

Chemical mimicry

Male ants disguised by the queen's bouquet

Males of the tropical ant *Cardiocondyla obscurior* are either wingless and aggressive or winged and docile, and both compete for access to virgin queens in the nest^{1,2}. Although the fighter males (ergatoids) attack and kill other ergatoids, they tolerate and even attempt to mate with their winged rivals. Here we show that the winged males avoid the aggression of wingless males by mimicking the chemical bouquet of virgin queens, but that their mating success is not reduced as a result. This example of female mimicry by vigorous males is surprising, as in other species it is typically used as a protective strategy by weaker

males, and may explain the coexistence and equal mating success of two male morphs.

Ants typically mate during short nuptial flights that give little opportunity for male–male combat³. By contrast, sexual individuals of *C. obscurior* mate inside their natal nests. Intensive intrasexual competition has led to the evolution of sabre-shaped mandibles and escalated fighting to the death among locally mating ergatoid males^{1,2}. Winged males, on the other hand, have weak mandibles, behave peacefully and leave the nest one to two weeks after emergence in order to mate outside. But, surprisingly, before dispersal they are as successful as ergatoid males in attaining copulations with virgin nestmate queens (*U*-test: $U=903.0$, $P=0.86$, $n_{\text{ergatoid}}=33$ observations for 24 min each, $n_{\text{winged}}=56$). Ergatoid males would therefore be expected to benefit from killing their winged rivals⁴.

Contrary to the aggression that might be expected towards winged males, ergatoid males typically restrict their fighting to other ergatoids, and attempt to mate with the winged males¹. Our behavioural observations indicate that young winged males (1–5 days old) are as attractive as young virgin queens to ergatoid males (ergatoid males mounted 11 out of 12 winged males and 15 out of 17 virgin queens; 72–120 min observation per individual; Fisher's exact test: d.f. = 1, $P=1.0$). By contrast, ergatoid males showed no interest in older winged males (6–10 days, $n=17$; old–young: $P<0.001$), whereas virgin queens remained attractive regardless of their age (old: 12 out of 14; old–young: $P=1.0$).

This toleration of winged males and attempts at homosexual mating with them can be explained by the chemical resemblance of winged males and virgin queens in their bouquet of cuticular hydrocarbons on the body surface, which are important for communication in social insects^{5–8}. In a discriminant analysis of hydrocarbon profiles obtained by gas chromatography with mass spectrometry⁹, 1-day-old winged males and virgin queens formed a single cluster that was distinct from those of ergatoid males and workers (Fig. 1a). However, for 10-day-old ants, all four groups were clearly separated (Fig. 1b). We conclude that the odour similarity of young — and only young — winged males to virgin queens explains their age-dependent attractiveness to ergatoid males.

Most examples of chemical deception occur between species⁵, whereas intra-specific female mimicry is typically based on morphological or behavioural similarities¹⁰. Chemical female mimicry occurs in male rove beetles¹¹ and garter snakes¹² when they find themselves in adverse physiological conditions. These males pay for avoiding competition with 'high-quality' males by suffering low mating success with females.

By contrast, in *Cardiocondyla*, the odour mimicry of virgin queens by young winged males does not affect their copulatory success when compared to older, non-mimicking winged males ($U=324.0$, $P=0.30$, $n_{\text{young}}=25$, $n_{\text{old}}=31$) and ergatoid males ($U=393.0$, $P=0.76$).

Cardiocondyla provides a new evolutionary context for chemical deception: it is deployed irrespective of condition by all young winged males and renders them simultaneously attractive to both sexes. This example of chemical female mimicry enables two alternative reproductive strategies to exist in the male sex.

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COMMUNICATIONS ARISING

Palaeoclimatology

Tropical temperatures in greenhouse episodes

Reconstruction from oxygen-isotope data of global sea-surface temperatures (SSTs) that prevailed during periods when greenhouse-gas levels were higher than at present (that is, in the early Eocene and Cretaceous epochs) indicates that temperatures were significantly warmer than present in mid- to high latitudes, but similar to or slightly cooler in the tropics. However, Pearson and colleagues¹ claim, on the basis of oxygen-isotope data from planktonic foraminifers recovered from clay beds in Tanzania and other localities, that the tropics were warm during

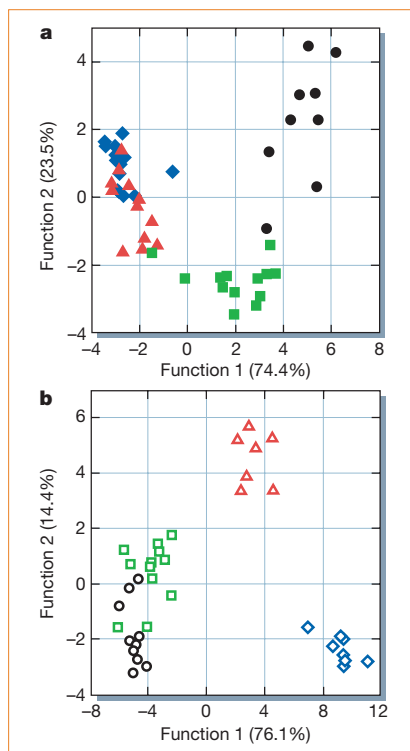


Figure 1 Discriminant analysis of the hydrocarbon profiles of 1-day-old (filled symbols) and 10-day-old (hollow symbols) *Cardiocondyla obscurior* ants. Hydrocarbons were extracted from workers (day 1: $n_1=10$, day 10: $n_{10}=10$; circles), ergatoid males ($n_1=13$, $n_{10}=12$; squares), winged males ($n_1=14$, $n_{10}=8$; diamonds) and virgin queens ($n_1=13$, $n_{10}=7$; triangles) by gas chromatography with mass spectrometry, and were statistically analysed by principal-components analysis followed by stepwise discriminant analysis¹³. Results show the first two canonical discriminant functions (percentage of variability is shown in parentheses). **a**, One-day-old ants: virgin queens and winged males cluster together but are distinct from ergatoid males and workers (81.6% of individuals classified correctly; $F1$: Wilks' $\lambda=0.018$, $P<0.001$; $F2$: Wilks' $\lambda=0.194$, $P<0.005$). **b**, Ten-day-old ants: all colony members form distinct groups (as the non-plotted third significant function discriminates workers and ergatoid males; 100% of individuals classified correctly; $F1$: Wilks' $\lambda=0.001$, $P<0.001$; $F2$: Wilks' $\lambda=0.023$, $P<0.001$).

the Eocene, attributing the discrepancy between these and previous tropical SST estimates to the effects of diagenetic overprinting of the latter. Here we note some potential flaws in their interpretation of the new oxygen-isotope data.

Although dissolution and incipient secondary calcification of tropical, deep-sea fossil planktonic foraminifera bias shell $\delta^{18}\text{O}$ ratios towards higher values²⁻⁴, we consider it unlikely that all tropical planktonic foraminifera tests are overprinted to the extent claimed by Pearson *et al.* Their estimate of up to 50% secondary calcite is based on a comparison of multi-species carbon and oxygen isotope values from planktonic foraminifera of "similar age" from Tanzanian outcrops and the Deep Sea Drilling Project Site 523 in the eastern South Atlantic Ocean, and their key assumption is that initial conditions are identical for both sets of samples.

However, given the differences in latitude, and the likely proximity of Tanzania and Site 523 to warm western and to cool eastern boundary currents, respectively, SST could have differed by as much as 6–8 °C between the two localities in the Eocene, just as it does today. This alone could account for 80% of the $\delta^{18}\text{O}$ difference between the two data sets. Moreover, as implied by the clay-rich depositional facies from which the Tanzanian fossils were extracted, it is likely that regional sea-surface salinities and seawater $\delta^{18}\text{O}$ were lower, possibly by as much as 3.0 p.p.t. and 1.0 p.p.t., respectively, than at Site 523. This local salinity difference would further bias the Tanzanian SST estimates towards higher values. These biases are compounded by the fact that the chronostratigraphic constraints on the Tanzanian sediment sequences are relatively coarse, a point that is reflected in the reported age errors of the Tanzanian samples, which is $\pm 1-2$ Myr.

As a result of these and other potential biases, it may prove difficult to constrain absolute estimates of SST in tropical coastal oceans to better than ± 3.0 °C for Eocene or Cretaceous 'greenhouse' intervals. This raises the issue of whether this is the most effective approach to resolving the enigma of greenhouse-gas tropical SSTs. We think not, and favour a more practical strategy that focuses on relative changes in temperature that were associated with episodes of rapid, short-lived climate change⁵⁻⁷.

Why? One reason is that it is easier to quantify relative changes in temperature on short timescales (about 10^2-10^4 yr), even in sediments that have been slightly to moderately overprinted. Because secondary calcification in sediments of uniform lithology is constant over short length scales, primary offsets in fossil-shell chemistry tend to be preserved, although slightly attenuated^{3,6}.

Second, by focusing on rapid, transient

events, the number of climate-forcing parameters can be reduced to greenhouse-gas levels, as all other non-astronomical parameters, such as changes in continental geography and elevation, operate on much longer timescales. However, this strategy will be most effective when dealing with well-dated, stratigraphically continuous (over millions of years) and lithologically uniform sedimentary sequences, such as those typically recovered from the deep sea.

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Pearson et al. reply — We agree with Zachos and colleagues that much can be learned about transient climate events from well-dated carbonate sediments from the deep ocean, and that the problem of recrystallization of such sediments (when tens of millions of years old) means that constraining relative temperature changes from oxygen-isotope data is more appropriate than attempting to measure absolute values.

We note, however, that this marks a shift of emphasis from studies spanning several decades, in which attempts have been made to determine actual temperatures from the deep-sea record and to compare them with the output of climate-model simulations (for example, see refs 1–3). We also warn against assuming that "primary offsets in fossil shell chemistry tend to be preserved", as diagenetic overprinting will tend markedly to reduce such offsets, as well as attenuating stratigraphic patterns.

We have suggested that recrystallization could account for as much as 50% of the mass of planktonic foraminifera in typical deep-sea samples, which would reduce estimated SSTs in the tropics by 10–15 °C. Zachos *et al.* have questioned our comparison of isotope data from well-preserved, middle-Eocene foraminifera from Tanzania and a recrystallized deep-sea assemblage. But we did not assume that initial conditions

were identical for the two sites — indeed, we were careful to point out the likely original difference in temperature. When this is taken into account, we calculate that the oxygen-isotope data suggest a 55% diagenetic overprint of the deep-sea sample towards an ocean bottom-water temperature of about 10 °C (ref. 4). A similar overprint is also implied by the greatly reduced inter-species carbon-isotope differentials.

We also discussed the question of $\delta^{18}\text{O}_{\text{sw}}$ on the Tanzanian margin. For several reasons (the narrow open shelf, probable onshore current, normal stratification, full plankton assemblages and results of palaeosalinity modelling), we think it unlikely that the salinity was as much as 3.0 p.p.t. lower than in the deep ocean. But even if it were, the probable relationship between $\delta^{18}\text{O}_{\text{sw}}$ and salinity at this latitude would imply a $\delta^{18}\text{O}_{\text{sw}}$ value that is only about 0.5 p.p.t. more negative, which corresponds to an estimated temperature increase of about 2 °C. This is a small effect when compared with the apparent difference of nearly 15 °C in estimated SST between the East African shelf and coeval open-ocean sites such as ODP Site 865 (ref. 2). We stress that our Tanzanian data are also supported by similar results from Mexico, Alabama and the Adriatic Sea.

Study of both deep-sea carbonates and hemipelagic clays is crucial to ensure that sampling is as spatially distributed as possible. But there is no reason why hemipelagic mudstones should not be as accurately dated as deep-sea carbonates, thereby combining the advantages of high-resolution stratigraphy and good microfossil preservation. Recent Ocean Drilling Program (ODP) coring in New Jersey has already demonstrated this potential⁵, and we anticipate further well-dated Cretaceous and Palaeogene mudstones from a forthcoming ODP leg to Demerara Rise (in the equatorial Atlantic Ocean) and from our own drilling in Tanzania. Such investigations will help to elucidate past variation in absolute palaeotemperatures and meridional temperature gradients, which remains critical for testing the greenhouse theory for past warm climates.

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