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

Robin J Southon, Emily F Bell, Peter Graystock, Seirian Sumner

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 is the primitively eusocial orders. 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 *Polistes canadensis*, in a captive setting removed of all environmental hazards. In comparison to other eusocial wasps' *P. canadensis* had an average lifespan of 193±10.5 days, with one individual living longer than 450 days. Although this is shorter than most highly eusocial bee and ant queens. Natal colony variation 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 caste and genome.

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Robin J. Southon[1], Emily Bell[1,2], Peter Graystock[1] and Seirian Sumner[1]

1. School of Biological Sciences, University of Bristol, 24 Tyndall Ave, Bristol, BS8 1TQ, UK

2. Institute of Zoology, Zoological Society of London, Regent's Park, London, NW1 4RY

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13 Introduction

14 Death comes to all, yet many seemingly ordinary insects have evolved some of the most
15 dramatic and extraordinary lifespans, delaying the call of death for remarkable periods (Finch, 1990).
16 Variation in insect longevity spans from *Ephemera simulans* males that live as adults for just 1.6 days
17 (Carey, 2002) to the ants *Pogonomyrmex owyheei* and *Lasius niger* whose queens can live up to 30
18 years (Porter *et al.*, 1988; Hölldobler *et al.*, 1990). Interestingly, eusocial insects such as ants, wasps
19 and bees feature heavily as examples of long-lived insects, but great variation exists not only
20 between these species but also within species and even among genotype. We understand little
21 about the roles of ecology, evolution, life-history and environment in generating variation in
22 longevity in social insects, largely due to the difficulty of disentangling intrinsic life-span (hence-forth
23 referred to as longevity) from survival (the abiotic and biotic environment pressures *i.e.* extrinsic
24 mortality) on individuals (Hölldobler & Wilson, 1990; Keller, 1998; Keeler, 2014; Giraldo & Traniello,
25 2014).

26 Eusocial insects are one of the most dominant, prolific, and diverse groups of organisms on
27 the planet (Wilson, 1975). Much of this groups' success is attributed to the division of labour within
28 the colony in the form of castes, with few or a single reproductive individual (*queen)*, supported by
29 tens to millions of non-reproductive individuals (*workers)* that forage, provision and care for sibling
30 brood (Crespi, 1993). Caste fate is primarily determined by environmental conditions, e.g. nutrition
31 during larval development, and occasionally genetic biasing (Oster & Wilson, 1978; Hölldobler &
32 Wilson, 1990; Hughes *et al*., 2003). Level of social complexity appears to be an important predictor
33 of longevity in the eusocial insects. Within species variation in longevity can be pronounced between
34 castes with queens living as much as 100-fold longer than their related workers (Ridley, 1993; Keller
35 & Genoud, 1997; Kramer & Schaible, 2013). This is a remarkable example of a how a single genome
36 can display plasticity in aging (Keller, 1998; Fjerdingstad & Crozier, 2006; Keeler, 2014). 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)). These long-lived queens live deep within the nest, sheltered from extrinsic pressures such as predation (Porter & Jorgensen, 1981; Keller & Genoud, 1997). Assuming there are costs associated with longevity, there may 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). Castes are unlikely to have been selected for such differential in the primitively eusocial species, where colonies are small each worker is valuable, and longevity of workers may be highly variable depending on the type or frequency of task each individual performs (Strassmann, 1985).

Group size may influence worker longevity and this is likely to be due to the changes in nutrition that developing brood receive through the colony cycle (Matsuura *et al.* 1990; Schmid-Hempel 1998). At the colony level, the first worker brood display a shorter lifespan than those produced later in the colony cycle, and this may be due to the increase in levels of nutrition available to brood as the colony grows (Oster & Wilson, 1978; Porter & Tschinkel, 1986). Productivity is therefore maximised when number of workers, and consequently rates of nutritional acquisition, are low in the early stages of the colony establishment (Oster & Wilson, 1978; Porter & Tschinkel, 1985; Hölldobler & Wilson, 1990). As the colony grows, the ratio of workers to larvae often increases, and the larvae will benefit from increased quality and quantity of food, which can result in longer adult life-spans (e.g. in honey bees: Groot, 1953; Eischen, 1982). To date there have been no studies on how worker longevity varies with colony size in primitively eusocial insects. We predict the same patterns will occur, as in the highly eusocial species, since workers 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 (Sumner *et al*., 2007).

Group identity may also influence longevity. This may be due to a genetic effects (VanRaden & Klaaskate, 1993; Herskind *et al*., 1996; Vollema & Groen, 1996; Klebanov *et al*., 2001; Sebastiani *et al*., 2012; Gems & Partridge, 2013), for example a genetic propensity to favour heavy or light feeding of larvae may translate into variable longevity of the resulting workers. Alternatively, the intrinsic environment of the group may influence longevity, for example through epigenetic effects (Keller & Jemielity, 2006; Yan *et al*., 2014). If group effects are important, we predict that variation in longevity will be greater between groups than within groups, even in the face of group size variation.

Here we provide primary data on longevity of females in captive colonies of the predatory and primitively eusocial Neotropical *Polistes canadensis* paper wasps. Primitively eusocial species such as those of 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). Yet, there are few systematic attempts to quantify longevity, and variation of, in this well-studied genus. Tropical species lack major seasonal constraints on longevity (Clutton-Brock, 1991) and so offer an excellent system for testing the influence of ecology, evolution and environment on longevity, in the absence of seasonal curtailment of longevity. 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 compare our data with estimates of longevity in other eusocial insects to determine the importance of level of sociality and ecology (Hypothesis 1). We quantify the effects of colony identity on worker longevity (Hypothesis 2). We then conduct manipulation experiments to determine the influence of group size on worker longevity (Hypothesis 3). 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: Ten colonies of the paper wasp, *Polistes canadensis* were collected from the Republic of Panamá in August 2013 for transportation. Adult wasps were captured with full nest carton containing brood (eggs, larvae, and pupae) during dusk. Nest cartons and wasps were transferred to individual containers (150mmx150mmx150mm) with wire mesh ventilation. Colonies were provided with sugar solution and water *ad libitum* during transfer to the United Kingdom. Turnaround from capture to settled maintenance in the laboratory was 48 hours.

Maintenance: Nests were housed in clear transparent acrylic containers 300mmx330mmx340mm each with two 525mm perimeter ventilation ducts (Figure 1). Food consisting of liquid cane sugar and live wax moth larvae *Achroia grisella*, along with distilled water and nest-building materials (cardboard & paper) were all supplied *ad libitum*. All sugar and food was obtained in batches and randomly 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, nest-boxes were also given artificial planting for environmental enhancement, to provide shelter from female aggression for males (Polak, 2010). Nest boxes were cleaned regularly and without disturbing wasps or nest. Natural conditions from the collection sites were mimicked with temperatures of 25±1^{o}C, 70±5% relative humidity, and a light cycle of 12h light (12h dark).

Data collection: Colonies were monitored and wasp deaths recorded weekly. Any dead adults found were immediately removed from the nest box. Recording continued until all individuals deceased. Only adult wasps that developed in the wild were monitored for longevity. This ensured our adult wasps developed under natural nutritional 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.

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

Hypothesis 1: If adult longevity correlates with level of social complexity, we expect mean adult longevity of *P. canadensis* to be more similar to that of other *Polistes* species than the more highly eusocial insects. Peer reviewed articles describing the longevity of eusocial Hymenoptera were collated to determine the longevity of species (and caste when described) - https://webofknowledge.com/. The average longevity of *P. canadensis*, as found in this study was included for comparison.

Hypothesis 2: Colony identity (e.g. genotype) explains variance in mean female longevity in *P. canadensis*. Using the data generated from colonies M1-M7, variance in longevity between colonies was quantified to determine whether colony identity (and by extension, genotype,) explains variation in wasp longevity better than colony size.

Hypothesis 3: Group size influences mean female longevity in *P. canadensis*. Three colonies (M8, M9, M10) were monitored every 10 days 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 (remaining with their related groups), giving six new groups in total and consisting of 18, 13, 12, 8, 8 and 9 females. A non-natal male was added to each new colony so that females had the opportunity to mate. These colonies were then maintained as above with wasp deaths monitored weekly for 220 days at which point all individuals were deceased.

Statistical analyses: Differences in adult survival where analysed using a Cox proportional hazards regression model where colony was used as a factor. Where differences in survival were found, pairwise comparisons between nests were made using Kaplan-Meier models with the Breslow χ^2 statistic to highlight specific patterns between the colonies.

Results

Hypothesis 1: The mean adult longevity of *P. canadensis* will be similar to that of other *Polistes* species but differ from those observed in highly eusocial hymenopterans such as ants and bees.

Literature suggests that the average lifespan of wasps can range from a maximum of 209 days in *Polistes lanio* down to 14 days in *Polistes exclamans,* with both studies carried out on wild *Polistes* colonies and so unable to account for extrinsic mortaility (Strassmann, 1985; Giannotti & Machado, 1994). The life-span of wasps in more highly eusocial species ranges from 59 days in *Vespa vulutina* to 14.5 days in both *Vespula germanica* and *Dolichovespula consobrina* (Akre, 1982; Dazhi & Yunzhen, 1989). Here found that 57% of adult *P. canadensis* colonies maintained in the lab can survive beyond 365 days with all but one colony having died after 450 days, providing data on longevity for 143 wasps in total (Figure 2) On average wasps lived for 193±10.5 days with one individual still alive after 450 days (Figure 3C; Figure 7).

Hypothesis 2: Colony identity (e.g. genotype) explains variance in mean female longevity in *P. canadensis*.

Colony identity has a significant influence on adult wasp longevity (Cox proportional hazard survival analyses Wald = 17.134, d.f. = 6, P = 0.009 (Figure 3A-D, Table S1-2)).

Hypothesis 3: Group size influences mean female longevity in *P. canadensis*. .

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 (Figure 6A). Colonies M8-M10 showed no difference in survival prior to splitting (Wald = 4.016, d.f. = 2, P = 0.134; Figure 4). However, after splitting into 6 cohorts of variable size, females exhibited

158 significantly different longevities (Wald = 12.544, d.f. = 5, p = 0.028; Figure 5). Pairwise analyses
159 show this is likely due to cohort M8A (the largest) living significantly longer than most other cohorts
160 (Figure 5D, Table S3-S4). Variation could not be attributed to natal colony identity. Cohorts from M9
161 (M9A & M9B) and from M10 (M10A & M10B) show no significant difference in adult longevity within
162 natal colony identity (χ^2 = 0.173, P = 0.677; χ^2 = 0.394, P = 0.530 respectively), cohorts from colony
163 M8 (M8A & M8B) do differ from each other and are, incidentally, the 2 cohorts with the largest size
164 difference (χ^2 = 3.829, P = 0.05; Table S6). Group size shows a positive trend with longevity (Figure
165 6B).

166 **Discussion**

167 Here we show *Polistes canadensis* to have the greatest longevity of any wasp recorded under
168 laboratory conditions to date, and 2nd greatest overall, with wasps living on average 193 days, and
169 up to 450 days. Our analyses suggest that colony identity and group size explain the variation in
170 longevity, as predicted by our hypotheses. We discuss the implications of this data in the context of
171 other species and ecology and evolution of eusociality.

172 Despite not monitoring the wasps from their day of eclosion (survival will be longer than our
173 data shows), *P. canadensis* that developed in the wild have an average longevity of 193 days when
174 maintained in the lab, free of extrinsic mortality pressures. This exceeds previous lifespan estimates
175 on *Polistes* species where workers live approximately one month (Miyano, 1980; Strassmann, 1985;
176 Giannotti & Machado, 1994; Giannotti, 1997, 2012; Gamboa, Greig & Thom, 2002; Torres, Gianotti &
177 Antonialli-Jr, 2013). There was no obvious difference in longevity between the 'worker force' and the
178 queens (defined by egg-laying). Instead we observe large cohorts of long lived individuals in multiple
179 colonies. The average longevity found is also greater than the survival of queens in many other wasp
180 species. This lack of differences between the castes may be, in part, a result of the biology of *Polistes*
181 wasps which are a primitively eusocial species with all members able to reproduce and perform like
182 a queen. Their eusocial structure is based on behaviour rather than the physiological constraints

observed in higher hymenopterans such as honey bees and many ants, which incidentally display the largest longevity disparities.

Colony identity was a clear predictor of wasp longevity. All colonies were collected at the same time from the same field site where 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 insect fruit fly and honey bees have 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 history, 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 identity was a predictor of longevity in the adult wasps, this did not correlate with wasp size, and so suggests that the explanation that larger colonies would produce longer lived workers due to enhanced nutrition during larval development is not correct. When groups of sister wasps were manipulated into varying group sizes, the effects of group size on longevity was diluted and an association with group size and longevity was observed.

To investigate the underlying variation in longevity in eusocial insects, data from captive colonies a range of eusocial insects is required. Predatory eusocial insects such as wasps are underrepresented in the literature. Here, for the first time we quantify longevity of adult *P. canadensis* in the absence of extrinsic mortality and provide some tantalising support for the link between group size and adult longevity. Our results suggest predictions founded on previous research using higher eusocial species such as honeybees may not be relevant to primitively eusocial species. 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. It is clear that *P. canadensis* adults can live for unexpectedly long periods with the oldest individual being at least 450 days old.

Acknowledgements

Thanks to Smithsonian Tropical Research Institute, particularly Jorge Morales and the staff at Galeta Point, and field-assistant Daniel Fabbro. Research was funded by NERC studentship awarded to Emily Bell at IOZ, STRI Pre-doctoral research fellowship and made possible following ANAM research permits SE/A-20-12 and SE/A-55-13. Thanks to Ian Warren & Jacob Podesta for wasp husbandry.

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371

372

373 **Figure legends**

374 **Figure 1.** Captive housing of *P. canadensis* colonies: **A** nest carton supported on reinforced celling
375 with shade; **B** artificial planting; **C** ventilation; **D** access hatch; **E** provisions and artificial planting.

376 **Figure 2.** Comparison of lifespans in a selections of ants (A), bees (B) and all records of wasps (C),
377 highlighting whether data is attained from wild (Black bars) or assisted (grey bars) colonies with
378 unknowns also included (grey bars). Data compiled from the result of this study (★ above column)
379 and those found following literature search (Pardi, 1948; Michener, 1969; West-Eberhard, 1969;
380 Matsuura, 1971; Wilson, 1971; Spradbery, 1973; Miyano, 1980; Haskins & Haskins, 1980; Akre, 1982;
381 Strassmann, 1985; Goldblatt & Fell, 1987; Dazhi & Yunzhen, 1989; Hölldobler & Wilson, 1990;
382 O'Donnell & Jeanne, 1992; Giannotti & Machado, 1994; Keller, 1998; Silva-Matos & Garófalo, 2000;
383 Page Jr & Peng, 2001; Gamboa, Greig & Thom, 2002; Jemielity et al., 2005; Hurd, Jeanne &
384 Nordheim, 2007; Archer, 2012; Giannotti, 2012; Torres, Gianotti & Antonialli-Jr, 2013; Halcroft,
385 Haigh & Spooner-Hart, 2013)

386

387 **Figure 3**. Survival of adults in seven *Polistes canadensis* colonies shown as raw numbers (A) and
388 proportions (B) over a period of 15 months post capture whilst maintained under laboratory
389 conditions. Their longevity estimates of adult wasps for each colony as estimated by Kaplan-Meier
390 survival analysis (C) with pairwise differences as calculated by the Breslow statistic shown by capped
391 horizontal bars (D)

392

393 **Figure 4.** Survival of adults in three *Polistes canadensis* colonies (92 adults) shown as raw numbers
394 (A) and proportions (B) over a period of 80 days post capture whilst maintained under laboratory
395 conditions, along with the survival estimates for each colony as estimated by Kaplan-Meier survival
396 analysis (C) Estimations used in C-D are limited to the largest survival time due to censorship.
397 Standard error bars in (D) calculated by Kaplan-Meier model.

398

399 **Figure 5.** Survival of 72 adult *Polistes canadensis* in 6 conspecific groups split from 3 colonies, shown
400 as raw numbers (A) and proportions (B) over a period of 220 days post split whilst maintained under
401 laboratory conditions. The survival estimates of these as estimated by Kaplan-Meier survival analysis
402 are shown (C) with pairwise differences as calculated by the Breslow statistic shown by capped
403 horizontal bars (D)

404

405 **Figure 6.** Associations between colony size and mean longevity of adult P. canadensis when
406 maintained in original colony (A) or when manipulated into cohorts of varying size (B). Standard
407 error bars calculated by Kaplan-Meier model.

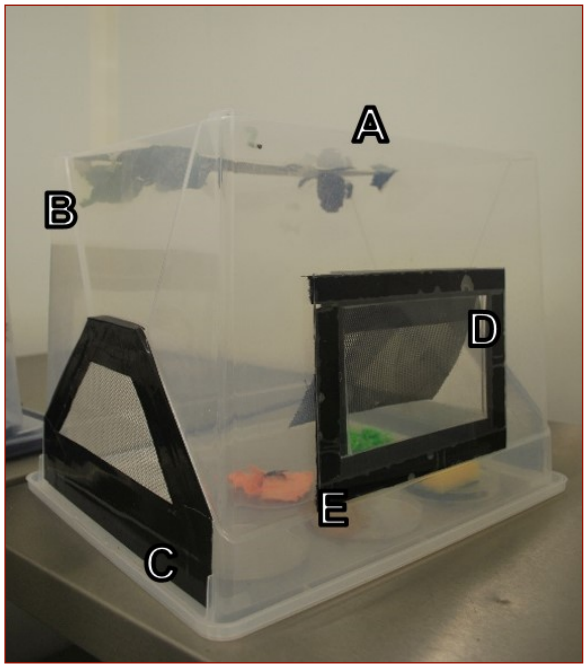
408

409 **Figure 7.** Individual M1-25, the oldest recorded *P. canadensis* at 450 days old.

410

411 **Figures**

412 Figure 1.



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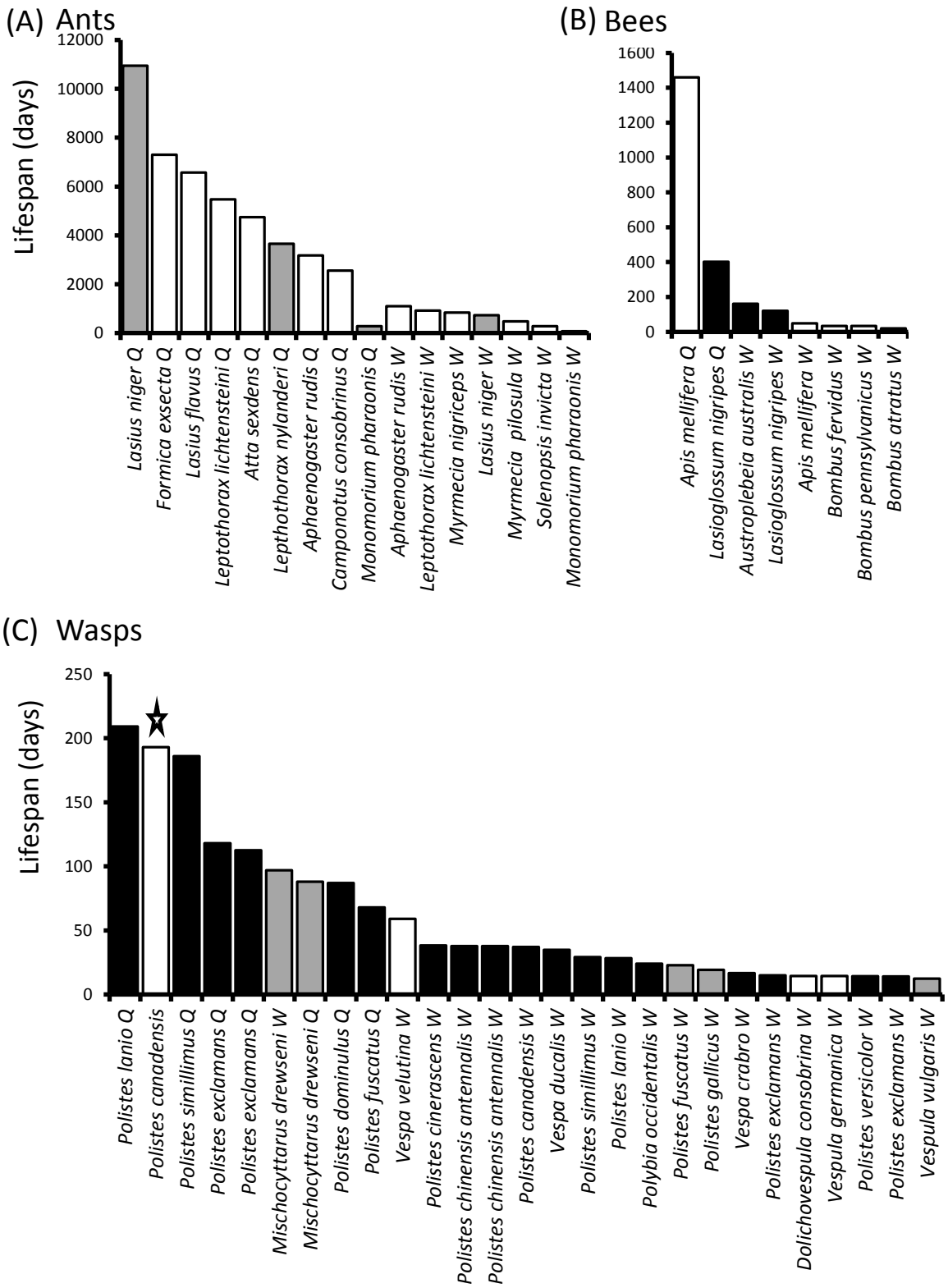
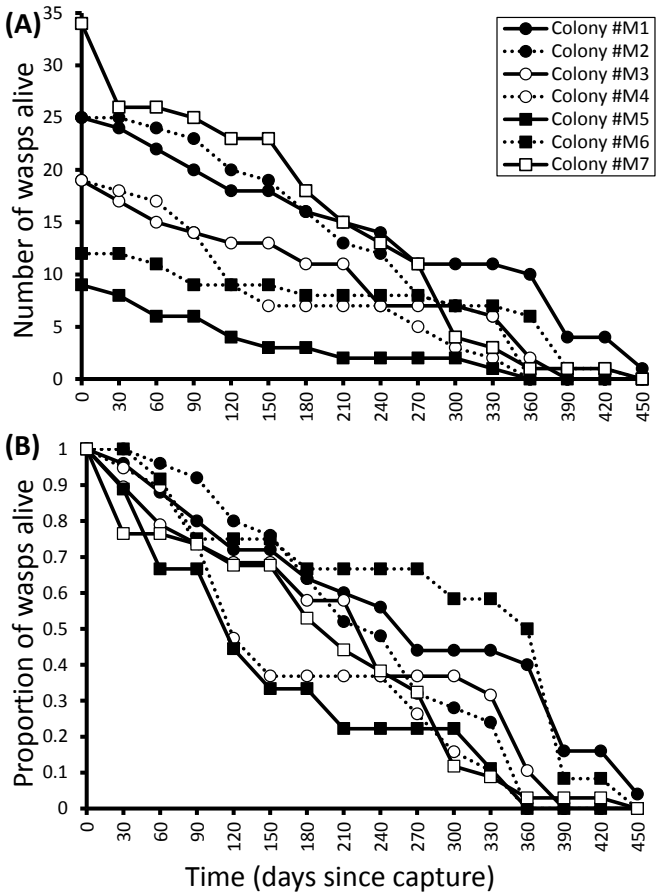
420 **Figure 2.**


(A) Ants
Lifespan (days)
12000
10000
8000
6000
4000
2000
0
Lasius niger Q
Formica exsecta Q
Lasius flavus Q
Leptothorax lichtensteini Q
Atta sexdens Q
Lepthothorax nylanderi Q
Aphaenogaster rudis Q
Camponotus consobrinus Q
Monomorium pharaonis Q
Aphaenogaster rudis W
Leptothorax lichtensteini W
Myrmecia nigriceps W
Lasius niger W
Myrmecia pilosula W
Solenopsis invicta W
Monomorium pharaonis W
(B) Bees
1600
1400
1200
1000
800
600
400
200
0
Apis mellifera Q
Lasioglossum nigripes Q
Austroplebeia australis W
Lasioglossum nigripes W
Apis mellifera W
Bombus fervidus W
Bombus pennsylvanicus W
Bombus atratus W
(C) Wasps
Lifespan (days)
250
200
150
100
50
0
Polistes lanio Q
Polistes canadensis
Polistes simillimus Q
Polistes exclamans Q
Polistes exclamans Q
Mischocyttarus drewseni W
Mischocyttarus drewseni Q
Polistes dominulus Q
Polistes fuscatus Q
Vespa velutina W
Polistes cinerascens W
Polistes chinensis antennalis W
Polistes chinensis antennalis W
Polistes canadensis W
Vespa ducalis W
Polistes simillimus W
Polistes lanio W
Polybia occidentalis W
Polistes fuscatus W
Polistes gallicus W
Vespa crabro W
Polistes exclamans W
Dolichovespula consobrina W
Vespula germanica W
Polistes versicolor W
Polistes exclamans W
Vespula vulgaris W

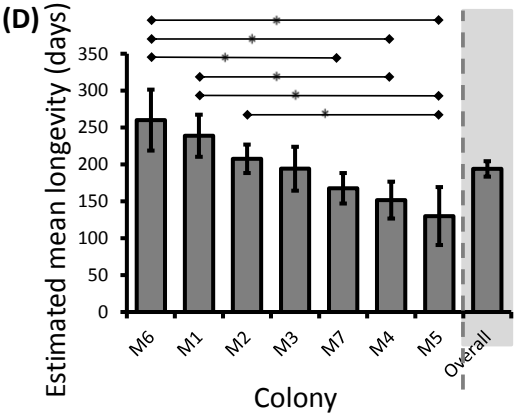
421

422 **Figure 3.**



(C)

Colony	Mean[a]			
	Estimate	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
M6	260.01	41.34	178.98	341.04
M1	238.8	28.62	182.7	294.9
M2	207.6	19.2	169.95	245.25
M3	194.22	29.76	135.87	252.57
M7	167.64	20.52	127.44	207.84
M4	151.59	24.96	102.63	200.52
M5	129.99	39.36	52.83	207.18
Overall	193.86	10.5	173.25	214.44



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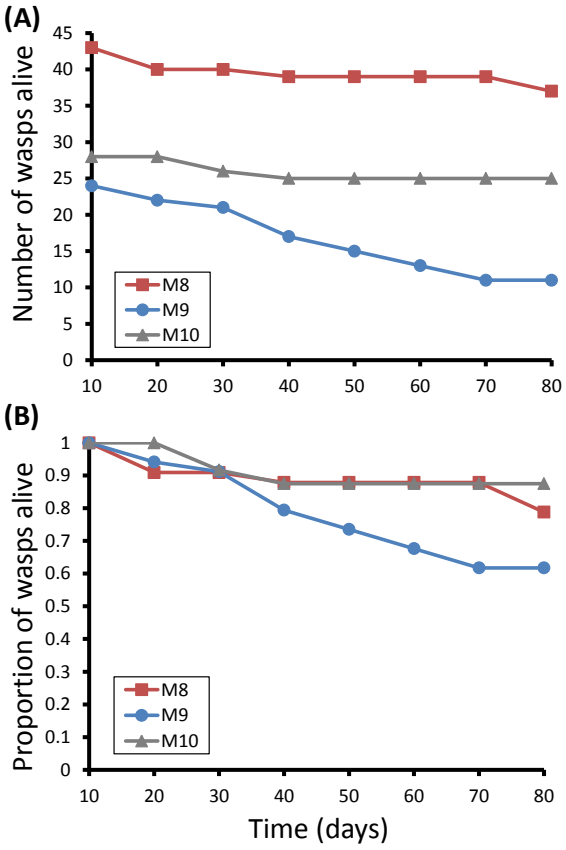
425 **Figure 4.**



(C)

Colony	Mean[a]			
	Estimate	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
M10	74.167	3.169	67.956	80.377
M8	71.471	3.829	63.967	78.975
M9	67.353	3.525	60.443	74.263
Overall	70.652	2.064	66.606	74.698

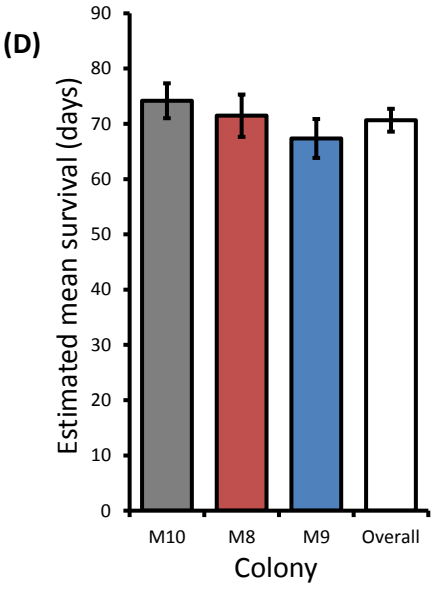


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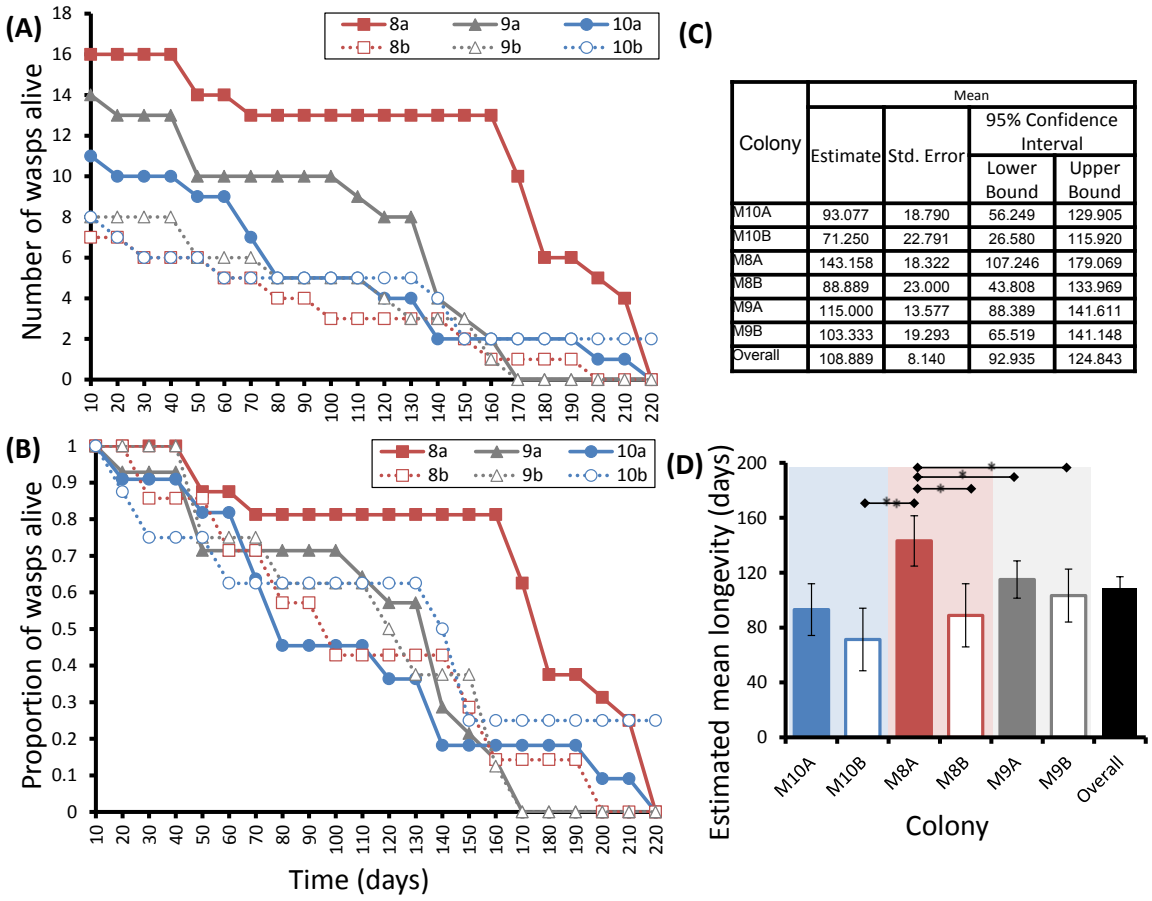
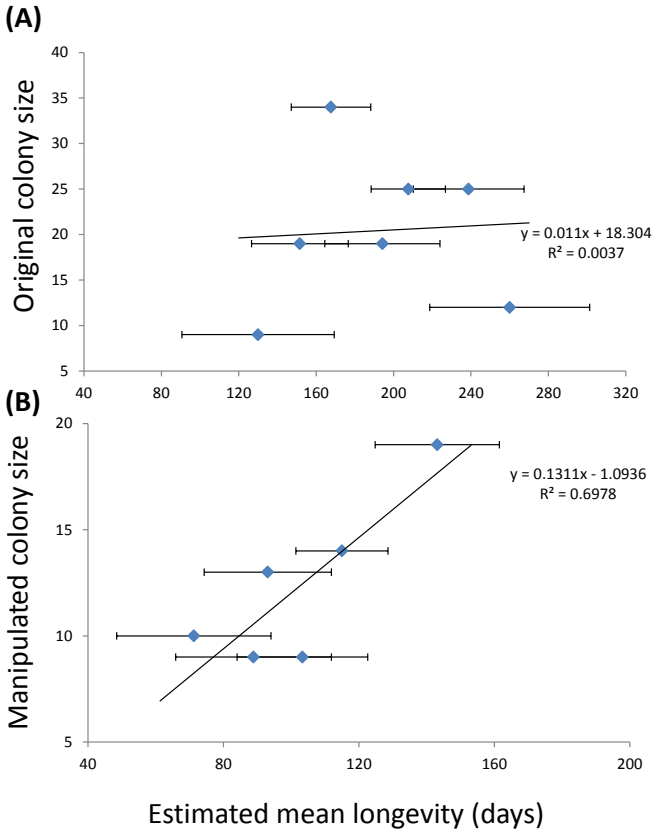
Figure 5.



Colony	Mean			
	Estimate	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
M10A	93.077	18.790	56.249	129.905
M10B	71.250	22.791	26.580	115.920
M8A	143.158	18.322	107.246	179.069
M8B	88.889	23.000	43.808	133.969
M9A	115.000	13.577	88.389	141.611
M9B	103.333	19.293	65.519	141.148
Overall	108.889	8.140	92.935	124.843

439 **Figure 6.**



440

441 **Figure 7.**

442

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445