Introduction

Conspecific males of many animal species employ different ways to increase their reproductive success. Such alternative reproductive tactics are easily recognized when associated with pronounced morphological differences, e.g., when territorial males have well-developed weapons while sneaker or female mimics have not [1,2]. In addition, morphologically uniform males sometimes adjust their breeding behaviour to changes in their social and ecological environment. For example, individuals may choose between philopatry and dispersal based on the local presence of mating partners and competitors, as occurs in some vertebrate species [1,3–5]. It is so far not clear whether also males of social insects are able to perform such adaptive mating decisions by behavioural plasticity.

Social insects (the social bees and wasps, ants and termites) typically mate within a swarm flight, in which scramble competition is the dominant form of male-male competition [6]. However, in some species, more complex sexual behaviour has evolved. Among these is our study system, the ant species *Cardiocondyla obscurior* that is characterized by a high social plasticity. First, colonies of this species can have variable queen numbers from a single to multiple queens and second, two male morphs co-occur and form a male diphenism with wingless fighter males (“ergatoid males”) and peaceful winged males. Wingless males engage in lethal combat for access to female nestmates, whereas winged males resemble the typical docile ant male in behaviour and physiology [7–11]. Wingless males stay lifelong in their natal nests, but the behaviour of winged males is more flexible: they mate within the nest early during their adult lives, but later disperse and search for female sexuals outside [7,12,13].

Here, we investigated whether winged males of *C. obscurior* can adaptively adjust the timing of their dispersal from the natal nest to local mating opportunities. We indeed observed that they stay longer in their natal nests when mating partners are available but leave earlier when male competitors are present. We also found that winged males adjust their departure time to the male morph with which they share the nest. They leave much earlier in the presence of a wingless fighter male than of a second peaceful winged male, revealing that the dispersal decision of winged males is also dependent on the type of male-male competition.

Methods

We collected 45 *Cardiocondyla obscurior* colonies from their nests in folded leaves in an experimental lemon plantation in Una, Bahia, Brazil. Collecting of colonies was allowed by Brazilian authorities (permit RMX 004/02). The experiments comply with the laws of Germany.

Ants were reared in the laboratory at a 30°C/25°C day/night cycle in three-chamber plastic boxes with a plaster floor [14]. One compartment contained a cavity in the ground covered with a microscope slide, where the ants formed their nests. Food (diluted honey and pieces of cockroaches) was offered in a second
Results

Winged males left colonies with virgin female sexuals 19.3 ± 6.7 (mean ± s.d.) days after emergence when they were the only male in the nest. They left the nest approximately five days earlier (14.0 ± 3.2 days) when sharing it with a second winged male and yet another five days earlier (9.0 ± 3.8 days) when they competed with a wingless male (Fig. 1A; ANOVA, \( F_{2,23} = 10.39, P < 0.001 \); pairwise SNK posthoc tests: all significant). As reported previously, winged males readily mated with the female sexuals and achieved a similar copulation frequency as wingless males [13].

In the absence of female sexuals, winged males left the nest after 12.7 ± 3.0 days when they were the only male in the colony and after 10.2 ± 6.5 days when they shared the nest with a wingless male. When comparing the timing of dispersal between colonies with and without female sexuals, we found that the presence of female sexuals delays dispersal by winged males only if no wingless males are present (Fig. 1B). This is indicated by the significant interaction term in a Two Way ANOVA (effect of presence/absence of wingless males: \( F_{1,47} = 13.29, P < 0.001 \); effect of presence/absence of female sexuals: \( F_{1,47} = 2.15, P = 0.15 \); interaction wingless males and female sexuals: \( F_{1,47} = 6.31, P < 0.016 \)).

Discussion

Our data show that winged males of Cardiocondyla obscurior adjust their reproductive behaviour to mating opportunities and the presence and type of male competitors. Winged males left the nest later when they were the only male in a colony than when other males were present. They stayed significantly longer in the natal nest in the presence of another docile winged male than in the presence of a wingless fighter male. This reflects different degrees of male-male competition. Whereas winged competitors only
decrease the availability of virgin queens and, if female sexuals mated multiply, potentially increasing sperm competition, the presence of wingless males introduces the risk of being killed or injured. Winged males chemically mimic female sexuals during the first few days of their adult lives and therefore are relatively safe against lethal attacks from wingless males [13,15]. However, their chemical female mimicry becomes less effective with age and the chemical profile of ten day old winged males does no longer overlap with that of virgin females [13]. Interestingly, we here found that winged males that share a nest with an aggressive wingless male leave already one day earlier, namely on average at the age of nine days. In contrast, winged males stay much longer in the nest if being the only male in a colony or if they share it with another peaceful winged male. This suggests that winged males ‘may be aware’ of the loss of their chemical protection against wingless males when they grow older and therefore leave the nest to prevent possible attacks, which are predicted by theory [12].

Over all, the reproductive behaviour of winged males of *C. obscurior* is surprisingly flexible. They appear to be capable of estimating their breeding chances in the natal nest in respect of the presence of competitors and the number of potential mating partners and adjust their dispersal behaviour accordingly. The behavioural plasticity shown by winged *Cardiocondyla* males allows context-dependent choices that resemble the often complex decision-making about staying or leaving in foraging animals [16] and the opportunistic breeding tactics known from vertebrate species [1,3].

**Acknowledgments**

We thank M. Sixt for comments on the manuscript.

**Author Contributions**

Conceived and designed the experiments: SC JH. Performed the experiments: SC AS. Analyzed the data: SC. Contributed reagents/materials/analysis tools: JH. Wrote the manuscript: SC AS JH.

**References**

1. Gross MR (1996) Alternative reproductive strategies and tactics: diversity within the sexes. Trends Ecol Evol 11: 92–98.
2. Oliveira RF, Taborsky M, Brockmann HJ, eds. Alternative reproductive tactics. Cambridge, UK: Cambridge University Press. 518 p.
3. Kodric-Brown A (1986) Satellites and sneakers: opportunistic male breeding tactics in pupfish (*Cyprinodon pupa*). Behav Ecol Sociobiol 18: 425–432.
4. Lawrence WS (1987) Dispersal: an alternative mating tactic conditional on sex ratio and body size. Behav Ecol Sociobiol 21: 367–373.
5. Thorpe R, Alcock J (1983) The evolution of insect mating systems. Cambridge, Mass.: Harvard University Press. 364 p.
6. Boomser JJ, Barr B, Heinze J (2005) The evolution of male traits in social insects. Annu Rev Entomol 50: 395–402.
7. Kinomura K, Yamauchi K (1987) Fighting and mating behaviors of dimorphic males in the ant *Cardiocondyla murrillii*. Journal of Ethology 5: 75–81.
8. Stann RJ, Francoeur A, Loselle R (1987) Lethal fighting among dimorphic males of the ant, *Cardiocondyla murrillii*. Naturwissenschaften 74: 548–549.
9. Heinze J, Hölldobler B (1993) Fighting for a harem of queens: physiology and reproduction in *Cardiocondyla* male ants. P Natl Acad Sci USA 90: 9412–9414.
10. Heinze J, Hölldobler B, Yamauchi K (1998) Male competition in *Cardiocondyla* ants. Behav Ecol Sociobiol 42: 239–246.
11. Heinze J, Trindl A, Seifert B, Yamauchi K (2005) Evolution of male morphology in the ant genus *Cardiocondyla*. Mol Phylogenet Evol 37: 278–288.
12. Anderson C, Cremer S, Heinze J (2003) Live and let die: why fighter males of the ant *Cardiocondyla* kill each other but tolerate their winged rivals. Behavioral Ecology 14: 54–62.
13. Cremer S, Sledge MF, Heinze J (2002) Male ants disguised by the queen’s bouquet. Nature 419: 497.
14. Cremer S, Heinze J (2003) Stress grows wings: environmental induction of winged dispersal males in *Cardiocondyla* ants. Curr Biol 13: 219–223.
15. Cremer S, D’Ettorre P, Drijfhout FP, Sledge MF, Turillazzi S, et al. (2008) Imperfect chemical female mimicry in males of the ant *Cardiocondyla obscurior*. Naturwissenschaften 95: 1101–1105.
16. Stephens DW, Brown JS, Ydenberg RC, eds. Foraging: behavior and ecology. Chicago: University of Chicago Press. 576 p.