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An abrupt transition in colony founding behaviour in the ant *Messor pergandei*

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Abstract. Transitions in behaviour across a continuous distribution of organisms can provide valuable information on how variation in behaviour is maintained. We used analyses developed for interspecific hybrid zones to examine geographic variation in colony founding strategy in the desert seed-harvester ant, *Messor pergandei*. Newly mated females initiate new colonies either alone (haplometrosis) or cooperatively with other foundresses (pleometrosis). The incidence of these founding strategies were surveyed across the species' range and found to occur in geographically distinct regions joined by a narrow transition zone. Foundresses collected from haplometrotic sites were more likely to display aggression and found solitary nests than foundresses from pleometrotic sites, suggesting that geographical variation in metrosis is due to genotypic divergence. Foundresses from transitional sites were generally not aggressive and tended to co-found nests in the laboratory, yet rarely formed associations in the field. Such an abrupt shift in behaviour indicates that variation in colony founding strategy is maintained by selection rather than the result of secondary contact of neutral characters. Level of aggression displays a wider cline than founding strategy and is likely under selection only when accompanied by active strategy preference.

Although species are often defined as cohesive evolutionary units (Templeton 1989), intraspecific phenotypic variation across populations is common (Ehrlich & Raven 1961; Slatkin 1987). Geographical variation can originate from fixation of alternative neutral characters due to isolation (Mayr 1942), or from geographically varying selective pressures causing local adaptation, as suggested for a variety of variable behaviours (e.g. Reichert 1981; Magurran & Seghers 1990). Testing these alternatives is not straightforward, however, as local populations may have accrued multiple phenotypic differences which prevent direct comparisons of fitness of alternative types. One solution to this problem is to examine behaviours across many isolated populations and correlate differences with variation in proposed environmental factors such as predation intensity or resource availability (Endler 1995). In this paper we propose a second approach, based on the dynamics of hybrid zones, which is applicable to continuous populations.

Hybrid zones occur when divergent populations or species interbreed across a contact zone. If alternative characters are selectively neutral, a steep cline produced by such contact will decay at a rate proportional to the rate of gene flow across the contact zone, leading to a broad phenotypic gradient relative to individual dispersal distance (Barton & Hewitt 1989). In contrast, selection acting in opposition to dispersal will prevent clinal decay and maintain steep transitions between alternative traits (Barton & Hewitt 1985). As strength of selection increases, the corresponding cline should narrow, so different traits displaying character transitions at the same location should show cline widths proportional to the level of selection acting on each trait (Hagen 1990; Sanderson et al. 1992; Nürnberger et al. 1995). Such selection estimates have been generated for a variety of characters, including morphology, plumage coloration, and life history characters (Szymura & Barton 1986; Mallet et al. 1990; Moore & Price 1993), and are supported in direct

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tests of proposed selective agents (e.g. Maccallum et al. 1995).

Although hybrid zone theory was developed for interspecific contact zones, its use is not restricted to cases where groups are highly divergent (Mallet et al. 1990). Hybrid zone analysis can therefore be a particularly useful tool for studies of intraspecific geographical variation. One such variable trait whose adaptive significance has not been resolved is colony founding behaviour in ants. During colony reproduction, females leave the colony to mate and start a new nest, either alone (haplometrosis), or cooperatively with one or more co-foundresses (pleometrosis). Cooperation may be adaptive because it reduces nest search time (Pfennig 1995) or because it confers a colony-level competitive advantage (Rissing & Pollock 1987, but see Pfennig 1995). Geographical variation in colony founding strategy has been demonstrated in several ant species, including the desert seed-harvester ant, *Messor pergandei* (formerly *Veromessor pergandei*; Ryti 1988; Rissing et al., in press). This species ranges throughout the Sonoran and Mojave deserts of the southwestern United States. In south-central Arizona, over 85% of foundresses initiate group nests (Pollock & Rissing 1985). Foundresses collected from these areas readily form associations in the laboratory without respect to relatedness, and show a preference for larger group sizes (Hagen et al. 1988; Rissing & Pollock 1988; Krebs & Rissing 1991). In contrast, only solitary nests were found at a location in southern California (Ryti 1988). Whether differences in incidence of cooperative founding result from genetically based variation in behaviour or from a facultative response to local environmental conditions is unknown.

In this study we investigated maintenance of geographical variation in mode of colony foundation in *M. pergandei*. To do this, we identified three behaviours that may influence founding decisions: the level of aggression between newly mated queens, queen preference for solitary or cooperative colony founding, and group size preference. For the first two, we assessed whether variation within and between sites was due to intrinsic differences among queens by testing foundress behaviour under uniform laboratory conditions. Group size preference was identified by analysing the distribution of foundress numbers per nest in the field. We then conducted a large scale survey of colony founding behaviour to determine the sites and widths of behavioural transitions and thus infer the strength of selection acting to maintain differences in colony founding strategy.

METHODS

We surveyed *M. pergandei* starting nests from 20 February to 10 March 1995 at 19 sites along a 200-km transect from western Arizona to south-central California (Table I). Most sites were located ca 45 km apart; sampling intervals were reduced to 3.75 km within one transitional area to increase survey resolution. At each location, we excavated starting nests and censused foundress numbers. No effort was made to control for proximity to adult nests, which has been shown to affect group size, although nests were generally further than 1 m from active entrances (Pfennig 1995). When possible, we excavated nests from natural desert areas, primarily ephemeral stream beds (washes) and other low areas. If sufficient numbers of nests (>10) could not be found in natural conditions, starting nests were also surveyed from disturbed areas with substantial bare soil which attract large numbers of foundresses (e.g. along unpaved roads).

Solitary founding in other ant species is generally mediated by aggressive behaviour towards other foundresses attempting to use the same nest site (e.g. Mintzer 1990). To test whether aggressive behaviour is associated with solitary founding in *M. pergandei*, we collected foundresses from solitary nests at 11 sites. We placed foundresses from all but one site (site 1) in pairs in covered 5.5 cm (diameter) × 1.5 cm (height) plastic petri dishes. Foundress pairs were observed for a 5-min period. Pairs were considered aggressive if fighting behaviours (biting and/or grappling) were observed at least once, and non-aggressive if no fights occurred. Sample sizes ranged from 9 to 33 pairs per site. The containers we used for foundresses from site 1 were somewhat smaller than those used for other sites; data from site 1 are illustrated but excluded from statistical analyses.

We identified regions of homogeneity in founding strategy and aggression with a simultaneous test procedure (STP) for multiple comparisons of categorical data (Gabriel 1966). This procedure

Table I. Summary statistics on foundress numbers per nest in *Messor pergandei* from study sites in south-central California to western Arizona

Site	Location	Number of nests	Mean number of foundresses per nest (range)
1	Whitewater Canyon Rd, 1 km N of I-10 (CA)	43	1.00 (1)
2	2 km N of Deep Canyon Research Station (CA)	177	1.00 (1)
3	Berdoo Canyon Rd (CA)	88	1.00 (1)
4	24 km S of Oasis (CA)	67	1.02 (1–2)
5	Aqueduct Rd, 6.8 km E of Fargo Canyon Rd (CA)	74	1.00 (1)
6	Painted Canyon Rd (CA)	42	1.00 (1)
7	Aqueduct Rd, 10 km E of Fargo Canyon Rd (CA)	64	1.09 (1–2)
8	Aqueduct Rd, 13.2 km E of Fargo Canyon Rd (CA)	73	1.36 (1–5)
9	Aqueduct Rd at Pinkham Wash (CA)	72	1.99 (1–8)
10	1.5 km N of North Shore (CA)	23	1.04 (1–2)
11	E mouth of Box Canyon (CA)	21	1.14 (1–2)
12	Frontage Rd Gas Pumping Station (CA)	124	3.67 (1–15)
13	Coachella Canal Rd, Canal crossing no. 26 (CA)	11	2.82 (1–7)
14	Maniobra Valley (CA)	13	3.77 (1–9)
15	Red Cloud Wash (CA)	17	3.24 (1–7)
16	Eagle Mountain Rd, 2.6 km N of I-10 (CA)	20	6.70 (1–18)
17	Highway 177, 23 km N of I-10 (CA)	10	2.70 (1–5)
18	Ford Dry Lake (CA)	19	3.58 (1–10)
19	Ehrenberg, AZ	36	7.39 (1–28)

uses an R × C table *G*-test of independence to identify heterogeneity within the entire sample. We subsequently tested all subsets of sites against the critical value for the entire sample to avoid inflating type I error due to repeated testing. We assembled subsets by pairing adjacent sites and re-testing for internally homogeneous groups (Gabriel & Sokal 1969). Sites A and B were considered adjacent if no other sites fell within a circle drawn between the two localities with a diameter of distance A–B (Gabriel & Sokal 1969; Seppä & Pamilo 1995). When an internally homogeneous subset was found, we added adjacent sites to the subset sequentially and re-tested. Subsets were considered maximally acceptable homogeneous regions when addition of each adjacent site produced significant heterogeneity (Gabriel & Sokal 1969).

Cooperative founding could result either from random encounters between foundresses at potential nest sites, or from active searching to locate co-foundresses. To determine whether cooperative founding results from active aggregation behaviour, we analysed field distributions of foundress numbers per nest for deviation from a truncated Poisson distribution with a *G*-test for goodness-of-fit (Cohen 1960; Johnson & Kotz 1969; Tschinkel & Howard 1983). Sample sizes were sufficient to conduct tests at three of the sites surveyed.

We estimated the shapes of clines in colony founding, aggression level and foundresses group size between regions homogeneous for solitary and cooperative colony founding. We scored founding strategy and aggression level as the frequency of the cooperative behavioural state (group founding and tolerance, respectively) across the cline. Group size was standardized to a 0–1 interval to fit the cline to a logistic model. For analytical simplicity, we estimated cline shape along a two-dimensional transect, rather than attempting to construct a three-dimensional cline map. This transect line crossed between regions at the narrowest point (100° SE from site 1). Sites were assigned the distance from the west edge of the transect line to the point at which a perpendicular line drawn from the site crossed the transect. Only those sites within 15 km of the transect were included in analyses (for haplometrosis/pleometrosis and group size clines: sites 1, 3, 5, 7, 8, 9, 12, 14, 15, 16, 18, 19; for aggression/tolerance cline: sites 3, 5, 8, 9, 12).

Clines maintained by a balance between dispersal and selection should show a sigmoidal, or logistic, shape regardless of which specific selective force is operating (Tucker et al. 1992; Barton & Gale 1993). We generated best-fit curves for clines in colony founding, aggression level and group size using the model $p = 1/\{1 + e^{-4(x-y)/w}\}$, where y = midpoint of the cline, w = width of the cline, p = frequency of the observed behavioural state, and x = distance of each site (N. Barton, personal communication).

To test whether founding preference differs among sites, we collected foundresses from a predominantly solitary founding site, a predominantly cooperative founding site, and a geographically intermediate site and allowed them to found nests in the laboratory. We compared the total numbers of haplometrotic and pleometrotic foundresses collected at each site in the nest survey to each of the other sites with two-tailed Fisher's exact tests in 2 × 2 tables to assure that sites significantly different in frequency were chosen for the experiment. To control for prior social interactions, foundresses from all sites were collected from solitary nests and used in only one trial.

To test for within-site differences, we collected additional foundresses from group nests at the site with the highest frequency of cooperative founding in the among-site comparison. Individuals were isolated from co-foundresses for at least 24 h before the start of the experiment, and were tested with individuals with whom they had no prior social contact.

For each of the three sites, we placed groups of five foundresses in 48 cm (diameter) × 23 cm (height) plastic arenas filled to 12 cm from the top with moist soil. We made five shallow refuge holes (0.8 cm in diameter × 3.0 cm in depth) in the soil at equidistant intervals around a circle one-half the radius of the arena. We placed each foundress in a separate refuge hole at the start of a trial and covered the arena with screen to prevent escape. We allowed foundresses to excavate nests over 24 h, at which time they were unearthed and censused. We compared numbers of foundresses from each location forming solitary and group nests in a 2 × 3 table with a *G*-test of independence, adjusted by Williams' correction (Sokal & Rohlf 1981). We performed post hoc pair-wise comparisons if significant table-wide differences were found. We also compared the numbers of foundresses collected from solitary and group nests within the cooperative site with a *G*-test of independence. Twenty-one of 177 foundresses in the experiment either did not occur in a nest or could not be located at the end of experiments and were disregarded in analyses. Individuals that could not be located were generally found later in the soil but could not be assigned reliably to an excavated nest hole. The remaining individuals from trials containing missing foundresses were included in analyses.

RESULTS

Solitary and cooperative colony founding occur in distinct geographical regions connected by a transition zone approximately 8.5 km wide. Two homogeneous regions were identified by the STP *G*-tests. The first region encompassed sites 1, 2, 3, 4, 5, 6 and 10, and was characterized by solitary founding ($G_{19} = 14.59$, $P > 0.5$; Fig. 1a). The second region encompassed all sites east of and including site 12 (12, 13, 14, 15, 16, 17, 18, 19; $G = 24.31$, $P > 0.1$). Over 90% of foundresses from these sites were in group nests.

The remaining sites (7, 8, 9, 11) were significantly different from regions 1 and 2, forming a zone of mixed founding behaviour connecting the two areas. This transition zone was most evident along 14 km south of the Cottonwood Mountains (sites 5–7–8–9–12; Fig. 1b). Another transition from haplometrosis to pleometrosis occurred south to northeast of the Mecca Hills (sites 6–11–12).

The geographical pattern of the Cottonwood Mountain transition zone closely matched a logistic model of cline structure ($r^2 = 0.99$, $F_{2,10} = 1785$, $P < 0.001$, logistic regression; Fig. 2), with the centre of the cline occurring between sites 8 and 9 ($y = 66.82 \pm 0.27$ km from the west edge of the transect) and a cline width of 8.65 ± 0.95 km.

The social behaviour of *M. pergandei* foundresses also differed between solitary and cooperative regions (Fig. 3). The behaviour of paired foundresses was heterogeneous across sampling sites ($G_{10} = 56.75$, $P < 0.001$). Pairs were more likely to fight if collected from solitary founding sites (sites 2, 3 and 4), and less likely to fight if collected from transitional or cooperatively founding sites (sites 5, 9, 10 and 12). One solitary founding and two transitional sites did not differ

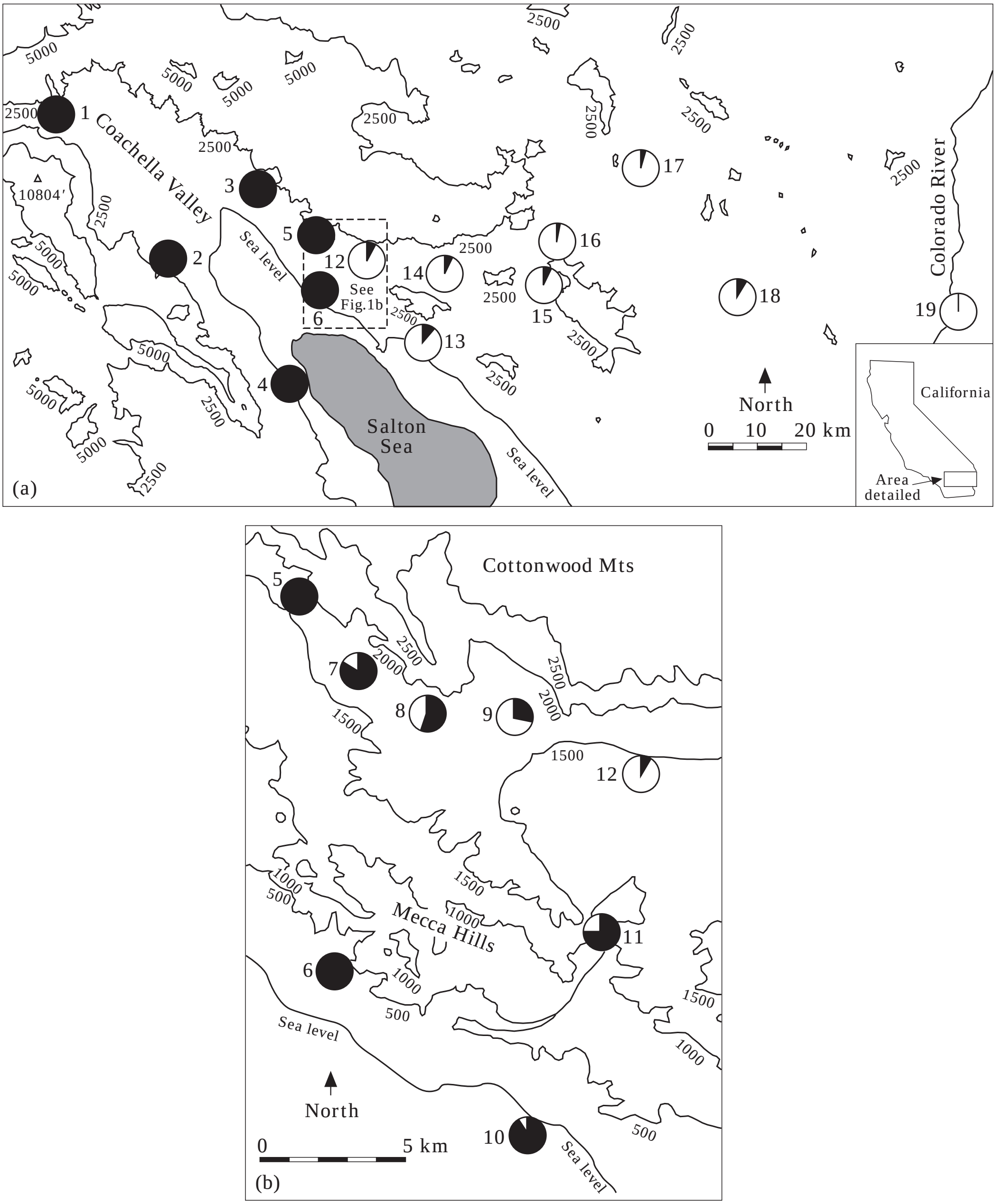

Figure 1. The geographical distribution of haplometrosis (solitary founding) and pleometrosis (cooperative founding) in the ant *M. pergandei* at sites surveyed across southern California. Black sections of the pie diagrams indicate the proportion of foundresses in haplometrotic nests. (a) Regional distribution of haplometrosis and pleometrosis. Map lines illustrate topography at 2500 ft (762.2 m) intervals. (b) Distribution of haplometrosis and pleometrosis in the transition zone. Map lines illustrate topography at 500 ft (152.2 m) intervals.

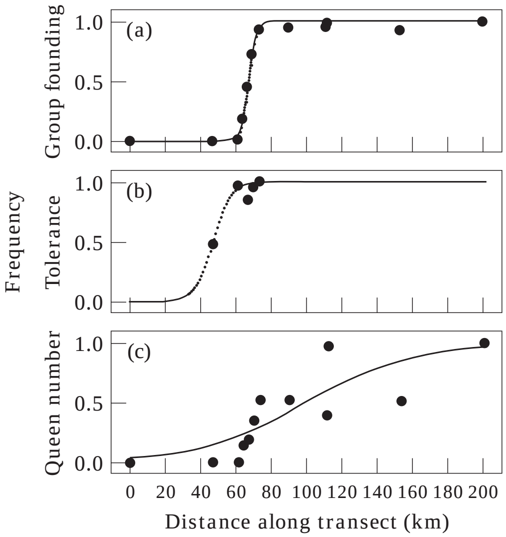

Figure 2. Behavioural clines in the ant *M. pergandei* estimated by logistic regression. (a) Transition from haplometrosis to pleometrosis ($r^2=0.99$, $N=12$ sites, $P<0.001$). The graph illustrates the relative frequency of pleometrosis across the transect. Colony founding data fit the equation $p=1/\{1+\exp(-4(x-66.82))/8.65\}$. (b) Transition from aggression to tolerance behaviour ($N=5$ sites, $r^2=0.91$, $P<0.001$). Graph illustrates relative frequency of tolerance across the transect. Behaviour data fit the equation $p=1/\{1+\exp(-4(x-46.67))/26.06\}$. (c) Shift in average queen number per nest ($r^2=0.657$, $N=12$ sites, $P<0.001$). Numbers are standardized to a 0–1 interval (range=1–7.88). Group size data fit the equation $p=1/\{1+\exp(-4(x-98.95))/121.455\}$.

significantly from either group (sites 6, 8 and 11). The shift from aggression to tolerance also matched a logistic cline model ($r^2=0.91$, $F_{2,3}=222.85$, $P<0.001$), although no sites surveyed were consistently aggressive. The centre of the behavioural cline occurred between sites 3 and 5, 20 km west of the transition from solitary to cooperative founding ($y=46.67 \pm 1.95$ km; Fig. 2). The estimated width of the social behaviour transition was 26.06 ± 8.79 km.

Within sites where the majority of foundresses occurred in group nests, comparisons of distributions of foundress numbers per nest to a truncated Poisson distribution revealed significantly different values from those expected if foundresses associated randomly (Fig. 4). Distributions were clumped, with fewer than expected numbers of nests having intermediate foundress numbers, and more nests than expected having small or large numbers of foundresses (Table I).

Logistic regression on foundress numbers per nest yielded a shallow cline in group size ($F_{2,10}=32.27$, $P<0.001$). The centre of the cline was located at 98.95 ± 14.17 km, between sites 13 and 14. Individual site data did not fit the generated cline as closely as did colony founding or tolerance behaviour ($r^2=0.66$), particularly in the eastern half of the transect (Fig. 2c). The estimated width of the cline was 121.46 ± 59.35 km.

We conducted tests for differences in founding preference with individuals from site 2 (100% haplometrotic in the field), site 10 (92% haplometrotic) and site 12 (7% haplometrotic; Fig. 1a). All sites showed significant differences in haplometrosis frequency in the field (Fisher's exact tests: site 2 versus site 10, $P=0.014$, site 2 versus site 12 and site 10 versus site 12, $P<0.0001$). Foundresses from these sites also differed in the frequency with which they founded single nests in the laboratory (G-test of independence: $G_2=50.10$, $P<0.001$). Foundresses from site 2 were significantly more likely to form haplometrotic nests than were foundresses from site 12 (Fig. 5). Foundresses from site 10, in the transition zone between haplometrosis and pleometrosis, formed haplometrotic nests at a significantly lower frequency than those from site 2 ($G=86.68$, $P<0.001$) but were not significantly different from those from site 12 ($G=3.01$, $P<0.1$). Foundresses collected from group nests at site 12 formed haplometrotic nests at nearly the identical frequency as those collected from single nests ($G=0.014$, $P>0.9$; Fig. 5).

DISCUSSION

The results of this survey confirm the existence of large-scale geographical variation in colony founding in *M. pergandei*. From south-central California to western Arizona, the range of this species is composed of two distinct behavioural regions: one in which cooperation rarely, if ever, occurs, and one in which cooperation is the dominant mode of colony foundation.

Variation in colony founding appears an intrinsic difference in strategy rather than a facultative response to regional founding conditions. In haplometrotic sites more than 20 km west of the

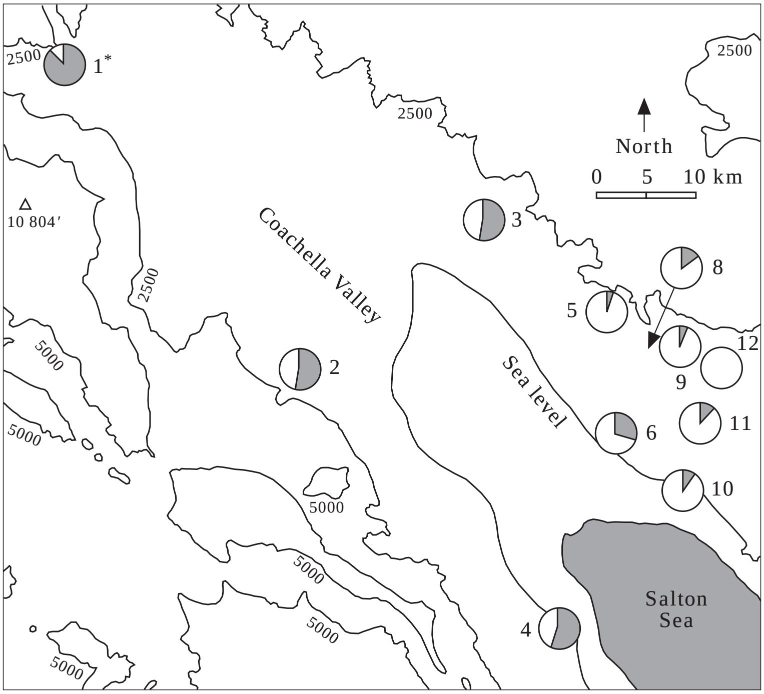

Figure 3. The geographical distribution of aggression and tolerance behaviour in the ant *M. pergandei*. Shaded sections of the pie graphs indicate the proportion of aggressive foundress pairs. Numbers in parentheses indicate the number of pairs observed from each site. Map lines illustrate topography at 2500 ft (762.2 m) intervals.

transition zone, a majority of foundresses reacted aggressively towards conspecifics and rarely co-founded a nest when given the opportunity in the laboratory. In contrast, foundresses from a highly pleometrotic location did not display aggression and readily co-founded nests under identical density conditions, even if they occurred in solitary nests in the field (Figs 3, 5).

In addition to differences in willingness to co-found, the behavioural shift from solitary to cooperative colony foundation also involves a change in aggregation behaviour. Consistent with a previous laboratory experiment (Krebs & Rissing 1991), field distributions of foundresses within nests indicate that individuals search actively for co-foundresses rather than co-operating simply by tolerating conspecifics during randomly occurring interactions. Aggregation appears to be a general feature of highly pleometrotic species, although pleometrosis can still occur, albeit with lower frequency, in the absence of active preference (Bartz & Hölldobler 1982; Tschinkel & Howard 1983; Rissing et al. 1986; Sommer & Hölldobler 1995). Foundresses may aggregate before nest excavation (Pollock & Rissing 1985), or join an established starting nest, as occurs in cooperatively founding wasps (e.g. Keeping 1990).

Intrinsic differences in behaviour can be attributable to genotypic differences (Arnold 1977; Reichert & Hedrick 1990) or environmental influences on behavioural development (review by Caro & Bateson 1986). An effect of environmental cues during development on founding behaviour has been reported in the fire ant *Solenopsis invicta* (Keller & Ross 1993). Females reared in monogynous and polygynous colonies of this species diverge in weight and founding behaviour during adult maturation, presumably due to the additive effect of pheromones emitted by queens in the mature colony. A similar colony-level effect is probably not applicable to this system, however, because cooperative colony founding does not result in polygyny in *M. pergandei* (Rissing & Pollock 1987; S. W. Rissing & J. D. Parker, unpublished data). Because mature colonies have a single queen regardless of initial founding strategy, there is no reason to suspect that the nest

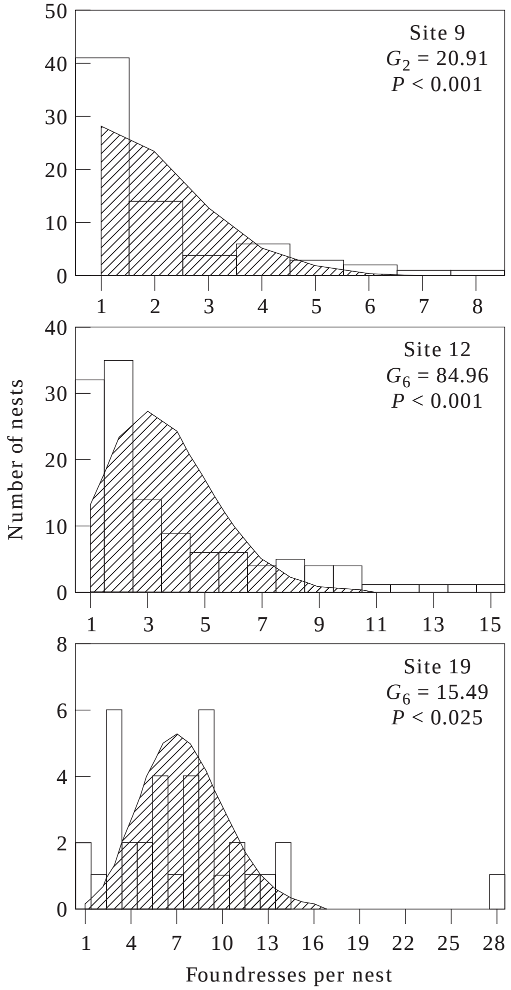

Figure 4. The distribution of foundress numbers per nest (bars) compared to a Poisson distribution truncated at 1 (shaded area) at three pleometrotic survey sites.

environment should differ between regions. It is possible that external environmental variation, such as resource or moisture availability, may affect reproductives during development, but these hypotheses could not be assessed because reproductive brood are inaccessible to study during development. Variation in post-flight cues is unlikely to affect founding strategy because significant differences in foundress behaviour were evident under controlled excavating conditions in the laboratory. We conclude that behavioural differences observed most likely indicate genotypic differences between regions.

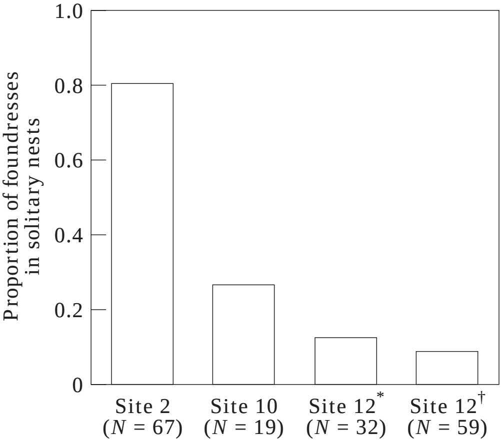

Figure 5. Proportion of *M. pergandei* foundresses forming haplometrotic nests under controlled density in laboratory arenas. *N* indicates number of foundresses tested from each site.

*Foundresses collected from haplometrotic field nests.

†Foundresses collected from pleometrotic field nests.

Colony founding strategies show a complete transition from solitary to cooperative founding over approximately 8.5 km along the east edge of the Coachella Valley. This sharp distinction exists despite the likelihood of gene flow over the transitional area. Both mature and starting nests were located at all intermediate sites across the transition zone, with freshly dug nests appearing across the entire zone after suitable flight days, suggesting that the two regions are not isolated from one another by differences in flight timing. Dispersal between sites also seems likely since *M. pergandei* mate in flight at least 20 m above ground, facilitating passive dispersal due to wind (S. Rissing, personal observation). Although dispersal distance has not been measured for *M. pergandei*, indirect genetic estimation of dispersal in *Solenopsis invicta*, which shows similar mating behaviour, suggests that movement of several kilometres or more is not uncommon (Ross & Keller 1995).

Geographical differentiation can result from secondary contact between populations possessing alternative neutral traits, or from selection maintaining differences despite ongoing mixing. The width of the transition zone between character states is a function of the average gene flow distance per generation, approximated by the standard deviation of parent–offspring distance (σ), as well as the forces operating to narrow or widen the cline. Under neutral mixing, cline width (w) depends on the number of generations since contact (T) according to Barton & Gale's (1993) equation:

$$w = 2.5\sigma\sqrt{T}$$

Assuming a dispersal range of 0.25–2 km, neutral diffusion of colony founding strategies between regions would create a cline 8.65 km wide in ca 3–190 generations. If *M. pergandei* colonies reproduce at an average of 10 years (S. Rissing, personal observation), this would make the transition zone a maximum of 1900 years old, an implausibly young age for an area where the climate has been relatively constant for at least 8000 years (Van Devender & Spaulding 1979; Spaulding & Graumlich 1986).

A more likely explanation for the narrowness of the transition zone is that selection is maintaining differentiation between non-cooperative and cooperative founding strategies. Because selection is acting in opposition to gene flow across the zone, the strength of selection required to maintain a zone of a given width is proportional to the ratio of dispersal distance to cline width (Barton & Hewitt 1989):

$$s \alpha (\sigma/w)^2$$

The specific constant used in this equation depends on the type of selection acting on the trait; however, the equations for heterozygote disadvantage, and habitat- and frequency-dependent selection are so similar that the magnitude of selection can be approximated without knowing the specific selective agent (Barton & Hewitt 1989). Application of cline width determined by this study and our estimate of dispersal distance to a habitat-dependent model of selection ($k = 3$) suggests that the transition zone in colony founding strategy could be maintained by a selection coefficient of 0.04, or a 4% decrease in mean fitness for an allele crossing the transition zone.

If geographical variation in colony founding strategy is maintained by selection, what type of selective agent is acting? Although cline structure cannot discriminate between selection regimes, two general categories of cline maintenance can be considered. First, the transition zone may correspond with an ecotone separating environments favouring alternative strategies. Two such habitat-dependent hypotheses have been proposed for this species: variation in surface exposure risk and intraspecific competition (Rissing & Pollock 1987; Pfennig 1995).

Differing levels of predation or dessication risk between regions may change the relative importance of nest-site quality versus search time, causing foundresses in high predation/dessication environments to enter a suboptimally occupied nest to minimize above-ground exposure. Co-founding would therefore be a side-effect of selection on foundresses to seek refuge underground (Pfennig 1995). The results of this study suggest that increased surface costs do not explain co-operative founding in this species. Foundresses accruing high search costs should adopt a ‘stay at any nest site’ decision rule, leading to a random distribution of foundress group sizes in the field (Nonacs 1989). The distributions of foundresses within nests in this study were not consistent with random nest joining; instead, large group sizes were consistently overrepresented. This distribution pattern may still be consistent with the refuge hypothesis if larger group nests are more easily located; however, females given a choice between a single and a three-foundress nest in the laboratory entered nests randomly, although they later abandoned single nests in favour of three-foundress nests, suggesting that group nests are not more conspicuous to searching foundresses (Krebs & Rissing 1991). These results were also evident in the laboratory arenas, in which a majority of foundresses from cooperative sites abandoned suitable nest holes to search above ground for conspecifics. If the negative consequences of above-ground exposure are important in maintaining geographical variation in nest founding behaviour, they may constrain the evolution of co-founding in high risk environments; however, an additional hypothesis would be required to explain the benefit of cooperation in the absence of such consequences.

Geographical variation in colony founding may also occur because the ratio of foundresses to quality nest sites differs across regions. Cooperation is predicted to evolve when this ratio is high because increased foundress density would raise the likelihood of competition for nest sites while simultaneously lowering the search cost associated with group formation. Joint nests tend to produce a larger initial workforce in less time (Waloff 1957; Bartz & Hölldobler 1982; Tschinkel & Howard 1983; Rissing & Pollock 1991), giving foundress associations a competitive advantage in inter-colony brood raids as well as increasing colony growth rate (Rissing & Pollock 1987; Vargo 1988; Tschinkel 1992). A field experiment designed to test for this advantage did not find evidence to support the hypothesis because brood raids were not seen among starting nests (Pfennig 1995). This study could not exclude later competitive interactions, however, because the field site was fully occupied by mature nests which quickly eliminate young nests regardless of foundress number (Ryti & Case 1988).

One way in which local foundress competition can increase is by spatial clumping of starting nests. However, spatial analyses of nest distributions at pleometrotic and haplometrotic sites indicate that nest clumping occurs across both founding types (Pollock & Rissing 1985; Ryti & Case 1988; Pfennig 1995; K. R. Helms, unpublished data).

Competition may also increase due to an increase in foundress density. This study provides modest support for density changes across the transition zone. When foundresses from a solitary founding site (site 2) were brought into the laboratory, approximately 20% formed co-operative nests, suggesting that individuals from this site may not normally experience high enough densities to encounter one another (Figs 1a and 5). The behaviour of transitional foundresses illustrates this even more clearly: under uniform density conditions, transition zone foundresses were as likely to co-found as foundresses from fully pleometrotic sites despite the low frequency of cooperative founding at this site in the field (8%, $N=23$ nests). Density differences may reflect differences in nest output between behavioural regions. Flights observed over a 1-month period at a solitary founding site (site 2) usually involved a minority of colonies on any given day, with each colony releasing fewer than 30 reproductives. In contrast, in a single flight observed at site 19, the most highly cooperative site in the survey (97% of foundresses in associations), large numbers of reproductives (often over 100 per colony) emerged from most colonies at the site.

The second category of selective hypotheses are those that affect fitness within the transition zone itself rather than in the regions on either side. The most common of these is a ‘tension zone,’ in which dispersal is balanced by reduced fitness of heterozygotes (Key 1968). Negative frequency-dependent selection has also been shown to produce a steep transition zone because dispersers across the zone move from high- to low-frequency conditions (Mallet et al. 1990). At present, nothing is known about the possible effects of hybridization or founding strategy frequency on foundress fitness. However, social behaviour may be particularly sensitive to frequency-dependent selection because aggregation behaviour forces interactions between individuals that may or may not have similar social strategies. Social incompatibility among males has been implicated as one agent maintaining a hybrid zone between two baboon species (Gabow 1975), and future research on the outcome of interactions between *M. pergandei* foundress types may reveal whether such a scenario is at work in this system.

If group formation is adaptive in at least part of the range of *M. pergandei*, the value of joining a group should be optimal at a certain group size, after which the cost of reproductive competition within the nest begins to outweigh the benefits of group membership (Bartz & Hölldobler 1982). Foundresses should therefore be able to assess group size within nests and only join nests with just below the optimal number. The over-representation of large foundress group sizes suggests that foundresses can recognize, and avoid, small groups; however, logistic regression on foundress numbers per nest indicates only weak, large-scale selection on group size, if any exists at all (Fig. 2c). If we look closer at the shape of the group size cline, however, we find that all of the points pulling the cline shallower are located in fully cooperative sites, while transitional sites show a much sharper increase in foundress number than that indicated by the regression (width = 121.46 km). Foundress group preference across the cooperative region may be masked by local density differences which would constrain an individual’s founding options. If density is as variable across years as it seems to be across sites, a simple ‘join the largest group available’ rule may be as effective as a more precise size assessment mechanism. A similar decision rule occurs in *Solenopsis invicta*, although not originally explained in an adaptive context (Tschinkel & Howard 1983).

Although colony founding strategy changes over a short geographical distance, the behavioural transition from aggression to tolerance is approximately three times wider and displaced 20 km west of the shift from haplometrosis to pleometrosis (Fig. 2b). These estimates were not as robust as those for founding strategy and queen number, as the regression fit using only five sites, four of which were located on the upper curve of the cline (Fig. 2b). The displacement of the cline westward, however, was corroborated by the *G*-test partitioning of the survey sites into an aggressive solitary founding region and a tolerant region that encompassed both the transitional and cooperatively founding sites. Differences between these two transition zones suggest that geographical variation in aggressive behaviour may be maintained by weaker selective forces than those affecting colony founding strategy. If haplometrotic foundresses rarely encounter one another, aggression level may be a selectively neutral trait, with aggression towards non-nestmates being expressed along with other worker-like behaviours (e.g. nest excavation, brood care) during colony foundation. However, individual interactions are significant if they lead to cooperation, and tolerance behaviour would be selected for when in conjunction with pleometrosis. This scenario is supported by the significant levels of foundress aggregation at site 12 at the east edge of the transition zone, despite the probability of ongoing gene flow with haplometrotic sites (Figs 1b and 4). Within the transition zone, dissociation of tolerance and aggregation through hybridization across the zone would allow tolerance behaviour to introgress into haplometrotic populations as a neutral trait. Although aggregation behaviour could not be tested in the field within the transition zone, it is likely that if the transition in colony founding corresponds with a density shift, aggregation behaviour within the low-density transition zone would be disadvantageous and would show a cline coincident with the shift in frequency of alternative colony founding strategies.

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