

Fecundity of *Thanasimus dubius* (Coleoptera: Cleridae) Rebounds after a Period of Prey Scarcity

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Abstract

We field-collected *Thanasimus dubius* (Fabricius) (Coleoptera: Cleridae) adults during spring, maintained them separately in the laboratory, and initially gave them four bark beetle adults [*Ips grandicollis* (Eichhoff) or *Tomicus piniperda* (L.) (Coleoptera: Curculionidae: Scolytinae)] daily as prey. Using a subset of the female clerids (N = 41), we assigned them to one of four feeding groups that varied in the number of prey provided daily. For the first four weeks of a 12-week study, the four diets were: four prey daily, two prey daily, one prey daily, and one prey every 2 days. After four weeks, all females were again given four prey daily until their death or to the end of the study. During the initial 4-week treatment period, females provided four prey daily laid the most eggs on average (106 eggs per female over four weeks). Average egg production by females provided two prey daily (63) or one prey daily (25) were intermediate, while females given one prey every two days laid the fewest eggs (10). Starting in week 5, when all females were given four prey daily, egg production by females that had been on the two most restricted diets matched the other two groups and surpassed them by week 6. At the end of 12 weeks, overall female longevity and fecundity did not differ significantly among the four feeding groups.

Keywords: Bark beetles, checkered beetles, fecundity, longevity, prey abundance

Beetles (Coleoptera) in the family Cleridae are commonly called checkered beetles and are often brightly colored. Clerids are found worldwide, on all continents except Antarctica, and there are currently about 4,710 recognized species (Chapman et al. 2025). In North America, Opitz (2002) recognized 291 clerid species; however, that total included three species that are now members of a separate family: Thanerocleridae. In Michigan, 35 species of clerids and one thaneroclerid have been documented (Gosling 1980, Ruesink et al. 2023).

Most clerids are predacious as both larvae and adults, and feed on a variety of insects (Opitz 2002, Chapman et al. 2025). Additionally, some species feed on pollen and a few are considered pests because they feed on stored food products (Hasan et al. 2022). Several clerids are predators of bark- and wood-infesting beetles, including species of Bostrichidae, Buprestidae, Cerambycidae, and Curculionidae, especially members of the subfamily Scolytinae (Böving and Champlain 1920, Gosling 1980).

Many clerids in the genera *Enoclerus* Gahan and *Thanasimus* Latreille are predators of conifer-infesting bark beetles

(Curculionidae: Scolytinae) (Böving and Champlain 1920). These clerids typically use bark beetle pheromones and host volatiles like α -pinene and ethanol to find their prey or trees where their prey likely occur (Vité and Williamson 1970, Nebeker et al. 1980, Bakke and Kvamme 1981, Chénier and Philogène 1989, Herms et al. 1991, Ross and Daterman 1995, Poland and Borden 1997, Schroeder 2003, Dahlsten et al. 2004, Miller 2023). The life histories of several *Enoclerus* and *Thanasimus* species have been reported, including information on adult female fecundity and longevity (Table 1) as well as prey consumption (Table 2).

Dozens of exotic scolytine beetles (including bark beetles and ambrosia beetles) have become established in the United States (Haack and Rabaglia 2013), as well as many other parts of the world (Neumann 1987, Tribe 1991, Brockerhoff et al. 2003, Kirkendall and Faccoli 2010, Kirkendall 2018, Li et al. 2021). In both Australia and New Zealand, several parasitoids and predators, including clerids, have been imported, reared, and introduced to control exotic pine (*Pinus*)-infesting bark beetles. In Australia, the North American clerid *Tha-*

Table 1. Fecundity and longevity data for various North American clerid species that are primarily bark beetle (Scolytinae) predators based on laboratory studies that used either field-collected or laboratory-reared clerids.

Clerid species	Collection method	Primary prey fed to clerids	Fecundity (eggs/female)	Adult female longevity (days)	Reference
<i>Enoclerus barri</i>	Field collected	<i>Dendroctonus rufipennis</i>	Mean 389 Max 1184	Mean 76 Max 131	Rice 1969
<i>Enoclerus lecontei</i>	Reared	<i>Dendroctonus brevicomis</i>	Mean 515 Max 1032	Mean 70 Max 114	Berryman 1966
<i>Enoclerus nigrifrons</i>	Field collected	<i>Ips avulsus</i> and <i>Ips grandicollis</i>	Max 54	Max 66	King 1966
<i>Enoclerus nigripes</i>	Field collected	<i>Ips avulsus</i> and <i>Ips grandicollis</i>	Max 86	Max 74	King 1966
<i>Enoclerus sphegeus</i>	Reared	<i>Dendroctonus pseudotsugae</i>	Mean 90 Max 289	Up to 6 months	Cowan and Nagel 1965
<i>Thanasimus dubius</i>	Reared	<i>Ips grandicollis</i>	Mean 123 Max 527	Mean 50 Max 358	Lawson and Morgan 1992
<i>Thanasimus dubius</i>	Reared	<i>Ips grandicollis</i>	Max 112	Max 57	Mignot and Anderson 1969
<i>Thanasimus dubius</i>	Reared	<i>Dendroctonus frontalis</i> and <i>Ips avulsus</i>	Mean 452 on <i>Df</i> Mean 361 on <i>Ia</i>	Mean 117 on <i>Df</i> Mean 129 on <i>Ia</i>	Mizell and Nebeker 1982
<i>Thanasimus dubius</i>	Field collected	<i>Callosobruchus maculatus</i>	Mean 252	Mean 127	Reeve et al. 2003
<i>Thanasimus dubius</i>	Reared	<i>Dendroctonus frontalis</i>	Max 367	Range 35–74	Thatcher and Pickard 1966
<i>Thanasimus dubius</i>	Reared	<i>Dendroctonus frontalis</i>	No data	Mean 97 when fed 1 <i>Df</i> /day Max 262	Turnbow et al. 1978
<i>Thanasimus undatulus</i>	Reared	<i>Dendroctonus pseudotsugae</i>	Max 395	Up to 7 months	Cowan and Nagel 1965

nasimus dubius (Fabricius) was introduced to control the exotic North American bark beetle *Ips grandicollis* (Eichhoff) (Lawson and Morgan 1992). In New Zealand, the Eurasian clerid *Thanasimus formicarius* (L.) was introduced for control of two exotic Eurasian bark beetles *Hylastes ater* Paykull and *Hylurgus ligniperda* (Fabricius) (Zondag 1979, Faulds 1988).

During the mid-1990s, the Eurasian clerid *Th. formicarius* was considered for possible release in the United States for control of the Eurasian bark beetle *Tomicus piniperda* (L.), known as the pine shoot beetle (Haack et al. 1997, Haack and Poland 2001). *Tomicus piniperda* was first discovered in the US state of Ohio in 1992 (Haack and Kucera 1993). Although there were quarantines in both Canada and the United States that regulated movement of potential host

material (e.g., pine logs, nursery stock, and Christmas trees) to regions outside known infested areas, *T. piniperda* spread rapidly, being found in eight US states and one Canadian province by 1996, and 12 states and two provinces by 2000 (Haack and Poland 2001). Given the initial concerns that *T. piniperda* would become a major pine pest in North America, more than 2,500 *Th. formicarius* adults and larvae were collected in France by USDA ARS (Agricultural Research Service) staff in 1995 and 1996 and shipped to the USDA ARS insect quarantine laboratory in Newark, DE, and later shipped to the USDA APHIS (Animal and Plant Health Inspection Service) biological control laboratory in Niles, MI. A mass-rearing program for *Th. formicarius* was developed at the APHIS facility in Niles, starting in 1995.

Table 2. Bark beetle consumption data by various *Enoclerus* and *Thanasimus* clerid species under laboratory conditions, including adult body length for both clerids and prey.

Clerid species	Adult clerid body length	Primary prey fed to clerids	Adult prey body length	Consumption rate (prey/day)	Reference
<i>Enoclerus lecontei</i>	5–9 mm (3)*	<i>Dendroctonus brevicomis</i>	2.0–4.7 mm (2) **	Mean 0.7	Berryman 1966
<i>Enoclerus lecontei</i>		<i>Dendroctonus brevicomis</i>		Mean 0.7	Person 1940
<i>Enoclerus nigrifrons</i>	6–7 mm (4)	<i>Ips avulsus</i> and <i>Ips grandicollis</i>	2.1–2.8 mm <i>Ia</i> (2) 2.9–4.6 mm <i>Ig</i> (2)	Up to 5 <i>Ia</i> , Up to 2 <i>Ig</i>	King 1966
<i>Enoclerus nigripes</i>	5–7 mm (4)	<i>Ips avulsus</i> and <i>Ips grandicollis</i>		Up to 5 <i>Ia</i> , Up to 2 <i>Ig</i>	King 1966
<i>Enoclerus sphegeus</i>	8–12 mm (2)	<i>Dendroctonus pseudotsugae</i>	4.4–7.0 mm (2)	Mean 1.7, Max 14	Cowan and Nagel 1965
<i>Enoclerus sphegeus</i>		<i>Dendroctonus ponderosae</i>	3.5–6.8 (2)	Mean 0.8	Schmid 1970
<i>Thanasimus dubius</i>	7–10 mm (1)	<i>Dendroctonus frontalis</i>	2.0–3.2 mm (2)	Mean 2.2, Max 20	Thatcher and Pickard 1966
<i>Thanasimus dubius</i>		<i>Dendroctonus frontalis</i>		Mean 1.4 (non-ovipositing) and 2.5 (ovipositing)	Turnbow et al. 1978
<i>Thanasimus formicarius</i>	7–11 mm (5)	<i>Ips typographus</i>	4.0–5.5 (1)	Mean 0.9 prey/day/pair	Weslien and Regnander 1992.

* Clerid size references: 1 = Drooz 1985, 2 = Furniss and Carolin 1977 , 3 = LeConte 1861, 4 = Leavengood 2008, and 5 = Thomaes et al. 2017.

** Scolytine size references: 1 = EPPO 2020, 2 = Wood 1982.

Thanasimus formicarius was considered for release in the United States despite the presence of the native clerid *Th. dubius* throughout eastern North America (Chapman et al. 2025). The life cycle of *Th. formicarius* was considered better synchronized with *T. piniperda* compared to *Th. dubius*, so *Th. formicarius* was deemed a potentially better candidate for biocontrol. For example, in the Great Lakes region, *T. piniperda* typically initiates spring flight about 3–6 weeks earlier than the native pine-infesting bark beetles and their associated natural enemies, including *Th. dubius* (Haack and Lawrence 1995a, 1995b). By contrast, timing of *Th. formicarius* spring flight closely matches that of *T. piniperda* (Herard and Mercadier 1996). In addition, *Th. formicarius* is recognized as a major mortality agent of *T. piniperda* in Europe (Schroeder 1996).

Although *Th. formicarius* had obvious advantages over *Th. dubius* for control of *T. piniperda*, concerns were raised regarding the potential that *Th. formicarius* could outcompete and replace *Th. dubius* over

time (Haack and Poland 2001). In response, we (Haack and Lawrence 2026) conducted a series of laboratory tests to evaluate the interactions of these two clerids when added to the same scolytine-infested pine bolts. As part of those studies, we developed a laboratory rearing program to produce larvae of *Th. dubius*. As a side project during this rearing program, we examined how egg production by *Th. dubius* varied with the number of prey (bark beetle adults) provided. Our main objective was to monitor changes in *Th. dubius* egg production during a 4-week treatment period when prey quantity varied from one prey every two days to as many as four prey daily, followed by eight weeks when all females were given four prey daily.

Materials and Methods

Field collections and laboratory colonies of scolytines and clerids. Starting in summer 1995, we initiated a laboratory colony of *I. grandicollis*, using adults that had been collected at Michigan State University’s W. K. Kellogg Forest Experi-

ment Station (Kalamazoo County, MI; 42.36° N, 85.36° W). The bark beetles were reared on red pine (*Pinus resinosa* Sol. ex Aiton) bolts held in cardboard rearing tubes (ca. 20–25 cm diameter, 66 cm length; Michigan Can and Tube, Saginaw, MI) with plastic lids that had attached collection cups (see details in Petrice and Haack 2006, Haack and Petrice 2022). Rearing occurred at room temperature (22–27° C) in our laboratory on the Michigan State University campus in East Lansing, MI. The pine bolts were 40–45 cm long and cut from trunks of small diameter trees growing at Kellogg Forest. The colony was maintained by using progeny adults from the most recent generation as parent adults to initiate the next generation of bark beetles.

Tomicus piniperda adults were collected by two methods in spring 1996. One method involved placing red pine trap logs at various sites in southern Lower Michigan where we had studied *T. piniperda* during the previous few years. Log placement was staggered from late March through early May so that we would have a steady supply of recently colonized logs. Once we saw bark beetle frass at several locations on the bark surface of the trap logs, indicating bark beetle infestation had occurred, the logs were returned to the laboratory. Some trap logs were placed in cold storage (ca. 4° C) and later removed and debarked to obtain *T. piniperda* parent adults as needed for various studies. The remaining trap logs were soon debarked with *T. piniperda* adults extracted and used to infest other red pine bolts in the laboratory so that their progeny could be used as clerid prey.

The second method involved using 12-unit Lindgren funnel traps (Phero Tech Inc., Delta, BC) to live-trap *T. piniperda* adults. The funnel traps were suspended from rebar poles so that the upper portion of the trap was about 2 m above ground. Traps were baited with α -pinene lures, which is a good attractant for *T. piniperda* (Schroeder 1988, Haack et al. 2025). Strips of unbleached, brown paper towels were placed in each collection cup to provide surfaces for the trapped insects to walk on. The traps were usually emptied every 1–2 days. The entire contents from each collection cup were placed in an individual 1-pint (473 ml) labelled cardboard food container with a tight-fitting lid. The containers were placed in chest coolers with some ice and returned to the laboratory for sorting, which usually occurred by the next day. Some *T. piniperda* adults were used to maintain the laboratory colony while others were used as clerid prey.

Starting in late April, we added racemic ipsdienol lures (Phero Tech Inc.) to the

funnel traps already baited with α -pinene to increase their attraction to the clerid *Th. dubius*. Both α -pinene and ipsdienol are known to attract *Th. dubius* (Hermes et al. 1991, Staeben et al. 2015, Miller 2023). We continued trapping *Th. dubius* through May 1996. As above, the traps were emptied multiple times per week, with all insects returned to the laboratory in 1-pint cardboard containers. Once there, the clerids were sexed with a single pair (one female and one male) of adults placed in individual 1-quart (ca. 0.95 l) plastic containers with lids that had screened ventilation holes. The containers were numbered and kept on countertops in the laboratory at room temperature. Mating usually occurred soon after both beetles were placed in a container. Moistened and crumbled paper towels were added to each container to serve as an ovipositional substrate. The male clerids were removed after a day and maintained separately but were reintroduced with the females for a day every 2–4 weeks in case multiple matings were required to maintain laying fertile eggs. Each adult clerid was given four scolytine adults daily as prey. We used adult *I. grandicollis* (2.9–4.6 mm long; Wood 1982) and *T. piniperda* (3–5 mm long; Haack and Kucera 1993) as prey, which are similar in size.

Clerid oviposition studies. We recorded the number of eggs each *Th. dubius* female laid daily, starting from the day after they were collected in the field and placed in containers in the laboratory. This was done by removing and labelling the paper towel from each container, examining it for eggs, and recording the number of eggs found. A new moistened and crumbled paper towel was then placed inside each container along with four new prey scolytines. By the end of May, we were collecting eggs from over 50 *Th. dubius* females each day. Using a subset of these females (N = 43) for which we had complete data for their day of collection and daily egg production, we assigned them to one of four feeding groups on 16 June. The feeding groups varied in the number of prey provided: four prey daily, two prey daily, one prey daily, and one prey every two days. After four weeks, all females were given four prey daily until their death or at the end of 12-week study. We only used apparently healthy females that had no damaged legs or antennae. Given that the test clerids had already been in the laboratory for 21 to 43 days prior to the start of the study, we divided the females into two age groups (those already held 21–32 days in the laboratory or 33–43 days), and then randomly assigned roughly equal numbers from each age group to the four feeding groups.

Table 3. Summary mean (± SE) age and fecundity data for field-collected *Thanasimus dubius* adult females that were maintained in the laboratory for 21–43 days before being assigned to one of four feeding groups that varied in the number of prey (bark beetles) provided daily for four weeks, after which all females were all given four prey daily for the next eight weeks. Means were compared using the nonparametric Kruskal-Wallis rank sum test.

	Initial feeding conditions during first four weeks of 12-week study				Range for all female clerids	Kruskal- Wallis test results
	Four prey/day	Two prey/day	One prey/day	One Prey prey		
Starting number of female clerids	10	9	11	11		
Number of female clerids alive after 12 weeks	6	5	1	5		
Mean age at start of 12-week study (days)	26 ± 1 a*	25 ± 2 a	30 ± 3 a	29 ± 3 a	21 - 43	H = 5.3; df = 3; P = 0.1516
Mean age at time of death or end of 12-week study (days)	96 ± 7 a	89 ± 11 a	90 ± 6 a	83 ± 10 a	36 - 127	H = 1.5; df = 3; P = 0.6739
Mean total No. eggs laid before study started (eggs)	75 ±12 a	84 ± 9 a	104 ± 12 a	85 ± 16 a	0 - 183	H = 2.7; df = 3; P = 0.4438
Mean No. eggs laid during the week before 12-week study started (eggs)	25 ± 5 a	25 ± 3 a	28 ± 3 a	21 ± 4a	0 - 50	H = 1.5; df = 3; P = 0.6933
Mean No. eggs laid during 4-week treatment period (eggs)	106 ± 9 a	63 ± 13 ab	25 ± 4 bc	10 ± 3 c	0 - 150	H = 26.1; df = 3; P < 0.0001
Mean No. eggs laid during entire 12-week study (eggs)	200 ± 21 a	167 ± 47 a	183 ± 34 a	148 ± 38 a	0 - 426	H = 1.6; df = 3; P = 0.6653
Mean No. eggs laid both before and during the 12-week study (eggs)	275 ± 25 a	251 ± 45 a	287 ± 33 a	233 ± 27 a	111 - 498	H = 2.5; df = 3; P = 0.4834

* Means followed by the same letter are not significantly different at 0.05 level (Dunn’s test).

We started with 10 or 11 females per feeding group (N = 43 females); however, two escaped during the study so that one group only had nine females total. To estimate adult longevity, we started with the day the females were first brought into the laboratory. We recognize that we do not know the exact age of each clerid but assume that they were captured in the funnel traps soon after they became active in spring 1996. We

also recorded the number of days that each female had been in captivity and number of eggs each had laid prior to initiation of the 4–week treatment period on 16 June. Next, for every female, we summed the number of eggs laid during each week of the study.

Data analysis. For the *Th. dubius* females in each feeding group, we calculated (1) mean female age at the start of the study i.e., days in captivity prior to 16 June, (2)

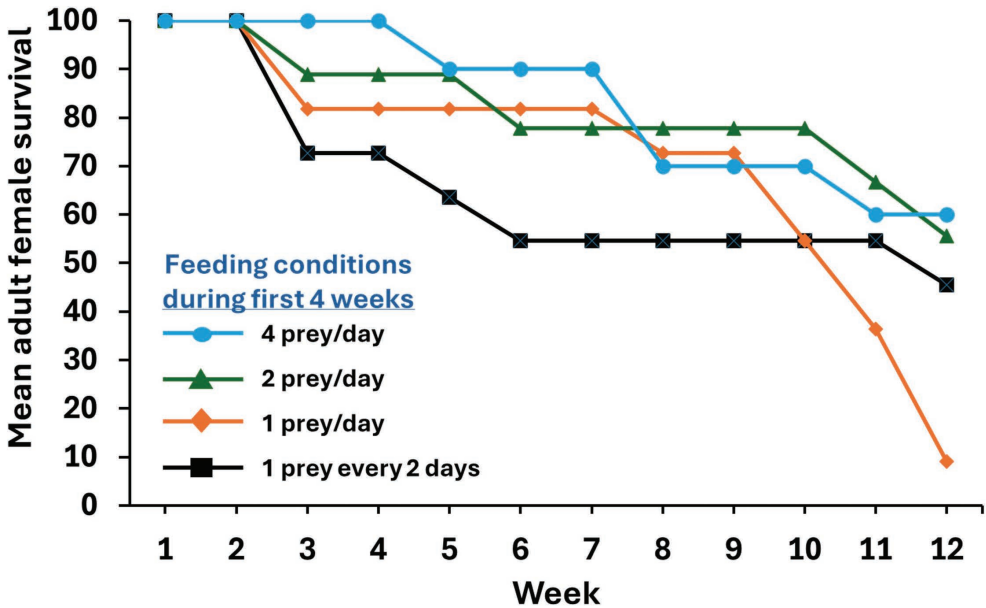


Figure 1. Survival curves of field-collected *Thanasimus dubius* adult females maintained in the laboratory for 21–43 days before being assigned to one of four feeding groups that varied in the number of prey (bark beetles) provided daily for the first four weeks of the study, after which all females were given four prey daily through week 12.

mean female age at time of death or age at the end of the study, starting when each female was collected in the field, (3) mean number of eggs laid before the 4-week treatment period began, (4) mean number of eggs laid during each week of the 12-week study and also the week prior to the start of the study, (5) mean number of eggs laid during the entire 4-week treatment period, and (6) mean total egg production during the entirety of beetle captivity up to the end of the study. For the weekly calculations, we only used egg production values for those females that were still alive at the end of each week. We compared means using the non-parametric Kruskal–Wallis rank sum test, followed by Dunn’s test for post-hoc pairwise comparisons (<https://astatsa.com>, <https://www.statskingdom.com>). An alpha level of 0.05 was used in all analyses.

Results

Mean adult female age (starting the day each female was field collected) at the start of the 4-week treatment period did not differ significantly among the four feeding groups, varying from 25 to 30 days (Table 3). Similarly, prior to the start of the 4-week treatment period, mean egg production per female did not differ significantly among feeding groups, ranging from 83 to 104 eggs

per female. However, for individual females the number of eggs laid prior to the start of the study ranged from 0 (for a female that was in captivity for 27 days before the 12-week study began, assigned to the “one prey every two days” group, but who eventually laid 334 eggs and was still alive when the study ended) to 183 (for a female that was in captivity for 43 days and eventually laid 189 eggs, dying in week three of the 12-week study, and being assigned to the “one prey daily” group). During the 4-week treatment period, six of the 41 females died, including three in the “one prey every two days” group, two in the “one prey daily” group, and one in the “two prey daily” group (Fig. 1).

There were no significant differences in mean egg production among feeding groups during the week prior to the start of the 4-week treatment period, averaging 21–28 eggs per female (Table 3). However, egg production responded quickly to changes in prey abundance even during the first week of the 4-week treatment period. For example, females given four prey daily laid on average the most eggs in absolute terms (27 eggs/week) while those given one prey every two days laid the fewest (7 eggs/week) (Fig. 2, Table 4). Females given either four or two prey daily continued a relatively high rate of egg production during the entire 4-week treatment period. By contrast, average egg

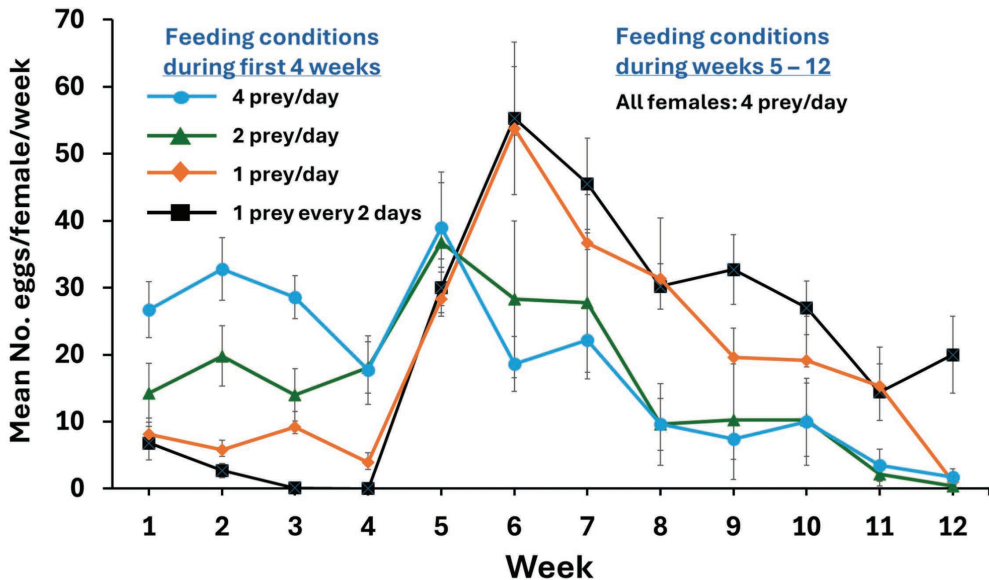


Figure 2. Mean ($\pm$ SE) number of eggs laid per female by week for four groups of field-collected *Thanasimus dubius* adult females that were maintained in the laboratory for 21–43 days before being assigned to one of four treatment groups that varied in the number of prey (bark beetles) provided daily for the first four weeks, after which all females were given four prey daily through week 12.

production by females given one prey daily or one prey every two days remained low during the 4-week treatment period. In fact, only one female in the group given one prey every two days laid a single egg in week three, and none laid eggs in week four (Fig. 2). For the entire 4-week treatment period, average egg production per female was highest for those given four prey daily (106 eggs over 4 weeks) and lowest for those provided one prey every two days (10 eggs) (Table 3).

Starting in week five, when all females were provided four prey daily, average egg production per female was similar among the four feeding groups, ranging from a mean of 28 to 39 eggs per female (Fig. 2, Table 4). By week six, the oviposition rate of females in the two groups provided the fewest prey during the 4-week treatment period surpassed the females in the groups that had been given more prey (means: 54–55 eggs per female vs. 19–28; Fig. 2, Table 4). This general pattern continued through to the end of the study.

Overall, mean fecundity per female did not differ significantly among the four feeding groups when considering the entire 12-week study, averaging 148 to 200 eggs per female (Table 3). For individual females, fecundity varied from 0 eggs during the 12-week study (for a female that was in captivity for 41 days and laid 165 eggs by the start of the study and was in the “one prey every two

days” group and died during week five) to 426 eggs (for a female that was in captivity for 24 days and laid 72 eggs by the start of the study and was in the “two prey daily” group and was still alive at the end of the study).

Total fecundity (from the day of field collection until death or the end of the study) did not differ significantly among feeding groups, ranging from an average of 233 to 287 eggs per female (Table 3). For individual females, total fecundity ranged from 111 eggs (for a female that was in captivity for 55 total days and in the “one prey every two days” group and had died in week six) to 498 eggs (for a female that was in captivity for 108 days and was in the “two prey daily” group and was still alive at the end of the study). Nevertheless, considering total fecundity for all 41 females revealed a moderately strong positive relationship between female longevity and fecundity (Fig. 3).

Of the original 41 females in the study, 17 (41%) were alive at the end of the 12-week study (Table 3). Mean longevity (from day of field collection to the day of death or end of the study) did not significantly differ among feeding groups, ranging from 83 days for the “one prey every two days” group to 96 days for the “four prey daily” group (Table 3). The shortest and longest laboratory lifetimes were 36 and 127 days, with both females having been members of the “one prey every two days” group. In fact, the longest-lived

Table 4. Statistical test results (Kruskal-Wallis test followed by Dunn post-hoc test) for the mean number of eggs laid per week by four groups of field-collected *Thanasimus dubius* adult females (shown in Fig. 2) that were maintained in the laboratory for 21-43 days before being assigned to one of four feeding groups that varied in the number of prey (bark beetles) provided daily during the first four weeks, after which all females were given four prey daily for the next eight weeks.

Dunn post-hoc test results for mean egg production per female by week					Kruskal-Wallis test results
Week	Four prey/day	Two prey/day	One prey/day	One prey/ two/days	
Females maintained on four different diets during weeks 1-4					
1	a*	ab	b	b	$H = 13.1$; df = 3; $P = 0.0045$
2	a	a	b	b	$H = 23.6$; df = 3; $P < 0.0001$
3	a	b	b	c	$H = 22.9$; df = 3; $P < 0.0001$
4	a	a	b	b	$H = 18.7$; df = 3; $P = 0.0003$
Females maintained on the same diet during weeks 5-12					
5	a	a	a	a	$H = 1.9$; df = 3; $P = 0.5896$
6	b	ab	a	a	$H = 12.4$; df = 3; $P = 0.0061$
7	a	a	a	a	$H = 3.2$; df = 3; $P = 0.3572$
8	b	b	a	a	$H = 8.2$; df = 3; $P = 0.0417$
9	b	b	a	a	$H = 12.4$; df = 3; $P = 0.0061$
10	a	a	a	a	$H = 6.7$; df = 3; $P = 0.0807$
11	b	b	ab	a	$H = 8.9$; df = 3; $P = 0.0311$
12	b	b	ab	a	$H = 10.5$; df = 3; $P = 0.0150$

* Mean fecundity values for the same week as shown in Fig. 2 followed by the same letter (within rows) are not significantly different at $\alpha = 0.05$.

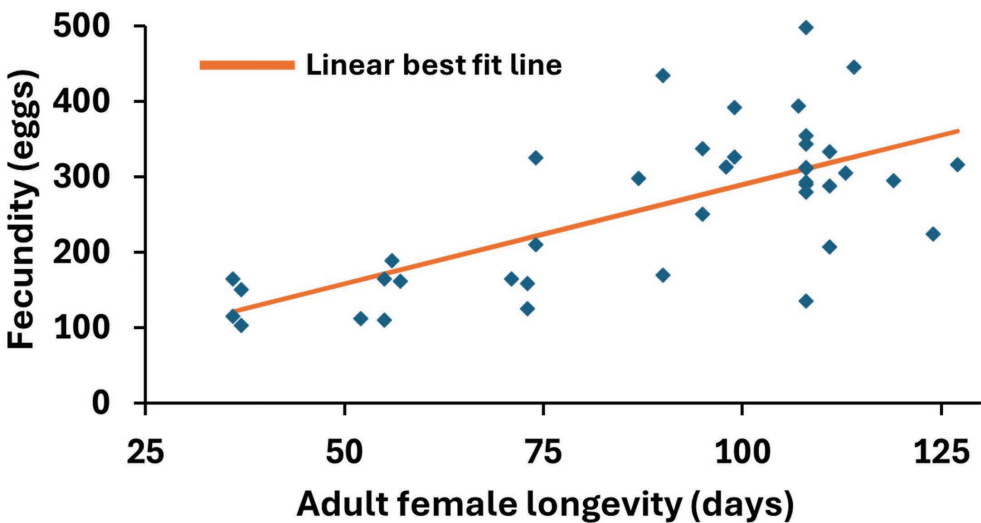


Figure 3. Linear regression curve ($R^2 = 0.47$; $df = 1,39$; $F = 35.1$; $P < 0.00001$) and scatterplot of fecundity vs. longevity data for 41 field-collected *Thanasimus dubius* adult females that were maintained in the laboratory and given similar numbers of prey daily except during a 4-week treatment period. The fecundity data reflect all eggs laid in the laboratory. The longevity data reflect the total number of days held in the laboratory from day of collection in the field to the day of death or to the end of the 12-week study if still alive.

female was still alive and laying eggs during the last week of the study.

Discussion

Egg production (oogenesis) in insects is usually limited by nutrients, particularly in iteroparous species that produce eggs multiple times throughout their adult lifespan (Wheeler 1996). For long-lived adult predatory insects there is often a trade-off between using available food resources for reproduction or survival when prey becomes scarce. There are several reports of lower egg production during periods of prey scarcity for various predatory insects, including hover flies (Diptera: Syrphidae; Amiri-Jami and Sadeghi-Namaghi 2014), ladybird beetles (Coleoptera: Coccinellidae; Bista 2014), minute pirate bugs (Hemiptera: Anthocoridae; Nakashima and Hirose 1999), and stink bugs (Hemiptera: Pentatomidae; Crum et al. 1998), to list a few. Additionally, oosorption (egg resorption) often occurs during periods of prey scarcity, allowing those resources to be used for adult survival i.e., somatic maintenance (Osawa 2005). However, we found no similar studies where the fecundity of the same predators was followed over time through periods of prey abundance, scarcity, and then prey abundance once again.

In the present study, *Th. dubius* clearly showed a reduction in egg production as prey scarcity intensified. However, once prey abundance was increased, *Th. dubius* egg production in the two low-prey groups not only rebounded quickly but exceeded the egg production by those females that had consistently been reared on a high-prey diet. Because we did not dissect any of the females in the present study, we cannot state if any oosorption occurred. However, given how quickly egg production rebounded in the low-prey groups starting in week five, suggests that little oosorption took place.

Since the adult clerids in the present study were collected in the field, we do not know the number of days they had been active or how many eggs they may have laid prior to collection. Moreover, given that 17 of the 41 adult females were still alive at the end of the study, and that 12 of the 17 living females laid eggs in week 12, our mean values for *Th. dubius* longevity and fecundity are underestimates. In other studies, using laboratory-reared *Th. dubius* (Table 1), the mean and maximum values for adult longevity and fecundity were higher than our values in one study (Mizell and Nebeker 1982), but similar to or lower than our values in the other studies (Thatcher and Pickard 1966, Mignot and Anderson 1969, Lawson and Morgan 1992, Turnbow et al. 1978). The maximum longevity of individual laborato-

ry-reared *Th. dubius* adults was reported as 262 days by Turnbow et al. (1978) and 358 days by Lawson and Morgan (1992). These extreme longevity values suggest that many of the adult females in the present study could have lived several more weeks after the study ended.

Compared to other clerid studies, our feeding rate of up to four prey items per day was much higher than the typical consumption rates reported for clerids that feed on bark beetles i.e., about one to two bark beetles per day (Table 2). However, King (1966) showed that the consumption rate of two *Enoclerus* species varied according to prey size. He reported that up to five smaller *Ips avulsus* (Eichhoff) (2.1–2.8 mm long) were killed daily, but only two larger *I. grandicollis* (2.9–4.6 mm long, Wood 1982). In the present study, nearly all bark beetle prey were killed within a day after being introduced. However, we did not record if the degree of consumption varied among the prey killed. Were the prey killed but not eaten? Nonetheless, during our 4-week treatment period, average egg production decreased in absolute terms within the first week after the number of prey offered daily dropped from four to two (Fig. 2). This suggests that a diet of two prey per day was suboptimal for egg production. We did not evaluate egg production at feeding rates greater than four prey per day; therefore, we cannot state whether *Th. dubius* could have produced more eggs.

The findings of the present study have implications for the mass-rearing of predatory insects, such as clerids. First, initial studies should determine how much prey a predator typically consumes in one or two days. Second, if the goal is to maintain high egg production, providing prey at a rate close to predator's daily consumption rate would be recommended.

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