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Development of some species of the *Anthrenus pimpinellae* (Fabricius, 1775) group (Coleoptera, Dermestidae, Megatominae) on feathers and dead insects

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Abstract: Some species of Dermestidae (Coleoptera) are pests of stored commodities or natural history museums, or are species of forensic significance. For these species, a lot of research has been carried out into their feeding habits. For the genus *Anthrenus* Geoffroy, 1762 pest species, we know what they will feed on or how long their development takes under different conditions, but rather less about the growth curves followed during development. For non-pest *Anthrenus* species, we know hardly anything about their feeding habits, let alone development periods and growth curves. In the current study, adult *Anthrenus amandae* Holloway, 2019, *Anthrenus angustefasciatus* Ganglbauer, 1904, and *Anthrenus isabellinus* Küster, 1848 from Mallorca (Balearic Islands, Spain) were placed on dry feathers and dead insects to assess developmental performance. All species developed on feathers, but only *A. angustefasciatus* was able to develop through to adult on dead insects. The developmental curves and relative growth rates of the three species on feathers are presented. *Anthrenus amandae* develops the fastest of the three species, whilst *A. isabellinus* was the slowest. Pupal weights and weight at adult eclosion from the final larval case were measured. Weight lost by adults whilst quiescent within the final larval case is linearly related to the length of time spent within the final larval case. Quiescing adults lose 0.2% of the weight accumulated during development per day.

Key words: Coleoptera, Dermestidae, *Anthrenus*, *A. amandae*, *A. angustefasciatus*, *A. isabellinus*, growth rates, foodstuffs, keratin, Mallorca, Spain.

Resumen: Desarrollo de algunas especies del grupo de *Anthrenus pimpinellae* (Fabricius, 1775) (Coleoptera: Dermestidae, Megatominae) sobre plumas e insectos muertos. Algunas especies de Dermestidae (Coleoptera) son plagas de productos almacenados o de museos de historia natural, o son especies de importancia forense. Para estas especies se han llevado a cabo muchas investigaciones sobre sus hábitos alimenticios. Para las especies plaga del género *Anthrenus* Geoffroy, 1762 sabemos de qué se alimentarán o cuánto tiempo lleva su desarrollo en diferentes condiciones, pero bastante menos sobre las curvas de crecimiento seguidas durante el desarrollo. En el caso de las especies de *Anthrenus* que no son plaga, apenas sabemos nada sobre sus hábitos alimenticios, y mucho menos sobre los períodos de desarrollo y las curvas de crecimiento. En el estudio actual, adultos de *Anthrenus amandae* Holloway, 2019, *Anthrenus angustefasciatus* Ganglbauer, 1904 y *Anthrenus isabellinus* Küster, 1848 procedentes de Mallorca (islas Baleares, España) se colocaron sobre plumas secas e insectos muertos para evaluar el rendimiento del desarrollo. Todas las especies se desarrollaron a partir de plumas, pero sólo *A. angustefasciatus* pudo desarrollarse hasta convertirse en adulto sobre insectos muertos. Se presentan las curvas de desarrollo y las tasas relativas de crecimiento de las tres especies en las plumas. *Anthrenus amandae* es la que se desarrolla más rápido de las tres especies, mientras que *A. isabellinus* fue la más lenta. Se midió el peso de las pupas y el peso a la eclosión adulta de la exuvia larvaria final. La pérdida de peso de los adultos mientras están inactivos en la exuvia larvaria final se relaciona linealmente con el tiempo que pasan en el dicha exuvia. Los adultos inactivos pierden un 0,2% del peso acumulado durante el desarrollo por día.

Palabras clave: Coleoptera, Dermestidae, *Anthrenus*, *A. amandae*, *A. angustefasciatus*, *A. isabellinus*, curvas de crecimiento, productos alimenticios, queratina, Mallorca, España.

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Introduction

The beetle family Dermestidae (Coleoptera) numbers over 1900 species (HÁVA, 2024). Although the majority are not synanthropic or pest species, some, such as *Dermestes maculatus* De Geer, 1774, and *Trogoderma granarium* Everts, 1898, are economically important pests of stored products (HINTON, 1945), species of forensic value (LAMBIASE *et al.*, 2018), whilst others such as *Anthrenus verbasci* (Linnaeus, 1767) (HINTON, 1945), *A. flavipes* LeConte, 1854 (HOLLOWAY & BAKALOUDIS, 2021), and *A. sarnicus* Mroczkowski, 1963 (HOLLOWAY & PINNIGER, 2020) are pests of natural history collections. Because of their significance, studies on life history have focussed on pest or forensically valuable Dermestidae (HINTON, 1945; LAMBIASE *et al.*, 2018). Beyond these relatively few species, the knowledge of the general life history and ecology of Dermestidae is remarkably sparse.

The genus *Anthrenus* Geoffroy, 1762 is one of the largest genera within Dermestidae with nearly 300 species (HÁVA, 2024), and within this genus sits the Palaearctic *A. pimpinellae* (Fabricius, 1775) group of species (HÁVA, 2024), which contains nearly 30 species (HOLLOWAY & HERRMANN, 2024c). Nearly all these closely related species have a similar colour pattern consisting of a trans elytral band of white (or cream) scales on a background of black or dark brown scales with a scattering of orange or brown scales. Many of the species within the *A. pimpinellae* group are common and widely spread, but despite this, the knowledge of their life histories is limited (YOKOYAMA, 1929 in HINTON, 1945; HOLLOWAY & BAKALOUDIS, 2020; HOLLOWAY & FOSTER, 2022). The common name of *A. pimpinellae* is the Bird Nest Carpet Beetle with an assumption therein that they and several of the species in the group can breed on feathers. This assumption, to our knowledge, has never been tested under laboratory conditions and as such we know little of their diet.

There are at least four species of the *A. pimpinellae* group on the Balearic island of Mallorca (Spain): *A. amandae* Holloway, 2019, *A. angustefasciatus* Ganglbauer, 1904, *A. isabellinus* Küster, 1848 (Fig. 1), and *A. munroi* Hinton, 1943 (HOLLOWAY, 2024a). This paper presents data on the growth rate, development and survival rates of the first three species when offered dry feathers or dead insects as a source of nourishment.

Material and methods

Adult insects were collected from the field on Apiaceae, north-eastern Mallorca 1st-7th May 2023. Twenty-four unsexed adults of each species were evenly split between feathers of *Columba palumbus* Linnaeus, 1758 (a mixture of flight and body feathers) and insects (a wide range of species but belonging mostly to Lepidoptera, Diptera, and Coleoptera caught from the wild by hand or with a light trap, and without the use of preservative fluids). Each species by food combination was allocated to a 7x7x4.5 cm plastic box with a loose lid allowing ventilation kept in the laboratory under constant temperature (21 ± 2°C) and ambient relative humidity. The adult insects were left on their respective oviposition substrates until death. Time to death was recorded. Since the precise moment of oviposition was not known, the exact development period for each individual was not known, so development times were minimum estimated values. The study was not concerned with generating accurate development periods, but rather was designed to answer which substrates the three species could feed on, and the associated growth curves.

Each treatment was visually inspected daily for the appearance of newly hatched larvae. At hatching, the larvae are very small and easy to damage, so they were left for four weeks before weighing to feed and gain bulk. Weighing (± 1 *μg*) was carried out using a Cahn 29 Automatic Electro balance. Each larva was picked up by their long lateral and terminal setae using needle tip forceps (changing to flexible forceps when they were bigger) and individually weighed once a week to enable a mean body weight to be calculated. Time to pupation was recorded, the pupa (inside the final larval case) was weighed and isolated to allow the adult to emerge. On emergence from the final larval case, each F1 adult and the immature insect cases were individually weighed to enable weight loss between pupation and adult emergence to be calculated. Each F1 adult was retained in isolation until death at which point the insect was dissected to establish sex.

Egg weight was estimated from adult female body weight assuming *Anthrenus* to be iteroparous using HOLLOWAY *et al.* (1987):

$\text{Log}_e EW = 0.698 \text{Log}_e BW - 1.7$

Where EW = egg weight and BW = body weight. Instantaneous growth rate (G) is $G = (\log_e BW - \log_e EW)/D$

Where D = development period in days (SIBLY & CALOW, 1985; HOLLOWAY *et al.*, 1987).

Statistical analysis was carried out using jamovi 2.3.28 (THE JAMOVI PROJECT, 2024). Data on adult longevity and time to pupation/emergence were not normally distributed (Anderson-Darling test) but fell into groups since the insects were inspected weekly. These data were compared using Kruskal Wallis (H) or Mann Whitney (W) non-parametric tests. Weight data and weight loss data were normally distributed and compared using analysis of variance (F) tests. Bonferroni adjustment was deployed reducing the critical significance value to $\alpha = 0.0167$ to counter the chance of increased Type 1 error during post hoc testing.

Figures were produced using Excel.

Results

Feathers

Median (field collected) adult longevity:

- *A. amandae* = 14 days (minimum 11 days, maximum 19 days)
- *A. angustefasciatus* = 14 days (minimum 11 days, maximum 23 days)
- *A. isabellinus* = 14 days (minimum 11 days, maximum 23 days).

There was a significant difference among the median longevities (H = 9.06, df = 2, $p < 0.01$), but no difference between *A. angustefasciatus* and *A. isabellinus* (W = 1751, $n_1 = 48$, $n_2 = 24$, ns [not significant]) indicating that *A. amandae* survived for a shorter period than *A. angustefasciatus* and *A. isabellinus*.

Larvae were noted in all species by food treatments 23 days after the adults were placed onto the oviposition medium (except *A. amandae* on insects which didn't lay any eggs). Increase in larval weight until pupation is shown in Fig. 2. On feathers, *A. amandae* reached maximum mean larval weight (4.9 ± 0.1 [SEM] mg, n = 24) 82 days after hatching, *A. angustefasciatus* reached maximum mean larval weight (4.8 ± 0.3 mg, n = 15) 110 days after hatching, *A. isabellinus* reached maximum mean larval weight (5.8 ± 0.1 mg, n = 28) 117 days after hatching.

All three species pupated within the final larval case, and the adult on emergence from the pupal case remained quiescent also within the final larval case. Larval survival from first weighing until pupation (L – P) and from pupation until adult eclosion from the final larval instar case (P – E) was over 90% for all species on feathers, except L – P for *A. isabellinus* which was 57% (Table 1). There was no significant difference in time to pupation between males and females for *A. amandae* (H = 0.94, df = 1, ns), *A. angustefasciatus* (H = 0.85, df = 1, ns), and *A. isabellinus* (H = 0.63, df = 1, ns). There was a difference in time to pupation among the species (H = 11.52. df = 2, $p < 0.01$) with median time to pupation for *A. angustefasciatus* at 139 days versus 146 days for both *A. amandae* and *A. isabellinus*.

Table 2 summarises the weights of pupae (plus the final larval case), adults at eclosion, and final larval cases. There was a significant difference in the weights of the pupae among species ($F_{2, 60} = 44.2$, $p < 0.001$), mostly because *A. isabellinus* was larger than the other two species. There was a significant difference between the sexes in pupal size ($F_{1,\,60} = 35.2$, $p < 0.001$) with females on average heavier than males. There was a significant interaction between species and sex ($F_{2,\,60} = 4.88$, $p = 0.011$) since the difference in weight between male and female *A. amandae* pupae was small relative to the differences between males and females of *A. angustefasciatus* and *A. isabellinus*, with females considerably heavier than males. The scenario was similar for adult body weight with a significant difference among species ($F_{2,\,60} = 67.9$, $p < 0.001$) because of the weight of *A. isabellinus*, and a significant difference between the sexes ($F_{1,\,60} = 19.27$, $p < 0.001$) because females are heavier than males. However, the interaction between species and sex noted for pupal weights was not present for adult weights ($F_{2,\,60} = 1.57$, ns).

Using adult female body weights, egg weights were estimated as 41 µg, 42 µg, and 60 µg for *A. amandae*, *A. angustefasciatus*, and *A. isabellinus*, respectively. Using estimated egg weight, mean body weight, and days until maximum larval weight produced *G* values of 0.0247, 0.0183, and 0.017 for *A. amandae*, *A. angustefasciatus*, and *A. isabellinus*, respectively. The *G* values show that rate of growth in *A. amandae* until cessation of feeding (i.e., maximum larval weight) was 35% greater than *A. angustefasciatus*, and 45% greater than *A. isabellinus*.

Table 2 also shows the proportion weight lost by insects during the quiescent phase. The proportion of weight lost was between 33% and 37% for *A. amandae* and *A. angustefasciatus* but under 22% for *A. isabellinus*. There was no difference in proportional weight loss between males and females ($F_{1,\,60} = 0.16$, p = ns). There was a significant difference in proportional weight loss among species ($F_{2,\,60} = 22$, $p < 0.001$) with *A. isabellinus* losing as a proportion significantly less weight than *A. amandae* ($p < 0.001$) and *A. angustefasciatus* ($p < 0.001$), but no difference between *A. amandae* and *A. angustefasciatus*. Fig. 3 illustrates the tight relationship between the length of time from pupation to adult eclosion and proportion weight lost. The relationship between proportion weight lost and time quiescing was very similar across the three species so the data were combined to produce Fig. 3. The regression line through the data points is:

$$\text{Proportion weight loss} = 0.002\ (\text{days } P - E) + 0.09341$$

The intercept indicates that over 9% of body weight was lost during the formation of the pupa and adult emergence. Thereafter, for every day the adult remains quiescing in the final larval case a further 0.2% of the initial pupal weight was lost. *Anthrenus isabellinus* adults spent less time in the final larval case prior to eclosion than *A. amandae* and *A. angustefasciatus* hence *A. isabellinus* lost less weight (Table 2).

Table 1.- Survival and median time (days) between first larval weighing and pupation (L – P) and from pupation until adult eclosion from final larval case (P – E) for *Anthrenus amandae*, *A. angustefasciatus*, and *A. isabellinus*.

Species	**Survival**		**Median days**	
	L – P	P – E	L – P	P – E
A. amandae	90%	100%	154	160
A. angustefasciatus	93%	97%	139	146
A. isabellinus	57%	94%	146	77

Table 2.- Weights (mg) of pupa + case (P), adult at eclosion (A), and empty final larval case (C) for male and female *Anthrenus amandae*, *A. angustefasciatus*, and *A. isabellinus*. N = sample size. (P-C-A)/P = proportion of final pupal weight lost during pupation and adult quiescence.

Species						
		N	P	A	C	(P-C-A)/P
A. amandae	Male	12	4.21 ± 0.12	2.53 ± 0.14	0.22 ± 0.01	0.366
	Female	9	4.43 ± 0.16	2.78 ± 0.16	0.24 ± 0.01	0.336
A. angustefasciatus	Male	14	3.88 ± 0.11	2.33 ± 0.09	0.19 ± 0.01	0.368
	Female	18	4.81 ± 0.1	2.86 ± 0.1	0.24 ± 0.01	0.374
A. isabellinus	Male	9	5.17 ± 0.21	3.85 ± 0.19	0.24 ± 0.02	0.219
	Female	6	6.51 ± 0.41	4.89 ± 026	0.27 ± 0.02	0.216

Dead Insects

Anthrenus amandae laid no eggs on dead insects. *Anthrenus isabellinus* laid eggs and seven larvae survived to be large enough to begin weighing (four weeks old). However, all of them remained small and died within three months. *Anthrenus angustefasciatus* laid eggs on dead insects and 10 larvae became large enough to weigh. Two female larvae pupated 24th October and 1st November, pupal weights 3.96 mg and 4.58 mg, the adults (2.39 mg and 2.65 mg, respectively) quiesced for 147 and 172 days, respectively. Six of the remaining larvae struggled to grow and died, but two increased in weight. However, neither larva became large enough to pupate. After about six months on insects the two remaining individuals slowly began to lose weight. After a year from the beginning of the experiment it was clear that both larvae were going to die so they were transferred to feathers, and they began to grow quickly. After three months on feathers they pupated at 7.08 mg and 6.71 mg.

Behavioural observations

The larvae of all three species chopped the feather up into fluff into which they buried themselves to feed. *Anthrenus amandae* larvae were docile and easy to pick up, especially when they reached maximum weight. *Anthrenus angustefasciatus* larvae were highly active when disturbed, diving into the feather fluff to protect themselves from being picked up. When removed from the feather fluff they were able to run fast. *Anthrenus isabellinus* larvae were more active than *A. amandae* but not as fast and mobile as *A. angustefasciatus*. The stiff lateral projecting hastisetae (HOLLOWAY *et al.*, 2024) made *A. isabellinus* and *A. angustefasciatus* difficult to pick up, especially *A. angustefasciatus* when moving quickly or diving into fluff. The stiff lateral setae served to shoot the larva forwards as the flexible forceps closed on them.

Discussion

The Palaearctic *Anthrenus pimpinellae* species group is proving to be highly speciose (HOLLOWAY & HERRMANN, 2024c; HOLLOWAY, 2025) and in most regions of Europe and Asia several species can be found coexisting (HÁVA, 2024; HOLLOWAY, 2024a; HOLLOWAY & HERRMANN, 2024a, 2024b). With overlapping distributions, different species are likely to be utilising different components of the environment, in other words, each species occupies a different niche (CHESSON, 1991; POLECHOVÁ & STORCH, 2008). However, very limited information exists on the ecological requirements of the *A. pimpinellae* group of species, largely because modern day studies of Dermestidae focus on taxonomy rather than ecology and life history. It is true that the taxonomy of the *A. pimpinellae* species group has been confused and it is only very recently that our understanding of the taxonomy has improved (e.g., HOLLOWAY *et al.*, 2020; HOLLOWAY & HERRMANN, 2023; HOLLOWAY, 2024b and references therein). The major reference dealing with *A. pimpinellae* life history is HINTON (1945) but here many species are confused. *Anthrenus pimpinellae*, *A. angustefasciatus*, *A. latefasciatus*, and *A. isabellinus* were all assumed to be variants of the same species so the life history data provided could have related to any one or more of these species. MOCQUERYS (1856) records *A. pimpinellae* attacking dried insect collections, whilst KALSHOVEN (1935) claims *A. pimpinellae* was found attacking horsehair on car upholstery and the tape of portfolios. YOKOYAMA (1929) stated that *A. pimpinellae* was a pest of woollens in Japan which cannot be the case as there is no evidence that *A. pimpinellae* occurs in Japan (HOLLOWAY & FOSTER, 2022). Many of these claims could have related to *A. oceanicus* (Fauvel, 1903) (HOLLOWAY, 2025) (or other misidentifications) but even where *A. oceanicus* was not involved there is no way of knowing which species was being referred to. With much better identification information now available (HOLLOWAY & CAÑADA LUNA, 2022), we are able to study life histories with greater accuracy.

Three species were studied here with overlapping distributions on Mallorca. *Anthrenus amandae* appears to be a feather specialist and refused to lay eggs on dried insects. The growth rate of *A.*

amandae on feathers was very high, much higher than *A. isabellinus* and *A. angustefasciatus*. The instantaneous growth rate of *A. angustefasciatus* was 7.5% higher than *A. isabellinus* but maximum mean weight of *A. angustefasciatus* peaked at just under 5 mg whilst *A. isabellinus* continued to grow to top out at a mean just under 6 mg. Both *A. isabellinus* and *A. angustefasciatus* were prepared to lay eggs on dead insects. *Anthrenus isabellinus* was not able to develop through to adult on dead insects whilst a small number of *A. angustefasciatus* developed through to adult. There were clear differences among the species in ability to process and grow on feathers, and to utilise another food source (dead insects) indicating a level of niche partitioning (CHESSON, 1991; POLECHOVÁ & STORCH, 2008).

HOLLOWAY *et al.* (2024) studied the field distribution of the three species studied here and found that *A. amandae* and *A. isabellinus* occupied pastoral landscapes and *A. angustefasciatus* appeared to be closely associated with large pine trees. It is possible that *A. angustefasciatus* feed on feathers in nests of birds associated with pines. The mobility of *A. angustefasciatus* larvae suggests that they are capable of foraging for suitable resource. Perhaps the birds nesting in pines produce nests containing relatively small quantities of feathers and *A. angustefasciatus* has evolved behaviours to cope with limited resource, leaving nests as food becomes exhausted, subsisting on dead insects over the winter months, if need be, until the following nesting season and returning to a feather-based diet (as was simulated with two larvae in the current study). The current study provides no evidence that *A. amandae* can do this, and perhaps also *A. isabellinus*. However, given the development and survival rate of *A. amandae* on feathers, it is possible that the dry woodpigeon feathers (a bird of lowland agricultural systems) offered feeding conditions close to ideal for *A. amandae*. Field observations suggest that *A. angustefasciatus* is a species associated with conifers (HOLLOWAY *et al.*, 2024) but despite that, *A. angustefasciatus* performed well on the woodpigeon feathers displaying a steady growth rate (although not as fast as *A. amandae*) and a high survival rate (Table 1), perhaps again indicating *A. angustefasciatus* has a versatile feeding capacity. *Anthrenus isabellinus* did the worst overall, with the lowest growth rate and the lowest survival rate. Although *A. isabellinus* produced some large F_1, the data suggest that the feeding conditions offered in the laboratory did not match ideal field conditions for the species.

All three study species having reached maximum larval weight stopped feeding for a period prior to pupating. *Anthrenus amandae* was the most extreme reaching maximum larval weight at 82 days after hatching (Fig. 2) but not pupating until 154 days after hatching (Table 1), representing 72 days without any evidence of larval feeding. *Anthrenus angustefasciatus* and *A. isabellinus* reached maximum larval weight at 110 and 117 days, respectively, but both species pupated on average 29 days later. About one week after pupation the adults emerged but remained in the final larval case for 160, 146, and 77 days for *A. amandae*, *A. angustefasciatus*, and *A. isabellinus*, respectively. Presumably, the delay in pupation after reaching maximum larval weight and adult quiescence in the final larval case is a strategy to ensure adult emergence into the field for optimum conditions for feeding and mating. *Anthrenus amandae* F_1 emerged on average during the first half of April, *A. angustefasciatus* emerged on average around the end of February beginning of March, and *A. isabellinus* emerged on average in January. It is possible that adults experiencing the coldest periods of winter would have delayed emergence further, but the study suggests that the lengths of the quiescent periods are not entirely under environmental control. Despite the lack of cold winter months, adults still emerged from quiescence at times relating to field activity. Little is known about *A. amandae* activity period under field conditions. The species was only described in 2019 (HOLLOWAY, 2019) and has only been noted by the authors in the field in May and June. Three further images of *A. amandae* can be found online (see here, last accessed 27th Nov. 2024) two from May and the third from June. *Anthrenus angustefasciatus* is found earlier in the field than *A. amandae*, with a small number of records from March (see here, last accessed 27 th Nov. 2024), peaking in May (but more in June than April suggesting a peak in late May), with an occasional record from August. *Anthrenus isabellinus* is active in the field still earlier from February, peaking in May but more April records relative to June records suggesting an earlier peak than *A. angustefasciatus*, with the last sightings occurring in the first week of July (see here, last accessed 27th Nov. 2024). The data on field activity for the three species correlates well with emergence in the current study.

Several Dermestidae species are known to overwinter as adults in the final larval case, e.g., *Dermestes maculatus* (HINTON, 1945) and *Attagenus rufiventris* (HERMAND & HOLLOWAY, 2020). The authors are not aware of any studies reporting on weight loss during the overwintering period. Both *A. amandae* and *A. angustefasciatus* adults lose on average about 35% of their maximum body weight whilst quiescing (Table 2). For *A. isabellinus* it is less (just over 20%) because *A. isabellinus* emerges sooner in the year than the other two species, so spends less time in quiescence. Every day the adult spends in the final larval case costs a further 0.2% of its pupal weight. This explains why the three study species can be found feeding voraciously on suitable flowers in the spring, particularly white flowers such as Apiaceae (HOLLOWAY, 2019; HOLLOWAY & BAKALOUDIS, 2019) and *Cistus* (HOLLOWAY *et al.*, 2024). There is often a relationship between adult size and egg laying capacity so to remain quiescent over winter carries a cost as adults lose weight (FORREST, 1987; ELLERS & VAN ALPHEN, 2002). There must also be a benefit to quiescing as an adult over winter rather than remaining as a larva, perhaps to reduce predation pressures, but the data collected here cannot address this question. With these points in mind, it is not clear why *A. amandae* larvae grow so fast and then stop feeding months in advance of pupation.

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Fig. 1.- Species of the *Anthrenus pimpinellae* group from Mallorca (Balearic Islands, Spain). **1a.-** *Anthrenus amandae*. **1b.-** *Anthrenus angustefasciatus*. **1c.-** *Anthrenus isabellinus*. Scale bars = 1 mm.

2

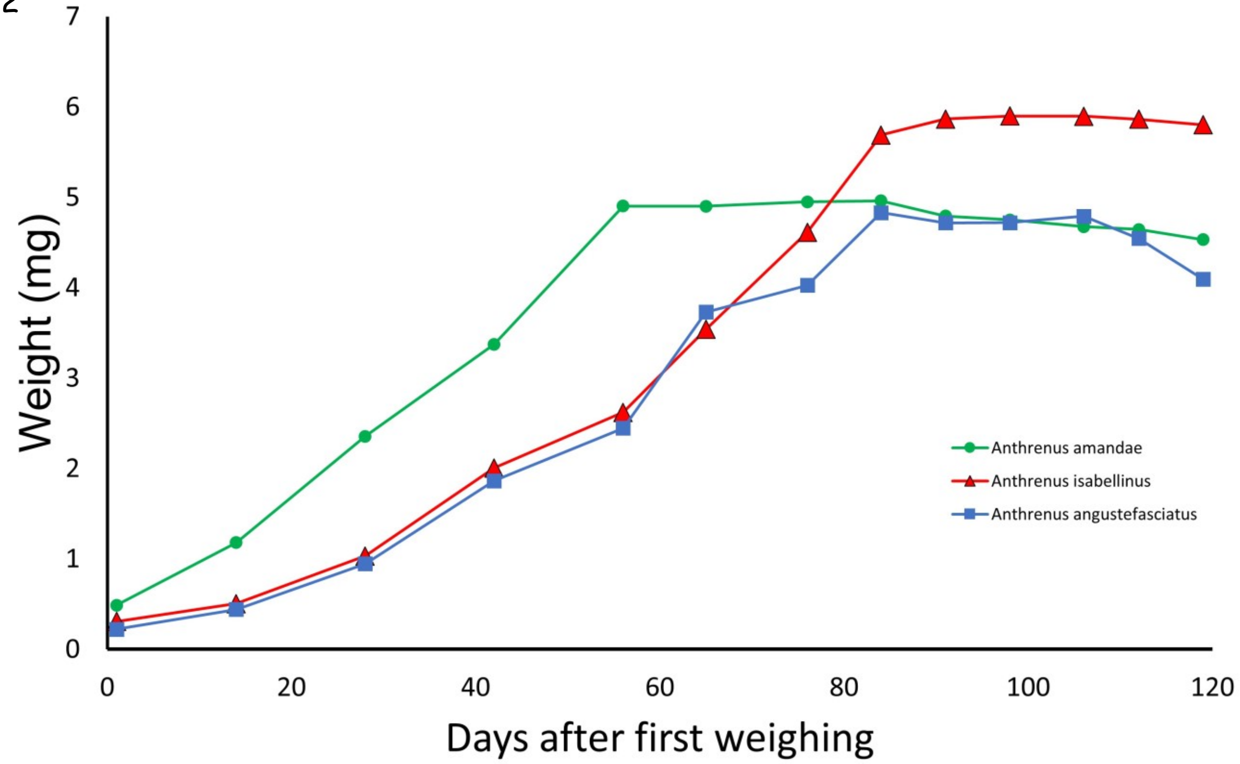

Fig. 2.- Mean change in weight (mg) against number of days since first weighing of all surviving larvae on feathers for *Anthrenus amandae*, *A. angustefasciatus* and *A. isabellinus*. Sample sizes varied from 29, 44, and 52, respectively, at first weighing down to 19, 12, and 11, respectively, at final weighing.

3

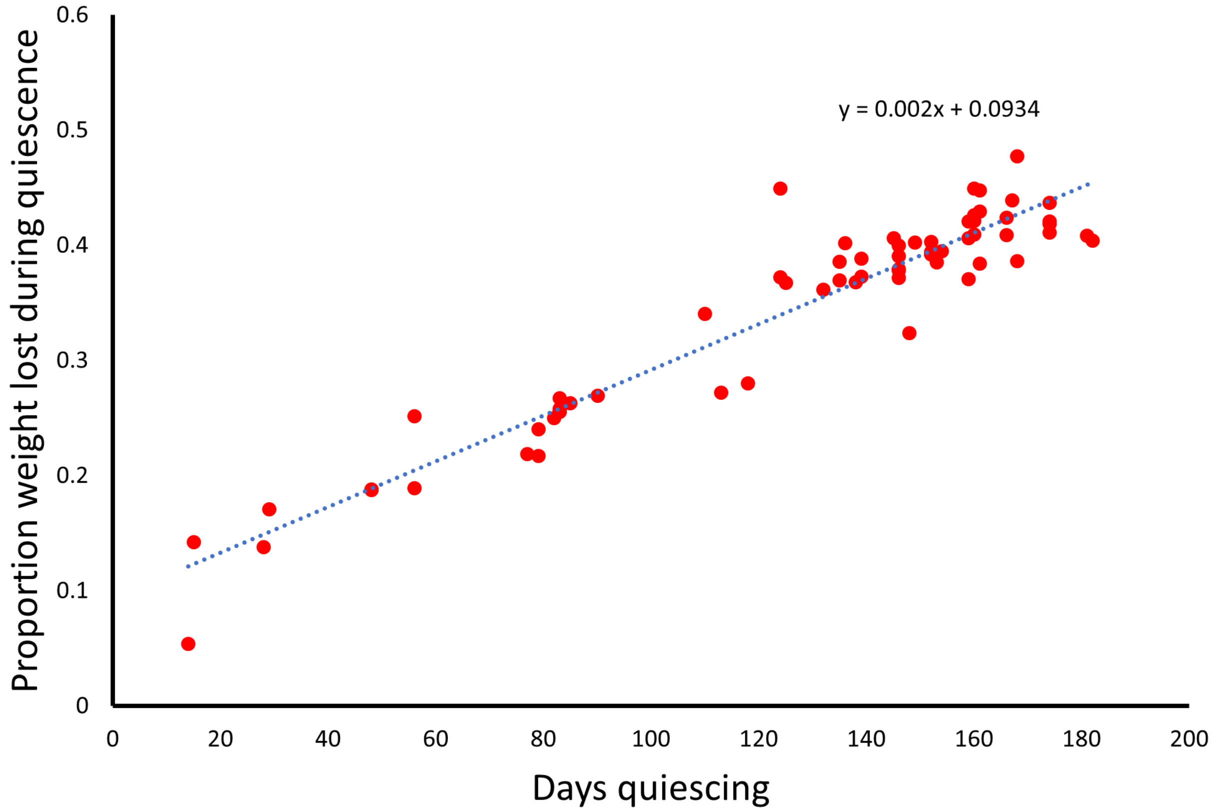

Fig. 3.- (Pupal weight – adult weight at eclosion)/pupal weight against number of days quiescing. All species data combined.