Parental quality in a subterranean termite

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An aspect of termite evolution that should be a source of envy to entomologists studying social Hymenoptera, is that the evolutionary antecedents of eusociality are well understood. Termites are clearly the sister group to subsocial wood roaches (genus *Cryptocercus*), whose biparental behaviour can be used to reconstruct the parental behaviour and life history of the common ancestor of wood roaches and termites (Bourguignon et al. 2015; Nalepa 2015). This ancestor would have lived in family groups in which both parents cared for slow-developing juveniles that took years to reach maturity at a relatively large body size. The necessity for high-cost parenting probably limited this ancestor to a semelparous life history like that of wood roaches, producing one batch of offspring over its lifetime. Since diverging from their roach-like ancestors, termites have “miniaturized”, increased their fecundity, and become iteroparous and eusocial, living in colonies in which the vast majority of juveniles are raised by alloparental workers rather than by their own parents (Nalepa 2010). Nevertheless, termites have retained a crucial subsocial phase in their life histories, because colonies are founded by a single female and male (queen and king) which raise the first offspring themselves. It can take months for these first offspring to mature into workers that raise subsequent offspring, taking over the parental care duties that then allow the royal pair to focus on egg production (Chouvenc and Su 2017). Therefore, just as in their subsocial ancestors, the ability of queen and king termites to care for this first brood is crucial to colony success. An important component of high-quality parenting in termites is their ability to produce the hindgut secretions with which they feed their offspring. In this, larger parents with more stored resources likely have an advantage, and so should produce more workers. The more workers they produce, the more likely it is that they and their offspring

will survive this first crucial, subsocial stage of colony development.

The Asian subterranean termite, *Coptotermes gestroi*, is a relatively small species endemic to southeast Asia. It is also one of the world’s most destructive invasive species, especially in urban cities in warm climates. Their wood-eating habits pose a threat to both human infrastructure and urban ecosystems. Like other members of this family (Rhinotermitidae), colonies are initiated by a single queen and king that pair up during a mating flight, then find a suitable nest site, create a nesting chamber, and lay their first batch of 15–30 eggs. From these modest beginnings, colonies eventually can grow to contain millions of individuals. In this issue, Chouvenc (2019) experimentally investigates the relationship between parental size and colony survival through the crucial subsocial stage of new colonies. Chouvenc collected thousands of alates during mating flights, then set up 175 pairs representing a range of female and male size combinations. Each pair was weighed and then introduced to a rearing unit, in which they lived for the next 9 months, when colony survival and productivity were assessed. The initial weights of the founding queen and king were significant predictors of both colony survival and total biomass. Larger queens and kings lost more weight over the 9 month period, probably because they had provided more resources to offspring. A biologically significant proportion of the variance (27%) in colony biomass was explained by parents’ initial weights, suggesting directional selection for larger alate body size as one important trait influencing parental quality in termites. In contrast, the small sizes of termite alates in comparison to subsocial wood roaches implies that since termites became eusocial, there has been long-term selection for smaller body size in concert with production of much higher numbers of offspring (Nalepa 2010). The limits to this “miniaturization” process can be seen in Chouvenc’s study. The current alate size of a given species likely represents a compromise between these two opposing selective forces, resulting in a presumably optimal balance between the quality and quantity of alates produced by a mature termite colony.

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In many animals, offspring requirements for parental care and other resource investments, constrain the number and size of offspring that they produce (Smith and Fretwell 1974). The evolution of eusociality in termites evidently has not removed this constraint on parental investment from their life history. The existence of a crucial subsocial phase in the life cycle of termites reminds us that it may be an oversimplification to conceptualize queens as specialized egg-layers and workers as brood-carers. Before they get to the “reproductive specialist” phase of their lives, termite queens and kings, as well as the queens of many ants, wasps, and bees, must first provide all the resources and parental care necessary for raising their brood, just as their non-social ancestors did, once upon a time.

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