

Evolution of Novel Mosaic Castes in Ants: Modularity, Phenotypic Plasticity, and Colonial Buffering

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ABSTRACT: Many ants have independently evolved castes with novel morphology as well as function, such as soldiers and permanently wingless (ergatoid) queens. We present a conceptual model, based on modularity in morphology and development, in which evolutionary innovation is facilitated by the ancestral ant polyphenism of winged queens and wingless workers. We suggest that novel castes evolved from rare intercastes, anomalous mosaics of winged queens and workers, erratically produced by colonies through environmental or genetic perturbations. The colonial environment is highly accommodating and buffers viable intercastes from individual selection. Their cost is limited because they are diluted by the large number of nestmates, yet some can bring disproportionate benefits to their colonies in the context of defense or reproduction (e.g., wingless intercastes able to mate). Useful intercastes will increase in frequency as their morphology is stabilized through genetic accommodation. We show that both soldiers and ergatoid queens are mosaics of winged queens and workers, and they are strikingly similar to some intercastes. Modularity and developmental plasticity together with winged/wingless polyphenism thus allow for the production of highly variable mosaic intercastes, and colonies incubate the advantageous mosaics.

Keywords: development, polyphenism, caste, intercaste, soldier, ergatoid queen.

Introduction

Modularity is a key feature of biological systems, from molecular complexes to whole organisms. A module is a set of traits that are internally integrated but relatively less linked to other modules (Wagner 1996; Rieppel 2005; Klingenberg 2008). Accordingly, traits belonging to different modules can evolve independently, and greater modularity could confer greater evolvability (Yang 2001; West-Eberhard 2003; Schlosser and Wagner 2004). Holometabolous insects show many layers of modularity, including imaginal discs, seg-

mental organization, and distinct larval and adult forms. Polyphenic insects exhibit an additional level of modularity: alternative adult phenotypes express different modular traits. Ants probably represent the most extreme example, with queen and worker female castes differing markedly in traits associated with two functions: flight and reproduction.

Polyphenism is a discrete case of a more general phenomenon known as phenotypic plasticity. The ability of a genotype to produce a variety of phenotypes in response to environmental variations is generally considered to be an adaptation. However, the fact that this plastic response to the environment can itself enhance the evolutionary potential of organisms has only recently been pointed out (reviewed in Pfennig et al. 2010).

Surprisingly, modularity in the polyphenic context of ant castes has received little attention (but see Miyazaki et al. 2010; Yang and Abouheif 2011), although it could have increased evolvability in this taxon. Here we explore the implications of such polyphenic modularity on the evolution of novel castes (novelty as reviewed in Moczek 2008; caste used in a strictly morphological sense; see Peeters and Crozier 1988). Novel castes, such as soldiers and permanently wingless queens, occur in numerous unrelated lineages. Their phenotypes are highly distinct from that of the winged queens and workers, and they perform distinct functions (e.g., colony defense, reproduction without solitary foundation of new colonies). We first show that both soldiers and wingless queens are mosaics of the standard worker and winged queen castes, uncoupling the modular traits associated with flight and reproduction. We then propose that intercastes, anomalous queen-worker mosaics produced erratically, are the first step toward the repeated evolution of these novel castes. Our proposed evolutionary mechanism is based on the accumulation of unexpressed genetic variation at loci that control the switches toward queen or worker pathways during larval development. Under strong environmental or genetic disturbances, this cryptic genetic variation becomes expressed (Rutherford 2000)

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and leads to the production of highly variable mosaic adult phenotypes (intercastes) combining queen and worker traits. Importantly, colonial life facilitates the survival and selection of intercastes. If some anomalous phenotypes bring benefits to colonies, then the propensity to produce them can be selected for because of their genetic background. Through such selection, developmental anomalies can become fully functional novel castes.

Modularity of Ant Castes

Modular Phenotypes Result from Modular Gene Expression

Over the course of embryonic and larval development, genes are expressed in networks with temporal and spatial specificities, yielding an adult phenotype that is an assemblage of modular traits (Von Dassow and Munro 1999; West-Eberhard 2003, pp. 56–88; Yang and Abouheif 2011). Following Yang (2001), modules are defined as phenotypic traits produced through underlying developmental processes. Two components are subject to selection: the switch mechanism, which regulates trait frequency, and the form of the expressed trait itself, which affects efficiency and functionality. The most important feature of modular development is tight internal integration, which contrasts with a high independence from other modules. This independence is of course relative; modular traits are more or less connected together. Metamerism in arthropods is an obvious example of modularity. Disassociation between developing segments has enhanced the evolution of segment-specific characteristics (Carroll et al. 2001; Prud'homme et al. 2011). Holometabolous insects offer great opportunities for studying the interconnection between the developmental and morphological aspects of modular traits. For example, larvae have imaginal discs, well-defined clusters of cells that develop into various adult body parts during metamorphosis (reviewed in *Drosophila*; Morata 2001). The concept of modularity has been applied to development and the morphology of monomorphic individuals. Here we extend it to polyphenic social insects with alternative versions of certain modular traits. Accordingly, for any body part or organ, only one version of a modular trait is expressed in a focal individual, although two or more versions of this trait occur across the colony.

Ant Castes Consist of Both Shared and Caste-Specific Modular Traits

Queen and worker castes in ants show more extreme differences than any other social hymenopterans. These differences result from distinct pathways of larval development in females. At a critical switching point, larvae

become sensitive to environmental factors that can direct them into either of two alternative developmental pathways with differential gene expression. Environmental determinates can be abiotic, such as temperature, and biotic, such as nutrition and pheromones (Beldade et al. 2011). Reinforcement through nutrition provided by workers ultimately leads to metamorphosis into distinct adult castes.

Queens typically have a large thorax, underlying both aerial dispersal and metabolic reserves for independent colony foundation, as well as large ovaries specialized for augmented egg production. In contrast, workers have a smaller and simpler wingless thorax, together with reduced ovaries (reviewed in Peeters and Molet 2010). The differences and similarities between queens and workers can be described in terms of two kinds of modular traits. Shared traits, such as legs and antennae, are very similar in both castes. In contrast, caste-specific modular traits occur as distinct versions in workers and queens (fig. 1a), such as parts of the flight, vision, and reproductive apparatus. The wingless workers have a reduced thorax in which most sclerites are fused, while queens have wing muscles and a thorax with the many articulated sclerites needed for flight. Eye size and ocelli, both important for flight in winged queens, are respectively smaller and nonfunctional or absent in workers (Bolton 1994; Krapp 2009). Queens often have more ovarioles than workers, and workers typically lack a functional spermatheca and are thus unable to store sperm (Gobin et al. 2006).

Imaginal discs give rise to various caste-specific modular traits (fig. 1a, 1b). For instance, the genital disc produces the oviducts and spermatheca, while the gonad primordia form the ovaries (e.g., *Drosophila*; Epper 1983). The antennal disc produces the eyes and ocelli (e.g., *Cyrtodiopsis dalmanni*; Hurley et al. 2002). Last, the anterior and posterior wing discs produce wings and parts of the articulated thorax, while their associated myoblasts form the flight muscles in queens but not in workers (e.g., *Drosophila*; Raghavan et al. 1996). The reproductive, vision, and flight apparatuses are highly independent of each other and are the highest-level caste-specific modular traits. Each can be split into lower-level modules showing various degrees of independence; for example, the reproductive apparatus includes ovarioles and the spermatheca (fig. 1a, 1b). The gene sets responsible for imaginal disc development are almost unstudied in ants, except for the wing discs. Portions of the gene sets in *Drosophila* are active in winged queens but not expressed in workers (Abouheif and Wray 2002). Another significant difference between ant castes is body size, ranging from small to enormous (see “Large Queen-Worker Dimorphism in Ants Allows a Greater Range of Intermediate Mosaics”). The mechanisms responsible for size determination in insects are not well understood, but they clearly involve regulation at both a

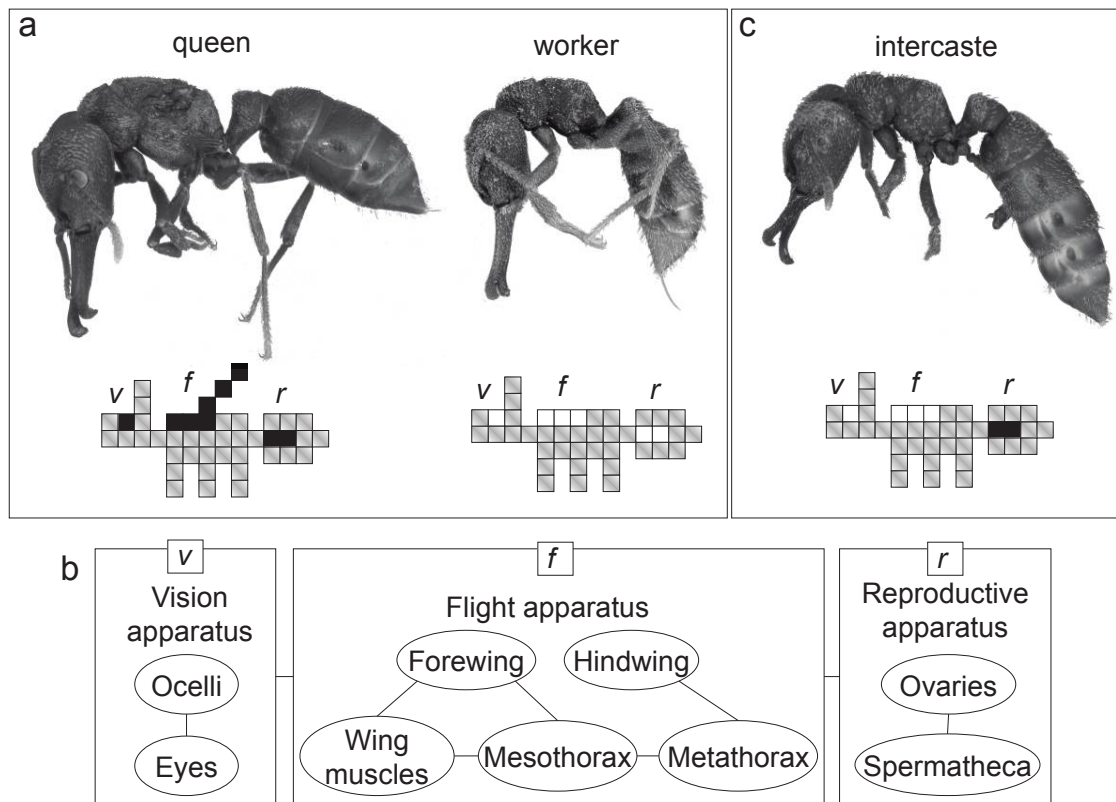


Figure 1: Modularity in ant castes (winged queens and workers) and intercastes. *a*, Dealate queen and worker of *Myrmica rogeri*, a poneroid with a relatively small degree of dimorphism. Ant queens shed wings after mating. Below images are schematic representations of shared (gray) and caste-specific (black, queen; white, worker) modular traits. *b*, Modular traits are embedded within and connected to one another. *c*, Intercaste of *M. rogeri* combining versions of traits that are specific to winged queens and workers. This individual had ovaries that resemble those of a queen (the presence of a spermatheca was not checked), but its vision and flight apparatus were reduced, as in workers. Photographs courtesy of April Nobile and <http://www.antweb.org>, holders of copyright.

large scale (whole body) and a smaller scale (organs, tissues; Mirth and Riddiford 2007). In ants, caste-specific modular traits likely include information about growth, resulting in distinct adult sizes.

Novel Ant Castes Are Mosaics of Queen-Specific and Worker-Specific Modular Traits

Wingless (Ergatoid) and Short-Winged Queens

Permanently wingless “ergatoid” queens reproduce in 55 genera (out of 295) scattered across the ant phylogeny (Peeters 2012). The thorax of ergatoid queens is typically reduced and often extremely so, similar to workers. This is associated with the absence of wing muscles. However, their reproductive apparatus consists of functional ovaries and spermatheca, similar to winged queens. Winged

queens may or may not be retained in species with ergatoid queens. Ergatoid queens differ from gamergates, which are true workers that mate and reproduce in about 200 species (Monnin and Peeters 2008). With only a few exceptions, both ergatoid queens and gamergates cannot found colonies independently, and they depend on nestmate workers during colony foundation (Peeters and Molet 2010).

Short-winged (brachypterous) queens are also flightless reproductives occurring in 15 genera belonging to six subfamilies (Peeters 2012). Wing muscles are generally absent, and the thorax is less simplified than in ergatoid queens. Like ergatoid queens, short-winged queens usually rely on nestmate workers during dependent colony foundation. Some species produce short-winged queens only, but others produce them together with fully winged queens (table 1).

Table 1: Assessment of the mosaic nature of novel ant castes: wingless (ergatoid) queens, short-winged queens, and soldiers

Species	Thorax	Abdomen	Ovaries	Spermatheca	Body size	Function	Reference
Wingless and short-winged queens:							
<i>Aphaenogaster senilis</i>	AQ	AQ	AQ	AQ	AQ	Reproduction	Tinaut and Ruano 1992
<i>Cardiocondyla batesi</i> [†]	AQ	AQ	AQ	AQ	AQ	Reproduction, independent colony founding	Heinze et al. 2002
<i>Eutetramorium mocquerysi</i>	W	W	AQ	AQ	W	Reproduction, brood care, foraging	Heinze et al. 1999b
<i>Harpagoxenus sublaevis</i> [‡]	AQ ↔ W	AQ ↔ W	AQ	AQ	AQ ↔ W	Reproduction	Buschinger and Winter 1975
<i>Leptothorax</i> sp. A ^a	AQ ↔ W	AQ ↔ W	AQ ↔ W	AQ ↔ W	AQ ↔ W	Reproduction, other?	Heinze and Buschinger 1987
<i>Monomorium leae</i> [‡]	AQ ↔ W	AQ	AQ	AQ	AQ	Reproduction	Fersch et al. 2000
<i>Monomorium opacior</i>	AQ	AQ	AQ	AQ	AQ	Reproduction	Bolton 1986
<i>Myrmecina nipponica</i> [‡]	AQ ↔ W	AQ ↔ W	AQ	AQ	AQ ↔ W	Reproduction, other?	Ohkawara et al. 1993
<i>Mystrium oberthueri</i>	W	W	AQ	AQ	W	Reproduction, brood care	Molet et al. 2009
<i>Odontomachus coquereli</i>	W	AQ	AQ	AQ	AQ	Reproduction	Molet et al. 2007
<i>Pogonomyrmex huachucanus</i>	W	AQ	AQ	AQ	AQ	Reproduction, independent colony founding	Johnson 2010
<i>Technomyrmex brunneus</i> [‡]	AQ ↔ W	AQ ↔ W	AQ ↔ W	AQ	AQ ↔ W	Reproduction, brood care, foraging	Tsuji et al. 1991
<i>Vollenhovia emeryi</i> [†]	AQ	AQ	AQ	AQ	AQ	Reproduction	Ohkawara et al. 2006
Soldiers:							
<i>Acanthomyrmex ferox</i> [‡]	W	AQ	AQ	W	AQ	Defense, trophic eggs, cut seeds	Gobin and Ito 2000
<i>Camponotus (Colobopsis) nipponicus</i> [‡]	W	AQ	AQ	?	AQ	Defense (block entrance), replete	Hasegawa 1993a, 1993b
<i>Cephalotes persimilis</i> [‡]	W	AQ	?	?	AQ	Defense (block entrance)	Powel 2008
<i>Crematogaster smithi</i> [†]	W	AQ	AQ	W	AQ	Trophic eggs only	Heinze et al. 1999a
<i>Pheidole</i> spp. ^a	W	AQ	?	?	AQ	Defense, cut insects, mill seeds	Wilson 2003

Note: Phenotypes vary across lineages, but they are generally intermediate between winged queens and workers. Four caste-specific modular traits are considered here: external morphology of thorax, size of abdomen, ovaries, and spermatheca. Body size is also included. Different types of combinations allow for different functions. W or AQ indicates whether morphology is closer to worker or conspecific/congeneric winged queen, respectively. AQ ↔ W indicates variable morphologies. Species were chosen to illustrate the diversity of mosaic combinations. Photographs of most of these lineages are in figure A1, available online.

^a Indicates species where winged queens occur.

The concept of modularity is well illustrated by the head, thorax, abdomen, and associated organs in ant queens that are winged, wingless, or short winged. Wing growth is halted in ergatoid queens without a decrease in ovariole numbers, which is evidence of the independence of modular traits (Yang 2001). Even more striking, ergatoid queens of *Megaponera foetens* have a reduced thorax, similar to workers, but many more ovarioles than do workers (32 vs. 13–15 per ovary) and a spermatheca, as in winged queens (Villet 1990; Peeters 1991). Ergatoid queens are thus developmental recombinations of the queen version of reproductive traits and the worker version of thoracic traits: ergatoid queens are a mosaic caste (examples in table 1). Independence of modular traits has also been shown during larval development in *Myrmecina nipponica*. Winged queens are typical in this species, but ergatoid queens reproduce in some colonies from two populations. A histological study of the developing larvae of ergatoid queens revealed their mosaic nature: gonads start devel-

oping at the same time as those in larvae of winged queens, but both the fore- and hindwings stop developing during the last instar, as in larvae of workers (Miyazaki et al. 2010).

The mosaic phenotypes of ergatoid queens are highly diverse (table 1; fig. A1, available online), partly because they have evolved convergently in unrelated lineages. For example, ergatoid queens in different species of the *Monomorium salomonis* group are much bigger than workers and have a spermatheca as well as large ovaries, similar to winged queens, but the thorax ranges from winged queen-like to worker-like externally (Bolton 1986; R. Keller and C. Peeters, unpublished manuscript). In contrast, ergatoid queens of both *Ocomyrmex* and *Eutetramorium mocquerysi* are externally indistinguishable from workers, including body size, but they have more ovarioles and a spermatheca (Bolton and Marsh 1989; Heinze et al. 1999b).

Soldiers: Mosaic Nonreproductive Caste

Various ant species have more than one morphological type of sterile adults, which is unknown in other social Hymenoptera. In addition to standard workers that predominate in colonies, bigger individuals function for guarding, food storage (repletes), or seed milling (Hölldobler and Wilson 1990). These bigger adults have evolved across lineages, which accounts for much heterogeneity in form and function. However, two kinds can be distinguished. First, in species where workers are highly polymorphic in size, the bigger (major) workers follow the same allometric growth rules as standard workers (fig. A2, available online; Wheeler 1991). Second, in fewer species, the bigger individuals, typically with enlarged heads, follow new growth rules distinct from workers'. The term "soldier" has been applied to both kinds and thus has an equivocal meaning in the literature, as illustrated by two definitions. Wheeler (1910, p. 97) described soldier as "characterized by a huge head and mandibles, often adapted to particular functions (fighting and guarding the nest, crushing seeds or hard parts of insects), and a thoracic structure sometimes approaching that of the winged queen in the development of the sclerites (*Pheidole*)."

Dornhaus and Powell (2010, p. 226) defined soldier as "a worker phenotype that is morphologically specialized for the role of colony defence." Thus, there is broad agreement about the importance of morphological adaptations and associated behaviors but disagreement about the inclusion of major workers and the exclusion of functions other than defense. In this discussion, we consider soldiers as a discrete caste of large individuals that are "neither worker, nor queen," after Heinze et al. (1995), irrespective of behavioral repertoires. In this more restrictive sense (major workers are excluded), soldiers are found in at least 15 genera scattered across ants (C. Peeters and F. Ito, unpublished data).

Distinctive head morphology generally differentiates soldiers from workers (fig. A1). However, as a result of independent evolution and idiosyncratic selective contexts, a broad diversity of body form and function is evident across genera. *Pheidole* soldiers have disproportionately large head capsules that hold enlarged muscles to power the mandibles, and across species mandibles can be long and sharp or heavy and blunt (Wilson 2003). In *Acanthomyrmex ferox*, soldiers cut seeds with their heavy mandibles, but they also lay trophic eggs, which gives them the function of repletes (Gobin and Ito 2000). In *Camponotus (Colobopsis)* and *Cephalotes*, the head is highly modified to plug nest entrances in wood (Hasegawa 1993b; Powell 2008); in *Camponotus (Colobopsis)* and *Pheidole*, the enlarged abdomen stores water and fat that are regurgitated to workers (e.g., Tsuji 1990; Hasegawa 1993a).

In species where soldiers function as both repletes and guards, these behaviors switch with age. In *Crematogaster smithi*, soldiers never behave as guards, and their head is not enlarged, but they have large abdomens with many ovarioles that convert food into trophic eggs to be given to nestmates during periods of reduced foraging (Heinze et al. 1995, 1999a). Interestingly, either major workers or soldiers can carry out the same tasks in distinct species. For example, food storage is done by major workers in *Myrmecocystus* and *Proformica* and by soldiers in *Camponotus (Colobopsis)*; (Rissing 1984; Hasegawa 1993a).

Soldiers across all species studied exhibit a mix of queen and worker traits (table 1). This mosaic nature was already suggested in Wheeler's (1910) definition above. The abdomen is usually enlarged relative to workers, reaching the same size as queens' in some species. In *A. ferox* and *C. smithi*, this reflects a larger number of ovarioles than in workers, and such soldiers produce trophic eggs. However, there is no spermatheca; thus, the queen version of the reproductive apparatus is only partly expressed in soldiers. Parts of the queen flight apparatus can also be expressed in soldiers, with thoracic size and sclerite fusion varying between lineages. The head is often bigger in soldiers than in workers and often similar to queens'. In *Cephalotes*, soldiers and queens share a cephalic shield (Powell 2008). Hence, caste-specific modular traits are combined in different ways according to species. Queen characteristics can allow soldiers to be bigger, which is appropriate for both defense and nutrient storage.

The mosaic nature of soldiers can also be revealed by studying their development, which reveals both worker and winged queen pathways of expression for modular traits. *Pheidole* worker larvae—and those of most other ants—develop vestigial imaginal wing discs (Brian 1955; Wheeler and Nijhout 1981; Abouheif and Wray 2002). What distinguishes the wing discs of *Pheidole* soldier larvae from other ants described to date is that they initially show rapid growth, equivalent to the rate of queen discs. Thus, a portion of the wing program that is normally expressed in queen larvae runs for a short time in developing soldiers (Wheeler and Nijhout 1981; Sameshima et al. 2004). The set of genes expressed in the anterior wing disc resemble that in winged queen larvae, whereas the gene set expressed in the posterior wing disc is similar to that in worker larvae (Abouheif and Wray 2002). Queen and worker traits thus develop together in larvae destined to be soldiers, making them a mosaic caste.

Assessment of Mosaics: Modular Traits Are Not Always Distinct

Mosaic phenotypes are easy to detect in some species because they recombine complete high-level modular traits

from the standard worker and winged queen castes. For example, soldiers of *Cephalotes* have a queen-like head, whereas ergatoid queens of *Eutetramorium* have a thorax identical to workers' (fig. A1). In other species, developmental recombination of lower-level modular traits results in mosaic phenotypes that look intermediate between winged queens and workers. For instance, ergatoid queens in many species retain distinct thoracic sclerites: although they are not articulated as in winged queens, they are not fused as in workers, for example, *Odontomachus* (fig. A1). Ovariole number in ergatoid queens is easy to compare: in some species, it is intermediate between winged queens and workers, and in others, it is the same as in winged queens. In species where the mosaic origin of morphology is blurred in adults, gene expression and morphology need to be studied during larval development.

Anomalous Mosaics Produced Erratically Are Buffered by Colonies

An Extensive Record of Anomalies in Ants: Gynandromorphs and Queen-Worker Intercastes

One kind of anomaly found in many insects is sexual mosaics, called gynandromorphs. In ants, gynandromorphs are especially common or perhaps especially noticeable because of strong sexual dimorphism, and they have been described in more than 40 species (Wheeler 1937; Jones and Phillips 1985). Bilateral mosaics of the head seem to be most frequent and often exhibit specific and repeatable patterns, which is consistent with the modular nature of both larval development and adult phenotypes (Yang and Abouheif 2011). Environmental stress, such as temperature shock (in Hymenoptera; Berndt and Kremer 1982), and genetic incompatibilities in hybrids (in butterflies; Scriber et al. 2009) have been associated with the production of gynandromorphs. This highlights the fundamental interchangeability of genomic and environmental influences on development (West-Eberhard 2003).

In addition to gynandromorphs, anomalous mosaics combining worker-like and winged queen-like traits called intercastes have long been known, especially in ants (Wheeler 1905, 1937; Hall and Smith 1953; Brian 1955; Passera 1976; Peeters 1991; fig. 1c). Intercastes are intermediate between winged queens and workers in both size and morphology. They can vary within species, ranging from very queen-like in thorax structure—though wings are absent or vestigial—to nearly worker-like (fig. A3, available online). Similarly, the reproductive organs vary. In *Temnothorax nylanderi*, Plateaux (1970) described an exceptionally large series of intercastes collected from many colonies reared in the laboratory over many years.

Intercastes varied in size and had diverse morphologies with various degrees of fusion of flight sclerites, various numbers of ocelli and ovarioles, and different levels of spermatheca development. There was no correlation in the degree of expression between each of these traits. For example, some smaller intercastes had a reduced thorax but six ovarioles, whereas larger ones had a complex thorax but only two ovarioles. The presence of a spermatheca was similarly uncoordinated and sometimes occurred in intercastes having only few ovarioles. In *Mystridium rogeri*, five intercastes from two colonies also showed various combinations of winged queen and worker traits: a smaller thorax with simplified flight sclerites, a single ocellus, an abdomen as large as the winged queens, and functional ovaries (the occurrence of a spermatheca could not be checked; Molet et al. 2009). In *Myrmica rubra*, Brian (1955) studied the ontogeny of six intercastes that had worker-like heads, unfused thoracic segments typical of winged queens, and three to eight ovarioles. Similarly, the intercastes described in other ant genera are variable mosaics of the winged queen and worker castes (Peeters 1991). Importantly, all these intercastes survive as adults, although their behaviors are unstudied (except in *T. nylanderi* [Plateaux 1970] and in *Pachycondyla obscuricornis* [Düßmann et al. 1996]). In short, intercastes can be small and wingless like workers but have ovaries and a spermatheca like the winged queens; hence, they are queen-worker mosaics that uncouple flight and reproduction. In other species, intercastes can be as large as winged queens (although wingless) but lacking a functional reproductive apparatus, that is, infertile mosaics larger than standard workers.

A key point about intercastes is that the caste-specific modular traits borrowed from workers and winged queens (fig. 1c) have already been tested for viability in the normally expressed worker and winged queen phenotypes. This probably explains why intercastes survive as adults. Assuming that the morphological heterogeneity of intercastes described in *T. nylanderi* (Plateaux 1970) is common across ants, a diversity of anomalous phenotypes is available to be tested for potential usefulness.

Mechanisms Causing the Development of Anomalous Queen-Worker Mosaics

Embryonic and postembryonic development in animals typically results in adult individuals well within the normal range of a species' characteristic phenotype (Siegal and Bergman 2002). The alternative phenotypes in polyphenic species—queen and worker castes in ants—are similarly canalized. Development can be stabilized despite environmental and genetic changes through the action of genetic factors (Rutherford 2000), regulatory homeostasis (Suzuki

and Nijhout 2008) and a variety of other processes (Gerhart and Kirschner 1997, p. 591). Even so, disturbances can exceed buffering capacity, resulting in abnormal development (Nijhout and Davidowitz 2003; West-Eberhard 2003; Suzuki and Nijhout 2008).

Since intercastes express a combination of caste-specific modular traits from the worker and winged queen castes, mechanisms of caste determination (see “Ant Castes Consist of Both Shared and Caste-Specific Modular Traits”) are certainly involved in their development. Any factor responsible for the switch between alternative queen and worker pathways of larval development could be the source of developmental instability, causing the production of intercastes. For instance, honeybee intercastes tend to develop when larval nutrition varies around its threshold for queen determination (West-Eberhard 2003, p. 130). Infection by pathogens such as nematodes can cause the production of intercastes in ants, presumably by affecting hormone levels (Wheeler 1928; Csősz and Majoros 2009). Genetic factors can also affect the processes that direct larval development toward alternative pathways (Fersch et al. 2000; Anderson et al. 2008).

Factors that stabilize development are called capacitors because they allow for cryptic genetic variation to accumulate (Moczek 2007; Masel and Siegal 2009). Indeed, capacitors prevent new alleles that appear through mutation from being expressed and modifying the course of development. These alleles are not exposed to natural selection; hence, individuals are not affected by the mutations they carry. Consequently, genetic variation remains cryptic and can rapidly accumulate over generations. However, when the system experiences excessive disruption that overrides the buffering abilities of capacitors, stored cryptic genetic variation is unleashed and results in new phenotypes that will then be exposed to selection (Rutherford 2000). Such cryptic genetic variation was found in dung flies by Berger et al. (2011): different female lineages have distinct propensities to develop an extra spermatheca when exposed to increasing temperature. In our scenario for ants, environmental or genetic perturbation releases cryptic genetic variation at loci involved in maintaining the integrity of caste-specific developmental pathways (see “Ant Castes Consist of Both Shared and Caste-Specific Modular Traits”), such that modular traits from more than one caste are expressed in the same individual. Intercastes result from the failure of the switch mechanisms that normally channel larvae along discrete developmental pathways. Heterochronic development of body parts leading to mosaic phenotypes has been shown in ergatoid queens of *Myrmecina nipponica* (Miyazaki et al. 2010) and intercastes of *Myrmica rubra* (Brian 1955). Accordingly, the queen-worker switch is likely to be composed of subordinate switches that have their own thresholds and sen-

sitive periods but respond to the same environmental cue (West-Eberhard 2003, pp. 129–131). This means that temporal fluctuations in external factors—or mutations that change the periods or thresholds of sensitivity—can affect some modular traits but not others. Consequently, individuals rarely exhibit changes in development and adult phenotype, and the extent of these changes varies between individuals. This fits with ant intercastes, which are rare and extremely variable in colonies. Importantly, intercastes can lead to the evolution of novel castes only if the propensity to develop such phenotypes following environmental perturbations is heritable (see “Selection and Stabilization of Frequency and Phenotype of Intercastes”).

Colonies Buffer Anomalies from Individual Selection

We suggest that insect colonies function as incubators for novelty, much in the way that homeostatic mechanisms act as capacitors. Any individual recognized as a colony member will be fed and protected. Only young founding queens and older foraging workers are active outside the nest, where colonial buffering stops. In solitary species, deviant traits directly affect the individual. In contrast, colonies shield intercastes (and the developmental process that produces them) from individual selection. Costs and benefits are transferred from the individual to the colony level. The extent of protection provided by a colony to deviant traits can be estimated by comparing survival in solitary and social contexts. For instance, in ant queens that found their colony alone (independent founding), solitary life starts with mating and dispersal flight and ends when the first workers emerge as adults. In the fire ant *Solenopsis invicta*, queen survival is lower than 0.1% during the few months of the founding stage, but it increases to about 75% per year in established colonies (Tschinkel 2006, pp. 184, 530). Colonial buffering can thus be very strong, although this should be investigated in more taxa.

Large Queen-Worker Dimorphism in Ants Allows a Greater Range of Intermediate Mosaics

Many ant species show strong divergence in size between winged queens and workers; thus, there is ample morphological space for a range of intercastes. Division of labor is generally enhanced by differences in size (Hasegawa 1993b; Billick and Carter 2007), so such variable intercastes may benefit colonies by providing a range of useful functions (fig. A3). In poneroid ants (as defined by Ward 2007) and other ants with low queen-worker dimorphism, the morphological and functional spaces between castes are too small to produce useful intercastes (fig. A4, available online). This is also the case in social bees and wasps, both of which have winged workers;

hence, the diversity and utility of intermediate mosaics are likely to be limited. Further support for the importance of large size dimorphism is the restriction of soldier castes to formicoid ants (as defined by Ward 2007; fig. A1).

Intercastes That Increase Colony Fitness Can Evolve into Novel Castes

Selection and Stabilization of Frequency and Phenotype of Intercastes

The usefulness of intercastes is tested by colony-level selection (Johnson and Linksvayer 2010). The benefits they provide are probably not symmetric with their costs.

First, the cost of producing intercastes is likely to be very low. As previously discussed, intercastes are built with modular traits that are fully functional in their castes of origin. It is thus likely that most intercastes will be able to perform some labor, even at a suboptimal level, and this will offset their cost of production and maintenance. Even if an intercaste performs poorly, the colony-level cost of producing it compares with that of a dead worker. Colonies lose workers all the time as a normal part of their foraging activity. If such a loss were devastating, then no ant colony could ever function. Second, some rare phenotypes can bring strong positive benefits to colonies. We suggest that, even though intercastes occur at very low frequencies, they can have much more than a marginal effect in three specific contexts: reproduction, defense, and management of trophic resources. For reproduction, an intercaste with a spermatheca can mate and reproduce, and just one such individual can have a huge positive effect on the colony. Strong evidence for this is the occurrence of only one winged or ergatoid reproductive in the colony of many species. For defense, a single intercaste with a bigger head or more powerful mandibles can similarly have a large positive effect on its colony. In all species with a soldier caste, these occur at low frequency in the colony; for example, *Acanthomyrmex ferox* colonies have 25 workers and two to three soldiers (Gobin and Ito 2000). For management of trophic resources, an intercaste with larger ovaries that converts and stores dietary proteins into trophic eggs can enhance colony fitness. In *Crematogaster smithi*, fewer than six such soldiers occur per colony (Heinze et al. 1999a). Thus, although intercastes are protected (colonial buffering) from negative selection, some can have strong positive effects even at very low frequencies and evolve into castes of ergatoid queens or soldiers.

Subsequent selection can then modify the intercaste phenotype. Selection of intercastes is possible if the levels of developmental plasticity and the propensity to produce intercastes are genetically encoded (see “Mechanisms Causing the Development of Anomalous Queen-Worker

Mosaics”). Repeated environmental perturbations can cause the release of variability hidden by capacitors. Genetic variants that express the more adaptive reaction norms can be selected for, a process known as genetic accommodation (West-Eberhard 2003; Nijhout and Suzuki 2008; Masel and Siegal 2009). The interchangeability between environmental and genetic inductions of developmental processes is due to their shared translation into endocrine signals. It is classically admitted that evolution is fueled by mutations. We support the recent complementary view that evolution strongly relies on phenotypic plasticity (West-Eberhard 2003, pp. 498–525; Schlichting 2008; Pfennig et al. 2010), and ants are a good example. Intercastes induced by an environmental change are produced in numerous colonies and can be selected for if their phenotypes are useful, thus quickly invading populations. If the environment changes back, intercastes are not produced anymore and are thus hidden from counterselection. Environment thus plays the role of both trigger and selection filter for intercastes. In striking contrast, genetic mutants are produced in only a limited number of colonies irrespective of environment, so their evolution may be much slower. Phenotypic plasticity can thus be crucial for the origin of novel castes in ants. The evolution of complex caste systems in ants is likely to be the result of multiple episodes of mosaic intercastes being integrated in the genome.

From Intercastes to Wingless Queens

Two main colony founding strategies exist in ants (reviewed in Peeters and Molet 2010). Independent founding is the ancestral strategy, whereby winged queens fly away from their natal nest, mate, and start colonies without the help of workers. Winged queens are capable of dispersing far, and they can also use their wing muscles and fat body reserves to feed the first generation of larvae. Independent founding is a resource-intensive strategy where many queens are produced, which compensates for high mortality during dispersal and solitary life. In contrast, many species in different lineages have shifted from independent to dependent colony foundation, where one or more reproductives leave their natal nest with a group of nestmate workers. Such reproductives never go through a solitary phase, and they disperse on foot. Hence, the constraints on their phenotype are greatly relaxed, and expensive wing muscles are selected against. Reproductive phenotypes that cost less—that is, having normal ovaries and a spermatheca but no flight apparatus—may be selected for. Ergatoid queens are indeed cheaper than winged queens (in *Monomorium viride* [DuBois 1986] and in *Myrmica obethuerei* vs. winged queens of *Myrmica rogeri* [Molet et al. 2009]).

We suggest that ergatoid queens evolved across ant species from intercastes capable of sexual reproduction. These can have a huge positive effect on colonies even if they occur at very low frequencies. It is known in *Pachycondyla verenae* (= *obscuricornis*) that two mated intercastes produced workers in a colony lacking the original winged queen (Düssmann et al. 1996), and this would have made all the difference to colony survival. Occasional intercastes able to mate can bring disproportionate benefits to their colonies; hence, they would be selected for and produced regularly.

Morphological evidence from congeneric species clearly points to an evolutionary transition from intercastes to ergatoid queens. In *Harpagoxenus sublaevis*, a single ergatoid queen reproduces, and colonies rarely produce winged queens. In contrast, colonies of *Harpagoxenus canadensis* have a single winged queen, but intercastes also occur occasionally (Buschinger and Winter 1975). Buschinger and Alloway (1978) reported that one-third of *H. canadensis* colonies had up to three individuals with mosaic phenotypes resembling the ergatoid queens of *H. sublaevis*, except they lacked a spermatheca. In *Odontomachus coquereli*, ergatoid queens have a small thorax and big abdomen, just like the nematode-infected intercastes of other *Odontomachus* species with winged queens (Wheeler 1928; Molet et al. 2007).

More evidence for an evolutionary transition from intercastes to ergatoid queens lies in the striking parallels between the morphological heterogeneity of intercastes within species (e.g., *Temnothorax nylanderii*; Plateaux 1970) and the heterogeneity of ergatoid queens across species (Peeters 2012). Assuming that different kinds of intercastes with a spermatheca are available intraspecifically for selection (especially in species with a large dimorphism between winged queens and workers), comparative evidence suggests that either queen-like or worker-like intercastes can be selected. Indeed, two general types of ergatoid queens (specialists vs. generalists) are found across species (Molet et al. 2009).

Wingless Queens: From Supplemental to Sole Reproductive Caste

Both winged and ergatoid queens exist in many species, and the latter generally function as secondary reproductives that can extend colony life span after the death of the winged foundress (Peeters 2012). Ergatoid queens can be morphologically variable in some of these species (*Myrmecina graminicola*; Buschinger and Schreiber 2002), ranging from winged queen-like (lacking wings but with similar size and unfused thorax) to worker-like (fig. A3). This gives an insight into the mechanisms of stabilization of the ergatoid queen phenotype. Indeed, comparative evi-

dence shows that, once winged queens have been lost, the variability of ergatoid queens decreases. In German populations of *H. sublaevis*, winged queens occur and ergatoid queens are extremely variable (Buschinger and Winter 1975), but in Sweden where winged queens are lost, ergatoid queens are morphologically fixed and externally very similar to workers (Bourke 1988). Hence, the retention of the winged queen caste in some species apparently prevents ergatoid queens from being morphologically fixed and restricts them to a size intermediate between winged queens and workers. Once independent colony foundation and winged queens have been lost, these constraints may be lifted. Subsequently, a self-accelerating process of developmental release can lead to the evolution of highly diversified phenotypes combining traits that were never associated before in the same phenotype (West-Eberhard 2003). The morphology of ergatoid queens can thus become highly modified, as illustrated hereafter. The giant specialist queens of army ants (Kronauer 2008) are much larger than any putative ancestral winged queen. In all army ants, winged queens are completely unknown, indicating that they were selected against early on in the evolutionary history of this lineage; hence, ergatoid queens have been evolving over millions of years. Another example is the dwarf ergatoid queens of *Myrmium*, which are smaller than workers (Molet et al. 2009). Selection favored dwarf queens efficient for both reproduction and brood care in addition to workers having long and sharp mandibles for hunting (Molet et al. 2007).

From Intercastes to Soldiers

Speculations about the evolutionary origin of a distinct soldier caste in ants have continued for many years. Some authors, such as Ward (1997), have suggested that soldiers evolved from within the worker caste. In contrast, Baroni Urbani and Passera (1996) proposed that soldiers evolved from within the queen caste, because in some species they share characters such as highly modified head or ovariole number. However, discussions have been compromised by semantic problems in distinguishing soldiers and major workers (discussed in "Soldiers: Mosaic Nonreproductive Caste"). On the basis of their mosaic nature, we propose that soldiers evolved from intercastes in the same way as ergatoid queens. A mosaic origin for soldiers resolves the apparent conflict between the hypotheses of worker versus queen derivation (Baroni Urbani and Passera 1996; Ward 1997). In addition, independent evolution of mosaics helps to account for the great morphological diversity of soldiers across lineages.

Wheeler (1937) alluded to the feminization (meaning queen-like nature) of soldiers, particularly in the head, which can be taken as corresponding to the expression of

caste-specific modular traits. A mosaic origin is supported by morphometric analysis of the largest ant genus, *Pheidole*, in which all species have soldiers. Pie and Traniello (2006) measured soldiers in 231 species and showed that their diversity in shape is limited because it is generated by allometry resulting from size change along the growth trajectories of workers. However, they also found that some diversity, notably in head shape, does not result from worker growth rules but from “extensive reorganization of developmental programs.” We suggest that this reorganization represents developmental recombination of queen and worker versions of traits: worker head traits have been replaced by queen head traits in soldiers. Combined with allometric growth rules, this can allow a much wider range of phenotypes with specialized morphologies. Studies about soldier evolution have classically compared them with the worker caste only. Future approaches that compare soldiers to both worker and queen castes are likely to bring important insights. In the case of *Eciton*, in addition to the queen, worker, and soldier castes, some species have an extra submajor caste, intermediate between workers and soldiers (Powell and Franks 2006; S. Powell, personal communication). The existence of novel mosaics between workers and soldiers underscores the principle that developmental pathways from all existing castes are available for recombination. Similarly, a few *Pheidole* species have an additional, even larger super-soldier caste, which is allometrically distinct from regular soldiers (Huang and Wheeler 2011). In super-soldiers of two species, the posterior wing disk is additionally expressed, reflecting even greater incorporation of the queen’s flight traits (Rajakumar et al. 2012).

As for ergatoid queens, anomalous mosaics provide only the starting point for the evolution of soldiers. Subsequent modifications can then evolve. For instance, the highly modified mandibles found in *Eciton* soldiers are absent from either queens or workers (Gotwald 1995), and the head of *Acanthomyrmex* and *Pheidole* soldiers is much larger than queen heads, although mandibles are similar (Gobin and Ito 2000; Wilson 2003), so modularity alone is not driving the process.

Are Mosaic Phenotypes Evolutionarily Useful in Other Insects?

Intercastes can be the basis for innovation in ants because the winged queen and worker castes are often highly dimorphic. As mentioned above, intercastes are likely to be less important in the other holometabolous social insects: bees and wasps have queen and worker castes that are both winged, and size dimorphism is limited. What about polyphenic taxa that are hemimetabolous (larvae develop gradually into adults, without metamorphosis)? In several

termite lineages, older larvae function as workers, but other lineages have specialized adult workers. Reproductives can be either the founding pair, which develop with wings, or wingless neotenic that are functionally equivalent to ergatoid queens in ants. Neotenic serve as replacement reproductives when the original pair dies. Hence, task division in termites relies both on divergent adult castes and on larval stages. Despite the existence of colonial buffering as in the ants, intercastes in termites would be functionally redundant with the graded morphologies and behaviors already occurring in the larval stages. Reproductive-soldier intermediates have been described in a variety of species (Thorne and Traniello 2003; Koshikawa et al. 2004), although it is not clear why they would be more advantageous than neotenic adults (Y. Roisin, personal communication). It is worth mentioning that, contrary to ants where soldiers are the derived form, in termites adult workers are the derived form, so intercastes cannot be involved in the evolution of soldiers. Aphids also express alternative traits: presence versus absence of wings, viviparous versus oviparous, seasonal phenotypes. Their bewildering array of forms may result from recombinations between modular developmental alternatives. A successful variant could quickly increase in numbers through clonal reproduction. Finally, migratory locusts tend to be polyphenic, with *Locusta migratoria* and *Schistocerca gregaria* having extreme forms (West-Eberhard 2003, p. 132). Environmental induction of the migratory phenotype from the solitary one takes several generations during which individuals exhibit varying gradations of the two forms, and it is possible that such intermediates would be advantageous under certain environmental pressures. In hemimetabolous insects then, phenotypic traits can be modularly expressed and could be recombined into mosaic phenotypes. However, there is neither colonial buffering nor division of labor in locusts and aphids, thus potentially limiting the survival and benefits of mosaic phenotypes. For similar reasons, intermediate forms would bring limited benefits to solitary holometabolous insects such as beetles showing horn polymorphism in males (Moczek 2003).

Concluding Remarks

Soldiers and wingless (ergatoid) queens occur widely across different ant lineages. Their adult morphology and development have not been compared up to now, and we suggest that both are mosaics of winged queens and workers. We propose that erratically produced intercastes are the source of variation that led to their repeated evolution. Three factors facilitate the production and survival of intercastes in ants (fig. 2). First, modularity enhances evolvability through relative independence of

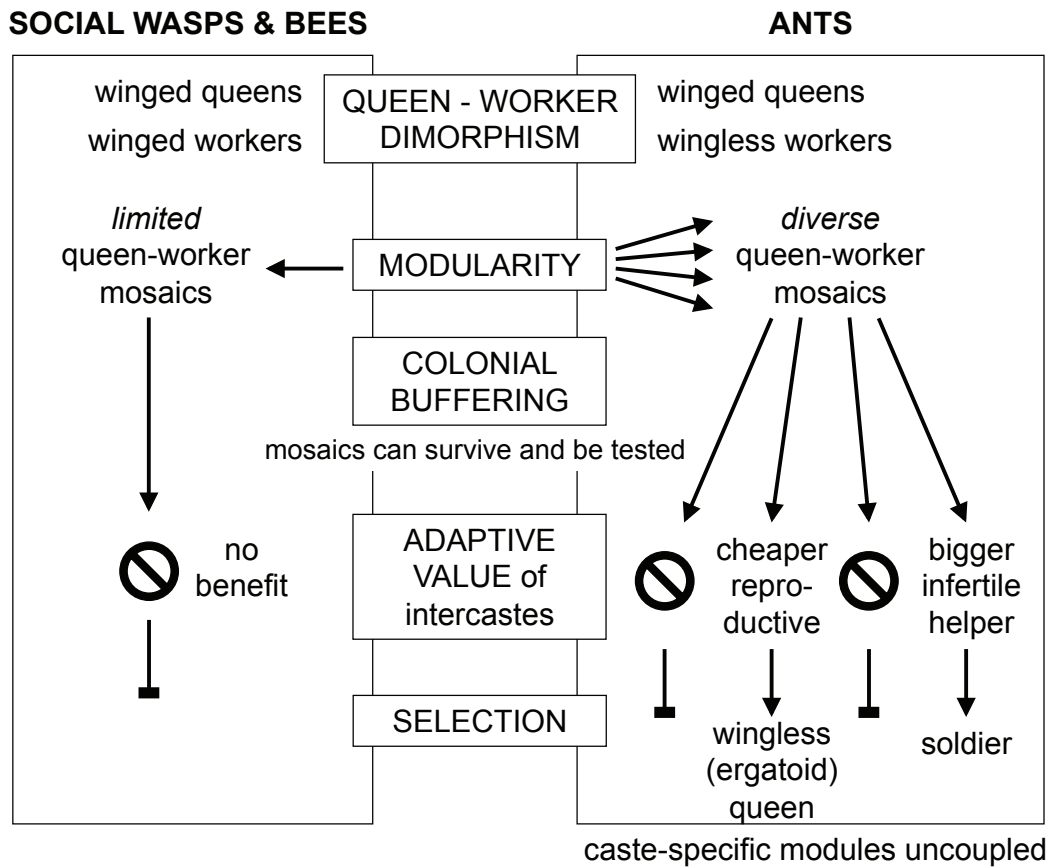


Figure 2: In ants, large queen-worker dimorphism allows for the production of a wide range of intercastes (rare anomalies) that are buffered by the colonial environment. Some can bring benefits to colonies and evolve into novel castes produced regularly.

traits, particularly flight and reproductive traits. Second, in many species, queens and workers differ markedly in size and morphology, which increases the chance that an intercaste will have an innovative phenotype. Third, the colonial environment protects developmental anomalies from purifying selection. Colony-level selection on the contribution of intercastes can then lead to regular castes. Once a novel caste is stabilized through genetic accommodation and its function improved by subsequent evolution, it too can serve as a source of modular traits to produce further intercastes. Our hypotheses and predictions can be tested empirically with comparative and experimental approaches.

Intercastes have been found in many ants but are seldom studied (Peeters 1991). They have the potential to provide fitness benefits to their colony and could approximate the idea of hopeful monsters (Dietrich 2003), unlike sexual mosaics lacking evolutionary potential that are hopeless

monsters (Yang and Abouheif 2011). And because colonial buffering can shield all deviant forms (intercastes as well as mutants) from individual selection, novel phenotypes can evolve more readily in social insects.

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Left, a mosaic monster of the ant *Mystridium rogeri* from Madagascar. It is neither a queen nor a worker: it has a single ocellus (three in queens, none in workers), a moderately simplified thorax with four tiny wing buds (thorax is complex in winged queens, simple in wingless workers), and ovaries that are bigger than workers'. *Right*, this monster can be seen in the central top section of the nest. It is well integrated in the colony and lives a normal life. However, it may provide benefits to the colony such as nest defense or egg laying. Photographs by Sylvain Londe.