

# Stress Grows Wings: Environmental Induction of Winged Dispersal Males in *Cardiocondyla* Ants

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## Summary

Dispersal is advantageous, but, at the same time, it implies high costs and risks [1]. Due to these counteracting selection pressures, many species evolved dispersal polymorphisms, which, in ants, are typically restricted to the female sex (queens) [2]. Male polymorphism is presently only known from a few genera, such as *Cardiocondyla*, in which winged dispersing males coexist with wingless fighter males that mate exclusively inside their maternal nests [3, 4]. We studied the developmental mechanisms underlying these alternative male morphs and found that, first, male dimorphism is not genetically determined, but is induced by environmental conditions (decreasing temperature and density). Second, male morph is not yet fixed at the egg stage, but it differentiates during larval development. This flexible developmental pattern of male morphs allows *Cardiocondyla* ant colonies to react quickly to changes in their environment. Under good conditions, they invest exclusively in philopatric wingless males. But, when environmental conditions turn bad, colonies start to produce winged dispersal males, even though these males require a many times higher investment by the colony than their much smaller wingless counterparts [5]. *Cardiocondyla* ants share this potential of optimal resource allocation with other colonial animals [6, 7] and some seed dimorphic plants [8, 9].

## Results and Discussion

In ant societies, dispersal is restricted to the winged female and male sexuals, which typically leave their wingless nestmates (workers and dealate queens) to form massive mating swarms. After mating, young queens shed their wings and found new colonies on their own [10, 11]. Where ecological conditions render such independent founding difficult, young queens mate in or near their natal nest and start to reproduce there [2, 10–14], leading to growth of the existing colonies. New societies can later be founded through the fragmentation or budding of colonies [12–15]. Similar to solitary species, in which conflicting selection pressures lead to an intraspecific dispersal dimorphism, in about 10% of all ant genera, winged dispersal queens co-

occur with smaller and often wingless nondispersing queens [12]. Male dimorphic ant species, on the other hand, are extremely rare [12, 15], and neither ultimate nor proximate explanations for their existence have as yet been described.

A particularly striking male dimorphism with wingless fighter males and winged dispersing males occurs in the genus *Cardiocondyla* [3–5, 16–20]. Wingless (ergatoid) males fight for access to virgin queens in their natal nests, while winged males, after a short period of sexual activity in the nest, disperse and mate outside with alien queens [4, 19, 20]. Male dimorphism in *C. obscurior* appears to be associated with a high behavioral plasticity in queens, which, after mating with males in the nest, either stay and begin to reproduce or leave the nest [4]. The philopatric queens and locally mating ergatoid males hence contribute to the local (“vegetative” [15]) growth of the ant colony, whereas the other fraction of queens and the winged males disperse. The life history of *Cardiocondyla* colonies thus provides an interesting parallel to some sessile organisms that can switch between local vegetative growth and dispersal of sexual propagules (“metagenesis”) [1, 6].

We were interested in the adaptive significance of the observed male dimorphism in *C. obscurior*. The simultaneous presence of alternative tactics generally increases the flexibility of a species to react to changing environmental conditions [21, 22]. The reaction time depends on the mechanism of phenotype development [22], being either rather fixed due to a genetic basis or more flexible due to an environmental induction [21–25]. To study the underlying mechanisms in *C. obscurior*, we first investigated the potential impact of genetic versus environmental (temperature and density) factors on male development. Second, by creating artificial colonies in which conditions of egg laying differed from those of brood rearing, we determined the developmental switch point after which male morph can no longer be changed.

## Crossing Experiment

To detect possible genetic influences on male morphology in *C. obscurior*, we conducted a crossing experiment over three generations and tested for a correlation between the morphology of males of the first and third generations. This was necessary, as, in haplodiploid organisms, males contribute genes to their daughters (fertilized eggs), but not to the sons of their mate (unfertilized eggs). Of the 118 sons produced by 14 daughters of ergatoid males, 23 (24%) were winged and 95 (76%) were ergatoid males. The 7 daughters of winged males produced a total of 62 sons, 7 (13%) of which were winged and 55 (87%) of which were ergatoid (Figure 1). The morph of the 180 grandsons thus did not depend on the morph of the grandfather (Fisher's exact test,  $p = 0.21$ ). Twelve (57%) of the 21 queens produced both ergatoid and winged sons, whereas the remaining 9 queens produced only ergatoid sons. Daughters of each

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Figure 1. Percentage of Ergatoid and Winged Sons Produced by Daughters of Ergatoid and Winged Males  
There was no significant influence of the morph of the grandfather (Fisher's exact test,  $p = 0.21$ ).

father morph were equally likely to produce both male morphs (3/7 winged males' daughters and 9/14 ergatoid males' daughters;  $p = 0.40$ ).

These data suggest that male morph in *C. obscurior* is not based on a genetic polymorphism, in contrast to queen polymorphism in related ant genera [26, 27]. Instead, it is likely influenced by environmental factors, as is typically the case for female caste (queen-worker) differentiation and worker polymorphism in social insects [15, 28, 29].

#### Manipulation of Environment

None of the 80 nests collected in two seasons from the field contained winged males, though half of them contained ergatoid males. Similarly, colonies reared under standard laboratory conditions (see the Experimental Procedures) produced ergatoid males only. But the production of winged males in addition to ergatoid males could be induced by manipulation of colonies in the laboratory. First, after reducing the mean rearing temperature by 5°C for at least 3 weeks, 87% (33/38) of the colonies started to produce winged males. Shorter exposure to cold temperature (<3 weeks) led to the production of winged males in 40% (4/10) of the colonies. In both cases, winged male production occurred with a significantly higher frequency than in controls reared under standard conditions (0/25; Fisher's exact test,  $p_{<3 \text{ weeks}} = 0.004$ ,  $p_{>3 \text{ weeks}} < 0.0001$ ; Figure 2A).

Second, after artificial fragmentation of colonies into small and large subunits, 78% (25/32) of the small colony fragments, but only 6% (2/32) of the large fragments, produced winged males. The frequency of winged male production did not depend on whether the nest fragment was transferred into a new nest site or remained in the old nest (small subunits:  $p = 0.70$ , large subunits:  $p = 1.0$ ). Winged male production was also not elicited by simply transferring complete colonies to a new nest site ( $n = 15$ ). Compared to these controls, winged male production occurred with a significantly higher frequency in the small subunits after fragmentation ( $p < 0.0001$ , significant after Bonferroni adjustment), but not in the large colony fragments ( $p = 1.0$ ; Figure 2B).

We assume that both our manipulative treatments represented a sign of deterioration of the environment

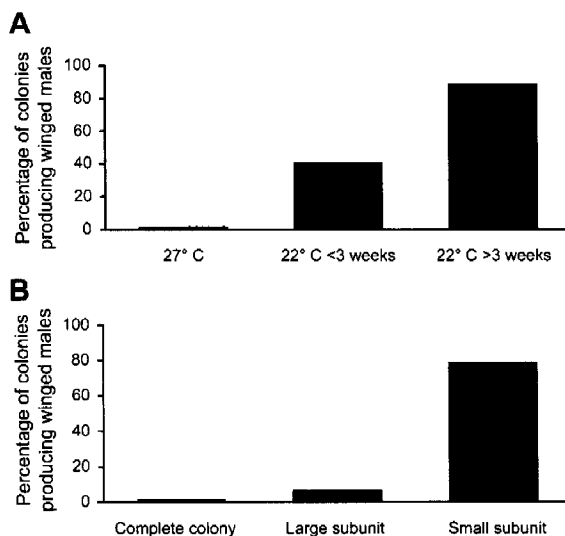


Figure 2. Percentage of Colonies that Produced Winged Males after Manipulation

(A) This graph shows a decrease of temperature by 5°C, from 27°C (controls) to 22°C, for shorter or longer than 3 weeks. Winged male production was significantly higher at both 22°C treatments compared to rearing conditions of 27°C (Fisher's exact test:  $p < 0.005$ ). (B) This graph shows a decrease of colony size to 90% (large subunit) and to 10% of the original colony size (small subunit) and control of complete colonies. Winged male production was increased compared to the control in the small colony subunits ( $p < 0.0001$ ), but not in the large subunits ( $p = 1.0$ ).

or "stress" for *Cardiocondyla* ants, either acting directly on the colony (decrease of temperature) or representing its effect (sudden decrease of colony size). The latter finding also explains the occurrence of winged males in the crossing experiment, as daughter colonies were obtained by creating small subsets of original colonies (see the Experimental Procedures). Furthermore, one laboratory colony that was accidentally starved for several weeks lost many colony members and started to produce winged males (data not shown), corroborating the finding that stressful conditions induce dispersal males in *C. obscurior*.

Temperature and density have previously been shown to influence wing dimorphism also in other taxa, such as aphids [22, 30] and locusts [1, 22]. Sensitivity to these environmental factors may be a general mechanism to estimate the present and future quality of the environment and may allow individuals to react to locally deteriorating conditions by dispersal or by producing a greater proportion of dispersing offspring [22]. In plants, a decreased temperature can similarly lower the investment in vegetative growth and leads to floral induction [31, 32].

#### Brood Exchange Experiment

To detect the developmental stage until which changes in environment can influence male morph determination, we performed a brood exchange experiment, in which conditions during egg laying and brood rearing were uncoupled. "ER" colonies were kept under warm, standard conditions, but they received eggs that had been laid under stressful, cold conditions. In contrary, "ED/

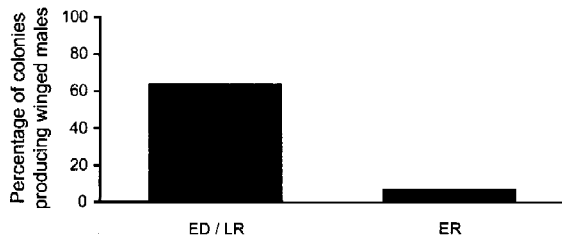


Figure 3. Percentage of Colonies that Produced Winged Males in the Brood Exchange Experiment

Winged male production was significantly higher in colonies that were kept under cold conditions but raised brood from warm, standard conditions (ED/LR) than in colonies that were kept at standard conditions but raised eggs laid under cold conditions (ER; Fisher's exact test,  $p = 0.002$ ).

LR" colonies were kept at stressful, cold conditions, but they received first instar larvae from colonies kept at standard conditions ("LD"; see the Experimental Procedures). The production of winged males was compared between ER and ED/LR treatments.

A single ER colony (1/16 = 6%) produced one single winged male. By contrast, winged males were frequently reared in ED/LR colonies (10/16 = 63%; Figure 3). As expected, no winged males eclosed in the ten LD colonies, which were used only as larvae donors without receiving any alien brood. The frequency of winged males in ED/LR colonies was significantly higher than in ER colonies (Fisher's exact test,  $p = 0.002$ , significant after Bonferroni adjustment), but did not differ from the treatments of the first experiment, in which colony size ( $p = 0.31$ ) and temperature had been decreased ( $p = 0.65$ ).

We therefore conclude that the conditions during brood rearing, but not egg laying, are decisive for male morph development. Thus, male morph is not yet fixed in the egg stage, but it is determined later during larval development. The exact critical period during which the bipotency is lost cannot yet be determined. Several switch points occur in the differentiation of the female sex, with the point of divergence between queens and workers occurring early in development but later in worker-worker polymorphism [29, 33]. Applying the conclusion that the earlier the timing of divergence, the more profound the morphological differences [33], would suggest that male morph in *C. obscurior* is determined during early larval development [5, 34], but after the first instar stage. Such relatively late developmental fixation allows a more flexible reaction to environmental changes than a genetic or blastogenic determination [25]. However, it is also more sensitive to "mistakes" [7, 22]. In *C. obscurior*, morphologically intermediate males may be produced when rearing conditions change during the development of a single male larva [34].

#### Time of Occurrence of Winged Males

In all of the above-described experiments that lead to the production of dispersal males, the first white, winged male pupae were detected approximately 5 weeks after manipulation (Kruskal Wallis test:  $H = 3.01$ , 2df,  $p =$

Table 1. Median, 25%, and 75% Quartile of Weeks until First Appearance of Winged Male Pupae in Colonies of *C. obscurior* after Start of the Different Treatments

Treatment	Number of Colonies	Week of Occurrence
Reduced Temperature	37	5 (3, 6)
Reduced Colony Size	27	5 (4, 6)
ED/LR Brood Exchange	11	6 (4, 6)

0.22; Table 1). The fact that winged males occurred with the same time lag after induction, despite the extremely different nature of the treatments, suggests that stress does not directly influence male morph development but induces a change in the workers' rearing behavior.

#### Adaptive Significance of Alternative Males in *Cardiocondyla*

The potential to produce alternative male morphs and their late developmental differentiation allows *Cardiocondyla* colonies to react to quickly changing environmental conditions. Two main questions arise in our study system: why is it adaptive to produce only wingless males under "default" conditions and why is it adaptive to produce winged males under "stress"?

*C. obscurior* is an invasive tramp ant [35] that colonizes isolated, patchy habitats, e.g., monocultural plantations, which are difficult to detect but, once located, offer optimal food and nest sites. The adaptive strategy for species living in such habitats is to avoid the costs and risks of dispersal [1] and to invest in local growth by budding as long as conditions are good [10, 12, 15, 36, 37]. Even though the dispersal behavior of young *Cardiocondyla* queens still requires more intensive research, it is likely that more queens mate and stay in their maternal colony under good conditions, which increases the fitness of wingless males and thus favors their production. Additionally, intranest mating assures the combination of locally adapted genotypes giving rise to the next generation of queens.

Even though flightlessness is beneficial in a predictable and permanent, patchy habitat [22, 30], dispersal is favored by temporary instability and deterioration of patch quality [9, 22]. In contrast to other species, sessile organisms, and also ant colonies, cannot escape when local survival is threatened [37], but they send out dispersal forms [9]. Plants have two options in this case: escape in space and time [1, 8, 9]. However, ants cannot use this second option, as there is no obvious parallel to seed dormancy in ants [10]. Instead of waiting for conditions to improve, they are forced to search for a new good place to live. Deteriorating conditions should thus lead to a higher proportion of dispersing queens. This increases winged males' fitness, not only because more receptive females will leave their sheltered nests, but also because changing conditions make outcrossing more valuable.

The fact that dispersing winged males are favorable under bad conditions poses the problem of resource management (availability versus allocation) for the colony. Dispersal forms usually require more investment than local forms in ants [38] and other taxa, e.g., plants

[8]. Winged *Cardiocondyla* males, being equipped with wings, large eyes, and energy stores for flight, even require a 60% higher investment than wingless ergatoid males [5]. How can an ant colony produce these expensive male forms when conditions are bad and resources constrained, whereas most other species need rich conditions to produce dispersal propagules [1]? Interestingly, this remarkable potential of optimal resource allocation is also found in colonial thrips [39] and colonial marine invertebrates [6, 7]. By resource sharing between the individuals of a colony, the energetic cost of polymorphism is likely reduced [7]. Thus, animals with a colonial organization, and also some plants with seed heteromorphism [8, 9], have the capacity to conduct different operations concurrently rather than sequentially [7, 40]. They thereby differ from most other taxa (e.g., locusts, aphids, and other plants) that are limited to produce only a single phenotype at a time and therefore react with a time lag to changing conditions.

Together, the observed flexibility and ability to switch adaptively between vegetative local growth and dispersal makes *Cardiocondyla* ants very well suited to colonize patchy habitats and explains their high success as an invasive species. Sharing this potential of optimal resource allocation under changing environmental conditions with other colonial animals and seed dimorphic plants reveals that evolution acts cross phyla borders and that equal selection pressures create parallel life histories in species groups as diverse as plants and ants.

#### Experimental Procedures

*C. obscurior* (previously referred to as *C. wroughtonii* [3, 4, 16–18]) is a cosmopolitan tramp ant [35] that lives in preformed cavities on trees and bushes. A total of 80 colonies were collected from their nests in aborted coconuts and rolled lemon tree leaves in an experimental plantation at Una, Bahia, Brazil in March 1998 and September 2000. Colonies were transferred into plaster nests and were cultivated in a climatic chamber in the laboratory at a 30°/25°C (mean = 27°C) day/night (12/12 hr) temperature and light cycle with constant humidity in the nest of 98%.

#### Crossing Experiment

A total of 21 virgin queens were mated with either a single ergatoid ( $n = 14$ ) or winged male ( $n = 7$ ). From each of the resulting families, 1 daughter queen, after mating, was transferred into a new nest with 20 workers. Colonies were kept as described above and were checked twice a week until all daughter queens had produced 5–10 sons.

#### Manipulation of Environment

Compared to rearing colonies under standard conditions (see above,  $n = 25$  colonies), two kinds of changes of environmental conditions were conducted. First, the mean rearing temperature was decreased by 5°C to a mean of 22°C, and humidity was kept constant at 98%. Ten colonies were kept in “cold conditions” for less than 3 weeks, and another 38 were kept in cold conditions for more than 3 (and up to 18) weeks. Second, we changed colony composition by artificially splitting 32 colonies into one large (with about 90% of the original colony members) and one small subunit each (with about 10% of the original colony members, but at least 1 queen and 20 workers). In 16 cases, the large fragment was placed into a new nest, and the remaining small subunit was kept in the original nest, and vice versa in the other 16 cases. To control for a potential influence of the new nest site alone, 15 additional colonies were completely moved into a new nest site without reduction of colony size. Male production was recorded twice a week over 18

weeks following manipulation. After the end of the experiment, colonies were again reared under standard conditions for at least 6 months before some colonies were reused in the second manipulation treatment. As the data of the small and large subunits were statistically compared both with the 15 controls and within each group for the effect of nest change, we used Bonferroni correction for multiple testing and adjusted the significance level  $\alpha$  to 0.025.

#### Brood Exchange Experiment

Three types of experimental colonies were created: 16 colonies reared under “cold conditions” served both as “egg donors” and “larvae receivers” (ED/LR), and 26 colonies reared under standard climatic conditions served either as “egg receivers” (ER,  $n = 16$ ) or as “larvae donors” (LD,  $n = 10$ ). All new eggs from ED/LR colonies were removed twice a week and were transferred into ER colonies. After removing the eggs, ED/LR colonies were provided with first instar larvae from LD colonies (to avoid mixing of own and added brood in ED/LR, larvae were added instead of eggs). All colonies were checked twice a week over 18 weeks for the occurrence of winged males. As the data of ED/LR were statistically compared both with ER colonies of the brood exchange experiment and the two other manipulated treatments of the first experiment (see above), we used Bonferroni correction for multiple testing and adjusted the significance level  $\alpha$  to 0.017.

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