Social Life in Arid Environments: The Case Study of *Cataglyphis* Ants

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Abstract

Unlike most desert-dwelling animals, *Cataglyphis* ants do not attempt to
escape the heat; rather, they apply their impressive heat tolerance to avoid
competitors and predators. This thermally defined niche has promoted a
range of adaptations both at the individual and colony levels. We have also
recently discovered that within the genus *Cataglyphis* there are incredibly
diverse social systems, modes of reproduction, and dispersal, prompting the
tantalizing question of whether social diversity may also be a consequence of
the harsh environment within which we find these charismatic ants. Here we
review recent advances regarding the physiological, behavioral, life-history,
colony, and ecological characteristics of *Cataglyphis* and consider perspectives
on future research that will build our understanding of organic adaptive
responses to desertification.

1. INTRODUCTION TO *CATAGLYPHIS*: AN ANT GENUS ADAPTED TO DESERT ENVIRONMENTS

Suppose you are outside in southern Morocco. It is 3:00 PM and the sand under your feet reaches 70°C. You would probably not expect to encounter any animal in such conditions. Still, you cross paths with an ant of silvery appearance. This *Cataglyphis bombycina* forager is only 1 cm long, but she is flitting about at great speed. In fact, wherever one might be in the Palearctic desert belt, from the Sahara to the Gobi and throughout the Mediterranean basin, you are very likely to find fast-running thermophilous *Cataglyphis* ants. This genus, which includes 110 recognized species (19), belongs to a lineage that diverged from *Formica* mesic wood ants more than 60 Myr (17, 100) and may have started to radiate with the expansion of xeric habitats during the Miocene. Today, these charismatic ants are commonly found in dunes, steppes, scrubland, and anthropic areas such as public dumps or dust roads from sea level up to altitudes of 3,000 m. These individually prodigious foragers, championed by Rüdiger Wehner and coworkers over the past 50 years (140), have become a model system for studies in ecology, neuroethology, and social evolution.

2. INDIVIDUAL AND COLONY-LEVEL TRAITS ENHANCING SURVIVAL IN DESERT ENVIRONMENTS

2.1. The Ecological Advantage of Foraging at High Temperatures

Arid and desert habitats offer a range of thermal conditions that can be used successively by different ant species to reduce competition among them. The way thermal niches are partitioned depends on species dominance (32). Dominant species live in large colonies with potentially hundreds of thousands of workers and can fiercely defend food resources. In contrast, subordinate species have relatively small colonies and behave less aggressively (23). *Cataglyphis* species typically belong to the second category, with colony sizes of generally less than a few hundred workers. In arid and semiarid Mediterranean ecosystems where ant communities are rich, foraging at high temperature allows *Cataglyphis* to exploit food resources through reduced competition (37, 38). Furthermore, at more southerly latitudes, ecosystem productivity and species richness decrease, but *Cataglyphis* ants persist because high thermal tolerance allows them to escape the pressure of predation by less thermotolerant vertebrates (141). More generally, many studies have documented that subordinate ant species are more tolerant to stressful temperatures than are dominant species (10, 11, 28, 31, 34, 69, 103), suggesting the existence of a dominance-thermal tolerance trade-off (34, 61). However, the evolutionary path that led to ant communities structured by temperature remains poorly understood. Did stress tolerance evolve in response to competitive interactions or independently in arid habitats? The predominant scenario to explain the evolution of thermophily is that heat tolerance has evolved in response to competitive interactions in relatively mesic environments, permitting subordinates to use thermally unfavorable time windows primarily for competitor-free foraging and then secondarily to colonize more extreme habitats (13).

2.2. The Thermophilia Syndrome

Foraging at high temperature requires a set of behavioral, morphological, and physiological adaptations that can be expressed at the individual and colony levels. These adaptations, which together constitute what Wehner & Wehner (144) term a thermophilia syndrome, have evolved independently in *Cataglyphis* and in other thermophilous ants (e.g., *Ocymyrmex*, *Melophorus*). Among them, behavioral traits are probably the most rapidly inducible and plastic. In the hot regions of Spain and North Africa, *Cataglyphis* colonies modulate their rhythm of foraging activity to seasonal and daily
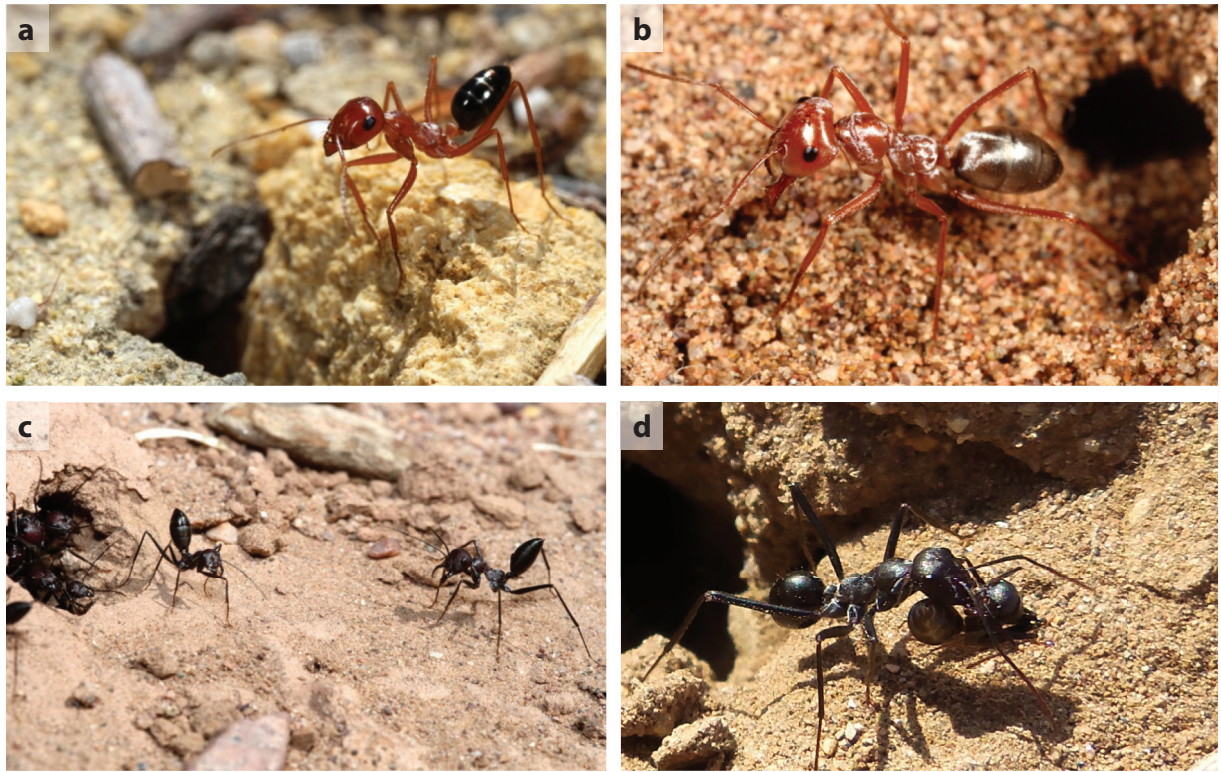
Figure 1

Cataglyphis ants show several adaptations to heat and desiccation. (*a*) *C. rosenhaueri* forager from southern Spain, whose long legs isolate its body from the hot ground surface. (*b*) Silver appearance of *C. bombycina* is produced by hairs that reflect sunrays. (*c*) Species of the *C. bicolor* group have a modified petiole for raising the abdomen, which increases maneuverability and speed. (*d*) During colony fission, *C. hispanica* workers are transported to a new nest location by a few individuals. Photo credits: (*a–c*) Fernando Amor, (*d*) Teresa Cerdá.

temperature oscillations, reverting from a unimodal rhythm of activity in the relatively cool spring to a bimodal rhythm in the more thermally stressful summer (5, 144). Individual foragers also use thermal refuges by climbing up sticks to alleviate heat stress at high ground temperatures (35, 144), a behavior that is triggered by the perception of ambient temperatures (144) and solar position (5).

Other important adaptations for heat tolerance are body size and morphology (**Figure 1**). *Cataglyphis* workers' legs are considerably longer than those of similarly sized, phylogenetically related species from mesic habitats (124). Longer legs raise them above the ground, reducing heat exposure, enhancing convective cooling (124), and increasing running speed (77) and foraging efficiency (7). Interestingly, in *C. tartessica* (formerly *C. floricola*), queens, which are less exposed to temperature than are workers, have relatively shorter legs (6). Species in the *albicans* and *bicolor* groups also have a modified petiole, allowing them to raise the gaster above the thorax (**Figure 1**). Adopted while running, this position not only protects organs from high temperatures (31) but also reduces the moment of inertia and increases maneuverability (99, 139), thus contributing to speed and convective cooling at a low energetic cost (114).

Cataglyphis species show a high degree of intra- and interspecific body-size variation. Some species, such as *C. tartessica*, have small monomorphic workers (36), whereas others, particularly in the *altisquamis* and *bicolor* groups, show marked polymorphism, which in some cases is bimodal

(35). Polymorphism may be a colony-level response to cope with high temperature. Large workers are costly to produce, but they are more heat tolerant and can prolong foraging activity into hotter hours (35, 42). Species also show marked differences in thermotolerance for ants of the same size, suggesting other thermotolerance mechanisms (35). Two independent studies have shown that the distinctive silvery appearance of *C. bombycina* is due to triangular hairs that cover the dorsal and lateral sides of the body and contribute to thermoregulation by reflecting solar radiation and increasing emissivity and heat discharge (103, 145).

Morphological thermoregulation is complemented by cellular processes such as the synthesis of heat shock proteins (HSPs), which prevent protein denaturation and maintain enzymatic activity even at elevated temperatures. In *C. bicolor* and *C. bombycina*, HSPs are synthesized at nonstressing (25°C) up to almost lethal (45°C) temperatures. This unusually high baseline production may constitute a preadaptation against sudden heat shock when a *Cataglyphis* forager exits from the relatively cool nest (64). Whether constitutive production of HSPs is a general phenomenon among *Cataglyphis* species awaits further investigation.

2.3. The Dual Function of Cuticular Hydrocarbons

Cuticular hydrocarbons (CHCs) serve a dual function in ants. They provide an external hydrophobic layer to prevent desiccation and also act in communication (71). They have a role as nestmate recognition cues (88, 137) and fertility signals (27, 54, 95, 97, 111). CHC composition is a blend of straight-chain alkanes and branched, generally monomethyl- and dimethyl-alkanes. Compared with branched alkanes, linear alkanes provide a much more effective impermeability to water (66). Methyl branching, by contrast, provides greater molecular diversity; therefore, branched alkanes may carry more information than do linear alkanes, facilitating their evolution as communicative molecules (1, 68). Moreover, the biosynthetic route of branched hydrocarbons differs from that of linear ones (18), suggesting their independent evolution. Thus, linear CHCs are well suited to preventing water loss, whereas branched CHCs meet the prerequisites for functioning in nestmate recognition. Accordingly, foragers of the desert-dwelling ant *Pogonomyrmex barbatus* have a greater abundance of linear alkanes than do their nestmate nurses that are less exposed to high temperatures (138).

The role of CHCs in nestmate recognition was shown experimentally in *C. niger* and probably occurs in other *Cataglyphis* species (88). Although *Cataglyphis* is not highly territorial and in many cases nests share foraging areas, the response to nestmate recognition cues is context dependent. In *C. fortis*, aggression toward foes is high around the nest entrance but declines rapidly with distance (82, 83). This is in accordance with *Cataglyphis* not being highly territorial and in many cases sharing foraging areas. At the population level, however [e.g., *C. niger* (119)], aggression toward neighboring nests is much greater than toward nests from distant populations, a result that is in line with the nasty neighbor hypothesis (101).

The role of CHCs in signaling fertility has also been shown in many ant species but has not been investigated in *Cataglyphis*. Nevertheless, in many ant species including *Cataglyphis*, the abundance of branched hydrocarbons allows for an idiosyncratic signal, but one that greatly reduces the waterproofing efficacy of the cuticle (67). This reduced efficacy may provide a handicap and contribute to the honesty of the fertility signal (72, 147).

2.4. Homing and Navigation

In contrast to most ant species that rely on chemical communication while foraging, *Cataglyphis* do not utilize trail pheromones, and there is little evidence for any type of recruitment (4, 115). For *Cataglyphis*, three factors may have rendered mass recruitment via trail pheromones ineffective.

Fertility signal:
a signal emitted by reproductive females (queens) intended for other females (workers and queens), resulting in reduced intracolonial conflicts

First, trail pheromones may be inefficient at high surface temperatures because they are slightly volatile and may rapidly degrade (118, 133, 134). Second, *Cataglyphis* workers are largely scavengers of sparsely dispersed food items (53), necessitating communication with nestmates only when the food item is too large to be carried alone. Third, in relatively small colony sizes, as occur in most *Cataglyphis* species, lone foraging is efficient enough for colony needs (12, 116). The second and third factors may explain why species that live in less arid environments (e.g., the *cursor* group) have not reverted to mass recruitment despite the alleviation of some ecological constraints.

A consequence of the lack of chemical recruitment is the recourse to individual strategies for orientation during foraging. As an individual, an ant forager has two main navigational strategies: path integration (PI) and environmental features. Central-place foragers when naive or with no trails to guide them need an innate strategy that is not dependent on experience. For most animals, this strategy is PI, wherein the direction and length of path segments are integrated to maintain a continuous estimate of the distance and direction back to the nest. For ants, distance information is provided by something akin to step counting for ordinary foragers (146) and optic flow for ants that are carried between nests (112). Sky cues, such as sun position and polarization patterns created by scattered sunlight, provide compass information (57, 142). To complement PI, individuals can also learn about environmental features (81) that can be used as guides to habitual foraging routes (44, 98, 120). This strategy is characteristic of experienced foragers.

PI is not precise enough to pinpoint a nest entrance, and *Cataglyphis* foragers readily learn visual and olfactory cues that define the nest position. Experimental addition of visual cues (125), odor cues (127), or both (126) has shown that ants rapidly learn the spatial configuration of sensory information around the nest entrance. Such learning is complemented by an innate strategy, shown in *C. fortis*, where foragers perceive and follow the plume of CO_2 emitted from a nest entrance (28). This reaction to CO_2 is dependent on ants having completed a route guided by PI; otherwise, they ignore any CO_2 plume they intersect to avoid homing to a neighboring nest and being attacked by its residents.

These individual strategies are important for *Cataglyphis* but are present even in ant species that show mass recruitment (81, 143). Indeed, when individual knowledge is in conflict with public information provided by trails, individuals will, in general, trust their own knowledge (69; but see 8). Because *Cataglyphis* species share a navigational tool kit with most other ants, the question becomes, how do ecological and social constraints manifest in individual orientation? Just as longer legs (see Section 2.2) lead to increased speed, desert ants also possess sensory systems that are adapted for navigation. *Cataglyphis* species living in featureless terrain, such as *C. fortis* in the North African salt pans, have a horizontal band of high-density photoreceptors across their compound eyes (148). This enables the extraction of landmark information that may be restricted to very small shrubs and bushes on the horizon of such terrain. The visual systems of desert ants also have sensory adaptations that extract celestial compass information. The dorsal rim area of the eyes of many insects contain polarization sensitive ommatidia (87). The eyes of *Cataglyphis* ants, in particular, have large dorsal rim areas, and tuning of their polarization sensitivity is precisely organized (86). Such adaptations are unlikely to be unique features of *Cataglyphis* species. However, compared with other desert ants, *Cataglyphis* show fast, very-long-distance foraging and accurate PI (28, 76), suggesting a behavioral benefit from an increased investment in sensory physiology.

Foragers of *Cataglyphis* and of many other ant species are excellent navigators. What sets *Cataglyphis* apart, in terms of navigation, learning, and memory, is a long history of studies of these species (120). Given the practicality of studying the individual foraging of *Cataglyphis* in open or semiopen habitats (140), these ants have become a model system for navigation studies. *Cataglyphis* may now be used to relate the development of specific neural structures to the organization of

foraging (128). Thus, *Cataglyphis* species are likely to be a rare system in the study of learning and memory, one in which we can study interactions among ecology, behavior, and neuroscience.

3. THE GREAT DIVERSITY OF SOCIAL TRAITS

3.1. Sociogenetics and Unusual Reproductive Systems

Cataglyphis ants are characterized by a remarkable diversity of breeding systems and modes of reproduction (**Table 1**). Phylogenetic inferences support the idea that monogyny and polyandry are the ancestral conditions and that several independent evolutionary transitions toward other breeding systems have subsequently occurred (11). For instance, in *C. niger*, tens of queens are distributed over several nests that extend over a large territory and that are interconnected by constant worker exchanges (91, 119). In addition, there is a tenfold variation in the level of polyandry across species: Although the majority of queens mate with 2 to 8 males (10), some species are monandrous, and *C. savignyi* queens mate with up to 14 males (**Table 1**). Males can also mate multiply in *C. cursor* (49).

Multiple mating by queens and males sets the stage for sexual selection. In species producing new colonies by colony fission (see Section 3.2), mating occurs near the nest entrance where workers may affect precopulatory mate choice (73, 74). Moreover, sperm competition may generate intense directional selection on sperm traits that enhance fertilization success, such as sperm production and size (16). A comparative study across 15 *Cataglyphis* species provides evidence that sperm production but not sperm length covaries with the level of sperm competition: Investment in sperm production decreases significantly with decreasing paternity frequency (10). In addition, in the highly polyandrous species *C. savignyi*, males ejaculate bundles of spermatozoa that collectively swim faster than do solitary cells (107). Such bundles, which also occur in other species, suggest that sperm cooperation (rather than sperm length) could be an evolutionary response to selection via sperm competition.

Queens of several *Cataglyphis* species conditionally use sexual and asexual reproduction for the production of nonreproductive and sexual offspring, respectively (60, 90, 106) (**Figure 2**). Although fertilized eggs yield workers, daughter queens commonly derive from thelytokous parthenogenesis (41, 108). In some species of the *altisquamis* group, asexual production of daughter queens also occurs through social hybridogenesis (51, 60, 90). All queens mate with males from a different genetic lineage and produce hybrid workers. In contrast, new queens are pure-lineage individuals produced asexually or, occasionally, from intralineage mating. As a consequence, lineages remain genetically distinct over generations. This corresponds to a unique case of hybridogenesis at the social scale, where both the maternal and paternal genomes are expressed in the worker force (i.e., the soma of the colony), whereas the new queens and males (i.e., the germ line) transmit the genetic material of the mother only. This unusual reproductive system leads to a strong caste-genotype association among females, whereby hybrid and pure-lineage eggs have lost the ability to develop into queens and workers, respectively (52). A few other forms of social hybridogenesis with strong genetic influence on caste determination have been documented in ants (122). Interestingly, more than half are from species living in arid environments, such as *Pogonomyrmex*. Whether living in harsh conditions influenced the evolution of hybridogenesis and other unusual reproductive systems in ants remains unknown. Unfortunately, the number of described cases in the literature is still too small to allow testing this kind of hypothesis.

Conditional use of sex and parthenogenesis for the production of workers and queens allows adult queens to benefit from a genetically diverse workforce without the cost of diluting the genetic material across generations. However, this should leave males with null fitness because they transmit their genes to nonreproductive workers only. Nevertheless, males may obtain some

Table 1 Diversity of social traits in *Cataglyphis* desert ants

Species groups	Species	Mating system[a]	Queen number[b]	Thelytoky[c] Workers	Queens	Colony foundation[d] Field observation/IBD	Reference(s)
cursor	*C. aenescens*	m-s	M+P	–	–	NA/No (nDNA)	45
	C. cursor (pilliscapa)	m	M	Yes	Yes	DCF/Yes (nDNA+mtDNA)	29, 40, 43, 70, 94, 106, 105, 109
altisquamis[e]	*C. mauritanica*	s-d	P	Yes	Yes	DCF/Yes (mtDNA)	60, 84
	C. velox	m-s	M/P	Yes	Yes	NA	60
	C. altisquamis	m-s	M	–	Yes	NA	85
	C. hispanica	s-d	M/M+P	Yes	Yes	NA	90, 51
bombycinus	*C. sabulosa*	m-s	M	Yes	No	ICF/No (nDNA)	123, 132
	C. bombycina	m	M	No	No	NA/No (nDNA)	93, 92
emmae	*C. emmae*	m-s	M	–	No	ICF/No (nDNA)	79
	C. tartessica	s-d	M	No	No	DCF/NA	6, 3
	C. floricola	s-d	M	No	No	DCF /NA	6
albicans	*C. theryi*	m	M	No	No	NA/No (nDNA)	93
	C. livida	m	M	No	No	NA/No (nDNA)	131
	C. iberica	–	M	No	–	NA	33
	C. cubica	–	M	No	–	NA	30
	C. ruber	–	M	No	–	NA	30
	C. albicans	–	M	No	–	NA	30
	C. rosenhaueri	–	M	No	–	NA	113
bicolor	*C. savignyi*	m	M	Yes	No	NA	91
	C. niger	m	P	No	No	NA/Yes (nDNA)	91, 119
	C. viatica	m	M	Yes	No	NA	9

Abbreviations: DCF, dependent colony foundation; IBD, isolation by distance; ICF, independent colony foundation; m, obligatory multiple mated (paternity frequency ≥2, and often ≥4); m-s, multiple-single mated (paternity frequency usually >1, with a variable minority of queens singly mated); M, monogyny (one queen); M + P, facultative polygyny (both monogynous and polygynous colonies co-occur in the same population); M/P, some populations have monogynous colonies and others have polygynous colonies; mtDNA, mitochondrial DNA; NA, no data available; nDNA, nuclear microsatellite DNA; P, polygyny (several queens); s-d, single-double mated (paternity frequency usually ≈1, with a minority of queens doubly mated) (modified from Reference 10).

[a]Mating system classes according to Reference 22. Mating frequency is determined from the arithmetic mean number of patrilines found from mother-offspring genetic combinations and/or from direct genotyping of sperm stored in the spermatheca of the queens.

[b]Queen number is determined from field observations and/or from workers genotypes.

[c]Thelytoky: occurrence of (yes) or failure to detect (no) thelytokous parthenogenesis by workers and queens (i.e., asexual production of new daughter queens). Thelytokous parthenogenesis is determined from laboratory observations (i.e., worker-produced females) and from queen-daughter genetic combinations. Worker reproduction usually occurs in queenless colonies.

[d]Mode of colony foundation as determined from field observation; because the population genetic structure is directly influenced by the mode of foundation, the presence (yes) or absence (no) of an IBD pattern at a local scale (less than a few kilometers), based on nDNA and/or mtDNA markers, is also given.

[e]All species of the *altisquamis* group sampled so far are characterized by a hybridogenetic mode of reproduction.

fitness through the occasional production of queens by sexual reproduction in some populations (55) and of queens and males by worker parthenogenesis. Indeed, workers of most *Cataglyphis* have ovaries and can produce males by arrhenotokous parthenogenesis and, in some species, females by thelytoky (**Table 1**). The production of males and females by queenless workers has been documented under laboratory conditions in the *bombycina*, *bicolor*, and *altisquamis* groups and in

Thelytoky: a type of parthenogenesis in which an unfertilized egg develops into a female individual
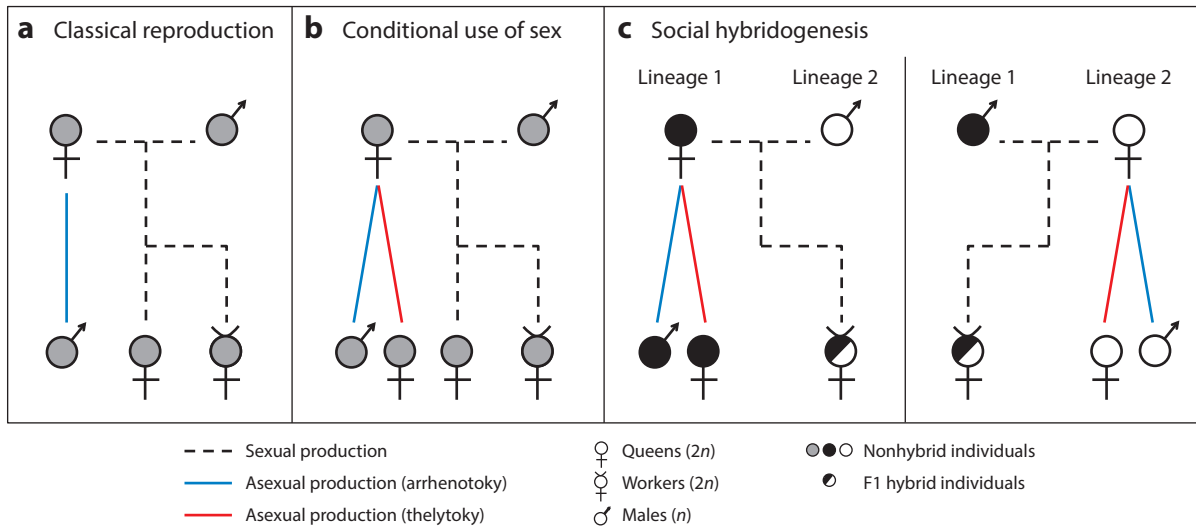
a Classical reproduction	**b** Conditional use of sex	**c** Social hybridogenesis

- - - - Sexual production ♀ Queens (2n) ⬤⬤◯ Nonhybrid individuals
——— Asexual production (arrhenotoky) ♀ Workers (2n) ◗ F1 hybrid individuals
——— Asexual production (thelytoky) ♂ Males (n)

Figure 2

Cataglyphis species show a great diversity of reproductive systems. (*a*) Classical sexual reproduction in hymenopterans: Males derive from arrhenotoky, whereas females (workers and queens) derive from sexual reproduction. (*b*) In some populations of *C. cursor*, conditional use of sex allows for the production of both males and queens by parthenogenesis, whereas workers derive from sexual reproduction. (*c*) In the *altisquamis* group, males and queens derive from parthenogenesis, whereas workers derive from interlineage fertilization.

semicaptive colonies of *C. cursor*. However, whether such eggs are laid under natural conditions and result in viable and fertile adult sexuals remains unknown.

Polyandry has multiple costs for females, including increased risk of predation and sexual infection (63, 75). Benefits that could outweigh these costs include obtaining sufficient sperm and reducing the production of diploid (sterile) males. These have not yet been supported by experimental data in *Cataglyphis* (56, 109, 132). However, *C. cursor* workers from different patrilines differ in their propensity to perform a given task (59), which may suggest that polyandry can enhance division of labor. Interestingly, in monandrous species of the *altisquamis* group, workers are hybrids of two lineages so the loss of genetic diversity within colonies due to monandry may be offset by high somatic heterozygosity in workers. Other fitness benefits of polyandry may be the reduction of queen-worker conflicts over the maternity of males and new queens (55, 132) and improved colony-level resistance to pathogens (121). This may be particularly relevant for scavengers such as *Cataglyphis* that are at risk from pathogens from dead arthropods.

Polygyny in the *altisquamis* group (and maybe in *C. niger*) results from the adoption of related queens into established nests. Here polygyny is closely linked with intralineage mating because queens mated with males from the same lineage cannot produce workers and are unable to found new colonies. Their only option is to stay in the natal nest and rely on the workforce produced by another queen (51). In some species, the risk of queen death during dispersal could have stimulated polygyny. Moreover, by increasing colony size, polygyny (and polydomy) in *C. niger* may also provide a competitive advantage against dominant species (23, 25).

3.2. Dispersal and Colony Foundation

Cataglyphis species show both modalities of colony formation that are typical of social insects, namely independent colony foundation (ICF) and dependent colony foundation (DCF; also known as colony fission) (48, 110). Under ICF, a mature colony produces numerous queens that disperse

Polydomy: the use of several above-ground interconnected nests by one colony

Dependent colony foundation (DCF): formation of a new colony by the fragmentation of an existing colony

Independent colony foundation (ICF): formation of new colonies by individual queens without the help of workers

individually by flight and start new colonies alone, i.e., breeding attempts with high dispersal and mortality. In contrast, under DCF, a mature colony splits to produce one (or a few) new colonies of significant size that disperse on foot. DCF thus yields low mortality at the cost of few breeding attempts and restricted dispersal.

ICF and DCF exemplify the trade-off between offspring number and offspring size faced by reproducing organisms balancing competition with colonization. Large offspring are better competitors, whereas small offspring are better colonizers, a dichotomy that allows the co-occurrence of species that differentially exploit the same habitat (65, 130). Overall, stable environments favor competitors, whereas environmental variability favors colonizers (2). However, habitat patchiness can select against colonizers when the risk of dispersing to an unsuitable patch is too high (21), and dispersal can also be selected against in stressful environments if colonizers are more stress sensitive, for instance, because they are smaller (102).

Deserts are patchy environments comprising limited viable habitats where colonies can establish a nest (e.g., roots of scattered plants) surrounded by extended inhospitable areas. Desert organisms are expected to be relatively bad dispersers, an hypothesis supported by the fact that desert plants show low seed dispersal relative to other plants (58, 135). Desert ants may follow the same pattern because they are comparable to plants regarding dispersal (mature colonies are sessile and offspring colonies follow a competition/colonization trade-off) (48). In ICF ants, queens are relatively poor flyers and have no knowledge of their environment when they take flight; hence, they may fail to find a favorable habitat in a desert environment. Moreover, even after finding an appropriate location, failing to dig a nest sufficiently rapidly will enhance mortality due to heat and desiccation stress. In contrast, DCF queens disperse on foot: They are more likely to remain in the same suitable patch as their mother and can count on a large workforce to excavate the nest.

Despite the above, it is still unclear whether DCF is more frequent in desert environments (48). For DCF in arid environments, data are available for three species, with further anecdotal observations. As expected, dispersal is restricted, although possibly less so for *Ocymyrmex* than for *Cataglyphis* (**Table 2**). Typically, only one offspring colony is produced, and it receives approximately a quarter to one-third of the workforce. That is, offspring colonies are very large. *C. cursor*, the northernmost and least thermophilous *Cataglyphis*, differs in producing four offspring colonies on average, which collectively receive approximately one-half of the workers. Although offspring colony size varies dramatically in this species, there is some evidence that increasing the size of the colony is favored over increasing the number of new colonies. Indeed, large mature colonies produce large offspring colonies but not more offspring colonies (40), and mature colonies seem to produce larger offspring colonies when colony density (competition) is higher (47), a trend similar to that found in the thermophilous ant *Aphaenogaster senilis* whereby colonies produce smaller colonies when colony density is low (24). In addition, workers allocated to offspring colonies are on average larger than those that remain in the mother colony (50), probably to increase the competitiveness and stress tolerance of offspring colonies because large foragers are more robust and efficient (see Section 2.2). Overall, these data suggest that desert ant species reproducing through DCF maximize the competitiveness and tolerance of their offspring colony. Yet, whether DCF is more common in *Cataglyphis* than in related species from mesic habitats and whether the same pattern occurs across different genera of desert ants are unclear.

3.3. Population Genetic Structure

The large diversity of reproductive systems, social organizations, and modes of colony foundation in *Cataglyphis* can translate into variation in the strength of evolutionary processes such as migration and genetic drift. For instance, in species with monogyny and single mating, the relatively

Table 2 Characteristics of dependent colony foundation (DCF) in *Cataglyphis* and in other desert-adapted genera

Species	Number of DCF observed	Number of new colonies (mean ± SD; range)	Number of workers in new colonies (mean ± SD; range)	Resource allocated to new colonies (% of mother colony's workforce)	Dispersal distance (m) of new colonies (mean ± SD; range)	Reference(s)
C. cursor	21	4.0 ± 1.3; 1 to 6	186 ± 214; 30 to 1,284	53 ± 23[a]	7.1 ± 5.3; 0.9 to 31.2	40, 94
C. tartessica	34	1	99 ± 7	33.6	7.7 ± 0.9; 1.9 to 28.4	6
C. mauritanica	1	1	–	–	30	84
Ocymyrmex picardi	1	1	108[b]	23	150	20
Ocymyrmex robustior	1	1	–	30	40	20
Proformica longiseta	22 (4 colonies excavated)	1.2 ± 0.6 (1 to 3)[c]	262 ± 42; 69 to 536	23 ± 9	3.25 ± 0.33; 0.45 to 7.2	62

[a]Resource allocated to new colonies could be determined in only 9 out of 19 colonies. The mother colony could not be identified in the remaining colonies because queen replacement coincided with colony fission, i.e., the mother queen had been replaced by a young queen indistinguishable from young queens heading new colonies (40).
[b]These included 20 ergatoid queens that were virgin and functioned as workers, as is typical in *Ocymyrmex* (20).
[c]Twenty colonies produced one new colony each, and two colonies produced three new colonies each.

low number of reproductive individuals in a population could enhance genetic drift and increase inbreeding, magnifying the effect of the low effective population sizes of eusocial hymenoptera (117). This effect may even be enhanced by the low carrying capacity of *Cataglyphis* desert environments. However, inbreeding is rare in *Cataglyphis* except in queens of species with thelytoky (60, 90, 106). The evolution of thelytoky could enhance inbreeding (39), reduce genetic diversity, and limit adaptive responses to environmental changes (15, 80).

In ants, breeding systems are often associated with female dispersal. Monogyny is often associated with ICF and polygyny with DCF (26), although there are many exceptions to this rule, particularly among *Cataglyphis* species. Because DCF limits female dispersal, it may enhance population viscosity (48), thereby affecting the evolution of altruistic behaviors (89, 104, 129) and life-history traits such as reproductive allocation (96). During DCF, restricted dispersal concerns females only. Thus, a pattern of population viscosity can occur in maternally inherited genes but not necessarily in nuclear genes because males generally fly and can mitigate the effect of restricted female dispersal (48). A pattern of isolation by distance for nuclear and/or mitochondrial DNA markers is shown for two *Cataglyphis* species with DCF (*C. cursor* and *C. mauritanica*) but not for two other species with ICF (*C. sabulosa* and *C. emmae*) (**Table 1**), thus supporting theoretical expectations. Yet, the expected connection between the mode of colony foundation and the pattern of population viscosity at local scales may be attenuated if ICF females remain near the mother nest (136) or if male dispersal and frequent nest relocation reduce population viscosity of DCF species.

At larger spatial scales (>10 km), dispersal may be limited for both ICF and DCF species (48). At this level, landscape connectivity may strongly impact population genetic structure, especially in stressful environments. For instance, in *C. cursor*, the distribution of genetic variability varies

Population viscosity: a spatial pattern of population genetics where genetic differentiation increases with increasing geographical distance

across habitats that differ in patchiness (43). Whatever the relative importance of geographical barriers and of restricted dispersal abilities, high genetic differentiation has been detected within populations over relatively short distances (43, 78, 79). This sets the scene for high levels of genetic and phenotypic divergence among populations that could be driven by either drift or natural selection and could ultimately lead to allopatric speciation. For instance, in southern Spain, molecular evidence suggests that recent (<1 Myr) allopatric speciation between *C. floricola* and *C. tartessica* occurred without ecological niche segregation (78). The relatively restricted range of some *Cataglyphis* species and their absence from most Mediterranean islands also support the idea of restricted dispersal, which, together with their thermophilous foraging activities, suggests *Cataglyphis* species likely retain a strong genetic signal of the impact of long-term environmental changes in the region in which they live. *Cataglyphis* species could therefore be very informative for phylogeographic studies to infer the historical dynamics of biological refuges during Pleistocene glaciation.

4. CONCLUSION AND FUTURE DIRECTIONS

Paleodeserts provide some of the harshest conditions of heat and dryness on Earth. However, some animals and plants take advantage of extreme climate to avoid competitors or predators. Adaptations in *Cataglyphis* are mainly quantitative exaggerations of traits that are present in most ant species, rather than qualitative innovations. In contrast, how climate and, more generally, environmental conditions shape the diversity of social systems observed across *Cataglyphis* species is unknown. Paleodeserts are relatively unstable, comprising patchy habitats that may both select for specific modes of reproduction and open opportunities for the evolution of unusual social systems. The degree of plasticity and the future evolutionary trajectory of these social traits are difficult to predict. Some traits may be evolutionary dead ends that limit the capacity of a species to adapt to new environmental conditions. Major limitations for our understanding of the evolution of *Cataglyphis* ants are the lack of a comprehensive phylogeny and many ambiguities concerning species delimitation and identification. Provided these problems are solved, *Cataglyphis* species may become a wonderful model system for integrative studies of species responses to desertification. Moreover, highly collaborative studies should be undertaken to compare the evolution of *Cataglyphis* with that of other desert-dwelling ants from other continents.

SUMMARY POINTS

1. Harsh environments drive unique ecological adaptations, allowing organisms to take advantage of extreme conditions to reduce competition and predation pressure.

2. *Cataglyphis* ants possess several adaptations at the individual and colony levels to increase thermotolerance and overcome the limitations of chemical communication in hot environments.

3. *Cataglyphis* ants also exhibit great diversity in social organization and mode of colony founding. The functional connection between such diversity and harsh environmental conditions is unclear.

4. Integrative and comparative studies between *Cataglyphis* and other desert-dwelling ants from other continents may shed light on the impact of environmental conditions on the evolutionary trajectory of social organisms and allow a better understanding of species responses to desertification.

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