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Dispersal and population structure of a New World predator, the army ant *Eciton burchellii*

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Abstract

The army ant *Eciton burchellii* is probably the most important arthropod predator in the Neotropics, and many animal species depend upon it. Sex-biased dispersal with winged males and permanently wingless queens may render this species especially sensitive to habitat fragmentation and natural barriers, which might have severe impacts on population structure and lead to population decline. Using nuclear microsatellite markers and mitochondrial sequences, we investigated genetic differentiation in a fragmented population in the Panama Canal area. While nuclear markers showed little differentiation between subpopulations (F_{ST} = 0.017), mitochondrial differentiation was maximal in some cases (Φ_{ST} = 1). This suggests that, while females are not capable of crossing barriers such as large rivers, flying males are able to promote nuclear gene flow between the studied forest patches. Consistent with this interpretation, we did not find any evidence for inbreeding or genetic deterioration on Barro Colorado Island over the last 90 years since its formation.

Introduction

Dispersal has profound consequences for the evolution and ecology of animal and plant species (Bullock *et al.*, 2002). It influences the spatial distribution and abundance of species, local community structure and the dynamics and stability of populations. Furthermore, if dispersal and thus gene flow is limited among populations, genetic drift and adaptations to local conditions may lead to differentiation and ultimately to the rise of new species (Mayr, 1947; Frankham *et al.*, 2002). On the other hand, limited dispersal between small and fragmented populations can have a major impact on the potential for adaptive evolution (Wright, 1931; Lande, 1995) and may lead to inbreeding depression (Keller & Waller, 2002). Given worldwide habitat destruction and fragmentation, it comes as no surprise that dispersal-related genetic population structure is more than ever a focus of scientific research (e.g. Damschen *et al.*, 2006; France & Duffy, 2006).

In many species, dispersal is more prevalent in one sex than in the other. For example, in group-living mammals, dispersal is normally male biased, whereas in birds the reverse pattern is generally found (Greenwood, 1980; Honer *et al.*, 2007; Lawson Handley & Perrin, 2007). Differing dispersal patterns may exacerbate the difficulties when investigating population structure, but when known, they can also lead to more detailed insights into a species' population ecology and potential threats due to population segregation.

In the social Hymenoptera (the ants, some bees and some wasps), dispersal potential and therefore genetic population structure is mainly associated with the mode of colony founding, which can be independent or dependent, or a mixture of both (Ross & Shoemaker, 1997; Peeters & Ito, 2001; Sanetra & Crozier, 2003; Seppä *et al.*, 2004). Species with independent colony founding normally produce many young queens and males that both participate in a nuptial flight. After mating, the queens shed their wings and found a new colony on their own. Similar to other animal species with potentially strong dispersal (Slatkin, 1987), this mode of colony

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founding is expected to lead to genetically homogenous local populations and to significant population structure only over distances that are beyond the species' dispersal abilities. Furthermore, because both sexes disperse, genetic structure should be similar over nuclear markers, which are inherited via both sexes, and mitochondrial markers, which are inherited only via females (Seppä *et al.*, 2004; Sundström *et al.*, 2005).

In certain ant species with dependent colony founding, workers accompany the young queens on foot, limiting dispersal to walking distances. In general, queens are permanently wingless or bad fliers and mate in or near their natal nest with males that disperse on the wing. This mode of colony founding, which parallels strongly sex-biased dispersal of numerous vertebrates, may lead to strong genetic structuring even on small geographic scales, and the genetic signature should be stronger for mitochondrial markers (Ross & Shoemaker, 1997; Doums *et al.*, 2002; Seppä *et al.*, 2004, 2006; Clémencet *et al.*, 2005; Sundström *et al.*, 2005). Dependent colony founding in ants in turn comes in two main forms: colony budding and colony fission (Franks & Hölldobler, 1987; Peeters & Ito, 2001). Colony budding occurs in species with many queens per colony, and new colonies remain close to their mother colony. The population genetic consequences of colony budding have been studied in detail in *Formica* wood ants (e.g. Liautard & Keller, 2001; Sundström *et al.*, 2005; Seppä *et al.*, 2006). During colony fission, on the other hand, a colony headed by a single queen, splits into two, more or less equal, parts, each again headed by a single queen. Daughter colonies are often able to disperse by emigrating on foot to new nest sites. Colony fission among the ants is mainly known from the three army ant subfamilies Aenictinae, Dorylinae and Ecitoninae. In spite of this intriguing system of highly differentiated dispersal abilities of the two sexes and the ecological importance of these army ants, the effect on their genetic population structure has not been studied.

Study system

The army ant *Eciton burchellii* is probably the prime predator of arthropods in Neotropical rain forests (Rettenmeyer, 1963) and thereby plays a pivotal role in structuring arthropod communities (Franks & Bossert, 1983; Kaspari & O'Donnell, 2003). Furthermore, many other organisms are associated with and dependent upon this species, ranging from birds (Sekercioglu *et al.*, 2002) to specialized mites (Rettenmeyer, 1962). Colonies are headed by a single queen and reproduce, approximately every 3 years, by colony fission (Franks, 1985). Queens are permanently wingless and mate inside the colony with approximately 10–20 males (Kronauer *et al.*, 2006), whereas males disperse on the wing. As is the case in all fissioning species, numerical sex ratios are highly male biased (Schneirla, 1971; Craig, 1980). Although female dispersal is limited to places the ants can walk to, colonies frequently emigrate and can disperse on average about 500 m month^{-1} (Franks, 1982). Nevertheless, natural barriers such as permanently broad rivers are impassable and colonies avoid crossing open and deforested areas (Suarez *et al.*, 1998; Roberts *et al.*, 2000; Meisel, 2006), making the species especially sensitive to habitat fragmentation (Partridge *et al.*, 1996).

Objectives of this study

Because of the species' crucial role in ecosystem functions and the peculiar mode of reproduction, it is important to achieve a better understanding of the underlying genetic structure in *E. burchellii* populations. This would eventually allow more efficient conservation planning, significantly contribute to the basic understanding of army ant life history, and provide comparative insights into how dispersal and reproductive systems affect the population structure of social insects and other organisms. We used a combination of nuclear and mitochondrial markers to address the following main questions: first, does mating regularly take place between relatives? Second, are the mates of a given queen related to each other? This information is important to understand to what extent the high mating frequencies lead to an increase in within-colony genetic diversity and effective population size. Third, do we find evidence for genetic deterioration in small, isolated populations, which eventually might lead to local extinction? And fourth, are populations genetically structured over distances that can potentially be covered by dispersing males, and to what extent is differential sex-linked dispersal reflected in the genetic population structure?

Materials and methods

Study area and sample collection

Fieldwork was conducted between March and May 2005 within the Barro Colorado Nature Monument, Panama (9°10′N, 79°51′W), which is contiguous to the 22 104-ha Soberanía National Park. Uniquely, the long-term fragmentation history in this area is well documented. This enabled us to investigate fragmentation effects on two time scales: long-term effects – associated with the original course of the later dammed river Chagres, and short-term effects – associated with the Panama Canal's creation 90 years ago, which resulted in various forest fragments, among them Barro Colorado Island (BCI). Ants were collected mainly at three sites (Table 1; Fig. 1): BCI, Gigante Peninsula (GIG), and the Soberanía National Park (Pipeline Road, PLR). A single colony was sampled along the nature-trail El Charco (CHA). We stored the ants directly in 96% ethanol. The sites GIG, BCI and CHA were on the western bank along the historic route of the river Chagres, whereas PLR was on

Table 1 Study sites and sample sizes.

Site	Fragment size (ha)	Resident army ant colonies	Sampled colonies	Reconstructed males
PLR	13 100	480	7	93
GIG	2500	91	10	133
BCI	1500	55	14*	168
CHA	9000	327	1	9

The estimates of fragment size and the number of resident army ant colonies follow Partridge *et al.* (1996). The number of sampled colonies is identical to the number of reconstructed queen genotypes. *Six of these colonies were sampled in 2002.

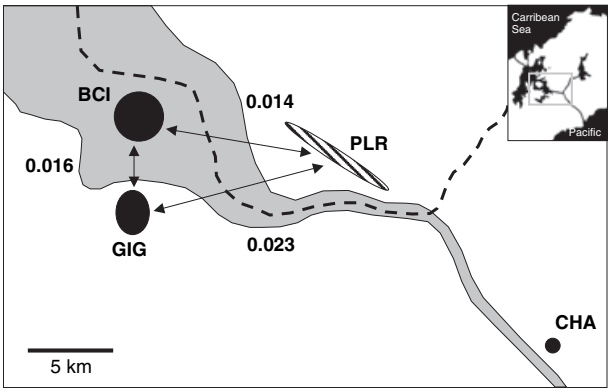

Fig. 1 Pairwise genetic differentiation between the subpopulations (F_{ST}; Weir & Cockerham, 1984) and their geographic position in relation to the waters of the Panama Canal (in grey). All estimates are significantly different from zero ($P < 0.05$) after adjustment for multiple comparisons. Populations fixed for mtDNA haplotypes H_1 and H_2 are depicted as filled and hatched areas respectively. The shape of the study sites indicates the approximate area where colonies were sampled. The hatched line represents the historic route of the river Chagres.

the former eastern bank of the river (Fig. 1). We also included the microsatellite data for six colonies from the BCI population from an earlier study (Denny *et al.*, 2004a; see Kronauer *et al.*, 2006 for more details on sampled colonies). Sample sizes are given in Table 1.

We assume that colony densities are comparable between sites. A census of a 100-ha plot each on BCI and PLR showed no significant differences in *E. burchellii* colony densities (Touchton, 2005). Likewise, the density of the ants' prey, which is known to be related to ant density (Kaspari & O'Donnell, 2003), did not differ significantly between the two sites (Touchton, 2005). No comparable data exist for GIG. However, habitat structure, geographic area and altitude are similar to the other two sites (Leigh *et al.*, 1982) and similar numbers of colonies were encountered per kilometre walked on BCI (0.069 colonies per km) and GIG (0.074 colonies per km), where trails were comparable in width and shading. The encounter rate of *E. burchellii* colonies on trail walks is a verified method to estimate the species' colony densities (Vidal-Riggs & Chaves-Campos, 2008).

Molecular protocols

We extracted DNA from 24 ants per colony using a standard phenol/chloroform protocol and genotyped them for eight polymorphic microsatellites as has been described in Denny *et al.* (2004b). Fragment sizing and allele calling were performed with the software GeneticProfiler 1.5 (Amersham Biosciences, Little Chalfont, UK) and allele scoring was checked by eye.

We sequenced one specimen per colony for a 525-bp region of the mitochondrial gene *cytochrome oxidase subunit 1* (*COI*) using the newly developed primers EbF2 (5′-AGGAGGATTAACTGGAATTATA-3′) and EbR2 (5′-TGAATTTTGTGTTCCTAATATT-3′). Amplifications of all sequences were carried out on a GeneAmp PCR system 9700 (Applied Biosystems, Foster City, California, USA). In 10-μL PCR reactions, we used 1 μL of template DNA, 3 pmol of each primer, 1.25 mM of each dNTP (Amersham), 0.4 units of HotStar *Taq* DNA polymerase (Qiagen) and 1x PCR reaction buffer (Qiagen, Crawley, UK). The thermal cycle profile was as follows: initial denaturation at 95 °C for 15 min, followed by 36 cycles of 94 °C for 30 s, 53 °C for 30 s and 72 °C for 1 min, with a terminal extension of 10 min at 72 °C. PCR products were purified with ExoSap-IT (GE Healthcare, Little Chalfont, UK) and subsequent ethanol precipitation. Sequences were generated with a MegaBACE automatic sequencer (Amersham), using the affiliated sequencing kit (DYEnamic ET dye Kit). Alignment and comparison of sequences between colonies and species was performed with the program Sequencher 4.0.5 (Gene Codes Cooperation, Anna Arbor, Michigan, USA).

Data analysis

Workers within social insect colonies are typically related and therefore should not be considered independent of each other in population analyses. Therefore, we initially determined genotypes of the queen and the fathering males for each colony using the broad deduction method of the program MATESOFT 1.0 (Moilanen *et al.*, 2004), as has been described in Kronauer *et al.* (2006). The queen genotypes were then duplicated and the male genotypes were entered as diploids, allowing alternative father genotypes to be entered as heterozygotes (Kronauer *et al.*, 2006). This data set was used only to calculate unbiased background allele frequencies for the overall population and the three subpopulations separately in FSTAT 2.9.3.2 (Goudet, 2001). Using background allele frequencies for the overall population, we then deduced the genotypes and their associated likelihoods for all colony queens and their mates in a second analysis in MATESOFT 1.0.

Exact tests for Hardy–Weinberg equilibrium for each locus and genotypic linkage equilibrium were calculated

with the software GENEPOP 3.4 (Raymond & Rousset, 1995), using only the derived queen genotypes.

We calculated the expected and observed heterozygosities per locus and subpopulation in the program FSTAT 2.9.3.2. Expected heterozygosities (H_s) were calculated from the derived queen and male genotypes, whereas observed heterozygosities (H_o) were based on the observed worker genotypes. These estimates were used to calculate an inbreeding coefficient $G_{IS} = 1 - H_o/H_s$ (Nei, 1987) with standard errors from jackknifing over loci. Again, because workers in social insect colonies are related, estimating H_s directly from the worker genotypes would have resulted in biased inbreeding estimates. We tested for differences in allele frequencies between the sexes in the parental generation by calculating pairwise Wright's fixation indices (F_{ST}; Weir & Cockerham, 1984) between the deduced queen and male genotypes for each subpopulation in FSTAT 2.9.3.2.

Allelic richness and the number of private alleles were calculated with the derived queen and male genotypes and corrected for differences in sample size using the rarefaction method (Kalinowski, 2004) with the program HP-Rare (Kalinowski, 2005). The data were normally distributed and we used one-way ANOVAS to test for differences between the subpopulations. These analyses were carried out to assess whether the BCI population was suffering detectable genetic deterioration and inbreeding in comparison with the mainland populations.

Calculations of F_{ST} (Weir & Cockerham, 1984) to quantify genetic differentiation at different hierarchical levels were based only on the derived male genotypes. These were 'diploidized' as above and analysed in FSTAT 2.9.3.2. This procedure has been used previously to analyse data for the Asian giant honeybee (*Apis dorsata*) by Paar *et al.* (2004). Initially, we ran three separate analyses to quantify genetic structure between colonies within each of the three subpopulations and to test whether the mates of single queens represent a random sample from the respective subpopulation. We then performed a fourth analysis to estimate genetic differentiation caused by geographic separation between the three subpopulations. Standard errors and 95% confidence intervals were obtained by jackknifing and bootstrapping over loci respectively. The significance of overall population differentiation in each analysis was tested with 15 000 randomizations not assuming Hardy–Weinberg equilibrium within samples. The nominal level for multiple comparisons in pairwise tests of differentiation was set to 0.05.

Genetic relatedness between individuals, *R*, was calculated in the program RELATEDNESS 5.0.8 (Goodnight & Queller, 1998), which uses the algorithm of Queller & Goodnight (1989). Standard deviations were obtained by jackknifing over loci. We calculated average *R* between the mates of a single queen (R_{MM}), and average *R* between queens and their mates (R_{QM}). The latter estimate was bidirectional using the settings Px = (Caste = Q) OR (Caste = M) and Py = (K-Colony = X) AND (Caste<>X). For relatedness analyses, we used separate background allele frequencies for each subpopulation and the most likely queen and male genotypes that had been determined by MATESOFT 1.0.

We estimated differentiation between subpopulations at the mitochondrial locus (Φ_{ST}) using FSTAT 2.9.3.2 following Weir & Cockerham (1984). We assume that mitochondrial DNA in *E. burchellii* is only inherited via females, as is the case in other ants (Seppä *et al.*, 2004; Sundström *et al.*, 2005).

Results

In total, we reconstructed 32 queen and 403 male genotypes (Table 1). The overall population and all three subpopulations were in Hardy–Weinberg equilibrium (Overall: $\chi^2 = 28.532$, $P = 0.808$; PLR: $\chi^2 = 3.665$, $P = 0.999$; GIG: $\chi^2 = 11.151$, $P = 0.800$; BCI: $\chi^2 = 13.716$, $P = 0.620$) and we did not detect significant linkage between any marker pair ($P > 0.05$ after Bonferroni correction for multiple comparisons).

The estimated inbreeding coefficient was significantly negative in all three subpopulations ($P < 0.05$; PLR: $G_{IS} = -0.046 \pm 0.010$ SE; GIG: $G_{IS} = -0.095 \pm 0.021$ SE; BCI: $G_{IS} = -0.074 \pm 0.014$ SE) and queens and their mates were not significantly related (PLR: $R_{QM} = -0.020 \pm 0.010$ SD; GIG: $R_{QM} = -0.012 \pm 0.013$ SD; BCI: $R_{QM} = -0.017 \pm 0.013$ SD; $P > 0.05$ in all cases). There was no significant genetic differentiation between parental queens and males in any of the subpopulations as indicated by pairwise F_{ST} estimates ($P > 0.05$ in all cases).

An analysis of between-colony genetic structure using F_{ST} estimates showed that the males that had mated with a given queen were not a random sample from the respective subpopulation. Overall, 53 of the 157 pairwise comparisons between colonies were significant, and F_{ST} values were significantly positive for all subpopulations (Table 2). Consistently, male genotypes deduced to have contributed to paternity in the same colony were, on average, significantly related to each other in all three subpopulations (Table 2).

Allelic richness (A) and private allelic richness (pA) were not significantly different between the subpopulations (details are given in the supplementary Table S1; A: $F_{2,21} = 0.072$, $P = 0.931$; pA: $F_{2,21} = 0.160$, $P = 0.853$).

Subpopulations were weakly but significantly differentiated at the nuclear microsatellite loci (overall $F_{ST} = 0.017 \pm 0.003$ SE; 95% CI: 0.011–0.023; $P < 0.00007$). Pairwise F_{ST} estimates among subpopulations are given in Fig. 1.

The 26 sampled *E. burchellii* colonies yielded two mtDNA haplotypes. Haplotype H_1 (GeneBank accession number: DQ644000) was shared among all 19 colonies collected from the sites GIG, BCI and CHA, whereas the

Table 2 Genetic differentiation between the male mates of different queens within a given subpopulation using Wright's fixation index (F_{ST}; Weir & Cockerham, 1984) as estimated in FSTAT 2.9.3.2 (Goudet, 2001). In addition, average pairwise relatedness of colony fathers (R_{MM}) are given as estimated in RELATEDNESS 5.0.8 (Goodnight & Queller, 1998). Significant differences from zero are indicated by *P*-values.

Subpopulation	F_{ST} ± SE	95% CI	*P*	R_{MM} ± SD	*P*
PLR	0.048 ± 0.005	0.040–0.058	< 0.00007	0.038 ± 0.005	< 0.05
GIG	0.113 ± 0.014	0.089–0.138	< 0.00007	0.088 ± 0.016	< 0.05
BCI	0.079 ± 0.006	0.068–0.090	< 0.00007	0.076 ± 0.008	< 0.05

remaining seven colonies from PLR carried haplotype H_2 (DQ644001). The two haplotypes differed at six bases (1.14% sequence divergence). The lack of detected variation in mitochondrial haplotypes within subpopulations translates into a maximum estimate of $\Phi_{ST} = 1$ between PLR and the other sites, and no detected differentiation between GIG and BCI.

Discussion

Inbreeding

No evidence for inbreeding was found in the study population and young queens were not related to their mates. In fact, the inbreeding coefficient was slightly but significantly negative in all three subpopulations. Such a bias could arise if allele frequencies differed between queens and males, e.g. if a significant proportion of males originated from a genetically distinct subpopulation. This could apply to *E. burchellii* if some males were dispersing over several kilometres because, as we show here, subpopulations that are separated by 5–10 km show low levels of genetic differentiation at nuclear loci. In contrast to this explanation, we did not find any significant genetic differentiation between parental queens and males. However, the power of this test is limited given the small sample size of queen genotypes. Alternatively, we could be dealing with a statistical artefact and the studied subpopulations are in fact panmictic (e.g. Seppä & Gertsch, 1996). Matings between young queens and their brothers could be avoided in army ants by a simple mechanism: young queens eclose several days before the males and probably also mate before their brothers become sexually active (Schneirla, 1971).

Relatedness among colony fathers

Both F_{ST} and regression relatedness estimates showed that the mates of a given queen were significantly related to each other and did not represent a random sample from the respective subpopulation. This is in contrast to the army ant *Neivamyrmex nigrescens*, where mates of single queens are not related to each other (Kronauer *et al.*, 2007). Numerical sex ratios in army ants are highly male biased. In *E. burchellii*, approximately 4000 males and only one or two successful young queens are produced by a reproducing colony (Schneirla, 1971; Franks, 1985). Reproduction in *E. burchellii* is seasonal (Schneirla, 1971), but only about one-third of the colonies contribute males to a given breeding season, and these males disperse from the colony within a few days (which is different from ant species where all colonies might contribute synchronously to a mating swarm). This increases the likelihood that some of a queen's mates will come from the same colony and are brothers. The average relatedness between queen mates over the three subpopulations was $R = 0.067$. Assuming that relatedness is zero for nonbrother males this means that, on average, two out of every 4.4 males that mate with a queen are brothers. Why the estimate for *E. burchellii* differs qualitatively from *N. nigrescens* is not clear, but it could be related to differences in basic life-history parameters such as male dispersal capacity, population level synchronization of the male flight period, or the duration of queen receptivity.

Genetic deterioration on BCI

We did not detect a decrease in nuclear genetic diversity or an increase in the level of inbreeding on BCI, when compared with the mainland sites. These results can be interpreted in the light of two nonexclusive underlying factors: the population's history and ongoing gene flow. Given the species' long generation time of about 3 years, the 90 years since the sites have been separated might not be sufficient for genetic drift to produce a measurable decline in genetic variation. In wood ants, such an effect of habitat fragmentation has been detected over a period of only 32 years, but the same study also showed that the intensity of this effect depends on the precise life history of a given species (Mäki-Petäys *et al.*, 2005). Although the recent unity of the subpopulations in our study is probably still traceable in their genetic structure and may also mask some effects (Ewers & Didham, 2006), the absence of a distinct reduction in nuclear genetic diversity in the island subpopulation could also point to current gene flow between BCI and the mainland. Because females are unable to disperse to the island, this would imply that males can cross the waters of the Panama Canal. This is also consistent with the very low observed levels of nuclear differentiation and the finding that colonies on the island show no

reduction in mating frequency compared with the mainland sites (Kronauer *et al.*, 2006). A reduction in mating frequency might have been expected if males were not able to reach and reproduce on the island (e.g. Neumann *et al.*, 1999; Griffith, 2000). Such male-mediated gene flow may be sufficient to counteract a decline in nuclear genetic diversity over several generations (Wright, 1931; Crozier *et al.*, 1984; Ross & Shoemaker, 1997). Yet to stop long-term genetic population differentiation even 10 migrants per generation might not be sufficient (Vucetich & Waite, 2000). Estimates of male dispersal capabilities in ants based on direct observation are scarce, but suggest that males can disperse over distances of a few kilometres (Vogt *et al.*, 2000). Army ant males are very large compared with other ants and therefore are probably good fliers. Subsequent investigations will need to show to what extent males cross between the forest fragments.

Genetic differentiation between subpopulations

As predicted from the life history of *E. burchellii*, mitochondrial differentiation between subpopulations was much more pronounced than nuclear differentiation. While the ratio Φ_{ST}/F_{ST} is expected to be 3/1 with equal numbers of dispersing males and females (due to the smaller effective population size of mitochondrial markers), in ants with male-biased dispersal this ratio typically ranges between 10 and 20 (Seppä *et al.*, 2006). The mitochondrial haplotype distribution in our study is consistent with a strict matriline separation by the historic route of the river Chagres (Fig. 1). The very high Φ_{ST}/F_{ST} ratios between subpopulations on both sides of the former river (BCI/PLR: 71; GIG/PLR: 43) are due to very low levels of nuclear differentiation and the complete separation in the mitochondrial marker. Such a very strong differentiation of mtDNA has also been found in a few other ants with dependent colony founding (Liautard & Keller, 2001; Doums *et al.*, 2002; Sanetra & Crozier, 2003). Although a longer mtDNA sequence and further sampling might reveal additional haplotypes, the present data demonstrate the profound effect that colony fission and male-biased dispersal have on genetic population structure. The data also strongly suggest that rivers act as barriers to mitochondrial gene flow in army ants. This is consistent with the observed barrier effect of rivers on gene flow in some vertebrates (i.e. the river hypothesis, reviewed in Moritz *et al.*, 2000). Our observations also imply that the waters of the Panama Canal will show long-term effects similar to those of the river Chagres in segregating Panamanian army ant populations. The very low levels of nuclear differentiation between subpopulations, also in comparison with other ant species with dependent colony founding (Doums *et al.*, 2002; Sanetra & Crozier, 2003; Clémencet *et al.*, 2005; Seppä *et al.*, 2006), again points to the likely ability of males to disperse over distances of several kilometres.

Conclusions

Sex-biased dispersal is the rule in many animal species (e.g. Lawson Handley & Perrin, 2007), and may have a very strong influence on the population genetic structure of such species and thus their potential for adaptive evolution. While showing many parallels to other animals, the army ants' reproductive and dispersal system – i.e. very high levels of multiple mating and colony fission, combined with sexually very distinct dispersal abilities – is possibly unique in the animal kingdom. Our results showing that these traits are mirrored in the small- and larger scale population structures of a fragmented *E. burchellii* population should further enhance our general understanding of interrelations between sex-biased dispersal and population genetics.

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Supplementary material

The following supplementary material is available for this article:

Table S1 Genetic diversity of the subpopulations. Values are given separately for each microsatellite locus.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/ 10.1111/j.1420-9101.2008.01531.x

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