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Supplementary information is available on *Nature*'s World-Wide Web site (http://www.nature.com) or as paper copy from the London editorial office of *Nature*.

Acknowledgements. We thank the Australian Museum for their award of a Visiting Fellowship to P.E.A. A. Ritchie for inviting us to work on the Canowindra material and J. Long and J. Jeffery for discussions and access to rhizodont material. Z.J. thanks J. Fairfax for financial support. This Letter is dedicated to the memory of S. M. Andrews.

Selfish genes: a green beard in the red fire ant

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A 'green-beard' gene is defined as a gene that causes a phenotypic effect (such as the presence of a green beard or any other conspicuous feature), allows the bearer of this feature to recognize it in other individuals, and causes the bearer to behave differently towards other individuals depending on whether or not they possess the feature[1–3]. Such genes have been proposed on theoretical grounds to be agents mediating both altruism and intragenomic conflicts[1,2], but until now few, if any, of these genes have been identified[4,5]. Here we provide evidence of a green-beard gene in the red imported fire ant, *Solenopsis invicta*. In polygyne (multiple-queen) colonies, all egg-laying queens are *Bb* heterozygotes at the locus *Gp-9* (ref. 6). Previous studies suggested that *bb* females die prematurely from intrinsic causes[6]; we now show that *BB* queens initiating reproduction are killed by workers, and that it is primarily *Bb* rather than *BB* workers that are responsible for these executions. This implies that allele *Gp-9^b* is linked to a green-beard allele that preferentially induces workers bearing the allele to kill all queens that do not bear it. Workers appear to distinguish *BB* from *Bb* queens on the basis of a transferable odour cue.

We mimicked the natural recruitment of new reproductive queens into polygyne nests by reintroducing young queens into their parental colonies after they had been kept in small colony fragments with workers but not other queens for three days. (The absence of mature reproductive queens induces reproductive development of young queens[7].) There was a strong association between queen genotype at *Gp-9* and the probability of being attacked: all attacked queens were homozygous for the *B* allele, whereas none of the queens with a copy of allele *b* faced significant worker aggression (Table 1). A separate experiment in which worker attacks were not interrupted showed that such attacks invariably led to the death of a queen within 15 minutes ($n = 50$).

We next compared the genotypes of workers attacking *BB* queens with those of workers sampled randomly from the same population and discovered that attackers were much more likely to carry the *b* allele (82.5 versus 59.3% of genotypes; $P < 0.01$). To confirm this, we did a second experiment in which we compared the genotypes of workers attacking *BB* queens with those of workers in the vicinity of non-attacked (*Bb*) queens in the same colonies. The proportion of *Bb* and *bb* workers surrounding attacked (*BB*) queens was significantly higher than the proportion surrounding non-attacked (*Bb*) queens (Table 2). Our assay may considerably underestimate the true extent of genotypic bias among workers attacking *BB* queens because these attacks elicited the formation of compact worker groups around the queens, making it impossible to collect only attacking workers. Thus, although our experiments demonstrate that such attacks are undertaken primarily by workers with at least one copy of allele *Gp-9^b*, they do not allow us to determine whether the attacks are carried out only by these workers. The possibility that these results are due to workers with the *b* allele generally having a lower threshold for aggression can be excluded, because such individuals were not overrepresented among the workers attacking foreign heterospecific ant workers (*Aphaenogaster* sp.) introduced into nests ($n = 788$; $G = 2.42$; d.f. $= 1$; $P = 0.12$; workers with the *b* allele actually were underrepresented among these attackers).

Some of the workers involved in attacks on *BB* queens subsequently were attacked by nestmates, suggesting that they might have acquired a distinctive odour from the attacked queens. To test this hypothesis, we rubbed randomly chosen workers against the cuticle of *BB* or *Bb* queens and then placed them in groups of nestmate

Table 1 Proportion of young queens of each *Gp-9* genotype attacked by workers

Age	Proportion of queens attacked, *Gp-9* genotype		
	BB	*Bb*	*bb*
7–10 days ($n = 19$ colonies)	0.61 ($n = 90$)	0.00 ($n = 275$)	0.00 ($n = 5$)
11–14 days ($n = 18$ colonies)	0.91 ($n = 11$)	0.00 ($n = 327$)	0.00 ($n = 11$)

The frequencies of attacks on 7–10-day-old queens varied significantly according to genotype ($G = 190.78$; d.f. $= 2$; $P < 0.0001$). The proportion of *BB* queens attacked was significantly greater than the proportion of either *Bb* queens ($G = 189.16$; d.f. $= 1$; $P < 0.0001$) or *bb* queens ($G = 9.04$; d.f. $= 1$; $P = 0.003$) attacked (the few *bb* queens found presumably had not yet succumbed to the age-dependent lethal effects of this genotype[6]). The same pattern was revealed within individual colonies: in each of the 16 colonies in which *BB* queens were present, the proportion of such queens attacked was significantly greater than the proportion of attacked queens with the other two genotypes (binomial probability, $P < 0.001$). A similar association between queen genotype and aggression occurred for 11–14-day-old queens ($G = 84.06$; d.f $= 2$; $P < 0.0001$), with the proportion of *BB* queens attacked again being significantly greater than the proportion of either *Bb* queens ($G = 83.41$; d.f. $= 1$; $P < 0.0001$) or *bb* queens ($G = 23.61$; d.f. $= 1$; $P < 0.001$) attacked. At the colony level, the proportion of attacked *BB* queens of this older class again was greater than the proportion of attacked queens with the other two genotypes in each of the three colonies in which *BB* queens were present. Two lines of evidence suggest that *BB* queens are killed as they approach sexual maturity and become potential egg layers (about 10 d after adult emergence[19,20]). First, the proportion of attacked *BB* queens was higher for 11–14-day-old queens than for 7–10 day old queens ($G = 4.58$; d.f. $= 1$; $P = 0.03$). Second, among queens in the younger age class, the non-attacked queens with genotype *BB* were significantly lighter (12.8 ± 1.3 mg; $n = 35$) than the attacked queens with this genotype (14.1 ± 1.1 mg; $n = 55$; two-way ANOVA, weight difference: $F = 23.55$, $P < 0.0001$; colony effect: $F = 1.95$, $P < 0.05$; interaction: $F = 0.831$, NS). Because weight is a good indicator of the age of maturing queens[20], these data suggest that younger and lighter *BB* queens were attacked relatively less frequently. Such age-associated attacks on *BB* queens may explain the decrease in the proportion of *BB* genotypes among queens as they age: this proportion was 0.24 in the 7–10-day-old queens, and 0.03 in the 11–14-day-old queens ($G = 77.69$; d.f. $= 1$; $P < 0.001$).

Table 2 Number of workers of each *Gp-9* genotype surrounding attacked, *Gp-9^{BB}* queens and non-attacked, *Gp-9^{Bb}* queens

Worker *Gp-9* genotype	Queen *Gp-9* genotype	
	BB (attacked)	*Bb* (non-attacked)
BB	50 (0.213)	81 (0.344)
Bb	184 (0.783)	147 (0.626)
bb	1 (0.004)	7 (0.030)
Total	235	235

Proportions of attacking and non-attacking workers with each genotype are shown in parentheses. There was a significant association between queen and worker genotypes ($G = 16.61$; d.f. $= 2$; $P = 0.0002$), with attacks on *BB* queens being made preferentially by workers having the *b* allele. The difference remains highly significant, both when *bb* workers are eliminated from the analysis ($G = 11.47$; d.f. $= 1$; $P < 0.001$) and when they are pooled with *Bb* workers ($G = 10.24$; d.f. $= 1$; $P = 0.001$). The same pattern was found within individual colonies. Of the nine colonies that contained three or more queens of each genotype, eight had a relative overrepresentation of workers with allele *b* attacking queens, an outcome that departs significantly from the null expectation that 50% of nests should have such overrepresentations (binomial test, $P < 0.02$). Furthermore, the overrepresentation of allele *b* in attacking workers was significant in two of these colonies ($G = 6.89$; d.f. $= 1$; $P < 0.01$ and $G = 5.07$; d.f. $= 1$; $P = 0.02$). The few *bb* workers found presumably were very young workers that had not yet succumbed to the age-dependent lethal effects of this genotype[6].

workers. Those rubbed against *BB* queens elicited significantly higher levels of aggression (aggression level was 2.5 ± 0.7 ($n = 10$); Mann–Whitney U test, $Z = 3.71$, $P = 0.0002$) and were killed significantly more often (40% ($n = 10$); $G = 6.56$, d.f. $= 1$, $P = 0.01$) than those rubbed against *Bb* queens (aggression level, 0.8 ± 0.4 ($n = 10$), 0% killed ($n = 10$)). These data, together with the finding that *BB* queens are attacked when they attain sexual maturity (Table 1), suggest that recognition and selective elimination of *BB* queens may be triggered by two chemical cues, one signalling a queen's sexual maturity and the other her *Gp-9*-linked genotype. Tight coupling between a queen's reproductive state and pheromone production has been demonstrated in *S. invicta*[8], as has the ability of workers to assess the level of pheromone production by individual queens[9]. Thus, the green-beard allele linked to $Gp\text{-}9^b$ may induce workers bearing it to kill all sexually mature queens except those possessing a specific chemical signature encoded by this allele.

The green-beard gene responsible for differences in queen odours and in the aggressive behaviour of workers with different *Gp-9* genotypes may be *Gp-9* itself, or one or more genes in very strong gametic disequilibrium with *Gp-9*. The enzyme-encoding locus *Pgm-3* (ref. 6) is tightly linked to and in strong disequilibrium with *Gp-9*. All females of genotype $Pgm\text{-}3^{AA}$ also have genotype $Gp\text{-}9^{BB}$ (ref. 6), accounting for the strong worker discrimination against $Pgm\text{-}3^{AA}$ queens reported previously for polygyne fire ants[7,10,11]. Analyses considering both genes simultaneously show that all described phenotypic and behavioural variation among queens and workers can be accounted for by *Gp-9* genotype alone in the Georgia population under study (our unpublished results). Moreover, although workers eliminated all 33 $Pgm\text{-}3^{AA}$ queens in the reintroduction experiments (Table 1), they also eliminated 26 $Pgm\text{-}3^{Aa}$ and five $Pgm\text{-}3^{aa}$ queens, indicating that $Pgm\text{-}3^{a}$ is not in complete disequilibrium with the green-beard allele. In contrast, workers eliminated no queens with allele $Gp\text{-}9^b$ in these same experiments. Finally, separate experiments show that workers destroy 100% of introduced $Gp\text{-}9^{BB}$ queens when these are fully sexually mature (our unpublished results), which explains the complete absence of egg-laying queens with this genotype in polygyne colonies in Georgia[6]. These data indicate that either *Gp-9* is directly responsible for the effects reported, or that the actual gene(s) involved is in complete disequilibrium with *Gp-9* but not *Pgm-3*.

The mechanism of selection against $Gp\text{-}9^{BB}$ queens is similar to the process of meiotic drive. Driving elements invade a population by distorting the outcomes of meiosis, such that these elements are carried by more than 50% of viable gametes produced by heterozygotes. Allele $Gp\text{-}9^b$ causes workers to destroy queens without the allele, biasing allele frequencies in sexuals produced by the colony. Fire-ant colony productivity is limited mostly by worker number rather than queen number[12], so selective elimination of *BB* queens results in an overall increase in the reproductive success of *Bb* queens and thus in the number of copies of the *b* allele transmitted to subsequent generations. Models show that, all else being equal, an outlaw gene[13], such as $Gp\text{-}9^b$, that causes the destruction of individuals not bearing it in favour of those that do, should spread rapidly and become fixed in a population[14,15], yet *Gp-9* is polymorphic in all polygyne *S. invicta* populations studied in South America and the USA (ref. 6, and C. J. DeHeer, D. D. Shoemaker and K.G.R., unpublished results). Fixation of $Gp\text{-}9^b$ apparently is prevented primarily because queens (as well as workers) homozygous for this allele die prematurely (that is, the allele behaves as a recessive lethal), although gene flow from a different social form fixed for the alternative allele probably also plays a role[6].

Our results show that all components of a green-beard effect[3]—a detectable phenotypic feature, the ability to recognize the feature, and different responses towards individuals possessing or not possessing the feature—are present in polygyne *S. invicta* and are mediated by a gene or group of genes closely linked to *Gp-9*. The analogy between the green-beard effect reported here and meiotic drive lies not only in the manner in which one allele biases its transmission, but also in the mechanism preventing its fixation. In both cases, the advantage of increased transmission is counteracted by negative viability and/or fertility effects of the allele when in the homozygous condition[16,17]. This trade-off may explain why green-beard genes have seldom been reported. In the absence of countervailing evolutionary pressures, polymorphisms at green-beard loci are expected to be present only as transient phases in the history of a population and thus will usually go undetected. □

Methods

Worker aggression towards queens. The queens originated from 37 polygyne colonies collected in northern Georgia, USA. Entire colonies were transferred into laboratory rearing units using standard procedures, and the number of reproductive queens in each colony was reduced to four[7]. All sexuals were removed from these colonies except for 40 adult winged queens with unsclerotized cuticles (0–3 days old). All winged queens in 19 of the colonies were removed four days later, and 18–20 of these queens from each colony were placed individually in small fragments of the source colony containing ~300 worker brood and adults but no other queens. After three days of separation, the queens (then 7–10 days old) were returned individually to their parent colony (each containing at least 5,000 workers) and the level of aggression directed towards them was recorded during the 5 min immediately following introduction. An identical procedure was followed with the remaining 18 colonies, except that queens were removed from their parent colony after 8 days (thus they were 11–14 days old when returned). Assessment of the level of aggression was done without knowledge of *Gp-9* genotypes, which were determined later by means of starch-gel electrophoresis[6]. Association between genotype and aggression was determined using G-tests[18]. Other experiments (ref. 7, and our unpublished results) showed that worker responses to queens of alternative genotypes are independent of whether queens are introduced sequentially (as in this experiment) or in larger groups.

Genotypes of workers attacking $Gp\text{-}9^{BB}$ queens and *Aphaenogaster* workers. The preliminary experiment in which genotype frequencies of attacking workers were compared to population frequencies was done using 10 polygyne colonies collected in northern Georgia. Twenty 10–13-day-old queens from each of these colonies were reintroduced into their parent colonies after having been separated for three days (see above). Attacked queens and the clusters of workers surrounding them were collected with forceps. All 22 queens attacked were found to be $Gp\text{-}9^{BB}$ homozygotes. We determined the *Gp-9* genotypes of 5–11 (average, 8.9) workers surrounding each of these queens, and the average frequencies were estimated using a resampling procedure in which a single worker genotype per colony was drawn at random (with replacement) 1,000 times. These frequencies were compared to genotype frequencies estimated in the source population in the same year (based on 406 workers sampled randomly from 181 colonies; the frequencies and their 99% confidence intervals were obtained using the resampling procedure[6]). The follow-up experiment was conducted with another 19 colonies, the same as were used to determine the level of aggression of workers against 7–10-day-old queens (see above). All 55 queens attacked were found to be *BB* homozygotes (Table 1). We determined the *Gp-9* genotype of five workers surrounding each of 47 of these queens. As a control, we collected and genotyped five workers in the vicinity of each of 47 *Bb* (non-attacked) queens. The same numbers of *BB* and *Bb* queens were used from each colony (maximum four per colony) to control for possible differences in genotype frequencies among colonies. To rule out the possibility that behavioural differences among workers with different *Gp-9* genotypes stem simply from intrinsic differences in their aggressiveness, we sequentially introduced four workers of another ant species (*Aphaenogaster* sp.) into each of 20 colonies and collected five fire ant workers attacking each alien ant. The genotype frequencies of the attacking fire ants were compared to those of 400 randomly sampled workers (20 workers from each of the 20 colonies). This procedure again controlled for possible differences in genotype frequencies among colonies. Associations between genotype frequencies were determined using G-tests[18].

Queen-odour transfer. Ten of the 11–14-day-old queens attacked by workers were kept individually for at least 10 min in a small isolation unit before a randomly selected live worker from the same parent colony was rubbed against the queen's thorax and abdomen. The worker was reintroduced into the parent

colony 2 min later and aggression was recorded during the 5 min immediately after introduction. The same procedure was followed for workers that were rubbed against non-attacked queens, with a single such queen being chosen randomly to match by colony each attacked queen. This procedure controlled for possible differences in worker behaviour among colonies. Subsequent genetic analysis revealed that all attacked queens were *Gp-9*^{BB} homozygotes, whereas all non-attacked queens were *Gp-9*^{Bb} heterozygotes. Levels of aggression were defined as: 0, no aggression; 1, infrequent biting; 2, frequent biting but attacked workers not immobilized; and 3, frequent biting with attacked workers immobilized. Scoring was done without knowledge of whether test workers had been rubbed against attacked (*BB*) or non-attacked (*Bb*) queens. In half of the replicates, we first introduced the worker rubbed against a *Gp-9*^{BB} queen and in the other half the worker rubbed against a *Gp-9*^{Bb} queen. This procedure controlled for possible changes in workers' behaviour in recipient colonies through time.

Received 7 November 1997; accepted 29 May 1998.

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Acknowledgements. We thank A. Bourke, C. DeHeer, J. Evans, M. Goodisman, D. Haig, L. Hurst and D. Queller for comments on the manuscript. This work was funded by grants from the Swiss and US National Science Foundations and the National Geographic Society.

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Visual search has no memory

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Humans spend a lot of time searching for things, such as roadside traffic signs[1], soccer balls[2] or tumours in mammograms[3]. These tasks involve the deployment of attention from one item in the visual field to the next. Common sense suggests that rejected items should be noted in some fashion so that effort is not expended in re-examining items that have been attended to and rejected. However, common sense is wrong. Here we asked human observers to search for a letter 'T' among letters 'L'. This search demands visual attention and normally proceeds at a rate of 20–30 milliseconds per item[4]. In the critical condition, we randomly relocated all letters every 111 milliseconds. This made it impossible for the subjects to keep track of the progress of the search. Nevertheless, the efficiency of the search was unchanged. Theories of visual search all assume that search relies on accumulating information about the identity of objects over time[5–7]. Such theories predict that search efficiency will be drastically reduced if the scene is continually shuffled while the observer is trying to search through it. As we show that efficiency is not impaired, the standard theories must be revised.

When a target item differs from distractors on a simple visual feature, such as a red bar among green bars, the target automatically grabs one's attention and can be detected independently of the number of distractor items present. When targets and distractors differ only in their spatial arrangement, however, the search becomes attention-demanding and the reaction time increases by 20–30 ms per item. Theories of visual search explain this phenomenon in one of two ways. 'Serial' models propose that attention can process the identity of only one item at a time. Once an item has been identified and rejected as a distractor, an inhibitory 'tagging' mechanism prevents that item from being revisited. As a result, a successful search for a target will require subjects to examine, on average, only half of the items in the display[5]. 'Parallel' theories assume that identity is computed in parallel for each item, and that an item's identity becomes gradually more certain over the course of a trial. A response is issued either when sufficient information confirms one item as the target, or when all of the items have proven to be distractors[6]. Both theories have in common the assumption that efficient search is based on accumulating information about the contents of the scene over the course of the trial; we refer to this as memory-driven search. We propose an alternative, that visual search processes are amnesic: they act on neural representations that are continually rewritten and have no permanent existence beyond the time span of visual persistence.

To test the hypothesis that visual search relies on memory-driven mechanisms, we designed our stimuli so that, during a trial, the scene would be constantly changing, yet the meaning of the scene (as defined by the required response) would remain constant. The task was to report as quickly as possible whether or not the target letter, T, was present in the display. In order to measure the increase in reaction time when extra items were present in the display, we varied the number of letters in the display (the set-size) between 8, 12 and 16. The slope of the target-present reaction-time × set-size function measures the efficiency of search through the display. This slope represents the added cost of each additional item. We focused on target-present slopes because their interpretation is more straightforward: the question of when to stop searching when you have not yet found a target is more complicated than the question of when to respond once you have found a target[8]. In half of the trials, all the letters were Ls, and these trials demanded a 'no' response. In the remaining trials, which required a 'yes' response, one of the letters was a T. Both Ts and Ls could appear, randomly, in any of four orientations: 0°, 90°, 180° or 270° to the vertical (Fig. 1).

There were two stimulus conditions in the experiments: random

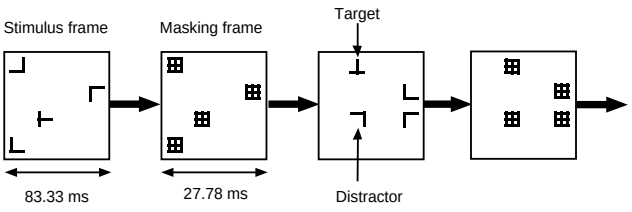

Figure 1 Two example stimulus frames from experiment 1, each followed by its corresponding masking frame. An actual trial in experiment 1 had four stimulus frames, repeated through five cycles. In experiment 2, the masking frames were eliminated and each stimulus frame was presented for 106.7 ms.