Assessing the costs of group living: Comparing metabolic physiology and growth in social and solitary spiders

Honors Thesis
Presented to the College of Agriculture and Life Sciences,
Department of Entomology
of Cornell University
in Partial Fulfillment of the Requirements for the
Research Honors Program

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May 2007
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Abstract:

Sociality in arachnids is extremely rare though well documented for the few cases that exist. However, no research to date has examined the metabolic and growth characteristics associated with social behavior. *Delena cancerides* is a social huntsman spider that closely overlaps in distribution with several closely related species of solitary huntsmen, providing a unique opportunity for comparison. I compared the metabolic rate of *D. cancerides* to other species of solitary huntsman using a closed-system respirometer. I also compared the growth, survival and molting frequency of *D. cancerides* spiderlings in solo and group treatments to those of solitary huntsman species. *Delena cancerides* had a significantly lower mass-specific metabolic rate than all other species to which it was compared. This is explained in the context of reduced food availability per individual for prolonged periods of time due to sharing. *Delena cancerides* spiderlings did not differ from other species when housed alone, but grew significantly more in group environments than did solitary species. Mortality was lowest for *D. cancerides* living in groups than for any other species living in groups. There was no difference for any species in molting patterns between solo and group treatments. *D. cancerides* molted consistently earlier and more often than the species to which it was compared. The consequences of these findings are discussed in the context of prey-sharing and avoidance of cannibalism.

Introduction

Sociality is uncommon in arachnids (Rayor and Taylor 2006). Of the ~40,000 spider species, only 53 are considered to be truly social (Whitehouse and Lubin 2005). Within the huntsman spiders (Family Sparassidae), only one species, *Delena cancerides* is social. *Delena cancerides* is an Australian species that lives under bark in colonies of up to 300 highly out-bred individuals (Rowell and Avilés 2005). Colonies of conspecifics regularly share prey, and cannibalism is rare among individuals, especially among young (Rayor, per comm). *Delena cancerides* is unusual among social spiders because they do not build shared webs for prey capture or shelter, because there is no inbreeding or sex-ratio bias, and because they are highly aggressive towards non-kin (Avilés 1997; Beavis et al 2007). While behavioral aspects of sociality have been well documented in the social arachnid species, there have been no comparisons of metabolic rate or growth rate between social spiders and their near relatives.

In light of the rarity of this form of spider sociality, I chose to investigate the physiological characteristics that are associated with the social lifestyle of *D. cancerides*. Metabolic rate and growth rate has been shown to be strongly interconnected with food availability, foraging behavior, and fitness in spiders (Greenstone and Bennet 1980; Uetz et al 1992; Higgins and Rankin 2001). With this investigation I hoped to identify some key differences in growth and metabolic rate between social and solitary Australian Huntsman that may be related to the unique social lifestyle of *Delena cancerides*. Pinpointing these physiological patterns that are closely tied to costs and benefits of sociality helps to distinguish between those plastic behaviors that are momentarily beneficial (such as aggregation) and those which are representative of long-term selection for social behavior.

For comparison with *D. cancerides* I used eight species of solitary huntsman spiders that are common throughout its native range and which do not differ in gross morphology. The solitary species were *Holconia flindersi* (Hirst, 1991), *Holconia nigrigularis* (Hirst, 1991), *Isopeda villosa* (Hirst 1990), *Isopeda canberrana* (Hirst 1992), *Isopedella pessleri* (Thorell, 1870), *Isopedella frenchi* (Hogg 1903), *Neosparassus calligaster* (Thorell 1870), *Pediana regina* (L. Koch, 1875), and *Heteropoda venatoria* (Linnaeus 1767). All of the aforementioned solitary species were obtained at the same collection locales where *D. cancerides* colonies were collected. Prey items, habitat, climate, seasonality, and day/night cycles for these species are not markedly different from *D. cancerides.* While little is known about the behavior of each, field observations indicate that habitats and resting behavior are very similar among all of these species with the exception of sociality in *D. cancerides*. While adult size and hatchling size are consistent in each of these species, laboratory observations have noted striking differences in the rate and pattern of development. This group of Australian Hunstman spiders was therefore ideal for physiological comparison because of the vast number of environmental variables that have been controlled for naturally.

Mass-specific metabolic rates in spiders are notably lower than for other taxa of comparable mass ranges (Anderson 1970; Anderson and Prestwick 1982). Within that low range the metabolic rate of spiders is highly dependent on food availability and on life stage of the individual, with lower metabolic rates being observed in non-reproducing stages and during periods of starvation (Anderson 1974; Tanaka and Ito 2006). While prey sharing may mean less prey on average per individual, there will be less variation in the availability of prey per individual compared to individuals that do not share. The presence of constant though smaller amounts of prey should favor long-term low-levels of metabolic activity. I therefore predicted that at a constant temperature, *D. cancerides* would sustain a lower metabolic rate than closely-related solitary huntsman. Respiratory rate (VO_2/hr) was used as a proxy for metabolic rate after Anderson (1974). Respiratory measurements were taken for one or more individuals of *Hc. flindersi, Hc. nigrigularis, Ip. villosa, Ip canberrana. Il. frenchi, Il. pessleri, N. calligaster, P. regina,* and *He. ventatoria.*

The rate of spiderling growth is dependent on both inherited and environmental characteristics (Uhl et al 2004). Within a species, spiderling growth varies with the regularity of available food resources, and is restricted by the ability of spiderlings to capture prey of larger sizes (Rypstra and Tirey 1990; Rypstra and Lehtinen 1990). For social species, prey-sharing distributes a prey item more evenly across multiple individuals than if sharing did not occur (Jones and Parker 2000). I predicted that spiderlings living in groups should develop more rapidly or grow to greater sizes in species where prey sharing occurs and prey is more consistently available. Selection should favor faster growth as a fixed trait, provided there is ample food to sustain growth. I hypothesized that the growth of *D. cancerides* will be faster compared to solitary counterparts and that this is a non-plastic characteristic which will be true in both social and solitary treatments. Molting frequency is a reliable indicator of growth in arthropods (Hutchinson et al 1997). Kim (2001) observed that molting frequency was highly synchronized for social *Amaurobius ferox* living in groups compared to those living singly, and stipulated that this was a mechanism for maintaining size homogeneity to avoid cannibalism. I therefore predicted that there would be marked differences in the molting patterns between social and solitary spiders in group and solitary situations. *Hc. flindersi, Hc. nigrigularis,* and *N. calligaster* were used for comparison of body mass and survivorship in growth experiments. For molt pattern comparisons, *Hc. flindersi* was used because there were more hatchlings available.

Methods

Animals

Hunstman spiders (Family Sparassidae), were collected from various localities in Australia during January – March 2004, February – April 2006, and November – December 2006. Spiders were identified by Australian huntsman taxonomist Dr. David Hirst of The South Australia Museum. All spiders were transported to Dr. Linda Rayor's laboratory at Cornell University with proper Austrailian export and USA import permits. One US huntsman species with a worldwide distribution, *Heteropoda ventatoria,* was also used in metabolic rate experiments. The juveniles used in this study were born in captivity from those wild-caught females from 2004 and 2006 collections. Individuals and colonies were housed in terraria in Ithaca, NY in a laboratory maintained between 24 ^{o}C and 29^{o}C with 12 h of artificial light per day. Animals were reared on a diet of primarily crickets fed on calcium fortified food and water, but their diet also included *Drosophila*, house flies, blow flies, and *Trichoplusia ni* moths.

Respirometry Protocol

Individuals were starved for a minimum of 24 h prior respirometry trials. Individuals were anesthetized with CO_2 and their mass, second leg length, and cephalothorax width were measured. Anesthetized individuals were then placed in a 100ml chamber of a closed system Scholander-style manometric respirometer (Griffin and George, Leicestershire, UK). For individuals weighing less than 0.29g, up to four individuals massed within 0.4mg of each other were placed in a chamber at the same time, separated from one another with metal baffles to minimize contact or social interactions. The bottom of the chamber contained a piece of filter paper wetted with a solution of 30% KOH (by weight) to absorb respired CO_2. A small metal baffle separated individuals from the moistened filter paper. The reference chamber was filled with a volume of water equivalent to that of the space occupied by the spider. Individuals were acclimated for 1h at 28 ^{o}C before the test chamber and reference chamber were connected and the trial began. A minimum displacement of 0.5ul of manometric fluid (Brodie's solution: 2% NaCl solution, traces of sodium dodecyl sulfate, trace of Congo red) was displaced before volumetric measurement and elapsed time were recorded. This protocol was repeated twice for each individual or group of individuals.

All trials were carried out in a walk-in environmental chamber maintained at 28^{o}C. Trials were conducted between 12:00pm and 12:00am with the lights on and minimal sound or physical disturbance. The masses of spiders used ranged from 0.0330g to 3.6500g, and included both male and female individuals. The lowest respiratory rate measured for each individual was used for analysis. For groups of individuals, the volumetric displacement was divided by the number of individuals in the chamber to calculate an average respiratory rate, the average body mass was used for data analysis. Respiratory rate in ul/hr was plotted against individual body mass. Plots were grouped by species or by lifestyle (social/solitary). An ANOVA was used to detect significant metabolic differences between species and social treatment. For species by species comparisons with *D. cancerides*, only those solitary species for which the sample size exceeded eight individuals were compared. The individuals used were restricted to those that were within the range of 0.7g and 1.2g, which was the most restrictive mass range of any species whose sample size exceeded 8. Using Jmp statistical software version 5.1.2, a regression analysis and a Tukey test was used to identify significant differences between each species.

Growth Protocol

In order to investigate how solitary and social species grow and develop differently in social and solitary treatments, newly emerged 3rd instar hatchlings of three species of huntsman were observed for a 76 day experimental period in each social treatment. Whole clutches of third-instar *Delena cancerides, Holonia flindersi, Holconia nigrigularis* and *Neosparassus calligaster* each originating from a single adult female were anesthetized with CO_2. The mass, second leg length, and cephalothorax width of each individual was recorded. Individuals from each species were then placed either individually (‘Solo’) or in groups of five (‘Group’) in small plastic containers with dirt substrate and airholes. Containers were 3.5cm x 3.5cm x 8cm tall for Solo and 5.5cm x 5.5 cm x 7.5 cm tall for Group. Individuals were partitioned into Group and Solo containers to create approximately equal replicate numbers for each treatment. *N. calligaster* offspring were housed in two groups of five originally, but after early escapes were in three groups of five and four groups of four. Solo individuals were fed one house fly, *Musca domesticus* two times per week. Groups of individuals were given two flies for groups of five twice a week, or fed one fly per two individuals after some individuals died. This feeding regime encourages sharing in group containers and thus highlights sharing effects on those traits measured. The discrepancy between group (0.8 flies/wk/individual) and solo (1fly/week/individual) feeding regimes was tolerated because of this particular analytical benefit. As some individuals died in group containers, the rations were given so as to approximate 1fly/week/individual as closely as possible.

For one of the two feeding sessions per week, all group setups were observed for 30 min after prey was presented and prey-sharing events were recorded. Feeding behavior was considered prey sharing if more than one individual was observed feeding on a single whole prey item for more than 60 sec. During the duration of the experiment, deaths and new molts were recorded every two days. In the groups of five, molts and deaths could not be associated with initial measurements as individuals were not marked in these groups. At the end of a 76- day period, the individuals from each setup were removed and anesthetized with CO_2, the mass, second leg length, and cephalothorax width of each was recorded. The experiment was terminated at this time to avoid losing extensive data to cannibalism among siblings.

Proportional increase in body mass was calculated as the difference between initial and final body mass divided by the initial body mass. For group containers, the initial and final body mass was an average of all individuals in a single enclosure at the start and end of the experiment. Body mass increase in relation to species and social setup was analyzed using an ANOVA, a Tukey test was used to compare treatments directly to one another. Survival was calculated as the proportion of individuals surviving within a container. For solo containers, this value was either 0 or 1. An ANOVA was used to compare the effects of species and social treatment on survivorship. A Tukey test was used to compare each treatment’s survival directly.

Variance of final body masses for each group container was calculated but was not analyzed as variance was biased by significant differences in survivorship between species. The number of molting events over the course of the experiment was compared qualitatively between treatments. The number of experimental days prior to the first molt recorded was compared by solo/group treatments and by species for *Hc. flindersi* and *D. cancerides* using an ANOVA and Tukey test. All statistical tests were performed using Jmp statistical computing software (v5.1.2).

Results

Metabolic Rate

The regression of metabolic rate by mass of *D. cancerides* was significantly lower (Figure 1; logistic regression; y = 21.414x + 0.3012, R^2 = 0.1439) than for the other solitary species taken together (y = 1.2969x + 50.726, R^2 = 0.0005). There was no significant difference in mass between social and solitary species (ANOVA, N = 114, p=0.5032). Social mean respiratory rate was X =18.25ul/hr ($\bar{\sigma}$± 5.35, N = 64), the solitary species collective mean respiratory rate was 51.94 ul/hr ± 6.06 (N = 50). As is expected from the prevailing literature, the relationship between respiratory rate and mass was positive and significant for *D. cancerides* (logistic regression, N = 64, p= 0.0020), however it was not significant for the combined pool of solitary species (logistic regression, N = 50, p = 0.8769). This was likely an effect of the extensive variability of body masses represented by both small and large species of huntsman.

The data were then separated out by species, giving consideration only to those species for which sample size exceeded eight. Three species, *Hc. nigrigularis, Il. pessleri,* and *Hc. flindersi* had sufficient sample sizes (N = 8, 16, and 14 respectively) for comparison with each other and with *D. cancerides*. The data used in these comparisons were restricted to individuals whose masses were included by the species with the smallest mass range (*I. pessleri,* 0.1225 –

1.1174g*)*. Mass and species were both highly significant effects ($p < 0.0001$) when modeling respiratory rate by species using a regression analysis, indicating that both parameters were relevant for predicting respiratory rate. *Delena cancerides* had a significantly lower respiratory rate (Figure 2; Tukey, N = 58, $\overline{X}$ = 13.27ul/hr, $\overline{\sigma}$ =6.05) compared to *Hc. flindersii* (Tukey, N = 14, $\overline{X}$ = 55.29ul/hr, $\overline{\sigma}$ =12.5), *Hc. nigrigularis* (Tukey, N = 8, $\overline{X}$ = 94.ul/hr, $\overline{\sigma}$ =16.50), and *Il. pessleri* (Tukey, N = 16 , $\overline{X}$ = 64.59 ul/hr, $\overline{\sigma}$ =11.64). ATukey test showed that the three solitary species did not differ significantly from one another (Figure 3). Again, there was no significant difference in mass between any of the species groups.

Growth

During the 76-day experimental period, all species grew in mass and molted in both solitary and group treatments. In solo treatments *D. cancerides, Hc. flindersi,* and *Hc. nigrigularis* did not differ in proportional increase in body mass relative to each other, solo *N. calligaster* grew significantly more than any other species in solo containers. The proportional increase in body mass of *D. cancerides* was not significantly different between group ($\overline{X}$ =1.00, $\overline{\sigma}$ =0.145) and solo ($\overline{X}$ =1.25, $\overline{\sigma}$ =0.145) treatments. This was also true for *N. calligaster* ($\overline{X}$ solo/group =2.47/1.90, SE = 0.18/0.26). However, both *Holconia* species (solitary) grew significantly less in group environments than in solitary environments (Figure 4). The decrease in growth associated with living in a group environment or “growth cost” was determined as a percentage of growth in the solo treatment [cost = (solo - group growth)/solo growth], where group growth was determined by averaging the start and end masses of individuals. Averages were used because it was too difficult to mark group spiderlings individually for the full experimental period. This cost of living in groups was lowest for *D. cancerides* and highest for *Hc. flindersi,* and *Hc. nigrigularis,* indicating that they suffered the most from enforced group living with siblings (Figure 5). These costs ignore the initial discrepancies in food availability, largely because those discrepancies were rectified early in during the experimental period.

Survival

D. cancerides was the only species that did not suffer mortality associated with living in groups. All solitary species had reduced survivorship in group treatments, tough *Hc. Nigrigularis* was the only species to reach statistical significance($\overline{X}$= 0.28, $\overline{\sigma}$ = 0.09. The effects of group/solo treatments and species on the survivorship of individuals were highly significant (ANOVA, N = 131, $p<0.0001$). In group treatments, *Hc. flindersi, Hc. nigrigularis,* and *N. calligaster* all had significantly lower survivorship than *D. cancerides,* despite the fact that there was no significant difference amongst their survival rates in solo treatments ((Tukey, $\overline{X}$ = 0.82 , $\overline{\sigma}$ = 0.06, Figure 6). Cannibalism was easily observed in the group treatments of *Hc. nigrigularis* and *Hc. flindersi,* and is suspected to be the leading factor in the differences in survivorship between group and solo treatments of these species.

Molting Frequency

Individuals of *D. cancerides* molted twice during the two-month experimental period in group and solo containers (Figure 7). Molts were highly synchronized across replicates over several days. *Holconia flindersi* molted twice in solo treatments but only once in group environments (Figure 7), concomitant with slower growth in group treatments (Figure 4). *Delena cancerides* molted significantly earlier ($\overline{X}$ = 18, $\overline{\sigma}$ = 1.5) than *Hc. flindersi* ($\overline{X}$ = 52, $\overline{\sigma}$ = 1.7, ANOVA, N = 61, $p<0.0001$, combined solo and group data), suggesting that *D. cancerides* grows faster initially. However, there was no significant difference in time until first molt between group and solo treatments for either species (Figure 8), thus it difficult to conclude that the differences in molting frequency between *D. cancerides* and *Hc. flindersi* are the result of social interaction.

Discussion

The consistently lower respiratory rate of *D. cancerides* is of considerable interest and represents the first evidence of differences in metabolic rates of social spiders when compared to closely-related solitary spider species of comparable morphology. While the foraging advantages of social spiders over solitary spiders are well-documented (Whitehouse and Lubin 2005), the metabolic consequences of these differences are not well known. These results represent the first detailed comparison that shows that metabolic depression may be a characteristic of sociality arachnids. The traditional pattern of seasonal changes in spider metabolism shows high levels of activity when warm seasons permit increased metabolic rate, corresponding to times when prey is readily available (Shoener 1971, Bennet VA et al 1999). In the Introduction, I reasoned that depressed metabolic rate was perhaps initially a plastic trait exhibited in times of low food availability as it is in most spiders (Anderson 1974) but that it later became fixed at a lower range for individuals living socially.

Contrary to my original prediction, it appeared that the proportional increase in body mass of *D. cancerides* spiders was not more than solitary species. Instead, they didn't *suffer* in group treatments the way *Holconia* (solitary) species did. While the prey difference between solo and group treatments was negligible, the parceling out of prey left room for uneven distribution of resources among individuals in groups. Individuals of *Delena cancerides* overcame this barrier through prey-sharing, so that all individuals had access to prey, and did not suffer a significant reduction in growth. Individuals of *Hc. flindersi* and *Hc. nigrigularis* suffered a cost when living in a group treatment due to a lack of frequent prey-sharing. Unexpectedly, the solitary species *Neosparassus calligaster* overcame this barrier, experiencing a cost of living in groups that was similar to that of *D. cancerides*. This evidence agrees with captive observations of prolonged tolerance and prey sharing among siblings up until the 5th instar in *N. calligaster* (Rayor, in prep). In a series of laboratory observations of prey-sharing in *D. cancerides* and *N. calligaster* through their 5th instar, *D. cancerides* were observed sharing prey in 23% of prey encounters, while *N. calligaster* shared prey in 22% of prey encounters. The results presented in this paper, taken in light of this other laboratory evidence suggest that prey-sharing is the key to permitting group living while avoiding growth (and cannibalism) costs. The near absence of prey-sharing behavior in both *Holonia* species further strengthens this conclusion.

The survivorship of individuals over the 75-day period was not significantly different among each species in solo treatments. However, in group setups, cannibalism clearly negatively affected survivorship for solitary species. While one might expect that increased cannibalism (and lower survivorship) might introduce a bias affecting growth patterns, *Hc. nigrigularis,* which suffered significant mortality in group situations, did not grow significantly more in group treatments than in solo treatments. If cannibalism allowed increased growth of surviving individuals, one would expect a greater increase in mean body mass of the surviving group individuals compared to those in solitary environments (due to increased “sibling-food” availability). In fact, the reverse was true for each solitary species. I therefore conclude that cannibalism does not support higher growth rates by increasing “food availability”, and should not be considered an adequate fitness benefit to offset the cost of eating one’s siblings. Based on this result, as long as siblings co-reside, one would expect selection for homogeneity of body mass and instar as a method of deterring siblicide. This phenomenon was observed by Kim (2001) in social *Amaurobius ferox,* but the relationship between the onset of cannibalism, dispersal, and the emergence of sibling size heterogeneity warrants further investigation in solitary species.

In light of the apparent genetic costs of sibling consumption, it is appropriate to bring up the positive relationship between resting metabolic rate and appetite (Waldbauer and Friedman 1991). A lower metabolic rate, analogous to a smaller appetite and therefore decreased foraging and prey-seeking behavior, can be seen as a benefit peculiar to sociality. A reduced metabolic rate in *D. cancerides* may serve as a preventative for voracious foraging behavior that would otherwise lead to the death of siblings. I reason that selection has favored a lower resting metabolic rate in *D. cancerides* in part to prevent predation on kin (in addition to prey-sharing implications stated above). This logic predicts that in subsocial species, the cessation of sibling tolerance (and initiation of dispersal) should be marked by an increase in metabolic rate. In agreement with this hypothesis, starvation, typically associated with depressed metabolic rate, was observed to spawn dispersal in Linyphiid spiders (Weyman et al 1994). However, Bodasing et al (2002) found that increased food initiated greater dispersal in the social spider *Stegodyphus mimosarum*, which starvation prevented. Though neither of these studies tested metabolic rates directly, given the known effects of food availability on metabolism, each supports the hypothesis that low metabolic rate reduces dispersal in social spiders, though not necessarily in solitary species. A direct metabolic comparison of dispersing and aggregating behavior in social and solitary spiders would resolve this prediction.

In summary, individuals of *D. cancerides* leads a unique energetic and developmental lifestyle shaped by the costs and benefits of living socially. This lifestyle can be described as a low-energy strategy in which feeding behavior is dictated by an even prey distribution among members of a colony. *Delena cancerides* is once again an exception to the rule in social arachnids. One of the prevailing hypotheses for the evolution of sociality in arachnids is an increased foraging efficiency, whereby multiple individuals are more likely to catch larger prey than single individuals (Uetz and Hieber 1997). *Delena cancerides* has evolved to sustain a socially-lowered amount of prey per individual resulting from prey sharing behavior. Field observations indicate that there are very few suitable refuges available for *D. cancerides* to live in (Rowell and Aviles 1995; Rayor, Yip, Rowell in prep). One consequence of this reduced availability may be that the costs of seeking out unoccupied suitable shelters far outweigh the costs of living with reduced prey availability. *Delena cancerides* therefore represents a novel solution to a unique set of selective pressures favoring sociality in arachnids.

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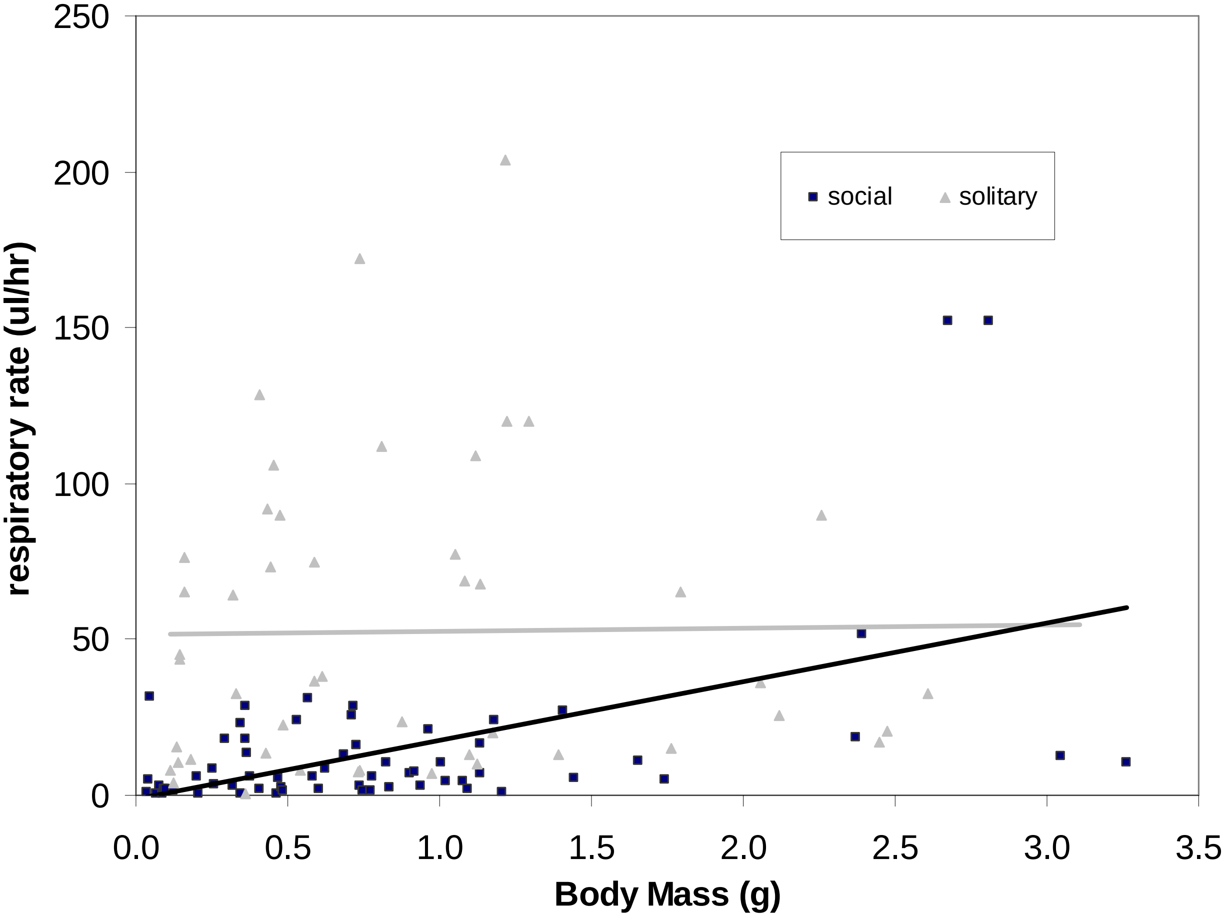

Figure 1: Respiratory rate (VO_2 ul/hr) plotted against body mass (g) for social and solitary huntsman spiders with linear trendlines. The mass-specific metabolic rate regressions of social and solitary species were significantly different from one another. The relationship between mass and respiratory rate was significant for the social species (*D. cancerides* N=2***)* but was not significant for the pooled solitary species (**_Hc. flindersi_ N=14, _Hc. nigrigularis_ N=8*, Ip. villosa* N=5*, Ip canberrana* N=1*. Il. frenchi* N=1*, Il. pessleri* N=15*, N. calligaster* N=2*, P. regina* N=1*,* and *He. ventatoria* N=2)

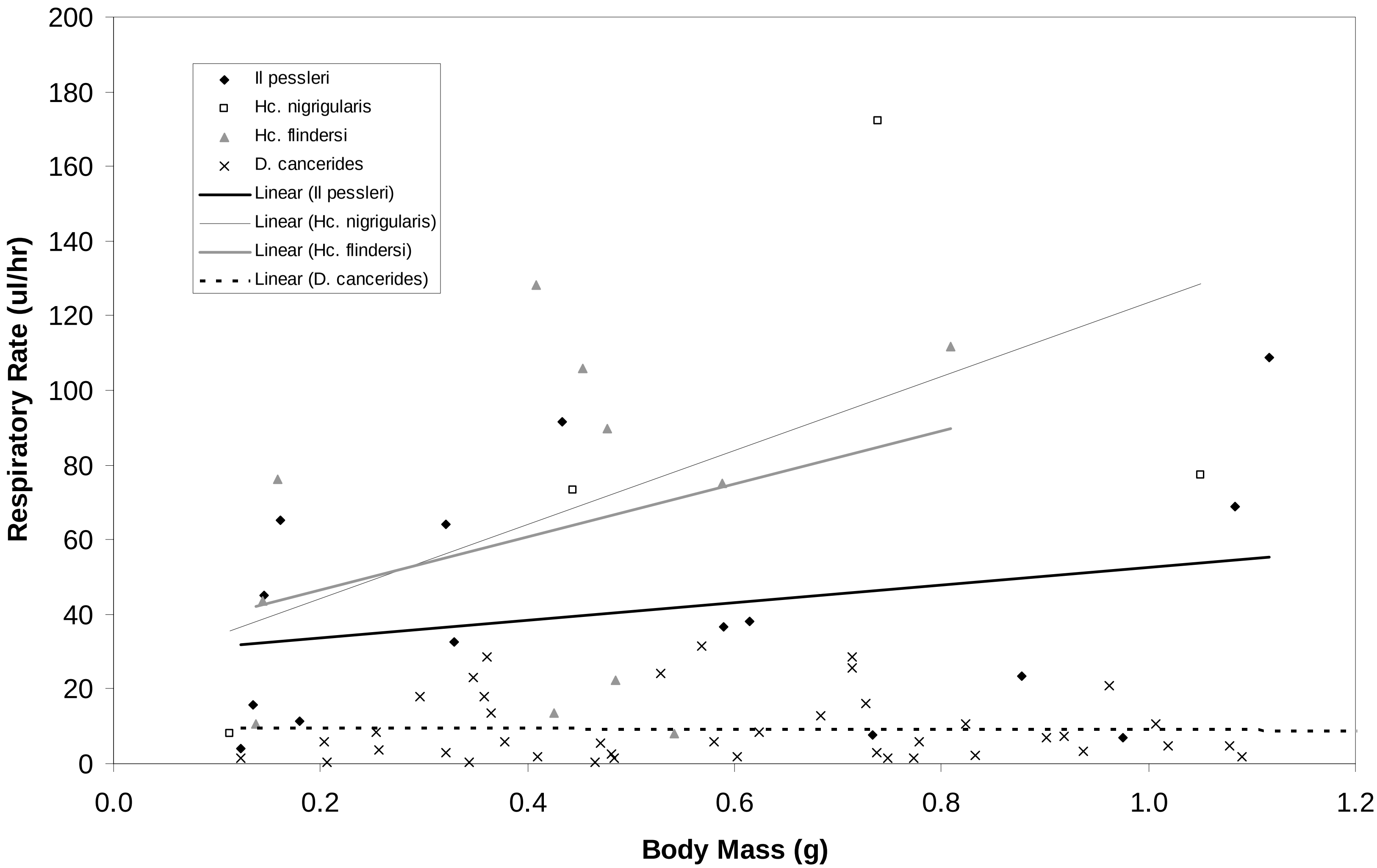

Figure 2: Metabolic rates of four species: Il. pessleri, Hc. nigrigularis, Hc. flindersi and D. cancerides. Delena cancerides has a significantly lower metabolic rate than the three other (solitary) species

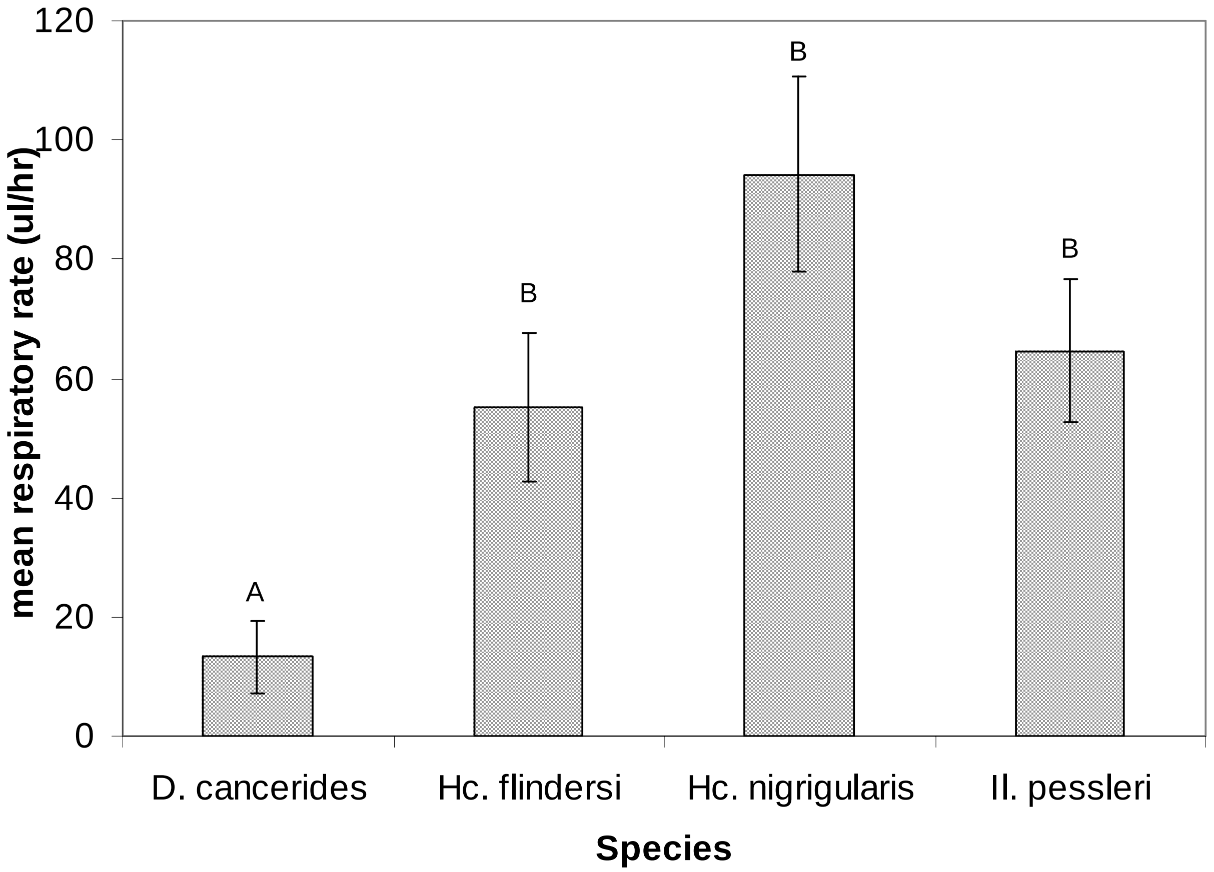

Figure 3: Comparison of mean respiratory rate between four species of huntsman spider. The social species, *Delena cancerides* has a significantly lower average respiratory rate despite there being no difference in overall masses between the four species. Different letters indicate groups that are significantly different.

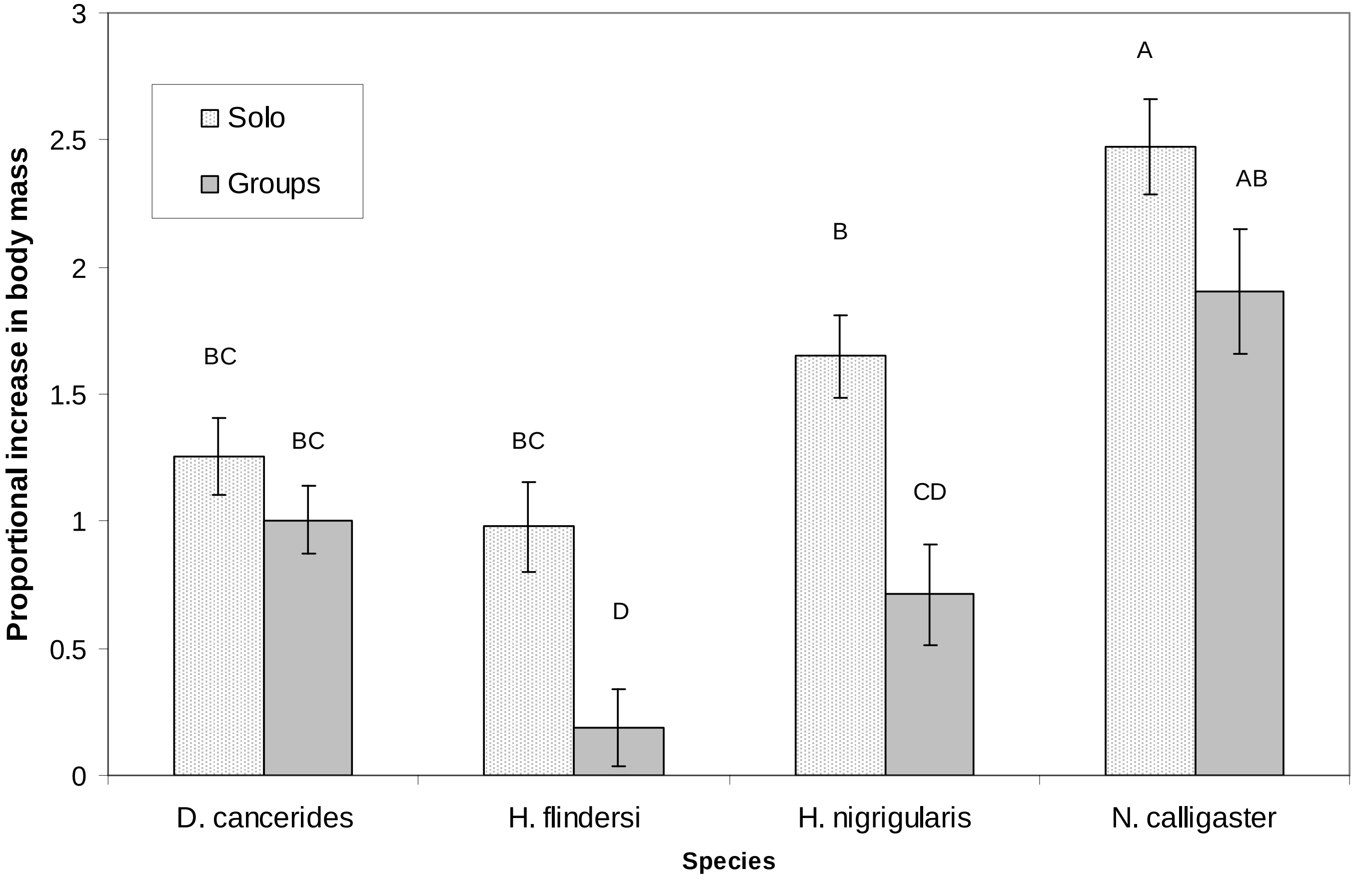

Fig 4: Comparison of proportional increase in body mass relative to initial mass of spiderlings raised in group and solitary containers. Different letters indicate groups that are significantly different.

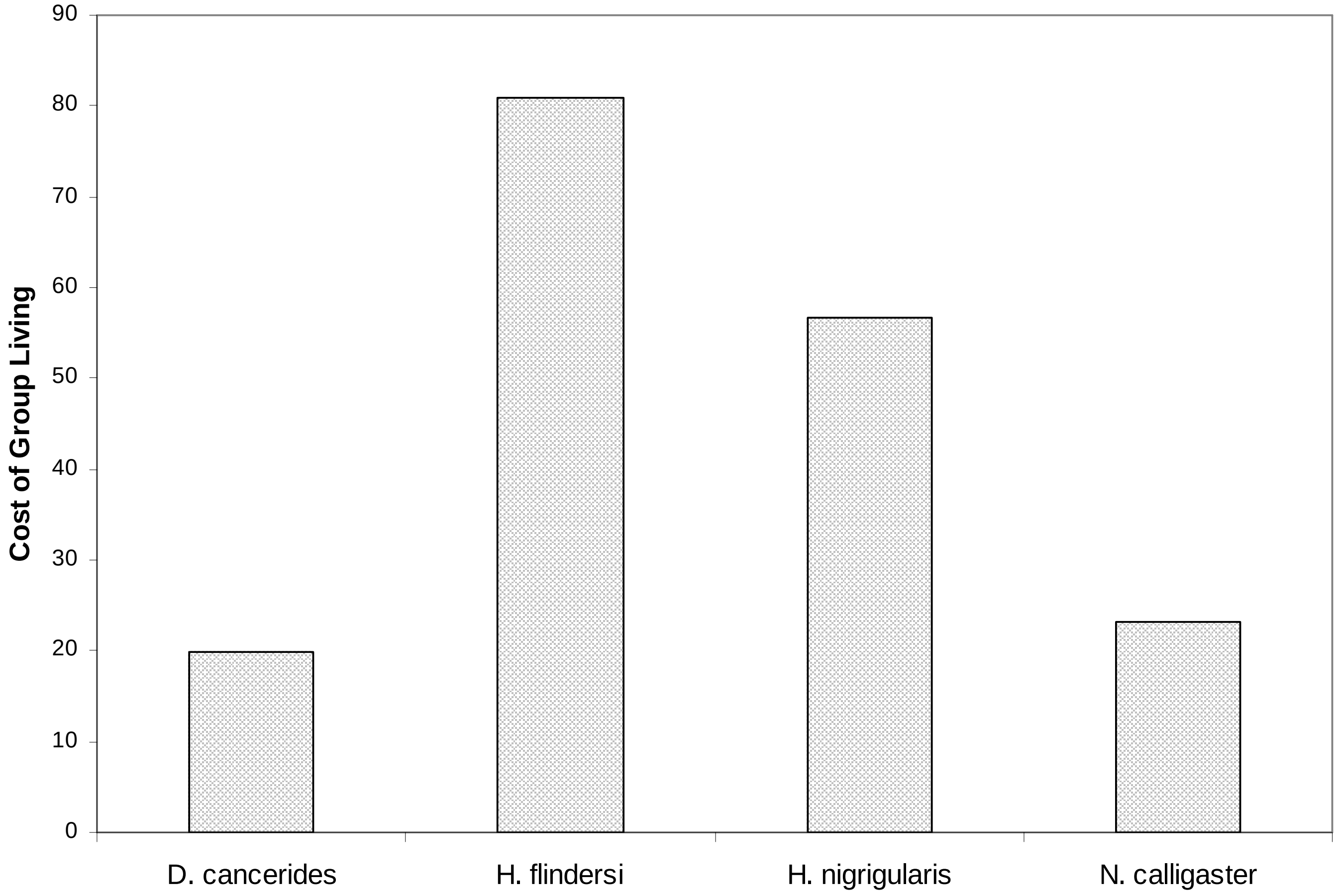

Fig 5: Cost of sociality as calculated by the difference in average body mass increase between group and solitary environments. All species suffered a decreased level of growth in group containers when compared to solo containers.

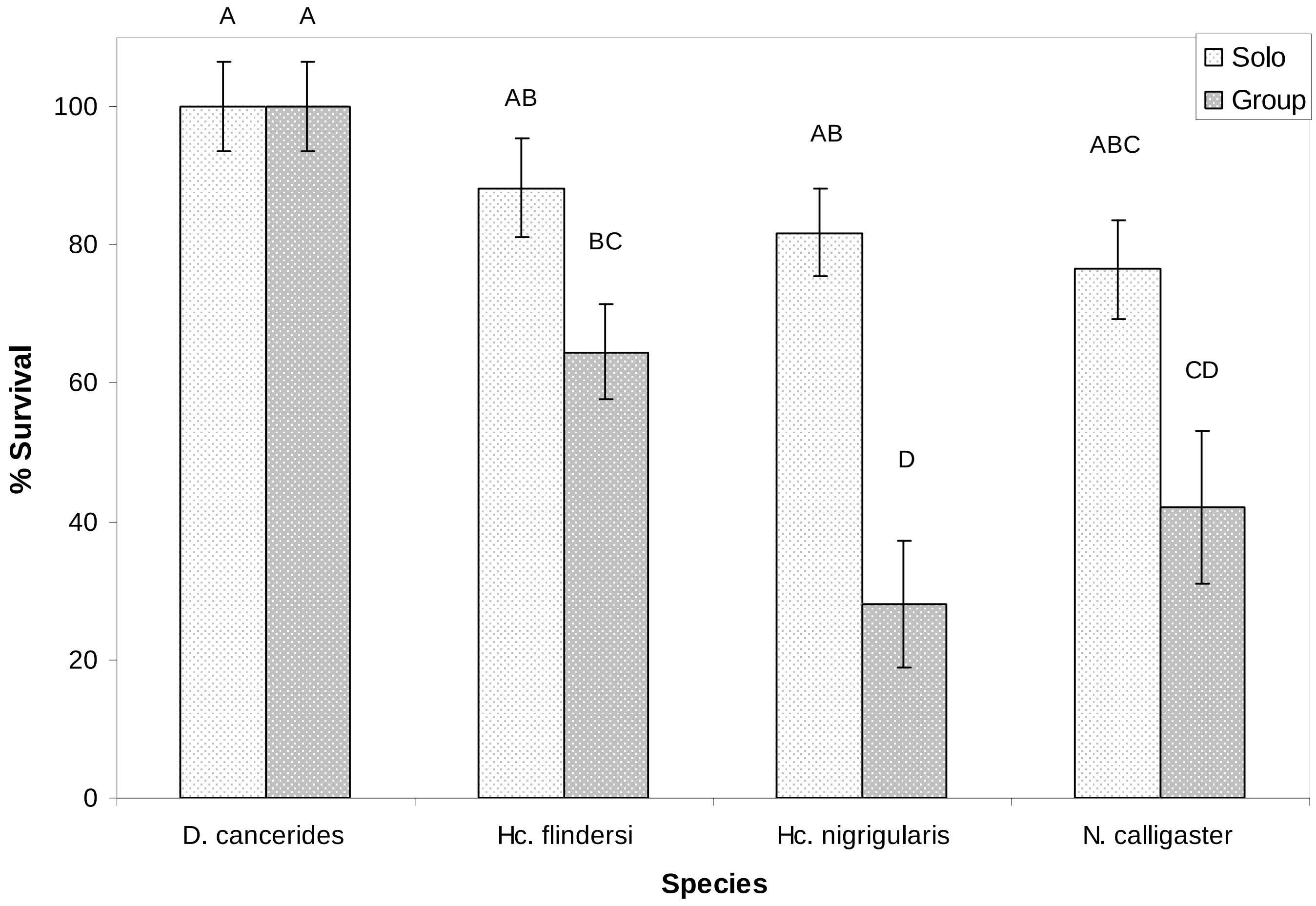

Figure 6: Survivorship in group and solo environments. Different letters indicate groups that are significantly different.

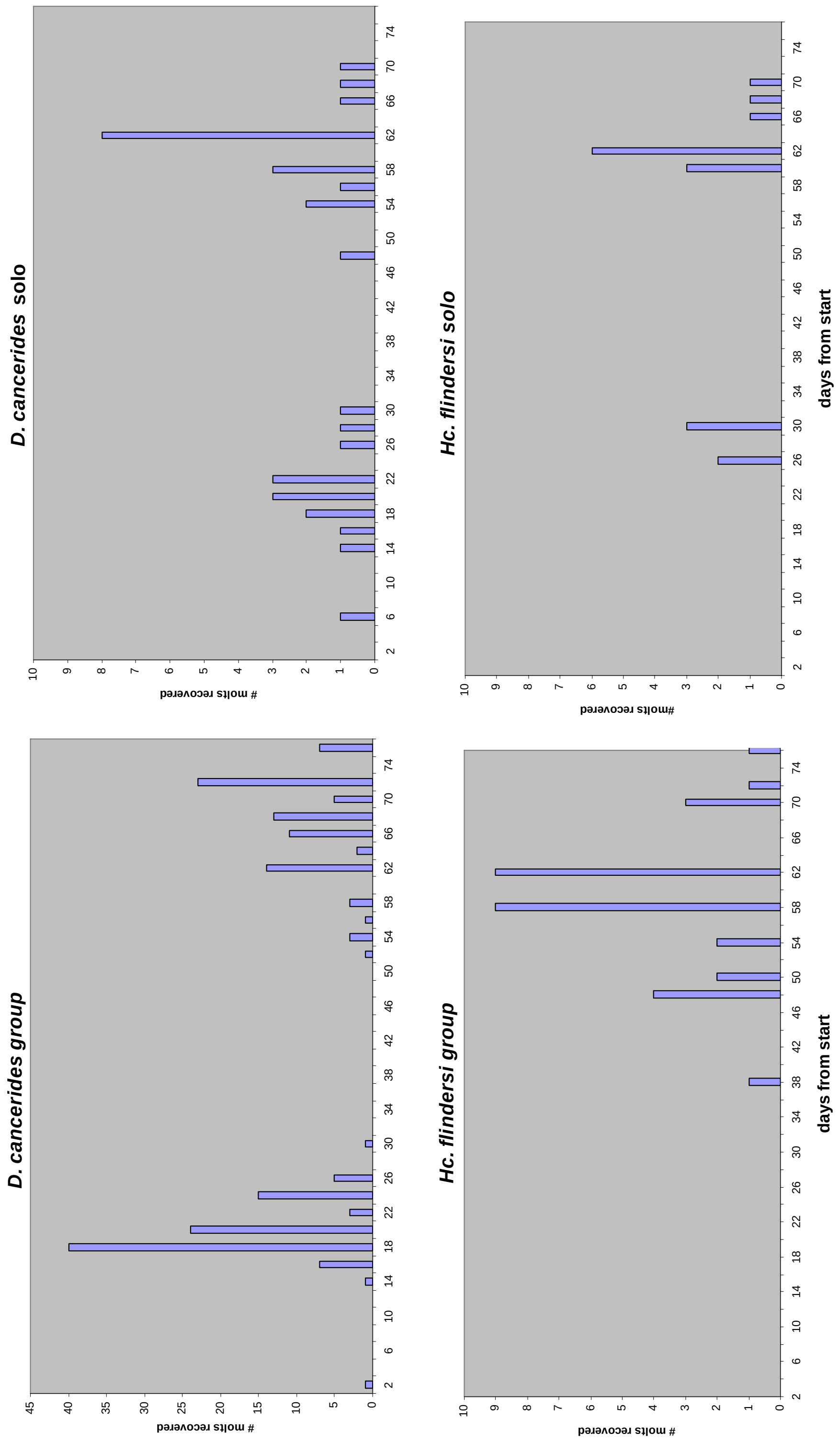

Fig 7: Molting patterns in group and solo environments for *D. cancerides* and *Hc. flindersi.*

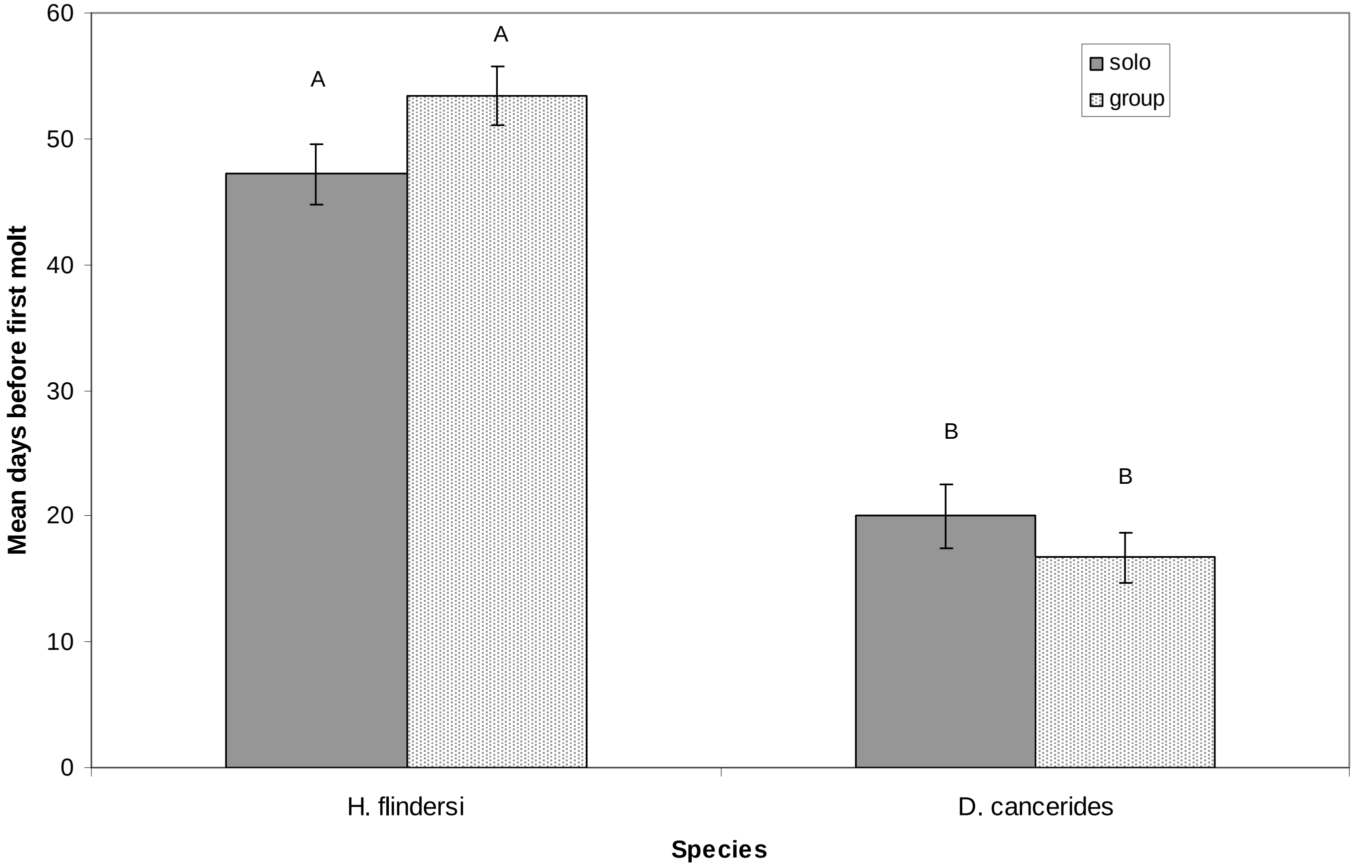

Fig 8: Average number of days prior to first molt in group and solo treatments of *D. cancerides* and *Hc. flindersi.* Different letters indicate groups that are significantly different.