Colony size explains the lifespan differences between queens and workers in eusocial Hymenoptera

BORIS H. KRAMER* and RALF SCHAIBLE

Max Planck Institute for Demographic Research, Rostock, Germany

Eusocial Hymenoptera show a unique divergence in lifespan of queens and workers; queens belong to the longest lived insects while workers in most eusocial species have significantly shorter lives. The different phenotypes within a colony emerge through reproductive division of labour, which is a characteristic trait of eusocial animals. Division of labour as a measure of organismal complexity increases with colony size in eusocial species similar to the increase of complexity with size that has been shown for the whole range of living organisms. We show that queen and worker lifespan diverge in closely related species representing the transition from solitary to social life and show that queen and worker lifespan are correlated if colony size is taken into account: with increasing colony size the lifespan differential between queen and worker increases, whereas neither queen nor worker lifespan is associated with colony size. Additionally, the lifespan differential is better explained by colony size than by the weight differences between the castes. The divergence of phenotypes found is in line with the increasing specialization of subunits in larger organisms, which leads to increasing complexity. We argue that division of labour is acting to increase colony efficiency, which in turn shapes the investments made into individuals leading to short-lived workers and long-lived queens. Additionally, maintenance investments may be shaped due to the variable extrinsic risk faced by different castes. © 2013 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2013, **109**, 710–724.

ADDITIONAL KEYWORDS: colony size – complexity – division of labour – Hymenoptera – lifespan – social insect.

INTRODUCTION

Biology is largely a matter of size: larger organisms tend to be more complex and this rule applies to the whole range of living organisms and to different levels of biological organization (Bell & Mooers, 1997; Bonner, 1988, 2004; Changizi, McDannald & Widders, 2002). Often organismal complexity is measured as the number of specialized subunits (Bell & Mooers, 1997) but it may also be measured by their phenotypic divergence (Changizi *et al.*, 2002). The increase in complexity results from increasing cooperative division of labour that appears at all levels of biological organization and which is a measure of the degree to which subunits (organelles, cells, and individuals) specialize on different tasks and thus reflects complexity (Bonner, 2004; Gadau, Fewell & Wilson, 2009; Rueffler, Hermisson & Wagner, 2011). Division of labour benefits the organism with increasing efficiency because it allows the organism to simultaneously accomplish several physiological processes (Hurd, Jeanne & Nordheim, 2007; Simpson, 2012). Once formerly autonomous units in a group shift to be intrinsically dependent upon one another they become integrated into a new hierarchical layer of biological organization representing an evolutionary transition such as that from unicellular to multicellular life or that from solitary to social life, which are accompanied by a shift in the level of selection (Smith & Szathmary, 1997; Heylighen, 2000; Wilson & Wilson, 2007; Goldsby *et al.*, 2012).

This latest evolutionary transition is accomplished by eusocial species (Michod, 2000). The emerging colonies have therefore been termed superorganisms, a collective organism consisting of many individual 'sub-unit' organisms (Wheeler, 1911; Wilson & Sober, 1989; but see Strassmann & Queller, 2009). The level of the superorganism is reached when societies are bound by altruism and division of labour (Gadau

*Corresponding author. E-mail: kramer@demogr.mpg.de

et al., 2009). The colony can thus be likened to the body of an individual organism. As a result of division of labour, the colony is composed of reproductive individuals (queens) that represent the germ line and workers that represent the soma, but as compared with a multicellular organism has lower genetic relatedness between its members, which gives rise to conflict and competing levels of selection (individual- and colony-level) (Wheeler, 1911; Wilson & Sober, 1989; Ross & Matthews, 1991; Boomsma, 2009).

Here we focus on queen–worker differences in lifespan that arise with changes in colony size. Increasing colony size has a number of consequences for the social organization and the evolution of life histories of different individuals within eusocial colonies, which are driven by increasing division of labour (Bourke, 1999; Dornhaus, Powell & Bengston, 2012). The positive association of colony size and division of labour leads to increasing morphological skew as the degree of task and caste specialization increases, as well as a divergence of lifespan between queens and workers and the loss of individual totipotency (e.g. reduced reproductive capabilities of workers), all of which increase efficiency gains for larger colonies (Holldobler & Wilson, 1990; Alexander, Noonan & Crespi, 1991; Schmid-Hempel, 1998; Bourke, 1999; Carey, 2001; Changizi *et al.*, 2002; Hurd *et al.*, 2007). Once group living has evolved, coevolutionary changes affecting lifespan evolution emerge (Alexander *et al.*, 1991; Carey, 2001). Disruptive selection becomes apparent once the chance or physiological ability of worker reproduction is minimized and leads to the evolution of distinct worker and queen phenotypes (Bourke, 2007). The divergence of phenotypes is a self-reinforcing process because early ageing in helpers with increasing colony sizes decreases the chance of future reproduction, promoting further phenotypic specialization (Alexander *et al.*, 1991). This leads from a reduced reproductive potential to complete worker sterility while the fertility and lifespan of the queen increases (Holldobler & Wilson, 1990). As a result, queens belong to the longest lived insects and generally live longer than workers, although in most species they do not differ genetically and develop from the same female larvae (Keller & Genoud, 1997; Heinze & Schrempf, 2008; but see Kerr, 1950).

However, beside the effect of colony size on lifespan evolution, lifespan in the social insects may also be correlated with body size (Porter & Tschinkel, 1985; Calabi & Porter, 1989), independent of size as a response to the level of extrinsic mortality (Chapuisat & Keller, 2002) or may be task dependent (Rueppell *et al.*, 2007). Therefore both, evolutionary (ultimate) and mechanistic (proximate) theories of ageing could explain the divergence of queen and worker lifespan

(Hughes & Reynolds, 2005). Evolutionary theories of ageing assume that high levels of extrinsic mortality select for a reduced investment in physiological maintenance leading to a shorter lifespan (Medawar, 1952; Williams, 1957; Hughes & Reynolds, 2005). Following this the evolution of the observed lifespan variation between different castes in social insects has been linked to the caste-specific differences of extrinsic mortality (Keller & Genoud, 1997; Heinze & Schrempf, 2008; Parker, 2011). Evolutionarily selected worker lifespan as a response to different levels of extrinsic mortality has been shown to be preserved under laboratory conditions (Chapuisat & Keller, 2002). Extended longevity, by contrast, is associated with adaptations that reduce the risk of predation. Examples are subterranean living (Buffenstein, 2005), the ability to fly (Austad & Fischer, 1991), group or social living (Carey, 2001; Carey & Judge, 2001; Buffenstein, 2005; Keller & Jemielity, 2006) and intergenerational transfers (Lee, 2003; Amdam & Page, 2005). In most cases the queens in eusocial colonies are long-lived, because they are protected in the centre of the colony while short-lived workers take over tasks that are correlated with higher levels of extrinsic risk (Schmid-Hempel, 1998). As a result the mean lifespan of queens in fire ant (*Solenopsis invicta*) is 30 times longer than that of small workers (Calabi & Porter, 1989; Holldobler & Wilson, 1990). Even species with less pronounced morphological caste differences such as *Diacamma rugosum* show a 1.3-fold difference of maximum lifespan between workers and queens (Tsuji, Nakata & Heinze, 1996). In contrast, mechanistic theories of ageing make predictions about the relationship between metabolic rate and lifespan. Larger organisms have a lower metabolic rate per unit of mass, a slower development and greater lifespan (Collatz & Sohal, 1986; Finch, 1990). For example, the lifespan of fire ant workers is affected by both temperature and body size, which both change metabolic expenditure (Calabi & Porter, 1989).

However, mechanistic and evolutionary theories of ageing have been broadly discussed (Schmid-Hempel & Wolf, 1988; Keller & Genoud, 1997; Moret & Schmid-Hempel, 2000; Jemielity *et al.*, 2005; Heinze & Schrempf, 2008; Parker, 2011) and therefore in this study we elaborate on the effect of colony size on changes in lifespan for both workers and queens. Highly eusocial species with larger colonies tend to have shorter lived workers (Matsuura, 1991; Schmid-Hempel, 1998) but for queens no such association was found (Holldobler & Wilson, 1990).

We first review trends in lifespan evolution associated with the transition from solitary to eusocial organization displayed by closely related species that show both solitary and social organization. Because

within the Hymenoptera only bees and wasps represent this transition, we also included other eusocial species (mole-rats, gall-inducing thrips and ambrosia beetles) in this analysis. This approach can give an indication on how lifespan changes with the onset of task specialization of different individuals within a group.

Second, because colony size is correlated with social complexity and division of labour, including reproductive potential and caste differentiation, we tested the hypotheses that colony size can explain the differences between queen and worker lifespan within the eusocial Hymenoptera as proposed by Carey (2001). As phenotypic specialization increases, the lifespan differential between queens and workers should increase as a result of disruptive selection. Disruptive selection should lead to the evolution of diverging caste-specific lifespan as a response to task-specific levels of extrinsic mortality. Additionally, because the differential lifespan of workers and queens emerges from group living and the associated reproductive division of labour we expect that the differences between worker and queen lifespan should be phylogenetically independent and apply to terrestrial (wasps, bees) as well as subterranean (ant) species similarly as a response to colony size. Alternatively, lifespan differences between worker and queen castes could result from the increasing morphological differences caused by increasing division of labour in larger colonies, which in turn affect metabolic rate and longevity. If so, we should find a correlation between the differences in lifespan and the differences in weight between queen and worker castes.

To analyse the association between colony size and lifespan we collected lifespan, colony size, and dry weight data on eusocial Hymenoptera from the published literature.

METHODS

DATA COLLECTION

Generally data on survival in social species were scarce. Apart from a few comparative studies or book chapters that focus on lifespan or colony size (Beckers et al., 1989; Holldobler & Wilson, 1990; Keller, 1998; Schmid-Hempel, 1998; Page & Peng, 2001; Hou et al., 2010), data needed for this study were often hidden in papers focusing on other topics. We collected data for eusocial Hymenopterans on lifespan, colony size, and dry weight by searching the scientific literature. We conducted queries on Google scholar and ISI web of knowledge for the following keywords: 'lifespan', 'survival', 'colony size', and 'worker/queen weight'. The collected data originated from a combination of laboratory, field observation, and anecdote (especially

data on lifespan). Sources for the data used in our analysis are given in the supplemental material (Table S1).

Lifespan

We collected lifespan data of solitary and closely related species that represent the steps from solitary towards eusocial organization as well as lifespan data for eusocial Hymenoptera. Within the Hymenoptera only bees and wasps represent recent examples of the transition from solitary to eusocial organization and thus we added eusocial species apart from the Hymenoptera (mole-rats, thrips, and ambrosia beetles) to analyse lifespan changes with changes in social organization. While data on survival would be more appropriate but rare we had to use data on mean or maximum lifespan, which was often complicated because sample sizes, especially for queens, were often low. Another problem was that published data can be obtained from laboratory or field colonies. For queens the difference between laboratory studies and field studies should be minimal; in both cases the queen lives in the centre of the colony protected from extrinsic risks. In the case of the workers laboratory lifespan could be higher than for field studies but bees and wasps were often allowed to forage outside in laboratory studies. Because we were interested in the intrinsic lifespan differences shaped by natural selection, which in turn result from differential investments into individuals or castes as a result of different levels of extrinsic mortality (Chapuisat & Keller, 2002; Heinze & Schrempf, 2008), we preferred laboratory over wild data, if both were available (e.g. *Harpagoxenus saltator*). Wild data, especially for workers, were often left truncated and did not cover the whole individual lifespan (e.g. workers of *Pogonomyrmex barbatus* were just monitored after first appearance outside the colony). We omitted such data from the analysis. In two cases field data were used because both queen and worker lifespan were available as field data but for just one caste as laboratory data and otherwise we would have mixed wild and laboratory data for one species, which we avoided if possible (e.g. *Vespa simillima*). If several maximum lifespan values were obtained we used the highest reported value because maximum lifespan usually represents maximum observed lifespan, which may vary between studies mainly depending on sample size. For species with polymorphic worker castes with differing lifespan (mean or maximum lifespan) we used the highest reported values because they would represent maximum worker lifespan (e.g. *Acromyrmex subterraneus brunneus*, *Solenopsis invicta*, *Apis mellifera diutinus* workers); if information was only available for one caste we used this. If survival curves were published we calculated mean lifespan

and used the age of the last survivor as maximum lifespan. When just life expectancy was reported (e.g. *Bombus ferdivus*) but no survival curve was published we used the reported value as mean lifespan. If the reported maximum lifespan value was obtained while the individual was still alive (LS > 3 years) we used the reported value (LS = 3 years) to avoid an overestimation of lifespan. Sometimes we just found estimates of queen lifespan derived from colony survival, which may be critical as unobserved queen turnover may have occurred (Keller, 1998). For some annual species lifespan was reported after the first egg was laid or colony lifespan alone is reported, so we then added the hibernation time, which is part of the adult lifespan (e.g. *Bombus melanopygus*). If a lifespan range was given we used the upper limit as maximum lifespan and the midpoint as mean lifespan (e.g. *Tetragonisca angustula*).

We collected mean queen lifespan of 72 species. Mean worker lifespan was collected for 82 species. Maximum lifespan was obtained for 79 species (queen) and 76 species (worker).

Colony size

Colony sizes were collected from the published literature (Table S1). If possible we used mean colony size of mature colonies. In cases where we just found one value we used that. If we found several reported colony sizes we took the mean, and if several mean values were obtained we used the mean weighted by the sample size (e.g. *Pogonomyrmex occidentalis*). If a range of colony sizes was given we used the midpoint of the reported values, and in cases where just a minimum size was given we used this. If we found a statement that the colonies are smaller than a certain value we reduced this by one-third because we found that average values are 20–50% smaller than reported maximum values, and additionally we did not want to overestimate colony size.

Dry weight

To account for the morphological differences between queens and workers we collected dry weight data for each caste. If we obtained several dry weight measures from different studies or several values for different worker castes we calculated the mean dry weight across castes and studies. Data sources can be found in Table S1.

DATA ANALYSIS

Mean and maximum lifespan calculation

For some species we collected both mean and maximum lifespan data but for others we obtained just mean lifespan for worker and maximum lifespan for queens or vice versa. To compare those species and to incorporate a higher variability of species into our analysis we calculated a conversion factor for both queens and workers to calculate the mean from maximum lifespan or vice versa. Instead of dividing maximum lifespan by 1.45 to obtain mean lifespan (Keller & Genoud, 1997; Hou *et al.*, 2010) we used a conversion factor retrieved from a linear regression (weighted by the study sample sizes) between mean and maximum lifespan of species where we collected both lifespan measures for either queens or workers. We chose linear regressions through the origin because of the clear relationship between mean and maximum queen lifespan (as seen in Fig. 1). For the regression we only used data from species where both mean and maximum lifespan were obtained either from the laboratory or the wild. For queens, the conversion factor (slope) obtained was 1.34 ± 0.05 ($t_{1,44} = 28.32$, $P < 0.001$, $R^2 = 0.95$, $F = 802.2$) and for workers 1.66 ± 0.07 ($t_{1,55} = 21.15$, $P < 0.001$, $R^2 = 0.89$, $F = 447.3$) (Fig. 1). After calculating maximum lifespan from mean lifespan (Fig. 1) we used the maximum lifespan data for all correlations between lifespan and colony size; using mean lifespan revealed similar results.

Lifespan and colony size

We used linear models to analyse the relationship between worker as well as queen lifespan and colony size. To test for a correlation between queen and worker lifespan we calculated the ratio of queen and worker lifespan (queen lifespan in days/worker lifespan in days) to obtain a dimensionless measure. We used linear regressions to analyse the relationship between the lifespan ratio and colony size. To normalize the residuals of the linear models we had to log-transform both the lifespan ratio and colony size. The species used and data sources can be found in Table S1.

For the Formicidae we also compared models including the mode of colony founding (dependent/independent) or queen number (monogyny/polygyny) along with colony size as explanatory variables. We used a backward elimination modelling approach starting with a maximal model. We then eliminated stepwise non-significant terms until a minimum adequate model with significant terms was reached (Crawley, 2002). We used ordinary least squares (OLS) linear models and model comparisons were performed using ANOVAs with χ^2 tests. Additionally, the models were compared using the Akaike information criterion (AIC).

Dry weight ratio

We were able to calculate the weight ratio (queen weight/worker weight) for 15 species, for which we also had the data to calculate the lifespan ratio
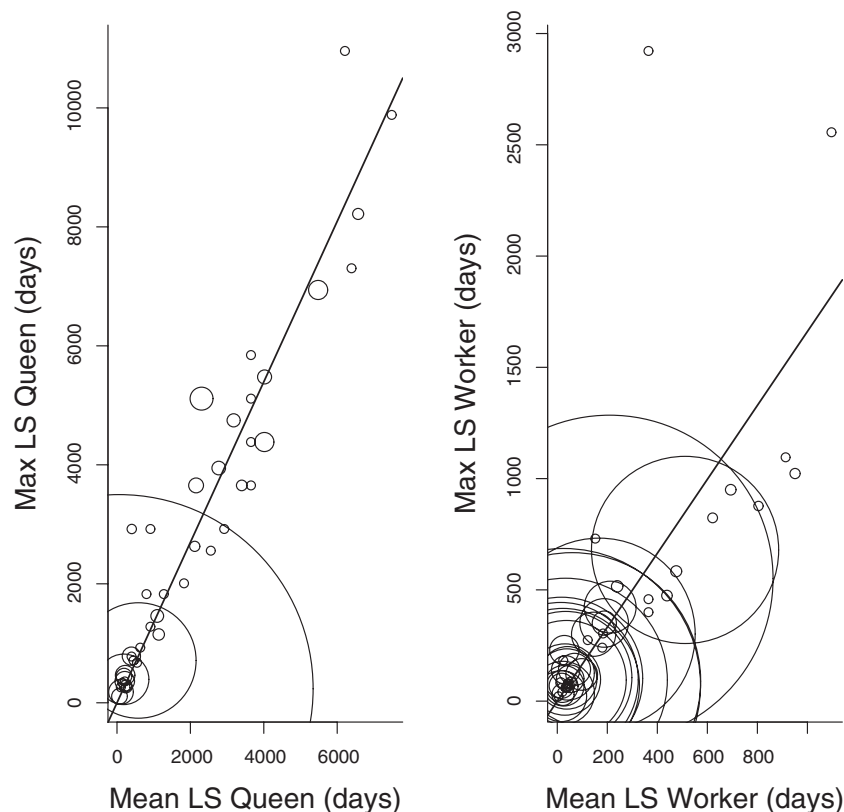
Figure 1. Linear regressions between mean and maximum lifespan for queens (left) and workers (right). Each circle represents mean and maximum lifespan of a species. The size of the circle represents sample size. The lines represent the slope (conversion factor) estimated from regression through the origin weighted by sample size. Left: mean and maximum queen lifespan; slope: 1.34 ± 0.05 ($t_{1,44} = 28.32$, $P < 0.001$, $R^2 = 0.95$, $F = 802.2$). Right: mean and maximum worker lifespan; slope: 1.66 ± 0.07 ($t_{1,55} = 21.15$, $P < 0.001$, $R^2 = 0.89$, $F = 447.3$).

(queen lifespan/worker lifespan). We were then able to test if either colony size or the dry weight differences between queens and workers can explain the lifespan differences between queens and workers.

We used a backward elimination modelling approach starting with a maximal model with lifespan ratio as the response variable and dry weight ratio and colony size, plus the interaction between them, as explanatory variables. We then eliminated stepwise non-significant terms until a minimum adequate model with significant terms was reached (Crawley, 2002). We used OLS linear models forced through the origin with log-transformed variables. Following a Lilliefors- (Kolmogorov–Smirnov) test the residuals were found to be normally distributed for all models. Model comparisons were done using ANOVAs with χ^2 tests. Additionally, the models were compared using AIC. The used species and data sources can be found in Table S1.

Comparative analysis
We used phylogenetically independent contrast (Felsenstein, 1985; Garland, Harvey & Ives, 1992)

for continuous variables to control for evolutionary relationships. Contrasts for continuous variables were obtained using the crunch option within the R-package caper (David *et al*., 2012) and were then subjected to regression analyses through the origin.

We used two different approaches. First we used an existing phylogeny for the Fomicidae (Moreau *et al*., 2006), which includes some species that appear in our dataset. We further added species if the genus was included in the existing phylogeny. We were able to include 13 ant species, the honey bee, and a wasp species as these where used as outgroups in the analysis of Moreau *et al*. (2006).

Second, we constructed a phylogeny from published trees of social Hymenoptera (Schmitz & Moritz, 1998; Danforth, 1999; Costa *et al*., 2003; Arevalo *et al*., 2004; Moreau *et al*., 2006). Because no information on branch lengths could be assigned to our composite phylogeny we set all branch lengths to the same value (Fjerdingstad & Crozier, 2006). Branch length information is not indispensable for independent contrast analyses, which are generally robust (Garland *et al*., 1992). We were able to include 29 species

representing all genera in our analysis (the tree and species used can be found in Table S2 and Fig. S1).

Statistical analysis

All statistical analyses were performed using the R-statistical software (R Core Development Team, 2010) and the packages nortest (Gross & Ligges, 2012), caper (David *et al*., 2012), and ape (Paradis, Claude & Strimmer, 2004).

RESULTS

LIFESPAN CHANGES DURING SOCIAL EVOLUTION

In our review of the literature an increased divergence of lifespan of queens versus workers with increasing sociality was found in all groups examined (including mole-rats, thrips, and ambrosia beetles in addition to bees and wasps, which represent the social Hymenoptera).

For African mole-rats (Bathyergidae) maximum recorded lifespan of solitary mole-rats was between 6 (*Bathyergus suillus*) and 11 (*Georychus capensis*) years (Dammann, 2006), but data were scarce and hence not as reliable as data for the social species. Maximum lifespan in the social species varied from 11 years (*Cryptomys hottentotus*) to 30 years (*Heterocephalus glaber*) (Dammann, 2006; Liang *et al*., 2010). Non-breeders of the genus *Fukomys* displayed significant differences in lifespan compared with breeders. Non-breeder lifespan was comparable to solitary species (*Fukomys anselli*, maximum lifespan = 8 years; *Fukomys mechowii*, 10 years) while breeder lifespan was prolonged (*Fukomys anselli*, maximum lifespan = 19 years; *Fukomys mechowii*, 16 years) (Dammann & Burda, 2006; Dammann *et al*., 2011). Breeders and non-breeders of *Heterocephalus glaber*, which forms the largest groups (up to 295 individuals) within the social mole-rats, showed similar lifespan (Brett, 1991; Buffenstein, 2005, 2008; Liang *et al*., 2010).

Several gall-inducing thrips are eusocial (Crespi, 1992; Kranz, 2005) and in the genus *Kladothrips* both solitary and eusocial species exist (Choe & Crespi, 1997). In solitary species (*Kladothrips rugosus* and *K. ellobus*) females lived for about 10–12 months (annual life cycle), and the same lifespan was found for foundresses in the eusocial species *K. intermedius* and *K. waterhousei*, while soldiers in the same species showed a reduced lifespan of about 3–6 months (Crespi, Morris & Mound, 2004).

In the solitary fungus-growing ambrosia beetles *Dolipygus dubius* and *Dendroplatypus impar* offspring leave the nest after emergence and individuals had lifespans of 14–16 weeks (Browne, 1962) and

1 year (Browne, 1961). Species in which cooperative breeding occurs, such as *Notoplatypus elongates*, reached a lifespan of more than 3 years (Kirkendall, Kent & Raffa, 1997). The only known eusocial species is *Austroplatypus incompertus*, which forms monogynic colonies that can last up to 37 years (Costa, 2006). Females in this species may live more than 4 years while it was not known how long the workers live (Kirkendall *et al*., 1997).

In the superfamily Apoidea eusociality has arisen at least eight times (Wilson, 1971). Solitary Apidae (*Ceratina calcarata*) had an average lifespan of approximately 14–16 months and a maximum lifespan of almost 2 years (22 months) (Rehan & Richards, 2010a, 2010b). In facultatively social Apidae (*Xylocopa virginica*) mean lifespan was below 11 months and maximum lifespan reached 26 months (Richards, 2011).

Wasp lifespan increased with increasing social complexity (Evans, 1958; Wilson, 1975; Carey, 2003). Solitary parasitoids had short lifespans of 14–60 days (*Natocyphus*), and extensive parental care in *Gorytes* and *Stenogaster* species led to an increase in lifespan (60–365 days) leading to advanced eusocial wasps (e.g. *Vespula*) with queen lifespans ranging from 180 to 1000 days (Evans, 1958; Wilson, 1975; Carey, 2003). However, worker lifespan in eusocial wasps (*Vespula*, *Vespa*) seemed to be similar to their related solitary species (20–65 days) (Strassmann, 1985). Data on eusocial wasps were also included in the following analyses.

COLONY SIZE EFFECTS ON LIFESPAN IN EUSOCIAL HYMENOPTERA

Worker lifespan and colony size

We did not find a general trend in the relationship between maximum worker lifespan and colony size. All regressions of maximum worker lifespan on colony size showed significant intercepts but not slopes (Table 1; Fig. 2). Due to the small sample size the Halictidae were only included in the regression on all Hymenopterans.

Queen lifespan and colony size

We did not find a general trend in the relationship between maximum queen lifespan and colony size. The regressions of maximum queen lifespan on colony size showed significant intercepts except for the Apidae; slopes were marginally significant for the Formicidae, Apidae, and all Hymenoptera combined (Table 1). In the Apidae the $R^2 = 0.761$ was large given the small sample size of five species. Long-lived queens were found at all colony sizes while short-lived queens do not appear at larger colony sizes

Table 1. Results of the linear regressions of worker lifespan, queen lifespan, and lifespan ratio (queen/worker) with colony size

|	Family	Intercept	P value	Slope	P value	R^2	d.f.
Worker	Formicidae	792.90	< 0.001	−0.0001	0.3620	0.021	39
	Vespidae	76.21	0.002	−0.0057	0.5030	0.046	10
	Apidae	74.42	0.002	0.0015	0.4475	0.074	8
	Hymenoptera	523.10	< 0.001	−0.0001	0.6140	0.004	64
Queen	Formicidae	3736.00	< 0.001	0.0010	0.0392	0.070	59
	Vespidae	286.89	< 0.001	0.0635	0.7445	0.014	8
	Apidae	698.62	0.139	0.0967	0.0539	0.761	3
	Hymenoptera	3026.00	< 0.001	0.0012	0.0117	0.080	77
Queen/worker	Formicidae	–	–	0.2060	< 0.001	0.898	30
	Vespidae	–	–	0.3220	< 0.001	0.855	9
	Apidae	–	–	0.3290	0.0023	0.904	4
	Hymenoptera	–	–	0.2300	< 0.001	0.867	48
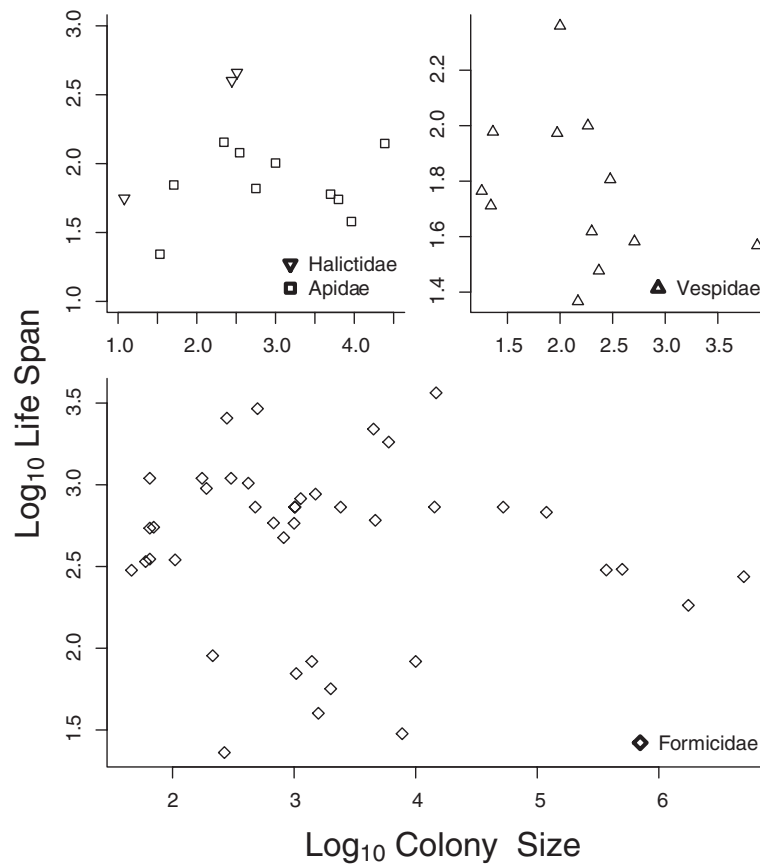
Figure 2. Maximum worker lifespan and group size. Sixty-six species (Hymenoptera) are included in this plot [Formicidae = 41 species (intercept = 792.9, $P < 0.001$, slope = −0.0001, $P = 0.362$, $R^2 = 0.021$, d.f. = 39, $F = 0.85$), Vespidae = 12 species (intercept = 76.21, $P = 0.002$, slope = −0.006, $P = 0.503$, $R^2 = 0.046$, d.f. = 10, $F = 0.483$), Apidae = 10 species (intercept = 74.42, $P = 0.002$, slope = 0.0015, $P = 0.448$, $R^2 = 0.074$, d.f. = 8, $F = 0.638$), Halictidae = 3 species].
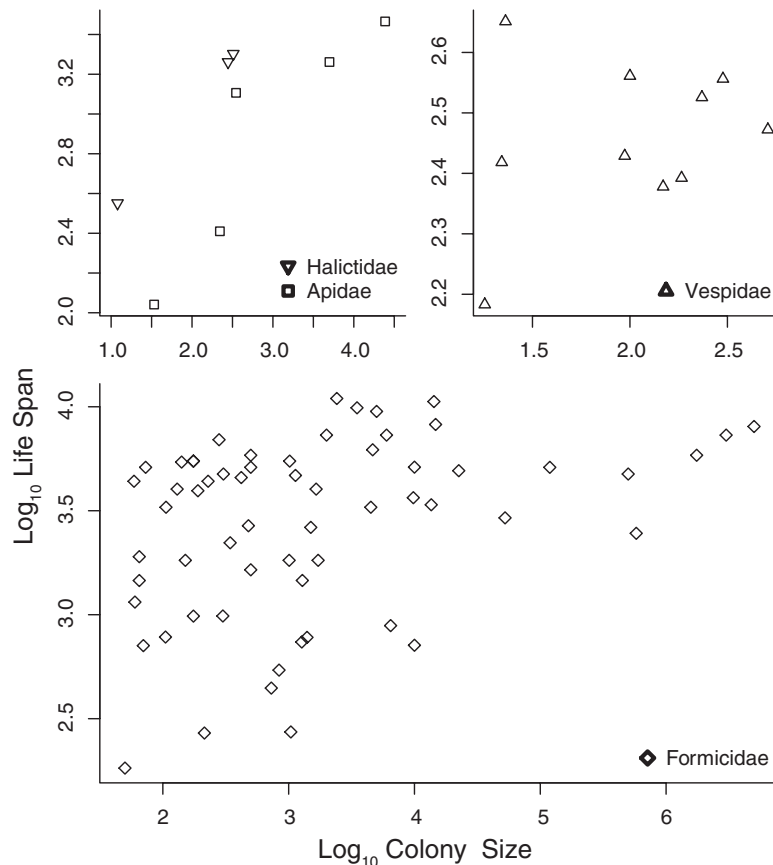
Figure 3. Maximum queen lifespan and colony size. Seventy-nine species (Hymenoptera) are included [Formicidae = 61 species (intercept = 3736, $P < 0.001$, slope = 0.001, $P = 0.039$, $R^2 = 0.07$, d.f. = 59, $F = 4.447$), *Vespidae* = 10 species (intercept = 286.89, $P < 0.001$, slope = 0.064, $P = 0.745$, $R^2 = 0.014$, d.f. = 8, $F = 0.114$), Apidae = 5 species (intercept = 698.62, $P = 0.139$, slope = 0.0967, $P = 0.054$, $R^2 = 0.761$, d.f. = 3, $F = 9.528$), Halictidae = 3 species)].

(Fig. 3). Due to the small sample size the Halictidae were only included in the regression on all Hymenopterans.

Lifespan ratio (queen / worker) and colony size
We found a positive association between the lifespan ratio, which represents the differences in the life-history trait lifespan between queens and workers and colony size, as follows: Hymenoptera: estimated slope = 0.23 ± 0.01 ($t_{1,48} = 17.14$, $P < 0.001$, $R^2 = 0.86$, $F = 293.7$); Apidae: estimated slope = 0.33 ± 0.3 ($t_{1,4} = 6.92$, $P = 0.002$, $R^2 = 0.92$, $F = 47.92$); Vespidae: estimated slope = 0.32 ± 0.04 ($t_{1,9} = 7.74$, $P < 0.001$, $R^2 = 0.86$, $F = 59.87$); Formicidae: estimated slope = 0.21 ± 0.01 ($t_{1,30} = 16.55$, $P < 0.001$, $R^2 = 0.9$, $F = 273.7$). Figure 4 shows the results for all Hymenoptera combined. For the Formicidae we also compared models including the mode of colony founding (dependent/independent) or queen number (monogyny/polygyny) along with colony size as explanatory variables. Neither of the additional vari-

ables was significant and the model just including colony size was preferable (ANOVA (queen number): change in the residual sum of squares = −0.530, d.f. = 1 on 46, $P = 0.22$; ANOVA (mode of colony founding): change in the residual sum of squares = −0.114, d.f. = 1 on 24, $P = 0.867$). The AIC was lower for the model using colony size as main effect (AIC = 4.81) than the model with colony size and queen number as explanatory variables (AIC = 12.78) or the model including colony size and the mode of colony founding (AIC = 13.02).

Independent contrast
Using the phylogeny of Moreau *et al.* (2006) revealed a slope of 0.2 ± 0.063 ($t_{1,13} = 3.17$, $P = 0.007$, $R^2 = 0.44$, $F = 10.04$). Using the tree created by merging different Hymenoptera revealed: slope = 0.21 ± 0.047 ($t_{1,24} = 4.38$, $P < 0.001$, $R^2 = 0.44$, $F = 19.18$). In both cases the relationship between the lifespan ratio and colony size did not change when controlling for phylogenetic effects.
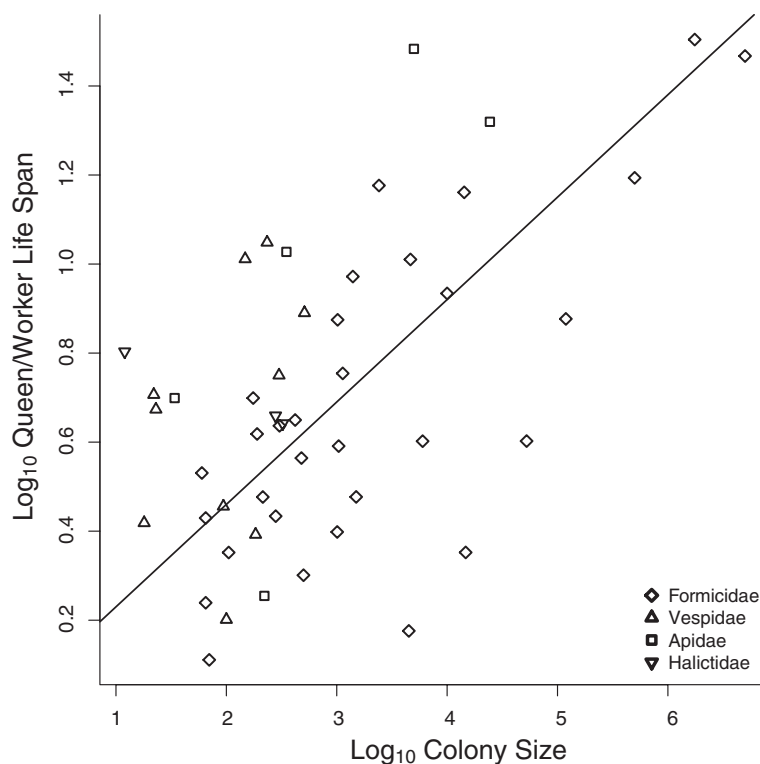
Figure 4. Maximum lifespan ratio and group size including 49 eusocial Hymenoptera species (Formicidae = 31 species, Vespidae = 10 species, Apidae = 5 species, Halictidae = 3 species). The line represents the results of the linear regression: slope = 0.23 ± 0.01 ($t_{1,48}$ = 17.14, $P < 0.001$, R^2 = 0.86, F = 293.7).

Lifespan ratio and weight ratio
After elimination of non-significant terms, only colony size remained in the model (slope = 0.21 ± 0.02, $t_{1,14}$ = 11.07, $P < 0.001$, R^2 = 0.89, F = 122.6). Both the interaction between colony size and dry weight ratio (ANOVA: change residual sum of squares = 0.086, d.f. = 1 on 13, P = 0.2961) and dry weight ratio as a main effect (ANOVA: change in residual sum of squares = 0.004, d.f. = 1 on 14, P = 0.8552) were not significant.

We also compared the AIC values of the minimum adequate model (with colony size as the only explanatory variable) with that of a model with dry weight ratio as the only explanatory variable (slope = 0.57 ± 0.09, $t_{1,14}$ = 6.42, $P < 0.001$, R^2 = 0.73, F = 41.16). The AIC was much lower for the model using colony size as the explanatory variable (AIC = 6.36) than the model with only dry weight ratio (AIC = 19.97). This is a strong indication that the model with colony size is the better model to explain the lifespan ratio of queens and workers than the model including the weight differences of queens and workers.

Colony size and weight ratio
We found a positive association between colony size and weight ratio using colony size as the explanatory variable: estimated slope = 0.31 ± 0.04 ($t_{1,14}$ = 8.69, $P < 0.001$, R^2 = 0.83, F = 75.62).

DISCUSSION

Our comparative study reveals a correlation between division of labour measured as colony size and the lifespan ratio of queens and workers in eusocial Hymenoptera (Fig. 4). The differences in lifespan increase with increasing colony size and point to a correlation between queen and worker lifespan when colony size is taken into account. Interestingly, the correlation with colony size is weak or disappears if workers and queens are considered independently (Table 1; Figs 2, 3). While weight differences between queens and workers increase with colony size, colony size itself is a better predictor for the lifespan differences found.

Throughout the transition from solitary to eusocial organization across different species from insects to vertebrates we find a divergence in lifespan between castes with increasing sociality, as did Carey (2001), probably caused by increasing reproductive division of labour (Bourke, 1999). In most groups lifespan of the reproductive individuals increases while worker lifespan stays within the range of the comparable

solitary species. However, we found two exceptions to this pattern. First, soldiers of the gall-inducing thrips show a reduced lifespan as compared with solitary species while the foundress lifespan remains constant. Another unique pattern is that soldiers in this species are larger than foundresses, while their main task is to defend the colony (Perry *et al.*, 2004). Second, within the social mole-rats, *Heterocephalus glaber* is an exception by showing the same lifespan of breeders and non-breeders. This may be caused by differences in maintaining the social system between the *Fukomys* species (incest avoidance) (Burda, 1995) and *Heterocephalus glaber* (dominant control), where the queen suppresses other colony members from reproduction but workers retain the ability to reproduce within their natal colony (Faulkes & Abbott, 1996).

However, when focusing on the social hymenoptera we find no correlation of worker lifespan with colony size (Fig. 2). Worker lifespan might decrease with colony size as in wasps but only within closely related species (Matsuura, 1984). Thus, phylogenetic constraints could drive the results of Matsuura (1984) and have also been suggested for the long lifespan of *Myrmecia* and ponerine workers (Holldobler & Wilson, 1990). Carey (2001) argued that worker lifespan or daily birth rate determine colony size, either of which needs to increase in order to obtain larger colonies (Carey, 2001). Because worker lifespan does not change with colony size the egg-laying rate of the queen must increase with increasing colony size.

We found marginally significant correlations of queen lifespan with colony size for the Formicidae and the Apidae (Fig. 3, Table 1). Within the Apidae a positive association between colony size and queen lifespan might exist but with our small sample size we cannot statistically confirm this. Within the Formicidae long queen lifespan occurs at all colony sizes while short-lived queens are only found in smaller colony sizes (Fig. 3). As pointed out by Keller & Genoud (1997) queens in polygyne colonies live significantly shorter than queens of monogyne species and for our dataset queen number would be a better predictor of queen lifespan than colony size. Interestingly, polygyne species appear with higher frequencies at smaller colony sizes. Short-lived queens do not occur in species with large colony sizes; this can either result from ancestral monogyny (Schrempf & Heinze, 2007) with the need for a longer lifespan in queens with larger colonies or it could be caused by a sampling bias because queen lifespan can be obtained by colony survival in monogyne but not in polygyne species (Gordon, 1991; Hou *et al.*, 2010). Larger colony sizes lead to an increased protection of the queen against extrinsic risks. Additionally, an increasing reproductive value and the dependency of colony fitness on the survival of the single queen should select for an increasing queen lifespan and survival, which is in line with the evolutionary theories of ageing (Stearns, 1992; Keller & Genoud, 1997).

If we could control for ecological factors or larger phylogenetic trends within the hymenoptera it might be possible that a correlation between lifespan (queen and worker) and colony size would appear. For example, queen lifespan of subterranean species (ants) is much greater than for terrestrial species (bees and wasps) (Carey, 2001) and colony size is likely to be set by ecological factors (Bourke, 1999). The relative differences of lifespan (lifespan ratio) and colony size used here are likely to control for phylogenetic and ecological constraints and offer an opportunity to compare different eusocial species as the result of the independent contrast analysis suggests. In our comparison bee, wasp, and ant species fit into the observed relationship of lifespan ratio and colony size. We could even include the social mole-rats of the genus *Fukomys* [which show long lifespans for queens and workers, but have small colony sizes (Dammann & Burda, 2006; Dammann *et al.*, 2011)] without changing the results.

We found that worker and queen lifespan diverge (increasing lifespan ratio) with increasing colony size in eusocial Hymenoptera. This may point to a general trend in eusocial organisms, which is already visible at the transition from solitary to social species also for species not belonging to the Hymenoptera. Two examples are the wasps and *Fukomys* species (mole-rats), in which worker lifespan remains at levels of the solitary ancestors while queen lifespan increases in the social species. In honey bees (*Apis mellifera*) the same pattern is observed throughout colony growth: in small colonies workers have longer lives when compared with workers living in larger colonies (Rueppell, Kaftanouglu & Page, 2009). Increasing colony size leads to a number of social consequences: the reproductive potential of workers decreases while the social complexity and the degree of caste differentiation increase (Alexander *et al.*, 1991; Bourke, 1999; Changizi *et al.*, 2002). Lifespan as a life-history trait appears to be affected by those changes.

Our finding generally points to an adaptive process of division of labour and increasing task specialization that eusocial Hymenoptera have in common and that could lead to an adaptive demography, where the demography of the colony is directly adaptive and not its causal parameters (Oster & Wilson, 1978; Holldobler & Wilson, 1990). As colony size increases the quality of individuals diverges and lifespan as an outcome of maintenance investments may be evolutionarily shaped to optimize productivity and hence fitness on the colony level by modifying the resource allocation into different castes. However, it is difficult

to disentangle the effect of larger colony size on the lifespan differential. Colony size is associated with increasing division of labour, which in turn leads to morphological differences and different patterns of resource allocation into individuals possibly as a response to different levels of extrinsic mortality (Bourke, 1999; Amdam & Omholt, 2002; Muench, Amdam & Wolschin, 2008; Dornhaus *et al*., 2012). Thus, it is difficult to identify exclusive explanatory factors for the observed lifespan differential.

Following the evolutionary theories of ageing maintenance, investment could be shaped according to the differences in extrinsic mortality and thus for social insects it has been argued that extrinsic mortality explains the lifespan of queens, the differences between worker and queen lifespan, as well as lifespan differences between different worker castes (Keller & Genoud, 1997; Chapuisat & Keller, 2002; Heinze & Schrempf, 2008). Following this, one possible explanation for the increasing lifespan ratio is that workers of larger colonies experience higher levels of extrinsic mortality while queens are more heavily protected by their colony. Larger colony sizes may force colonies to increase their foraging range and to defend more distant food patches. The distance each forager has to cover during a foraging trip increases and thus the risk of dying from predation (Jorgensen & Porter, 1982). Additionally, competition with other colonies might increase for species with larger foraging ranges (Gordon & Kulig, 1996). Selection may act on the colony level to ensure resources within the protected colony and minimize losses caused by the early death of a worker. Individual worker productivity should be optimized: applying a model of intergenerational transfers to honey bees suggests that task- or caste-dependent senescence patterns may occur as a result of different schedules of resource allocation to individuals dependent on the task carried out (Amdam & Page, 2005). In larger colonies selection for morphological or physiological changes that increase worker productivity should be more efficiently selected for because the benefits would be multiplied by the number of workers. This trait could be selected for at the colony level to increase colony fitness by changing the life histories of the individuals within, resulting in disposable workers (Porter & Jorgensen, 1981) and highly reproductive and long-lived queens. Additionally, redundancy and parallel operations leads to a reduced dependency of the superorganism on the precise functioning of single individuals (Oster & Wilson, 1978). As long as the required tasks are accomplished and no fitness compromises are made, selection on worker lifespan might be weak, leading to workers that expend fewer resources independent of extrinsic mortality. It has been shown that small short-lived workers of *Solenopsis invicta* are less costly for the colony than large workers (Calabi & Porter, 1989).

Alternatively, the differences in lifespan could be explained by the morphological differences, but in our study we find that colony size and not the increasing morphological differences measured by the dry weight ratio explain the difference in lifespan between queens and workers. Even in species with morphologically identical castes, which differ in social or reproductive status, lifespan may differ. Examples are ant species with gamergate systems such as *Platythyrea punctata* or *Diacamma* cf. *rugosum* (Tsuji *et al*., 1996; Hartmann & Heinze, 2003) or social wasps such as *Roplidia marginata* (Gadagkar *et al*., 1993), which are included in our dataset.

However, worker lifespan may be correlated with body size (Porter & Tschinkel, 1985; Calabi & Porter, 1989), independent of size as a response to the level of extrinsic mortality (Chapuisat & Keller, 2002) or may be task-dependent (Rueppell *et al*., 2007), and a combination of those factors may ultimately explain the interspecific differences of worker lifespan as a response to colony size. Thus, in this study we cannot be certain which factors drive the positive association of colony size and lifespan.

In general, we cannot be sure why the observed lifespan differences appear as a response to changes in colony size. But we can confirm a larger organismal trend, namely the increasing specialization with increasing size within the superorganism. As a general rule governing the evolution of organismal complexity, larger entities [organisms, nervous systems, ecosystems, and ant colonies (superorganisms)] are composed of increasing numbers of subunits (Bell & Mooers, 1997; Changizi *et al*., 2002). In multicellular organisms division of labour measured as the number of cell types increases with body size (Bell & Mooers, 1997), and in ant colonies the number of castes increases with colony size (Changizi *et al*., 2002). Here we can show for the social insects that the increasing number of phenotypes also leads to an increasing divergence and specialization of those phenotypes. Although we can confirm the increasing morphological differences with colony size measured as weight (this study) or size differences (Changizi *et al*., 2002), we can also show that life-history traits may also be affected. The measured trait lifespan diverges as a response to colony size and increasing complexity.

CONCLUSIONS

For social Hymenoptera lifespan shows a strong association with colony size once the differences between workers and queens are taken into account. The queen–worker lifespan ratio (queen lifespan/worker

lifespan) is positively associated with colony size, while the association between queen or worker lifespan with colony size is not existent or weak. If we assume that the differences in lifespan between queen and worker of a species arise from increasing task specialization in larger groups we find a general pattern in eusocial Hymenoptera that confirms increasing task specialization of individuals, consistent with increasing organismal complexity found in the evolution of nervous systems, multicellular organisms, ant colonies, and ecosystems (Bell & Mooers, 1997; Changizi *et al.*, 2002). In social insects, caste specialization and reproductive division of labour are often accompanied by different levels of extrinsic mortality, which may lead to the correlation of lifespan differences with increasing colony size. To elaborate further the link between extrinsic mortality it would be interesting to test if workers in larger colonies generally experience higher levels of extrinsic mortality.

ACKNOWLEDGEMENTS

REFERENCES

Alexander RD, Noonan KM, Crespi BJ. 1991. The evolution of eusociality. In: Sherman RW, Jarvis JUM, Alexander RD, eds. *The biology of the naked mole-rat*. Princeton, NJ: Princeton University Press, 3–44.

Amdam GV, Omholt SW. 2002. The regulatory anatomy of honeybee lifespan. *Journal of Theoretical Biology* **216:** 209–228.

Amdam GV, Page RP. 2005. Intergenerational transfers may have decoupled physiological and chronological age in a eusocial insect. *Ageing Research Reviews* **4:** 398–408.

Arevalo E, Zhu Y, Carpenter JM, Strassmann JE. 2004. The phylogeny of the social wasp subfamily Polistinae: evidence from microsatellite flanking sequences, mitochondrial COI sequence, and morphological characters. *BMC Evolutionary Biology* **4:** 1–16.

Austad SN, Fischer KE. 1991. Mammalian aging, metabolism, and ecology – evidence from the bats and marsupials. *Journals of Gerontology* **46:** B47–B53.

Beckers R, Goss S, Deneubourg JL, Pasteels JM. 1989. Colony size, communication and ant foraging strategy. *Psyche (Cambridge)* **96:** 239–256.

Bell G, Mooers AO. 1997. Size and complexity among multicellular organisms. *Biological Journal of the Linnean Society* **60:** 345–363.

Bonner JT. 1988. *The evolution of complexity: by means of natural selection*. Princeton, NJ: Princeton University Press.

Bonner JT. 2004. Perspective: the size–complexity rule. *Evolution* **58:** 1883–1890.

Boomsma JJ. 2009. Lifetime monogamy and the evolution of eusociality. *Philosophical Transactions of the Royal Society B: Biological Sciences* **364:** 3191–3207.

Bourke AFG. 1999. Colony size, social complexity and reproductive conflict in social insects. *Journal of Evolutionary Biology* **12:** 245–257.

Bourke AFG. 2007. Kin Selection and the Evolutionary Theory of Aging. *Annual Review of Ecology, Evolution, and Systematics* **38:** 103–128.

Brett RA. 1991. The population structure of naked mole-rat colonies. In: Sherman PW, Jarvis JUM, Alexander RD, eds. *The biology of the naked mole-rat*. Princeton, NJ: Princeton University Press, 97–136.

Browne FG. 1961. The biology of Malayan Scolytidae and Platypodidae. *Malayan Forest Records* **22:** 1–255.

Browne FG. 1962. Preliminary observations on *Doliopygus dubius* (Samps.), (Coleopt: Platypodidae). *Report of the West African Timber Borer Research Unit London* **1961:** 15–30.

Buffenstein R. 2005. The naked mole-rat? A new long-living model for human aging research. *Journals of Gerontology Series a-Biological Sciences and Medical Sciences* **60:** 1369–1377.

Buffenstein R. 2008. Negligible senescence in the longest living rodent, the naked mole-rat: insights from a successfully aging species. *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology* **178:** 439–445.

Burda H. 1995. Individual recognition and incest avoidance in eusocial common mole-rats rather than reproductive suppression by parents. *Experientia* **51:** 411–413.

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

Carey JR. 2001. Demographic mechanisms for the evolution of long life in social insects. *Experimental Gerontology* **36:** 713–722.

Carey JR. 2003. *Longevity: the biology and demography of life span*. Princeton, NJ: Princeton University Press.

Carey JR, Judge DS. 2001. Life span extension in humans is self-reinforcing: a general theory of longevity. *Population and Development Review* **27:** 411–436.

Changizi MA, McDannald MA, Widders D. 2002. Scaling of differentiation in networks: nervous systems, organisms, ant colonies, ecosystems, businesses, universities, cities, electronic circuits, and legos. *Journal of Theoretical Biology* **218:** 215–237.

Chapuisat M, Keller L. 2002. Division of labour influences the rate of ageing in weaver ant workers. *Proceedings of the Royal Society of London Series B-Biological Sciences* **269:** 909–913.

Choe JC, Crespi BJ. 1997. *The evolution of social behavior in insects and arachnids*. Cambridge: Cambridge University Press.

Collatz KG, Sohal RS. 1986. *Insect aging: strategies and mechanisms*. Berlin: Springer.

Costa JT. 2006. *The other insect societies*. Cambridge, MA: Belknap Press of Harvard University Press.

Costa MA, Del Lama MA, Melo GAR, Sheppard WS. 2003. Molecular phylogeny of the stingless bees (Apidae, Apinae, Meliponini) inferred from mitochondrial 16S rDNA sequences. *Apidologie* **34:** 73–84.

Crawley MJ. 2002. *Statistical computing: an introduction to data analysis using S-plus*. New York: Wiley.

Crespi BJ. 1992. Eusociality in Australian gall thrips. *Nature* **359:** 724–726.

Crespi BJ, Morris DC, Mound LA. 2004. *Evolution of ecological and behavioural diversity: Australian acacia thrips as model organisms*. Canberra: Australian Biological Resources Study.

Dammann P. 2006. *Seneszenz bei afrikanischen Sandgräbern (Bathyergidae, Rodentia) unter besonderer Berücksichtigung der Gattung Fukomys* Fakultät für Biologie und Geografie. Essen: Universität Duisburg-Essen.

Dammann P, Burda H. 2006. Sexual activity and reproduction delay ageing in a mammal. *Current Biology* **16:** R117–R118.

Dammann P, Sumbera R, Massmann C, Scherag A, Burda H. 2011. Extended Longevity of reproductives appears to be common in *Fukomys* mole-rats (Rodentia, Bathyergidae). *PLoS ONE* **6:** e18757.

Danforth BN. 1999. Phylogeny of the bee genus *Lasioglossum* (Hymenoptera: Halictidae) based on mitochondrial COI sequence data. *Systematic Entomology* **24:** 377–393.

David O, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, Pearse W. 2012. caper: Comparative analyses of phylogenetics and evolution in R.

Dornhaus A, Powell S, Bengston S. 2012. Group size and its effects on collective organization. *Annual Review of Entomology* **57:** 123–141.

Evans HE. 1958. The evolution of social life in wasps. *Proceedings of the 10th International Congress of Entomology*, Montreal 1956, **2:** 449–457.

Faulkes CG, Abbott DH. 1996. The physiology of a reproductive dictatorship: regulation of male and female reproduction by a single breeding female in colonies of naked mole-rats. In: Solomon NG, French JA, eds. *Cooperative breeding in mammals*. New York: Cambridge University Press, 302–334.

Felsenstein J. 1985. Phylogenies and the comparative method. *American Naturalist* **125:** 1–15.

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

Fjerdingstad EJ, Crozier RH. 2006. The evolution of worker caste diversity in social insects. *American Naturalist* **167:** 390–400.

Gadagkar R, Chandrashekara K, Chandran S, Bhagavan S. 1993. Serial polygyny in the primitively eusocial wasp *Ropalidia marginata*: implications for the evolution of sociality. In: Keller L, ed. *Queen number and sociality in insects*. Oxford: Oxford University Press, 188–214.

Gadau J, Fewell JH, Wilson EO. 2009. *Organization of insect societies: from genome to sociocomplexity*. Cambridge, MA: Harvard University Press.

Garland T, Harvey PH, Ives AR. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology* **41:** 18–32.

Goldsby HJ, Dornhaus A, Kerr B, Ofria C. 2012. Task-switching costs promote the evolution of division of labor and shifts in individuality. *Proceedings of the National Academy of Sciences of the United States of America* **109:** 13686–13691.

Gordon DM. 1991. Behavioral flexibility and the foraging ecology of seed-eating ants. *American Naturalist* **138:** 379–411.

Gordon DM, Kulig AW. 1996. Founding, foraging, and fighting: colony size and the spatial distribution of harvester ant nests. *Ecology* **77:** 2393–2409.

Gross J, Ligges U. 2012. nortest: Tests for normality. R package version 1.0-2 ed.

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

Heinze J, Schrempf A. 2008. Aging and reproduction in social insects – a mini-review. *Gerontology* **54:** 160–167.

Heylighen F. 2000. Evolutionary transitions: how do levels of complexity emerge? *Complexity* **6:** 53–57.

Holldobler B, Wilson EO. 1990. *The ants*. Xiii+732p. Illus. Maps: XIII+732P. Cambridge, MA: Harvard University Press.

Hou C, Kaspari M, Vander Zanden HB, Gillooly JF. 2010. Energetic basis of colonial living in social insects. *Proceedings of the National Academy of Sciences of the United States of America* **107:** 3634–3638.

Hughes KA, Reynolds RM. 2005. Evolutionary and mechanistic theories of aging. *Annual Review of Entomology* **50:** 421–445.

Hurd CR, Jeanne RL, Nordheim EV. 2007. Temporal polyethism and worker specialization in the wasp, *Vespula germanica*. *Journal of Insect Science* **7:** 43.

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

Jorgensen CD, Porter SD. 1982. Foraging behavior of *Pogonomyrmex owyheei* in Southeast Idaho. *Environmental Entomology* **11:** 381–384.

Keller L. 1998. Queen lifespan and colony characteristics in ants and termites. *Insectes Sociaux* **45:** 235–246.

Keller L, Genoud M. 1997. Extraordinary lifespans in ants: a test of evolutionary theories of ageing. *Nature* **389:** 958–960.

Keller L, Jemielity S. 2006. Social insects as a model to study the molecular basis of ageing. *Experimental Gerontology* **41:** 553–556.

Kerr WE. 1950. Genetic determination of castes in the genus *Melipona*. *Genetics* **35:** 143–152.

Kirkendall LR, Kent DS, Raffa KF. 1997. Interactions among males, females and offspring in bark and ambrosia beetles: the significance of living in tunnels for the evolution of social behavior. In: Choe JC, Crespi BJ, eds. *The evolution of social behavior in insects and arachnids*. Cambridge: Cambridge University Press, 181–215.

Kranz BD. 2005. Egg size and reproductive allocation in eusocial thrips. *Behavioral Ecology* **16:** 779–787.

Lee RD. 2003. Rethinking the evolutionary theory of aging: transfers, not births, shape social species. *Proceedings of the National Academy of Sciences of the United States of America* **100:** 9637–9642.

Liang S, Mele J, Wu Y, Buffenstein R, Hornsby PJ. 2010. Resistance to experimental tumorigenesis in cells of a long-lived mammal, the naked mole-rat (*Heterocephalus glaber*). *Aging Cell* **9:** 626–635.

Matsuura M. 1984. Comparative biology of the five Japanese species of the genus *Vespa* (Hymenoptera, Vespidae). *Bulletin of the Faculty of Agriculture Mie University*: 1–131.

Matsuura M. 1991. *Vespa* and *Provespa*. In: Ross KG, Matthews RW, eds. *The social biology of wasps*. Ithaca, NY: Cornell University Press, 232–262.

Medawar PB. 1952. *An unsolved problem of biology*. London: Lewis.

Michod RE. 2000. *Darwinian dynamics: evolutionary transitions in fitness and individuality*. Princeton, NJ: Princeton University Press.

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

Moret Y, Schmid-Hempel P. 2000. Survival for immunity: the price of immune system activation for bumblebee workers. *Science* **290:** 1166–1168.

Muench D, Amdam GV, Wolschin F. 2008. Ageing in a eusocial insect: molecular and physiological characteristics of life span plasticity in the honey bee. *Functional Ecology* **22:** 407–421.

Oster G, Wilson EO. 1978. *Caste and ecology in the social insects*. Princeton, NJ: Princeton University Press.

Page RE Jr, Peng CYS. 2001. Aging and development in social insects with emphasis on the honey bee, *Apis mellifera* L. *Experimental Gerontology* **36:** 695–711.

Paradis E, Claude J, Strimmer K. 2004. A{PE}: analyses of phylogenetics and evolution in {R} language. *Bioinformatics* **20:** 289–290.

Parker JD. 2011. What are social insects telling us about aging? *Myrmecological News* **13:** 103–110.

Perry S, Chapman T, Schwarz M, Crespi B. 2004. Proclivity and effectiveness in gall defence by soldiers in five species of gall-inducing thrips: benefits of morphological caste dimorphism in two species (*Kladothrips intermedius* and *K. habrus*). *Behavioral Ecology and Sociobiology* **56:** 602–610.

Porter SD, Jorgensen CD. 1981. Foragers of the harvester ant, *Pogonomyrmex owyheei* – a disposable caste. *Behavioral Ecology and Sociobiology* **9:** 247–256.

Porter SD, Tschinkel WR. 1985. Fire ant polymorphism – the ergonomics of brood production. *Behavioral Ecology and Sociobiology* **16:** 323–336.

R Core Development Team. 2010. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Rehan SM, Richards MH. 2010a. The influence of maternal quality on brood sex allocation in the small carpenter bee, *Ceratina calcarata*. *Ethology* **116:** 876–887.

Rehan SM, Richards MH. 2010b. Nesting biology and subsociality in *Ceratina calcarata* (Hymenoptera: Apidae). *Canadian Entomologist* **142:** 65–74.

Richards MH. 2011. Colony social organisation and alternative social strategies in the eastern carpenter bee, *Xylocopa virginica*. *Journal of Insect Behavior* **24:** 399–411.

Ross KG, Matthews RW. 1991. *The social biology of wasps*. Ithaca, NY: Comstock Pub. Associates.

Rueffler C, Hermisson J, Wagner GP. 2011. Evolution of functional specialization and division of labor. *Proceedings of the National Academy of Sciences of the United States of America* **109:** E326–E335.

Rueppell O, Bachelier C, Fondrk MK, Page RE. 2007. Regulation of life history determines lifespan of worker honey bees (*Apis mellifera* L.). *Experimental Gerontology* **42:** 1020–1032.

Rueppell O, Kaftanouglu O, Page RE. 2009. Honey bee (*Apis mellifera*) workers live longer in small than in large colonies. *Experimental Gerontology* **44:** 447–452.

Schmid-Hempel P. 1998. *Parasites in social insects*. Princeton, NJ: Princeton University Press.

Schmid-Hempel P, Wolf T. 1988. Foraging effort and life span of workers in a social insect. *Journal of Animal Ecology* **57:** 509–521.

Schmitz J, Moritz RFA. 1998. Molecular phylogeny of Vespidae (Hymenoptera) and the evolution of sociality in wasps. *Molecular Phylogenetics and Evolution* **9:** 183–191.

Schrempf A, Heinze J. 2007. Back to one: consequences of derived monogyny in an ant with polygynous ancestors. *Journal of Evolutionary Biology* **20:** 792–799.

Simpson C. 2012. The evolutionary history of division of labour. *Proceedings of the Royal Society B-Biological Sciences* **279:** 116–121.

Smith JM, Szathmary E. 1997. *The major transitions in evolution*. Oxford: Oxfors University Press.

Stearns SC. 1992. *The evolution of life histories*. Oxford and New York: Oxford University Press, xii + 249 pp

Strassmann J. 1985. Worker mortality and the evolution of castes in the social wasp *Polistes exclamans*. *Insectes Sociaux* **32:** 275–285.

Strassmann JE, Queller DC. 2009. The social organism: congresses, parties, and committees. *Evolution* **64:** 605–616.

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

Wheeler WM. 1911. The antcolony as an organism. *Journal of Morphology* **22:** 307–325.

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

Wilson DS, Sober E. 1989. Reviving the superorganism. *Journal of Theoretical Biology* **136:** 337–356.

Wilson DS, Wilson EO. 2007. Rethinking the theoretical foundation of sociobiology. *The Quarterly Review of Biology* **82:** 327–348.

Wilson EO. 1971. *The insect societies*., Cambridge, MA: Belknap Press of Harvard University Press.

Wilson EO. 1975. *Sociobiology: the new synthesis*. Cambridge, MA: Belknap Press of Harvard University Press.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Phylogenetic trees used for the independent contrasts analysis. A, inferred from Moreau, Bell, Vila, Archibald & Pierce (2006) including branch length; B, inferred from (Arevalo, Zhu, Carpenter & Strassmann, (2004), Costa, Del Lama, Melo & Sheppard (2003), Danforth (1999), Moreau *et al*. (2006), and Schmitz & Moritz (1998) using equal branch length.
Table S1. Species list and used citations.
Table S2. Species used in the independent contrast analysis.