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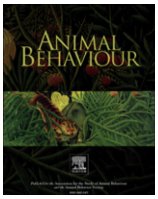

Review

The mating biology of termites: a comparative review

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Eusocial living influences mating system evolution if kin selection selects for a low number of fathers to increase helper relatedness and helping incentive. Consequently, polyandry resulting in pre- and postcopulatory sexual selection is restricted in social compared to nonsocial species. Despite a growing body of literature, empirical studies are still needed to understand fully the effects of kin selection on mating system evolution or vice versa. Here we review the mating biology of termites and conclude that they make interesting study species to unravel the evolutionary interplay between mating system evolution and eusociality. A number of reproductive characteristics of termites differ substantially from those of other insects. Polyandry appears to be mostly absent in termites and lifetime pair formation is achieved early in life, after an initial dispersal flight. The consequent absence of postcopulatory sexual selection coincides with the loss of a number of reproductive traits, such as elaborate male and female genitalia, flagellated sperm and seminal fluid-producing male accessory glands. The absence of sexually selected, female-harming male traits suggests that the interests of males and females are well aligned in most termites, fostering the evolution of kings, males with life expectancies comparable to those of queens and the ability to supply sperm continuously. Comparative work on mating system evolution between the diplodiploid termites and the haplodiploid hymenopteran social insects can be used to explain the influence of kin selection. We conclude that the study of social insect reproduction offers exciting opportunities to understand the evolutionary interplay between sexual, natural and kin selection.

The reproductive biology of social insects has received increasing interest over recent years because the mode of reproduction ultimately defines helper relatedness, which is assumed to be a driver for kin selection (Hölldobler & Bartz 1985; Baer 2003; 2005; Boomsma 2007; Hughes et al. 2008). With few exceptions known so far (Himler et al. 2009), social insects have all maintained the ability to reproduce sexually, thereby lowering helper relatedness and the helping incentive compared to hypothetical clonal systems. Furthermore, polyandry has evolved independently in several social insect species (Boomsma & Ratnieks 1996; Strassmann 2001; Kronauer et al. 2004; Baer 2011), which further reduces helper relatedness and results in additional kin-related conflicts (Boomsma 1996). A number of studies have investigated the costs and benefits of sex and polyandry in social insects; the vast majority have been conducted on hymenopterans (Boomsma & Ratnieks 1996; Boomsma et al. 2005) and some isopterans, being the termites (Calleri et al. 2005, 2006a, b). These studies provide multiple independent lines of evidence that pair formation and mating have a substantial influence on the performance and fitness of the subsequent colony, and that costs associated with lower helper relatedness (Baer & Schmid-Hempel 2001) can be offset with fitness-enhancing benefits such as reduced parasitism (Baer & Schmid-Hempel 1999, 2001; Tarpy 2003; Hughes & Boomsma 2005; Calleri et al. 2006b; Tarpy & Seeley 2006; Seeley & Tarpy 2007) or more efficient division of labour (Wiernasz et al. 2008).

Kin selection is assumed to be the driver of eusociality in both groups, and termites and hymenopterans share a number of key traits supporting this idea. First, both termites and social hymenopterans possess life history traits that result in high helper relatedness. Colony foundation is typically by a single mated pair, such as a queen and king in termites or a single queen storing sperm of her deceased mate(s) in hymenopterans. Furthermore, pair bonding for life appears to be maintained throughout virtually all clades (Boomsma et al. 2005; Boomsma 2009), such that a colony is a closed system throughout its life span with no additional genetic contributions after initial pair formation. In both groups, pair formation is typically achieved during swarming events away from the maternal colony, and new colonies are generally founded in the absence of helpers. Finally, spectacularly large and long-lived societies with extreme male and female

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fecundity, sophisticated division of labour and complex symbiotic interactions have evolved in both groups. As a consequence of their successful social lifestyle, the ants and termites, and to a lesser extent also the bees and wasps, have become ecologically dominant components of many tropical and temperate ecosystems.

The focus on kin selection has resulted in a neglect of sexual selection as a possible force in the evolution of mating systems in social insects. While sexual selection is well documented in many taxa, it is only beginning to be studied in the social Hymenoptera (reviewed in Crozier & Page 1985; Simmons 2001; see also Kraus et al. 2003; Schlüns et al. 2003; Kronauer et al. 2007; Couvillon et al. 2010) and is little understood in termites. The short pair formation period early in life has fitness consequences spanning years or decades (Keller 1998) and competition for mates able to produce large numbers of nonreproductive offspring can result in intra- and intersexual conflicts. As we point out below, these conflicts and their effects may be very different for social hymenopterans and termites and this provides fertile ground for disentangling the effects of natural selection, sexual selection and eusociality on reproductive traits.

In this review we compare the mating biology of termites with that of the better-studied hymenopteran social insects. In spite of a similar number of recent papers published on these two groups of eusocial insects (ISI Web of Science 2000–2010: 1562 articles and reviews found using ‘Isoptera’ as a search word and 1839 publications using ‘hymenoptera’ and ‘social’), far less attention has been paid to the mating biology of termites (ISI Web of Science: 20 hits for search for ‘Isoptera’ and ‘mating’ versus 390 hits for ‘Hymenoptera’, ‘social’ and ‘mating’). We begin with an overview of the mating biology of termites and develop an evolutionary comparison to the hymenopteran social insects. To conclude, we discuss avenues for future research.

ISOPTERA AND SOCIAL HYMENOPTERA

There are currently about 3000 described termite species (Engel et al. 2009), far fewer than the 19 000, eusocial hymenopterans (Schmid-Hempel 1998). All known termite species are eusocial and diverged from a common ancestor with the subsocial cryptocercid roaches in the late Jurassic, about 35 million years before the ants first arose (Engel et al. 2009). Ecological dominance and the development of large colonies with extreme division of labour occurred in the Tertiary, coinciding with similar developments in ants and marked by the greatest radiation of the termites, the family Termitidae, 20–40 million years ago. Like some eusocial hymenopterans, termites dominate many terrestrial ecosystems: termite densities may exceed 1000 individuals/m^2 or 2000 mg/m^2 (Sugimoto et al. 2000). Termites are major consumers of cellulose and lignocellulose, and it is estimated that they process 50–100% of dead plant biomass in the tropics (Bignell & Eggleton 2000).

Termites are more geographically restricted than the social Hymenoptera. Of the living species of termites, 70% belong to the derived family Termitidae (the ‘higher’ termites; Engel et al. 2009; Inward et al. 2007), distributed throughout the tropics. Many of these species build mounds or arboreal carton nests, housing large colonies with extreme division of labour. Most Termitidae have a queen (whose abdomen becomes substantially enlarged after colony foundation, referred to as physogastric), a king, and sterile worker and soldier castes. Diets range from dead wood, soil, grass and forest litter to microepiphytes and cultivated fungi (Eggleton & Tayasu 2001). Gut symbionts are fungi and prokaryotes.

The remaining basal termite species, currently classified into eight extant families (Engel et al. 2009), are collectively referred to as ‘lower’ termites. With the exception of the grass-feeding Hodotermitidae and the inquiline Serritermitidae, which live in and feed on the nest material of other termites, lower termites feed exclusively on wood, which they digest with the help of flagellated protistan symbionts. Lower termites are found in both temperate and tropical regions, and include some of the most important pest species in the world (Vargo & Husseneder 2009). With the exception of two rare lineages (Inward et al. 2007), the most basal species form smaller colonies and live within their only food source, while more derived taxa forage outside the central nest site and achieve larger colony sizes (Eggleton & Tayasu 2001). Division of labour is not fixed in these taxa owing to totipotency (see below) of the helpers. Indeed, helpers in some basal termites, such as *Archotermopsis* (Imms 1920), have the same degree of gonad development as mature alates (the dispersing winged sexuals). Reproduction by helpers may be pheromonally suppressed in lower termites (Lüscher 1961), but caste regulation or fertility-signalling substances have only recently been identified (Liebig et al. 2009; Weil et al. 2009; Hanus et al. 2010) and require further study.

Caste development and determination is more complex and plastic in termites than in hymenopterans (Fig. 1), although sexually reproducing castes of termites are, as in the hymenopterans, developmental endpoints. Caste development follows either a ‘linear’ pathway (highly plastic development, lower termites) or a ‘bifurcated’ pathway (fixed castes, Termitidae; Roisin & Korb 2010). In the lower termites, developmental plasticity allows helpers in the nest to maintain their reproductive potential. They can either reproduce at low levels in their natal colony with low developmental investment (neotenic reproductives) or undergo additional moults to become alate primary reproductives and disperse to establish independent colonies. In some taxa, even the most morphologically differentiated caste, the soldiers, can undergo regressive moults to develop into reproductives (Roisin 2000). In higher termites, caste is determined early in development and is irreversible, similar to most hymenopterans in that workers and soldiers are unable to reproduce or develop into alates. This variation and plasticity of caste determination offers interesting opportunities for comparative studies, for example to study conflicts over reproduction within colonies (e.g. Hoffmann & Korb 2011).

Similar to most hymenopterans, colony foundation occurs after a dispersal event of the sexuals (Nutting 1969). While in most social hymenopterans newly inseminated females found new colonies solitarily, termites initiate a new society as a (de-alated) pair of primary reproductives, the queen and the king. Over time, the queen and king in basal termites can be supplemented with or replaced by neotenic reproductives developed from their offspring (Myles 1999). This is rare in the higher termites, and, similar to many social hymenopterans, colony life span is directly linked to the survival of the primary queen and her mate.

THE MATING BIOLOGY OF TERMITES

Most work conducted so far on the mating biology of termites has investigated the dynamics of pair formation and colony foundation during and after nuptial flights (Thorne & Haverty 2000; Kaib et al. 2001; Matsuura & Nishida 2001; Shellman-Reeve 2001; Fei & Henderson 2003; Long et al. 2003; Raina et al. 2003a; Rosengaus et al. 2003; Matsuura et al. 2004; Park et al. 2004; Calleri et al. 2005, 2006a, b, 2007; DeHeer & Vargo 2006; Husseneder & Simms 2008; Adam & Mitchell 2009). The physiological details of sperm production, transfer, storage and use have received little attention (Dean & Gold 2004; Raina et al. 2007; Ye et al. 2009), although the ability of termite kings to provide large numbers of viable sperm to the queen continuously for up to several decades is as remarkable as that of some social hymenopteran queens to store sperm of their deceased mates for similar amounts of time (Pamilo