Parasitoid secretions provoke ant warfare

Subterfuge used by a rare wasp may be the key to an alternative type of pest control.

Insect social parasites are extreme specialists that typically use mimicry or stealth to enter ant colonies to exploit the rich, but fiercely protected, resources within their nests[1–3]. Here we show how a parasitic wasp (parasitoid)[4] contrives to reach its host, itself an endangered species of social parasite that lives inside the brood chambers of ant nests, by releasing semiochemicals to induce in-fighting between worker ants, locking the colony in combat and leaving it underprotected. Four of these chemicals are new to biology and have the potential to control pest species by inducing different agonistic behaviours in ants.

Ichneumon eumerus is an endangered hymenopteran parasitoid that is found in less than 20% of populations of its host, the butterfly *Maculinea rebeli*[5], which is listed by the World Conservation Union. *I. eumerus* females deposit their eggs in *M. rebeli* larvae, and their progeny emerge 11 months later as adults from their host's pupae[5]. Both stages of *M. rebeli* inhabit colonies of the ant *Myrmica schencki*, where the larvae mimic *M. schencki* larvae in their behaviour and surface chemistry[6]. *I. eumerus* seeks its host by first detecting *M. schencki* colonies that contain *M. rebeli*, and then inducing the fighting that enables it to penetrate nests[5].

We confirmed that *I. eumerus* uses agonistic chemicals to provoke *M. schencki* (Fig. 1). Empty *M. rebeli* pupal cases from which parasitoids had already emerged induced fierce fighting in laboratory ant colonies, as did solvent extracts from these cases painted onto dummies. In contrast, pupal cases produced no reaction after being washed in solvent (Fig. 1a, and see supplementary information).

Analysis by gas chromatography with mass spectrometry revealed that these extracts contained three alcohols and three aldehydes: 0.3 μg μl^{-1} *Z*-9-icosen-1-ol (*Z*-9-C_{20}-ol); 5 μg μl^{-1} *Z*-9-docosen-1-ol (*Z*-9-C_{22}-ol); 14 μg μl^{-1} *Z*-9-tetracosen-1-ol (*Z*-9-C_{24}-ol); 0.3 μg μl^{-1} icosanal (*Z*-9-C_{20}-al); 7 μg μl^{-1} docosanal (*Z*-9-C_{22}-al); and 20 μg μl^{-1} tetracosanal (*Z*-9-C_{24}-al). Four of these compounds are new to biology; the functions of the others (*Z*-9-C_{22}-al and *Z*-9-C_{24}-al) were previously unknown[7].

We synthesized each chemical in the laboratory and presented it to *M. schencki* colonies on dummies, either separately or mixed in the relative concentrations found in the extract. Four chemicals provoked at least one significant response (Fig. 1b, and see supplementary information). *Z*-9-C_{20}-ol attracted workers to the dummy and
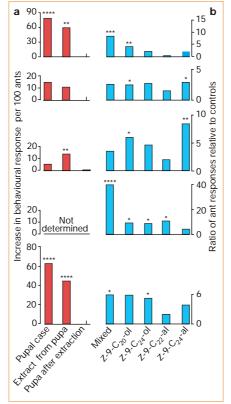

Figure 1 Responses of *Myrmica schencki* ants to chemicals produced by the parasitoid wasp *Ichneumon eumerus* and to artificially synthesized chemicals. The behaviours shown are (from top): ants run towards the source; they investigate the source; they attack it; they are repelled; they attack kin ants. **a**, Effects of biological samples produced by wasps (red), showing ants' increased behavioural responses when presented with: empty *Maculinea rebeli* butterfly pupal cases that had produced wasps, compared with cases that produced *M. rebeli*; teflon dummies dosed with hexane, ethyl acetate and methanol extracts from wasp pupae, compared with dummies dosed with solvents alone; or pupal cases after extraction. **b**, Effects of individual and mixed synthetic chemicals (blue; see text for abbreviation definitions) on ant responses relative to controls. Dummies were dosed with >99.5% pure chemicals and presented to ant colonies. The significance of results relative to controls was assessed using STATXACT (**a**) and Mann–Witney (**b**) analyses; *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, ****$P < 0.0001$. For further details, see supplementary information.

encouraged them to investigate it but, having touched it, the ants became aggressive and ran away, so that they attacked sister ants instead. *Z*-9-C_{24}-al promoted the initial investigation and, with *Z*-9-C_{24}-ol, amplified ant aggression; *Z*-9-C_{22}-al and *Z*-9-C_{24}-ol strongly repelled ants. Mixed together, these chemicals drew ants to the parasitoid, where, having become aroused to a state of high aggression, they were quickly repelled. This resulted in three to eight times more attacks ($P = 0.001$, $n = 9$)

being made on kin ants than on *I. eumerus*, the stimulator of the aggression.

The controlled propagation of alarm plays a key part in ant societies, casting a social 'immune barrier' around them and affording workers instant recognition of nestmates and discrimination against foreigners[2]. Most of the pheromones involved in this process are volatile, short-chain hydrocarbons, which allow the rapid expansion and dissipation of alarm[2,8,9]. Only the slave-making ant *Formica subintegra*, whose C_{12}–C_{16} aldehydes are the most persistent and longest-chain semiochemicals known to provoke ants, has been found to use alarm in the same way as *I. eumerus* to raid other ants' nests[2,9]. The allomones used by *I. eumerus* are more persistent still, provoking aggression for 50 days after secretion[5].

Our bioassays induced only 56–79% of the ferocity unleashed by a living parasitoid[5]. This may be due to the small size of our test colonies — larger ones reacted more strongly ($r^2 = 92\%$, $P = 0.04$, $n = 5$), which supports our observation that the ants themselves amplify and propagate a sense of panic after contact with the wasp, creating a chain reaction of in-fighting across their society.

No other known secretion enables an individual insect to immobilize up to 80% of an ant colony. The strength and persistence of this reaction suggests that similar cocktails of long-chain hydrocarbons might provide an alternative to the use of poisons and repellents to control pest ants[10]. If so, this would be an unexpected benefit of studying obscure taxa[11] — sadly, just four unprotected European meadows now support all of the *I. eumerus* individuals found in recent decades.

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Sports statistics

Trends and random fluctuations in athletics

Improvements in the results of athletic competitions are often considered to stem from better training and equipment, but elements of chance are always present in athletics and these also contribute. Here we distinguish between these two effects by estimating the range into which athletic records would have fallen in the absence of systematic progress and then comparing this with actual performance results. We find that only 4 out of 22 disciplines have shown a systematic improvement, and that annual best results worldwide[1] show saturation in some disciplines.

We investigated the development of sporting records by means of order statistics[2] that provide estimates of the maxima and minima of stochastic time series. We used the results to predict (retrospectively) how athletes' records would have evolved during the German championships[3,4] in the absence of systematic improvements. (These can arise from an increase in the number of competition participants, a major effect during the past century.)

We assumed that the stochastic variations are the result of a strongly stationary process in which two consecutive values are independent and all values obey the same statistical distribution, $\rho(x)$. The records considered here may be either maxima (jumping and throwing distances) or minima (running times); we rendered these two types directly comparable by converting running times into average speeds, allowing us to discuss only the case of maxima. We used the values of one time interval (here, annual best results) to determine the most probable record, $x_{max,th}$ (expectation value), and its standard deviation, σ_E, for the succeeding interval.

Assuming that $\rho(x)$ is gaussian (with mean μ and standard deviation σ), the expectation value for the record during the subsequent period of N years can be estimated as
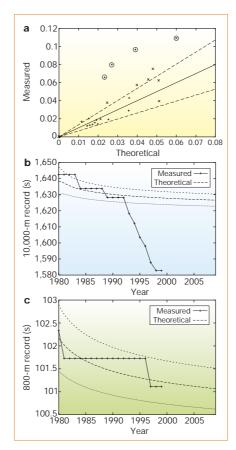
$$x_{max,th} = \mu + \sigma(a_0 + a_1 \ln\ln(N) + a_2(\ln\ln(N))^2) \quad (1)$$

where the optimal coefficients for $2 \leq N \leq 100$ are (the error of the approximation of $x_{max,th}$ for $\mu = 0$ and $\sigma = 1$ being $< 0.06\%$ over this interval): $a_0 = 0.818$, $a_1 = 0.574$ and $a_2 = 0.349$ (D.G., J.G.T. and

Figure 1 Trends versus random fluctuations in athletics. **a**, Comparison of actual and theoretical results for the relative differences between the best performances of the second 12-yr interval and the mean annual best result of the first 12-yr interval for the German championships. 'Theoretical' (*x*-axis): $(x_{max,th}/\mu) - 1$; 'measured' (*y*-axis): $x_{max,real}/\mu) - 1$; $+$, running disciplines; $\times$, jumping and throwing disciplines. The solid line $y = x$ represents perfect theoretical predictions, dashed lines (not symmetrical to the $y = x$ line) indicate $\pm$ s.d. intervals (σ_t). The greatest deviations correspond to the 110-m hurdles, 50-km and 20-km walking races, and pole vault. **b, c**, Representative forecasts of world records obtained using equation (1) and the annual best results from the period 1980–89. The time course in **b** (for the 10,000 m) shows a strong trend beginning in 1992; that in **c** for the 800 m seems to be purely stochastic.

D.S., manuscript in preparation). Analogously, we find that

$$\sigma_E = \sigma(b_0 + b_1 \ln\ln(N) + b_2(\ln\ln(N))^2) \quad (2)$$

where $b_0 = 0.8023$, $b_1 = -0.2751$ and $b_2 = 0.0020$ (approximation error $< 0.15\%$). We derived these equations from formulae for maxima estimation that hold in the limit of large N (ref. 5).

We applied this method to the top performances of men in 22 disciplines during

the German championships of 1973–96. We divided the data into two groups: those for the years 1973–84 served as a reference period from which we predicted the best result for the period 1985–96. A Kolmogorov–Smirnov test showed that a gaussian function is a suitable approximation of the probability distributions of our data. The distribution should have cut-offs at zero and at some physiological limit[6], but we found that these hypothetical cut-offs could be safely neglected.

Figure 1a compares the stochastic predictions with the actual data for all 22 disciplines. Most of the experimentally determined points are well described by the statistical analysis. Only four disciplines show a significant deviation — for these, the results achieved are better than the predictions, indicating systematic improvement. A previous analysis of world records[7] ignored trends and considered only record-breaking events.

We also analysed a similar data set for worldwide annual best results (for the outcome of the statistical test, see supplementary information), and found that 7 out of 19 estimates do not fall into a $3\sigma_E$ interval around $x_{max,th}$ for the time-interval pairs 1985–97 and 1990–99. Compared with the German results, stronger non-stationarities occur, indicating more systematic progress, but tend to decrease over time (D.G., J.G.T. and D.S., manuscript in preparation).

We also used the available data for 1980–89 to predict the development of world records (N here being the number of years since the pre-1980 onset of the stationary process; Fig. 1).

The method we describe here should be useful for assessing the relevance of any small signal in a noisy environment[8,9], and in obtaining estimations for the quality of the best (unknown) solutions of computationally complex optimization problems.

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