Long live the wasp: adult longevity in captive colonies of the eusocial paper wasp *Polistes canadensis* (L.)

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ABSTRACT

Insects have been used as an exemplary model in studying longevity, from extrinsic mortality pressures to intrinsic senescence. In the highly eusocial insects, great degrees of variation in lifespan exist between morphological castes in relation to extreme divisions of labour, but of particular interest are the primitively eusocial insects. These species represent the ancestral beginnings of eusociality, in which castes are flexible and based on behaviour rather than morphology. Here we present data on the longevity of the primitively eusocial Neotropical paper wasp *P. canadensis*, in a captive setting removed of environmental hazards. Captive *Polistes canadensis* had an average lifespan of 193 ± 10.5 days; although this average is shorter than most bee and ant queens, one individual lived for 506 days in the lab—longer than most recorded wasps and bees. Natal colony variation in longevity does exist between *P. canadensis* colonies, possibly due to nutritional and genetic factors. This study provides a foundation for future investigations on the effects of intrinsic and extrinsic factors on longevity in primitively eusocial insects, as well as the relationship with natal group and cohort size.

INTRODUCTION

Death comes to all, yet many seemingly ordinary insects have evolved some of the most dramatic and extraordinary lifespans, delaying the call of death for remarkable periods (*Finch, 1990*). Variation in insect longevity spans from *Ephemera simulans* males that live as adults for just 1.6 days (*Carey, 2002*) to the ants *Pogonomyrmex owyhee* and *Lasius niger* whose queens can live up to 30 years (*Porter & Jorgensen, 1988; Hölldobler & Wilson, 1990*). Interestingly, eusocial insects such as ants, wasps, and bees feature heavily as examples of long-lived insects, but great variation exists not only between these species but also within species and even among genotypes. We understand little about the roles of ecology, evolution, life-history, and environment in generating variation in longevity in social insects, largely due to the difficulty of disentangling intrinsic life-span (henceforth referred to as longevity) from survival (the abiotic and biotic environment pressures i.e., extrinsic mortality) on individuals (*Hölldobler & Wilson, 1990; Keller, 1998; Keeler, 1993; Giraldo & Traniello, 2014*).
Eusocial insects are one of the most dominant, prolific, and diverse groups of organisms on the planet (Wilson, 1975). Much of this groups’ success is attributed to the division of labour within the colony in the form of castes, with few or a single reproductive individual (queen), supported by tens to millions of non-reproductive individuals (workers) that forage, provision, and care for sibling brood (Crespi, 1994). Caste fate is primarily determined by environmental conditions, e.g., nutrition during larval development, and occasionally genetic biasing (Oster & Wilson, 1978; Hölldobler & Wilson, 1990; Hughes et al., 2003). Within species, variation in longevity can be pronounced between castes, with queens living as much as 100-fold longer than their related workers (e.g., general: Kramer & Schaible, 2013; Lucas & Keller, 2014; ants: Hölldobler & Wilson, 1990; Keller & Genoud, 1997; wasps: Ridley, 1993). This is a remarkable example of how a single genome can display plasticity in aging (Keller, 1998; Fjerdingstad & Crozier, 2006; Keeler, 1993). Few individuals are selected to specialise in egg production and therefore colony survival is likely to be highly associated with and dependent on queen longevity (in the absence of reproductive succession, see Bourke (2007)). As a result, specialised egg layers are frequently protected from extrinsic pressures such as predation, for example the long-lived queens of the Harvester ant (Pogonomyrmex owyheei) live deep within the nest where they are sheltered (Porter & Jorgensen, 1981). Assuming there are costs associated with longevity (e.g., nutritional demands during larval development, development time), evolutionary theory would predict there would be selection for short lifespan in workers, and long-life span in queens, especially in highly eusocial species where colonies are large enough to support highly specialised, short-lived workers (Evans, 1958; Carey, 2001; De Loof, 2011; Ferguson-Gow et al., 2014). This has been shown to be the case with weaver ants in a protected lab environment whereby major workers (who take on more risky tasks) have a shorter intrinsic lifespan than minor workers who adopt less risky tasks (Chapuisat & Keller, 2002). The level of social complexity appears to be an important predictor of longevity in the eusocial insects. Castes are unlikely to have been selected for such differential longevity in the primitively eusocial species, where colonies are small, each worker is valuable, and survival of workers may be highly variable depending on the type or frequency of task each individual performs (Strassmann, 1985).

Between species, individual longevity is often correlated with mature colony size, as shown in several wasp (Vespa spp.) and ant (Myrmica, Leptothorax, Solenopsis, Cataglyphis) species (Matsuura & Yamane, 1990; Schmid-Hempel, 1998). In ants, at the colony level, the first worker brood are often physically smaller with shorter lifespans than those produced later in the colony cycle, such as nanitic workers of ants (Porter & Tschinkel, 1986). It is hypothesised that this may be due to the increase in levels of nutrition available to brood as the colony grows (Oster & Wilson, 1978; Porter & Tschinkel, 1986). As the colony grows, the ratio of workers to larvae often increases, the larvae will then benefit from increased quality and quantity of food, which can result in longer adult life-spans (e.g., in honey bees Apis mellifera: de Groot, 1953; Eischen, 1982). Conversely in the primitively eusocial paper wasp Polistes exclamans, Strassmann (1985) identified that late emerging workers survived less
time than early emerging workers in 1977 and 1978. This pattern was not detected in 1979
and its cause was suggested to be due to extrinsic factors.

Extrinsic factors such as parasitism, prey availability, and abiotic conditions can be
powerful determinants of survival to wild individuals (Gibb & Metcalf, 1978; Strassman,
1979; Strassmann, 1981; Tibbetts & Reeve, 2003). To date there have been no studies on
how individual longevity varies with colony size in primitively eusocial insects in the
absence of such extrinsic factors. Based on the larval nutrition quality to adult longevity
theory, we predict the same patterns will occur as in the highly eusocial species, since
individuals emerging early in the colony cycle are subject to low worker:larvae ratio
and therefore low quality nutrition. Conversely, those emerging late in the colony cycle
experience high worker:larvae ratio and thus high quality nutrition (Summer et al., 2007).
Additionally, there may be a genetic link to longevity whereby some colonies are more
likely to produce long living individuals than others, potentially due to heritable differences
in feeding/hunting propensity (VanRaden & Klaaskate, 1993; Herskind et al., 1996; Vollema
& Groen, 1996; Klebanov et al., 2001; Sebastiani et al., 2012; Gems & Partridge, 2013). If
colony effects are important, we predict that variation in longevity will be greater between
colonies than within colony, even in the face of group size variation. Finally, positive
correlations between colony size and longevity may be due to social-behavioural and
metabolic factors such as increased per capita work rate in small colonies (Karsai & Wenzel,
1998).

Here we provide primary data on longevity of females in captive colonies of the
predatory and primitively eusocial Neotropical P. canadensis paper wasp. Primitively
eusocial species, such as those of the paper wasp genus Polistes, have been used to
extensively study the evolution of eusociality, with their lack of morphological differences
and plasticity in caste (Turillazzi & West-Eberhard, 1996; although see Hunt, 2006).
Although some studies have addressed the survivorship and colony phenology of some
Polistes species (e.g., O'Donnell & Jeanne, 1992b; Giannotti, 1997a; Clapperton & Dymock,
1997), there remain few systematic attempts to quantify longevity, and variation of, in this
well-studied genus. Many tropical Polistinae such as P. canadensis, although influenced by
wet/dry seasonality in food abundance (and resulting colony productivity), mate and have
colonies of various life-stages throughout the year (Pickering, 1980; Clutton-Brock, 1991).
These study systems offer an excellent system for testing the influence of ecology, evolution,
and environment on longevity, in the absence of seasonal curtailment of longevity found
in temperate species. Studying insect lifespans in captivity, in the absence of predation and
parasitism, is a valuable approach that allows us to quantify longevity in the absence of
extrinsic mortality pressures (Chapuisat & Keller, 2002). We assess how natal colony size
correlates with longevity under laboratory conditions and follow this up by comparing
longevity in experimentally manipulated group sizes. Understanding variation in longevity
in these organisms provides an excellent foundation to explore similar questions in the
higher-order social vertebrates (Carey, 2001).
METHODS

Collection: We collected ten colonies (M1–M10) of the paper wasp, *P. canadensis* from the Province of Colón in Republic of Panamá in August 2013 for transportation to the UK (9°24′03″N 79°52′11″W). Adult wasps were captured with full nest carton containing brood (eggs, larvae, and pupae) during dusk. The nest cartons and wasps were transferred to individual containers (15 cm x 15 cm x 15 cm) with wire mesh ventilation. Colonies were then provided with sugar solution and water *ad libitum* during transfer to the United Kingdom in luggage kept at ambient temperature. Turnaround from capture to settled maintenance in the laboratory was 48 h. To ensure that no colony was heavily infected with entomopathogens from the field, a subset (5 individuals per colony) of cadavers were placed in isolated petri dishes to observe any resulting sporulation of any infecting fungal entomopathogens. The common fungal agent *Aspergillus* spp. sporulated from 10% of these cadavers. *Aspergillus* is an opportunistic and largely ubiquitous fungus, commonly regarded as non-lethal to social insects unless under extreme stress or ingested at unnaturally high concentrations (*Bailey, 1968; Foley et al., 2014*).

Maintenance: Once in the UK, we housed nests in clear transparent acrylic containers 30 cm x 33 cm x 34 cm each with two 525 mm perimeter ventilation ducts (Fig. 1). The food provided consisted of liquid cane sugar and live wax moth larvae *Achroia grisella*, along with distilled water and nest-building materials (cardboard & paper) all were supplied *ad libitum*. All sugar and food was obtained in batches and haphazardly split between colonies to ensure equal food quality provided to the adults to prevent any longevity variability as a result of adult nutrition (*Johanowicz & Mitchell, 2000; Harvey et al., 2012*). In addition to food, in each nest-box we provided plastic artificial planting in the form of...
a strip of 7 cm × 7 cm × 2.5 cm grass sp. and a 5 cm × 5cm × 5 cm plastic Hedera sp. for environmental enhancement to provide shelter from female aggression for males (Polak, 2010). The nest boxes were cleaned regularly with distilled water without disturbing wasps or nest. Natural conditions from the collection sites were mimicked with temperatures of 25 ± 1 °C, 70 ± 5% relative humidity, and a light cycle of 12 h light (12 h dark).

**Data collection:** The colonies were surveyed three to four times a week and any deceased adults found immediately removed from the nest box. Total deaths per colony/cohort were tallied on a weekly basis and this recording method continued until all individuals were deceased. Whilst newly laid eggs were left in the nest for the adults to tend to, brood were eventually removed before pupation ensuring that only the original adult wasps captured from the wild were monitored for longevity and the colony/cohort sizes remained constant. This ensured all of the adult wasps developed under semi-natural conditions. Since all nests were collected from the same field site at the same time, local environmental conditions for development are controlled for as best as possible, though the colonies will differ from each other genetically.

As we do not know the eclosion date for each adult wasp, measures of longevity will be underestimates.

**Hypothesis 1: Adult longevity of female P. canadensis will show some positive correlation with the size of the natal group due to nutrition during colony development theory**

Using the data generated from colonies M1–M7, we were able to quantify variance in longevity between colonies to determine whether colony identity explains variation in wasp longevity better than colony size. Using average survival per colony, correlations between initial colony size upon permanent laboratory setup were investigated.

**Hypothesis 2: Group size will correlate positively with mean female longevity in P. canadensis once the influence of colony genotype is controlled for**

Three colonies (M8, M9, M10) were monitored for a period of 3 months, at which point their group sizes were of 28, 23 and 23 workers respectively. Each colony was then split, and randomly allocated between two new nest boxes lacking nest cartons, giving six new groups in total and consisting of 18, 13, 12, 8, 8 and 9 females. A non-natal male was also added to each the new colony nest boxes so that females had the opportunity to mate. All cohorts then started to build nest cartons and lay eggs suggesting mating may have occurred. The colonies were maintained as above with wasp deaths monitored weekly for 220 days, at which point all individuals were deceased.

**Statistical analyses:** Differences in adult survival were analysed using a Cox proportional hazards regression model where colony was used as a factor. Where differences in survival were found, we conducted pairwise comparisons between nests using Kaplan–Meier models with the Breslow $\chi^2$ statistic to highlight specific patterns between the colonies. Pearson product-moment correlations were carried out to look for patterns between
colony size and average colony longevity. All analyses were carried out in SPSS Statistics 21 (IBM, Armonk, NY, USA).

RESULTS

Hypothesis 1: Adult longevity of female *P. canadensis* will show some positive correlation with the size of the natal group

Here we found that 57% of adult *P. canadensis* colonies maintained in the lab can survive beyond 365 days with one individual living for 506 days, providing data on longevity for 143 wasps in total (Fig. 2). On average wasps lived for 193 ± 10.5 days with the oldest individual living for 506 days (Fig. 2 and Fig. S1). Colony identity has a significant influence on adult wasp longevity (Cox proportional hazard survival analyses, *Wald* = 17.134, d.f. = 6, *P* = 0.009 (Fig. 2 and Table S2). There was no correlation between colony size and the colonies’ average longevity (*r* = 0.06, *n* = 7, *P* = 0.89; Fig. 3A). Regular observations did not identify any behavioural differences between colonies. All colonies built nests, maintained social cohesion, and regular egg laying was observed throughout.
Hypothesis 2: Group size will correlate positively with mean female longevity in *P. canadensis* once the influence of colony genotype is controlled for.

Group sizes ranged from 9 (M5) to 34 (M7) wasps with average longevity within different nests ranging from 130 ± 39.4 days (in M5) up to 206 ± 41.3 days (in M6). Comparing the mean adult longevity of colonies M1–M7 against their original size gives no clear association (Fig. 3A). Colonies M8–M10 showed no difference in survival prior to splitting.
Figure 4 Survival details of three colonies of *P. canadensis* over 80 days. Survival of adults in three *P. canadensis* colonies (92 adults) shown as raw numbers (A) and proportions (B) over a period of 80 days post capture whilst maintained under laboratory conditions, along with the survival estimates for each colony as estimated by Kaplan–Meier survival analysis. (C) Estimations used in C-D are limited to the largest survival time due to censorship. Standard error bars in (D) calculated by Kaplan–Meier model.

(Wald = 4.016, d.f. = 2, \( P = 0.134 \); Fig. 4). However, after splitting into 6 cohorts of variable size, females exhibited significantly different longevities (Wald = 12.544, d.f. = 5, \( P = 0.028 \); Fig. 5). Cohorts from M9 (M9A & M9B) and from M10 (M10A & M10B) show no significant difference in adult longevity within natal colony identity (\( \chi^2 = 0.173, P = 0.677 \); \( \chi^2 = 0.394, P = 0.530 \) respectively; Table S3), cohorts from colony M8 (M8A & M8B) do differ from each other and are, incidentally, the 2 cohorts with the largest size difference (\( \chi^2 = 3.829, P = 0.05 \); Fig. 5). Group size shows a positive correlation with longevity (\( r = 0.84 \) \( n = 6 \) \( P = 0.038 \); Fig. 3B). Regular observations did not identify any behavioural differences between cohorts. All cohorts built nests, maintained social cohesion, and regular egg laying was observed throughout.

**DISCUSSION**

Here we show that with an average lifespan of 193 days, *P. canadensis* have some of the longest lifespans of recorded wasps under laboratory conditions to date. The oldest wasp in our study lived for a staggering 506 days which is one of the longest living lab assisted, or wild recorded wasp—and most recorded wild and assisted bees, with the notable exception
Figure 5 Survival details of six cohorts of *P. canadensis* wasps from 3 natal colonies. Survival of 72 adult *Polistes canadensis* in 6 conspecific groups split from 3 colonies, shown as raw numbers (A) and proportions (B) over a period of 220 days post split whilst maintained under laboratory conditions. The survival estimates of these as estimated by Kaplan–Meier survival analysis are shown (C) with pairwise differences as calculated by the Breslow statistic shown by capped horizontal bars (D).

of assisted honeybee queens tending to live around 3,000 days (Fig. 6 and Table S3). The natal group was a significant predictor of longevity with wasps living on average between 260 days and 130 days depending on nest, though the size of the natal groups had no correlation with longevity. When natal groups were split in to varying cohort sizes, the largest cohort lived the longest and a correlation between longevity and cohort size was identified. We discuss the implications of these data in the context of other species and ecology and evolution of eusociality.

We observed large cohorts of long lived individuals in multiple colonies, although we cannot say whether individuals were of queen, worker, or in a quiescence (Hunt, 2006) status/state. In the most general sense, eusocial structure is based on behaviour rather than the physiological constraints observed in more highly eusocial hymenopterans such as honey bees and many ants, which incidentally display the largest longevity disparities between castes. Though there are no directly comparable studies that use *Polistes* in a lab setting such as this study, the lifespan estimates on workers of wild or assisted *Polistes* species tends to be approximately one month, with the longest average life span
Figure 6 Comparative mean lifespans in ants, bees and wasps. Comparison of lifespans in a selection of ants (A), bees (B) and all records of wasps (C), highlighting whether data is attained from wild (Black bars) or assisted (grey bars) colonies with unknowns also included (grey bars). Queen lifespans in minimum age, as most studies/literature start from colony creation. Data compiled from the result of this study (above column) and those found following literature search (continued on next page...
being 37 days in *P. lanio* and shortest life span being 14 days in *P. exclamans* (Miyano, 1980; Strassmann, 1985; Giannotti & Machado, 1994b; Giannotti, 1997a; Giannotti, 2012; Gamboa, Greig & Thom, 2002; Torres, Gianotti & Antoniali-Jr, 2013).

The average lifespan of egg laying *Polistes* wasps can range from a maximum of 209 days in wild *Polistes lanio* queens down to 66 days in wild queens of *Polistes fuscatus* wasps (Giannotti & Machado, 1994b; Gamboa, Greig & Thom, 2002). Whilst there is an observation from Phil Rau (West-Eberhard, 1969) of a marked wild temperate *Polistes* queen living for approximately 2 years, it seems tropical species may have some of the longest lifespans, although further empirical studies are needed to tease apart seasonal affects. In each case, the studies were carried out on wild *Polistes* colonies and so cannot account for extrinsic mortality (Strassmann, 1985; Giannotti & Machado, 1994b). The life-span of wasps in more highly eusocial species ranges from 1,000 days in queens of some wild *Vespa* spp. to 14.5 days in lab maintained *Vespula germanica* and *Vespula consobrina* (Akre, 1982; Dazhi & Yunzhen, 1989; Hölldobler & Wilson, 1990).

On average there is a positive correlation between the maximum lifespan of eusocial queens and the degree of eusociality displayed by that species (Carey, 2001; Kramer & Schaible, 2013) and differences found among species tend to be due to extrinsic mortality (Keller, 1998). Here we cannot differentiate between egg layers and helpers in our primitively eusocial species, yet evolutionary theory dictates that when a colony is small and the lifespans of both the reproductive individuals and helpers are equal, the helpers will resist evolutionary specialisation to workers as that would ultimately reduce their direct fitness potential (Alexander, Noonan & Crespi, 1991). We may therefore expect to find similar lifespans in both egg layers and workers in *P. canadensis*. However differences in lifespan are observed between helpers and egg layers in other *Polistes* species (Fig. 6).

These studies use wild species though and describe the extrinsic mortality, unlike our study which had minimal extrinsic pressures.

Colony identity was a clear predictor of wasp longevity. All colonies were collected at the same time from the same field site, in which adults on all nests would have shared the same developmental and environmental conditions. The potential causes for the effect of colony identity could be: (1) genetic differences between the colonies. Genetic influences on longevity have been found in a number of model species from mammals to nematodes and insects (VanRaden & Klaaskate, 1993; Herskind et al., 1996; Vollema & Groen, 1996; Klebanov et al., 2001; Sebastiani et al., 2012; Gems & Partridge, 2013) and evidence for heritability of increased longevity in the fruit fly and honey bee has been observed (Rinderer, Collins & Brown, 1983; Luckinbill & Clare, 1985) with some gene
expression patterns being associated with longevity in queen honey bees (Corona et al., 2005). (2) Queen ‘quality’ which can be the result of extrinsic or intrinsic factors. Variation in fecundity of reproductive and dominance over other individuals in a colony is known as queen quality and this can vary between queens (Harris & Beggs, 1995; Liebig, Monnin & Turillazzi, 2005; Holman, 2012). This queen quality variation can be inherited (Rinderer & Sylvester, 1978; Corona et al., 2005) or driven by environmental factors (Hatch, Tarpy & Fletcher, 1999; Tarpy et al., 2011). (3) Unobserved differences in extrinsic factors that the nests had experienced before collection. Since the colonies were not monitored for their entire life cycle, there is the possibility that something affected each one differently in order to cause varying longevity within their workers. What we can conclude is that although colony genotype was a predictor of longevity in the adult wasps, this did not correlate with wasp group size unless the size was manipulated. This suggests that the colony influences are greater than those of group size, and whilst an overall correlation between manipulated group size and longevity was identified, only one out of three split colonies displayed this trend. This suggests that the explanation that larger colonies produce longer lived workers due to enhanced nutrition during larval development is not a major component.

To investigate the underlying variation in longevity in eusocial insects, data from captive colonies of a range of eusocial insects is a useful tool and can help uncover variation in investment for longevity based on extrinsic factors faced by a given species, individual, or caste (Chapuisat & Keller, 2002). Longevity studies on predatory eusocial insects such as wasps are underrepresented in the literature, and while several excellent studies have been identified, no studies have followed maintained Polistes in a protected lab environment. Here, for the first time we quantify longevity of adult P. canadensis in the absence of extrinsic mortality and provide some support for the link between group size and adult longevity but show that natal origin (i.e., genotype) is a more powerful predictor. Our results suggest that predictions founded on previous research using higher eusocial species such as honey bees may not be relevant to primitively eusocial species since their caste/fate is not fixed during development. A particular challenge will be for future studies to also control for all of the described extrinsic and intrinsic factors such as wild nest site condition and the presence of symbionts.

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Author Contributions
• Robin J. Southon and Emily F. Bell conceived and designed the experiments, performed the experiments, contributed reagents/materials/analysis tools, wrote the paper, reviewed drafts of the paper.
• Peter Graystock conceived and designed the experiments, analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
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REFERENCES
Akre RD. 1982. Economics and control of yellowjackets (Vesoula, Dolichovespula). In: Breed MD, Michener CD, Evans HE, eds. Proceedings of 9th Congress, International Union for the Study of Social Insects, August, 1982. Boulder: Westview Press, 109–112.
Alexander R, Noonan K, Crespi B. 1991. The evolution of eusociality. In: The biology of the naked mole-rat. Princeton: Princeton University Press, 3–44.
Archer ME. 2012. Vespine wasps of the world: behaviour, ecology & taxonomy of the Vespinae. Castleton: Siri Scientific Press.
Bailey L. 1968. Honey bee pathology. Annual Review of Entomology 13:191 DOI 10.1146/annurev.en.13.010168.001203.
Bourke AFG. 2007. Kin selection and the evolutionary theory of aging. Annual Review of Ecology, Evolution, and Systematics 38:103–128 DOI 10.1146/annurev.ecolsys.38.091206.095528.
Carey JR. 2001. Demographic mechanisms for the evolution of long life in social insects. Experimental Gerontology 36:713–722 DOI 10.1016/S0531-5565(00)00237-0.
Carey J. 2002. Longevity minimalists: life table studies of two species of northern Michigan adult mayflies. Experimental Gerontology 37:567–570 DOI 10.1016/S0531-5565(01)00180-2.
Chapuisat M, Keller L. 2002. Division of labour influences the rate of ageing in weaver ant workers. Proceedings of the Royal Society B: Biological Sciences 269:909–913 DOI 10.1098/rspb.2002.1962.
Clapperton BK, Dymock JJ. 1997. Growth and survival of colonies of the Asian paper wasp, *Polistes chinensis antennalis* (Hymenoptera: Vespidae), in New Zealand. *New Zealand Journal of Zoology* 24:9–15 DOI 10.1080/03014223.1997.9518101.

Clutton-Brock TH. 1991. *The evolution of parental care*. Princeton: Princeton University Press.

Corona M, Hughes KA, Weaver DB, Robinson GE. 2005. Gene expression patterns associated with queen honey bee longevity. *Mechanisms of Ageing and Development* 126:1230–1238 DOI 10.1016/j.mad.2005.07.004.

Crespi BJ. 1994. The definition of eusociality. *Behavioral Psychology* 6:109–115.

Dazhi D, Yunzhen W. 1989. A preliminary study on the biology of wasps *Vespa velutina auraria* Smith and *Vespa tropica ducalis* Smith. *Zoological Research* 10:162–163.

da Silva-Matos E, Garófalo C. 2000. Worker life tables, survivorship, and longevity in colonies of *Bombus (Fervidobombus) atratus* (Hymenoptera: Apidae). *Revista de Biología Tropical* 48:657–663.

de Groot A. 1953. Protein and amino acid requirements of the honeybee (*Apis mellifica* L.). *Physiologia Comparata et Oecologia* 3:197–285.

De Loof A. 2011. Longevity and aging in insects: is reproduction costly; cheap; beneficial or irrelevant? A critical evaluation of the “trade-off” concept. *Journal of Insect Physiology* 57:1–11 DOI 10.1016/j.jinsphys.2010.08.018.

Eischen F. 1982. Length of life and dry weight of worker honeybees reared in colonies with different worker-larva ratios. *Journal of Apicultural Research* 21:19–25.

Evans HE. 1958. The evolution of social life in wasps. In: *Proceedings of the 10th international congress of entomology*, Ottawa: Mortimer, 449–457.

Ferguson-Gow H, Sumner S, Bourke AFG, Jones KE. 2014. Colony size predicts division of labour in attine ants. *Proceedings of the Royal Society B: Biological Sciences* 281(1793):20141411 DOI 10.1098/rspb.2014.1411.

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

Fjerdingstad E, Crozier R. 2006. The evolution of worker caste diversity in social insects. *The American Naturalist* 167:390–400 DOI 10.1086/499545.

Foley K, Fazio G, Jensen AB, Hughes WOH. 2014. The distribution of *Aspergillus* spp. opportunistic parasites in hives and their pathogenicity to honey bees. *Veterinary Microbiology* 169:203–210 DOI 10.1016/j.vetmic.2013.11.029.

Gamboa GJ, Greig EI, Thom MC. 2002. The comparative biology of two sympatric paper wasps, the native *Polistes fuscatus* and the invasive *Polistes dominulus* (Hymenoptera, Vespidae). *Insectes Sociaux* 49:45–49 DOI 10.1007/s00040-002-8278-y.

Gems D, Partridge L. 2013. Genetics of longevity in model organisms: debates and paradigm shifts. *Annual Review of Physiology* 75:621–644 DOI 10.1146/annurev-physiol-030212-183712.

Giannotti E. 1997a. Biology of the wasp *Polistes (epicnemius) cinerascens* Saussure (Hymenoptera: Vespidae). *Anais da Sociedade Entomológica do Brasil* 26:61–67 DOI 10.1590/S0301-80591997000100008.

Giannotti E. 2012. Notes on the biology of *Polistes simillimus* Zikán (Hymenoptera, Vespidae). *Bioikos* 8:41–49.

Giannotti E, Machado V. 1994a. Colonial phenology of *Polistes lanio lanio* (Fabricius, 1775) (Hymenoptera, Vespidae). *The Revista Brasileira de Entomologia* 38:639–643.

Giannotti E, Machado V. 1994b. Longevity, life table and age polyethism in *Polistes lanio lanio* (Hymenoptera, Vespidae), a primitive eusocial wasp. *Journal of Advanced Zoology* 15:95–101.
Gibo DL, Metcalf RA. 1978. Early survival of Polistes apachus (Hymenoptera: Vespidae) colonies in California: a field study of an introduced species. The Canadian Entomologist 110:1339–1343 DOI 10.4039/Ent1101339-12.

Giraldo YM, Traniello JFA. 2014. Worker senescence and the sociobiology of aging in ants. Behavioral Ecology and Sociobiology 68:1901–1919 DOI 10.1007/s00265-014-1826-4.

Goldblatt JW, Fell R. 1987. Adult longevity of workers of the bumble bees Bombus fervidus (F.) and Bombus pennsylvanicus (De Geer) (Hymenoptera: Apidae). Canadian Journal of Zoology 65:2349–2353 DOI 10.1139/z87-354.

Halcroft M, Haigh AM, Spooner-Hart R. 2013. Ontogenic time and worker longevity in the Australian stingless bee, Austroplebeia australis. Insectes Sociaux 60:259–264 DOI 10.1007/s00040-013-0291-9.

Harris RJ, Beggs JR. 1995. Variation in the quality of Vespula vulgaris (L.) queens (Hymenoptera: Vespidae) and its significance in wasp population dynamics. New Zealand Journal of Zoology 22:131–142 DOI 10.1080/03014223.1995.9518030.

Harvey JA, Cloutier J, Visser B, Ellers J, Wackers FL, Gols R. 2012. The effect of different dietary sugars and honey on longevity and fecundity in two hyperparasitoid wasps. Journal of Insect Physiology 58:816–823 DOI 10.1016/j.jinsphys.2012.03.002.

Haskins C, Haskins E. 1980. Notes on female and worker survivorship in the archaic ant genus Myrmecia. Insectes Sociaux 27:345–350 DOI 10.1007/BF02223727.

Hatch S, Tarpy DR, Fletcher DJC. 1999. Worker regulation of emergency queen rearing in honey bee colonies and the resultant variation in queen quality. Insectes Sociaux 46:372–377 DOI 10.1007/s000400050159.

Herskind AM, McGue M, Holm NV, Sorensen TIA, Harvald B, Vaupel JW. 1996. The heritability of human longevity: a population-based study of 2872 Danish twin pairs born 1870–1900. Human Genetics 97:319–323 DOI 10.1007/BF02185763.

Hölldobler B, Wilson EO. 1990. The ants. Cambridge: Harvard University Press.

Holman L. 2012. Costs and constraints conspire to produce honest signaling: insights from an ant queen pheromone. Evolution 66:2094–2105 DOI 10.1111/j.1558-5646.2012.01603.x.

Hughes WOH, Sumner S, Van Borm S, Boomsma JJ. 2003. Worker caste polymorphism has a genetic basis in Acromyrmex leaf-cutting ants. Proceedings of the National Academy of Sciences of the United States of America 100:9394–9397 DOI 10.1073/pnas.1633701100.

Hunt J. 2006. Evolution of castes in Polistes. In: Annales Zoologici Fennici. Helsinki: Finnish Zoological and Botanical Publishing Board, 407–422.

Hurd CR, Jeannie RL, Nordheim EV. 2007. Temporal polyethism and worker specialization in the wasp, Vespula germanica. Journal of Insect Science 7:1–13 DOI 10.1673/031.007.4301.

Jeanne R. 1975. The adaptiveness of social wasp nest architecture. Quarterly Review of Biology 50:267–287 DOI 10.1086/408564.

Jernielity S, Chapuisat M, Parker JD, Keller L. 2005. Long live the queen: studying aging in social insects. Age 27:241–248 DOI 10.1007/s11357-005-2916-z.

Johanowicz D, Mitchell E. 2000. Effects of sweet alyssum flowers on the longevity of the parasitoid wasps Cotesia marginiventris (Hymenoptera: Braconidae) and Diadegma insulare. Florida Entomologist 83:41–47 DOI 10.2307/3496226.

Karsai I, Wenzel J. 1998. Productivity, individual-level and colony-level flexibility, and organization of work as consequences of colony size. Proceedings of the National Academy of Sciences of the United States of America 95:8665–8669 DOI 10.1073/pnas.95.15.8665.
Keeler KH. 1993. Fifteen years of colony dynamics in *Pogonomyrmex occidentalis*, the western harvester ant, in western Nebraska. *Southwestern Naturalist* 8(3):286–289 DOI 10.2307/3671438.

Keller L. 1998. Queen lifespan and colony characteristics in ants and termites. *Insectes Sociaux* 45:235–246 DOI 10.1007/s000400050084.

Keller L, Genoud M. 1997. Extraordinary lifespans in ants: a test of evolutionary theories of ageing. *Nature* 389:3–5 DOI 10.1038/40130.

Klebanov S, Flurkey K, Roderick TH, Archer JR, Astle MC, Chen J, Harrison DE. 2001. Heritability of life span in mice and its implication for direct and indirect selection for longevity. *Genetica* 110:209–218 DOI 10.1023/A:1012790600571.

Kramer BH, Schaible R. 2013. Colony size explains the lifespan differences between queens and workers in eusocial Hymenoptera. *Biological Journal of the Linnean Society* 109:710–724 DOI 10.1111/bij.12072.

Liebig J, Monnin T, Turillazzi S. 2005. Direct assessment of queen quality and lack of worker suppression in a paper wasp. *Proceedings of the Royal Society B: Biological Sciences* 272:1339–1344 DOI 10.1098/rspb.2005.3073.

Lucas ER, Keller L. 2014. Ageing and somatic maintenance in social insects. *Current Opinion in Insect Science* 5:31–36 DOI 10.1016/j.cois.2014.09.009.

Luckinbill LS, Clare MJ. 1985. Selection for increased longevity in *Drosophila melanogaster*. *Heredity* 55(1):9–18 DOI 10.1038/hdy.1985.66.

Matsuura M. 1971. Nest foundation by the female wasps of the genus *Vespa* (Hymenoptera, Vespidae). *Japanese Journal of Entomology* 39:99–105.

Matsuura M, Yamane S. 1990. *Biology of the vespine wasps*. Berlin, Heidelberg: Springer Verlag.

Michener C. 1969. Comparative social behavior of bees. *Annual Review of Entomology* 14:299–342 DOI 10.1146/annurev.en.14.010169.001503.

Miyano S. 1980. Life tables of colonies and workers in a paper wasp, *Polistes chinensis antennalis*, in central Japan (Hymenoptera: Vespidae). *Researches on Population Ecology* 22:69–88 DOI 10.1007/BF02513536.

O’Donnell S, Jeanne R. 1992a. The effects of colony characteristics on life span and foraging behavior of individual wasps (*Polybia occidentalis*, Hymenoptera: Vespidae). *Insectes Sociaux* 80:73–80 DOI 10.1007/BF01240532.

O’Donnell S, Jeanne RL. 1992b. Lifelong patterns of forager behaviour in a tropical swarm-founding wasp: effects of specialization and activity level on longevity. *Animal Behaviour* 44:1021–1027 DOI 10.1016/S0003-3472(05)80314-8.

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

Page Jr RE, Peng C. 2001. Aging and development in social insects with emphasis on the honey bee, *Apis mellifera* L. *Experimental Gerontology* 36:695–711 DOI 10.1016/S0531-5565(00)00236-9.

Pamilo P. 1991. Life span of queens in the ant *Formica exsecta*. *Insectes Sociaux* 119:111–119 DOI 10.1007/BF01240961.

Pardi L. 1948. Dominance order in *Polistes* wasps. *Physiological Zoology* 21:1–13.

Pickering J. 1980. *Sex ratio, social behaviour and ecology in Polistes* (Hymenoptera, Vespidae), *Pachysonoides* (Hymenoptera, Ichneumonidae) and *Plasmodium* (Protozoa, Haemosporida). Cambridge: Harvard University.
Polak M. 2010. Landmark territoriality in the neotropical paper wasps *Polistes canadensis* (L.) and *P. carnifex* (F.) (Hymenoptera: Vespidae). *Ethology* **95:**278–290 DOI 10.1111/j.1439-0310.1993.tb00477.x.

Porter SD, Jorgensen CD. 1981. Foragers of the harvester ant, *Pogonomyrmex owyheei*: a disposable caste? *Behavioral Ecology and Sociobiology* **9:**247–256 DOI 10.1007/BF00299879.

Porter SD, Jorgensen CD. 1988. Longevity of Harvester Ant Colonies in Southern Idaho. *Journal of Range Management* **41:**104–107 DOI 10.2307/3898942.

Porter SD, Tschinkel WWR. 1986. Adaptive value of nanitic workers in newly founded red imported fire ant colonies (Hymenoptera: Formicidae). *Annals of the Entomological Society of America* **79:**723–726 DOI 10.1093/aesa/79.4.723.

Ridley M. 1993. Clutch size and mating frequency in parasitic Hymenoptera. *American Naturalist* **142:**893–910 DOI 10.1086/285579.

Rinderer TE, Collins A, Brown M. 1983. Heritabilities and correlations of the honey bee: response to *Nosema apis*, longevity, and alarm response to isopentyl acetate. *Apidologie* **14:**79–85 DOI 10.1051/apido:19830202.

Rinderer TE, Sylvester HA. 1978. Variation in response to *Nosema apis*, longevity, and hoarding behavior in a free-mating population of the honey bee. *Annals of the Entomological Society of America* **71:**372–374 DOI 10.1093/aesa/71.3.372.

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

Sebastiani P, Solovieff N, Dewan AT, Walsh KM, Puca A, Hartley SW, Melista E, Andersen S, Dworkis DA, Wilk JB, Sebastiani P, Solovieff N, DeWan AT, Walsh KM, Puca A, Hartley SW, Melista E, Andersen S, Dworkis DA, Wilk JB, Myers RH, Steinberg MH, Montano M, Baldwin CT, Hoh J, Perls TT. 2012. Genetic signatures of exceptional longevity in humans. *PLoS ONE* **7:**e29848 DOI 10.1371/journal.pone.0029848.

Spradbery J. 1973. *Wasps. An account of the biology and natural history of social and solitary wasps*, with particular reference to those of the British Isles. London: Sidgwick & Jackson Ltd.

Strassman JE. 1979. Honey caches help female paper wasps (*Polistes annularis*) survive texas winters. *Science* **204:**207–209 DOI 10.1126/science.204.4389.207.

Strassmann J. 1981. Parasitoids, predators, and group size in the paper wasp, *Polistes exclamans*. *Ecology* **62:**1225–1233 DOI 10.2307/1937287.

Strassmann J. 1985. Worker mortality and the evolution of castes in the social wasp *Polistes exclamans*. *Insectes Sociaux* **32:**275–285 DOI 10.1007/BF02224916.

Sumner S, Lucas E, Barker J, Isaac N. 2007. Radio-tagging technology reveals extreme nest-drifting behavior in a eusocial insect. *Current Biology* **17:**140–145 DOI 10.1016/j.cub.2006.11.064.

Tibbetts E, Reeve H. 2003. Benefits of foundress associations in the paper wasp *Polistes dominulus*: increased productivity and survival, but no assurance of fitness returns. *Behavioral Ecology* **14:**510–514 DOI 10.1093/beheco/arg037.

Torres V de O, Gianotti E, Antoniali-Jr W. 2013. Temporal polyethism and life expectancy of workers in the eusocial wasp *Polistes canadensis canadensis* Linnaeus (Hymenoptera: Vespidae). *Sociobiology* **60:**107–113 DOI 10.13102/sociobiology.v60i1.107-113.
Turillazzi S, West-Eberhard MJ. 1996. *Natural history and evolution of paper-wasps*. Oxford: Oxford University Press.

VanRaden PM, Klaaskate EJ. 1993. Genetic evaluation of length of productive life including predicted longevity of live cows. *Journal of Dairy Science* 76:2758–2764 DOI 10.3168/jds.S0022-0302(93)77613-4.

Vollema AR, Groen AF. 1996. Genetic parameters of longevity traits of an upgrading population of dairy cattle. *Journal of Dairy Science* 79:2261–2267 DOI 10.3168/jds.S0022-0302(96)76603-1.

West-Eberhard MJ. 1969. *The social biology of polistine wasps*. Museum of Zoology, University of Michigan Miscellaneous publications, 140.

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

Wilson E. 1975. *Sociobiology: the new synthesis*. Cambridge: Harvard University Press.