

## Queen and male longevity in the Southeast Asian ant *Cardiocondyla tjibodana* Karavaiev, 1935

MARION FUESSL, JÜRGEN HEINZE AND ALEXANDRA SCHREMPF\*

Biologie I, Universität Regensburg,  
D-93040 Regensburg, Germany

\*Corresponding author's e-mail: alexandra.schrempf@ur.de

**ABSTRACT.** Many species of the ant genus *Cardiocondyla* are characterized by a bizarre polyphenism with winged disperser males and wingless males that engage in lethal fighting for access to nestmate queens. In *C. obscurior*, winged males have a stronger life-prolonging and fecundity-enhancing effect for their female mates than wingless males. Here we examine whether the same is true for males of the Southeast Asian *C. tjibodana*. Male phenotype did not have an effect on queen life expectancy and fecundity. Like the queens of other *Cardiocondyla* species, *C. tjibodana* queens were relatively short-lived, with a maximum lifespan of 273 days. Males of both phenotypes survived for a median of 25 days, with one wingless male reaching an age of 194 days. Data from additional species of *Cardiocondyla* are needed to determine how life expectancy of males and queens and the male influence on queen traits have evolved in this genus.

**Keywords:** life history trade-off, male polyphenism, longevity

### INTRODUCTION

In many animal species, males pursue different approaches to increase their mating success (Oliveira *et al.* 2008). Dominant males may provide females with access to their territories or nutritious nuptial gifts in exchange for copulations, while sneaker males do not deliver such direct benefits (e.g., Brockmann 2008). In the male-diphenic ant *Cardiocondyla obscurior*, queens that mate with a winged male have on average a longer lifespan, and thereby a larger reproductive success than queens that mate with a wingless fighter male (Schrempf & Heinze 2008). The mechanisms of this beneficial effect of mating with winged males are not yet understood but presumably involve seminal fluids (Schrempf *et al.* 2005), which indeed differ strikingly between winged and wingless males (M. Fuessler, unpublished). Ultimately it appears to be linked with different colony founding

strategies and environmental stress. Female sexuals and wingless males are reared year-round, and most young queens remain in their natal nest after mating and found new colonies assisted by workers in the immediate vicinity (“budding”, Cremer & Heinze 2003, Heinze & Delabie 2005). In contrast, winged males are produced during periods of environmental changes when the natal colony declines (Cremer & Heinze 2003). Young queens may then be forced to disperse on the wing and to found solitarily without the help of workers. Independently founding queens need considerably more time before they produce sexuals and the life-prolonging effect of winged males can be seen as a postmating investment into their joint offspring.

Winged and wingless males co-occur also in other species of *Cardiocondyla*, but the production pattern appears to differ considerably among species. In the Southeast Asian endemic *Cardiocondyla tjibodana* Karavaiev, 1935,

winged males appear to occur regularly in colonies in the laboratory, and have also been collected in the field. In contrast to *C. obscurior*, where winged males readily emigrate from the natal nest to mate with queens away from it (Kinomura & Yamauchi 1987), winged males of *C. tjibodana* may stay and mate there throughout their entire lives (M. Fuessl, unpublished).

Our study documents that male phene does not differently affect female longevity and fecundity in *C. tjibodana*. In addition, it increases the data base on life expectancies and age-specific fecundity of *Cardiocondyla* queens and thus contributes to insect sociometry, “a field in search of data” (Tschinkel 1991).

## MATERIAL AND METHODS

*C. tjibodana* is a species of the *C. minutior* group, which is widely distributed throughout disturbed and ruderal habitats in Southeast Asia (Seifert 2003). Several small, polygynous (multi-queen) colonies were excavated from their nests in soil in various places in Indonesia. The study is based on experimental colonies derived from a single stock colony collected on Oct, 19, 2008 from its nest in sandy soil on a parking lot near Gua Londron Cave, Pangkajene, Sulawesi Selatan, Indonesia. Because of intranidal mating and colony budding, populations of many *Cardiocondyla* in such anthropogenically influenced places form interconnected colonies with limited genetic differentiation. Using different stock colonies from the same location would presumably not have resulted in larger genetic diversity and thus not have affected the results of our study. However, we would like to stress that the results of our study can be considered as representative of only the studied supercolony and might depart in other populations.

Winged males of *C. tjibodana* resemble typical ant males in morphology and behaviour – they have long antennae, well-developed eyes, and a bulky thorax. They are dark brown in colour, and their mandibles are worker-like. Contrary, but in agreement with many other species of *Cardiocondyla*, wingless males are amber in colouration, have small eyes and strong, shear-shaped mandibles. Their antennae and

thorax are worker-like, though the shoulders are more pronounced in comparison to workers. They attempt to monopolize mating with all queens eclosing in their natal nest by eliminating newly emerging wingless male rivals with their strong mandibles but rarely savage adult males. Young males occasionally escape attacks by an older male and in particular large colonies may therefore contain sometimes two or more wingless males.

Following Schrempf *et al.* (2005) we set up experimental colonies consisting of one female sexual pupa, 20 workers, a few larvae, but no eggs and the pupa of either a winged ( $n = 26$ ) or a wingless male ( $n = 23$ ). After eclosion, the sexuals mated in the nest and young queens shed their wings. We checked for the presence of the queen and male as well as that of eggs and pupae twice per week. The number of adult workers was kept constant at 20 to avoid positive feedback between colony size, queen fecundity, and lifespan (e.g., see Heinze & Schrempf 2012).

## RESULTS AND DISCUSSION

Winged and wingless males did not differ in average lifespan (19 wingless males: 4 – 194 days, median, quartiles 25 [11 – 46]; 25 winged males: 7 – 41 days, 25, [16 – 27]; Mann-Whitney U-test,  $U = 218.5$ ,  $P = 0.652$ ). However, wingless males reached a considerably higher maximum lifespan than winged males (194 vs. 41 days). Male phene did not affect the lifespan of queens (23 queens mated with wingless males: 32 – 243 days, median, quartiles 154, [89 – 206]; 26 queens mated with winged males: 31 – 273 days, median, quartiles 112.5, [63 – 200];  $U = 237$ ,  $P = 0.214$ ; all 49 queens: median, quartiles 122, [80 – 205], Fig. 1). Interestingly, the lifespan of wingless males and their mates was positively correlated ( $n = 19$ , Spearman rank correlation,  $r_s = 0.550$ ,  $P = 0.015$ ), whereas those of winged males and their mates was not ( $n = 25$ ,  $r_s = 0.030$ ,  $P = 0.888$ ).

Queen longevity was positively associated with the number of eggs observed per scan ( $n = 49$ ,  $r_s = 0.410$ ,  $P = 0.0035$ ). Male phene did not have an influence on median egg laying rate (number of eggs per scan: queens mated with wingless males: median, quartiles 5.27, [4.25 –

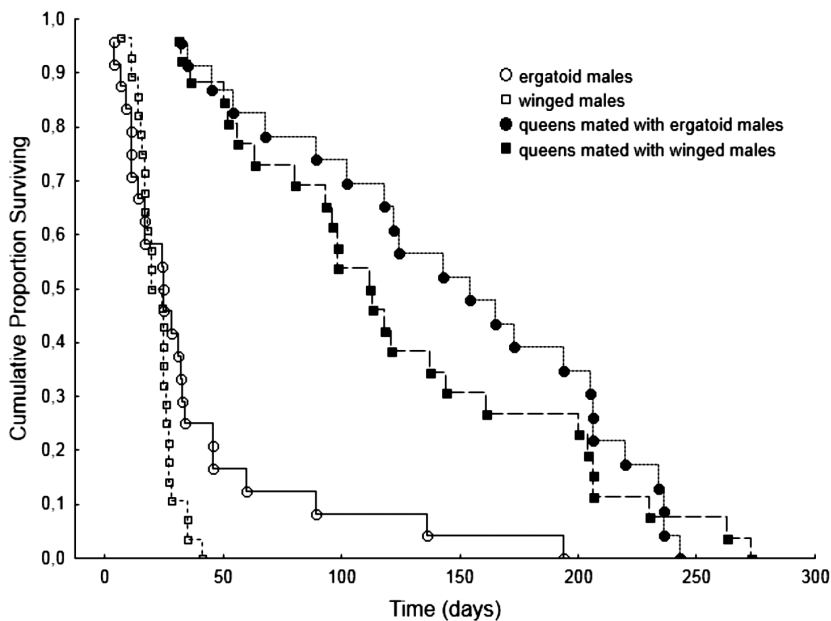


Fig. 1. Cumulative proportion surviving of the the two male phenes and of queens that mated with either a winged or an ergatoid male (age in days).

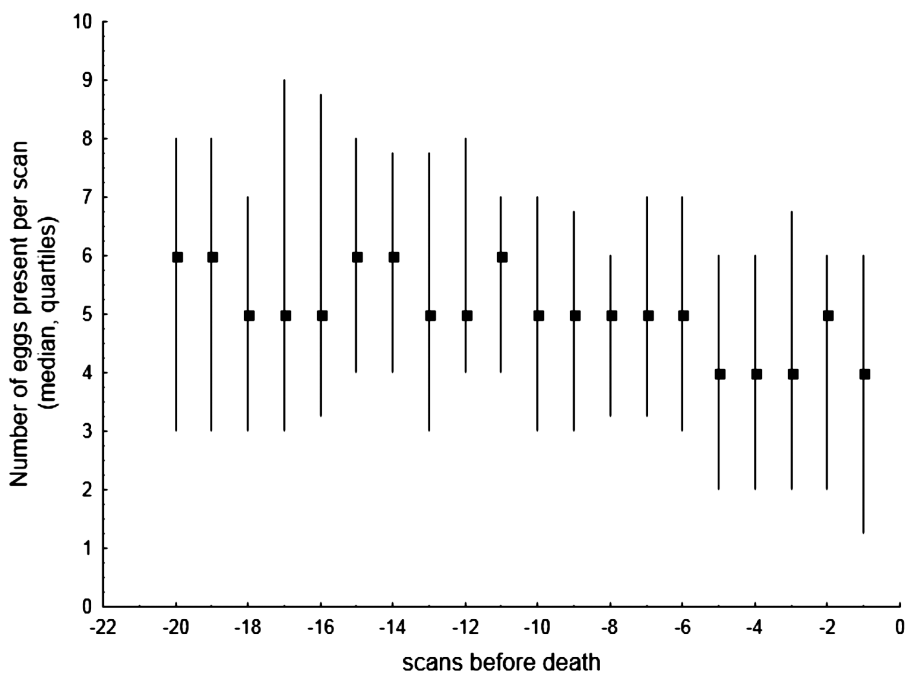


Fig. 2. Median ( $\pm$  quartiles) egg laying rate of the queens throughout their lifetime, from the beginning till death (0).

6.09]; queens mated with winged males: 5.12 [4.14 – 6.49];  $U = 245$ ,  $P = 0.287$ ). Throughout almost the complete lifetime of queens the median number of eggs observed per scan stayed on a plateau of 4 to 6 eggs (Fig. 2). Brood production was low under our experimental conditions with the reduction of worker numbers to 20, and only 19 of 49 colonies produced worker offspring.

Results from our experiment with *C. tjobodana* in part are in accordance with data from previous studies on the longevity of *Cardiocondyla*. Winged and wingless males of *C. tjobodana* have almost the same median lifespans as those of the close relative *C. minutior*; and like in other *Cardiocondyla*, the maximal lifespan obtained by wingless males greatly surpasses that of most winged ant males, including those of *Cardiocondyla* (Heinze *et al.* 1998; Yamauchi *et al.* 2006; Schrempf *et al.* 2007; Shik & Kaspari 2009, Shik *et al.* 2013). With lifespans of less than one year, queens of *C. tjobodana* and other tropical *Cardiocondyla* are ephemeral compared to the notoriously long-lived queens of monogynous ant species (Keller 1998). However, this matches their polygynous and r-selected life history with frequent queen replacements, colony propagation by budding, and rapid population growth (Tsuji & Tsuji 1996; Tsuji 2006). Queens of monogynous *Cardiocondyla* from temperate habitats appear to be more long-lived (Schrempf & Heinze 2007).

In other aspects, *C. tjobodana* is surprisingly different from other *Cardiocondyla*. First, whereas in *C. obscurior* and *C. kagutsuchi* (Heinze *et al.* 2014) egg laying rates increased with queen age, egg numbers remained at a rather constant value in our experimental sub-colonies of *C. tjobodana*. The limitation of worker numbers did apparently not have a negative effect on oviposition rates, because in two colonies, which were allowed to increase in size, we also counted only maximally 19 eggs per scan. Furthermore, the two queens in the unmanipulated sub-colonies lived for only 80 and 125 days, respectively, indicating that larger worker numbers do not necessarily prolong the life of queens. Egg laying rates did not considerably decline in the last days before death, indicating negligible reproductive senescence like in *C. obscurior* (Heinze & Schrempf 2012).

The second difference between *C. obscurior* and *C. tjobodana* is that male phenotype did not affect the life expectancy of *C. tjobodana* queens, while in *C. obscurior* mating with a winged male has a considerably stronger positive effect on queen life expectancy than mating with a wingless male (Schrempf & Heinze 2008). Unfortunately, nothing is known about the influence of mating with winged vs. wingless males in other male-diphenic *Cardiocondyla* and it is thus futile to speculate about possible explanations for this striking difference.

In any case, winged males of *C. tjobodana* seem to have lost their function as an exclusive disperser phenone (Cremer & Heinze 2003), and further studies are needed to elucidate the factors that influence the occurrence and ratio of winged and ergatoid males in the colonies.

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