Worker senescence and the sociobiology of aging in ants

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Abstract

Senescence, the decline in physiological and behavioral function with increasing age, has been the focus of significant theoretical and empirical research in a broad array of animal taxa. Preeminent among invertebrate social models of aging are ants, a diverse and ecologically dominant clade of eusocial insects characterized by reproductive and sterile phenotypes. In this review, we critically examine selection for worker lifespan in ants and discuss the relationship between functional senescence, longevity, task performance, and colony fitness. We did not find strong or consistent support for the hypothesis that demographic senescence in ants is programmed, or its corollary prediction that workers that do not experience extrinsic mortality die at an age approximating their lifespan in nature. We present seven hypotheses concerning how selection could favor extended worker lifespan through its positive relationship to colony size and predict that large colony size, under some conditions, should confer multiple and significant fitness advantages. Fitness benefits derived from long worker lifespan could be mediated by increased resource acquisition, efficient division of labor, accuracy of collective decision-making, enhanced allomaternal care and colony defense, lower infection risk, and decreased energetic costs of workforce maintenance. We suggest future avenues of research to examine the evolution of worker lifespan and its relationship to colony fitness, and conclude that an innovative fusion of sociobiology, senescence theory, and mechanistic studies of aging can improve our understanding of the adaptive nature of worker lifespan in ants.

Keywords

life history; social insect; division of labor; demography; caste evolution

Introduction

The longevity of ants can be remarkable. Queens may live up to 45 years in the laboratory or field (Keeler 1993; Keller 1998), and the lifespans of reproductives are more than an order of magnitude greater than those of related taxa (Ridley 1993). Prominent in ant caste polyphenisms are sterile workers that may show task-related survival risk, and in sharp contrast to the longevity of queens, live only weeks to months (Kramer and Schaible 2013),

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Dedicated to the memory of Professor Henry Hagedorn, mentor, colleague and friend, and his generous spirit.

illustrating remarkable aging plasticity specified by a single genome (Fjerdingstad and Crozier 2006). Extensive variation in life-history characteristics, colony size and social organization in ants provide opportunities to explore how differences in extrinsic mortality and social structure have led to the evolution of lifespan variation between and within morphological castes. Ants therefore present species-rich and ecologically diverse models to understand how selection shapes worker life history, enabling predictions of senescence theory to be critically evaluated in respect to sociality and its influence on the ecology and evolution of gerontological patterns and the maintenance of physiological performance throughout the lifespan (Austad 2009; Nussey et al. 2013). Here we present an integrated analysis of sociobiological and gerontological factors influencing the evolution of worker lifespan in ants. We explore potential relationships between worker longevity and colony fitness to characterize aging in the context of sociality and colony-level processes (Keller and Genoud 1997; Rueppell 2009), including the impact of selection on lifespan, senescence, and the structure of age-related patterns of task performance.

Senescence theory

Senescence is defined functionally as the decline in cognitive, motor, and physiological performance associated with increasing age, or demographically as an increase in mortality over the lifetime (Finch 1990; Williams 1999). Functional degeneration and declining survivorship are often assumed to be coupled. Although demographic senescence has been a primary focus of aging research, examining *how* animals age rather than simply *when* they die has received less attention (Williams 1999). Indeed, senescence does not necessarily increase until death; selection can operate differentially across the lifespan (Rauser et al. 2006, Shahrestani et al. 2009). Individuals that survive environmental insults are expected to functionally decline due to endogenous molecular damage and age-specific impacts of selection. Evolutionary theories of aging (mutation accumulation [Medawar 1952]; antagonistic pleiotropy [Williams 1957]) have attempted to predict patterns of senescence and explain intra- and interspecific variation in aging rates. Disposable soma theory (Kirkwood 1977) complements these concepts and suggests that deleterious mutations affecting non-reproductive tissue could accumulate if resources are allocated preferentially to the germ line, a notion particularly significant for the study of life-history evolution in eusocial insects, given differential selection on queens as germ line and workers as soma (Jemielity et al. 2005; Heinze and Schrempf 2008; Rueppell 2009). Empirical studies on model systems other than eusocial insects both support and refute predictions of senescence theories (Kirkwood 1977; Partridge and Gems 2006), and fail to identify a universal pattern of aging. Although there has been progress understanding the genetic basis of aging in some taxa, the question of the evolutionary programming of aging has been controversial (Austad 2004a, b; Bredesen 2004; Kirkwood and Melov 2011). Negligible senescence - no increase in age-related mortality, little or no decline in fertility late in life, and no age-related deterioration in physiological condition – characterizes some species, possibly ants (Finch 1990, 1998, 2009; Garcia et al. 2011; Traniello et al. 2013). Theories of aging have been prominent in seminal treatments of caste evolution (Oster and Wilson 1978), but there has been modest progress evaluating these concepts in respect to the evolution of worker longevity in ants.

Senescence and eusociality

Euociality impacts longevity in naked mole rats (Lacey and Sherman 1991): individuals have lifespans of up to 30 years, ~9 times longer than those of comparably sized rodents (Buffenstein 2008). Naked mole rats appear to show negligible senescence, and lack several physiological hallmarks of aging (Buffenstein 2008; Lewis et al. 2012). How can evolutionary and mechanistic theories of aging be applied to eusocial species, and conversely, how do the life histories of these social groups influence our understanding of senescence? Amdam and Page (2005) note that no major theory of aging was developed in respect to eusociality, or in particular, the evolutionary ecology of ants. Nevertheless, their application of intergenerational transfer theory, which considers energetic investment in offspring (Lee 2003), may in part explain social insect aging polyphenisms, although it does not adequately explain aging in reproductives (Amdam and Page 2005). Amdam and Page (2005) note that a comprehensive theoretical framework for understanding social insect aging must integrate individual and colony-level selection, which are not specifically addressed by Lee's theory. Development of a model explicitly for eusocial insects is essential to generate predictions and empirical tests of the evolution of aging in these remarkably plastic taxa. Broad analysis of costs and benefits of cooperative brood care suggests that selection can increase or decrease longevity, in part due to inclusive fitness benefits (Bourke 2007). Worker longevity should be under positive selection if its colony-level benefits exceed costs resulting from errors in task attendance, declines in performance efficiency, and metabolic maintenance associated with increasing age. Given the uncoupling of reproduction and worker labor, the fecundity/longevity tradeoff preeminent in life-history models appears to be inverted because reproductive females have the longest lifespans, and worker longevity increases following mating in species whose workers can become reproductive (Tsuji et al. 1996; Hartmann and Heinze 2003; Heinze and Schrempf 2008). Fecundity and longevity are positively correlated in facultatively polygynous *Cardicondyla obscurior* queens (Schrempf et al. 2011). Insights can be gained through such studies on ants to address key problems in gerontology (Heinze and Schrempf 2008; Rueppell 2009; Parker 2010; Amdam 2011; Lucas and Keller 2014). However, little attention has been paid to the interplay of selection on worker- and colony-level traits related to aging.

Worker aging in the eusocial Hymenoptera: honey bees

Honey bees have been the premier model of social insect aging (Rueppell et al. 2007a; Rueppell 2009; Münch and Amdam 2010; Amdam 2011). Workers generally progress from nursing to foraging through physiological, hormonal, and neurobiological changes (Münch et al. 2008). Social role (nurse or forager), rather than chronological age, appears to be the primary driver of senescence (Amdam et al. 2005; Behrends et al. 2007; Rueppell et al. 2007a; Behrends and Scheiner 2010). Foragers show age-related flight performance deficits, independent of wing wear (Vance et al. 2009), and foraging itself may be costly in respect to learning (Behrends et al. 2007). Behavioral deficits could be related to the high metabolic costs of flight and decreased antioxidant activity (Williams et al. 2008). Nursing may also shorten lifespan (Amdam et al. 2009), and the negative correlation between the age of foraging and foraging duration (Rueppell et al. 2007a, e.g.) suggests that nurses senesce demographically. Nurses also show age-related deficits in stress responses at 50 days, older

than in typically age-structured colonies (Remolina et al. 2007). Nevertheless, not all worker functions necessarily decline with age or tenure as a forager. In fact, Rueppell et al. (2007b) found that workers did not decline in phototaxis, locomotion, or sucrose responsiveness from 26 to 52 days, although mortality increased with age, suggesting the uncoupling of functional and demographic senescence. How comparable is the social nature of aging in worker ants, and what evolutionary patterns do they suggest?

Age-related behavior and the development of task repertoires in ants

In ants, behavioral development and aging impact chronological task schedules and behavioral responsiveness in multiple social contexts, including labor efficiency, outcomes of ecological interaction, body size-related worker survivorship, and ultimately colony fitness. Although the study of age-related behavior has been prominent in the analysis of the organization of labor (Robinson et al. 1994; Beshers and Fewell 2001; Toth and Robinson 2007; Duarte et al. 2011), we have only a basic understanding of how worker task performance and dynamic colony-level task allocation change over the worker lifespan, and how internal physiological states impact response thresholds and social behavior (Table 1). Age-related transitions in task performance (temporal polyethism; Wilson 1971, 1985) generally have been studied from adult eclosion to the first 3–5 weeks of adult life, or in workers of unknown age (Wilson 1976a; Seid and Traniello 2006; Muscedere et al. 2009, 2013). Chronological age is often estimated through cuticular pigmentation, which is reasonably accurate for only the first few weeks following adult eclosion (Wilson 1976a; Seid and Traniello 2006) or mandibular wear, which may confound the relationship of age and task performance (Porter and Jorgensen 1981; Schofield et al. 2011). Physiological influences on worker behavioral development begin with larval nutrition (Kaptein et al. 2005) and encompass age-related responsiveness to task stimuli (Wilson 1976a; Beshers and Fewell 2001; Seid and Traniello 2006; Duarte et al. 2011; Mersch et al. 2013), task-related mortality risk (Schmid-Hempel and Schmid-Hempel 1984; Kwapich and Tschinkel 2013), the aminergic control of task performance in workers (Seid and Traniello 2005; Muscedere et al. 2012; Kamhi and Traniello 2013; Smith et al. 2013), and neurodegeneration (Fig. 1). Ant species may differ substantially in the extent of the influence of age on behavior and its underlying physiological processes (Sendova-Franks and Franks 1993, 1995; Seid and Traniello 2006; Muscedere et al. 2009, 2011; Robinson et al. 2012, e.g.). The role of age in task performance has sparked controversy (Tofts and Franks 1992; Robson and Beshers 1997; Traniello and Rosengaus 1997); in some ants the effects of age on behavior may be weak (Sendova-Franks and Franks 1993, 1995). Workers that undergo considerable behavioral and physiological maturation following eclosion (*Pheidole dentata*: Seid and Traniello 2006; Muscedere et al. 2009, 2011) could continue to show plasticity throughout their lifespan, ultimately affecting social organization. Integrating models of division of labor (Wilson 1976a; Beshers and Fewell 2001; Seid and Traniello 2006; Duarte et al. 2011) with senescence theory will yield a deeper understanding of the evolution of worker function and colony life history.

Extrinsic mortality and worker lifespan in ants

One key prediction of aging theories is that low levels of extrinsic mortality select for long lifespan and decreased senescence (Ricklefs 1998; Amdam and Page 2005; Baudisch and

Vaupel 2010, e.g.). Ant queens surviving colony foundation are largely protected by their nests, the social organization of their colonies, and their reproductive specialization, which apart from partially claustral founding species, minimizes risks associated with extranidal activity. Similarly, worker lifespans should show effects of senescence when workers are shielded from extrinsic mortality. Oster and Wilson (1978) hypothesized that worker senescence is programmed: in the absence of extrinsic mortality, such as under laboratory conditions, worker lifespan should approximate longevity in nature. However, limited studies indicate that worker lifespan may often be significantly greater in the laboratory than in the field. *Cataglyphis bicolor* workers forage solitarily under harsh conditions of temperature and predation; they have a life expectancy of only 6.1 days in the field after initiating foraging (Schmid-Hempel and Schmid-Hempel 1984), but can nevertheless live months in the lab (Schmid-Hempel 1983). Moreover, rearing *C. fortis* workers in the dark can extend their lifespan several years (S. Stieb, pers. comm.). *Pogonomyrmex badius* workers in the field survive on average one month after they begin foraging (Kwapich and Tschinkel 2013). Foragers collected in the field and reared in the lab can live approximately 200 days longer (C. Kwapich, pers. comm.), again suggesting that short worker lifespans in the field are due to extrinsic rather than intrinsic factors.

Programmed senescence can be tested by lifespan comparisons of worker subcastes that differ in levels of extrinsic mortality. In the weaver ant *Oecophylla smaragdina,* major workers perform colony defense and foraging whereas minor workers remain in the nest caring for brood (Crozier et al. 2010). Majors are thus predicted to experience higher mortality. Despite their larger body size, majors exhibit shorter laboratory lifespans than minors (Chapuisat and Keller 2002), although field longevity data are needed. Overall, the limited data on ants show mixed, if any, support for programmed worker senescence (Table 2).

Worker life history and lifespan polyphenism

Queens initiating new colonies produce a first brood, often of nanitic workers smaller in body size than workers eclosing from later broods, to maximize initial colony growth during a vulnerable life history stage (Oster and Wilson 1978; Porter and Tschinkel 1986). During the ergonomic and reproductive stages, colony-level selection can act separately on worker and queen phenotypes to maximize reproductive success (Oster and Wilson 1978). Adaptive worker size-frequency distributions change throughout the colony lifespan (Porter and Tschinkel 1986), as does the production of increasingly large workers and/or large-bodied defensive specialists (Wilson 1983a). Colonies attain a critical size before initiating alate production (Cassill 2002; Cole 2009), indicating the dynamics of worker and reproductive production are critical to understanding colony life history.

Life history characteristics of colonies are additionally shaped by the ontogeny of individual workers and reproductives from birth to death. Ant queens appear to universally exhibit longer lifespans than workers (Keller and Genoud 1997), and workers vary in longevity. Indeed, eusociality may create circumstances conducive to long-lived workers and colonies in addition to special adaptations to group living. Ant colonies share life-history characteristics with sessile colonial invertebrates characterized by indeterminate growth and

functional modularity. Colonies of sponges, corals and ascidians, for example, increase in size through component replication and theoretically may continue to expand vegetatively (Sebens 1987; Turon and Becerro 1992). In these sessile colonial invertebrates, competition for space and resources can limit reproductive success (Ferrari et al. 2012). Thus the importance of size in shaping life-history patterns may be a general feature of colonial organisms, including ants.

Worker longevity can impact colony size. Relatively large ant colonies, under some ecological circumstances, are predicted to have fitness advantages over smaller colonies (Dornhaus et al. 2012). Al-Khafaji et al. (2009) suggest that increasing worker lifespan could interact with worker production rate to shape colony reproduction, depending on environmental conditions. Selection for worker longevity and/or production rate can increase and maintain larger colony size in ants (Asano and Cassill 2011). Honey bee workers in small colonies actually live longer than those in large colonies; this may reflect an increase in risk-taking behavior in large colonies, which are better able to buffer worker loss, or a switch in colony life history stage from growth and survival to reproduction (Rueppell et al. 2009). Differences in colony ontogeny could thus confound assessment of direct effects of group size. In ants, nesting ecology could physically constrain colony size, but this may be restricted to twig-nesting species (Wilson 1959). Nevertheless, relatively large colony size in twig-nesting ants could be beneficial even if nest size limits maximum colony size. Therefore, colonies of most ant species should theoretically benefit from expanding their worker populations. Sperm depletion could limit queen fertility, affecting colony growth, age-specific mortality and hence colony lifespan (Tschinkel 1987; den Boer et al. 2009), but selection could nevertheless produce males with greater sperm number and volume, multiple mating, or longer sperm longevity. Sperm limitation, therefore, does not seem a likely *causal* explanation for the evolution of maximum colony size (Crozier and Page 1985; Kronauer et al. 2007).

The role of colony size in shaping social structure in ant colonies and the fitness consequences of group size have been examined in light of reproductive conflict (Bourke 1999) and metabolic maintenance costs of worker subcastes (Shik 2010). Selection for worker longevity in respect to its adaptive impact on colony size has received little attention. Asano and Cassill (2011) found that when egg-laying rate was simulated to vary with the number of 4th instar larvae, colony size was determined by worker longevity. Relatively short worker lifespans are attributed to extrinsic mortality resulting from high-risk worker behaviors that buffer the queen to environmental hazards (Asano and Cassill 2011).

Increasing worker lifespan, in addition to production rates, may increase colony size, but do larger colonies have a positive effect on worker lifespan? Kramer and Schaible (2013) did not find a correlation between colony size and lifespans of workers or queens, although short-lived queens were only found in small colonies. However, colony size was positively correlated with the difference in queen and worker lifespans, a relationship potentially driven by greater division of labor in larger colonies and differential selection on caste lifespan. Below, we examine how selection for worker longevity could contribute to fitness in large colonies.

Worker longevity and colony fitness

We begin by reviewing the literature on effects of colony size on productivity to determine if larger colonies have greater reproductive success, and then present seven hypotheses concerning the relationship between worker age and colony function and how ecological advantages of large colony size could select for long lifespan in workers (Table 3). Although we heuristically list adaptive hypotheses concerning potential benefits of long-lived workers, we recognize that negative or neutral effects of worker age on colony fitness could occur, and reference these studies where applicable.

Colony size and productivity

Ant colonies grow by increasing worker population size; fitness is ultimately dependent on the production of virgin queens and males that successfully mate and establish daughter colonies. Cole (2009) notes there is little evidence that colony size directly correlates with reproductive output in mature colonies. If size were the only important factor, small colonies would be universally outcompeted by larger colonies, although small colonies can be successful (Dornhaus et al. 2012). Colony size in ants is species-typical and can range from 8 to 300 million (Kaspari and Vargo 1995). Nest-size constraints potentially important in tropical litter-nesting ants (Wilson 1959; Kaspari 1993) may not occur in other taxa (Kaspari and Vargo 1995). Even in species in which nesting ecology could constrain maximum colony size, larger colonies could nevertheless show fitness advantages. The range of effects of colony size on productivity are illustrated in *Solenopsis invicta*: manipulations of colony size and subcaste composition showed that worker size but not worker biomass affect egg production (Porter and Tschinkel 1985). Also, queen fecundity increases with the number of fourth-instar larvae, but not overall colony size, and is likely to be regulated by larval secretions fed to the queen (Tschinkel 1988). Queen starvation resistance is improved in larger colonies, indicating the important buffering capacity of a large workforce (Kaspari and Vargo 1995). Colony productivity increases with colony size for immature colonies (Tschinkel 1993). However, when immature colonies were excluded, colony size had no significant relationship with alate production (Cassill 2002). Asano and Cassill (2002) suggested that workers could buffer unpredictable challenges, particularly during overwintering. However, when mature colonies were experimentally reduced to less than one-half their size, they produced significantly fewer sexuals and increased worker production (Vargo 1988). In *Camponotus impressus*, colony size positively correlates with the production of alate males and females: the number of sexuals increases with the number of phragmotic major workers but is negatively correlated with the number of minor workers at large colony sizes (Walker and Stamps 1986). Ant species with larger colonies tended to invest in proportionately fewer but larger reproductives (Shik 2008). Per-capita production of workers and reproductives has been shown to decline with increasing colony size, without controlling explicitly for colony age (Kramer et al. 2014). The wide variation among taxa, as well as differences in seasonality, metrics used (worker number versus biomass), and age-associated effects such as queen fecundity, suggest there may not be a universal effect of colony size on per capita productivity in ants. Alternatively, such an effect may be masked by a lack of standardized methodology or confounding effects of season and interannual variability.

The complexity of the relationship between colony size and worker longevity is seen in *Temnothorax* (=*Leptothorax*) *albipennis*, whose workers can live up to 5 years in the lab (Sendova-Franks and Franks 1995), although colony size remains small (200–400 workers). In *T. longispinosus,* nests can be polydomous, and queen and nest number can respond flexibly to environmental or seasonal conditions (Herbers 1986). Colony size may be most accurately measured in these species as a composite of colonies derived from budding over time, but without queen fecundity data, it is not possible to fully assess the role of worker lifespan in shaping colony growth and reproduction. Although the relationship between colony size and worker lifespan may be elusive (Kramer and Schaible 2013), comparisons of closely related and ecologically distinct species may provide important insights. Below we present multiple hypotheses concerning how aging workers could enhance colony size by contributing to colony function and review studies that support or refute them.

1. Increased competitive ability results from the contributions of long-lived workers to a larger foraging workforce—A larger worker population having an age distribution containing older, experienced, and more efficient foragers could increase search effort and food encounter rates, and thus increase caloric intake to enhance colony fitness. Support for this hypothesis has been equivocal. Colony size in the army ant *Eciton hamatum* did not affect average or peak intake during a raid, but large colonies had higher peak intake when summed across all simultaneous raids; larger colonies do not appear to be more efficient at prey capture on the time scale of a single raid, but are likely better able to successfully attack larger prey colonies (Powell 2011). Studies of *Pogonomyrmex* species that vary in colony size suggest that the number of foragers does not affect the efficacy of harvesting a clumped food supply (Flanagan et al. 2012). *Temnothorax rugatulus* colonies with low worker density have lower foraging rates than high-density colonies, indicating that group size could interact with other characteristics, such as density effects on interaction rates, to shape mechanisms of resource exploitation (Cao 2013).

2. Efficiency of division of labor and task performance is enhanced by the presence of long-lived workers and hence larger colony size—As noted, worker age is often linked to behavioral, developmental and physiological aspects of task performance (Beshers and Fewell 2001; Muscedere et al. 2011, 2012, 2013). Few studies, however, have attempted to track labor throughout the worker lifespan in ants (Lenoir 1979; Porter and Jorgensen 1981; Schmid-Hempel and Schmid-Hempel 1984; Kwapich and Tschinkel 2013) or measure age-specific task efficiencies (Muscedere et al. 2009, 2013; Robinson et al. 2009; Amador-Vargas 2012; Constant et al. 2012). Recent studies on the completely dimorphic *Pheidole dentata* indicate that newly eclosed workers are not behaviorally mature and that age-related myological, neuroanatomical, and neurochemical changes underscore the ability of workers to labor productively (Muscedere et al. 2009, 2011, 2012). In other species, experience may affect task efficiency: mandibular wear in *Atta cephalotes* foragers increases with age, impairing leaf-cutting ability and thus colony energy expenditure (Schofield et al. 2011). Foragers having the greatest wear are more likely to carry leaves than cut them, suggesting task switching can mitigate costs of wear, thereby increasing the value of individual workers, albeit suboptimally (Schofield et al. 2011). *Pogonomyrmex owyheei* foragers also experience mandibular wear that prevents carrying

small items (Porter and Jorgensen 1981). Although no studies test whether task switching extends worker lifespan, selection may not have favored terminating workers that decline in the performance of their primary task.

The association of age and task performance appears flexible in respect to colony age structure, and demographic distributions do not appear to vary predictably with local ecological factors that likely influence caste distribution patterns (*Pheidole dentata:* Calabi and Traniello 1989a). The expanded task repertoires of older minors may compensate for the apparent inability of colonies to rapidly adjust worker age demography (Calabi and Traniello 1989b; Seid and Traniello 2006; Muscedere et al. 2009). In other ant species (*Pogonomyrmex barbatus*: Gordon 1989; Gordon and Mehdiabadi 1999; Gordon et al. 2005; *Pheidole morrisi*: Brown and Traniello 1998; Yang 2006; *Atta cephalotes*: Wilson 1983b), task flexibility may enable adaptive responses to environmental perturbations without the need to alter colony demography (Schmid-Hempel 1992). Mechanisms of adaptive skewing of physical subcaste investment have been described (Passera et al. 1996), but colony-level modification of age demography is not understood. Colonies that invest in long-lived workers may maximize plasticity in response to environmental variation, by enhancing both the experience and physiological variability of workers. This strategy may benefit colony energetic investment, particularly if worker maintenance costs are low relative to production costs (see hypothesis 7).

Results of empirical studies are mixed, but tend to support a positive association between colony size and the efficacy of partitioning tasks among different age cohorts, physical subcastes, or worker social roles. Larger colony size correlated broadly with a greater number of morphological subcastes in ants (Bonner 1993). In *Pogonomyrmex californicus,* workers became more specialized with increasing colony size (Holbrook et al. 2011), although experimentally increasing colony size did not lead to a short-term change in worker task specialization (Holbrook et al. 2013). In *Temnothorax albipennis,* colony size had no significant effect on indices of division of labor that measure the extent of worker task specialization, although the most productive workers performed more labor in small colonies (Dornhaus et al. 2009). In contrast, larger colonies of *Rhytidoponera metallica* showed temporal polyethism, with older workers spending more time foraging and younger workers more time tending brood, indicating a positive association between division of labor and colony size (Thomas and Elgar 2003). Partitioning tasks is generally considered adaptive, but the costs of increasing division of labor by dividing tasks more finely may result in delays in task switching (Anderson and Ratnieks 1999) or the presence of idle (Dornhaus et al. 2008) or specialized workers, thus outweighing the benefits of task specialization and fidelity. Response threshold models indicate that group size may have a positive effect on division of labor, although outcomes depended on interactions between group size, number of tasks and colony need (Jeanson et al. 2007). Additionally, simulations showed that recruitment rate rose with increasing colony size, producing a four-fold advantage (O'Donnell and Bulova 2007).

3. Collective decision-making is improved by long-lived workers in larger colonies—Ant colonies face ecology-based cognitive challenges that require group decisions (Conradt and Roper 2005; Couzin 2009). Highly integrated colonies provide

opportunities to examine the contribution of worker longevity, through its influence on colony size, to the emergence of cooperative group actions and collective decision-making. Larger groups are better able to average limited, individual information, improving the accuracy of collective decisions (Simons 2004) and efficiently solve problems (Morand-Ferron and Quinn 2011; Donaldson-Matasci et al. 2013). Quorum rules can be rendered in large groups when only a few individuals have information (Couzin 2009), and larger groups can utilize a smaller proportion of informed individuals to arrive at a decision (Couzin et al. 2005). *Temnothorax* colonies select the best nest available using quorum sensing (Pratt et al. 2002). Large colonies found quality nests faster, presumably through the deployment of a greater number of scouts; small colonies appear to compensate for a lower number of scouts by lowering the quorum threshold (Franks et al. 2006), although potentially compromising accuracy (Franks et al. 2003). Long-lived workers could facilitate collective decision-making by contributing to larger colony size and providing improved information based on experience, but how group size is involved in applying local information to arrive at effective group decisions is not well-studied.

Emergent group behavior is based upon stimulus detection and sensory processing by individual workers; both may be age-dependent (Hara 2003; Muscedere et al. 2009, 2012, 2013). As noted, physiological processes, including neuromodulation, may format behavioral development and/or responsiveness to task-related stimuli, and hence determine task performance (Kamhi and Traniello 2013). In *Pheidole dentata*, brain titers of serotonin and dopamine increase with age in association with the onset of foraging behavior (Seid and Traniello 2005) and are causally linked to trail-following behavior (Muscedere et al. 2012), a central component of collective foraging in which worker age may be important. Titers of serotonin continue to increase with age throughout the minor worker lifespan (YMG), but identifying how worker age, colony size, colony needs, and interactions with nestmates shape behavioral responsiveness in senescing workers remains unexplored. Large colonies of long-lived workers could have heterogenous age demographies, creating an environment of labor in which workers that vary in sensory perception or responsiveness to task cues and signals could compensate for the deficiencies of less-responsive nestmates. If chemosensory and/or cognitive abilities decline with age, then task performance efficiency would be predicted to decline. Social compensation, however, could allow colonies to accrue fitness benefits associated with emergent properties in the presence of behaviorally immature or physiologically compromised workers.

4. Nest and territory defense is improved by an older and larger workforce—
Larger colonies appear to be more effective at patrolling larger areas and recruiting a greater number of nestmates more rapidly to defend against nest invasions and territory intrusions. Moreover, theory predicts that the oldest workers, with the least residual value to the colony, should be the most likely to take risks in the context of colony defense (Wilson 1971; Agarwal et al. 2011). Larger colony size has been correlated with increased aggression, successful defense being accomplished by a smaller proportion of the workforce and higher levels of aggression by the oldest workers (Forsyth 1978; London and Jeanne 2003). *Formica rufa* workers fight harder per capita in smaller groups, but larger groups exhibit higher total levels of aggression, suggesting that workers may compensate behaviorally for

the disadvantages of smaller group size (Batchelor and Briffa 2011). In contrast, small *Formica xerophila* worker groups showed lower aggression (Tanner 2006). In *Myrmica scabrinodis*, foragers whose life expectancy was experimentally shortened foraged in riskier environments than their uncompromised nestmates (Moro et al. 2012) and may increase their risk-taking during territorial defense. *Oecophylla longinoda* colonies with the highest local density of major workers (likely a consequence of larger colony size) tended to win intraspecific territorial battles (Hölldobler and Wilson 1978). If fighting ability is experience-dependent, long-lived workers could contribute to more effective colony defense, although this remains to be tested empirically. *Pheidole dentata* major workers ("soldiers") are differentially recruited to defend against threats from fire ants, which possess a numerical advantage; therefore, a swift and strong response by majors is required to repel an attack (Wilson 1976b). Southern populations of *P. morrisi*, which are also under threat of fire ant attack, are characterized by a higher proportion of majors (15% vs. 10%), resulting in significantly more effective defense (Yang et al. 2004).

Larger colonies may achieve their size in part through defense of feeding territory. In experimental plots of fire ant (*Solenopsis invicta*) colonies, removal of ~30% of foragers decreased territory size (Adams 1998, 2003). In *Azteca trigona,* outcomes of staged battles between neighbors indicated that colonies with greater worker density won 80% of asymmetric contests, and those experimentally weakened by worker removal tended to lose territory (Adams 1990). These studies illustrate not only the benefit of numerical advantage, but also increased flexibility in allocating workers to defense in large colonies.

5. Extended worker lifespan increases colony size to combat infection risk with more effective colony-level immunocompetence—Disease risk is a cost of insect sociality (Rosengaus et al. 1998; Rosengaus and Traniello 2001; Pie et al. 2004; Cremer et al. 2007; Fefferman et al. 2007). Frequent interactions within a nest, and in the case of the eusocial Hymenoptera, close genetic relatedness, compound infection risk (Schmid-Hempel 1998; Cremer et al. 2007). Colony immunocompetence, which can depend upon group size (Rosengaus et al. 1998; Hughes et al. 2002), arises from individual immune physiology and specialized antimicrobial glands, most prominently the metapleural glands of ants (Yek and Mueller 2011), and social behaviors such as allogrooming (Calleri et al. 2006) contribute to collective defenses (Wilson-Rich et al. 2009). Group size may improve social mechanisms of infection control. *Temnothorax nylanderi* colonies infected with a cestode parasite were larger than uninfected colonies; worker productivity did not differ with infection state, suggesting that larger colonies may buffer parasitism (Scharf et al. 2012). In *Acromyrmex echinatior*, workers experimentally infected with the fungus *Metarhizium* had significantly lower survival in isolation than when maintained with nestmates (Hughes et al. 2002). Fungus-cultivating species with larger colonies relied more heavily on chemical and behavioral defenses than bacterial defenses to cope with the fungal pathogen *Escovopsis* (Fernández-Marín et al. 2009). Similar adaptive associations between colony organization and infection control have been described in other social insects (Rosengaus et al. 1998; Gao et al. 2012), and increasing worker density, a potential correlate of colony size, had a positive effect on the rate of disease transmission (Pie et al. 2004). Although these studies do not indicate a clear relationship between colony size, immune

function, and disease resistance, indirect linkages are supported. For example, a positive correlation between polyandry, which may reduce infection risk through genetic diversity (Tarpy 2003; Hughes and Boomsma 2004), and colony size have been described (Cole 1983; Boomsma and Ratnieks 1996; Hughes and Boomsma 2004; Ugelvig et al. 2010).

Disentangling causal from correlative relationships among group size, worker longevity, and social and individual immunity requires additional study. Questions remain, for example, concerning the relationship of worker age and disease susceptibility and its impact on colony-level immunocompetence. Immunosenescence is most thoroughly understood in honey bee workers (Münch et al. 2008; Amdam 2011), which decline in disease resistance with the age-associated shift from nurse to forager (Amdam et al. 2004) but recover immune function when bees revert to nurses (Amdam et al. 2005). In ants, these relationships are unknown. The presence of the metapleural gland in ants could minimize negative age-associated consequences if workers can effectively provide protection through self-grooming and allogrooming. Decreased immune function in foragers relative to nurses could indicate that foragers are essentially programmed to decrease immunocompetence, or could also represent increased investment in immune function in nurses that interact regularly with susceptible brood. Are workers with inherently weaker immune systems more likely to become foragers? What would be the potential costs and benefits of allocating immunocompromised workers to outside- or inside-nest tasks? While diseased or parasitized workers are likely less effective at performing a task than their healthy counterparts, a colony could benefit from having those individuals continue to labor at any level rather than eliminate them, provided those workers are not infective, in which self-removal from the nest would be advantageous (Heinze and Walker 2010; Rueppell et al. 2010). Furthermore, outside-nest tasks, to a degree, can spatially isolate infected workers from the queen and brood. Therefore, allocation of potentially immunocompromised workers to outside nest tasks could represent the least costly, even if suboptimal, division of labor for colonies living under infectious conditions.

6. Workers with long lifespan provide large colonies with increased allomaternal care through adaptive partitioning of nursing—Colony fitness depends on the maintenance of a social infrastructure that provides labor to successfully rear immatures to adulthood. Although overlapping generations and alloparental care in part define eusociality, the organization of brood care is understudied (Burd 1996; Schulz and Robinson 2001; Wehner et al. 2004; Muscedere et al. 2013, e.g.), and hence its relationship to worker lifespan in ants is unclear. In honey bees, the presence of brood has a small but significant negative effect on lifespan, likely through the vitellogenin-mediated onset of foraging as well as foraging-independent effects (Amdam et al. 2009), but no comparable study is available for ants. We predict that a larger workforce could lead to increased and more efficacious alloparental care. If queen oviposition rate is nutritionally limited, a larger forager population may obtain more resources to support ovarian growth and egg production although these predictions remain to be empirically verified. If larval growth rates are similarly limited by nutrition, large colonies may have a higher success rate of rearing immatures. Foraging and nursing ability, through their potential coupling to age, are likely important determinants of colony productivity. How does the delivery of nursing services by

older workers impact the efficacy of brood care? Are individuals of different ages equally adept at responding to larval needs and maximizing their growth? Do larger colonies accrue nursing efficiencies through the maintenance of aging workers?

Workers are able to assess nutritional and hygienic requirements of brood. *Pheidole dentata* minor worker nursing is positively and significantly correlated with the number of immatures in a colony; older workers are the most responsive to colony needs (Seid and Traniello 2006). *Acromyrmex spp.* minim workers respond to isolated and thus presumably hungry larvae by increasing nursing (Lopes et al. 2005), and *Solenopsis invicta* workers adjust their nursing to larval need and instar (Cassill and Tschinkel 1995). We expect that brood-care behavior across the worker lifespan is adapted to larval and colony requirements and the capability of workers to complete nursing task suites efficiently. The *presumed* relationship of worker age and brood care in ants is well-known: young workers remain in the nest to nurse until they mature and initiate extranidal tasks (Wilson 1971, 1985). However, the association of age and nursing in ants is more flexible than assumed, and age-related sensory and motor capabilities and their potential decline with senescence are poorly understood. Minor workers of all ages in *P. dentata* attempt to perform brood care (Seid and Traniello 2006), but mature workers are more effective at ensuring the survival and growth of larvae than callows (Muscedere et al. 2009). The efficiency of nursing by "elderly" workers is only beginning to be understood. *Camponotus fellah* nurses are typically younger than foragers, and midden workers ("cleaners") are of intermediate age; some nurses never forage and individuals in each labor group can be of any age, suggesting a flexible and dynamic system of polyethism (Mersch et al. 2013). *P. dentata* minor workers in the last quarter of their lifespan in laboratory colonies contribute to labor without any apparent deficits in the performance of nursing or foraging tasks (Giraldo et al., unpublished data), a finding consistent with the maintenance of some behaviors throughout life in honey bees (Rueppell et al. 2007b). It remains unknown whether *P. dentata* workers senesce rapidly before death and if behavioral functions essential for brood care are maintained independent of age. Lifetime task performance may be shaped by a "self-assessment" of behavioral competence: senescent workers could switch to less physiologically or biomechanically demanding tasks if their behavior is in fact compromised by advancing age.

Larger colonies characterized by demographics biased toward older workers may allow more brood to be raised per capita. In *S. invicta*, colony size of 100 or more workers did not affect brood-care efficiency and nursing was upregulated in response to increasing numbers of larvae until the ratio of workers:larvae exceeded one; only subcolonies of 10 workers showed a complete lack of feeding and grooming behavior (Cassill and Tschinkel 1999). Intermediate ratios of workers to brood had the highest egg-to-eclosion survival in *Formica selysi* (Purcell et al. 2011). However, colony size was not controlled and a 1:1 ratio at the largest group sizes was not tested, potentially confounding the effects of group size and worker:larva ratio.

7. Lower energetic costs of maintenance relative to replacement favor worker longevity—Ant colonies are expected to minimize energy costs of worker manufacture and maintenance to maximize reproduction (Oster and Wilson 1978). If the cost of new workers is high relative to the maintenance costs of existing workers, we expect selection will

prolong worker lifespan if sensory, motor and mechanical components of task performance do not decline with age and result in unattended or inefficiently performed tasks that compromise colony productivity and security. However, if levels of extrinsic mortality are high, then selection may favor a "disposable" workforce (Porter and Jorgensen 1981). Nevertheless, such high levels of mortality may be restricted to relatively few taxa and be associated with specific habitats and life histories. Maintenance costs are dependent on body size, temperature and activity level; production costs depend on biomass, but if prorated over the lifetime, decline with increasing worker longevity (Calabi and Porter 1989). Maintenance costs can be affected by group size as well as body size, with metabolic efficiencies gained in larger groups (Shik 2010). Therefore, lower energetic requirements of larger groups could compensate for lower per capita productivity rates (as noted above), as colony biomass production is a relatively constant proportion of colony metabolism (Shik et al. 2012). A significant portion of worker metabolic costs may be due to maintaining a potentially energetically expensive nervous system (Aiello and Wheeler 1995). Brain metabolic rates scale allometrically with body size: smaller insects have higher brain-specific metabolic rates (Kern 1985) that could change with age (Kern et al. 1984). However, the initial cost of the central nervous system is unknown. Similarly, immune function maintenance costs may be high (Poulsen et al. 2002), but production costs have not been assessed.

Benefits of maintaining long-lived workers could be related to foraging ecology. In two species of *Pogonomyrmex,* energetic benefits to the colony of a successful foraging bout are nearly one hundred times that of the cost of a forager's excursion (Weier and Feener 1995). High-cost foraging may contribute to selection for lower investment in foragers: *P. owyheei* foragers experience high mortality but have the lowest body weight of all task groups, perhaps reflecting preferential allocation of nutrition to workers with lower morality risk (Porter and Jorgensen 1981). However, in pterous social insects, flight may greatly increase forager maintenance costs (Schmid-Hempel et al. 1985; Dukas and Dukas 2011).

Production costs of workers across subcaste and the costs and benefits of maintaining the existing workforce must be determined by measuring colony energetics and task efficiency. As noted, foraging performance has to date only been demonstrated to decline in older workers due to loss of efficiency from mechanical wear; there are no studies that describe declines in foraging consequential to physiological or cognitive senescence in ants (for honey bees, see Behrends et al. 2007 and Rueppell et al. 2007b). If navigation and/or other biocomputational skills of central place foragers improve with experience, then older workers should increase their foraging performance unless sensory perception, sensorimotor functions, cognitive processing, and information storage abilities decline with advancing age, as in senescence-associated declines in foraging performance observed in honey bees (Tofilski 2000). Desert ants of the genus *Cataglyphis* shorten the distance to a food source over the course of several foraging bouts (Wolf 2008); older and presumably more experienced foragers, if they were longer lived, may improve efficiency. We anticipate that mechanical and/or physiological damage would not sufficiently accumulate and cause significant functional deficits.

Advantages of allocating older workers to risky tasks depend in part on the declining residual value of a worker as its age increases (Wilson 1971; Heinze and Schrempf 2008; Moro et al. 2012). For example, a one-month old worker has a longer potential lifespan than her nine-month old sister, and therefore the colony minimizes its losses through the allocation of the older worker to high-risk tasks. Nevertheless, the probability of death might not change substantially with age: workers that leave the safety of the nest expose themselves to risk with every departure and survivorship would only be age-dependent if elderly workers are inferior at avoiding causes of mortality. Older workers may perform the majority of defense and foraging behaviors, but this does not necessarily imply they are more efficient, or that they have lower energy costs. Furthermore, worker condition may predict task allocation (Moro et al. 2012); age itself is therefore insufficient to understand how senescence can influence risk-taking behaviors.

Nursing is also a critical context for the analysis of worker age, productivity, and maintenance costs. In ants, unlike honey bees (Robinson 1992), it appears that there are no age-related physiological limitations that preclude brood care; however, the age-related function of digestive and trophic glands has not been examined in most taxa. In *Monomorium pharaonis*, the postpharyngeal gland is likely used to feed young or sexual larvae, but nurses have thinner glandular epithelia than repletes or foragers, contrary to expectations (Eelen et al. 2006). Therefore, the relationship between glandular anatomical characteristics and age-related task performance may be complex. Foraging and larval feeding may be directly coupled, particularly in basal ant subfamilies (Hölldobler and Wilson 1990), and nursing efficiency may improve with worker age (Muscedere et al. 2009). We hypothesize that selection has acted to maintain the efficacy of both suites of behaviors throughout the worker lifespan, perhaps through maintenance of olfactory sensitivity, which is critical for both tasks.

Future studies

Our review applies sociobiological concepts framed in senescence theory and mechanistic analyses of aging to improve our understanding of how selection may act on worker lifespan and encourage the development of a comprehensive theory of aging in social insects. The benefits of our synthesis and analysis, illustrated by identifying areas of interdisciplinary fusion (Fig. 2), have yet to be fully realized. The impressive lifespan plasticity of queens and workers likely reflects variation in molecular and neural mechanisms of aging; such analyses are in their incipient stages. Historically separate theoretical constructs of senescence and proximate explanations of aging are increasingly being bridged, and further integration of neurobiology can be insightful, using ants as social models to explore brain-based aging. If worker longevity does not show evidence of programmed senescence, then physiological, neural, and molecular processes underscoring sensorimotor functions could remain intact until old age, perhaps until death, although stochastic wear and tear could lead to gradual decline in function at ages beyond which few workers survive in nature. Alternatively functional senescence could occur precipitously at the end of life. Indeed, programmed senescence and functional senescence may not be necessarily directly linked. If worker function does not decline with age, the efficacy of task performance by older workers may even be enhanced by experience through changes in gene expression or

synaptic connectivity that maintain sensory perception, integrative processing, and motor output in "elderly" workers. Assessments of neuroanatomical and neurochemical changes throughout the worker lifespan, as well as between workers that experience different levels of extrinsic mortality, could identify neural substrates associated with age-related task performance and sensecence. Alternatively, workers could continue to contribute productively to colony labor although they functionally decline, the consequences of which could be compensated for by system redundancies associated with sociality. Neuroplasticity could allow workers exhibiting mechanical wear or cognitive decline to shift their task performance profiles to more effectively fulfill colony needs. This integrative approach facilitates the genesis and testing of hypotheses central to recognizing the effects of worker lifespan on social organization, how social life shapes longevity in individuals and colonies, and the ultimate and proximate bases of aging. Critical questions identified by the overlap in sociobiology, sensecence theory, and mechanisms of aging remain largely unexplored.

A comprehensive test of the hypothesis that worker lifespan has been a target of selection in the context of benefits of larger colony size and reduced maintenance costs requires further investigation. Comparative studies in ants will be facilitated by the collection of behavioral, ecological, and sociometric data, which in conjunction with molecular phylogenies (Brady et al. 2006; Moreau et al. 2006) can provide critical analyses. We suggest several avenues of investigation.

Inter- and intraspecific comparisons of worker lifespan and senescence

A robust, phylogenetically controlled analysis of worker field and laboratory lifespans across diverse ant subfamilies can test hypotheses concerning the origin of patterns of senescence in ants and identify social and ecological factors underscoring intrinsic and extrinsic mortality. Independent contrasts could determine if worker lifespans in the lab or field are constrained by evolutionary history. Workers in socially basic species, generally characterized by smaller colony size and greater individual responsibility for a broad range of tasks, are predicted to have longer lifespans than workers of socially complex taxa characterized by larger colony size and increased age-related division of labor. The greater dependence of colonies of socially basic species on a smaller number of individuals with relatively large task repertoires may enhance selection for longer lifespan. Nevertheless, at any level of social organization, the potential benefits of large colony size we have described could lead to selection for long-lived workers: while socially complex taxa may be better able to absorb the costs of losing individual workers to extrinsic or intrinsic mortality, these colonies could nevertheless benefit from long-lived workers. Many factors are of course expected to shape selection on life history traits such as colony size and worker lifespan and have numerous fitness consequences; the relationships between these traits are unresolved (Kramer and Schaible 2013, e.g.). Furthermore, reconstruction of ancestral traits can identify how lifespan and senescence have evolved in ants in response to specific social innovations, such as the evolution of morphologically distinct worker subcastes, or nesting ecology.

Detailed analyses of specific taxa that exhibit extensive variation in levels of extrinsic mortality between worker groups could be used to evaluate the prediction that shielding a subset of workers from risk leads to selection for longevity. A comparison of lifespans

between foragers and intranidal workers in taxa in which these social roles are distinct and/or spatially segregated could identify whether the presence of a subset of workers in a protected environment endows all workers with long life. Age-based models of division of labor generally assume, sometimes implicitly, that all individuals pass through all stages of behavioral development as they age; all nurses are typically thought to become foragers (Wilson 1976a; Robinson 1992; Beshers and Fewell 2001), or expand their repertoires as they mature (Seid and Traniello 2006). However, few studies (Lenoir 1979; Mersch et al. 2013) have tracked lifetime task performance in ants. If some workers remain primarily or wholly within the nest for their entire lives, they may be subject to greater selection for longevity. In general, we lack information on how individual behavioral roles change throughout the worker lifespan in the field. If only a subset of workers become foragers, then the often implicit assumption that all workers become foragers might significantly underestimate field lifespans if longevity data are collected only on workers that leave the nest. Additionally, ecological manipulations (field enclosures, e.g.) that either increase or decrease extrinsic mortality by eliminating predation or changing local humidity or temperature could reveal how colonies respond in the short term to increases in extrinsic mortality.

Senescence and sociogenomics

Examinations of worker and queen lifespans, both intra- and interspecifically, have the potential to reveal the extent of plasticity and constraints on longevity in ants. Sociogenomic studies of ants (Libbrecht et al. 2013) enable molecular technologies to address long-standing questions concerning the evolutionary ecology and behavioral organization of division of labor and senescence. For example, *Harpegnathos saltator* gamergates upregulate gene expression in association with slower aging relative to workers (notably telomerase, involved in telomere replacement, and sirturins [Bonasio et al. 2010], responsible for many cellular functions including DNA-repair [Vaquero and Reinberg 2009]). Molecular homologies between ants and vertebrates in aging-related genes (Bonasio et al. 2010) further demonstrate the value of developing ants as social models of aging. By utilizing enhanced abilities to characterize the molecular, genetic, and neural underpinnings of the aging process in ants, an integrative understanding of senescence in social organisms can be achieved.

Conclusions

Potential benefits of large colony size, achievable in part through extended worker lifespan, appear to argue against the programming of worker senescence and suggest colony-level selection promotes worker longevity under conditions that realistically affect colony fitness. To date, there have been limited tests of Oster and Wilson's (1978) programmed senescence theory and other evolutionary theories of aging in ants; the few available studies fail to strongly support the prediction that field and laboratory lifespans are tightly linked. We hypothesize that long worker lifespan will be under positive selection to achieve larger colony size and thus provide colony-level fitness advantages under some circumstances. Enhanced colony growth and reproduction could be realized through improved resource acquisition, division of labor, group decision-making, defense, immunocompetence,

allomaternal care, and cost savings in worker maintenance. Our review identified mixed support for the proposed benefits of large colony size. Worker task efficiency is influenced by physiological and behavioral development, experience, and mechanical wear, all of which may change throughout the lifespan (Fig. 1). From eclosion to death, workers undergo neuronal restructuring and changes in sensory abilities that shape their roles within the colony. Ant workers may therefore be considerably more plastic than assumed in their behavioral repertoires, leading to flexible responses to colony needs and the potential to compensate for efficiency declines in senescent colony members, if they occur.

Acknowledgments

References

Adams ES. Boundary disputes in the territorial ant *Azteca trigona*: effects of asymmetries in colony size. Anim Behav. 1990; 39:321–328.

Adams ES. Territory size and shape in fire ants: a model based on neighborhood interactions. Ecology. 1998; 79:1125–1134.

Adams ES. Experimental analysis of territory size in a population of the fire ant *Solenopsis invicta*. Behav Ecol. 2003; 14:48–53.

Agarwal M, Giannoni Guzmán M, Morales-Matos C, Del Valle Díaz RA, Abramson CI, Giray T. Dopamine and octopamine influence avoidance learning of honey bees in a place preference assay. PLoS ONE. 2011; 6:e25371. [PubMed: 21980435]

Aiello LC, Wheeler P. The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. Curr Anthropol. 1995; 36:199–221.

Al-Khafaji K, Tuljapurkar S, Carey JR, Page RE. Hierarchical demography: a general approach with an application to honey bees. Ecology. 2009; 90:556–566. [PubMed: 19323239]

Amador-Vargas S. Behavioral responses of acacia ants correlate with age and location on the host plant. Insect Soc. 2012; 59:341–350.

Amdam GV. Social context, stress, and plasticity of aging. Aging Cell. 2011; 10:18–27. [PubMed: 21070589]

Amdam GV, Aase ALTO, Seehuus S-C, Fondrk MK, Norberg K, Hartfelder K. Social reversal of immunosenescence in honey bee workers. Exp Gerontol. 2005; 40:939–947. [PubMed: 16169181]

Amdam GV, Page RE. Intergenerational transfers may have decoupled physiological and chronological age in a eusocial insect. Ageing Res Rev. 2005; 4:398–408. [PubMed: 16039913]

Amdam GV, Rueppell O, Fondrk MK, Page RE, Nelson CM. The nurse's load: early life exposure to brood-rearing affects behavior and lifespan in honey bees (*Apis mellifera*). Exp Gerontol. 2009; 44:467–471. [PubMed: 19264121]

Amdam GV, Simões ZLP, Hagen A, Norberg K, Schrøder K, Mikkelsen Ø, Kirkwood TBL, Omholt SW. Hormonal control of the yolk precursor vitellogenin regulates immune function and longevity in honeybees. Exp Gerontol. 2004; 39:767–773. [PubMed: 15130671]

Anderson C, Ratnieks F. Task partitioning in insect societies. I. Effect of colony size on queueing delay and colony ergonomic efficiency. Am Nat. 1999; 154:521–535. [PubMed: 10561125]

Asano E, Cassill DL. Impact of worker longevity and other endogenous factors on colony size in the fire ant, *Solenopsis invicta*. Insect Soc. 2011; 58:551–557.

Austad SN. Is there a role for new invertebrate models for aging research? J Gerontol Biol Sci. 2009; 64:192–194.

Batchelor TP, Briffa M. Fight tactics in wood ants: individuals in smaller groups fight harder but die faster. Proc R Soc Lond B. 2011; 278:3243–3250.

Baudisch A, Vaupel J. Senescence vs. sustenance: evolutionary-demographic models of aging. Demogr Res. 2010; 23:655–668.

Behrends A, Scheiner R. Learning at old age: a study on winter bees. Front Behav Neurosci. 2010; 4:15. [PubMed: 20428511]

Behrends A, Scheiner R, Baker N, Amdam GV. Cognitive aging is linked to social role in honey bees (*Apis mellifera*). Exp Gerontol. 2007; 42:1146–1153. [PubMed: 17976939]

Beshers SN, Fewell JH. Models of division of labor in social insects. Annu Rev Entomol. 2001; 46:413–440. [PubMed: 11112175]

den Boer SPA, Baer B, Dreier S, Aron S, Nash DR, Boomsma JJ. Prudent sperm use by leaf-cutter ant queens. Proc R Soc Lond B. 2009; 276:3945–3953.

Bonasio R, Zhang G, Ye C, Mutti NS, Fang X, et al. Genomic comparison of the ants *Camponotus floridanus* and *Harpegnathos saltator*. Science. 2010; 329:1068–1071. [PubMed: 20798317]

Bonner JT. Dividing the labour in cells and societies. Curr Sci. 1993; 64:459–466.

Boomsma JJ, Ratnieks FLW. Paternity in eusocial hymenoptera. Philos T Roy Soc B. 1996; 351:947–975.

Bourke AFG. Colony size, social complexity and reproductive conflict in social insects. J Evol Biol. 1999; 12:245–257.

Bourke AFG. Kin selection and the evolutionary theory of aging. Annu Rev Ecol Evol S. 2007; 38:103–128.

Brady SG, Schultz TR, Fisher BL, Ward PS. Evaluating alternative hypotheses for the early evolution and diversification of ants. P Natl Acad Sci USA. 2006; 103:18172–18177.

Bredesen DE. The non-existent aging program: how does it work? Aging Cell. 2004; 3:255–259. [PubMed: 15379848]

Brown JJ, Traniello JFA. Regulation of brood-care behavior in the dimorphic castes of the ant *Pheidole morrisi* (Hymenoptera: Formicidae): effects of caste ratio, colony size, and colony needs. J Insect Behav. 1998; 11:209–219.

Buffenstein R. Negligible senescence in the longest living rodent, the naked mole-rat: insights from a successfully aging species. J Comp Physiol B. 2008; 178:439–445. [PubMed: 18180931]

Burd M. Foraging performance by *Atta colombica*, a leaf-cutting ant. Am Nat. 1996; 148:597–612.

Calabi P, Porter SD. Worker longevity in the fire ant *Solenopsis invicta*: ergonomic considerations of correlations between temperature, size and metabolic rates. J Insect Physiol. 1989; 35:643–649.

Calabi P, Traniello JFA. Social organization in the ant *Pheidole dentata*: physical and temporal caste ratios lack ecological correlates. Behav Ecol Sociobiol. 1989a; 24:69–78.

Calabi P, Traniello JFA. Behavioral flexibility in age castes of the ant *Pheidole dentata*. J Insect Behav. 1989b; 2:663–677.

Calleri DV, McGrail Reid E, Rosengaus RB, Vargo EL, Traniello JFA. Inbreeding and disease resistance in a social insect: effects of heterozygosity on immunocompetence in the termite *Zootermopsis angusticollis*. Proc R Soc Lond B. 2006; 273:2633–2640.

Cao TT. High social density increases foraging and scouting rates and induces polydomy in *Temnothorax* ants. Behav Ecol Sociobiol. 2013; 67:1799–1807.

Cassill D. Yoyo-bang: a risk-aversion investment strategy by a perennial insect society. Oecologia. 2002; 132:150–158.

Cassill DL, Tschinkel WR. Allocation of liquid food to larvae via trophallaxis in colonies of the fire ant, *Solenopsis invicta*. Anim Behav. 1995; 50:801–813.

Cassill DL, Tschinkel WR. Effects of colony-level attributes on larval feeding in the fire ant, *Solenopsis invicta*. Insect Soc. 1999; 46:261–266.

Chapuisat M, Keller L. Division of labour influences the rate of ageing in weaver ant workers. Proc R Soc Lond B. 2002; 269:909–913.

Cole BJ. Multiple mating and the evolution of social behavior in the Hymenoptera. Behav Ecol Sociobiol. 1983; 12:191–201.

Cole, BJ. The ecological setting of social evolution: the demography of ant populations. In: Fewell, JH.; Gadau, J., editors. New Frontiers for Behavioral Ecology: From Gene to Society. Harvard University Press; 2009. p. 74-104.

Conradt L, Roper TJ. Consensus decision making in animals. Trends Ecol Evol. 2005; 20:449–456. [PubMed: 16701416]

Constant N, Santorelli LA, Lopes JFS, Hughes WOH. The effects of genotype, caste, and age on foraging performance in leaf-cutting ants. Behav Ecol. 2012; 23:1284–1288.

Couzin ID. Collective cognition in animal groups. Trends Cogn Sci. 2009; 13:36–43. [PubMed: 19058992]

Couzin ID, Krause J, Franks NR, Levin SA. Effective leadership and decision-making in animal groups on the move. Nature. 2005; 433:513–516. [PubMed: 15690039]

Cremer S, Armitage SAO, Schmid-Hempel P. Social immunity. Curr Biol. 2007; 17:R693–R702. [PubMed: 17714663]

Crozier RH, Newey PS, Schlüns EA, Robson SKA. A masterpiece of evolution – *Oecophylla* weaver ants (Hymenoptera: Formicidae). Myrmecol News. 2010; 13:57–71.

Crozier RH, Page RE. On being the right size: male contributions and multiple mating in social Hymenoptera. Behav Ecol Sociobiol. 1985; 18:105–115.

Donaldson-Matasci MC, DeGrandi-Hoffman G, Dornhaus A. Bigger is better: honeybee colonies as distributed information-gathering systems. Anim Behav. 2013; 85:585–592.

Dornhaus A, Holley J-A, Franks NR. Larger colonies do not have more specialized workers in the ant *Temnothorax albipennis*. Behav Ecol. 2009; 20:922–929.

Dornhaus A, Holley J-A, Pook VG, Worswick G, Franks NR. Why do not all workers work? Colony size and workload during emigrations in the ant *Temnothorax albipennis*. Behav Ecol Sociobiol. 2008; 63:43–51.

Dornhaus A, Powell S, Bengston S. Group size and its effects on collective organization. Annu Rev Entomol. 2012; 57:123–141. [PubMed: 21888521]

Duarte A, Weissing FJ, Pen I, Keller L. An evolutionary perspective on self-organized division of labor in social insects. Annu Rev Ecol Evol S. 2011; 42:91–110.

Dukas R, Dukas L. Coping with nonrepairable body damage: effects of wing damage on foraging performance in bees. Anim Behav. 2011; 81:635–638.

Eelen D, Børgesen L, Billen J. Functional morphology of the postpharyngeal gland of queens and workers of the ant *Monomorium pharaonis* (L.). Acta Zool. 2006; 87:101–111.

Fefferman NH, Traniello JFA, Rosengaus RB, Calleri DV. Disease prevention and resistance in social insects: modeling the survival consequences of immunity, hygienic behavior, and colony organization. Behav Ecol Sociobiol. 2007; 61:565–577.

Fernández-Marín H, Zimmerman JK, Nash DR, Boomsma JJ, Wcislo WT. Reduced biological control and enhanced chemical pest management in the evolution of fungus farming in ants. Proc R Soc Lond B. 2009; 276:2263–2269.

Ferrari R, Gonzalez-Rivero M, Mumby P. Size matters in competition between corals and macroalgae. Mar Ecol Prog Ser. 2012; 467:77–88.

Finch, CE. Longevity, senescence, and the genome. University of Chicago Press; Chicago: 1990.

Finch CE. Variations in senescence and longevity include the possibility of negligible senescence. J Gerontol. 1998; 53A:B235–B239.

Finch CE. Update on slow aging and negligible senescence--a mini-review. Gerontology. 2009; 55:307–313. [PubMed: 19439974]

Fjerdingstad EJ, Crozier RH. The evolution of worker caste diversity in social insects. Am Nat. 2006; 167:390–400. [PubMed: 16673347]

Flanagan TP, Letendre K, Burnside WR, Fricke GM, Moses ME. Quantifying the effect of colony size and food distribution on harvester ant foraging. PLoS ONE. 2012; 7:e39427. [PubMed: 22808035]

Forsyth, A. Dissertation. Harvard University; 1978. Studies on the behavioral ecology of polygynous social wasps.

Franks NR, Dornhaus A, Best CS, Jones EL. Decision making by small and large house-hunting ant colonies: one size fits all. Anim Behav. 2006; 72:611–616.

Franks NR, Dornhaus A, Fitzsimmons JP, Stevens M. Speed versus accuracy in collective decision making. Proc R Soc Lond B. 2003; 270:2457–2463.

Gao Q, Bidochka MJ, Thompson GJ. Effect of group size and caste ratio on individual survivorship and social immunity in a subterranean termite. Acta Ethol. 2012; 15:55–63.

Garcia MB, Dahlgren JP, Ehrlén J. No evidence of senescence in a 300-year-old mountain herb. J Ecol. 2011; 99:1424–1430.

Gordon DM. Dynamics of task switching in harvester ants. Anim Behav. 1989; 38:194–204.

Gordon DM, Chu J, Lillie A, Tissot M, Pinter N. Variation in the transition from inside to outside work in the red harvester ant *Pogonomyrmex barbatus*. Insect Soc. 2005; 52:212–217.

Gordon DM, Mehdiabadi NJ. Encounter rate and task allocation in harvester ants. Behav Ecol Sociobiol. 1999; 45:370–377.

Hara K. Queen discrimination ability of ant workers (*Camponotus japonicus*) coincides with brain maturation. Brain Behav Evol. 2003; 62:56–64. [PubMed: 12907860]

Hartmann A, Heinze J. Lay eggs, live longer: division of labor and life span in a clonal ant species. Evolution. 2003; 57:2424–2429. [PubMed: 14628930]

Heinze J, Schrempf A. Aging and reproduction in social insects--a mini-review. Gerontology. 2008; 54:160–167. [PubMed: 18367827]

Heinze J, Walter B. Moribund ants leave their nests to die in social isolation. Curr Biol. 2010; 20:249–252. [PubMed: 20116243]

Herbers JM. Nest site limitation and facultative polygyny in the ant *Leptothorax longispinosus*. Behav Ecol Sociobiol. 1986; 19:115–122.

Holbrook CT, Barden PM, Fewell JH. Division of labor increases with colony size in the harvester ant *Pogonomyrmex californicus*. Behav Ecol. 2011; 22:960–966.

Holbrook CT, Eriksson TH, Overson RP, Gadau J, Fewell JH. Colony-size effects on task organization in the harvester ant *Pogonomyrmex californicus*. Insect Soc. 2013; 60:191–201.

Hölldobler B, Wilson EO. The multiple recruitment systems of the African weaver ant *Oecophylla longinoda* (Latreille)(Hymenoptera: Formicidae). Behav Ecol Sociobiol. 1978; 3:19–60.

Hölldobler, B.; Wilson, EO. The Ants. Belknap Press of Harvard University Press; Cambridge, MA: 1990.

Hughes WOH, Boomsma JJ. Genetic diversity and disease resistance in leaf-cutting ant societies. Evolution. 2004; 58:1251–1260. [PubMed: 15266974]

Hughes WOH, Eilenberg J, Boomsma JJ. Trade-offs in group living: transmission and disease resistance in leaf-cutting ants. Proc R Soc Lond B. 2002; 269:1811–1819.

Jeanson R, Fewell JH, Gorelick R, Bertram SM. Emergence of increased division of labor as a function of group size. Behav Ecol Sociobiol. 2007; 62:289–298.

Jemielity S, Chapuisat M, Parker JD, Keller L. Long live the queen: studying aging in social insects. Age. 2005; 27:241–248. [PubMed: 23598656]

Kamhi JF, Traniello JFA. Biogenic amines and collective organization in a superorganism: neuromodulation of social behavior in ants. Brain Behav Evol. 2013; 82:220–236. [PubMed: 24281765]

Kaptein N, Billen J, Gobin B. Larval begging for food enhances reproductive options in the ponerine ant *Gnamptogenys striatula*. Anim Behav. 2005; 69:293–299.

Kaspari M. Removal of seeds from neotropical frugivore droppings: ant responses to seed number. Oecologia. 1993; 95:81–88.

Kaspari M, Vargo E. Colony size as a buffer against seasonality: Bergmann's rule in social insects. Am Nat. 1995; 145:610–632.

Keeler KH. Fifteen years of colony dynamics in *Pogonomyrmex occidentalis*, the western harvester ant, in western Nebraska. Southwest Nat. 1993; 38:286–289.

Keller L. Queen lifespan and colony characteristics in ants and termites. Insect Soc. 1998; 45:235–246.

Keller L, Genoud M. Extraordinary lifespans in ants: a test of evolutionary theories of ageing. Nature. 1997; 389:3–6. [PubMed: 9288950]

Kern M, Wegener G. Age affects the metabolic rate of insect brain. Mech Ageing Dev. 1984; 28:237–242. [PubMed: 6521504]

Kern MJ. Metabolic rate of the insect brain in relaiton to body size and phylogeny. Comp Biochem Phys Part A. 1985; 81A:501–506.

Kirkwood TBL. Evolution of ageing. Nature. 1977; 270:301–304. [PubMed: 593350]

Kirkwood TBL, Melov S. On the programmed/non-programmed nature of ageing within the life history. Curr Biol. 2011; 21:R701–R707. [PubMed: 21959160]

Kramer BH, Schaible R. Colony size explains the lifespan differences between queens and workers in eusocial Hymenoptera. Biol J Linn Soc. 2013; 109:710–724.

Kramer BH, Scharf I, Foitzik S. The role of per-capita productivity in the evolution of small colony sizes in ants. Behav Ecol Sociobiol. 2014; 68:41–53.

Kronauer DJC, Johnson RA, Boomsma JJ. The evolution of multiple mating in army ants. Evolution. 2007; 61:413–422. [PubMed: 17348950]

Kwapich CL, Tschinkel WR. Demography, demand, death, and the seasonal allocation of labor in the Florida harvester ant (*Pogonomyrmex badius*). Behav Ecol Sociobiol. 2013; 67:2011–2027.

Lacey, EA.; Sherman, PW. Social organization of naked mole-rat colonies: evidence for division of labor. In: Sherman, PW.; Jarvis, JUM.; Alexander, R., editors. The biology of the naked mole-rat. Princeton University Press; Princeton, NJ: 1991. p. 275-336.

Lee RD. Rethinking the evolutionary theory of aging: transfers, not births, shape senescence in social species. P Natl Acad Sci USA. 2003; 100:9637–9642.

Lenoir A. Le comportement alimentaire et la division du travail chez la fourmi *Lasius niger* (L.). Bull Biol Fr Belg. 1979; 113:79–314.

Lewis KN, Mele J, Hornsby PJ, Buffenstein R. Stress resistance in the naked mole-rat: the bare essentials - a mini-review. Gerontology. 2012; 58:453–462. [PubMed: 22572398]

Libbrecht R, Oxley PR, Kronauer DJ, Keller L. Ant genomics sheds light on the molecular regulation of social organization. Genome Biol. 2013; 14:212. [PubMed: 23895728]

London KB, Jeanne RL. Effects of colony size and stage of development on defense response by the swarm-founding wasp *Polybia occidentalis*. Behav Ecol Sociobiol. 2003; 54:539–546.

Lopes JFS, Hughes WOH, Camargo RS, Forti LC. Larval isolation and brood care in *Acromyrmex* leaf-cutting ants. Insect Soc. 2005; 52:333–338.

Lucas E, Keller L. Ageing and somatic maintenance in social insects. Curr Op Insect Sci. 201410.1016/j.cois.2014.09.009

Medawar, PB. An unsolved problem of biology. H. K. Lewis; London: 1952.

Mersch DP, Crespi A, Keller L. Tracking individuals shows spatial fidelity is a key regulator of ant social organization. Science. 2013; 340:1090–1093. [PubMed: 23599264]

Morand-Ferron J, Quinn JL. Larger groups of passerines are more efficient problem solvers in the wild. P Natl Acad Sci USA. 2011; 108:15898–15903.

Moreau CS, Bell CD, Vila R, Archibald SB, Pierce NE. Phylogeny of the ants: diversification in the age of angiosperms. Science. 2006; 312:101–104. [PubMed: 16601190]

Moro D, Lenda M, Skórka P, Woyciechowski M. Short-lived ants take greater risks during food collection. Am Nat. 2012; 180:744–750. [PubMed: 23149399]

Münch D, Amdam GV. The curious case of aging plasticity in honey bees. FEBS Lett. 2010; 584:2496–2503. [PubMed: 20385132]

Münch D, Amdam GV, Wolschin F. Ageing in a eusocial insect: molecular and physiological characteristics of life span plasticity in the honey bee. Funct Ecol. 2008; 22:407–421. [PubMed: 18728759]

Muscedere ML, Djermoun A, Traniello JFA. Brood-care experience, nursing performance, and neural development in the ant *Pheidole dentata*. Behav Ecol Sociobiol. 2013; 67:775–784.

Muscedere ML, Johnson N, Gillis BC, Kamhi JF, Traniello JFA. Serotonin modulates worker responsiveness to trail pheromone in the ant *Pheidole dentata*. J Comp Physiol A. 2012; 198:219–227.

Muscedere ML, Traniello JFA, Gronenberg W. Coming of age in an ant colony: cephalic muscle maturation accompanies behavioral development in *Pheidole dentata*. Naturwissenschaften. 2011; 98:783–793. [PubMed: 21792597]

Muscedere ML, Willey TA, Traniello JFA. Age and task efficiency in the ant *Pheidole dentata*: young minor workers are not specialist nurses. Anim Behav. 2009; 77:911–918.

Nussey DH, Froy H, Lemaitre J-F, Gaillard J-M, Austad SN. Senescence in natural populations of animals: widespread evidence and its implications for bio-gerontology. Ageing Res Rev. 2013; 12:214–225. [PubMed: 22884974]

O'Donnell S, Bulova SJ. Worker connectivity: a simulation model of variation in worker communication and its effects on task performance. Insect Soc. 2007; 54:211–218.

Oster, GF.; Wilson, EO. Caste and Ecology in the Social Insects. Princeton University Press; Princeton, NJ: 1978.

Parker JD. What are social insects telling us about aging? Myrmecol News. 2010; 13:103–110.

Partridge L, Gems D. Beyond the evolutionary theory of ageing, from functional genomics to evo-gero. Trends Ecol Evol. 2006; 21:334–340. [PubMed: 16769434]

Passera L, Roncin E, Kaufmann B, Keller L. Increased soldier production in ant colonies exposed to intraspecific competition. Nature. 1996; 379:630–631.

Pie MR, Rosengaus RB, Traniello JFA. Nest architecture, activity pattern, worker density and the dynamics of disease transmission in social insects. J Theor Biol. 2004; 226:45–51. [PubMed: 14637053]

Porter SD, Jorgensen CD. Foragers of the harvester ant, *Pogonomyrmex owyheei*: a disposable caste? Behav Ecol Sociobiol. 1981; 9:247–256.

Porter SD, Tschinkel WR. Fire ant polymorphism: the ergonomics of brood production. Behav Ecol Sociobiol. 1985; 16:323–336.

Porter SD, Tschinkel WR. Adaptive value of nanitic workers in newly founded red imported fire ant colonies (Hymenoptera: Formicidae). Ann Entomol Soc Am. 1986; 79:723–726.

Poulsen M, Bot ANM, Nielsen MG, Boomsma JJ. Experimental evidence for the costs and hygienic significance of the antibiotic metapleural ants gland secretion in leaf-cutting ants. Behav Ecol Sociobiol. 2002; 52:151–157.

Powell S. How much do army ants eat? On the prey intake of a neotropical top-predator. Insect Soc. 2011; 58:317–324.

Pratt S, Mallon E, Sumpter D, Franks N. Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *Leptothorax albipennis*. Behav Ecol Sociobiol. 2002; 52:117–127.

Purcell J, Brütsch T, Chapuisat M. Effects of the social environment on the survival and fungal resistance of ant brood. Behav Ecol Sociobiol. 2011; 66:467–474.

Rauser CL, Mueller LD, Rose MR. The evolution of late life. Ageing Res Rev. 2006; 5:14–32. [PubMed: 16085467]

Remolina SC, Hafez DM, Robinson GE, Hughes KA. Senescence in the worker honey bee *Apis mellifera*. J Insect Physiol. 2007; 53:1027–1033. [PubMed: 17692333]

Ricklefs RE. Evolutionary theories of aging: confirmation of a fundamental prediction, with implications for the genetic basis and evolution of life span. Am Nat. 1998; 152:24–44. [PubMed: 18811399]

Ridley M. Clutch size and mating frequency in parasitic Hymenoptera. Am Nat. 1993; 142:893–910.

Robinson EJH, Feinerman O, Franks NR. Flexible task allocation and the organization of work in ants. Proc R Soc Lond B. 2009; 276:4373–4380.

Robinson EJH, Feinerman O, Franks NR. Experience, corpulence and decision making in ant foraging. J Exp Biol. 2012; 215:2653–2659. [PubMed: 22786642]

Robinson GE. Regulation of division of labor in insect societies. Annu Rev Entomol. 1992; 37:637–665. [PubMed: 1539941]

Robinson GE, Page R Jr, Huang Z. Temporal polyethism in social insects is a developmental process. Anim Behav. 1994; 48:467–469.

Robson SK, Beshers SN. Division of labour and "foraging for work": simulating reality versus the reality of simulations. Anim Behav. 1997; 53:214–218.

Rosengaus RB, Maxmen AB, Coates LE, Traniello JFA. Disease resistance: a benefit of sociality in the dampwood termite *Zootermopsis angusticollis* (Isoptera: Termopsidae). Behav Ecol Sociobiol. 1998; 44:125–134.

Rosengaus RB, Traniello JFA. Disease susceptibility and the adaptive nature of colony demography in the dampwood termite *Zootermopsis angusticollis*. Behav Ecol Sociobiol. 2001; 50:546–556.

Rueppell, O. Aging of social insects. In: Gadeau, J.; Fewell, J.; Wilson, EO., editors. Organization of Insect Societies: From Genome to Sociocomplexity. Harvard University Press; Cambridge, MA: 2009. p. 51-73.

Rueppell O, Bachelier C, Fondrk MK, Page RE. Regulation of life history determines lifespan of worker honey bees (*Apis mellifera* L.). Exp Gerontol. 2007a; 42:1020–1032. [PubMed: 17689041]

Rueppell O, Christine S, Mulcrone C, Groves L. Aging without functional senescence in honey bee workers. Curr Biol. 2007b; 17:R274–R275. [PubMed: 17437701]

Rueppell O, Hayworth MK, Ross NP. Altruistic self-removal of health-compromised honey bee workers from their hive. J Evol Biol. 2010; 23:1538–1546. [PubMed: 20500363]

Rueppell O, Kaftanouglu O, Page RE. Honey bee (*Apis mellifera*) workers live longer in small than large colonies. Exp Gerontol. 2009; 44:447–452. [PubMed: 19389467]

Scharf I, Modlmeier AP, Beros S, Foitzik S. Ant societies buffer individual-level effects of parasite infections. Am Nat. 2012; 180:671–683. [PubMed: 23070326]

Schmid-Hempel, P. Dissertation. Universität Zürich; 1983. Foraging ecology and colony structure of two sympatric species of desert ants *Cataglyphis bicolor* and *Cataglyphis albicans*.

Schmid-Hempel P. Worker castes and adaptive demography. J Evol Biol. 1992; 5:1–12.

Schmid-Hempel, P. Parasites in Social Insects. Princeton University Press; Princeton, NJ: 1998.

Schmid-Hempel P, Kacelnik A, Houston AI. Honeybees maximize efficiency by not filling their crop. Behav Ecol Sociobiol. 1985; 17:61–66.

Schmid-Hempel P, Schmid-Hempel R. Life duration and turnover of foragers in the ant *Cataglyphis bicolor* (Hymenoptera, Formicidae). Insect Soc. 1984; 31:345–360.

Schofield RMS, Emmett KD, Niedbala JC, Nesson MH. Leaf-cutter ants with worn mandibles cut half as fast, spend twice the energy, and tend to carry instead of cut. Behav Ecol Sociobiol. 2011; 65:969–982.

Schrempf A, Cremer S, Heinze J. Social influence on age and reproduction: reduced lifespan and fecundity in multi-queen ant colonies. J Evol Biol. 2011; 24:1455–1461. [PubMed: 21507120]

Schulz DJ, Robinson GE. Octopamine influences division of labor in honey bee colonies. J Comp Physiol A. 2001; 187:53–61. [PubMed: 11318378]

Sebens KP. The ecology of indeterminant growth in animals. Annu Rev Ecol Syst. 1987; 18:371–407.

Seid MA, Traniello JFA. Age-related changes in biogenic amines in individual brains of the ant *Pheidole dentata*. Naturwissenschaften. 2005; 92:198–201. [PubMed: 15776257]

Seid MA, Traniello JFA. Age-related repertoire expansion and division of labor in *Pheidole dentata* (Hymenoptera: Formicidae): a new perspective on temporal polyethism and behavioral plasticity in ants. Behav Ecol Sociobiol. 2006; 60:631–644.

Sendova-Franks A, Franks NR. Task allocation in ant colonies within variable environments (a study of temporal polyethism: experimental). Bull Math Biol. 1993; 55:75–96.

Sendova-Franks AB, Franks NR. Spatial relationships within nests of the ant *Leptothorax unifasciatus* (Latr.) and their implications for division of labor. Anim Behav. 1995; 50:121–136.

Shahrestani P, Mueller LD, Rose MD. Does aging stop? Curr Aging Sci. 2009; 2:3–11. [PubMed: 20021395]

Shik JZ. Ant colony size and the scaling of reproductive effort. Funct Ecol. 2008; 22:674–681.

Shik JZ. The metabolic costs of building ant colonies from variably sized subunits. Behav Ecol Sociobiol. 2010; 64:1981–1990.

Shik JZ, Hou C, Kay A, Kaspari M, Gillooly JF. Towards a general life-history model of the superorganism: predicting the survival, growth and reproduction of ant societies. Biol Lett. 2012; 8:1059–1062. [PubMed: 22896271]

Simons AM. Many wrongs: the advantage of group navigation. Trends Ecol Evol. 2004; 19:453–455. [PubMed: 16701304]

Smith AR, Muscedere ML, Seid MA, Traniello JFA, Hughes WOH. Biogenic amines are associated with worker task but not patriline in the leaf-cutting ant *Acromyrmex echinatior*. J Comp Physiol A. 2013; 199:1117–1127.

Tanner CJ. Numerical assessment affects aggression and competitive ability: a team-fighting strategy for the ant *Formica xerophila*. Proc R Soc Lond B. 2006; 273:2737–2742.

Tarpy DR. Genetic diversity within honeybee colonies prevents severe infections and promotes colony growth. Proc R Soc Lond B. 2003; 270:99–103.

Thomas ML, Elgar MA. Colony size affects division of labour in the ponerine ant *Rhytidoponera metallica*. Naturwissenschaften. 2003; 90:88–92. [PubMed: 12590305]

Tofilski A. Senescence and learning in honeybee (*Apis mellifera*) workers. Acta Neurobiol Exp. 2000; 60:35–39.

Tofts C, Franks NR. Doing the right thing: ants, honeybees and naked mole-rats. Trends Ecol Evol. 1992; 7:346–349. [PubMed: 21236060]

Toth AL, Robinson GE. Evo-devo and the evolution of social behavior. Trends Genet. 2007; 23:334–341. [PubMed: 17509723]

Traniello IM, Sîrbulescu RF, Ilie I, Zupanc GKH. Age-related changes in stem cell dynamics, neurogenesis, apoptosis, and gliosis in the adult brain: A novel teleost fish model of negligible senescence. Dev Neurobiol. 2013; 74:514–530. [PubMed: 24293183]

Traniello JFA, Rosengaus RB. Ecology, evolution and division of labour in social insects. Anim Behav. 1997; 53:209–213.

Tschinkel WR. Sociometry and sociogenesis of colonies of the fire ant *Solenopsis invicta* during one annual cycle. Ecol Monogr. 1993; 63:425–457.

Tschinkel WR. Fire ant queen longevity and age: estimation by sperm depletion. Ann Entomol Soc Am. 1987; 80:263–266.

Tschinkel WR. Social control of egg-laying rate in queens of the fire ant, *Solenopsis invicta*. Physiol Entomol. 1988; 13:327–350.

Tsuji K, Nakata K, Heinze J. Lifespan and reproduction in a queenless ant. Naturwissenschaften. 1996; 83:577–578.

Turon X, Becerro MA. Growth and survival of several ascidian species from the northwest Mediterranean. Mar Ecol Prog Ser. 1992; 82:235–247.

Ugelvig LV, Kronauer DJC, Schrempf A, Heinze J, Cremer S. Rapid anti-pathogen response in ant societies relies on high genetic diversity. Proc R Soc Lond B. 2010; 277:2821–2828.

Vance JT, Williams JB, Elekonich MM, Roberts SP. The effects of age and behavioral development on honey bee (*Apis mellifera*) flight performance. J Exp Biol. 2009; 212:2604–2611. [PubMed: 19648405]

Vaquero A, Reinberg D. Calorie restriction and the exercise of chromatin. Genes Dev. 2009; 23:1849–1869. [PubMed: 19608767]

Vargo, EL. Effect of pleometrosis and colony size on the production of sexuals in monogyne colonies of the fire ant *Solenopsis invicta*. In: Trager, JC., editor. Advances in Myrmecology. E. J. Brill; New York: 1988. p. 217-225.

Walker J, Stamps J. A test of optimal caste ratio theory using the ant *Camponotus* (*Colobopsis*) *impressus*. Ecology. 1986; 67:1052–1062.

Wehner R, Meier C, Zollikofer C. The ontogeny of foraging behaviour in desert ants, *Cataglyphis bicolor*. Ecol Entomol. 2004; 29:240–250.

Weier J, Feener D. Foraging in the seed-harvester ant genus *Pogonomyrmex*: are energy costs important? Behav Ecol Sociobiol. 1995; 36:291–300.

Williams GC. The Tithonus error in modern gerontology. Q Rev Biol. 1999; 74:405–415. [PubMed: 10672642]

Williams GC. Pleiotropy, natural selection, and the evolution of senescence. Evolution. 1957; 11:398–411.

Williams JB, Roberts SP, Elekonich MM. Age and natural metabolically-intensive behavior affect oxidative stress and antioxidant mechanisms. Exp Gerontol. 2008; 43:538–549. [PubMed: 18342467]

Wilson EO. Some ecological characteristics of ants in New Guinea rain forests. Ecology. 1959; 40:437–447.

Wilson, EO. The Insect Societies. Oxford University Press; London: 1971.

Wilson EO. Behavioral discretization and the number of castes in an ant species. Behav Ecol Sociobiol. 1976a; 154:141–154.

Wilson EO. The organization of colony defense in the ant *Pheidole dentata* Mayr (Hymenoptera: Formicidae). Behav Ecol Sociobiol. 1976b; 1:63–81.

Wilson EO. Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*): IV. Colony ontogeny of *A. cephalotes*. Behav Ecol Sociobiol. 1983a; 14:55–60.

Wilson EO. Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*): III. Ergonomic resiliency in foraging by *A. cephalotes*. Behav Ecol Sociobiol. 1983b; 14:47–54.

Wilson EO. The sociogenesis of insect colonies. Science. 1985; 228:1489–1495. [PubMed: 17831241]

Wilson-Rich N, Spivak M, Fefferman NH, Starks PT. Genetic, individual, and group facilitation of disease resistance in insect societies. Annu Rev Entomol. 2009; 54:405–423. [PubMed: 18793100]

Wolf H. Desert ants adjust their approach to a foraging site according to experience. Behav Ecol Sociobiol. 2008; 62:415–425.

Yang AS. Seasonality, division of labor, and dynamics of colony-level nutrient storage in the ant *Pheidole morrisi*. Insect Soc. 2006; 53:456–462.

Yang AS, Martin CH, Nijhout HF. Geographic variation of caste structure among ant populations. Curr Biol. 2004; 14:514–519. [PubMed: 15043818]

Yek SH, Mueller UG. The metapleural gland of ants. Biol Rev Camb Philos Soc. 2011; 86:774–791. [PubMed: 21504532]
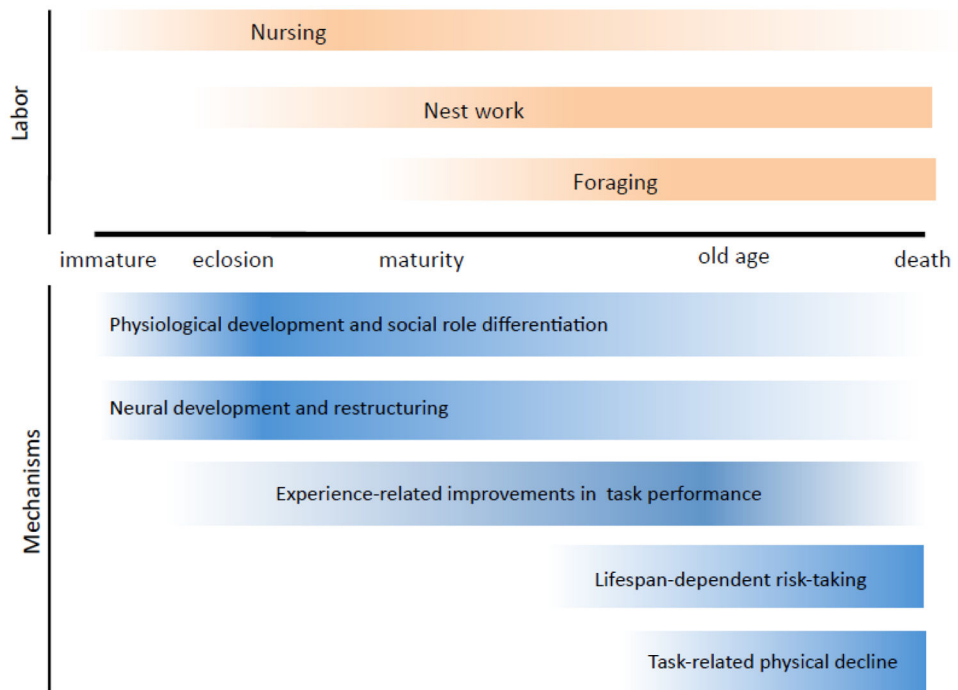
Fig. 1.
Model of task attendance across the worker lifespan in ants. Task suites are indicated in orange (top); internal drivers of behavior and other factors shaping worker function are in blue (bottom). Intensity of shading indicates expected task frequency among age groups. Patterns illustrated are generalized approximations based on published data and personal observations. Details are expected to vary among taxa
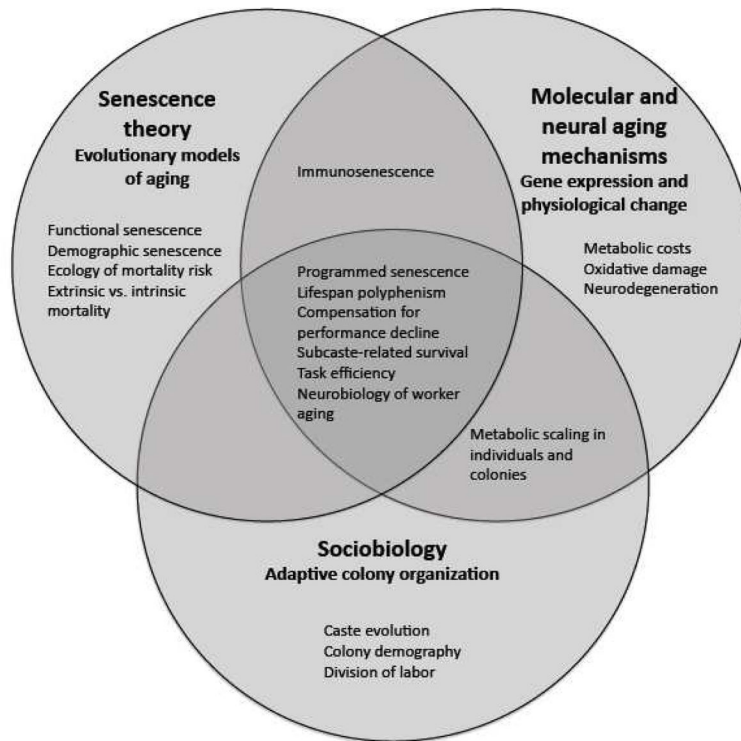
Fig. 2.
Integration of sociobiology, senescence theory, and molecular and neurobiological approaches to identify mechanisms of aging illustrating current and potential interdisciplinary analyses of aging in ants

Table 1

Association of worker aging and colony function

Behavioral effects of mechanical wear or shortened lifespan on task performance.

Species	Age-related effect	Notes	Reference
Atta cephalotes	Switch task following mandibular wear	Workers that cut experience mandibular wear with increased age (assumed) and switch to carrying leaves	Schofield et al. 2011
Pogonomyrmex owyheei	Foragers experience mandibular wear	Impaired ability to pick up small food items	Porter and Jorgensen 1981
Myrmica scabrinodis	Increase in risk-taking with shortened lifespan	Workers experimentally harmed to shorten lifespan were more likely to forage under higher risk	Moro et al. 2012

Table 2

Tests for programmed senescence in ants

Species	Evidence for programmed senescence	Notes	Reference
Cataglyphis bicolor	None	High forager mortality (6 days) but long laboratory lifespan (months)	Schmid-Hempel 1983; Schmid-Hempel and Schmid-Hempel 1984
Pogonomyrmex badius	None	Foragers live only 1 month but can live >200 days in the lab	Kwapich and Tschinkel 2013
Oecophylla smaragdina	Subcaste differences in lab survival	Majors experience higher extrinsic mortality (predicted) and have shorter lifespans	Chapuisat and Keller 2002

Table 3

Association of colony size and fitness in ants

Evidence supporting and refuting fitness-enhancing contributions of long-lived workers to increased colony size. Research has concentrated on species in the Subfamilies Myrmicinae and Formicinae.

Factor	Species	Effect of colony size	Notes	Reference
Colony growth and reproduction	*Solenopsis invicta*	None	Positive effect of number of 4th instar larvae on queen laying rate	Tschinkel 1988
		Positive	For immature colonies	Tschinkel 1993
		Mixed	No effect: mature colonies; Positive: when immature colonies included; effect appears to be driven by immature and adolescent colonies	Cassill 2002
		None	Effects of worker size class on brood production/survival	Porter and Tschinkel 1985
		Positive	Reduction of workforce size in mature colonies led to a reduction in production of sexuals and an increase in worker production	Vargo 1988
	Camponotus impressus	Mixed	Positive: alate males and females; in large colonies positively with number of majors Negative: in large colonies with number of minors	Walker and Stamps 1986
	Meta-analysis of 15–65 spp.	Mixed	Negative: larger colonies had proportionately fewer alates per worker Neutral: biomass scaled isometrically	Shik 2008
	Temnothorax crassispinus, T. longispinosus, T. nylanderi, Leptothorax acervorum, L. muscorum, Myrmica punctiventris, Protomognathus americanus, Harpagoxenus sublaevis	Mixed	Negative: Per capita productivity declined in 6 of 8 species Mixed: some populations differed in the direction of the effect within species Production was pooled across all castes	Kramer et al. 2014
Resource acquisition	*Pogonomyrmex spp.*	Neutral	Intraspecific comparison between species with different colony sizes; larger numbers of foragers no better at harvesting clumped food; but larger colonies given larger territories	Flanagan et al. 2012
	Eciton hamatum	Mixed	Neutral: effect on average or peak raid intake Positive: peak colony intake	Powell 2011
	Temnothorax rugatulus	Mixed	Higher density colonies had higher foraging rates; field density relatively constant among colonies	Cao 2013
Global division of labor	*Pogonomyrmex californicus*	Positive	During ontogeny and with age-matched colonies	Holbrook et al. 2011
		Neutral	Experiment only conducted over ~ 3 days	Holbrook et al. 2013
	Temnothorax albipennis	Neutral	In small colonies, a smaller proportion of workers did most of the work	Dornhaus et al. 2009
	Rhytidoponera metallica	Positive	Greater task specialization in larger colonies; older workers spent more time foraging in larger colonies but no effect of age in small colonies	Thomas and Elgar 2003

Factor	Species	Effect of colony size	Notes	Reference
	140 spp.	Positive	Not phylogenetically controlled, based on number of morphological castes	Bonner 1993
Group decision-making	*Temnothorax sp.*	Mixed	Neutral: no difference in ability to select nests Positive: larger colonies found good nests faster	Franks et al. 2006
Defense	*Oecophylla longinoda*	Positive	Colonies with highest density of majors win intraspecific contests	Hölldobler and Wilson 1978
	Solenopsis invicta	Positive	Experimental removal of workers	Adams 2003
	Formica rufa	Mixed	Negative: workers in smaller groups fight more aggressively Positive: larger groups have higher levels of total aggression	Batchelor and Briffa 2011
	Formica xerophila	Positive	Workers housed in larger and denser subcolonies prior to fighting were more aggressive (fighting groups held at equal sizes)	Tanner 2006
Immunocompetence	Attine species	Positive	Larger colony sizes necessitated a switch to behavioral and chemical defense	Fernández-Marín et al. 2009
	Acromyrmex echinatior	Positive	Isolated ants had compromised immune function	Hughes et al. 2002
	Temnothorax nylanderi	Positive	Cestode-infected colonies were larger than unifected colonies; no effect of infection on per worker productivity	Scharf et al. 2012
Nursing	*Solenopsis invicta*	Neutral	Required minimum number of workers but otherwise no effect	Cassill and Tschinkel 1999
	Formica selysi	Mixed	Non-linear; intermediate ratios and sizes had highest rate of brood eclosion; confounds of group size and worker:brood ratio	Purcell et al. 2011