least 1 1	Nearctic, Palearctic Nearctic, Palearctic Palearctic	12,44 12,38,44 44
Subtotal	3 genera	Facultative social parasitism, inquilinism	76	7 (9%)	At least 3	Nearctic, Palearctic	
Total VESPIDAE	4 genera	Facultative social parasitism, inquilinism	~5000	10 (0.2%)	At least 4	Nearctic, Palearctic	

(continued)

Social Parasitism, Table 1 (continued)

Family/Subfamily	Genus including social parasite species	Socially parasitic life history syndrome	Total species diversity	Social parasite diversity	Independent evolutionary origins of social parasitism	Biogeography of socially parasitic species	References
5. GRAND TOTAL EUSOCIAL HYMENOPTERA	58 genera	Social parasitism		492	At least 88	Afrotropic, Australasia, Indomalaya, Malagasy, Nearctic, Neotropic, Palearctic	

The numbered references in the table correspond to: [1] Agosti D. 1994. *J. Nat. Hist.* 28:913–9; [2] Albuquerque NL & Brandão CRF. 2004. *Pap Avulsos Zool.* 44:55–80; [3] Aron S et al. 2004. *Insect. Soc.* 51:395–9; [4] Beibei J et al. 2005. *Insect. Soc.* 52:291–7; [5] Bharti H. 2012. *Myrmecol. News* 16:149–56; [6] Bharti H et al. 2016. *ZooKeys* 605:113–29; [7] Biani NB & Weislo WT. 2007. *J. Kansas Entomol. Soc.* 80:392–4; [8] Blaimer BB. 2012. *Syst. Entomol.* 37:240–60; [9] Bolton B. 1982. *Bull. Br. Mus. Nat. Hist.* 45:307–70; [10] Borowiec ML & Rabeling C. 2018. XVIII Int. Conf. IUSSI, Brazil; [11] Cameron SA et al. 2007. *Biol. J. Linn. Soc.* 91:161–188; [12] Carpenter JM & Perera EP. 2006. *Am. Mus. Nov.* 3507:1–19; [13] Casevits-Weulerse L. 2014. *Bull. D. Arthropoda* 47:27–33; [14] Cervo R. 2006. *Ann. Zool. Fennici* 43:531–49; [15] Chomiccki G et al. 2015. *Proc. R. Soc. B* 282:20152200; [16] Choudhary M et al. 1994. *Proc. R. Soc. B* 257:31–5; [17] Creighton WS. 1934. *Psyche* 41:185–200; [18] Danforth BN et al. 2019. *The Solitary Bees*. PUP; [19] Deyrup M & Cover SP. 1998. *Proc. Entomol. Soc. Wash.* 100:214–221; [20] Douglas A & Brown WL. 1959. *Insect. Soc.* 6:13–9; [21] Dubovikoff DA. 2005. *Caucas. Entomol. Bull.* 1:89–94; [22] Economo EP et al. 2018. *Glob. Ecol. Biogeogr.* 28:456–70; [23] Eickwort GC & Eickwort KR. 1972. *J. Kansas Entomol. Soc.* 45:529–41; [24] Elmes GW. 1978. *Syst. Entomol. Hym. Res.* 19:51–65; [25] Engel MS. 2013. *J. Melittol.* 24:1–9; [26] Feitosa RM et al. 2008. *Zootaxa* 1713:47–52; [27] Gibbs J et al. 2012. *Cladistics* 28:195–207; [28] Guerrero RJ et al. 2010. *J. Hym. Res.* 19:51–65; [29] Hasegawa E et al. 2002. *Ann. Zool. Fennici* 39:267–271; [30] Heinze J et al. 2015. *PLoS ONE* 10:e0131023; [31] Hines HM & Cameron SA. 2010. *Insect. Soc.* 57:379–83; [32] Hölldobler B & Wilson EO. 1990. *The Ants*. HUP; [33] Hosoiishi S. 2015. *J. Hym. Res.* 42:63–92; [34] Janda M. et al. 2004. *Mol. Phylog. Evol.* 33:595–614; [35] Jansen G et al. 2010. *Mol. Phylog. Evol.* 56:294–304; [36] Karaman C. 2012. *J. Kansas Entomol. Soc.* 85:309–17; [37] Kempf WW. 1974. *Stud. Entomol.* 17:471–512; [38] Kinsey LS & Carpenter JM. 2012. *J. Hym. Res.* 28:37–65; [39] Kobayashi K et al. 2012. *J. Kansas Entomol. Soc.* 85:309–17; [40] Lhomme P & Hines HM. 2018. *Ann. Entomol. Soc. Am.* 112:122–40; [41] Longino JT. 2003. *Zootaxa* 151:1–150; [42] Longino JT. 2006. *Zootaxa* 1141:1–54; [43] Longino JT. 2007. *Zootaxa* 1491: 1–63; [44] Lopez-Osorio F et al. 2015. *R. Soc. open sci.* 2:150159; [45] Manyama M et al. 2008. *BMC Evol. Biol.* 8:237; [46] Messer SJ et al. 2016. *ZooKeys* 552:49–65; [47] Messer SJ et al. 2020. *ZooKeys* 921:23–48; [48] Michener CD. 2000. *The bees of the world*. JHUP; [49] Moreau CS. 2008. *Mol. Phylog. Evol.* 48:224–39; [50] Nettel-Hernanz A et al. 2015. *Org. Divers. Evol.* 15:543–53; [51] Parker JD & Rissing SW. 2002. *Evolution* 56:2017–28; [52] Prebus M. 2017. *BMC Evol. Biol.* 17:250; [53] Rabeling C & Bacci M. 2010. *Syst. Entomol.* 35:379–92; [54] Rabeling C et al. 2014. *Curr. Biol.* 24:2047–52; [55] Rabeling C et al. 2015. *Insect. Soc.* 62:335–49; [56] Rabeling C et al. 2018. XVIII Int. Conf. IUSSI, Brazil; [57] Rabeling C et al. 2019. *Insect. Soc.* 66:435–51; [58] Radchenko AG. 1997. *Ann. Zoologica* 46:207–10; [59] Radchenko AG & Elmes GW. 2003. *Ann. Zoologica* 53:217–43; [60] Romiguier J et al. 2018. *BMC Evol. Biol.* 18:40; [61] Sanetra M & Buschinger A. 2000. *Eur. J. Entomol.* 97:95–117; [62] Sanlloriente O et al. 2018. *J. Zool. Syst. Evol. Res.* 56:48–60; [63] Santischi F. 1917. *Ann. Soc. Entomol. France* 85:279–96; [64] Savolainen R & Vepsäläinen K. 2003. *PNAS* 100:7169–74; [65] Shoemaker DD et al. 2006. *Mol. Phylog. Evol.* 38:200–15; [66] Smith JA et al. 2013. *Biol. J. Linn. Soc.* 109:320–31; [67] Smith CR et al. 2015. *Mol. Biol. Evol.* 32:2919–31; [68] Summer S et al. 2004. *Insect. Soc.* 51:37–42; [69] Tierney SM et al. 2008. *Apidologie* 39:3–15; [70] Tinaut A et al. 1992. *Nov. Revue Ent.* 9:233–8; [71] Trager JC. 1988. *Florida Entomol.* 71:11–29; [72] Trager JC. 2013. *Zootaxa* 3722:501–48; [73] Ward PS. 1996. *Syst. Entomol.* 21:253–63; [74] Ward PS et al. 2010. *Syst. Biol.* 59:342–62; [75] Ward PS et al. 2015. *Syst. Entomol.* 40:61–81; [76] Weislo WT. 1997. *Ethology* 103:1–11; [77] Wilson EO. 1984. *Insect. Soc.* 31:316–334; [78] Wilson EO. 1989. *Insect. Soc.* 36:62–9; [79] Wilson EO. 2003. *Pheidole in the New World*. HUP

monophyletic group in the Dolichoderinae consisting of the three genera *Arnoldius*, *Bothriomyrmex*, and *Chronoxenus*.

In temporary social parasites, behavioral and life history traits can be rather heterogeneously distributed among species. In the genus *Formica*, for example, some species in the Palearctic and Nearctic *rufa*- and *exsecta*-groups are temporary social parasites where newly mated queens are adopted into the colonies of heterospecific host species. In addition, young queens seek readoption into conspecific colonies leading to secondary polygynous colonies, which then propagate via colony fission, leading to large, unicolonial populations. In contrast, temporary social parasites in the Nearctic *Formica microgyna*-group do not seek readoption into conspecific colonies, nor do they establish new nests via colony fission. Instead, newly mated queens obligately depend on being adopted by their respective host species.

Temporary social parasites in the genera *Lasius* and *Bothriomyrmex* famously assassinate the host queen(s) by either “throttling” or decapitating the resident queen(s) before the social parasite takes over the role of the reproductive individual. These gruesome natural history observations have captivated the imagination of lay-naturalists and professional biologists alike and they remind us that detailed natural history observations are absent for many, if not most, social parasite species. Frequently, socially parasitic behavior is inferred from diagnostic morphological characters, such as falcate mandibles or diminutive queen sizes, and the biology of entire groups of putative social parasites especially from tropical habitats, such as species in the genera *Azteca*, *Crematogaster*, *Myrmelachista*, among many other, are unknown. To gain a better understanding of social parasite biology, it is important to study the natural and life histories of these species.

Dulotic Social Parasites

The ► [dulotic or slave-making](#) social parasites depend on their host species throughout their life cycles. The queens of dulotic social parasites start

the colony life cycle as temporary social parasites, where the newly mated queen infiltrates a host colony, usually kills the resident host queen(s), and assumes the function as the sole reproductively active queen [5, 10]. The host workers care for the dulotic queen and raise her brood, and once sufficient parasitic workers have been reared, the dulotic workers conduct well-organized raids of nearby host colonies to capture their larvae and pupae. Some brood is eaten, but most captured workers eclose inside the parasite’s nest. Because the host workers eclose in the parasite’s nest, they acquire the parasite’s colony odor and contribute to the workforce of the colony in which they eclose. Interestingly, the workers of some dulotic ant species lost the ability to perform colony maintenance, such as brood care and nest construction, and in some cases, such as *Polyergus* and *Strongylognathus*, the specialized saber-shaped mandibles of workers prevent the dulotic ants from feeding themselves. The high degree of morphological specialization highlights the obligate dependence of dulotic social parasites on their hosts for colony founding, feeding, and brood care.

Approximately 80 species, translating to roughly 20% of all ant social parasites, are dulotic, and species in the genera *Formica*, *Polyergus*, *Strongylognathus*, and ► [Temnothorax](#) are well-known for their fascinating and eponymous brood stealing behavior. Dulosis evolved at least nine times in the ant subfamilies Formicinae and Myrmicinae (Table 1), and therefore, dulosis has significantly fewer independent evolutionary origins than temporary or inquiline social parasitism. However, once dulotic behavior originated, these dulotic ant lineages repeatedly diversified into moderately diverse clades of 10–25 species, suggesting that dulosis evolves rarely but once it originates this socially parasitic life history strategy is successful leading to moderate secondary diversification.

The eye-catching mass raids of *Polyergus* ants are a fascinating spectacle to witness first hand in nature. Hence, it is not surprising that the European species *Polyergus rufescens* was the first ant social parasite species to be studied in detail by Pierre Huber 210 years ago.

Inquiline Social Parasites

Inquiline social parasites are obligately dependent on their hosts throughout their life cycles for nest founding, survival, and reproduction [10, 25]. Most inquiline species have lost their worker caste in part or entirely. In contrast to temporary or dulotic social parasites, most inquiline species tolerate and coexist with the host queen inside the host colony, allowing the host to continuously produce workers. Consequently, inquilines and their hosts form permanent symbioses that can last multiple years. Queens of workerless inquiline social parasite allocate all of their reproductive effort to sexual offspring.

Inquiline social parasites are the phylogenetically most diverse group of social parasites and inquilinism evolved convergently across the ant tree of life. Currently, approximately 100 species are known from 25 ant genera that are distributed across six different subfamilies of the formicoid clade. However, with approximately 40 origins, the number of independent evolutionary origins of ant inquiline social parasites is higher than the number of genera containing inquilines, because some speciose genera, such as *Acromyrmex*, ► *Leptothorax*, *Myrmica*, ► *Pheidole*, and *Pseudomyrmex*, harbor multiple inquiline species and some of those social parasites originated independently (Table 1).

Among ants, many inquilines convergently evolved a suite of similar morphological, behavioral, and life history characteristics known as the “inquiline syndrome” (Fig. 2). These traits include important modifications associated with the socially parasitic life history, such as reduced mouthparts, reduced body size, smooth and shiny cuticle, reduction or absence of the worker caste, intranidal mating with close relatives, and polygyny. Interestingly, independently evolved inquiline species exhibit a mosaic of inquiline syndrome characteristics, frequently converging on a similar albeit not identical adaptive parasitic phenotype [10, 25]. The mosaic evolution and convergence on the inquiline syndrome likely reflect the adaptiveness of inquiline syndrome traits as well as the diverse and

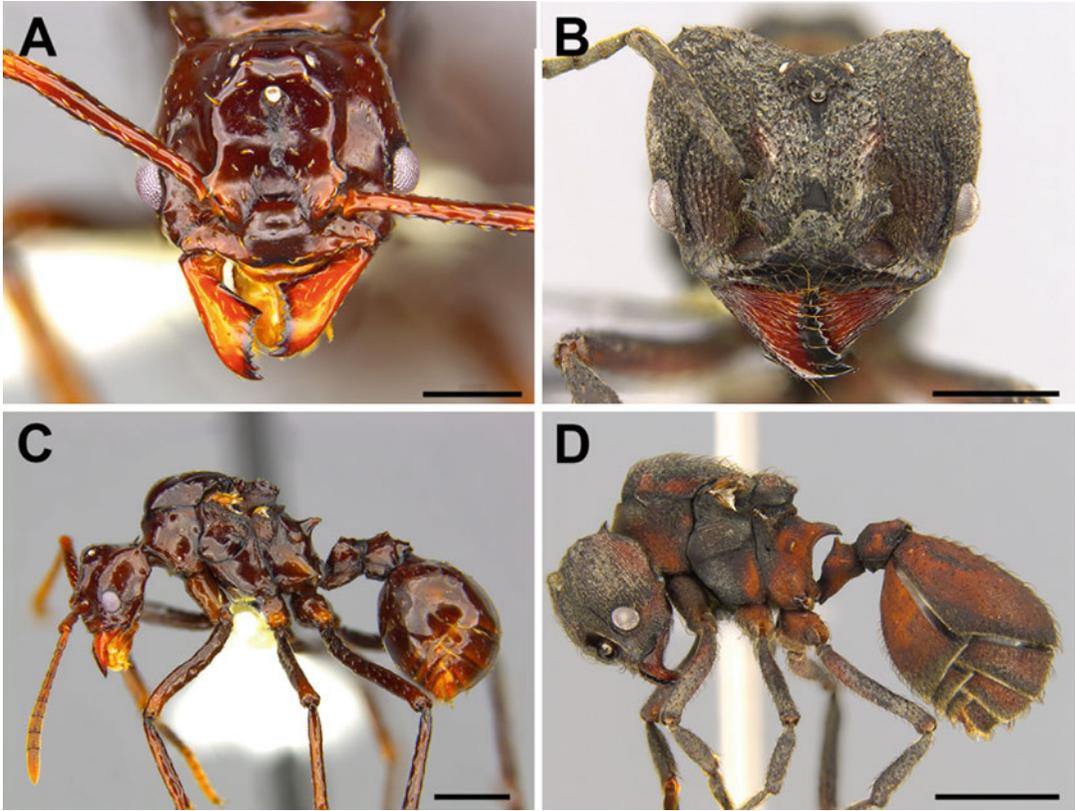
heterogeneous ancestry from which inquiline species evolved.

Xenobionts

Xenobionts or guest ants live inside the nest of another ant species, but keep the brood separate. They move freely inside the host nest and some species, such as *Formicoxenus* ants, obtain food from their hosts via trophallaxis. Xenobiosis is a collective term describing facultative or obligate interactions between ant species. Xenobionts are not true social parasites as defined above (final paragraph of introduction) because the behavioral interactions between xenobiotic species and their hosts cover the entire spectrum of species interactions ranging from mutualism over commensalism to parasitism and predation [9]. Some mutualistic and commensalistic xenobionts, such as species in the genera *Formicoxenus* and *Strumigenys*, do not seem to bear a significant cost to the hosts, whereas some *Megalomyrmex* species are specialized predators of their fungus-growing ant hosts. The species interaction dynamics can also be context dependent, and *Megalomyrmex* ants were shown to be either parasites or mutualists of their fungus-growing ant hosts, depending on whether they consumed the host brood or defended their nests against predators [1]. Therefore, species interactions between xenobionts and their hosts are heterogeneous and potential socially parasitic interactions need to be evaluated individually. For those reasons, xenobionts most closely resemble myrmecophiles, and although some xenobionts may be obligately dependent on their hosts, they are not true social parasites.

Bee Social Parasites

Among the approximately 20,000 described species of bees, a total of at least 81 social parasite species have been recognized from the two bee families Apidae and ► Halictidae (Table 1). Bee social parasites are known from 12 different genera and at least 23 origins of social parasitism



Social Parasitism, Fig. 2 The inquiline syndrome in leaf-cutting ants. The queen of the workerless inquiline social parasite *Pseudoatta argentina* (a, c) is compared to its closely related host, the leaf-cutting ant *Acromyrmex heyeri* (b, d). Note the morphological modifications of the

parasite in comparison to the host, including its shiny integument, rounded posterior margin of the head, as well as the reductions in body size, integumental sculpturing, and pilosity. The scale bars represent 0.5 mm in A, 1 mm in B & C, and 2 mm in D

were inferred from phylogenetic analyses. In the family Apidae, a high diversity of social parasites is known from the bumble bees with 31 *Bombus* species that independently evolved three times [13]. The social parasites belong to the subgenera *Alpinobombus*, *Psithyrus*, and *Thoracobombus* with the subgeneric classification reflecting their independent evolutionary origins. The 28 socially parasitic ► *Psithyrus* species are considered one of the major radiations of social parasite species in bees [13]. In contrast, the 25 social parasite species that are distributed among eight genera in the tribe Allodapini (subfamily Xylocopinae) (Fig. 3), exhibit the highest phylogenetic diversity of bee social parasites with at least 14 independent evolutionary origins [20, 21]. In the sweat bee family Halictidae, social parasites are known from the

genera *Lasioglossum*, *Megalopta*, and *Microsphecodes*. In *Lasioglossum* the 15 socially parasitic species evolved at least four times independently, whereas social parasitism evolved likely once in the ancestor of the nine extant *Microsphecodes* species [8]. The crepuscular sweat bee genus *Megalopta* contains multiple kleptoparasitic species, and evidence accumulated that *Megalopta byroni* exploits social host species. Similar to other socially parasitic Hymenoptera, the putatively socially parasitic *Megalopta* bees are extremely rare, and additional observations are needed to characterize the interactions between parasite and host.

Distinguishing between brood and social parasites can be difficult [6, 15], because a high diversity of social and socially parasitic behaviors



Social Parasitism, Fig. 3 Bee inquiline social parasites in the tribe Allodapini. Left side: Line drawing of a female *Eucondylops reducta*. Right side: Micrograph of a female *Inquilina schwarzi*. Note the modifications of the social parasites, including the scythe-like mandibles lacking dentition, the reductions in wing venation, compound eyes,

proboscis, and scopa, as well as the enlarged legs and tibial spines. Drawing modified from Michener 1970 *Zool. J. Linn. Soc.* 49:199–215. (Photo by Laurence Packer; image bank of the bee genera of the world at York University)



Social Parasitism, Fig. 4 Inquiline social parasite of *Polistes* paper wasps. Left side: A queen of the workerless inquiline social parasite *Polistes atrimandibularis* on the nest of its host *P. biglumis*. Right side: Full-face view of *Polistes atrimandibularis*. The social parasite is larger than

its host, has stronger mandibles and a thicker cuticle, all traits that are advantageous during nest invasion. (Photos from the image library Entomologie/Botanik at ETH Zürich and the photographer Albert Krebs)

exists in bees and the definition of social parasitism rests on two main criteria: (a) that the parasite exploits a eusocial host, and (b) that the parasite functionally replaces the host queen and tricks the host workers in raising its offspring. In bees, some kleptoparasites usurp non-eusocial hosts, such as *Aglae* and *Exaerete* orchid bees as well as species in the sweat bee genus *Sphecodes*, and therefore, they are not regarded as true social parasites. In addition, other socially parasitic bees live inside

the host colony alongside the host queen but do not functionally replace the host queen. Nonetheless, the obligate social parasites depend on their social hosts for survival and raising their brood, thereby invading and exploiting the social environment provided by their hosts. The highest degree of social integration was achieved by *Psithyrus* bumble bee social parasites and the allodapine social parasite *Braunsapis kaliago* [13, 20]. These biological nuances are a reminder

that convergent evolution may result in highly congruent but not exactly identical social parasite morphologies, behaviors, and life histories, and detailed knowledge about the natural history and evolution is required to navigate the complex biology of socially parasitic eusocial Hymenoptera.

Wasp Social Parasites

Social parasitism evolved rarely in wasps. Among the approximately 5000 wasp species only 10 species of obligate social parasites are known from the eusocial subfamilies Vespinae and Polistinae (Table 1). Seven species of yellowjackets and hornets (Vespinae) and three species of paper wasps (Polistinae) are socially parasitic. *Polistes* social parasites are workerless inquilines that lost the ability to build nests and care for brood, and hence *Polistes* parasites obligately depend on their hosts (Fig. 4). Among the vespine social parasites in the yellowjackets (*Dolichovespula* & *Vespula*) and hornets (*Vespa*), both temporary and inquiline social parasitism can be observed. Across the wasp parasites, at least four independent origins of social parasitism occurred: once in the paper wasp genus *Polistes* and once in each of the three vespine genera *Dolichovespula*, *Vespula*, and *Vespa*.

Classification of Social Parasites

Before the rise of phylogenetic systematics, social parasite species were regularly placed in their own higher taxonomic groups separated from their close relatives. These taxonomic placements were justifiable at the time because many social parasite species, especially the permanent inquiline social parasites, are morphologically and behaviorally modified and thus clearly distinct from their hosts. Notwithstanding, for more than 150 years, entomologists have also been noticing that hosts and parasites are often close relatives (see section “► [Origins and Evolution of Social Parasites](#)”), and evolutionary relationships should

be reflected in the higher classification of Hymenoptera.

W.T. Brown offered a comprehensive revision of ant genus names in 1973, proposing a large number of actual and provisional synonyms including many socially parasitic ant genera, such as *Anergatides* (= *Pheidole*), *Bruchomyrma* (= *Pheidole*), *Parapheidole* (= *Pheidole*), *Sifolinia* (= *Myrmica*), among many others. Other genera of highly diagnostic social parasites were maintained at first, including, for example, *Anergates* (= *Tetramorium*), *Chalepoxenus* (= *Temnothorax*), *Myrmoxenus* (= *Temnothorax*), and *Teleutomyrme* (= *Tetramorium*). Molecular phylogenetic studies then demonstrated that these social parasite genera are nested inside larger genera including close relatives and their host species [22]. To ban paraphyletic taxa and restrict higher-level taxa to monophyletic groups, thereby achieving long-term nomenclatural stability, a significant number of ant social parasite genera in the subfamily Myrmicinae were synonymized [22]. Synonymizing names of parasitic ant genera caused controversy in the myrmecological community. Opponents of a strict phylogenetic classification argued that information about the biology of a social parasite clades was lost, or not immediately evident, when the genus name was synonymized under the host genus name. Proponents of a phylogenetic classification emphasized that paraphyletic groups cause nomenclatural instability and only monophyletic groups should be recognized as taxa. As for the social parasites, it is understandable that some scientists prefer to continue the use of names they have been using throughout their careers because they associate a rich library of biological information with these names. However, to prevent major reclassification exercises that are reoccurring roughly every generation in ant taxonomy, it seems to be in the best interest of transgenerational, long-term nomenclatural stability to agree on a single nomenclatural system instead of dividing the biological information associated with taxonomic names and the literature into two or more parallel systems. In fact, the use of parallel taxonomies will inevitably cause the loss of biological information, which cannot be in the

best interest of any scientist. To emphasize a positive effect, integrating social parasite species into larger clades, which often include the host species, also adds valuable information about the biology and evolutionary history of the social parasite. Adding the parasite to a clade of close relatives immediately provides information about the biology of the host clade and the ancestry from which the social parasite evolved. When integrating evolutionary history into the taxonomic classification, information about the biogeography, behavior, ecology, and many other aspects of the parasite's biology come for free with the genus name.

While not everyone will agree with the current genus-level and higher classification, describing new social parasite species as members of their host genera has already been common practice for the past decades. Even new social parasite species that are truly morphologically distinct from their hosts, and therefore highly diagnosable, have been described as new species in their respective host genera instead of being described as monotypic social parasite genera. To only name a few examples, recently described parasite species that are members of their host genera include *Acromyrmex fowleri*, *Myrmica latra*, *Nylanderia deyrupei*, and *Temnothorax pilagens*.

In bees, social parasite taxonomy and nomenclature followed a similar trend. Early bee taxonomists in the nineteenth century placed parasitic and nonparasitic bees in separate families, and during the twentieth century parasites were more frequently grouped with nonparasitic relatives [15]. Since the advent of phylogenetic systematics, clades were recognized as genera and social parasite taxa that rendered larger clades paraphyletic were synonymized under those generic names [15]. Diagnostic names of monophyletic social parasite groups, such as *Psithyrus*, were often kept as subgeneric names. Melittologists also recognized that convergently evolved (homoplastic) traits associated with the social parasitic lifestyle repeatedly misled morphology-based phylogenetic reconstructions [8]. Estimates for the number of origins of kleptoparasitism in apid bees, for example, ranged from four to 11 independent origins when comparing results from

morphology-based and molecular phylogenetic studies [6]. The socially parasitic Allopadini are morphologically and behaviorally distinct from their hosts and are therefore recognized as separate genera [20, 21], whereas socially parasitic Halictidae are recognized as series or species groups [6, 8, 15].

Phylogenetic studies have demonstrated that socially parasitic paper wasps, which were previously placed in the subgenera *Sulcopolistes* and *Pseudopolistes*, are both monophyletic and nested within *Polistes* [4]. Therefore, elevating parasitic taxa to subgenus or genus rank is not practiced in wasp taxonomy and parasitic species are grouped within monophyletic groups with close relatives and hosts [14].

Origins and Evolution of Social Parasites

The evolutionary origins of social parasitism have been debated since Charles Darwin's "Origin of Species." Myrmecologists and melittologists of the nineteenth century noticed early on that social parasites exploit their close relatives [7, 16]. That parasites and hosts are closely related makes immediate intuitive sense because due to their common ancestry hosts and parasites use similar channels of communication and share ecological, behavioral, as well as physiological preferences, which allow the social parasite to successfully integrate into the host colony. Hermann Müller [16] suggested that cuckoo bumble bees diverged recently from free-living, pollen-collecting bumble bees, and Auguste-Henri Forel and Erich Wasmann suggested that dulotic ants derived from their "host stocks." Once sufficient natural history observations had accumulated, Carlo Emery [7] systematically compared the relationships of ant social parasites with different life histories to their hosts and noticed a couple of generalizable patterns: First, the socially parasitic ants (i.e., temporary, dulotic, and inquiline social parasites) are directly derived from close relatives, which serve them as hosts, and second, the myrmecophilous ants (i.e., "xenobionts") are not derived from relatives of their hosts but instead originated in different genera or even subfamilies.

The first part of Emery's generalizations was later called ► **Emery's Rule**. Wheeler [24] supported Emery's observations, and perspicaciously asked how interbreeding between emerging social parasite and host populations was prevented when the social parasites evolved directly from their hosts? Thereby, Wheeler outlined a century ago the most critical condition that needs to be accounted for when testing a case of sympatric speciation! Since then the origin and evolution of social parasites has been discussed in great detail in the light of fascinating new discoveries [1–6, 8–15, 17–25].

To explain the origin of social parasite species, two main hypotheses prevail: the *interspecific* hypothesis proposes that a nonparasitic species evolves parasitic behavior allopatrically and starts exploiting a second, free-living species, whereas the *intraspecific* hypothesis postulates that the parasite evolves directly from its host in sympatry [2]. Phylogenetic studies allow for distinguishing between the two hypotheses by interpreting Emery's Rule in its strict and its loose version. Strictly interpreted, Emery's Rule postulates a sister group relationship between host and parasite, whereas a less restrictive or "loose" interpretation signifies for example a congeneric, but not necessarily a sister taxon relationship [14, 18, 20]. Only strict cases of Emery's Rule where host and parasite are each other's closest relatives can provide insights about *intraspecific* social parasite evolution via sympatric speciation. Secondary evolutionary events, such as secondary speciation events of host and/or parasite, host shifts, or extinction events of either species are expected to obliterate the phylogenetic signal of the social parasite's origin, irrespective of the parasite having speciated via the intra- or interspecific route of social parasite evolution. During the past decades an increasing body of case studies accumulated allowing to draw first conclusions about social parasite evolution across the eusocial Hymenoptera.

In ants, *intraspecific* origins of social parasites via sympatric speciation could only be inferred for some queen-tolerant ant inquiline social parasites in the genera *Acromyrmex*, *Ectatomma*, *Mycocetopus*, and *Myrmica* (Table 1 and references therein). In contrast, empirical studies of

temporary, dulotic, and queen-intolerant workerless ant social parasites generally provided support for the interspecific hypothesis, and in some cases, secondary speciation events of host and/or parasite taxa obscured the original evolutionary conditions under which the social parasite originated (Table 1 and references therein). Notably, the temporary and dulotic social parasites often radiated into speciose clades, whereas the inquiline social parasites evolved independently at high frequency. Some dulotic ant genera, such as *Harpagoxenus*, *Polyergus*, *Rossomyrmex*, and *Strongylognathus*, constitute speciose monophyletic groups that are closely related to the genera of free-living species that include their hosts. In other cases, such as *Formica* and *Temnothorax*, the dulotic species form specialized clades that are nested inside larger genera. The temporary social parasites include some genera that consist exclusively of social parasite species, such as the three monophyletic dolichoderine genera *Arnoldius*, *Bothriomyrmex*, and *Chronoxenus*, whereas temporary socially parasitic *Crematogaster*, *Formica*, and *Lasius* species mark speciose radiations within larger genera of free-living species. In addition, temporary social parasitic behavior evolved repeatedly in single lineages or small groups of species that originated convergently across the ant tree of life (Table 1).

In bees, the independent origins of social parasitism were carefully examined in the Apidae (Allodapini and *Bombus*) and Halictidae. Empirical phylogenetic studies generally supported the origin of bee social parasites via the interspecific, allopatric route of social parasite evolution. In the Allodapini, the loose version of Emery's Rule was generally supported and social parasite species were closely related to clades that included their host species [20, 21]. A sister species relationship was only recovered between the facultative coinhabiting species *Braunsapis paradoxa* and *Braunsapis elizabethana*, but the facultatively socially parasitic behavior is inconsistent with a sympatric speciation scenario because it does not allow for consistent spatial or temporal isolation between host and parasite populations during the speciation process [20]. The Allodapini probably owe the high number of independent origins of

social parasitism to their particular life history with progressive rearing of brood in an open nest tunnel lacking individual brood cells. In this regard, allopapine brood rearing is more similar to ants than to most bees, and their inquiline may persist in host nests across multiple seasons, which may give rise to novel origins of social parasitism [20, 21].

In the bumble bees, social parasitism evolved thrice. The large radiation of 28 socially parasitic species in the subgenus *Psithyrus* is monophyletic and nested within the genus *Bombus* [13]. The obligate social parasites *Bombus hyperboreus*, *B. navigi*, and *B. inexpectatus* were also not inferred as sister species to their respective hosts [13]. Therefore, the phylogenetic relationships of socially parasitic *Bombus* and their hosts are consistent with a loose version of Emery's Rule, providing support for the interspecific, allopatric route of social parasite speciation.

Lastly, of the 25 social parasite species in the sweat bee family Halictidae, the evolutionary history of six *Lasioglossum* species was reconstructed, recovering two independent origins of social parasitism in *Lasioglossum* [8]. Social parasites and their hosts were inferred as close relatives but not as sister species, suggesting interspecific origins of social parasitism in the sweat bees.

In contrast to the social parasites, the vast number of kleptoparasitic bees originated less frequently than previously anticipated in the families Apidae and Megachilidae, and the majority of kleptoparasites form speciose clades usurping a phylogenetically diverse array of host species [6]. The relationships of kleptoparasitic bees and their hosts are not consistent with Emery's Rule, indirectly supporting the notion that the symbioses between social parasites and their hosts are particularly intimate.

In wasps, social parasitism evolved once in the paper wasps (Polistinae) and at least thrice in the yellowjackets and hornets (► *Vespinae*). The three polistine social parasites were inferred as a monophyletic group that is nested in the host genus *Polistes* [4]. Similarly, the socially parasitic *Vespinae* in the genera *Dolichovespula*, *Vespa*, and *Vespula* were inferred as members of their

respective host genera with parasites and host being close relatives but not sister species [14]. For the genus *Dolichovespula*, three social parasite species were included in a recent phylogenetic analysis [14], inferring all three parasites as originating from a single common ancestor. Hence, the phylogenetic relationships between wasp social parasites and their hosts suggest an interspecific origin of social parasitism via allopatric speciation.

In summary, empirical studies support the intraspecific, sympatric speciation hypothesis for some host queen tolerant ant inquiline social parasite species, whereas allopatric speciation was inferred, or could not be ruled out, to account for the evolutionary origins of temporary, dulotic, and other inquiline social parasites of ants, as well as for social parasites of bees and wasps. Individual case studies supporting one speciation hypothesis over the other should not be used to draw generalizations regarding the speciation patterns across social parasite groups with similar life history traits. Social parasites evolved at least 88 times convergently across the eusocial Hymenoptera, and future studies may identify cases of allopatric speciation among ant inquilines or sympatric origins among socially parasitic Hymenoptera other than the inquiline ants. Neither allopatric nor sympatric speciation should be regarded as null hypotheses for the origin of social parasite species, and empirical studies need to individually test for speciation patterns across independently evolved social parasite lineages.

Geographic Distribution of Social Parasites: The Kutter-Wilson Paradox

Social parasites are rarely encountered in nature but at the same time they are also highly diverse. With almost 500 known species, entomologists discovered a remarkable diversity of socially parasitic Hymenoptera worldwide (Table 1), and biogeographical studies of ants and bees demonstrated that the biodiversity of free-living eusocial Hymenoptera increased towards the equator, whereas the social parasite diversity seems to increase towards high latitudes,

contradicting the general biogeographical pattern of their hosts.

Heinrich Kutter's detailed studies of the Swiss ant biodiversity illustrate this pattern nicely. He [11] estimated that approximately 30% of the Swiss ant diversity were social parasites, which is an incredibly high proportion considering that at the time the global social parasite diversity amounted to roughly 2% of the world's ant species. Although the number of Neotropical ant social parasite species, for example, doubled to currently 45 described species during the past 50 years, the number of free-living ant species also increased significantly. Consequently, the proportion of social parasite to free-living species in the Neotropical region did not change significantly since Kutter's 1968 census [19].

The brood parasitic bees are also distributed along an inverse latitudinal gradient, similar to the pattern observed in ants. Free-living bees, when including both solitary and social species, are most diverse in warm-temperate, xeric regions of the world. However, it should be noted that the high bee diversity in desert regions is caused by the high diversity of solitary bees, whereas the social bees are most diverse in the humid tropics [15]. Weislo [23] studied the biogeography of brood parasitic bees, including kleptoparasites and social parasites, and found that the proportion of brood parasitic species increased in the surveyed bee communities with increasing latitude. The inverse latitudinal gradient of brood parasitic bee species is a particularly strong biogeographic pattern, especially when considering that the communities of free-living bees are reaching their highest diversity in temperate regions.

The geographic distribution of vespine wasp social parasites overlaps broadly with the main distribution of their host genera in the Palearctic and Nearctic regions, and the three *Polistes* social parasite species are distributed in the Mediterranean region whereas the free-living paper wasps are most diverse in the tropics [4]. Considering the low number of origins of social parasitism in wasps, a biogeographic pattern contrasting the distribution of social parasites with that of their host genera could not be identified.

Unraveling the underlying causes responsible for the paradoxical biogeographic distribution of ant and bee social parasites is still an active area of research. Kutter [11] reasoned that the disproportionately low number of ant social parasite species in the tropics reflected a sampling bias, testifying to the incomplete knowledge about tropical ant biology and natural history. Wilson [25] generally agreed but also emphasized the role of ecological, life history, and climatic factors contributing to the frequent evolution of ant social parasites in temperate regions. For the brood parasitic bees, Weislo [23] emphasized the importance of developmental synchrony between host and parasite for the evolution of brood parasitic behavior, and suggested that populations in temperate regions are more tightly synchronized by climatic factors than in tropical regions where temperatures limiting bee activity are less variable.

Our current knowledge about the biology and taxonomy of tropical social parasite species and their hosts suggests that the "Kutter-Wilson Paradox" is a genuine biogeographical phenomenon instead of a mere sampling artifact [19]. However, the discovery of additional social parasites, especially in the tropical regions, and quantitative biogeographic studies are needed to better understand the dynamics shaping the biogeographic distribution of social parasites.

Morphological and Behavioral Modifications Associated with Social Parasitism

Despite the high diversity of social parasite species, the high diversity of socially parasitic syndromes, and the high number of independent evolutionary origins, one aspect is common to all social parasites: socially parasitic Hymenoptera obligately depend on their hosts' societies for their survival and successful reproduction. During the process of switching from a eusocial to a socially parasitic life history, social parasites evolved many different morphological and behavioral modifications to a parasitic lifestyle, some of which are clearly adaptive. Across ants, bees, and

wasps, social parasites developed diverse strategies to (i) locate the colonies of their hosts, (ii) gain access to the host colonies, (iii) communicate with their hosts and integrate into the host societies, (iv) establish as the reproductive individuals in the host colonies, and (v) trick their hosts into raising their offspring. A few examples across well-studied groups of social parasites shall illustrate the diversity of morphological and behavioral modifications these fascinating organisms evolved.

In ants, the morphological and behavioral syndromes of some socially parasitic life histories are highly diagnostic (Figs. 1,2). For example, the dulotic ants assault colonies of their host species, kill workers defending their maternal colonies, and steal the host brood to raise a domestic work force. Workers of *Polyergus* and *Strongylognathus* ants have sickle-shaped mandibles that are used to pierce and kill host workers during brood raids. The mandibles attach to relatively large, bulbous heads providing an increased surface for muscle attachment, indicating the increased mandibular strength of the dulotic species. Instead of piercing mandibles, *Harpagoxenus* ants have clipper-like mandibles to cut off appendages of their opponents. In addition, some dulotic *Temnothorax* species use their stings to kill their adversaries with their venom.

In contrast to the dulotic species that steal pupae to integrate the host workers into their colonies, the inquiline social parasites enter the host nest integrating themselves into the host society. Despite their numerous evolutionary origins, at least 40 independent origins are known, inquiline social parasites are quite diagnostic due to their convergence on the so-called inquiline syndrome. Wilson [25, p. 374] and Hölldobler & Wilson [10, p. 467] defined the inquiline syndrome and listed 19 morphological, behavioral, and life history traits that evolved convergently in inquiline social parasites. Comparative studies of inquiline social parasite species in the ant genera *Myrmica*, *Nylanderia*, *Pheidole*, and fungus-growing ants showed that the characters of the inquiline syndrome evolved in a mosaic fashion where some but not all traits were present in the inquiline species, and the inquiline traits did not

necessarily occur in the same combination. Among the key characteristics of the inquiline syndrome are for example (i) the reduced body size of the parasite, (ii) the complete or partial loss of the worker caste, (iii) the unusual modifications of the males becoming queen-like or pupa-like, (iv) the sib-mating behavior of the parasite sexuals copulating inside the nest, instead of mating during nuptial flights, (v) the reduction of internal and external mouthparts, as well as of antennal segments, and (vi) the reduction of integumental sculpturing and thinning of the cuticle (Fig. 2). These extreme modifications of the inquiline species illustrate why these social parasites are not capable of living independently outside the colonies of their eusocial hosts. The life histories, such as sib and intranidal mating, also have significant consequences on the population biology of inquiline social parasites, which are often rare, have inbred populations, and have geographically restricted distribution ranges. Some entomologists suggested that ant inquiline social parasites are ephemeral species bound for extinction, but this interpretation remains to be tested with reliable data about the parasites' population biology. In contrast, some inquilines in the allodapine bee genus *Inquilina* persisted for tens of millions of years [20].

In addition to their modified morphologies and life histories, social parasites also employ chemical weaponry to deceive their hosts and fight the hosts' recognition systems. Social parasites communicate chemically with their hosts to gain entry and acceptance into the host colony, and the diverse chemical strategies were classified into three main categories [12, 17]. First, chemical insignificance is a strategy used by young social parasite queens entering a new host colony. The queens lack chemical cues, such as cuticular hydrocarbons, which are primarily used by social insects to discriminate nestmates from intruders, and thereby avoid detection by the host gaining access to the host colony. Second, camouflage describes the acquisition of chemical signals from the host or the host environment, which is then utilized by the social parasite to disguise itself from the host. Third, mimicry was observed in some social parasites that are capable of

synthesizing the chemical cues used to hide from host recognition, integrating into the host's chemical environment. In addition to the strategies social parasites utilize to hide their true identities from their hosts, some social parasites produce appeasement, propaganda, and/or repellent substances directly attacking, confusing, or manipulating the host communication system [12, 17]. To successfully invade a host colony, dulotic ants use propaganda substances mimicking the hosts' alarm pheromones. These pheromones solicit flight responses from the host workers, and allow the dulotic raiders to steal the host brood while the nest is being abandoned. Contrary to offensive propaganda substances, appeasement pheromones mitigate aggressive host behavior and were suggested to decrease aggressive behavior during usurpation. Social insects are generally regarded as miniature chemical factories producing a plethora of chemical compounds and the chemical ecology of host-parasite interactions has not been explored in detail. Therefore, exciting discoveries are expected from this field of research.

The socially parasitic bees differ significantly from their free-living, pollen-collecting relatives, because they have lost morphological structures and behaviors related to social colony life and nest building [6, 15]. The *Psithyrus* cuckoo bumble bees, for example, are workerless and depend on their hosts for foraging [13]. *Psithyrus* females do not actively collect pollen and nectar and their corbiculae or pollen-baskets are reduced because they not maintained by natural selection. Although still functional, the wax glands of *Psithyrus* females are also reduced and produce insufficient amounts of wax for nest construction. In addition to traits related to pollen-collecting, nest construction, and social colony life, cuckoo bumble bees are also well-protected to defend themselves against host attacks when entering a new host colony. Protective adaptations include strongly sclerotized integuments, fused intersegmental membranes, enlarged mandibles, and a more powerful sting with an enlarged venom gland. Cuckoo bumble bees are also chemically armed with an enlarged Dufour's gland from which a repellent chemical can be everted

protecting the parasite females from host worker attacks. To integrate into the host society, different species of cuckoo bumble bees developed different strategies including chemical insignificance, camouflage, and mimicry depending on the species' host specificity. The most host-specific social parasites mimic their hosts, synthesizing their proper cuticular hydrocarbon profiles, whereas host generalists acquire the colony odor from their hosts. The chemo-ecological dynamics suggest a co-evolutionary arms race between host deceit and parasite detection. In comparison to workerless ant inquiline social parasites, it is eye-catching that cuckoo bumble bees aggressively invade the host colony and co-evolved with their hosts to successfully attack and defend themselves, whereas ant inquilines seek rapid integration into the host colony avoiding openly hostile and aggressive interactions.

Social parasites of allodapine bees were also rarely collected on flowers, indicating that foraging is left to the host. The obligate inquiline species show strongly reduced mouthparts, scopa, compound eyes and wing venation, enlarged legs and tibial spines, as well as modified scythe-like mandibles which lack the indentation of host species specialized for excavating burrows from wood [20, 21] (Fig. 3). Furthermore, observations revealed that the inquilines were incapable of rearing their brood [20, 21]. In contrast, facultative social parasites, such as two Malagasy *Macrogalea* species, are still capable of raising their own brood, even though they show some morphological modifications associated with a socially parasitic lifestyle, such as reduced pollen-collecting structures.

Socially parasitic sweat bees convergently arrived at morphologies indicative of their socially parasitic lifestyles [8]. Similar to cuckoo bumble bees and inquiline allodapines, socially parasitic halictid bees lost morphological structures related to nest digging and pollen-collecting and gained traits associated with aggressive and defensive behaviors. The most conspicuous adaptations to aggressive behavior include a thicker integument, larger mandibles, and stronger mandibular adductor muscles, delivering a stronger bite.

Interestingly, the kleptoparasitic brood parasites and the social parasites share similar modification associated with their parasitic lifestyles, such as the heavily sclerotized integuments and both lack morphological structures related to pollen-collecting and nest construction. However, among the kleptoparasitic bees, not only the adult females but also the larvae can be adapted to their parasitic life history [6, 15]. In case of these “hospicidal” larval parasites, one or more larval instars are equipped with scythe-like mandibles that are especially used for killing the host larvae and/or larvae of other kleptoparasites inhabiting the same brood cell. Such fascinating adaptations of the larvae have so far not been discovered in inquiline social parasites.

The social parasites of polistine and vespine wasps are adapted for aggressive interactions with their hosts during nest invasions. For example, *Polistes* social parasites have thicker and stronger mandibles than their hosts, thicker integuments with more tightly fitting sclerites protecting them from being stung, and stronger developed femurs on their front legs, which are advantageous during battles with host females during nest invasion [4] (Fig. 4).

Polistes atrimandibularis and *P. semenowi*, in contrast to *P. sulcifer*, do not kill the host queen but coinhabit the nest alongside the host queen. To gain acceptance into the host colony, *P. atrimandibularis* queens are chemically insignificant at first, and then secondarily adopt the host’s chemical profile. Distinct behaviors of the parasite queens unique to *Polistes* social parasites include intense rubbing of the metasoma on the host nest surface and licking the host’s body. Both behaviors are thought to facilitate the parasite’s integration into the host society. Larvae of the social parasite species do not differ morphologically and behaviorally from their hosts.

Outlook

During the past couple of centuries, entomologists unearthed a remarkable diversity of social parasites species. With every new discovery, intricate and highly fascinating behaviors came to light

fueling our curiosity. Studying the biology of socially parasitic Hymenoptera is a highly integrative endeavor, and with every piece of new information the rich mosaic of social parasite biology is becoming more complete. Unfortunately, most social parasite species are rare. However, the rareness could also be viewed as a challenge, reminding us, the students of social insects, to jump at a chance to study the unknowns of social parasite biology. Only by utilizing a multidisciplinary approach, integrating biodiversity discovery, natural history, chemo-ecology, behavioral and evolutionary biology, as well as genetic and genomic approaches, will we be able to understand both the fascinating patterns of social parasite biology as well as the convergent mechanisms by which this intriguing diversity has evolved.

References

1. Adams, R. M., Liberti, J., Illum, A. A., Jones, T. H., Nash, D. R., & Boomsma, J. J. (2013). Chemically armed mercenary ants protect fungus-farming societies. *Proceedings of the National Academy of Sciences of the USA*, *110*, 15752–15757.
2. Bourke, A. F., & Franks, N. R. (1991). Alternative adaptations, sympatric speciation and the evolution of parasitic, inquiline ants. *Biological Journal of the Linnean Society*, *43*, 157–178.
3. Buschinger, A. (2009). Social parasitism among ants: A review (Hymenoptera: Formicidae). *Myrmecological News*, *12*, 219–235.
4. Cervo, R. (2006). *Polistes* wasps and their social parasites: An overview. *Annales Zoologici Fennici*, *43*, 531–549.
5. D’Ettorre, P., & Heinze, J. (2001). Sociobiology of slave-making ants. *Acta Ethologica*, *3*, 67–82.
6. Danforth, B. N., Minckley, R. L., & Neff, J. L. (2019). *The solitary bees: Biology, evolution, conservation*. Princeton, NJ: Princeton University Press.
7. Emery, C. (1909). Über den Ursprung der dulotischen, parasitischen und myrmekophilen Ameisen. *Biologisches Zentralblatt*, *29*, 352–362.
8. Gibbs, J., Albert, J., & Packer, L. (2012). Dual origins of social parasitism in North American *Dialictus* (Hymenoptera: Halictidae) confirmed using a phylogenetic approach. *Cladistics*, *28*, 195–207.
9. Gray, K., Cover, S., Johnson, R., & Rabeling, C. (2018). The dacetine ant *Strumigenys arizonica*, an apparent obligate commensal of the fungus-growing ant *Trachymyrmex arizonensis* in southwestern North America. *Insectes Sociaux*, *65*, 401–410.

10. Hölldobler, B., & Wilson, E. O. (1990). *The ants*. Cambridge, MA: Harvard University Press.
11. Kutter, H. (1968). Die sozialparasitischen Ameisen der Schweiz. *Neujahrsblatt der Naturforschenden Gesellschaft in Zürich*, 171, 1–62.
12. Lenoir, A., D'Ettorre, P., Errard, C., & Hefetz, A. (2001). Chemical ecology and social parasitism in ants. *Annual Review of Entomology*, 46, 573–599.
13. Lhomme, P., & Hines, H. M. (2018). Ecology and evolution of cuckoo bumble bees. *Annals of the Entomological Society of America*, 112, 122–140.
14. Lopez-Osorio, F., Perrard, A., Pickett, K. M., Carpenter, J. M., & Agnarsson, I. (2015). Phylogenetic tests reject Emery's rule in the evolution of social parasitism in yellowjackets and hornets (Hymenoptera: Vespidae, Vespinae). *Royal Society Open Science*, 2, 150–159.
15. Michener, C. D. (2000). *The bees of the world*. Baltimore: The Johns Hopkins University Press.
16. Müller, H. (1872). Anwendung der Darwinischen Lehre auf Bienen. *Verhandlungen des naturhistorischen Vereines der preussischen Rheinlande und Westphalens* 29; 3. Folge; 9. Band; Seiten 1–96 + 2 Tafeln.
17. Nash, D. R., & Boomsma, J. J. (2008). Communication between hosts and social parasites. In D. P. Hughes & P. D'Ettorre (Eds.), *Sociobiology of communication: An interdisciplinary perspective* (pp. 55–79). Oxford, UK: Oxford University Press.
18. Rabeling, C., Schultz, T. R., Pierce, N. E., & Bacci, M., Jr. (2014). A social parasite evolved reproductive isolation from its fungus-growing ant host in sympatry. *Current Biology*, 24, 2047–2052.
19. Rabeling, C., Messer, S., Lacau, S., do Nascimento, I., Bacci, M., & Delabie, J. (2019). *Acromyrmex fowleri*: A new inquiline social parasite species of leaf-cutting ants from South America, with a discussion of social parasite biogeography in the Neotropical region. *Insectes Sociaux*, 66, 435–451.
20. Smith, J. A., Chenoweth, L. B., Tierney, S. M., & Schwarz, M. P. (2013). Repeated origins of social parasitism in allodapine bees indicate that the weak form of Emery's rule is widespread, yet sympatric speciation remains highly problematic. *Biological Journal of the Linnean Society*, 109, 320–331.
21. Tierney, S. M., Smith, J. A., Chenoweth, L., & Schwarz, M. P. (2012). Phylogenetics of allodapine bees: A review of social evolution, parasitism and biogeography. *Apidologie*, 39, 3–15.
22. Ward, P. S., Brady, S. G., Fisher, B. L., & Schultz, T. R. (2015). The evolution of myrmicine ants: Phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae). *Systematic Entomology*, 40, 61–81.
23. Wcislo, W. T. (1987). The roles of seasonality, host synchrony, and behaviour in the evolutions and distributions of nest parasites in Hymenoptera (Insecta) with special reference to bees (Apoidea). *Biological Reviews*, 62, 515–542.
24. Wheeler, W. M. (1919). The parasitic Aculeata, a study in evolution. *Proceedings of the American Philosophical Society*, 58, 1–40.
25. Wilson, E. O. (1971). *The insect societies*. Cambridge, MA: Harvard University Press.