that mean extraction generalizes to other emotions (Figure S1A) and even other face dimensions, such as gender (Figure S1B). In these cases, mean discrimination performance was at least as good as regular discrimination. Further precise mean discrimination occurred for stimulus durations as brief as 500 ms (Figure S3).

It is unlikely that the mean extraction revealed here was driven by feature-based processing. Noise added to the faces to reduce low-level cues, such as brightness differences and facial marks, did not impair mean discrimination (Figure S1B). Moreover, when presented with sets of scrambled faces, stimuli thought to require a feature-based strategy [7], observers' ability to discriminate the mean emotion significantly declined.

Our findings — the statistical extraction of mean emotion or gender — contrast with the prototype effect, in which individuals form an idealized representation of a face based on the frequent occurrence of various features over an extended time period, even though that ideal, or prototype, was never viewed [8,9]. Whereas the prototype and other statistical learning effects [10] take several minutes of exposure and cannot be quickly modified in sequential trials, mean extraction occurs rapidly and flexibly on a trial-by-trial basis and takes less than 500 ms — two sequential trials can have very different means, yet observers code each mean precisely. Naïve observers were even able to extract a mean from a novel set of faces that had never been seen before (Figure S4), providing further evidence against a prototype effect. More importantly, unlike the prototype effect, the rapid extraction of mean emotion may reflect an adaptive mechanism for coalescing information into computationally efficient chunks.

We have demonstrated that observers precisely and automatically extract the mean emotion or gender from a set of faces while lacking a representation of its constituents. This sort of statistical representation could serve two primary functions. First, a single mean can succinctly and efficiently represent copious amounts of information. Second, statistical representation may facilitate visual search, as detecting deviants becomes easier when summary statistics are available [4]. Our results suggest that the adaptive nature of ensemble coding or summary statistics is not restricted to the level of surface perception but extends to face recognition as well.

**Supplemental data**

Supplemental data are available at http://www.current-biology.com/cgi/content/full/17/17/R751/DC1

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[1]The Center for Mind and Brain, and [2]The Department of Psychology, The University of California, Davis, California 95618, USA.
E-mail: jmhaberman@ucdavis.edu

# Multiple queens means fewer mates

**Daniel J.C. Kronauer and Jacobus J. Boomsma**

Obligate multiple mating by social insect queens has evolved in some derived clades where higher genetic diversity is likely to enhance colony fitness [1–3]. The rare and derived nature of this behaviour is probably related to copulations being costly for queens, but fitness trade-offs between immediate survival and future reproductive success are difficult to measure and not well understood [1]. A corollary of this logic, that multiple mating should be less common or lost when genetic diversity among workers is achieved through multiple queens per colony, was suggested more than ten years ago [4]. However, large scale comparative analyses did not support this prediction, quite possibly because they did not contain any informative contrasts [1,2]. Only comparisons between closely related species with similar ecology and high queen-mating frequencies as ancestral state would provide decisive information, but such species pairs are exceedingly rare so that no case studies have been conducted and a comparative statistical approach [5] is impossible. Here we document for the first time that there is a clear link between the number of queens and the average number of matings of these queens, using the army ant *Neivamyrmex carolinensis* as a model system.

While all other studied Old World and New World army ants have very high queen-mating frequencies and a single queen per colony [3,6], up to 13 queens have been found in *N. carolinensis* colonies [6]. However, the species is entirely subterranean and so elusive that it has hardly been studied. It occurs in the southern and

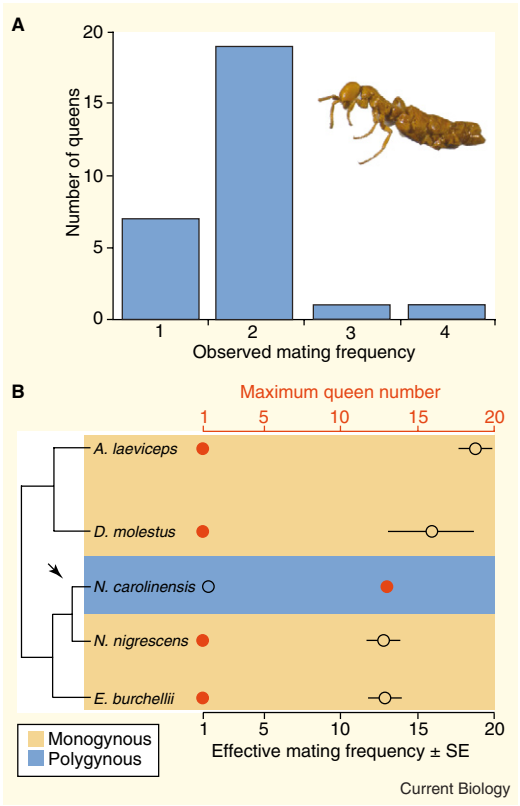


Figure 1. Low queen-mating frequencies in a polygynous army ant.

(A) The observed mating frequencies of 28 *Neivamyrmex carolinensis* queens from two colonies. (B) The mating system transition in *N. carolinensis* (arrow) from an ancestor with single-queen (monogynous) colonies and extremely high queen-mating frequencies to multi-queen (polygynous) colonies with low queen-mating frequencies, mapped on a partial army ant phylogeny with relevant branches represented [7]. The maximum number of queens per colony (filled red circles) [6] and the effective queen-mating frequency (open black circles) — the number of equally contributing fathers that would produce the average relatedness observed among the worker offspring, harmonic mean ± SE from jackknifing over queens — are shown for different *Aenictus*, *Dorylus*, *Neivamyrmex* and *Eciton* army ants for which genetic marker studies are available [3]. The SE for *N. carolinensis* is too small to be visible.

central USA in areas with cold winters and hot, dry summers, at the very northern edge of the overall army ant distribution. Harsh environments make accidental queen death more likely, so that multi-queen colonies are probably adaptive in *N. carolinensis* [6].

We collected samples from six colonies (I–VI) in tallgrass prairie habitat at the Konza Prairie Research Natural Area in eastern Kansas and investigated the genetic structure of colonies using five highly polymorphic microsatellite loci (see Supplemental data available on-line with this issue). The average relatedness between nestmate workers of all colonies was significantly positive ($r = 0.048 \pm 0.007$ SE; 95% CI: ± 0.019), but substantially lower than the minimum value of 0.25 that is expected for daughters of a single queen mated with an infinite number of unrelated males.

We were able to reconstruct the genotypes of 28 queens and their mates with high confidence (9 and 19 queens from colonies I and II, respectively; the two colonies with sufficiently large sample sizes; Supplemental data). Queen number in colony II exceeded the maximum of 13 reported so far [6], possibly because of a recent turnover of queens (Supplemental data). In sharp contrast to all other studied army ants [3], over 90% of the *N. carolinensis* queens had been inseminated by only one or two males, so that average mating frequencies were low (observed: 1.9 ± 0.1 SE; effective: 1.4 ± 0.1 SE; Figure 1). Relatedness among nestmate queens and among queens and their mates was indistinguishable from zero, which indicates outbreeding and suggests that multiple nest queens are permanently present and can be considered as independent data points for mating frequency analyses (Supplemental data).

Multiple queen-mating arose in a common ancestor of all army ants just over 100 million years ago and has been maintained since [3,7]: queens of all investigated monogynous species, including *N. nigrescens*, a very close relative of *N. carolinensis* that occurs sympatrically at the study site, typically mate with ten to twenty males [3] (Figure 1B). The dramatic and relatively recent mating system transition in *N. carolinensis* demonstrates that multiple mating can secondarily be selected against when the benefits no longer apply. Although other factors, such as sperm limitation of queens, could be associated with reduced queen-mating frequency, we regard selection for offspring genetic diversity as the most likely evolutionary driving force (Supplemental data). This interpretation is consistent with a previous study showing that a socially parasitic leaf-cutting ant has reverted to single/double mating from an ancestor with high queen mating frequency, presumably because social parasites exploit the genetic diversity of the host workers [8]. Our results suggest that the costs of mating in army ants are non-negligible, albeit comparatively small because queens do not have to leave the nest to mate [3].

We hypothesize that previous large scale comparative analyses [1,2] and case studies [9] failed to confirm a negative association between multi-queen colonies and multiple mating by queens, because they only included contrasts that concerned species with facultative multiple mating — some queens mate a few times while others mate once — rather than those with high levels of obligate multiple mating. Facultative multiple mating probably evolves for other reasons than increasing genetic diversity [1], and it may often be an unselected consequence of the breeding system [9]. A negative correlation between queen number and queen-mating frequency is therefore not necessarily predicted for clades where queens have retained the option to either mate singly or

multiply [9]. This implies that the army ant contrast of this study may be the only one in existence to directly test the hypothesis that queen number and queen-mating frequency are negatively associated via selection for genetic diversity [4].

**Supplemental data**

Supplemental data are available at http://www.current-biology.com/cgi/content/full/17/17/R753/DC1

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Institute of Biology, Department of Population Biology, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen, Denmark.
E-mail: djckronauer@bi.ku.dk

# Involvement of deoxycytidylate deaminase in the response to $S_n1$-type methylation DNA damage in budding yeast

**R. Michael Liskay[1,*], Linda J. Wheeler[2], Christopher K. Mathews[2] and Naz Erdeniz[1]**

In addition to spellchecking during DNA replication and modulating recombination, DNA mismatch repair (MMR) promotes cytotoxic responses to certain DNA-damaging agents [1]. In mammalian cells, the best-studied response is to $S_n1$-type methylating agents, including N-methyl-N'-nitro-N-nitrosoguanidine (MNNG) [1]. Notably, MMR-deficient mammalian cells are resistant to the cytotoxic effects of these agents. A recent report showed that MMR deficiency conferred resistance to MNNG in yeast cells crippled for both homologous recombination (*rad52*Δ) and the detoxifying enzyme methylguanine methyltransferase (*mgt1*Δ) [2]. To better understand the response, we searched for additional genes modulating sensitivity to MNNG in *rad52*Δ *mgt1*Δ budding yeast. In addition to alleles of known MMR genes, we isolated an allele of *DCD1* encoding the enzyme deoxycytidylate deaminase, which influences the dCTP:dTTP nucleotide pool ratio by catalyzing the conversion of dCMP to dUMP [3]. Models of the MMR-dependent cytotoxic response to $S_n1$-type methylating agents have included the incorporation of dTTP opposite $O^6$-methyl guanine ($O^{6met}G$) in the template [1]. Our findings lend further support to this aspect of the MMR-dependent response and highlight a mechanism for 'methylation' resistance that may be of therapeutic relevance for human cancer.

To better understand the response of budding yeast to DNA methylation damage, we mutagenized a *rad52*Δ *mgt1*Δ strain to ~33% survival with ethyl methanesulfonate, and screened for mutants resistant to MNNG. After screening ~10,000 colonies, 18 colonies repeatedly tested resistant. In appropriate crosses, one-half of the *rad52*Δ *mgt1*Δ segregants were MNNG resistant, suggesting that a single gene mutation was responsible for the resistance trait and that the mutation was unlinked to either *RAD52* or *MGT1* (data not shown). Crosses to a *rad52*Δ *mgt1*Δ strain produced diploids that were each sensitive to MNNG, indicating that all 18 $MNNG^r$ mutations were recessive. Next, we performed complementation tests amongst the mutant collection and with MMR genes that, when mutated, have been found to confer resistance to MNNG, i.e. *mlh1*Δ, *msh2*Δ, *pms1*Δ, *msh6*Δ ([2] and our unpublished data). Not surprisingly, complementation tests suggested that we had isolated multiple alleles of *MLH1* (6), *MSH2* (2), *PMS1* (3) *and MSH6* (6). However, one recessive mutation defined a separate complementation group, initially designated *drm1-1* (damage response to methylation).

To identify, by complementation, the gene associated with the MNNG resistance, we transformed the *drm1-1* strain with a centromere-based yeast genomic library. Among ~20,000 transformants screened for MNNG sensitivity, two complemented colonies were identified and the library clones isolated. Sequencing revealed that these clones harbored identical genomic inserts containing seven potential open reading frames, including the *DCD1* gene. We sequenced the *DCD1* gene in the MNNG-resistant (*rad52*Δ *mgt1*Δ) strain and detected a mutation (G to T) predicted to cause a serine to phenylalanine change at residue 178, a residue conserved in the human deoxycytidylate deaminase gene *Dctd1* (Figure S1 in Supplemental Data).

To further substantiate that the S178F change in Dcd1 was responsible for MNNG resistance in the *drm1-1* strain, we introduced the *dcd1-S178F* mutation into the genome of the wild-type