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Title: Chapter 11. Patterns of longevity across a sociality gradient in vespid wasps

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Abstract

The reversal of the fecundity/longevity tradeoff in social insects is striking, but we lack understanding of when and how this reversal evolved. Vespid wasps are excellent models for studying social evolution because species show different levels of sociality from solitary to primitively to advanced eusocial. We provide the first synthesis of existing, but scanty, data available on longevity in vespids. We explore whether the fecundity/longevity tradeoff reversal is exaggerated in species with more derived sociality. Although the reversal is evident in primitively social wasps, the available data suggest it may be stronger in large-colonied species, which show a trend toward shorter worker longevity. More data are needed on additional species and underlying mechanisms, but vespids hold promise for understanding the evolution of the fecundity/longevity tradeoff reversal.

Social insects as models for understanding the evolution of aging and longevity

In most organisms, high reproductive output is associated with reduced longevity due to the costs of reproduction and mating [1,2]. Social insects have become important models for understanding the biology of aging, due to the reversal of this fecundity/longevity tradeoff [3,4]. Specifically, in queens of advanced eusocial species such as honey bees and many species of ants and termites, we find not only some of the most long-lived individuals in the whole insect world but, paradoxically, these queens also have among the highest known reproductive rates [5]. Thus, comparisons of social insect queens and workers have the potential to provide important insights into the mechanisms and evolution of aging. Several studies to date have investigated the mechanisms underlying extended lifespan and high reproductive capacity of social insect queens, especially using the model social insect, the honey bee *Apis mellifera* [6]. However, fewer studies have addressed the evolution of these unique and extreme patterns of aging, longevity, and reproduction.

The reversal of the typical fecundity/longevity tradeoff in social insects raises the question of whether this unusual reversal accompanied the origin of sociality or whether it is a derived trait found only in advanced eusocial species such as ants, honey bees, and higher termites [7]. Here, we suggest that comparative studies of patterns of aging and longevity in social insects can provide insights into how and when this reversal evolved during social evolution. In particular, wasps in the family Vespidae provide a particularly attractive model for comparative studies investigating the evolution of longevity in the context of sociality.

Vespid wasps as a model system for comparative social evolution

Mechanisms of aging and longevity in relation sociality have been studied most extensively in other hymenopteran families, especially bees (Apidae) and ants (Formicidae) [3]. However, the family Vespidae offers an unparalleled opportunity to study the evolution of longevity, as vespid species exhibit the complete spectrum of social complexity from solitary to highly eusocial (**Figure 1; Table 1**) within a single monophyletic lineage [8-10], making it one of the best systems for studying the evolution of sociality [11**]. In addition, studies of wasps, paired with those of other independently evolved social lineages such as bees, ants, and termites, provide an informative “natural experiment” to examine whether convergently evolved patterns of aging and longevity are associated with the same or different physiological and genetic mechanisms.

There are six recognized subfamilies of vespid wasps: Eumeninae, Euparagiinae, Masarinae, Stenogastrinae, Polistinae, and Vespinae (**Figure 1**). The former three are solitary or subsocial (showing maternal care), while the latter three show different degrees of social behavior, from facultatively social to advanced eusocial. Within the social subfamilies, independent founding (nest initiation by a single generation) is considered to be less derived than swarm founding (nest initiation by a multigeneration group). In **Table 1**, we provide brief descriptions of the different grades of sociality in vespid wasps and in **Figure 1**, which subfamilies and model genera exhibit this behavior.

General patterns of vespid longevity related to caste and sociality

There are few experimental studies on longevity (age at death) in vespid wasps [12**], making it difficult to determine whether death occurs due to old age or extrinsic mortality effects. The patterns we report, therefore, are tentative. In order to provide a synthesis of patterns across castes and across species, we first review the existing data on longevity in adult female vespid wasps. Conspicuously, there are almost no actual longevity data available for solitary vespid subfamilies (**Figure 1**). Although a few solitary vespid life cycles are typified by fairly long-lived adult females (up to a year, i.e. in univoltine species undergoing adult diapause and subsequent nesting), most solitary wasps in temperate zones overwinter as pre-pupae, suggesting adult lifespans of a few months at most [13-15]. Solitary vespids have very low lifetime reproductive potential (e.g., eumenine species span lifetime totals of 5-14 eggs), and reproduction may be limited by the energetic demands of maternal care [14]. Thus, while solitary vespids are certainly characterized by low reproductive potential, lifespans may be highly variable. More data are needed to address whether the solitary vespids exhibit the typical fecundity/longevity tradeoff. Due to the paucity of data on solitary species, the remainder of our review will focus on studies from the three social subfamilies (Stenogastrinae, Polistinae, and Vespinae).

Queen vs. Worker Longevities in the Social Vespids. We identified three patterns concerning caste-related differences in vespid longevity, which relate to two life-history traits: level of social complexity and seasonality. First, primitively eusocial

species (**Table 1**) of the aseasonal tropics show little difference in longevity between the castes. Wasp sociality is believed to have originated in the tropics [8], which posits the idea that there was little or no difference in longevity between reproductives and non-reproductives at the origin of sociality in wasps. In aseasonal tropical species, reproductive diapause is absent and queens of independent-founding polistine species (e.g., *Polistes*, *Mischocyttarus*) initiate new colonies shortly after leaving the natal colony, and at any time of the year [16,17]. Colonies typically last only a few months before reproducing and declining. In many cases queen supersedure is common [18], resulting in much lower lifespans for queens. In *Mischocyttarus drewseni*, mean queen lifespan was only 61 (± 18.7 ; $n = 6$) days, compared to 31 (± 16.9 ; $n = 148$) days for workers, a ratio of 2:1 [16]. Mean longevity for *Liostenogaster flavolineata* was 132 days for queens ($n = 112$) and 58 days for workers ($n = 211$), a ratio of 2.3:1 [19]. Much greater longevity was recorded in the only lab-experimental study on longevity in wasps, in which tropical *Polistes canadensis* females lived up to 506 days (mean 193 ± 10.5 days) [12**], although reproductive status was not examined. This species may be exceptional because nest re-founding by family groups occur [20], with queens surviving and reproducing during multiple nesting cycles [21].

Second, primitively eusocial wasp species that live in seasonal environments show greater differential longevity among castes, suggesting that seasonality could play a role in evolution of the reproduction-longevity relationship that characterizes social insects. In strongly seasonal climates, e.g. temperate zones and tropical regions with a strong dry season, queens often live for close to a year, whereas workers live for 2-5 weeks [22,23]. Thus, queens live 10-25x as long as workers. This difference is marked,

given that in these seasonal environments longevity is limited by the demands of entering diapause during overwintering (e.g. most vespines and some *Polistes*) or altitudinal migration (e.g. some tropical *Polistes* and *Mischocyttarus*) [24]. Extended lifespan as an overwintering adaptation is well known in other social insects, e.g. *Apis mellifera* worker “winter bees” [25]. However, despite marked queen-worker differences in longevity, queen longevities may be limited to a little more than a year in vespids. Even where colonies persist across years (e.g. some *Vespula* species at the equatorial edges of their ranges), the original founding queen does not live long enough to reproduce in the second year [26,27].

Third, the more socially complex swarm-founding species of the tropics (Polistinae: Epiponini) show intermediate levels of caste-related differences in longevity. New colonies are initiated by swarms of many workers and a smaller number of queens. During the first part of the colony cycle queen numbers are gradually reduced to one (or a few), a process called cyclical oligogyny. When the last queen dies, the colony rears many new queens (‘requeening’) and the cycle repeats [28]. In one colony of *Metapolybia aztecoides* in Costa Rica, the polygynous stage lasted at least six months, during which the number of queens decreased from over 30 to just one, who continued as the sole egg-layer for another six months [28]. Given the likelihood that she was among the original polygynous cohort, she lived and reproduced for about a year, although the average would be much less if all the founding queens are taken into account. If worker lifespans of this species are comparable to those of other epiponines (3-4 weeks), she outlived her workers by a ratio of at least 13 to 1. We are aware of only one study of an epiponine in which longevities of queens were measured. Simões et al.

[29] found that queens in *Protopolybia exigua* lived an average of 256 days, compared with workers' mean lifespan of 25.6 days [30], a ratio of 10:1. Thus, although the data for the swarm-founding Polistinae are very scant, they suggest that queens live for a few months to a year.

In a recent study of longevity in eusocial Hymenoptera, Kramer and Schaible [31**] found that colony size correlated with the ratio of queen to worker lifespans, but not with either queen or worker lifespans alone. The above analysis suggests that lifespan ratios are closely tied to climate and type of founding.

Correlates of Worker Longevity—Social Complexity. Strassmann noted that maximum worker lifespans for primitively eusocial wasps (the independently founding polistine genera *Polistes* and *Mischocyttarus*) tended to be longer than those for highly eusocial genera (*Vespula*, *Vespa*, *Apis*) [32]. This suggests that in the small colonies of the former, helpers may resist specialization as workers so as to retain the flexibility to replace their mother as the sole reproductive female [32,33].

We used the currently available information on worker longevity from 27 species [16,19,22,23,30,32,34-47] for an initial, exploratory test of this idea. To do this, we grouped species into three rough categories, from lowest to highest social complexity: (1) primitively or facultatively eusocial (including one Stenogastrinae and several independent founding Polistinae, n=13), (2) advanced eusocial with independent founding (Vespinae, n=11, and (3) advanced eusocial with swarm founding (Epiponini, n=3). Although there were no significant differences between the three social complexity groups (**Figure 2A**, ANOVA: $F = 3.24$, $p = 0.057$), there was a non-significant

trend in the predicted direction. Worker longevity was fairly low for epiponines, somewhat intermediate for vespines, and there was a large range in worker longevity among independent founding species, including some species with the most long-lived workers known in the Vespidae. Based on this preliminary analysis, the data are suggestive, but inconclusive to support or reject the social complexity hypothesis. The analysis is based on relatively few species and the social complexity grouping is confounded by taxonomy (e.g., all of the intermediately social species are in the subfamily Vespinae) and correlated life history traits (e.g. differences in tropical vs temperate distribution).

Correlates of Worker Longevity—Colony Size. To further explore the possible relationship between social complexity and worker longevity, we used colony size as a rough indicator for social complexity. Although not a perfect correlate of social complexity, large colony size is typically related to more advanced social traits such as queen-worker morphological caste differences, worker sterility, more complex nest architecture and a more pronounced reproductive and worker division of labor [48]. We examined the relationship between mean colony sizes from reports in the literature with available data on mean worker longevity for 22 vespid species [16,19,22,23,30,32,34-45,49-58], ranging from independent-founding, primitively eusocial polistines (e.g. *Polistes* and *Mischocyttarus*) to independent-founding advanced eusocial vespines (e.g. *Vespula*) to swarm-founding polistines (e.g. *Polybia*). We found a significant negative association between mean colony size and mean worker longevity (Linear regression; $R^2 = 0.314$, $R^2_{\text{adj}} = 0.279$, $p=0.007$, **Figure 2B**). Although there is substantial variation and colony size is not a perfect predictor of worker longevity, the fact that we found a

significant relationship is noteworthy considering the noisy nature of the data, which are based on relatively few species, and colony size and longevity data were not necessarily taken from the same colonies or populations. These data also fit well with the disposable soma (i.e. “disposable caste”) idea [59**] that colonies should reduce investment in maintenance and lifespan of non-reproductive members with high extrinsic mortality [60], and this effect should be most pronounced in species with large colonies.

Mechanistic basis of wasp longevity differences

The exaggeration of individual longevity differences (long-lived queens vs very short-lived workers) is a life history trait in the evolution of sociality [3]. Such differences could be related to correlated suites of deeply conserved physiological and behavioral traits including reproductive physiology and diapause. Indeed, bivoltinism and diapause (which are intimately tied to the regulation of aging/senescence) in wasps have been proposed as pre-adaptations for the evolution of sociality [10].

To date, there have been no studies directly examining the underlying mechanisms of longevity regulation in vespids. However, there have been numerous studies examining physiological and molecular correlates of differences in caste development and behavior (reviewed in [11**]). Previous studies in honey bees have implicated JH signaling, in conjunction with regulation of the yolk protein vitellogenin (Vg) as being related to the regulation of lifespan in honey bees [61]. JH and Vg are also known to be associated with caste, dominance, and foraging behavior differences in some vespid wasps [62-67]. Thus, it is possible that JH, Vg, and their dynamic

interaction may also affect longevity in vespids, but more empirical work is needed to understand these relationships.

Studies of gene expression differences between queens and workers in social vespids show differences in the expression of storage proteins (including Vg and hexamerins), and genes related to metabolism and oxidation-reduction, and immunity [62,67-70*,71*]. There are also massive changes in the expression of thousands of genes during the one-year lifespan of *Polistes* queens as they shift social roles and ages. Some of these are related to oxidation-reduction, stress response, and heat shock [62] and could be active or causal regulators of lifespan, but the roles of these genes and pathways have not yet been tested experimentally.

In contrast to classic aging theory, where reproduction appears to be costly and associated with reduced longevity, in social insects reproduction appears to carry longevity benefits, somehow slowing down the aging process [4]. Workers in species that have retained reproductive potential (i.e. primitive species, like *Polistes*) appear to be longer lived (relative to queens) than those in more complex societies (i.e. advanced species, like *Polybia*), where workers have reduced capacity to reproduce. A fruitful avenue for understanding the mechanisms underpinning the evolution of long-lived queens and short-lived workers therefore lies in explaining how workers lose reproductive potential, whereas queens retain (and augment) it. Tropical wasps such as *Polistes canadensis* may offer insights into these mechanisms, as workers apparently lose the ability to reproduce as they grow older [72]. Similarly, workers in swarm-founding *Metapolybia* lose the ability to develop their ovaries after about 2 weeks of age [28]. Loss of worker reproductive potential may be an important transitional step in the

evolution of long lived queens and short lived workers in social insects. Epigenetic factors such as DNA methylation are possible candidates for regulating this loss of reproductive ability, as they have been broadly implicated in aging [73].

Future directions

Our synthesis of available vespid longevity data highlight several testable hypotheses on the evolution and mechanisms of aging and longevity patterns in social insects (**Figure 3**) : 1) queens are longer lived than workers, and the extent of this difference may depend on climatic factors and level of social complexity, 2) workers are shorter lived in large-colonied species and this *may* reflect a “disposable caste” with reduced investment in mechanisms promoting longevity in workers, and 3) loss of worker reproductive potential may be an important mechanism in the evolution of queen-worker longevity differences. We emphasize that these are only hypotheses and more rigorous tests of each are needed. In particular, there is a great need for more work on solitary species for comparison to social species to fruitfully test these hypotheses (**Figure 3**).

The vespids are also an ideal group to examine how both individual-level and colony-level selection may drive the evolution of lifespans of colony members. Colony cycles among tropical species vary from a few months in some species to years in some of the swarm founders. What would we predict, for example, about lifespans of queens and workers in long-cycle species that have evolved hardened defenses that reduce colony mortality rates to relatively low levels?

We suggest that more work on regulation of aging and lifespan in a comparative context, using vespids as a key model system, can provide new insights into the evolution of the reversal of the fecundity-lifespan tradeoff in social insects. If paired with studies on mechanisms, including manipulation of candidate genes/pathways, we may also understand which genomic and molecular systems have been utilized or co-opted for lifespan regulation in the context of sociality.

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Figure Legends

Figure 1. Phylogenetic representation (based on [9]) of vespid wasp subfamilies, including information on the forms of sociality exhibited by the subfamilies and most commonly studied genera within each, with indications on where there are available data on patterns of longevity. Photos from Wikimedia except *Euparagia* (from BugGuide.net by Dennis Haines) and *Polybia* (by Mario Palma).

Figure 2. A. Worker longevity data for 27 species of Vespidae, grouped by level of sociality and taxon: primitively and facultatively eusocial (independent-founding Polistinae and Stenogastrinae) (n=13), advanced eusocial with independent-founding (Vespinae) (n=11), and advanced eusocial with swarm founding (Polistinae: Epiponini) (n=3). There were no significant differences between the groups (ANOVA $p=0.057$). Middle line = median; box gives middle 50% of the data; upper and lower whiskers extend to maximum and minimum data points within 1.5 box heights from the top and bottom of the box, respectively. Filled circles are outliers. **B.** There was a significant negative relationship between worker longevity and colony size across 22 species of Vespidae (Linear Regression R-squared = 0.314, R-squared (adj) = 0.279, $p=0.007$). Data are species means for colonies under field conditions. In some cases longevity data and colony-size data come from different populations. Generic abbreviations: A. = *Agelaia*; B. = *Belonogaster*; D. = *Dolichovespula*; L. = *Liostenogaster*; M. = *Mischocyttarus*; Pb. = *Polybia*; Pl. = *Polistes*; Pr. = *Protopolybia*; Va. = *Vespa*; Vl. = *Vespula*.

Figure 3. Possible evolutionary scenario for the reversal of the longevity/reproduction tradeoff during social evolution. We hypothesize a gradual evolution of this reversal, with the reversal already present in primitively eusocial species and further exaggerated in advanced eusocial species. Comparisons between worker longevity in primitively eusocial and advanced eusocial species provide some support for this hypothesis, but we currently lack data to test the other comparisons. Wasp drawing by Amy C. Geffre.

Table 1: Descriptions of the types of social behavior found in vespid wasps.

Form of sociality	Description
Solitary/subsocial	Nests are built and inhabited by a single, solitary female who shows extended maternal care to her offspring (subsociability).
Facultatively social	Within a population, females may nest as solitary individuals or may nest with workers (daughters), who may or may not end up reproducing themselves.
Primitively eusocial	Nests are independently founded by a single female or small group of same-generation females. Queen and worker castes exist but there is extensive caste flexibility and the presence of dominance hierarchies.
Advanced eusocial with independent-founding	Nests are independently founded by a single female. Queen and worker castes are very distinct, with extensive size, morphological, and behavioral differences that are established early in development.
Advanced eusocial with swarm-founding	Nests are founded by a multigeneration swarm including queen(s) and workers. Queen and worker reproductive division of labor is complete, but level of morphological differences vary across species. Multiple queens may exist.

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	Subfamily	Example Genera	Image	Sociality	Longevity Data Available
<pre> graph LR Root --- Node1 Node1 --- Node2 Node1 --- Node3 Node2 --- Node4 Node2 --- Node5 Node3 --- Node6 Node3 --- Node7 Node4 --- Node8 Node5 --- Node9 Node6 --- Node10 Node7 --- Node11 Node8 --- Node12 Node9 --- Node13 Node10 --- Node14 Node11 --- Node15 Node12 --- Node16 Node13 --- Node17 Node14 --- Node18 Node15 --- Node19 Node16 --- Node20 Node17 --- Node21 Node18 --- Node22 Node19 --- Node23 Node20 --- Node24 Node21 --- Node25 Node22 --- Node26 Node23 --- Node27 Node24 --- Node28 Node25 --- Node29 Node26 --- Node30 Node27 --- Node31 Node28 --- Node32 Node29 --- Node33 Node30 --- Node34 Node31 --- Node35 Node32 --- Node36 Node33 --- Node37 Node34 --- Node38 Node35 --- Node39 Node36 --- Node40 Node37 --- Node41 Node38 --- Node42 Node39 --- Node43 Node40 --- Node44 Node41 --- Node45 Node42 --- Node46 Node43 --- Node47 Node44 --- Node48 Node45 --- Node49 Node46 --- Node50 Node47 --- Node51 Node48 --- Node52 Node49 --- Node53 Node50 --- Node54 Node51 --- Node55 Node52 --- Node56 Node53 --- Node57 Node54 --- Node58 Node55 --- Node59 Node56 --- Node60 Node57 --- Node61 Node58 --- Node62 Node59 --- Node63 Node60 --- Node64 Node61 --- Node65 Node62 --- Node66 Node63 --- Node67 Node64 --- Node68 Node65 --- Node69 Node66 --- Node70 Node67 --- Node71 Node68 --- Node72 Node69 --- Node73 Node70 --- Node74 Node71 --- Node75 Node72 --- Node76 Node73 --- Node77 Node74 --- Node78 Node75 --- Node79 Node76 --- Node80 Node77 --- Node81 Node78 --- Node82 Node79 --- Node83 Node80 --- Node84 Node81 --- Node85 Node82 --- Node86 Node83 --- Node87 Node84 --- Node88 Node85 --- Node89 Node86 --- Node90 Node87 --- Node91 Node88 --- Node92 Node89 --- Node93 Node90 --- Node94 Node91 --- Node95 Node92 --- Node96 Node93 --- Node97 Node94 --- Node98 Node95 --- Node99 Node96 --- Node100 </pre>	Masarinae	<i>Pseudomasaris</i>		Solitary	None
	Euparagiinae	<i>Euparagia</i>		Solitary	None
	Stenogastrinae	<i>Liostenogaster</i> , <i>Parischnogaster</i>		Facultatively eusocial	1 species
	Eumeninae	<i>Zethus</i> , <i>Ancistrocerus</i> (pic)		Solitary	None
	Vespinae	<i>Vespula</i> (pic), <i>Vespa</i> , <i>Dolichovespula</i>		Advanced eusocial with independent founding	11 species
	Polistinae	Polistini and Ropalidiini: <i>Polistes</i> (pic), <i>Mischocyttarus</i> , <i>Ropalidia</i>		Primitively eusocial	12 species
	Polistinae	Epiponini: (<i>Polybia</i> (pic), <i>Apoica</i> , <i>Agelaia</i> , <i>Protopolybia</i>)		Advanced eusocial with swarm founding	3 species

A

B

SOLITARY

PRIMITIVELY EUSOCIAL

ADVANCED EUSOCIAL