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Development of alary muscles in single- and multiple-queen populations of the wood ant *Formica truncorum*

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Formica truncorum is an ant species that maintains populations dominated by either single-queen (monogyne) or multiple-queen (polygyne) colonies. New queens (gynes) from monogyne colonies disperse after mating whereas gynes from polygyne colonies are philopatric. Gyne physical condition frequently reflects the overall dispersal propensity of the maternal colony, with dispersers heavier and with larger wings than philopatric morphs. Little, however, is known about the musculature that powers flight dispersal. Our histological examination of alary muscle tissue revealed that mitochondrion and sarcomere numbers did not differ in newly emerged gynes from monogyne and polygyne populations. Significantly greater numbers of mitochondria and sarcomeres were, however, detected in mature virgin gynes from monogyne nests. Within both populations, gynes that had shed their wings had significantly fewer mitochondria than winged gynes. Wingless mated gynes from monogyne nests also had greater numbers of mitochondria. As the sites of ATP production, mitochondria are critical to any biochemical process and reduced numbers are likely to influence the success of flight dispersal. Differential provisioning of new gynes post-emergence in the two populations may account for the variation in flight musculature, which may provide a reliable mechanism by which current dispersal conditions can be assessed. As flight capability generally represents a trade-off with ovarian growth for many insect species, gynes able to forgo flight dispersal and redirect resources from flight muscle development into oocyte development may gain an early reproductive edge compared to their dispersing counterparts.

Introduction

Dispersal is a risky business, with threats of predation (Weisser 2001), starvation or death by natural elements such as wind, desiccation and rain (Cody & Overton 1996). Yet, despite these potential dangers, most animals disperse, motivated by the need for new habitat and resources (Roff 1984), the negative effects of inbreeding (e.g., Moritz 1983, Chesser & Ryman 1986), and the benefits of maintaining genetic variation (Keller & Reeve 1994). Movement out of the natal range can furthermore minimize the potential for competition among kin (Hamilton & May 1977). Nonetheless, the benefits of natal senescence for numerous vertebrate and invertebrate taxa outweigh the risks of dispersal (e.g., Moses & Millar 1994, Blumstein & Armitage 1998, Ekman *et al*. 2000) and individuals with dispersal potential remain home, often at a reduction in personal reproduction (Wiley & Rabenold 1984, Koenig *et al*. 1992).

Natal philopatry is frequently facultative and strongly associated with intra-sexual dispersal morphs (e.g., naked mole rat: O'Riain *et al*. 1996). Nearly every insect order contains species that are polymorphic with respect to dispersal propensity and, consequently, flight ability or flight-muscle development (Johnson 1969, Harrison 1980, Roff 1986, 1990, Zera & Denno 1997). In some species, dispersal morphs are distinguishable on the basis of mitochondrial ultrastructure (Blackmer *et al*. 1995, Strohm & Daniels 2003). Thus, a sometimes-high proportion of reproducing individuals disperse only short distances or not at all (e.g., *Jadera haematoloma* (Rhopalidae): Carrol *et al*. 2003; *Bembidion lampros* (Carabidae) in some populations: Langor & Larson 1983). The development and maintenance of flight muscle requires a great deal of energy and resources, as up to 65% of total body mass may consist of flight muscle mass in individuals capable of flight (Marden 2000). Metabolic products and resting rate of the thoracic muscle in flight capable individuals are substantially higher than in flight incapable counterparts, and nine times higher than the metabolic rate of ovarian tissue (e.g., the polymorphic cricket *Gryllus firmus*: Zera *et al*. 1997). Sustenance of metabolic activities devoted to muscle tissue frequently overshadows the energy need for ovarian activities and ultimately has a negative impact on female fecundity (Zera & Mole 1994, Zera & Denno 1997, Zera *et al*. 1997, Marden 2000). In species that undergo temporary or permanent histolysis of flight muscles, the percentage of total body mass apportioned to thoracic musculature drops to nearly zero just prior to or during ovarian development and oogenesis (Langor 1987, Marden 2000). Hence, the amount of energy investment required for flight dispersal at the expense of reproduction may be a strong selective pressure to forgo dispersal altogether, particularly in conjunction with other dispersal stressors (e.g., Roff 1984, Denno *et al*. 1989, Crespi & Taylor 1990, Roff 1994, Cody & Overton 1996, Weisser 2001).

Intra-specific dispersal polymorphism is known for several genera of ants (*Formica*: Sundström 1995, *Leptothorax*: Heinze & Buschinger 1989, *Solenopsis*: McInnes & Tschinkel 1995). Typically, ants have two morphologically distinct female castes: queens that disperse by flight and are primarily responsible for dispersal and reproduction, and workers, which have limited or no reproductive ability. Non-dispersal within the dispersal-equipped (sexual) caste usually results in colonies with multiple reproducing queens (secondary polygyny) (Heinze & Tsuji 1995) and is considered a response to unfavorable ecological conditions (Tsuji & Tsuji 1996). Comparative studies of such facultatively polygyne species have shown there to be a strong association between different mating and dispersal habits of new gynes and the queen number of a colony. Whereas new gynes from monogyne nests are typically inclined to disperse by flight, new gynes originating from polygyne colonies are not (but *see* e.g., Sundström *et al*. 2003). The generally smaller body size (Keller & Passera 1989), shorter wing length (Kikuchi 2002, C. A. Johnson & L. Sundström unpubl. data), lower nutrient reserves (Passera & Keller 1990, Sundström 1995), and an earlier wing shedding (Fortelius 1987, Sundström 1995) of new gynes from polygyne nests suggest overall inferior flight (dispersal) and colony establishment abilities of these queens. Yet for most ant species, almost nothing is known about the alary musculature, which is crucial for successful long-distance dispersal and intricately linked to oogenesis and, hence, reproduction.

The wood ant, *Formica truncorum* Fabricius, maintains populations that are dominated by either monogyne (single-queen) or polygyne (multiple-queen) colonies (Sundström 1993). Genetic investigations indicate that within the polygyne populations there is little long-distance dispersal but that new gynes from monogyne colonies disperse (Sundström 1989, 1993), although dispersal dimorphism is evident in colonies of both social structures (Sundström 1995). The physiological condition of reproductive females and males is strongly associated with dispersal tendencies, such that individuals in better nutritional condition tend to disperse and those nutritionally deficient tend to remain in the natal colony (Sundström 1995). To examine the developmental trajectory of alary musculature relative to natal colony social structure, we conducted a histological examination of thoracic musculature of new gynes at different stages (callow, mature virgin, newly mated). Although all winged ant gynes eventually dealate (shed their wings), typically after mating and dispersing, some gynes shed their wings beforehand, completely curtailing any potential for long-distance dispersal. Alary musculature of alate (winged) and dealate (wingless) virgin gynes were, thus, also compared. Well-developed and mitochondrion rich alary muscle is critical for successful dispersal by flight (Tribe & Ashhurst 1972, e.g., *Atta sexdens*: Cruz Landim & Silva de Moraes 1979), as mitochondria fuel the energetically costly flight (*see* Marden 2000 for review) by producing adenosine triphosphate (ATP) (Alberts *et al*. 1994). We therefore quantified the number of mitochondria and sarcomeres in longitudinal sections of thoraces from new gynes to provide an estimate of the development of flight ability during adult maturation.

Material and methods

New *F. truncorum* gynes were collected from one monogyne archipelagic population (Hanko) and one polygyne archipelagic population (Siuntio) in south-west Finland, during the summer of 2002. From the monogyne population, we collected alate callow (5), alate (5) and dealate (6) virgin, and dealate mated (6) gynes from six colonies on four islands. From the polygyne population, we collected alate callow (10), alate (9) and dealate (6) virgin, and dealate mated (8) gynes from six colonies on three islands. Spermathecal contents were examined to verify virginity or insemination. Thoraces were separated from other body parts, and a section of the cuticle supporting the forelegs was removed to enable fixation in cold 2% glutaraldehyde for 24 hrs. Samples were thereafter maintained in buffer solution (pH 7.3 with 50 mM Na-cacodylate and 150 mM saccharose) and shipped to the Laboratory of Entomology at the Catholic University of Leuven, Belgium, for further processing. Fixed thoraces were post-fixed in 2% osmium tetroxide, subjected to dehydration in a graded acetone series, and embedded in Araldite resin. The resin blocks of thorax muscle tissues were ultra-thin sectioned longitudinally (70 nm) using a Reichert Ultracut E microtome and placed on 50 mesh copper grids. The sections were contrasted using uranyl acetate and lead citrate, and examined with a Zeiss EM 900 transmission electron microscope. The number of mitochondria and the number of sarcomeres in a 27.5 μm × 27.5 μm area of the ultra-thin thorax muscle sections were quantified by direct measurement from micrographs taken at 3000× magnification. Distributions were analyzed for non-normality and heteroscedasticity, and data were analyzed accordingly, using the least squares fit model and the Wilcoxon 2-group test in JMP 4.0.2 (SAS Institute, Inc., NC, USA).

Results

Callow gynes from monogyne and polygyne nests did not differ in the number of mitochondria ($z_{13} = 0.79$, $p = 0.42$) or in the number of sarcomeres ($z_{13} = -1.84$, $p = 0.07$), although there was a tendency for polygyne callows to have more sarcomeres (Fig. 1). In mated dealate queens, the number of mitochondria but not the number of sarcomeres differed significantly between monogyne and polygyne colonies ($z_{12} = 2.23$ and 0.00, $p = 0.02$ and 1, respectively; Fig. 1), with monogyne individuals having more mitochondria. In mature, virgin gynes, the number of mitochondria was significantly greater in individuals from monogyne colonies and in individuals with wings, but there was no interaction (Table 1 and Fig. 1). The number of sarcomeres, however, differed only with respect to colony type and not with respect to wing status, i.e., gynes from monogyne colonies had significantly more sarcomeres than gynes from polygyne colonies (Table 1 and Fig. 1).

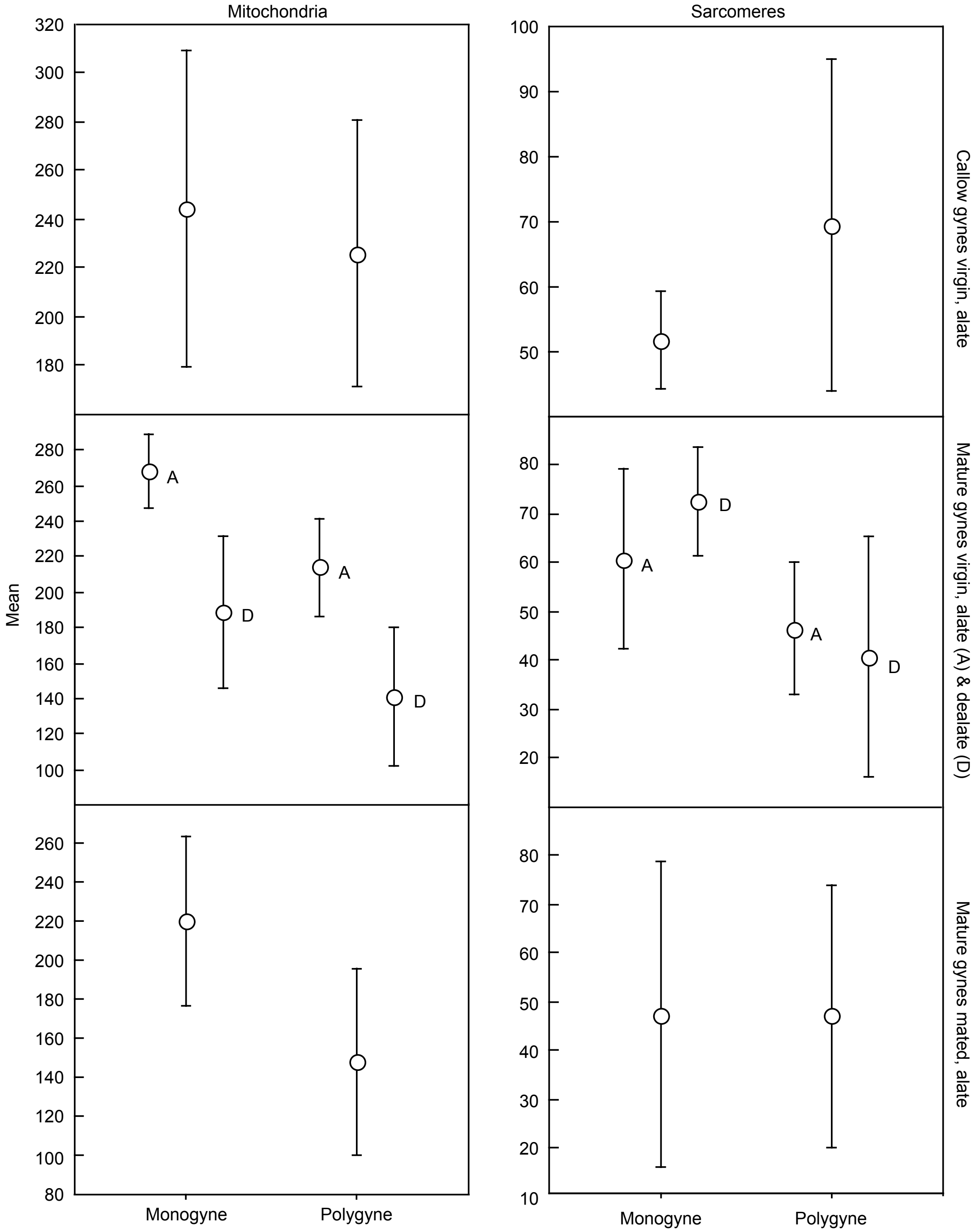

Fig. 1. Mean number (± 95% confidence intervals) of mitochondria and of sarcomeres in longitudinal ultra-thin sections (27.5 μm × 27.5 μm) of indirect alary muscle from callow, mature virgin and mated gynes from monogyne and polygyne *F. truncorum* nests.

Overall, sarcomere number was not significantly correlated with mitochondrion number in any gyne category (alate callow: $b = 0.36$, $R^2 = 0.003$, $F_{1,13} = 0.038$, $p = 0.85$; alate virgin: $b =$

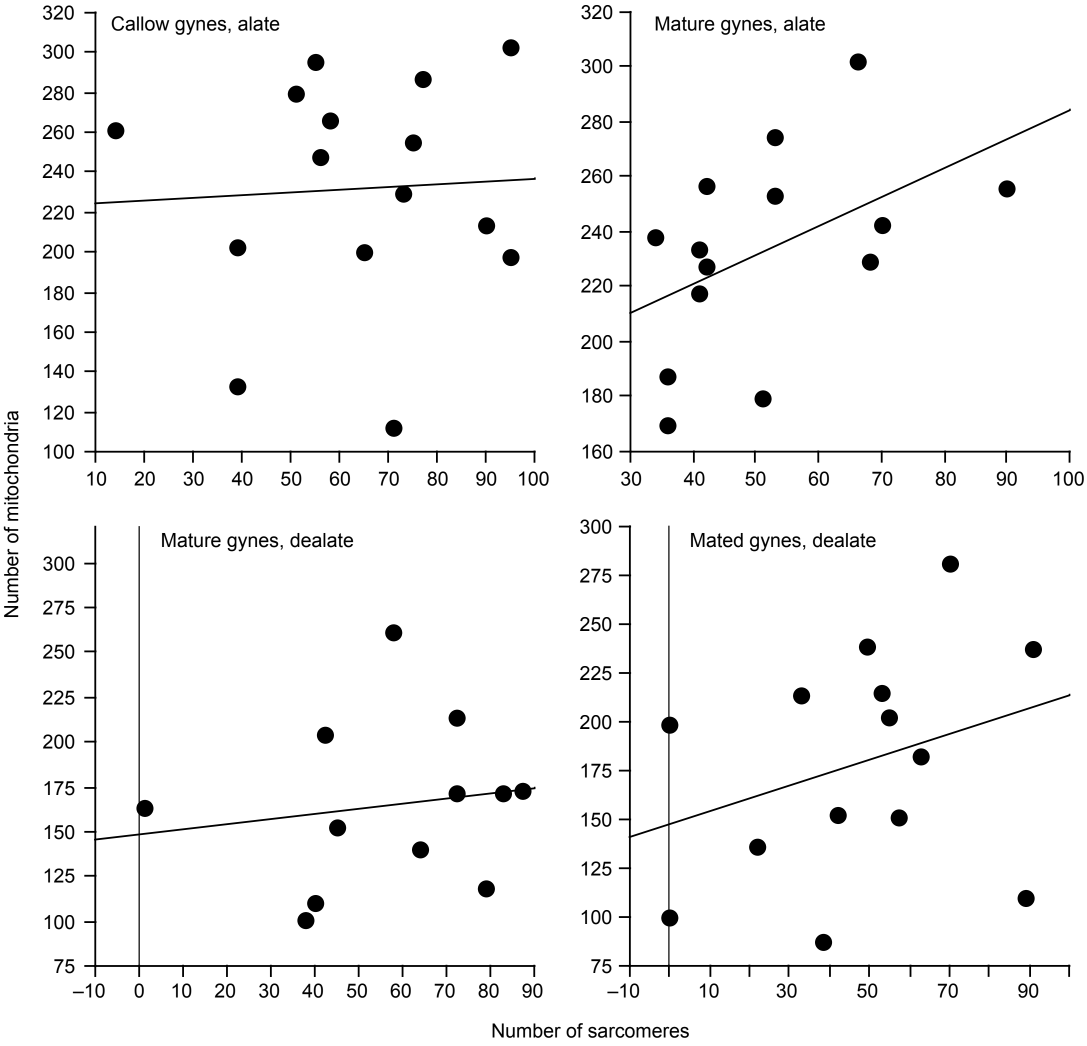

Fig. 2. Relationships between the number of sarcomeres and mitochondria in ultra-thin sections (27.5 μm × 27.5 μm) of thoracic musculature from new *F. truncorum* gynes at different developmental stages and states post-emergence.

1.05, $R^2 = 0.224$, $F_{1,13} = 3.47$, $p = 0.087$; dealate virgin: $b = 0.293$, $R^2 = 0.024$, $F_{1,10} = 0.25$, $p = 0.63$; dealate mated: $b = 0.658$, $R^2 = 0.1$, $F_{1,12} = 1.33$, $p = 0.27$; Fig. 2). In callow gynes from both populations, the myofibrils appear compact and the mitochondria are numerous and intact (Fig. 3). The mitochondria and myofibrils in mature alate virgin gynes from the polygyne population are noticeably less compact than in monogyne counterparts. The pattern of muscle degeneration after gyne self-amputation also appears to be quite different between the two populations. The myofibrils are collapsed and sarcomeric Z-lines

Table 1. Differences in thoracic musculature between mature virgin *F. truncorum* gynes as a function of colony social structure and wing status (general linear model, analysis of variance).

	F	df	*p*
Mitochondria			
Colony type	14.36	1	0.001
Wing status	32.41	1	< 0.0001
Colony type × Wing status	0.07	1	0.79
Sarcomeres			
Colony type	11.12	1	0.03
Wing status	0.20	1	0.66
Colony type × Wing status	1.62	1	0.22

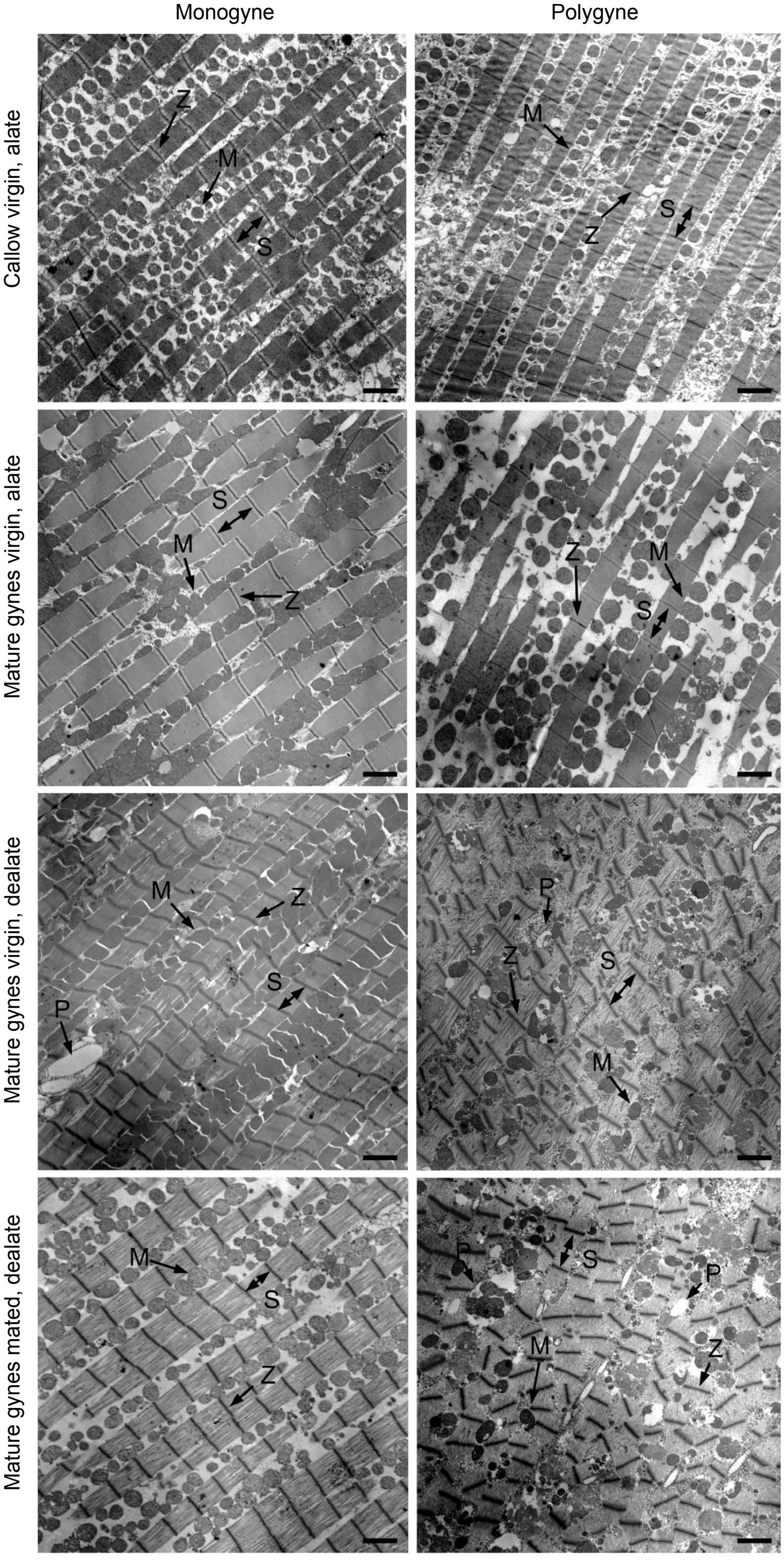

Fig. 3. Representative transmission electron micrographs of longitutinal ultra-thin sections from alate callow, alate and dealate mature virgin and dealate mated *Formica truncorum* gynes from monogyne and polygyne nests, which illustrate the diverging trajectory of thoracic musculature development. Arrows indicate mitochondria, phagocytes, sarcomeres, Z-disks and phagocytes. Scale bar = 2.5 μm.

become chaotically arranged in the gynes from polygyne colonies. In gynes from monogyne colonies, the sarcomeric Z-lines are intact and the muscle appears to thin rather than rupture at least at this stage after dealation (Fig. 3).

Discussion

Our results show that whereas alary muscle of new gynes at the callow stage does not differ between the monogyne and polygyne populations, the difference is significant at later stages, when pigmentation and hardening of the cuticle has been completed. Differences in alary musculature were also apparent within monogyne and polygyne populations between gynes that maintained their wings and those that had undergone self-amputation, with gross distortions observed early after dealation in the polygyne population. The primary difference in thoracic musculature was in the number of mitochondria, although mature virgins from polygyne nests also had fewer sarcomeres. The range in the number of mitochondria among the sampled gynes particularly within the polygyne population suggests a continuum within populations and probably also within nests. Some of this variation may be a consequence of slight differences in the ages of the individuals sampled and our results may underestimate larger actual differences. Nevertheless, these results reveal a diverging trajectory of alary tissue development and degeneration in new gynes relative to queen number in the colony of origin.

The deviate changes in alary tissue after the callow stage suggest that the degree to which energy is shunted to muscle development may be determined in part during adult maturation, which may be contingent on available resources or worker behavior during post-emergence development. In virgin gynes from both the monogyne and polygyne populations, the number of mitochondria plummeted after self-amputation, whereas the sarcomere numbers remained rather constant. However, wingless virgins from monogyne colonies rivaled winged virgins from polygyne colonies in mitochondria number, and sarcomere numbers of wingless virgins were overall much lower in the polygyne population. Hence, some winged gynes from polygyne colonies may never acquire mitochondrial or sarcomeric reserves necessary for 'successful' flight. However, by not expending energy on flight, flight-deficient gynes may have a greater net energy available for initial ovarian and egg development. In general, queens in nests with multiple queens have lower life-time reproductive outputs than a queen that is the sole reproductive of a colony if she survives the founding stage (Bourke & Franks 1995). Nonetheless, egg production in independent colony founders peaks much later than in philopatric gynes, which reach their maximal rate of egg output soon after mating (Brian 1983, Keller & Passera 1990). The disarray in dealate thoracic tissue from our polygyne population certainly seems to chronicle a race to degeneration by virgin and mated gynes.

A number of insect species, including ants, undergo rapid degeneration of their flight muscles just prior to ovarian growth and oogenesis. This transition between high flight capability and ovarian development is referred to as the oogenesis-flight syndrome (Johnson 1969) and is believed to represent a common mechanism via apoptosis (programmed cell death) to reorganize existing resources. The resorption products generated by histolysis provide metabolites for ovarian development and vitellogenesis (Bhakthan *et al.* 1970, Nair & Prabhu 1985, Rankin *et al.* 1986). Consistently, flight endurance is positively correlated with muscle size and negatively correlated with female ovarian development, although some females show high flight capacity even when ovaries are highly developed (Marden 2000). Muscle condition in birds (Houston *et al.* 1995b) and reptiles (Schwarzkopf & Shine 1992) also appears to be compromised during periods of egg production with muscle proteins being made available for egg formation in birds (Houston *et al.* 1995a).

Polygyny in ants has been an evolutionary conundrum for decades, yet it may be the predominant state of queen number (Hölldobler & Wilson 1977, Keller & Vargo 1993). In *Formica truncorum*, dispersal risks and colony founding limitations may in part drive polgyny, and our examination of alary muscle indicates that new gynes from polygyne nests may be less well equipped to disperse than new gynes from monogyne nests. In general, the majority of flight muscle development takes place during the juvenile stage, although in some taxa muscle development continues during adult maturation (Marden 2000). Muscle and wing development and morph determination are regulated by the relative concentration of juvenile hormone with respect to a particular time course (Rankin 1989, Abouheif & Wray 2002, for review *see* Dingle & Winchell 1997). Because environmental stimuli (photoperiod, temperature variations, and food availability) can affect juvenile hormone titres, flight muscle and wing development is relatively labile in a number of species (Johnson 1969, Harrison 1980, Roff 1986, 1990, Zera & Denno 1997, Abouheif & Wray 2002). This flexibility allows for an appropriate response to environmental conditions, and individuals can either prepare to colonize better habitats by directing resources to muscle building or increase their reproductive effort by redirecting nutrients from construction and maintenance of flight musculature or structures to reproductive organs (Wheeler 1995). In other species, the converse seems to be true. Unfavorable conditions seem to stimulate the production of phenotypes that promote dispersal capability, which allows these individuals to potentially locate richer habitats (Cremer & Heinze 2003). In either instance, environmental conditions have the potential to profoundly influence social structure of eusocial insects by affecting dispersal capability.

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