Ant parasite queens revert to mating singly

A parasitic ant has abandoned the multiple mating habit of the queens of its related host.

Multiple mating (polyandry) is widespread among animal groups, particularly insects[1]. But the factors that maintain it and underlie its evolution are hard to verify because benefits and costs are not easily quantified and they tend to be similar in related species. Here we compare the mating strategies of the leaf-cutting ant *Acromyrmex echinatior* and its recently derived social parasite *Acromyrmex insinuator*, which is also its closest relative[2] (see Fig. 1). We find that although the host queens mate with up to a dozen different males, the social parasite mates only singly. This rapid and surprising reversion to single mating in a socially parasitic ant indicates that the costs of polyandry are probably specific to a free-living lifestyle.

In social insects, obligate polyandry has evolved independently in four groups (honeybees, vespid wasps, harvester ants and leaf-cutting ants[3]), among which every species was previously believed to be multiply mated. All free-living leaf-cutting ants are multiply mated[4], so the common ancestor of both parasite and host ants must have had multiply mated queens. Because social parasite queens exploit the resources and workers of a host colony to produce reproductive offspring (sexuals) without investing in a large worker force of their own[5–7], we investigated whether this dramatic change in lifestyle could have altered the costs and benefits of polyandry, and thereby driven a shift in mating strategy.

Parasitized *A. echinatior* colonies were collected from Gamboa, Panama, where the species is common[7]. We compared the mating frequencies of host and parasite by analysing the genotypes of queens and their female offspring to estimate the number of fathers contributing to a queen's progeny. Host queens mated with 10.6 ± 1.0 males (mean $\pm$ s.e; $n = 10$) but social parasite queens were predominantly singly mated (average number of matings per queen, 1.19 ± 0.10; only 2 out of 13 queens doubly mated; see Fig. 2).

This difference is statistically highly significant (Mann–Whitney U-test, $P < 0.0001$) and robust to alternative measures of queen-mating frequency. For example, the observed number of queen matings was 9.3 ± 0.7 *versus* 1.15 ± 0.10 ($P < 0.0001$), the effective number of queen matings was 5.3 ± 0.6 *versus* 1.09 ± 0.09 ($P < 0.0001$), the estimated proportion of multiply mated queens was 1.00 (95% confidence interval, 0.69–1.00) *versus* 0.19 (0.034–0.51; binomial test,

$P = 0.0006$), and genetic relatedness among the offspring was 0.380 ± 0.042 *versus* 0.693 ± 0.053 (t-test, $P = 0.0002$) for the host and parasite, respectively. The difference cannot be attributed to low variability in the genetic markers[8], sampling error[8] or inbreeding: neither species was inbred ($F = 0.006$, $n = 10$, $P = 0.19$ and $F = -0.035$, $n = 19$, $P = 0.88$ for *A. echinatior* and *A. insinuator*, respectively).

These findings provide insight into the selective forces affecting the evolution of polyandry. Like its host, *A. insinuator* is outbred and produces hundreds of winged sexuals in discrete batches that leave their natal colonies within the same brief time period[7]. This indicates that females of both species mate with unrelated males in swarms outside the colony. The parasite is also very abundant, infecting 44% of host colonies at our study site[7]. Mating behaviour, mate availability and thus the costs of mating are therefore likely to be similar for the two species. That *A. insinuator* has reverted to single mating suggests that the benefits of polyandry are reduced for the social parasite. The reversion to single mating seems to have been rapid compared with the evolution of other adaptive traits[5–7], supporting the widely held but rarely demonstrated assumption[1,2] that multiple mating is costly.

The association between a reversion to single mating and a switch to social parasitism indicates that the benefits of polyandry for *Acromyrmex* ants may be specific to being free-living and social. Four proposed benefits of multiple mating for social insect queens (nutrient transfer, sperm competition, variable daughter queens and avoidance of genetic incompatibility[3]) are unlikely to be important in the maintenance of polyandry in *Acromyrmex*, because they

would apply equally to social parasites and free-living species. Other likely benefits (greater sperm store, convergence of sex-allocation interests between queens and workers, reduced fitness cost of producing sterile diploid males and increased genetic diversity among workers[3]) are specific to free-living social insects and so are the most likely explanations for polyandry in *Acromyrmex* ants. The benefits of polyandry in these ants are therefore related to their social lifestyle, indicating that the selective forces affecting the evolution of polyandry in free-living social insects differ from those in other animals. We would expect workerless social parasites of other polyandrous social insects to have also reverted to mating singly. The identification of additional reversions to single mating, both in social and non-social animals, will be important in further distinguishing the factors
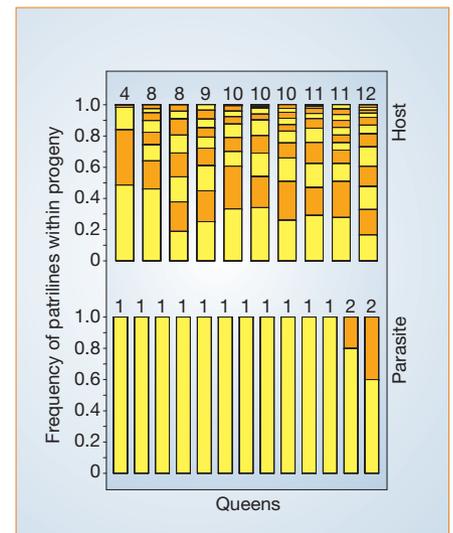

Figure 1 A multiply mated queen of the leaf-cutting ant *Acromyrmex echinatior* (right) and its singly mated socially parasitic companion queen *A. insinuator* (left) on their joint fungus garden. Small worker ants cluster around the parasite queen.

Figure 2 The observed frequency distributions of patrilines (offspring sired by different males) of the social parasite *Acromyrmex insinuator* ($n = 13$) and its host *A. echinatior* ($n = 10$), as derived from genetic analysis of the progeny of single queens. Patrilines are shown by alternate shading patterns, with their total number in each colony given above the bars. Host queens and an average of 203 (range, 35–672) female offspring per queen were genotyped at four microsatellite loci (*Ech*1390, *Ech*3385, *Ech*4126 and *Ech*4225)[9]. Parasite queens and an average of 14.7 (6–20) female progeny per queen were genotyped at two loci (*Trachy*11_12 and *Ech*3385)[9,10]. Genotypes of queens and their offspring were analysed using the software MATESOFT 1.0b (by A. Moilanen, L. Sundström and J. S. Pedersen; available at http://www.zi.ku.dk/popecol/personal/JSPedersen/Mate-Soft.htm) to obtain mating-frequency statistics[8], and the total mate number for host queens was further estimated using a modified version of the coverage statistics calculated by the program CHAO[11].

involved in the evolution and maintenance of multiple mating by females.

Seirian Sumner*, William O. H. Hughes, Jes S. Pedersen, Jacobus J. Boomsma
Biological Institute, Department of Population Biology, University of Copenhagen, 2100 Copenhagen, Denmark
e-mail: jjboomsma@zi.ku.dk
*Present addresses: Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002, USA, and Institute of Zoology, Zoological Society of London, Regents Park, London N1 4RY, UK.

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COMMUNICATIONS ARISING

Arctic Ocean

Hydrothermal activity on Gakkel Ridge

In the hydrothermal circulation at mid-ocean ridges, sea water penetrates the fractured crust, becomes heated by its proximity to the hot magma, and returns to the sea floor as hot fluids enriched in various chemical elements. In contradiction to earlier results[1] that predict diminishing hydrothermal activity with decreasing spreading rate, a survey of the ultra-slowly spreading Gakkel Ridge (Arctic Ocean) by Edmonds *et al.*[2] and Michael *et al.*[3] suggests that, instead of being rare, the hydrothermal activity is abundant — exceeding by at least a factor of two to three[3] what would be expected by extrapolation from observation on faster spreading ridges. Here we use helium-3 (^{3}He), a hydrothermal tracer[4], to show that this abundance of venting sites does not translate, as would be expected, into an anomalous hydrothermal ^{3}He output from the ridge. Because of the wide implications of the submarine hydrothermal processes for mantle heat and mass fluxes to the ocean, these conflicting results call for clarification of the link between hydrothermal activity and crustal production at mid-ocean ridges.

On the basis of the axial distribution of light scattering and manganese tracer anomalies measured during the Arctic mid-ocean ridge experiment (AMORE), hydrothermal activity on Gakkel Ridge has been reported to be "far more abundant than predicted on the basis of previous correlations with spreading rate"[3]. Owing to the high enrichment of the hydrothermal fluids in mantle ^{3}He (typically a factor of 10^4 relative to ambient sea water), this abundant hydrothermal activity should logically correspond to an enhanced ^{3}He output from the ridge.

At a global scale, three-dimensional oceanic general circulation models make a good job of simulating the oceanic distribution of hydrothermal ^{3}He by using the simple assumption that the ^{3}He source intensity is linearly correlated with the spreading rate[5,6]. The slope of the ^{3}He flux–spreading rate relationship is close to 330 ^{3}He mol km^{-2} of crustal spreading, translating into a world average ^{3}He annual flux of 0.33 mmol km^{-2} of ridge and per mm yr^{-1} of full spreading rate. Available ^{3}He fluxes determined for active portions of ridge show results consistent with this global trend (Fig.1a).

Gakkel Ridge stretches 1,800 km across the Eurasian basin of the Arctic Ocean. Residence time of deep and bottom waters in the Greenland/Norwegian seas and the Eurasian basin have been studied in detail in the recent past using multi-tracer balances[7]. ^{3}He concentrations are relatively low in the deep waters of the Arctic Ocean: Eurasian basin deep waters (EBDW), which are at 1,500–2,600 m depth, show a ^{3}He excess relative to solubility equilibrium of $4.3 \pm 0.8\%$, whereas the Eurasian basin bottom waters (EBBW) average ^{3}He excess is $3.7 \pm 0.6\%$ (refs 7,8).

The ^{3}He input from Gakkel Ridge to the EBBW and EBDW can be calculated using a simplified version of a box model[7] (Fig.1b). Water fluxes are derived from the ^{39}Ar radioactive tracer budget (^{39}Ar is a cosmogenic isotope with a half-life of 269 years), allowing the mantle ^{3}He flux to be calculated from the ^{3}He budget. Taking into account the uncertainties in the data, a maximum ^{3}He input of 3.4 mol yr^{-1} is inferred. Scaled to the length and spreading rate of Gakkel Ridge, the mantle ^{3}He input translates into an annual flux of 0.15–0.32 mmol km^{-1} of ridge and per mm yr^{-1} of full spreading rate (Fig.1a), showing no positive anomaly with respect to that expected from the value of the spreading rate.

One explanation mentioned by Michael *et al.*[3] for the observed discrepancy could be that the high plume incidence observed during the survey (80% plume incidence on the 145 profiles) overestimated the abundance of vents because of the confined nature of the deep unsegmented rift valley. It is possible that plume meanders originating from a single vent site may have been interpreted as corresponding to different sources. Alternatively, if the inferred number of vent sites is right, an explanation may rest on the fact that vent frequency is not a direct measurement of hydrothermal activity.

It is also possible that, on ultra-slowly spreading ridges, individual plumes carry
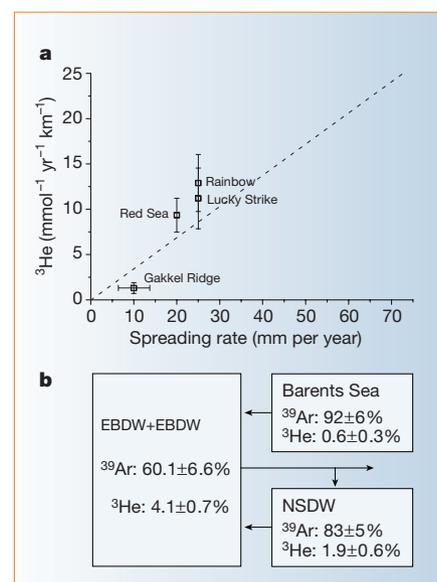

Figure 1 ^{3}He fluxes at mid-ocean ridges. **a,** ^{3}He annual flux per kilometre of ridge as a function of spreading rate. The linear relationship used in GCM simulations[5,6] is shown (dashed line). The Mid-Atlantic Ridge (MAR) Lucky Strike site and Red Sea values are from refs 9,10. The Rainbow site (MAR) value is unpublished data. **b,** Eurasian basin box model : Eurasian basin deep and bottom waters (EBDW and EBBW respectively) are directly ventilated by the sinking of dense shelf waters from the Barents Sea. They leave the basin through the western part of the Fram Strait and mix with the Greenland Sea and Norwegian Sea deep waters (NSDW). In addition to the Barents Sea waters, some NSDW also return to the north and re-enter the deep Arctic through the eastern part of the Fram strait[7]. ^{39}Ar values[7] are expressed as a percentage δ of modern concentration. ^{3}He data are expressed using the isotope δ notation.

fewer chemicals and less heat, so higher frequency does not necessarily mean higher hydrothermal activity. The apparent discrepancy between the enhancement factor of two to three in the vent site frequency deduced from along axis tracer surveys and the low ^{3}He flux may therefore primarily reflect the unusual characteristics of the hydrothermal circulation on this ultra-slowly spreading ridge.

Detailed investigation of individual venting sites in such environments is needed to resolve this issue and to reassess the geological parameters that control ridge processes, including hydrothermal plume and vent frequency, fluid circulation and fluxes.

Philippe Jean-Baptiste, Elise Fourré
Laboratoire des Sciences du Climat et de l'Environnement, IPSL, CEA-CNRS, Centre d'Etudes de Saclay, 91191 Gif-sur-Yvette, France
e-mail : pjb@lsce.saclay.cea.fr

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