30th Annual Edition

T.J. Walker *Editor*

UFBIR

University *of* Florida Book *of* Insect Records

2023

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Preface

BEGINNING IN 1994, graduate students in the Insect Ecology course at the University of Florida have contributed chapters to the University of Florida Book of Insect Records (UFBIR), a book that names insect champions and documents their achievements. Each chapter deals with a different category of record. For comparison, see the PDF of the 8th annual edition (2001) with 39 chapters:

https://web.archive.org/web/20011120070847/http://www.ifas.ufl.edu/~tjw/ufbir.pdf

Preparation of chapters

Before 1999, chapters were written by graduate students in an Insect Ecology course at the University of Florida, except for chapters 17 and 18, prepared by graduate students at the University of Bergen, Norway. Members of the Insect Ecology class proposed categories for new chapters, with the final list being determined by vote of the class. Each student chose a topic from the approved list, solicited nominations for champions, searched the secondary and primary literature, and wrote a chapter of no more than 1,500 words, including a brief abstract. The instructor/editor and two class members reviewed each chapter. The authors revised their chapters on the basis of the reviews. They then submitted new versions of their chapters to the editor for final review and acceptance for publication.

Now chapters are solicited from anyone interested in researching an insect record and lengthier chapters are permitted. What is required is good scholarship and a willingness to augment or improve the content of UFBIR.

Publication of chapters

Completed chapters are put on the World Wide Web as HTML documents in which the user's browser controls the document's format by referring to markup tags. Through 1999, complete chapters were also put on the web as PDF documents, which can be viewed and printed with a free download of Adobe Reader [*https://get.adobe.com/reader*] exactly as desktop-published.

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Submissions

Contributed chapters and nominations for new chapters or for new champions for old chapters should be sent to:

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NOTE: I will not answer questions that do not deal directly with UFBIR.

Chapter 1. Fastest flyer

T.J. Dean - School of Physics, University of New South Wales at the Australian Defence Force Academy - 2003-IV-01

Editor's note: This version replaces an early version (1994-V-31) of **chapter 1** by J.H. Byrd. - T.J. Walker, 2003-IV.

ABSTRACT. The insects with the highest *reliably measured* airspeeds are desert locusts *Schistocerca gregaria* (Forskål 1775) and corn earworm moths *Helicoverpa zea* Boddie 1850. These fly at average airspeeds of 33 and 28 km/h respectively, ~21 and 17 mph. Many insects surely fly faster, but their airspeeds have yet to be studied with modern methods. The highest sustained ground speed recorded is that of the black cutworm *Agrotis ipsilon* (Hufnagel 1766) which flies at speeds of 97-113 km/h (Showers & Sappington 1992).

INTRODUCTION. Insect airspeed is affected by mass, size, age, gender, feeding, water content, activity type, temperature, humidity, solar radiation, wind, oxygen level, ascent angle and even habitat isolation. The speed attainable by insects is currently poorly understood (Gauthreaux & al. 1998); indeed Dudley 1997 states that insect airspeed is one of the least known features of flight performance. This chapter details the current state of insect flight speed measurements and includes the most complete list of measured speeds to date (**Table 1**).

METHODS. Stevenson & al. 1995 attribute the large range of flight speeds measured being due to the different methodologies used (e.g. timing with stopwatches; wind tunnels; flight mills etc.). Insects flying freely often have higher speeds than those that are confined to small cages or tethered, although Wagner 1986 states that cage size has no influence on basic flight performance. While measurements have been made for insects flying up pheromone plumes, they are generally slower than freely flying insects (Kuenen & Carde 1993) and their speed decreases with proximity (Willis & al. 1991) and strength of the source (Meats & Osborne 2000; March & McNeil 2000). Riley & al. 1997 found that insects flying on flight mills partitioned their effort between lift and thrust substantially differently from those in free flight. Cooter & Armes 1997, Gatehouse & Hacket 1980, and Gatehouse & Woodrow 1987 consider that mills do not adversely affect the behaviour of the cotton bollworm *Helicoverpa armigera* (Hübner 1808). They do emphasize, however, that the results are meaningful only when used to provide comparative estimates of flight performance between experimental treatments. Other methods of monitoring insect activity include cameras (El-Sayed & al. 2000; Fry & al. 2000; Noldus & al. 2002; Hardie & Powell 2002), Doppler-radar autocorrelation analysis (Buchan & Satelle 1979; Sohal & Buchan 1981; Buchan & Moreton 1981; Renou & al. 1999; Knoppien & al. 2000), telescopic observation against the moon (Preuss & Preuss 1971), and roundabouts (Michel & al. 1977). For a full review of remote-sensing, telemetric and computer-based technologies see Reynolds & Riley 2002. In addition to effects of the methods employed on the measured speed, speed has been found to vary between laboratory and naturally reared specimens. McKibben & al. 1988 found that naturally reared cotton boll weevils *Anthonomus grandis* Boheman 1843 specimens had an average speed 1.2× greater than that of the laboratory reared specimens, although this was not found for 6 generations of the fruit fly *Ceratitis capitata* (Wiedemann 1824) (Economopoulos 1992). Significant variation has also been found within single species; a total of 7 authors have made over 400 measurements of the speed of the desert locust *Schistocerca gregaria* and found ground speeds ranging from 3 to 33 km/h (**Table 1**).

RESULTS. The most famous and oft-quoted insect flight speed is that of the deer botfly (genus *Cephenemyia* Latreille 1818), reputed to be able to fly at over 1,287 km/h (Townsend 1926). However, Langmuir 1938 refuted this claim, calculating that to attain this speed (equivalent to 0.5 horse power) the fly would have to consume 1.5 its own mass in fuel every second. Further observations by Langmuir 1938 found the maximum speed was more likely to be around 40 km/h. Some of the difficulties with early measurements arose from the difficulty separating airspeed from ground speed. Airspeed is the speed relative to the air whereas ground speed (often the quantity actually measured) is the speed relative to the ground (**Figure 1**). This difficulty in separating airspeeds from ground speeds makes some early measurements obtained using 'less than conventional' methods (e.g., comparisons with the speed of trains, Twinn & al. 1948) useless for comparison purposes. This is why the reported (Hocking 1953) speed of 98 km/h for *Austrophlebia costalis* (Tillyard 1907) is not included here.

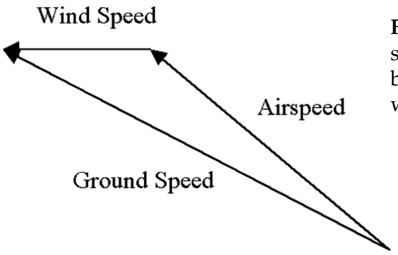

Figure 1. Vector diagram showing the relationship between insect airspeed, wind speed and ground speed.

The highest airspeeds reported in refereed literature obtained using a reliable method are those of the desert locust *Schistocerca gregaria*, 15 individuals having an average speed of reached 33 ± 3 km/h (mean ± SE) (Waloff 1972), and the corn earworm moth *Helicoverpa zea*, 10 individuals reaching an average speed of 28 ± 8 km/h (Quero & al. 2001). In the unrefereed literature, a noteworthy record is that of a ♂ horsefly *Hybomitra hinei* that was estimated to achieve an airspeed of ~145 km/h (89 mph) while chasing an air rifle pellet (Kunzig 2000). The highest sustained ground speed recorded is that of the black cutworm *Agrotis ipsilon* which flies at speeds of 97-113 km/h at heights of 300-600 m 'riding' on winds ahead of cold fronts (Showers & Sappington 1992) although this species only has an airspeed of 9-13 km/h (Jia & Cao 1992).

DISCUSSION. Insect flight speed has been found to be affected by the following insect characteristics:

1. Mass (Dudley & Srygley 1994; Dudley 1997);
2. Size (Larkin 1991; Fischer & Kutsch 2000);
3. Age (Karlsson 1994; Banjaree 1988);
4. Gender (Rogowitz & Chappell 2000; Willmott & Ellington 1997; Lingren & al. 1995);
5. Amount of feeding (David 1978; Fadamiro & Wyatt 1995);
6. Water content (Danks 2000; Lehmann & al. 2000);
7. Activity type (David & Hardie 1988; Quero & al. 2001; May 1999);

Also, insect flight speed is affected by the following environmental factors:

1. Temperature (Gilchrist & al. 1997; Isard & al. 2000; Fitzgerald & Underwood 2000; Elliott & al. 2000);
2. Humidity (Gunn 1937; Pielou & Gunn 1940; Dorner & Mulla 1962);
3. Solar radiation (Rudinsky & Vite 1956; Ostrand & al. 2000; Carde & Knowls 2000; Vicens & Bosch 2000; Lloyd 2000; Schneider 1965);
4. Wind (Aluja & al. 1993; Hardie & Young 1997);
5. Oxygen levels (Ellington & al. 1990; Joos & al. 1997; Harrison & Lighton 1998; Dekker & al. 2001);
6. Habitat isolation (Denno & al. 2001);
7. Ascent angle (Kutsch & al. 1999);

Given the wide variety of possible effects on insect flight speed, studies of large numbers of insects from a single species have found that the distribution of speeds approximately follows a normal distribution (Tuxhorn & McShaffrey 1998; Nachtigall 2001; Dean & Drake 2002). Most insects have airspeeds of less than 21 km/h. All currently available measured insect speeds are listed in **Table 1**. It should be borne in mind, however, that many of the early measurements were made using inaccurate methods and may reflect only a single speed measurement.

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Table 1. Published insect speeds in ms^{-1}, errors in brackets; 1 m/s = 3.6 km/h ≅ 2.2 mph. **N**, number. **R**, range: A, average R; X, max R; N, min R. **T**, type: A, air-speed; G, ground-speed. This was difficult to determine especially for some early studies; readers are advised to check original reference. **M**, method: WT, wind tunnel; FF, free flying; FC, flight chamber; T, tethered; M, mill.

o	f	sp	m/s	N/R/T/M	reference
Coleoptera	Bostrichidae	*Prostephanus truncatus*	0.2	/ A / A / WT	Fadamiro 1996
		Prostephanus truncatus 20m/s wind	0.07 (0.01)	15 / A / A / WT	Fadamiro 1996b
		Prostephanus truncatus 25m/s wind	0.08 (0.01)	15 / A / A / WT	Fadamiro 1996b
		Prostephanus truncatus 32m/s wind	0.1 (0.01)	9 / A / A / WT	Fadamiro 1996b
	Cerambycidae	*Phoracantha semipunctata* in plume	0.66 (0.21)	32 / A / A / WT	Barata & Araujo 2001
		P. semipunctata outside plume	0.52 (0.14)	40 / A / A / WT	Barata & Araujo 2001
	Cicindelidae	*Cicindela hybrida*	0.6	/ A / A / FF	Nachtigall 1996
			3	/ X / A / FF	Nachtigall 1996b
	Dytiscidae	unknown	1.97	/ ? / G / ?	Lane 1941
	Lampyridae	*Photinus collustrans*	1.2	123 / A / G / FF	Lloyd 2000
			0.14-2.1	123 / A / G / FF	Lloyd 2000
	Nitidulidae	*Carpophilus hemipterus* f	0.44	/ A / A / T	Wu & Laughlin 1994
		Carpophilus hemipterus m	0.33	/ A / A / T	Wu & Laughlin 1994
	Scolytidae	*Dendroctonus pseudotsugae*	0.34-0.72	/ A / A / T	Rudinsky & Vite 1956
		Ips typographus	0.15	/ N / G / FF	Zolubas & Skirkevicius 1992
		various	2	/ X / G / FF	Byers 1996
Diptera	Calliphoridae	*Calliphora vicina*	1.2	/ X / A / FC	Schilstra & Hateren 1999a;b
			1	/ X / A / FC	Schilstra 1999
			1.2	/ X / A / FC	Schilstra 1999
		Phaenicia sericata	1.45-2.05	/ A / A / FC	Yurkiewicz & Smyth 1966
	Cecidomyiidae	*Mayetiola destructor*	7	/ A / G / FC	Lewis & Taylor 1967
	Chloropidae	*Hister merdarius*	1.92	/ A / G / FC	Lewis & Taylor 1967
		Oscinella frit	0.76	/ A / G / FC	Lewis & Taylor 1967
	Culicidae	*Aedes aegypti* female	0.18	/ A / A / M	Briegel & al. 2001
		Aedes aegypti poor	0.13	/ A / A / M	Briegel & al. 2001
		Aedes aegypti fast	0.28	/ A / A / M	Briegel & al. 2001
			0.33	/ X / A / M	Briegel & al. 2001
		Aedes aegypti	1.5	/ A / G / FF	Kennedy 1939
			0.08-0.33	/ A / A / FF	Kennedy 1939
		Aedes flavescens	1.1	3 / A / A / M	Hocking 1953
		Aedes nearcticus	1.0	10 / A / A / M	Hocking 1953
		Anopheles fuliginosus	0.08-0.33	/ A / A / FC	Bentley 1914
		Anopheles melas	1.2	/ X / G / FF	Snow 1980
		Culex tarsalis	2.15	/ A / G / FF	Bailey & al. 1965
		Culex thalassius	1.2	/ A / G / FF	Snow 1980
		unknown	1.39	/ ? / G / ?	Lane 1941
	Drosophilidae	*Drosophila hydei* fed	0.3 (0.085)	/ A / G / WT	David 1978
		Drosophila hydei starved	0.46 (0.11)	/ A / G / WT	David 1978
			0.5	/ A / A	Lehmann 2001
		Drosophila virilis	2	/ A / A / WT	Vogel 1967
			2	/ A / A / T	Vogel 1966
		Drosophila melanogaster	1.37	/ A / G / FC	Lewis & Taylor 1967
			0.70 (0.01)	113 / A / A / WT	Marden & al. 1997
			0.64 (0.02)	88 / A / A / WT	Marden & al. 1997
			0.46 (0.02)	99 / A / A / WT	Marden & al. 1999
			0.52 (0.01)	144 / A / A / WT	Marden & al. 2000
		Drosophila sp.	1.4	26 / A / A / M	Hocking 1953
	Empididae	*Rhamphomyia* sp.	3.05	/ A / G / FC	Lewis & Taylor 1967
	Equidae	*Hippelates collusor*	0.9	/ A / A / WT	Dorner & Mulla 1962
	Fanniidae	*Fannia canicularis*	0.4-0.8	/ A / A / FC	Nachtigall 1999
			0.5-0.65	/ A / A / FC	Nachtigall 1999b
	Glossinidae	*Glossina morsitans morsitans*	1.8	/ A / G / WT	Colvin & al. 1989
			4.8 (0.1)	/ A / G / FF	Brady 1991
	Muscidae	*Musca domestica*	2.23	/ ? / G / ?	Lane 1941
			3.05	/ A / G / FC	Lewis & Taylor 1967
			1.8	/ A / G / FF	McKeown 1944
		Stomoxys calcitrans	0.33	/ A / A / FF	Bailey & al. 1973
			0.55	/ A / A / FF	Eddy & al. 1962
		Musca sp.	0.28 (0.032)	8 / A / G / FF	Golding & al. 2001
	Oestridae	*Tracheomyia macropi*	11.17	/ X / G / ?	Lane 1941
	Psychodidae	*Phlebotomus ariasi*	0.65-0.70	/ X / A / WT	Killick-Kendrick & al. 1986
	Schizophora	Calliphoridae	2.68	/ ? / G / ?	Lane 1941
	Simuliidae	*Simulium venustum*	1.5	16 / A / A / M	Hocking 1953
			2.4	3 / A / A / M	Hocking 1953
	Syrphidae	*Eristalis tenax*	0.19 (0.03)	8 / A / G / FF	Golding & al. 2001
		Syritta pipiens	1.4-4.6	/ A / A / FC	Collet & Land 1975
		Syrphus ribesii	0.19 (0.01)	9 / A / G / FF	Golding & al. 2001
	Tabanidae	*Hybomitra hinei*	40.3	/ X / G / FF	Kunzig 2000
		Tabanidae unspecified	18	/ N / G / FF	Schwardt 1932
		Tabanus affinis	2.3	71 / A / A / T&M	Hocking 1953
			6.5	/ A / G / FC	Lewis & Taylor 1967
			12.5	/ X / G / FF	Twinn & al. 1948
		Tabanus bovinus	14	/ X / A / FF	Demoll 1918
			4	/ A / A / T	Magnan 1934
		Tabanus septentrionalis	2.4	10 / A / A / M	Hocking 1953
			6.5	/ A / G / FC	Lewis & Taylor 1967
		various	13.4	/ ? / G / ?	Lane 1941
		various	12.5	/ A / G / FF	McKeown 1944
Ephemeroptera	unknown	unknown	0.5	/ ? / G / ?	Lane 1941
Hemiptera	Aphididae	*Aphis fabae*	0.76	/ A / G / FC	Lewis & Taylor 1967
			0.13-0.28	/ A / A / WT	Kennedy & Thomas 1974
		various	0.54-0.67	/ A / A / WT	Haine 1955
		various	3.15 (0.19)	/ A / A / WT	Hardie & Young 1997
		various	2.76 (0.19)	/ A / A / WT	Hardie & Young 1997
	Cicadellidae	*Circulifer tenellus*	0.27-0.85	/ A / A / WT	Lawson & al. 1951
	Miridae	*Lygus lineolaris*	0.45	/ A / A / M	Stewart & Gaylor 1994
	various	various	3	/ A / G / FF	Nilakhe & Buainain 1988
Homoptera	Aleyrodidae	*Aleyrodes* sp.	0.46	/ A / G / FC	Lewis & Taylor 1967
		Bemisia tabaci	0.04-0.16	/ A / / FC	Byrne 1999
			0.16-0.23	30 / A / G / WT	Isaacs & al. 1999
			0.16-0.49	30 / A / A / WT	Isaacs & al. 1999
	Aphididae	*Drepanosiphum platanoidis*	0.91	/ A / G / FC	Lewis & Taylor 1967
		Jacksonia papillata	0.37	/ A / G / FC	Lewis & Taylor 1967
		Macrosiphum pisum	0.55	/ A / G / FC	Lewis & Taylor 1967
		Myzus persicae	0.3-0.75	/ A / A / FF	Kennedy & Thomas 1974
		Phorodon humili	7	/ A / A / FC	Hardie & al. 1996
	Cicadellidae	*Typhlocyba sp.*	1.16	/ A / G / FC	Lewis & Taylor 1967
	Delphacidae	*Nilaparvata lugens*	22.4	/ X / A / M	Chen & al. 1984
Hymenoptera	Apidae	unknown	3-15.7	100 / A / G / FF	Osborne & al. 1999
		unknown	4.9	/ ? / G / ?	Lane 1941
		Apis mellifera	2.6	16 / A / A / M	Hocking 1953
			4.14	/ A / G / FC	Lewis & Taylor 1967
			3.3-5.1	/ A / A / T	Nachtigall & al. 1995
			0.19 (0.025)	11 / A / G / FF	Golding & al. 2001
			2.2-3.6	/ A / G / FF	McKeown 1944
		Apis mellifera drone	1.8	/ A / G / FF	Park 1923
			1.8	/ A / A / FF	Schnell-larsen 1934
		A. mellifera worker empty	8.3	/ A / A / T	Hansson 1945
			4.9	/ ? / G / ?	Lane 1941
			5.6	/ A / G / HR	Capaldi & al. 2000
			3.6	/ A / G / HR	Capaldi & al. 2000
		A. mellifera worker full	7.2	/ A / A / T	Hansson 1945
			2.4	/ ? / G / ?	Lane 1941
		Apis mellifera worker	5.56	/ A / G / FF	Beutler 1950
			3.75	/ A / G / FF	Demoll 1918
			2.5	/ A / A / T	Magnan 1934
			6.12	/ A / G / FF	Park 1923
			6	/ A / A / T	Von Frisch 1927
			14	/ A / G / FF	Wenner 1963
	Ichneumonidae	*Ichneumon* sp.	1.67	/ A / G / FC	Lewis & Taylor 1967
	Vespidae	*Vespa crabro*	5.9	/ ? / G / ?	Lane 1941
	unknown	unknown	5.4	/ ? / G / ?	Lane 1941
Lepidoptera	Hesperiidae	*Chioides catillus*	3.6 (0.2)	2 / A / A / FF	Srygley 2001
		Dryas julia	3.1 (0.6)	6 / A / A / FF	Srygley 2001
		unknown	5.1	1 / A / A / FF	Srygley 2001
		Urbanus simplicius	3.5	1 / A / A / FF	Srygley 2001
		unknown	5.3	1 / A / A / FF	Srygley 2001
		Calpodes ethlius	7.5	2 / A / A / FF	Dudley & Srygley 1994
		Cyclosemia anastomosis	5.7	1 / A / A / FF	Dudley & Srygley 1994
		Heliopetes sp.	4.1	2 / A / A / FF	Dudley & Srygley 1994
		Typhedanus undulatus	7.4	1 / A / A / FF	Dudley & Srygley 1994
		Urbanus proteus	4.5	98 / A / G / FF	Balciunas & Knopf 1977
			6.1	98 / A / A / FF	Balciunas & Knopf 1977
	Libytheidae	*Libythia bachmani*	4.47-6.7	/ A / G / FF	Parman 1926
	Lycaenidae	*Lycaena phlaeas*	2.86	/ A / G / FC	Lewis & Taylor 1967
	Lymantriidae	*Lymantria dispar*	4.5	24 / A / G / WT	Kuenen & Carde 1993
			4.7	24 / A / G / WT	Kuenen & Carde 1993
			5.3	24 / A / G / WT	Kuenen & Carde 1993
			0.64 (0.18)	20 / A / A / WT	Carde & Knols 2000
			0.53 (0.06)	20 / A / A / WT	Carde & Knols 2000
			0.48 (0.06)	20 / A / A / WT	Carde & Knols 2000
	Noctuidae	*Agrochola lychnidis*	4.35	/ A / G / FC	Lewis & Taylor 1967
		Agrotis ipsilon	26.8-31.3	/ A / G / T	Showers & Sappington 1992
		Schistocerca gregaria	3.5	47 / A / G / FF	Lingren & al. 1995
			7.9 (2.3)	10 / A / A / WT	Quero & al. 2001
		S. gregaria casting	5.7 (2.4)	10 / A / A / WT	Quero & al. 2001
	Noctuidae-Sphingidae	unknown	4.47-6.7	/ A / A / FC	Callahan 1965
	Nymphalidae	*Adelpha iphiclus*	3.6	1 / A / A / FF	Dudley & Srygley 1994
		Agranlis vanillae	3.6	1 / A / A / FF	Srygley 2001
			2.8	2 / A / G / FF	Correale & Crocker 1976
			5	1 / A / A / FF	Dudley & Srygley 1994
		Anartia fatima	3.6	7 / A / A / FF	Dudley & Srygley 1994
		Anartia fatima females	2.6 (0.2)	5 / A / A / FF	Srygley & Kingsolver 2000
		Anartia fatima males	2.5 (0.4)	27 / A / A / FF	Srygley & Kingsolver 2000
		Archaeoprepona demophon	7	1 / A / A / FF	Dudley & Srygley 1994
		Cissia sp.	2.2	1 / A / A / FF	Dudley & Srygley 1994
Lepidoptera (continued)	Nymphalidae (continued)	*Danaus eresimus*	3.9	2 / A / A / FF	Dudley & Srygley 1994
			3	2 / A / A / FF	Srygley 2001
		Danaus gilippus	3.6	4 / A / A / FF	Dudley & Srygley 1994
		Danaus plexippus	4.9	/ A / G / FF	Urquhart 1960
			8.9-11.2	/ A / G / FF	Urquhart 1960
		D. plexippus parasite infected	0.9622	20 / A / A / M	Yueh 1999
			0.9345	20 / A / A / M	Yueh 1999
		Dione juno	3.8	3 / A / A / FF	Dudley & Srygley 1994
		Dryadula phaetusa	3.7	8 / A / A / FF	Dudley & Srygley 1994
		Dryas iulia	4.5	5 / A / A / FF	Dudley & Srygley 1994
		Eueides lybia	2.3	1 / A / A / FF	Dudley & Srygley 1994
		Eunica alcmena	3	1 / A / A / FF	Dudley & Srygley 1994
		Eunica sp.	4.8	1 / A / A / FF	Dudley & Srygley 1994
		Hamadryas feronia	4.4	3 / A / A / FF	Dudley & Srygley 1994
		Hamadryas ipthime	4.5	1 / A / A / FF	Dudley & Srygley 1994
		Heliconius charitonius	2.3	1 / A / A / FF	Dudley & Srygley 1994
		Heliconius eleuchia	1.9	1 / A / A / FF	Dudley & Srygley 1994
			3.3	1 / A / A / FF	Dudley & Srygley 1994
		Heliconius erato	1.7	3 / A / A / FF	Dudley & Srygley 1994
		Heliconius hecale	2.1	7 / A / A / FF	Dudley & Srygley 1994
		Heliconius melpomene	2.6	1 / A / A / FF	Dudley & Srygley 1994
		Heliconius sapho	2	1 / A / A / FF	Dudley & Srygley 1994
		Heliconius sara	2.7	7 / A / A / FF	Dudley & Srygley 1994
		Historis acheronta	6.5	11 / A / A / FF	Dudley & Srygley 1994
			4.3	1 / A / A / FF	Srygley 2001
		Junonia evarete	2.3	2 / A / A / FF	Dudley & Srygley 1994
			3.8	1 / A / A / FF	Srygley 2001
		Laparus doris	2.7	1 / A / A / FF	Dudley & Srygley 1994
		Marpesia chiron	4.6	23 / A / A / FF	Dudley & Srygley 1994
		Marpesia petreus	4.9	13 / A / A / FF	Dudley & Srygley 1994
		Mechanitis lysimnia	0.7	1 / A / A / FF	Dudley & Srygley 1994
		Mechanitis polymnia	2.5	1 / A / A / FF	Dudley & Srygley 1994
		Melinaea parallelis	2.5	2 / A / A / FF	Dudley & Srygley 1994
		Melinaea scylax	3.5	1 / A / A / FF	Dudley & Srygley 1994
		Morpho amathonte	2.6	1 / A / A / FF	Dudley & Srygley 1994
		Olyras insignis	2.5	1 / A / A / FF	Dudley & Srygley 1994
		Philaethria dido	2.5	5 / A / A / FF	Dudley & Srygley 1994
		Precis coenia	2.8	10 / A / G / FF	Balciunas & Knopf 1977
			5.3	10 / A / A / FF	Balciunas & Knopf 1977
		Precis lavinae	2.7	7 / A / G / FF	Correale & Crocker 1976
		Pyrrhogyra crameir	2.2	1 / A / A / FF	Dudley & Srygley 1994
		Pyrrhogyra neaerea	1.8	1 / A / A / FF	Dudley & Srygley 1994
		Pyrrhogyra otolais	3.6	1 / A / A / FF	Dudley & Srygley 1994
		Siproeta stelenes	3.7	2 / A / A / FF	Dudley & Srygley 1994
		Vanessa atalanta	3.9	/ ? / G / ?	Lane 1941
		Vanessa cardui	2.2-6.1	/ A / G / FF	Abbott 1951
			4.9-8	/ A / G / FF	Williams 1930
	Papilionidae	*Battus polydamas*	5.8	3 / A / A / FF	Dudley & Srygley 1994
		Eurytides dolicaon	4.5	1 / A / A / FF	Dudley & Srygley 1994
		Eurytides ilus	4.5	3 / A / A / FF	Dudley & Srygley 1994
		Eurytides protesilaus	5.3	3 / A / A / FF	Dudley & Srygley 1994
		Papilio anchisiades	4.6	2 / A / A / FF	Dudley & Srygley 1994
		Papilio thoas	4.6	6 / A / A / FF	Dudley & Srygley 1994
		Parides arcas	2.9	3 / A / A / FF	Dudley & Srygley 1994
		Parides sesostris	3.1	2 / A / A / FF	Dudley & Srygley 1994
	Pieridae	*Anteos maerula*	5.4	4 / A / A / FF	Srygley 2001
		Aphrissa boisduvallii	5.1	29 / A / A / FF	Dudley & Srygley 1994
		Aphrissa statira	5.3	36 / A / A / FF	Dudley & Srygley 1994
			4	3 / A / A / FF	Srygley 2001
		Appias drusilla	4	5 / A / A / FF	Dudley & Srygley 1994
			4	1 / A / A / FF	Srygley 2001
		Ascia monuste	3.1-4.5	/ A / G / FF	Nielsen 1961
			3.4	14 / A / A / FF	Srygley 2001
		Colia philodice	1.3-2	/ A / G / FF	Leigh & Smith 1959
		Colias eurytheme	2.45 (0.15)	9 / A / G / FF	Srygley & Kingsolver 1998
		Eurema proterpia	2.9	1 / A / A / FF	Dudley & Srygley 1994
		Itaballia demophile	2.7	3 / A / A / FF	Dudley & Srygley 1994
		Itaballia pandosia	2.2	2 / A / A / FF	Dudley & Srygley 1994
		Melete florinda	1.8	1 / A / A / FF	Dudley & Srygley 1994
		Phoebis agarithe	4.1	3 / A / A / FF	Srygley 2001
		Phoebis argante	4.9	18 / A / A / FF	Dudley & Srygley 1994
		Phoebis philea	4.9	6 / A / A / FF	Dudley & Srygley 1994
		Phoebis sennae	3.61	66 / A / G / FF	Correale & Crocker 1976
			4.1	45 / A / G / FF	Balciunas & Knopf 1977
			5.1	45 / A / A / FF	Balciunas & Knopf 1977
			6.2	3 / A / A / FF	Dudley & Srygley 1994
			4	25 / A / A / FF	Srygley 2001
		Phoebis triste	4.8	2 / A / A / FF	Dudley & Srygley 1994
Lepidoptera (continued)	Pieridae (continued)	*Pieris rapae*	2.35 (0.28)	9 / A / G / FF	Srygley & Kingsolver 1998
		Pontia occidentalis	2.1 (0.43)	9 / A / G / FF	Srygley & Kingsolver 1998
	Sphingidae	*Manduca sexta*	5	/ X / A / FC	Willmott & Ellington 1997/97b
		M. sexta towards light	0.4 (0.03)	61 / A / A / FC	Spencer & al. 1997
		M. sexta away from light	0.29 (0.02)	61 / A / A / FC	Spencer & al. 1997
			0.57	38 / A / A / FC	Stevenson & al. 1995
			1.02	37 / A / A / FC	Stevenson & al. 1995
			1.58	62 / A / A / FC	Stevenson & al. 1995
			3.38	93 / A / A / FC	Stevenson & al. 1995
			22.3	/ ? / G / ?	Lane 1941
			13.4	/ X / G / FF	McKeown 1944
	Tortricidae	*Grapholita molesta*	0.80 (0.27)	/ A / A / WT	Baker & al. 1984
	Uraniidae	*Urania fulgens* female	3.74 (0.26)	14 / A / A / FF	DeVries & Dudley 1990
		Urania fulgens male	4.08 (0.21)	13 / A / A / FF	DeVries & Dudley 1990
Mantodea	Mantidae	unknown	1.9-3.8	/ A / A / FC	May 1999
Neuroptera	Chrysopidae	*Chrysopa carnea*	0.76	/ A / G / FC	Lewis & Taylor 1967
Odonata	Aeshnidae	*Austrophlebia costalis*	25-27	/ ? / G / ?	Lane 1941
	Libellulidae	*Sympetrum sanguineum*	2-5	/ A / A / FC	Wakeling & Ellington 1997
		Libellula luctuosa	1.86 (0.58)	1805 / A / G / FF	Tuxhorn & McShaffrey 1998
			0.41-4.44	1805 / R / G / FF	Tuxhorn & McShaffrey 1998
		Libellula lydia	2.12 (0.62)	4411 / A / G / FF	Tuxhorn & McShaffrey 1998
			0.68-6.64	4411 / R / G / FF	Tuxhorn & McShaffrey 1998
		Pachydiplax longipennis	1.54 (0.55)	59 / A / G / FF	Tuxhorn & McShaffrey 1998
			0.53-2.89	59 / R / G / FF	Tuxhorn & McShaffrey 1998
		Tramea lacerata	2.61 (0.85)	93 / A / G / FF	Tuxhorn & McShaffrey 1998
			1.59-6.88	93 / R / G / FF	Tuxhorn & McShaffrey 1998
Orthoptera	Acrididae	*Locusta migratora*	3.6 (0.2)	/ A / A / FC	Kutsch & Fuchs 2000
			4.6	/ A / G / FF	Baker & al. 1981
			4.6	/ A / G / FF	Gewecke
		Schistocerca gregaria	4.1	77 / A / A / FC	Fischer & Ebert 1999
			4.48	37 / A / A / FF	Fischer & Kutsch 1999
			2.5	/ N / A / FP	Katz & Gosline 1993
			4.5-5	/ A / A / T	Riley & al. 1988
			0.89	/ A / A / FF	Sayer 1965
			5.36	/ A / G / FF	Sayer 1965
			3.1	16 / A / A / FF	Waloff 1972
			4.3	17 / A / A / FF	Waloff 1972
			5.3	/ A / A / FF	Waloff 1972
			5.0	/ A / A / FF	Waloff 1972
			5.0	12 / A / A / FF	Waloff 1972
			6.1	17 / A / A / FF	Waloff 1972
			5.1	11 / A / A / FF	Waloff 1972
			8.1	17 / A / A / FF	Waloff 1972
			6.1	21 / A / A / FF	Waloff 1972
			6.3	/ A / A / FF	Waloff 1972
			7.8	16 / A / A / FF	Waloff 1972
			6.2	23 / A / A / FF	Waloff 1972
			9.3	12 / A / A / FF	Waloff 1972
			4.9-8	/ A / G / FF	Waloff & Rainey 1951
			3.5	/ A / A / FC	Weis-Fogh 1976
			3.0-4.5	158 / A / A / FC	Weis-Fogh 1956
			3.5-5.5	/ A / G / FF	Weis-Fogh 1956
			2.99	/ A / A / FF	Weis-Fogh 1952
			2.3-3.5	/ A / A / FC	Weis-Fogh 1952
			0.5-7	/ R / A / WT	Zarnack & Wortmann 1989
			3	/ A / A / WT	Zarnack & Wortmann 1989
			3.7	/ A / A / FC	Kutsch & al. 1999
Plecoptera	Austroperlidae	*Acruroperla atra*	2.24	/ A / G / FF	Marden & al. 2000
		Tasmoperla thalia	1.56	3 / A / G / FF	Marden & al. 2000
	Caopniidae	various	3.2 (0.29)	/ A / G / FF	Marden & al. 2000
	Capniidae	*Paracapnia angulata*	2.4	1 / A / G / FF	Kramer & Marden 1997
	Chloroperlidae	*Swelta onkos*	2.9	1 / A / G / FF	Kramer & Marden 1997
		various	6.3 (1.5)	/ A / G / FF	Marden & al. 2000
	Gripopterygidae	various	4.4 (1.66)	/ A / G / FF	Marden & al. 2000
	Leuctridae	various	4.2 (0.19)	/ A / G / FF	Marden & al. 2000
		Leuctra hippopus	3.7 (0.7)	28 / A / G / FF	Kramer & Marden 1997
		Leuctra sibleyi	3.4 (0.54)	4 / A / G / FF	Kramer & Marden 1997
	Nemouridae	*Amphinemura nigritta*	2.3 (0.66)	7 / A / G / FF	Kramer & Marden 1997
		Ostrocerca spp.	1.6 (0.42)	4 / A / G / FF	Kramer & Marden 1997
		Paranemoura perfecta	2.6 (0.54)	8 / A / G / FF	Kramer & Marden 1997
		various	3.2 (0.29)	/ A / G / FF	Marden & al. 2000
	Notonemouridae	various	6.3 (1.5)	/ A / G / FF	Marden & al. 2000
	Perlodidae	*Isoperla* sp.	2.4	1 / A / G / FF	Kramer & Marden 1997
	Perlodidae	various	6.3 (1.5)	/ A / G / FF	Marden & al. 2000
	Taeniopterygidae	various	3.2 (0.29)	/ A / G / FF	Marden & al. 2000
		Taeniopteryx burski	2.3 (0.36)	5 / A / G / FF	Kramer & Marden 1997
			2.9 (0.9)	5 / A / G / FF	Marden & Kramer 1994
Psocoptera	Stenopsocidae	*Stenopsocus immaculatus*	0.85	/ A / G / FC	Lewis & Taylor 1967

Chapter 2. Greatest host range

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ABSTRACT. The fall webworm, *Hyphantria cunea* (Drury 1773) (Lepidoptera Arctiidae), probably has the widest host range for any insect. The larvae feed on an estimated 636 species of plants worldwide. This number appears to be higher than the records for gypsy moth and for japanese beetle. The gypsy moth seems to be limited by secondary plant metabolites but feeds on plants containing tannins. This factor does not appear to restrict the fall webworm.

INTRODUCTION. Polyphagy is well known in the animal kingdom, and though many insects are specialists, some exploit the generalist way of life. Being a generalist has at least 2 advantages in terms of survival:

1. A ♀ may have an easier time finding a suitable host for oviposition using chemical cues if more hosts are acceptable;
2. An insect that finds a suitable food source easily can spend more time eating and growing and less time searching.

Insect consumers can be grouped into four types: predators and parasitoids, parasites, detritivores, and herbivores. Each consumer has some potential for being a generalist in its category. Herbivores are apparently the best group to search for host records. Predators and parasitoids contain many specialists, but also some generalists which have poorly studied host preferences. Few insects are themselves parasites but they vector diseases. Detritus feeders feed on dead or organic matter but these are hard to classify as to specific host. Also, information on these is limited. Herbivores are more studied relative to their hosts due to the high number of agricultural pests. Also, a plant species is a well documented single unit. Thus I consider herbivores as the insects most likely to have the greatest host range. Defining what makes a host is difficult. Herbivores may be tested against plants to show willingness to feed, ability to feed, ability to develop fully, or the ability to develop partially. Some insects need more than one host to complete full development. In this chapter observed feeding will constitute a host record regardless of the effect on development of the insect and whether or not it was a lab or field observation. One host will equal one species of plant fed upon.

METHODS. Professors and graduate students were asked to nominate candidates. Standard library techniques were used to investigate candidates, but the best results came from literature volunteered by a professor.

RESULTS. Promising candidates were the gypsy moth, *Lymantria dispar* (Linnaeus 1758), and the japanese beetle *Popillia japonica* Newman 1838, but the most polyphagous insect appears to be the fall webworm moth, *Hyphantria cunea* (Drury 1773) (Lepidoptera Arctiidae). A native of North America, *H. cunea* had spread to Hungary by 1940, to Japan by 1947 and soon after into Korea (Warren & Tadic 1970). It is now a resident of most of the holarctic region. The number of plant species that are hosts for the fall webworm is staggering. An early report by Doane 1936 says that it "feeds on almost any tree except conifers... when almost full grown they scatter, feeding upon anything green." It has been collected from over 200 host species in the United States (Coulson & Witter 1984). In Europe, Warren & Tadic 1970 noted that it feeds on 219 species with 103 hosts in Hungary, 85 hosts in Yugoslavia, as well as 48 species in the former Soviet Union. In Japan more than 300 species of plants are hosts including trees, shrubs, weeds, and vegetables (Masaki & Umeya 1977), and in Korea 65 hosts are recorded (Woo 1961). The total number of observed hosts is 636 species (Warren & Tadic 1970).

DISCUSSION. It is unlikely that 636 is the exact number of hosts as this is based on different reports from different parts of the world. Warren and Tadic 1970 compiled the data of others and stated that their list is not considered final or complete and no distinction was made between food preferences for the black-headed and red-headed races. The Japanese beetle, *Popillia japonica*, was dismissed as a candidate for the most polyphagous because Fleming 1972 stated that it feeds on just under 300 species. The gypsy moth, *Lymantria dispar*, the other close candidate, is known for its damage in the United States and Canada to a wide number of hosts including some conifers. Miller & Hanson 1989 combined previous studies on host preference by *L. dispar* and reported that a total of 658 species had been tested and/or observed for suitability as hosts. The tests revealed that gypsy moth rejected many plants due to the presence of secondary plant metabolites, apparently toxic to it. It generally accepted plants containing tannins but lacking alkaloids, terpenoids, and glucosinolates. These plant compounds may partly restrict the host range of gypsy moth as compared to fall webworm. Some arctiid moths are known to sequester highly toxic chemical (Krasnoff & Dussourd 1989). *H. cunea* is by no means a specialist on poisonous plants, but considering its relationship to other Arctiidae, it may have mechanisms for handling plant toxins that the gypsy moth just cannot keep up with.

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Chapter 3. Longest diapause among insects

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ABSTRACT. The yucca moth *Prodoxus y-inversus* Riley 1892 (Lepidoptera Prodoxidae) has the longest reported diapause. Structures of *Yucca baccata* (Agavaceae) containing prepupae of this species were collected in Nevada, and successful emergence of adults was observed 19 years later, under artificial conditions.

INTRODUCTION. Prolonged periods of dormancy are well-known among invertebrates. Brusca & Brusca 1990 reported that a dried museum specimen of moss yielded living tardigrades, a small phylum that appears to be closely tied to the annelid-arthropod line, when moistened after 120 years on the shelf. Some insects, such as the golden buprestid *Buprestis aurulenta* Linnaeus 1767, have an extended larval life. According to Linsley 1943, the larvae usually require from 1 to 3 years to complete their development, but Huguenin 1915 reported delayed emergence of specimens from structural timbers as long as 26 years after infestation. In a critical review, Smith 1962 presented 32 additional cases in British Columbia, with 11 of the cases being between 26 and 51 years. However, other cases of delayed emergence in insects may reflect diapause rather than prolonged larval development. Diapause, as defined by Tauber & al. 1986, is a neurohormonally mediated, dynamic state of low activity that occurs during a genetically determined stage(s) of metamorphosis, usually in response to environmental stimuli that precede unfavorable conditions. The objective of this chapter is to determine the longest diapause recorded for insects.

METHODS. AGRICOLA, Biological Abstracts, CAB Abstracts and Life Science Collection were searched from year 1986 to the present. Secondary literature, mainly textbooks in entomology and ecology, also proved useful.

RESULTS. Diapause lasting more than a year, also called "prolonged" or "extended" diapause, is known in many species of insects (Danks 1987). Sunose 1983 summarized cases of prolonged diapause and tabulated 64 insect species that present this phenomenon. In fact, prolonged diapause seems to be more common than one could imagine. Powell 1987 referred to approximately 90 species of Lepidoptera, in 10 superfamilies, that diapause for over one year. Barnes 1952, studying wheat-blossom midges (Diptera Cecidomyiidae), reported the emergence of *Contarinia tritici* Kirby 1798 after the larvae had been in soil up to 3 years, whereas larvae of *Sitodiplosis mosellana* (Géhin 1857) spent as many as 12 winters in the soil before emergence of the adults. However, Powell 1989 reported the emergence of adults of *Prodoxus y-inversus* Riley 1892, after prepupae spent 19 years in diapause.

DISCUSSION. Prolonged diapause may have appreciable adaptive value in habitats where resources are available only briefly each season and/or undergo erratic fluctuations in abundance (Sunose 1978). The prolonged diapause for *P. y-inversus* was observed under unnatural environmental conditions. The prepupae of this prodoxid insect were housed in sealed cardboard boxes, and then exposed to variable temperature and humidity regimes, subdued light, and without direct moisture from rainfall (Powell 1987). Powell 1989 pointed out that this example indicates a potential for successful dormancy of insects adapted to extremely arid climates for much greater periods than previously supposed. The physiological mechanisms of prolonged diapause are poorly understood (Tauber & al. 1986). Powell 1987 suggested that particular token stimuli needed to promote the late phases of diapause maintenance and diapause termination are not received. Hence, when thermal or other thresholds are reached that would have resulted in post diapause development, the diapause maintenance period continues. According to Powell 1984, the study of two prodoxid species, *Prodoxus aenescens* Riley 1881 and *P. cinereus* Riley 1881, indicated that temperature is the key factor in diapause development. Powell 1989 pointed out that exposure to temperatures that are colder than preceding winters are likely to interrupt the diapause maintenance in *P. y-inversus*.

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Chapter 4. Most tolerant of cold

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ABSTRACT. In laboratory tests, Hinton 1960 found that dehydrated larvae of the African chironomid *Polypedilum vanderplanki* Hinton 1951 (Diptera) could survive submersion in liquid helium (-270°C). This phenomenon seems related to its ability to tolerate extreme desiccation.

INTRODUCTION. The aim of this chapter is to identify the insect species most tolerant to cold. "Most tolerant to cold" is here taken to mean ability to survive the lowest temperature. The search was an open ended one, such that the results could come from individuals studied under natural or laboratory conditions.

METHODS. I first searched the secondary literature, such as general ecology, entomology and physiology textbooks. All author's names associated with work on cold tolerance were then subjected to a literature search. AGRICOLA 1970-93 was also searched for reference to papers on cold tolerance in insects.

RESULTS. Hinton 1960 found that the dehydrated larvae of the African chironomid *Polypedilum vanderplanki* were able to withstand exposure to liquid helium (-270°C) for up to 5 min. with a 100% survival rate.

DISCUSSION. Surprisingly, the insect able to survive the lowest temperature is not found in polar regions, but in tropical West Africa. *Polypedilum vanderplanki* inhabits shallow pools which are subjected to repeated dehydration, and accordingly *P. vanderplanki* has evolved the capacity to tolerate severe desiccation in an anhydrobiotic state. It seems likely that it is due to this phenomenon that the insect is able to survive extreme temperatures. Hinton 1960 placed the larvae directly in liquid helium from room temperature. Only larvae that had been desiccated to a water content of 8% survived freezing at -270°C and subsequently metamorphosed, after warming and rehydration. When frozen fully hydrated, the larvae failed to recover, apparently because of damage to the fat body (Leader 1962). In contrast, elimination of body water in freezing-tolerant nonanhydrobiotic species can often be detrimental to the chances of survival at low temperatures (Salt 1961). The lowest temperature survived by any insect in a nonanhydrobiotic state is -196°C by the prepupae of the sawfly *Trichiocampus populi* Okamoto 1912. Tanno 1968 employed a 3-step procedure consisting of freezing the prepupae at -20°C, transferring them to -5°C for several hours and then slowly cooling them to -30°C before placing them in liquid nitrogen. After slow thawing, 75% survived and emerged as adults. It is possible that *T. populi* could also survive -270°C in liquid helium, but it has never been tested. Asahina & Tanno 1964 attributed this freeze tolerance ability to the presence of very high levels of the sugar trehalose. It is generally believed that survival of freezing occurs only if the site of ice formation is restricted to the extracellular space (Mazur 1984). This is also assumed to be true in the above two cases, although intracellular freeze tolerance has been reported by Salt 1959 in the fat body cells of the goldenrod gall fly *Eurosta solidaginis* (Fitch 1855). In the case of *P. vanderplanki*, it is clear that tolerance of freezing is in no way adaptive, since it is never subjected to sub-zero temperatures in its natural tropical environment, but is instead linked with its extraordinary ability to withstand a water content as low as 3%, which certainly is adaptive. The insect able to survive the lowest temperature for adaptive reasons is *Pterostichus brevicornis* (Kirby 1837). In laboratory tests, Miller 1969 found that the winter adult of this carabid beetle tolerates temperatures as low as -87°C, through use of the cryoprotectant glycerol. This beetle should thus be able to survive any natural temperatures in its Arctic environment. In many freeze tolerance experiments, workers define survival on the basis of directed coordinated activity like walking, feeding, and avoidance responses after rewarming (Miller 1969, Lee & Denlinger 1991). However, Baust & Rojas 1985 have rightly questioned this definition of survival in a biological context. For the purposes of this chapter, Miller's definition is adequate, but it could be argued that the only adaptive survival is reproductive survival. Few workers have tested whether insects that survive low temperatures maintain their ability to reproduce.

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Chapter 5. Most tolerant of desiccation

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ABSTRACT. The larvae of the chironomid, *Polypedilum vanderplanki* Hinton, breed in small pools on unshaded rocks in northern Nigeria and Uganda where they withstand an environment which is alternately dry and flooded. *Polypedilum vanderplanki* is the only insect definitely known to endure cryptobiosis and survive drying to <3% moisture. However, the hemolymph and certain tissues of some insects also tolerate the extreme desiccation associated with the cryptobiotic state.

INTRODUCTION. Organisms have a variety of strategies which allow them to tolerate extremely dry environments and avoid desiccation. These strategies range from physiological adaptations such as the use of metabolic water, to behavioral adaptations such as moving from the sun to the shade during the hottest part of the day. One very peculiar tactic used by a few organisms is a phenomenon known as cryptobiosis. According to Keilin 1959 cryptobiosis is defined as "the state of an organism when it shows no visible signs of life and when its metabolic activity becomes hardly measurable, or comes to a standstill". Recovery after exposure when dry to temperatures of over 100°C is evidence that the organism or tissue had been in a state of cryptobiosis (Hinton 1960a). Cryptobiosis is known to occur in a wide variety of organisms including viruses, bacteria, fungi, seeds of higher plants, and even in animals - including tardigrades, eelworms (Keilin 1953), and eggs of some crustacea (Hinton 1960a). An insect which can undergo cryptobiosis would surely be able to withstand drier conditions than an insect that cannot.

METHODS. In order to find whether there is an insect that can undergo cryptobiosis I searched general entomology texts (Blum 1985; Chapman 1982; Borror & al. 1989; Edwards 1991) and the CD-ROM version of Biological Abstracts from 1991 to 1993.

RESULTS. *Polypedilum vanderplanki* is the only insect known to endure the cryptobiotic state and survive dehydration to a moisture content of <3%. *P. vanderplanki* breeds in small pools in shallow depressions on unshaded rocks in northern Nigeria and Uganda. The pools are alternately dry and flooded. During the dry periods the larvae dry out on the mud under 4 to 8 mm of plant debris in depressions. Larvae are exposed to temperatures as high as 70°C (Hinton 1952). Hinton 1951 brought the larvae into the laboratory to determine how the larvae survive. The larvae were dried to <3% moisture and were heated at several temperatures for varied amounts of time. Some of the larvae metamorphosed after exposure to 102-104°C for 1 minute, and some recovered temporarily after exposure to 106°C for 3 hr or 200°C for 5 min (Hinton 1960b). According to Hinton 1960a, the ability to survive these temperatures is indisputable evidence that the larvae were in a state of cryptobiosis.

DISCUSSION. Since virtually all insects are not capable of entering the cryptobiotic state, they cannot tolerate a moisture content lower than 10-20% (Hinton 1960a). Dehydration is generally slowed in insects by the impermeability of the embryonic membrane, chorion, or cuticle, or by the production of metabolic water (Hinton 1960a). The eggs of *Locustana pardalina* (Walker 1870) survive moisture contents as low as 40% (Matthee 1951). The American coccid, *Margarodes vitis* (Philippi 1884) was found alive after at least 17 years in a museum (Ferris 1919), and the development of the larva of the wood boring beetle, *Eburia quadrigeminata* (Say 1827), has been delayed for up to 40 years in dry wood (Jaques 1918); however, their moisture contents are not know. Although many insects are resistant to moisture loss they tolerate a drop in moisture only to a critical level (Hinton 1960a). However, some insect tissues are capable of surviving the cryptobiotic state. For example, the epidermis of several species of Coleoptera and Diptera (Hinton 1957) and the hemocytes of *Sialis lutaria* Linnaeus 1758 (Megaloptera) survive cryptobiosis (Selman 1961). Although *Polypedilum vanderplanki* is the only insect known to survive the extreme desiccation associated with the cryptobiotic state, other insects may have this ability; for example, the larva of the mycetophylid, *Sciara medullaris* (Giard 1902) and a ceratopogonid larva occur in the same environment in Africa as *P. vanderplanki* (Hinton 1960a). Further investigation is needed to confirm whether these or other insects can enter cryptobiosis.

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Chapter 6. Shortest generation time

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ABSTRACT. Generation time is the time needed to complete one generation. Insects of short generation time have higher rates of increase and develop resistance to insecticides more quickly than insects of comparatively longer generation time. Temperature and food quality are two key factors that may influence the generation time. The aphid *Sitobion avenae* ssp. *avenae* (= *Rhopalosiphum prunifoliae* Fitch 1855) has the shortest generation time, 4.7 days @ 25°C.

INTRODUCTION. A generation is from a given stage in the life cycle to the same stage in the offspring (Borror & al 1981). Generation time is the time required to complete a generation. Based on this definition, I sought the insect that has the shortest generation time.

METHODS. Candidates were sought in general entomology textbooks from the 1950s to 1980s and via personal communications. AGRICOLA 1970-1994, Biological Abstracts 1985-1994 and CAB Abstracts 1985-1992 were searched for primary literature.

RESULTS. Aphids may have the shortest generation time for their parthenogenetic reproduction. Gutierrez & al. 1971 reported that *Aphis craccivora* C.L. Koch 1854 needed 5.8 days to complete a generation @ 20°C. Elliot & Kieckefer 1989 reared aphid *Rhopalosiphum padi* Linnaeus 1758 with barley under constant temperatures. They found that apterae take 5.1 days @ 26°C to finish 1 generation. *Aphis gossypii* Glover 1877 one of the most serious insect pest of crops, also requires only 5.0 days to complete 1 generation (Petitt & al. 1994). Noda 1960 reported that *Rhopalosiphum maidis* (Fitch 1856) finishes one generation in 5.0 days @ 25°C. *R. prunifoliae* takes only 4.7 days to fulfill its generation @ 25°C (Noda 1960). This may be the shortest generation time in insects.

DISCUSSION. What is the significance for insects to have a short generation time? They may have prodigious rates of increase once environmental conditions are suitable (Dixon 1987). The population can develop resistance to insecticides. Georghiou & Taylor 1986 reported that the time needed for development of aldrin resistance decreased with shorter generation time. The aphids *Aphis gossypii* Glover 1877 and *Myzus persicae* (Sulzer 1776) have a broad spectrum of insecticide resistance. What factors affect the generation time? Dixon 1987 reported that temperature and food quality are important factors which determine the developmental rate. Radford 1967 demonstrated that food supply affects mean relative growth rate. *Sitobion avenae ssp. avenae* takes 21.3 days for 1 generation @ 10°C while only 4.7 days @ 25°C (Noda 1960). Other factors may shorten or extend the generation time. The yucca moth *Prodoxus y-inversus* diapaused for 19 years (Powell 1989). This extends the generation time. The same species usually develop more quickly in tropical areas than in temperate areas. For various reasons the generation time may be much different under laboratory conditions compared with field conditions. In this paper, the conclusion was based on laboratory conditions that optimize development.

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Chapter 7. Smallest eggs

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ABSTRACT. Taking into account ♀ size, the smallest insect eggs are the microtype eggs of Tachinidae, which are usually 0.02 to 0.2 mm long but very rarely as long as 0.4 mm. The eggs of *Clemelis pullata* (Meigen 1824) (= *Zenillia pullata*) are exceptionally minute, only 0.027 × 0.02 mm. The volume of the macrotype egg of *Gymnosoma* sp., another tachinid, is approximately 2,000× the volume of the microtype egg of *C. pullata*.

INTRODUCTION. The eggs of insects vary greatly in appearance, size and number. Regarding size, a common belief has been that hemimetabolous insects have large eggs with much yolk and therefore develop within the shell into a form resembling that of their parents. The holometabolous insects, on the other hand, are supposed to have small eggs with little yolk and therefore hatch in an undeveloped form that does not resemble that of their parents (Hinton 1981). The present paper is a literature review of the smallest eggs in the class Insecta.

METHODS. Bibliographic data were gathered from CD-ROM Biological Abstracts (1985-1993) and AGRICOLA (1970-1993). In addition, several general entomology, Hymenoptera, and Diptera books were consulted.

RESULTS. In general, the eggs of insect parasites are the smallest eggs of insects. Relative to ♀ size, the smallest insect eggs reported in the literature are the microtype eggs of Tachinidae (Hinton 1981). These eggs are usually 0.02 to 0.2 mm long, very rarely as much as 0.4 mm long (Hinton 1981). The eggs of *Clemelis pullata* are exceptionally minute, only 0.027 by 0.02 mm (Clausen 1940, Hinton 1981). Townsend 1938, 1942 calculated the volume of a considerable number of Tachinid eggs and found that the largest macrotype egg of *Gymnosoma* Meigen 1803 sp., which is 0.9 mm long, is ~2000× the volume of the microtype egg of *C. pullata*.

DISCUSSION. Traditionally holometabolous insect eggs have been considered smaller than hemimetabolous insect eggs. Anderson 1972ab published dimensions of holometabolous and hemimetabolous eggs. He maintained that with a few exceptions mainly among Coleoptera and Lepidoptera, the eggs of holometabolous insects have dimensions of ~1 mm or less and develop and hatch in only a few days. Hinton 1981 criticized Anderson's data because he compared hemimetabolous spp that on the average are much larger than those of the holometabolous spp. In addition, he did not include the size of the ♀, although large animals tend to lay larger eggs than small animals. Hinton 1981 suggested that a realistic comparison would be the ratio of the dry weight of the ♀♀ to that of their eggs. However, he recognized that data were insufficient for this kind of comparison and instead listed the major axis of the egg as a percentage of the body length of ♀ from vertex of head to the tip of abdomen. He included 102 spp of hemimetabolous and holometabolous insects. Based on these data he concluded there is no difference in the size of eggs of hemimetabolous and holometabolous insects, and insects that lay thousands of eggs, like Ephemeroptera and Tachinidae with microtype eggs, have very small eggs in relation to the size of ♀. It is important to point out that Hinton did not consider Mymaridae and Trichogramatidae, which consist entirely of species that are egg parasites and consequently are usually very minute, some adults being < 0.25 mm in L (Debach & Rosen 1991). The mymarids contain some of the smallest insects known. One sp of *Alaptus* Westwood 1839 has a BL of 0.21 mm (Borror & al. 1981), and the eggs of *Anagrus atomus* Linnaeus 1767 (Mymaridae) are 0.06 mm in L (Clausen 1940). The trichogramatids also contains some spp of the genus *Megaphragma* Timberlake 1924, parasites of the eggs of thrips, that are ≯ 0.18 mm in total L (Borror & al. 1989). In general, the data on egg size are scarce and it is difficult to determine a record without extensive data on egg size for the families mentioned above. However, *C. pullata* has an exceedingly minute egg, probably the smallest insect egg that has been measured.

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Chapter 8. Most spectacular mating

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ABSTRACT. The extensively cultivated insect, *Apis mellifera* Linnaeus 1758 is judged to have the most spectacular mating because a "comet" of drones pursues the female with the winner forfeiting a portion of his phallus at the end of coitus and dying soon thereafter (Woyke & Ruttner 1958; Winston 1987).

INTRODUCTION. Copulation in the honey bee usually occurs above ground in flight (Gary 1963). Consequently, many of the observations of the mating process have been accomplished through manipulation of the queen and/or drone (Woyke & Ruttner 1958; Gary 1963; Koeniger & al. 1979). The queen is pursued by a large swarm of drones, "drone comets," where copulation occurs (Winston 1987). Insemination ends with the eventual death of the drone, and the queen receiving the "mating sign" (Woyke & Ruttner 1958; Winston 1987). The queen mates multiple times but the drone inevitably only once (Gary 1963; Starr 1984; Winston 1987). The aforementioned features warrant my designation of it being the most spectacular mating among insects.

METHODS. An initial search was performed on AGRICOLA. The more useful resources were personal communication with faculty members of the Univ. of FL, review books about animal and/or insect mating, journal articles on the reproductive behavior of *Apis mellifera*, and correspondence with individuals on the Internet.

RESULTS. Copulation occurs on the wing, within a drone congregation site 15-30 m above ground (Gary 1963). An aggregation of drones "lazily" fly within their congregation site awaiting the arrival of a queen, and once she appears a fast-paced chase commences where copulation is attempted (Winston 1987). The term "drone comets" visually describe the continual consolidation and disassembly of this following drone swarm (Winston 1987). Koeniger & al. 1979, utilizing a tethered queen, report that the drone clasps the queen in a dorso-ventral position and everts his endophallus directly into the queen's sting chamber. The drone then becomes "paralysed" and falls backwards (Koeniger & al. 1979). Woyke and Ruttner 1958 state the eversion of the endophallus occurs from haemostatic pressure caused by abdominal muscles. Ejaculation occurs into the bulb portion of the drone's endophallus prior to full eversion, and semen is discharged through a small opening in the bulb into the queen's vagina during copulation (Woyke & Ruttner 1958). Winston 1987 figuratively asserts that the drones "explode" their semen into the queen's copulatory orifice, and consequently toward her oviduct. Through subsequent pressure the bow of the bulb and chitinized plates, the "mating sign," detaches from the endophallus of the drone and remains inside the queen (Woyke & Ruttner 1958). Winston 1987 concludes this may help thwart the flow of sperm from the queen's vagina after copulation, and that it does not function as a "mating plug" used to discourage multiple matings. After the pair separate the endophallus is still fully everted with its associated strong pressure, and with loss of the "mating plug" the endophallus may burst at the tip (Woyke & Ruttner 1958). At the end of copulation, the drone falls to the ground and dies either in minutes or hours (Woyke & Ruttner 1958; Winston 1987). Woyke 1962 calculated that a single drone on average contains 1/8 to 1/9 the semen required to fill the queen's spermatheca. The average number of times a queen mates has been reported to be from 7-10 (Woyke 1962) and up to 17.25 (Adams & al. 1977). Sperm mixing occurs within the queen's spermatheca, and comparable spermatozoa representation of all mates follows at fluctuating intervals (Laidlaw & Page 1984), leading to a low average relatedness among the ☿ caste, i.e. potentially 0.25 (Page & Metcalf 1982, Laidlaw & Page 1984).

DISCUSSION. The conditions intrinsic to the mating process of *A. mellifera*, whether it be the death of the drone or the decrease in relatedness among the sterile caste, obviously is to the betterment of the queen and unfortunate to the effected. However, the possible prevention of sperm flow out of the vagina after copulation (Winston 1987) would be to the advantage of the drone, and given the alternatives of mating or not mating, the former should most definitely be chosen at least if the drone's genes are in control! The properties of the drone comet, partial phallus detachment and the resultant death of the drone warrant its title of the most spectacular mating.

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Chapter 9. Fastest wing beat

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ABSTRACT. Using a beat-frequency oscillator as well as personal auditory analysis, Sotavalta 1953 found that a midge of the genus *Forcipomyia* Meigen 1818 (Diptera Ceratopogonidae) attained a wing beat frequency of 1,046 Hz.

INTRODUCTION. Insects require enormous amounts of energy to beat their wings rapidly. To lessen the demand for energy, insects have reduced the weight of the wings, the amount of drag created during wing movement, and the overall body size and weight. Appropriately the fastest recorded wing beat was achieved by a small, lightweight ceratopogonid midge.

METHODS. To locate references on wing beat frequencies, I consulted general entomology texts and keyword searched WebLUIS Search System, the University of Florida's computerized library catalog. I also searched Biological Abstracts on CD-ROM but it was not helpful. The most useful technique was locating citations of primary literature in published books on insect flight.

RESULTS AND DISCUSSION. A Polish researcher, Sotavalta 1947, 1953 published extensively on insect flight, particularly concerning flight-tone frequency. Using a beat-frequency oscillator as well as personal auditory analysis (Sotavalta had perfect pitch), Sotavalta found that a species of *Chironomus* Meigen 1803 (Diptera Chironomidae) had a wing beat frequency between 650-700 Hz. However, a member of the genus *Forcipomyia* Meigen 1818 (Diptera Ceratopogonidae) (no species given) had most masterfully exploited its asynchronous muscle system by achieving a wing beat frequency of 1046 Hz. Through experimental manipulation of this insect (removal of most of the wing area as well as exposing it to temperatures up to 37°C) Sotavalta recorded flight tones over 2,200 Hz. Insect muscle systems have been categorized into 2 groups; synchronous and asynchronous. Most insects with synchronous muscle systems cannot produce muscle contractions greater than about 100/s, because of delays involved in conduction of the motor nerve impulses and the activation of the contractile system of muscle fibers (Pringle 1976; Smyth 1985). However, insects do not read our texts on physiology and biochemistry and there are currently 2 recorded exceptions to this limit. The tymbal muscles used in sound production in the cicada *Chlorocysta viridis* (Goding & Froggatt 1904) (Cicadidae), have been recorded up to 224 Hz (Young & Josephson 1983). When singing, the cone-head *Neoconocephalus robustus* (Scudder 1862) (Orthoptera Tettigoniidae) has thoracic muscle contractions of 212 Hz (Josephson & Halverson 1971). In asynchronous muscle systems (Hymenoptera, Diptera, Coleoptera, Hemiptera), the impulses in the motor nerves and the mechanical activity of the muscles do not occur at the same frequency (Pringle 1976). The arrangement of muscles in the asynchronous system is antagonistic which causes cyclic deformations of the thorax (Smyth 1985). It is this asynchronous muscle system that allows some insects to produce such high muscle contraction rates. Although these recordings are over 40 years old they seem to be the only evidence of such feats, as the most modern publications continue to cite Sotavalta's work. One advantage for rapid wing beat is the ability of the insect to remain relatively stationary in air (hover). This talent would certainly be helpful in times of mating.

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Chapter 10. Least specific sucker of vertebrate blood

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ABSTRACT. The tsetse fly *Glossina palpalis* (Robineau-Desvoidy 1830) (Diptera Glossinidae) probably has no match among haematophagous insects in its vertebrate host range. According to Jordan & al. 1962 this fly can feed on any vertebrate it contacts. It is also not responsive to host derived odors presently being evaluated as olfactory baits and incorporated in trapping technology strategies for tsetse flies (Williemse & Taken 1994).

INTRODUCTION. Haematophagy or the utilization of blood as food occurs in six insect orders. The order Diptera (true flies) has the largest number of haematophagous species and includes endoparasitic and ectoparasitic forms (Lehane 1991). The ectoparasites include those that stay permanently on their hosts and those that are off their hosts except when feeding. Those ectoparasites that stay off their hosts, range from most to least host specific with regard to both their host locating (trailing) and host preference patterns. According to Askew 1971 tsetse flies are not at all restricted in their choice of hosts; different spp have different habitat preferences and are classified into 3 major ecological groupings on the basis of habitat preferences: open savanna or grassland [*G. morsitans* Westwood 1851 species-group] dense humid forests associated with water bodies [*G. palpalis*]; and other forests [*G. (Austenina) fusca* (Walker 1849)].

METHODS. Vertebrate host specificity of haematophagous insects was obtained from medical and veterinary entomology textbooks and journals. Help in finding a champion was obtained from the Entomo-L Listserv.

RESULTS. *Stomoxys calcitrans* (Linnaeus 1758) was a candidate on the basis of being a cosmopolitan livestock pest and attacking up to 30 different spp. among mammals, birds, reptiles, and even amphibians (Bishop 1913; Surcouf 1923; Hoskins 1933; Haefez & Gammal-Eddin 1959; Greenberg 1971). According to Jordan & al. 1961, 1962, *Glossina palpalis* has a wider range of acceptable hosts than any other species in West Africa. Species of the *palpalis* group of tsetse flies feed on any vertebrate they encounter ranging from mammals and reptiles to birds (Weitz 1963, 1971; Harwood & James 1979). Information on feeding habits and preferences by tsetse flies relies on identifying blood meals of wild caught tsetse flies using the precipitin test described by Weitz 1956. Weitz & Glasgow 1956 observed that the host range for *G. palpalis fuscipes* in East Africa included mammals, with birds and reptiles having equal importance and even suggested that lungfish (genus *Protopterus* Owen 1839) could be a source of blood meals. Nash 1948 in West Africa, compared *G. palpalis* to *G. tachinoides* Westwood 1851 and observed that *G. palpalis* will fly higher and hunt for hosts in dense undergrowth. Williemse & Taken 1994 state that tsetse flies of the *palpalis* group are not responsive to conventional vertebrate host derived odor cues that tsetse flies of the *morsitans* group readily respond to.

DISCUSSION. The least host specific vertebrate blood sucker should be an insect documented to feed on any available vertebrate host. Greenberg 1971 discussed *Glossina* spp. as vectors of trypanosomes, having bimodal flight activity, etc., but did not attempt to categorize tsetse fly hosts in the same way as he did for *Stomoxys calcitrans* and other flies. *G. palpalis* is probably least specialized in host selectivity as there is no limit documented for vertebrate species that it can feed on (Weitz & Glasgow 1956; Jordan & al. 1961, 1962; Weitz 1963). This tsetse fly generally feeds while inside dense humid forest habitats where trailing hosts by olfaction would be arduous. Under such circumstances, it would be advantageous to compromise by feeding on any vertebrate host encountered by sight rather than by relying on olfactory cues.

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Chapter 11. The longest migration

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ABSTRACT. A definition of migration that does not require migrants to have navigational abilities or to return to the point of origin has been used in this chapter in an attempt to determine the longest insect migration. The desert locust *Schistocerca gregaria*, a dynamic migrator, migrated westward across theAtlantic ocean 4,500 Km during the fall of 1988.

INTRODUCTION. "In many books published in the past a distinction was made between migration and other forms of movements. But in recent years it has become increasingly accepted that this distinction is artificial and that movement and migration are one in the same thing" (Baker 1981). This statement perhaps best describes the problem with an exact definition of migration. Migration in insects serves not only for escape from old habitats but also for reproduction and colonization in new ones (Dingle 1978). Because insects exhibit an extremely wide range of lifestyles and life histories, two of the four kinds of migration described by Taylor 1986, dynamic migration and homeostatic migration, were examined to determine the farthest insect migration. Dynamic migration is directed movement controlled by tides or wind, with navigation abilities not essential. The desert locust *Schistocerca gregaria* (Forskål 1775) found in Africa is a good example of this type of migration. The majority of migratory insects fall into this category. Homeostatic migrations are two-way movements with migrants or offspring returning to breeding areas, hence the need for navigational abilities. The monarch butterfly [*Danaus plexippus plexippus* (Linnaeus 1758)] is a good example of this type of migration. This insect migrates to overwintering sites and then migrates back toward its summer range taking several generations (Urquhart & Urquhart 1977). Weather appears to be an important factor for the majority of insect migrations. Insect migrations are usually completely confined to the lowest 2 Km of the atmosphere, the Planetary Boundary Layer (PBL) (Drake & Farrow 1988). While migratory insects are within the PBL, they are subject to weather effects such as thermals, downvalley wind jets, and fronts (Pedgley 1982). Many insects that migrate with help from the wind such as the six-spotted leaf hopper, *Macrosteles fascifrons* (Stål 1858), travel on the wind by flying vertically until they encounter ideal currents that carry them north from locations of over wintering (Meade & Peterson 1964). They then fly down to ground when they encounter suitable habitats. The migratory aphid *Aphis fabae* Scopoli 1763 also disperses with local winds. Winged adult forms take off on strong vertical flights, attracted to the blue light of the sky (Johnson 1963). After several hours of flight and often many Km from their takeoff site, the aphids begin to descend, now attracted to yellow or green colors. Some insects can rise above lower air turbulence by wind currents or powered flight. Glider pilots have observed monarch butterflies at an altitude of 1,200 m (Gibo 1981). *Schistocerca gregaria* has been seen to reach heights of 1-2 Km by riding thermals (Rainey 1974). Migratory flights at these altitudes can allow insects to disperse against wind directions found at lower altitudes.

METHODS. Determination of the longest flyer was made after a search of AGRICOLA 1970-1994, secondary literature, including ecology and entomology texts, and discussion with several professors.

RESULTS. The desert locust, *Schistocerca gregaria* inhabits the dry areas of northern Africa. Their breeding is synchronized with the arrival of the rainy season (Gillot 1980). Their wind borne migrations are associated with the movement of the convective air currents of the Inter-Tropical Convergence Zone (ITCZ). Within the ITCZ "opposing warm and humidity-laden trade winds meet, air ascends and, in cooling off, precipitates its humidity in the form of tropical rain" (Schmidt-Koenig 1975). Waloff 1959 reported that in 1950 individual swarms had been tracked from the Arabian peninsula over 5,000 Km to the west coast of Africa at Mauritania in less than 2 months. However, recruitment and die-off of individuals making the entire trip from start to finish was not mentioned or recorded. During 1988-X many individuals of *S. gregaria* were found along a front reaching north from the island of St. Croix in the West Indies, south to the eastern coasts of the South American countries of Suriname and Guyana (Rainey 1989). These individuals were arriving with a sub tropical wave of low pressure that later spawned a hurricane. The distance traveled from the west coast of Africa to islands in the West Indies was 4,500 Km.

DISCUSSION. The longest insect migration was performed by desert locust *Schistocerca gregaria*. The records of *S. gregaria* found in many Caribbean islands and parts of the east coast of South America during 1988-X indicate that they flew within with a tropical wave pattern for a distance of 4,500 Km. The close observation of weather records for that particular region of the Atlantic made it possible to track their flight with a fair degree of accuracy. Also, members of the swarms probably flew for some distance in Africa before they began the trip across the Atlantic ocean. The report of the 1950 swarm could be misleading due to the unknown history of the individuals.

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Chapter 12. Longest life cycle

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ABSTRACT. Under exceptional conditions, some individuals of wood-boring beetles (Cerambycidae, Buprestidae) have the longest life cycle. One *Buprestis aurulenta* larva emerged after 51 years. 3 species of 17-year periodical cicadas, *Magicicada septendecim*, *M. cassini*, *M. septendecula*, are well-known to have the longest synchronized development times in natural conditions.

INTRODUCTION. Life cycle is defined as the sequence of events from egg to reproducing adult. Metamorphosis is a characteristic of insect life cycles, and the different stages become distinct units of development time. Each of these units must face environmental exigencies often quite different from those of the others. Insects have solved the problems of synchronizing life cycles to seasonal periodicities and responding to other biotic and abiotic factors with an impressive array of tactical alternatives. These include flexibility in diapause and development rates (Dingle 1986). On the other hand, there are many cases in which life cycles are made longer by prolonged development time rather than diapause. This chapter is a literature review of the longest life cycles in the class Insecta.

METHODS. CD-ROM versions of Biological Abstracts and AGRICOLA were searched from year 1989 to the present. The more useful resources were personal communications with scientists, and secondary literature.

RESULTS. In some insect species, different individuals have different spans of life cycle depending on individual inhabited environment. On the other hand, some species have an unchangeable period for their life cycle regardless of inhabited environment. Many recorded cases of prolonged of life cycle are in Coleoptera. The adults of the old house borer *Hylotrupes bajulus* Audinet-Serville 1834 (Cerambycidae) do not feed on wood; the main damage to wood is done by their larvae. Grosser 1985 reported that their development can continue for 1-6 years and sometimes up to 10 years. The wood boring beetle *Eburia quadrigeminata* (Say 1826) (Cerambycidae), when feeding in dry wood, may have its development so greatly retarded that adults emerge from furniture and flooring many years after manufacture or installation. Delayed emergence of *E. quadrigeminata* was discovered from a birch bookcase 40 years old (Jaques 1918). Huguenin 1915 was the first to record a development time of *Buprestis aurulenta* Linnaeus 1767 (Buprestidae) from structural timbers as long as 26 years after infestation. 32 additional cases of delayed emergence in *Buprestis* were presented by Smith 1962, with 11 of the total cases between 26 and 51 years. For some of these cases, infestation by later direct attack was suggested. However, considering the potential of these wood beetle species for prolonged larval development, Smith 1962 believed that when wood beetles emerge from a structure, it indicates larval development at least equivalent to the age of the structural members they emerged from, unless local and more recent repairs have introduced the infestation. Compared with the lack of convincing concrete evidence of prolonged development time for these two beetle species, the periodical cicada's requirement of 17 years to complete nymphal development is well documented. Marlatt 1907 studied the development in the 17-year nymphs by digging up specimens from the same grove of trees over a period of 17 years. This 17-year development time is shared by 3 distinct species: *Magicicada septendecim* (Linnaeus 1758), *M. cassini* (Fisher 1852), *M. septendecula* Alexander & Moore 1962. The 3 spp. are sympatric, but are separated microspatially by preferring different but overlapping forest types. Within the same brood, emergences co-occur with definite synchrony.

DISCUSSION. As described above, some cases of prolonged development time are extrinsically mediated by direct effects the environment, such as *Buprestis aurulenta*. Smith 1962 suggested there are innate differences in rate of development amongst individuals of the same *B. aurulenta* brood; some have short rates of development and others prolonged development under the same environmental conditions. Obviously, the poor nutritional quality of dead wood causes significantly prolonged development (Haack & Slansky 1987). As Howard 1942 pointed out, under these exceptional conditions, the larvae of certain wood-boring beetles (Cerambycidae and Buprestidae) in furniture and manufactured wooden articles may have the longest lives recorded among insects. Conversely, for 3 species of 17-year periodical cicadas, the prolonged development time is the result of an endogenous mechanism. Cicadas feed exclusively on xylem fluid as nymphs and as adults (Cheung & Marshall 1973). Slow development in cicadas could be comprehensible due to their exceedingly dilute diet of xylem fluid that is energetically expensive to procure (White & Strehl 1978; Lloyd 1984). Furthermore, nymphs may only be able to feed during the limited period when xylem pressures are positive or when the negative pressures are not impossible to overcome. In addition, the size of the cibarial pump may limit the rate of ingestion. Karban 1986 advanced a detailed hypothesis for the relationship between nutrition and prolonged development in cicadas. The mechanism that maintains the precise developmental periodicity is not simply a uniform determined development rate. The first individuals to complete their growth have to wait to emerge until the "scheduled" number of years has elapsed (Lloyd & Dybas 1966). In summary, although 17-year cicadas are well-known for their long life cycle in natural habitats, some wood beetle spp. definitely have the longest life cycles in exceptional habitats.

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Chapter 13. Most instars

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ABSTRACT. If instar refers to any stage between molts, then the fire brat, *Thermobia domestica* Packard 1873 (Thysanura Lepismatidae), holds this record with 60 molts. If the larval stage is defined as the only stage that contains instars, then the mayfly, *Stenacron interpunctatum canadense* (Walker 1853) [Cfr. *Stenacron interpunctatum* (Say 1839)] (Ephemeroptera Heptageniidae), would be our champion with 45 molts.

INTRODUCTION. The first objective was to determine a definition for instar. After asking professors and fellow graduate students, I found there were two ideas of what an instar is. One definition for instar is the stage of the insect between successive molts (Chapman 1982; Borror & al. 1989). This definition does not state anything about immatures or adults. The other definition states that an instar is the stage between molts of the immature insect (De la Torre-Bueno 1989). Therefore I looked for record holders using both these definitions.

METHODS. The first method employed was to ask professors and graduate students in the UF Entomology & Nematology Dept. to nominate candidates for this record. At this time the discrepancy as to how instar should be defined was noted. Therefore, general entomology text books were studied to try an arrive at a usable definition of the word for this chapter. Because two definitions seemed established, both were used. Insects that were nominated were then searched using standard library methods (i.e., CAB Abstracts, AGRICOLA, and secondary literature).

RESULTS. The record for most instars is dependent on which definition is used for instars. If the definition is used that restricts the term to immatures, then the mayfly, *Stenacron interpunctatum canadense* (Walker 1853), holds the record with 45 larval molts observed by Ide 1935. If we use the definition that any insect stage between molts is an instar then the fire brat, *Thermobia domestica* Packard 1873, is the overall champion with 60 molts (Sweetman & Whittemore 1937). Thysanura molt through-out their life, so no definite number can be assigned. The number of instars is dependent on age.

DISCUSSION. It seems as though entomologists have done little research on the number of molts an insect has. Very little information is available, and the information that is available is old. Nymphal and larval size seem to be of more interest to researchers than the actual number of times an insect molts. The number of molts a particular insect experiences is affected by temperature, humidity, and food quality (Sweetman 1934; Sweetman & Whittemore 1937; Clifford & al. 1979; Brittian 1982; Berner & Pascador 1988; Brittian 1990; Mallis 1990). Laboratory conditions may also have an impact on insect molting (Clifford & al. 1979). Many insects have a variable number of molts, and it is not known whether laboratory conditions significantly increase or decrease this number from the natural population.

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Chapter 14. Most parental sharing of brood care

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ABSTRACT. Shared brood care or parenting chores are rare behaviors in insects. While a number of species exhibit biparental care, including wood roaches, passalid beetles and some bark and dung beetles, only burying beetle ♂♂ (*Nicrophorus orbicollis* Say 1825) participate in all activities, remain with the brood throughout development, and can take over all parenting responsibilities if the ♀ disappears. In general, extended parenting by both sexes is linked to insects that use rich but ephemeral resources to provision their young.

INTRODUCTION. Maternal care and protection of offspring have been well documented in insects; some examples include lace bugs, reduviids and of course many Hymenoptera. More rare is unassisted care of the young by the father, as in Belostomatidae and the reduviid gg. *Rhinocoris* Hahn 1834 and *Zelus* Fabricius 1803 (Tallamy & Wood 1986). Among insects, cooperation between the sexes in brood care is very unusual.

METHODS. There are risks associated with increased parental care. Defending young from predators could put the adult in jeopardy, aggregations of prey (as a mother with young) may attract predators, and parents must put energy into the care of a few offspring rather than many (Wilson 1975). Paternal cooperation in offspring rearing has evolved a number of times in divergent groups, most of which feed on carrion, dung, or rotting wood. This convergence of social behaviors associated with dietary constraints is no coincidence. Dung and carrion are rich resources that decompose rapidly and must be used within a very short time. Many beetles excavate chambers underground to store and protect the resource and the larvae developing within it from predators and desiccation. This intensive processing requires the collaboration of both parents (Halffter & Edmonds 1982). Rotting wood presents a unique resource; while not rich or particularly ephemeral, it requires processing before it can be used as food (Tallamy & Wood 1986). A number of insect species could be nominated as candidates for the most parental sharing in brood care, depending on how one defines "sharing". Below I list several examples. *Cryptocercus* Scudder 1862 roaches pair for life. The adults chew a series of galleries interspersed with large rearing chambers in rotting logs. Young nymphs require the transmission of intestinal flagellates through proctodeal trophallaxis (you don't want to know) from their parents. Nymphal growth is slow (5 yrs), and the nymphs' diet is supplemented in the early stages with parental hindgut fluids and fecal pellets (Nalepa 1984). Passalid beetles are also monogamous, and cooperate in construction and defense of interconnected galleries in rotting wood. Larvae of different species have differing abilities to chew and process wood for food; however, all depend on their parents to some extent in this endeavor. Colonies generally have overlapping generations and cooperative brood care. Colonizing adults share galleries with offspring in all stages of development, and with first generation nonreproductive adults. In some cases, young adults assist parents in the construction and repair of sibling pupal cases and other tasks (Schuster & Schuster 1985). Cooperation in excavation of brood galleries and rearing young is also known in the *Monarthrum* Kirsch 1866 bark beetles (Hubbard 1897), and other scolytids (Tallamy & Wood 1986). Complex cooperation between the sexes, with division of labor, occurs in many species of scarabaeine dung beetles. ♀♀ in the genus *Copris* Geoffroy 1762 and many *Ontophagus* Latreille 1802 species dig tunnels and brood chambers under dung, pushing dirt up to ♂♂ higher in the tunnel, who in turn push it out. When excavation is complete, ♂♂ transfer dung from the surface to the ♀ in the tunnel and she constructs the brood ball. Typically the ♂ remains with the ♀ for most of this process, but disappears from the nest soon after eggs are laid in the dung (Halffter & Edmonds 1982). Some *Cephalodesmius* Westwood 1842 dung beetles pair bond for life and cooperate extensively while rearing larvae (Monteith & Storey 1981). The ♀ excavates the brood chamber while the ♂ stands guard at the entrance. The ♂ then forages for detritus (leaves, flowers, fruits), which he passes to the ♀. She adds feces and shapes the material into a ball, which is allowed to ferment for a week. The ♀ then divides the ball into smaller sections for each larva. For several weeks, while the larvae are growing, the ♂ continues to provision the nest. When the young approach pupation, both parents seal themselves inside the chamber with the larvae.

Results

The insects with the reputation for the greatest amount of shared responsibility in offspring care are burying beetles, genus *Nicrophorus* Fabricius 1775 (Fetherston & al. 1994). ♂♂ and ♀♀ *Nicrophorus orbicollis* Say 1825 pair off at a carcass, and after defending it from others, bury it. Underground, the carcass is rolled into a ball, fur or feathers are removed, and it is covered with anal and oral secretions. Eggs are laid in the soil nearby, and hatch into altricial larvae, which are fed regurgitant by both parents. Although larvae may be able to feed themselves relatively quickly, they may still be fed by both parents (Scott & Traniello 1990). ♂ and ♀ beetles have identical brood care behaviors; however, in biparental broods, ♀♀ spend more time provisioning the brood, and ♂♂ spend more time guarding. Nevertheless, when one member of the pair is removed, the other member compensates by taking over all responsibilities. Furthermore, single ♂♂ are as successful at raising broods as single ♀♀ (Fetherston & al. 1994).

DISCUSSION. I award burying beetles the prize for most parental sharing in brood rearing. I base this decision on the following reasons:

1. Burying beetles share the same tasks; they do not exhibit absolute division of labor, as do dung beetles;
2. Unlike wood roaches and termites, many tasks (defense, nest and food preparation, feeding larvae) are required;
3. ♂♂ will take over sole responsibility if a ♀ disappears, like many bird spp., but unknown in any other insect.

When food resources are patchy and decompose quickly, insect parents are faced with a dilemma in reproduction. Young cannot be abandoned, as in most insect species, but require extended periods of parental assistance. The resource has a short "shelf life", thus the labor-intensive nesting, processing, and, in some species, care and feeding of the larvae, necessitates shared parenting (Wilson 1975).

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Chapter 15. Resistant to most insecticides

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ABSTRACT. The green peach aphid, *Myzus persicae* (Sulzer 1776) (Homoptera Aphidae), is resistant to more insecticides than any other insect. Two other agricultural pests that are notoriously resistant, the Colorado potato beetle *Leptinotarsa decemlineata* Say 1824 (Coleoptera Chrysomelidae) and the diamondback moth *Plutella xylostella* (Linnaeus 1758) (Lepidoptera Plutellidae), are strong runners-up.

INTRODUCTION. Since Melander 1914 first reported insecticide resistance, the subject has received ever greater attention due to increasing inability to control agricultural pests and disease vectors through chemical means (Forgash 1984; Georghiou 1986). A population is considered resistant if its response to an insecticide in detection tests drops significantly below its normal response (Georghiou & Mellon 1983). In 1984 there were 1797 cases of resistance in arthropods (including all spp. and all insecticides); by 1991, resistance to at least one insecticide had been recorded for 504 spp. (Georghiou 1986; Georghiou & Lagunes-Tejada 1991). A population may develop cross resistance to several closely related chemicals, in the absence of selection pressure against each, when one compound causes selection for a detoxication mechanism common to both. More serious is multiple resistance, the presence of separate detoxication mechanisms for unrelated insecticides, selected for independently (French & al. 1992). By 1984 at least 17 insect spp. were resistant to all major classes of insecticides (Georghiou 1986). There are several ways to define "most resistant" insect, including frequency of resistant genes in a population or geographic range of resistant populations (Forgash 1984; Georghiou 1986) and even seriousness of control failure, given the enormous socio-economic costs of multiple resistance. In this chapter, "most resistant" is limited to degree of cross and multiple resistance, the champion being the species with documented resistance to the greatest number of insecticides.

METHODS. Secondary literature and advice from entomologists provided initial candidates. CD-ROM databases of AGRICOLA and CAB Abstracts were searched for the years 1984-1994 for references to insecticide resistance in the principal candidates.

RESULTS. In terms of the total number of insecticides to which populations are resistant, the two candidates closest to the champion are *L. decemlineata*, resistant to 37 compounds as of 1989, and *P. xylostella*, resistant to 51 compounds, also in 1989. However, the insect species with populations resistant to the greatest number of insecticides is *Myzus persicae*, which has documented resistance to 71 synthetic chemical insecticides (Georghiou & Lagunes-Tejada 1991).

DISCUSSION. Species that have developed resistance to most insecticides used against them include the cotton leafworm, *Spodoptera littoralis* (Boisduval 1833) in Egypt; the cattle tick *Rhipicephalus microplus* (Canestrini 1888) (= *Boophilus microplus* Lahille 1905) (Ixodidae) in Australia; the housefly *Musca domestica*; and many species of *Anopheles* mosquitoes worldwide (Forgash 1984; Georghiou 1986). Two of the most striking examples of resistant insect species are and, both of which have developed extensive populations resistant to all synthetic insecticides registered for use against them, as well as biological insecticides like *Bacillus thuringiensis* Berliner 1915 (see **RESULTS**) (Georghiou 1986; Hare 1990; Jansson & Lecrome 1990; Olkowski & al. 1992; Yu & Nguyen 1992; Talekar & Shelton 1993). *L. decemlineata* has been especially devastating to potato on Long Island and other parts of the NE US while the *P. xylostella* has been most uncontrollable on crucifers throughout SE Asia (Forgash 1984). Furthermore, their resistance has been influential in the development of Integrated Pest Management (IPM) strategies, and both cases demonstrate the risk of reliance on one control method (Hare 1990; Olkowski & al. 1992; Talekar & Shelton 1993). Additionally, these cases highlight the importance of monitoring pest populations for insecticide resistance and incorporating resistance management into integrated control measures. Many would therefore argue that the rapidity with which populations of these 2 species develop resistance to newly applied insecticides, leading to inherent difficulties in their chemical control, would make them the champions of the category "resistant to most insecticides". However, *M. persicae*, while receiving less attention in terms of its resistance, has a greater number of documented cases of resistance to individual insecticides, and therefore is the most resistant according to the definition utilized here. This has important implications for IPM strategies, since *M. persicae*, in addition to causing direct damage to various crop species, is the most efficient vector of several viruses attacking potato and other crops (Radcliffe & al. 1991), resulting in severe economic losses. Perhaps because of the high number of cases of resistance in this species, resistance management programs are being refined. With the determination that the biochemical resistance mechanism in *M. persicae* is based on increased levels of Esterase-4, biochemical assay techniques have been developed to monitor populations for resistance (Scott 1990). As a vector of plant disease, a low population density of green peach aphids can cause severe economic losses, so multiple resistance in this species is a serious matter. Given the severe resistance problem already present, the refinement of IPM programs for *M. persicae* is vital, and should be pursued with as much effort as has been extended to IPM programs for *L. decemlineata* and *P. xylostella*.

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Chapter 16. Shortest sexual life cycle

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ABSTRACT. The mosquito *Psorophora confinnis* (Diptera Culicidae), probably has the shortest sexual life cycle. Temperature and geographical origin are the most important factors affecting how quickly the cycle is completed. In Coachella Valley, under optimum environmental conditions, *P. confinnis* can complete an entire life cycle within a week.

INTRODUCTION. The sexual life cycle of insects depends on species characteristics and environmental conditions. Most insects can complete their entire life cycle within 1 year. Some may be much longer, while others may be only a few weeks or less (Borror & al. 1981). For mosquitoes, the time spent in the immature stages depends largely upon temperature (Breeland & Pickard 1963). In this chapter I will attempt to identify the insect requiring the shortest time to complete a sexual life cycle under optimum environmental conditions.

METHODS. Professors and graduate students were asked to nominate candidates. AGRICOLA, Biological Abstracts and CAB Abstracts were searched from 1970 to the present. Secondary literature, mainly text books in entomology and life history, were consulted.

RESULTS. Gunstream 1967 reported that the developmental times, hatching to emergence, of 18 broods of *Psorophora confinnis* (Lynch Arribálzaga 1891) observed in irrigated date groves in Coachella Valley, US-CA, ranged 78-126 h with a mean of 97 h @ average water temperature of 77-88°F. Usual incubation period is 1-3 h (Breeland & Pickard 1963), preoviposition period is 2-3 days (J. Jackson, USDA, Medical & Veterinary Entomological Research Laboratory, Gainesville, US-FL, personal observation). Therefore, the entire life cycle (egg to egg) of *P. confinnis* can be completed within a week.

DISCUSSION. *Psorophora confinnis* is the most abundant mosquito in the desert agricultural regions of southeastern US-CA. The aquatic stages develop in shallow temporary pools formed by irrigation water, especially in crops irrigated by flooding. Usually these pools persist only 1-5 days. *P. confinnis* must tolerate high temperatures and develop rapidly to use such habitats (Azawi & Chew 1959; Gunstream & Chew 1967). Several investigators have studied the effect of temperature on the growth rate of immature *Psorophora* Robineau-Desvoidy 1827 mosquitoes (Chew & Gunstream 1964; Gunstream & Chew 1967; McHugh & Olson 1982; etc.). According to Chew & Gunstream 1964, the developmental time of *P. confinnis* from hatching to emergence is between 86 h @ 32°C and 108 h @ 23°C. The developmental times reported by Gunstream & Chew 1967, 78-126 h, are much shorter than the previously reported times of 144-168 h @ similar water temperatures of 30-35°C in US-AK ricefields (Horsfall 1942) and 133-266 h @ somewhat cooler average water temperatures of 22-29°C in Alabama (Breeland & Pickard 1963). This fact suggests that the shorter developmental time of *P. confinnis* in the Coachella valley is an adaptation evolved under selective pressure of rapidly drying irrigation water. Compared with *P. confinnis*, the developmental times of *P. columbiae*, *P. cyanescens*, and *P. ciliata* were 105 h (McHugh & Olson 1982), 118 h and 114 h (Breeland & Pickard 1963) respectively. For 2 other promising candidates, the horn fly *Haematobia irritans* (Linnaeus 1758) and certain parasitic chalcid wasps, the developmental time (hatching to emergence) are 9.3 d (Depner 1961) and within 7 d respectively (Wootton 1984). *P. confinnis* is apparently the insect with the shortest sexual life cycle.

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Chapter 17. Lowest lifetime fecundity

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ABSTRACT. Insect species from at least three orders are thought to have extremely low lifetime fecundity, producing less than ten offspring. These species rank among the lowest fecundity animals in the world. Choice of a champion is difficult, but from the published estimates the louse fly *Hippobosca variegata* Megerle 1803 is the species with the lowest lifetime fecundity, producing an average of 4.5 offspring.

INTRODUCTION. Extremely low lifetime fecundity is found in insects of several different orders, and with different diets and foraging behaviors. The one thing most of these insects have in common is that parental investment per progeny is very large. The parental care ranges from the most extreme, such as giving birth to prepupae in blood-feeding flies, to the production of large eggs that provide the embryo with a rich food source. The main purpose of this care is, of course, to increase the offspring's survival. When organisms invest heavily in each young, the number they can produce has to be reduced. There is a trade off between having few offspring with low mortality, or having a large number with high mortality but which are less costly to produce (Stearns 1992).

METHODS. The most useful sources were the textbooks by Hinton 1981 and Engelmann 1970, both of which have extensive tables of insect egg numbers. Biological Abstracts 1989-1994 was also searched. Combinations of the keywords "lifetime fecundity", "low" and "insects" proved useful. General textbooks of entomology also provided references that were used.

RESULTS & DISCUSSION. The tsetse fly *Glossina palpalis* (Robineau-Desvoidy 1830) (Glossinidae) produces 6-12 larvae in its life (Hoffmann 1954). Another dipteran, the louse fly *Hippobosca variegata* Megerle 1803 (Hippoboscidae) has an average of only 4.5 larvae (Schuurmans 1923). These flies are not closely related, but they have evolved very similar feeding habits and reproductive strategies. Both feed on blood from mammals, and both are viviparous. ♀♀ produce 1 egg at a time, and the larva develops inside the uterus where it feeds on a "milk gland" inside the mother. When it is born, the larva pupates almost immediately; vivipary in these flies is thus analogous to giving birth to teenagers. Their protein rich diet is probably one of the reasons these flies have been able to evolve vivipary, a reproduction strategy which is very demanding to the mother. Vivipary allows only a low reproduction rate, but it gives the growing larva exceptional protection and a very high survivorship. Beetles that live in dung and carrion generally have low fecundities (Hinton 1981). Among the most extreme examples are scarabaeid beetles of the genus *Phanaeus* MacLeay 1819. Under natural conditions, these beetles are said to produce about 6 offspring in their lifetime (Halffter 1977). The parents provide their young with very elaborate brood "chambers". Each egg is placed on a ball of dung on which the larva feeds while growing. This brood ball is encapsulated by the parents in a thin layer of clay; the larva is thus almost completely protected from parasites and predators. The low fecundity is probably a result of this time- and resource-intensive nest-building process. Under optimal conditions in the laboratory, the beetles still laid only 12 eggs. The solitary bee *Dieunomia triangulifera* (Vachal 1897) is a host specialist that feeds exclusively on pollen from *Helianthus annuus* sunflowers. ♀♀ produce on average 2-6 offspring in their lifetime (Minckley & al. 1994). Adult activity is timed to coincide with the flowering of their food source. The eggs they produce are large compared to other social and parasitic bees. These eggs provide the young with a rich food source and increase their chance of survival. The adult bees also supply the larva with a pollen ball on which they feed before they emerge. Bark beetles breeding in leafstalks also appear to be among the animals with lowest absolute lifetime fecundity. The habitats of bark beetles are quite varied. Most common are the ones that live in the bark of dead or dying trees, but several other habitats are utilized, including leafstalks of fallen leaves from tropical trees. Some of the bark beetles breeding in fallen leaves may have broods as small as 3 eggs (Beaver 1979). Bark beetles in *Cecropia* Loefling 1758 leafstalks in Costa Rica, show similar extremely low fecundities (Bjarte Jordal, Univ. Bergen, Zool. Inst., pers. comm.). The reason for these low numbers is probably a combination of parental care and a very poor habitat. The trees presumably extract most of the valuable substances out of the leaf before they shed it, so one would expect the leafstalks to have a very low nutritional value. These beetles were the focus of thesis work this summer (Bianca Nygård & Henning Brueland, Univ. of Bergen); preliminary data for one species, *Scolytodes cecropiavorus* Wood 1969 indicate an average fecundity of five offspring per pair. It is still not clear, however, if these small broods really are lifetime fecundity, or if females lay further broods. Of the insects reviewed in this article, *Hippobosca variegata* is most likely the species with lowest lifetime fecundity. An average of 4.5 offspring is extremely low even among these insects that have lower fecundity than most other living animals.

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Chapter 18. Highest lifetime fecundity

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ABSTRACT. An Australian ghost moth, *Trictena atripalpis* Walker 1856, is the insect with the highest recorded fecundity among nonsocial species. One ♀ was reported to lay 2.91E4 eggs, and when dissected, 1.5E4 fully developed eggs were found in the ovaries. Among eusocial insects, queens of the African driver ant *Dorylus wilverthi* Emery 1899 can lay broods with up to 3-4 million eggs every 25 days. This is probably the species with the highest lifetime fecundity among eusocial insects.

INTRODUCTION. Life history theory predicts a trade off between fecundity and parental care (Roff 1992), both of which vary considerably among insects. Although lifetime fecundity varies from < 10 to several millions of eggs, most insects lay between 1E2 or 2E2 and 2E3 eggs (Hinton 1981). There are different reasons why some insects have unusually high fecundities. To explain this variation it is easiest to discuss separately eusocial insects and insects with no social organization.

METHODS. Biological Abstracts 1989-1994 was searched. Most info came from text-books in entomology and general books about social insects (Clausen 1940; Wilson 1971; Holldöbler & Wilson 1990). The extensive table with data on insect fecundity in Hinton 1981 was especially useful.

RESULTS & DISCUSSION

Nonsocial insects. *Leschenaultia adusta* (Loew 1872) (Diptera Tachinidae), a parasite of salt marsh caterpillar (*Estigmene acrea* Drury 1773), has been reported to lay 4,572 eggs (Jackson & al. 1970). The eggs are laid on plant foliage, and must be ingested by the host larvae. A wax scale insect, *Ceroplastes pseudoceriferus* (Green 1935) (Hemiptera Coccidae), is capable of laying more than 1E4 eggs (Sankaran 1954). It infests a number of plants, including the economically important mango. *Kapala terminalis* Ashmead 1892 and *Stilbula cynipiformis* Kirby 1886 (Hymenoptera Eucharitidae), can lay up to 1.5E4 eggs (Clausen 1940). All Eucharitidae are internal or external parasitoids of Formicidae immature stages. They lay large numbers of eggs on vegetation. Larvae that emerge attach themselves to ants. It is not clear if they search for ants or if they just wait for ants to pass nearby (Gauld & Bolton 1988). When they reach the ant nest they actively seek out ant larvae which they attach themselves to or enter. Further development usually occurs when the ant larvae reach prepupal stage. The highest lifetime fecundity among non-social insects appears to be a lepidopteran. An Australian ghost moth ♀, *Trictena atripalpis* Walker 1856 (Hepialidae), captured at Adelaide, laid 2.91E4 eggs (Tindale 1932), and when it was dissected 1.5E4 eggs were found in the ovaries. These moths oviposit while in flight and tend to lay their eggs in the vicinity of the red gumtree (*Eucalyptus camaldulensis* ssp. *camaldulensis* Dehnhardt 1832) on the roots of which their larvae feed. There are other ghost moths that are larger, which may have an even higher fecundity, but I've found no literature on egg number in these species. Most of the nonsocial insects with extremely high fecundity have an uncommon life cycle. None of these species have parental care. Both *L. adusta* and *K. terminalis* rely upon chance encounters between eggs or larvae and their intended hosts. This is also true for *T. atripalpis*, although it drops its eggs in the general vicinity of the host tree. The species seem to share an unusually risky oviposition strategy with unavoidably high juvenile mortality, which selects strongly for high fecundity.

Eusocial insects. The highest recorded fecundities are found in the eusocial insects. Indeed most eusocial insects have high fecundity. Fenton 1952 states in his textbook that the queen of the termite *Macrotermes bellicosus* (Smeathman 1781) [Cfr. *Macrotermes natalensis* (Haviland 1898)] lays an estimated 3E4 eggs each day and, on average, lives 10 years. This calculates to more than 1.09E8 in a lifetime. However, Fenton gives no primary source for his estimates, making it difficult to evaluate their worth. The honey bee queen (*Apis mellifera* Linnaeus 1758) can produce up to 2E5 eggs each year (Bodenheimer & Nerya 1937), and has a life span of 3-4 years. Army ants and driver ants appear to have the highest fecundities among ants, though the longevity of the queens is not known. The army ant *Eciton burchelli* Westwood 1842 can lay a new brood of 1.2E5 eggs every 36 days (Schneirla 1957). Queens of the African driver ant *Dorylus wilverthi* Emery 1899 can lay broods with up to 3-4E6 eggs every 25 days (Raigner & Van Boven 1955). Other driver ants have similar fecundity, 1-2E6 eggs in a month (Holldöbler & Wilson 1990). The queens are the largest among the ants and have up to 1.5E4 ovarioles. They lay egg more or less continually, but with bursts of high production every 3 weeks that last for 5-6 days. All values for egg number in eusocial insects are fairly rough estimates. The insect with the highest fecundity is certainly eusocial, but it is impossible to say which is really highest. The best candidate so far is *D. wilverthi*. The eusocial insects have a highly organized social system, usually with only 1♀ that does all of the egg laying (Wilson 1971). The other members of the colony provide her with food, and tend her eggs as well as doing all of the foraging and nest defense; instead of laying their own eggs, they help the ♀ to achieve as high a fecundity as possible. Generally, increasing parental care is associated with decreasing fecundity (Roff 1992). In eusocial insects we have intensive care of offspring, but not by the mother, who is freed of all responsibilities other than egg-laying. This division of labor makes it possible for a queen to have extreme specializations for fecundity.

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Chapter 19. Adapted to greatest depth

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ABSTRACT. Lake Baikal in the Siberian region of Russia is the world's deepest lake, with a maximum depth of 1,620 m. Although many different orders of insects live in Lake Baikal, only non-biting midges (Diptera Chironomidae) survive in its deeper waters. *Sergentia koschowi* Linevich 1948 larvae have been found in the open waters of Lake Baikal at a depth of 1,360 m, making it the only insect known to survive in waters so deep.

INTRODUCTION. The goal of this chapter is to identify the insect species that lives in water at the greatest depths. The search was limited to the world's deepest lake, Lake Baikal in the Siberian region of Russia. Of all insect spp. living in or around Baikal area, only one sp. of insect is able to live as deep as 1,360 m.

METHODS. To locate references on aquatic insects, I consulted aquatic insect textbooks, general entomology textbooks, and keyword searches on the WebLUIS Search System, the computerized library catalog at the University of FL. I also searched AGRICOLA 1970-1990. Help in finding a champion was obtained from posting a request to the Entomo-L Listserv.

RESULTS. Only a few spp. of Chironomidae live in the deeper portions of Lake Baikal. The depth record belongs to *Sergentia koschowi* larvae, which occur in the fine oozes of lake bottom at 1,360 m (Linevich 1971). Larvae of related sp. *S. baikalensis* Chernovsky 1949 also live in Lake Baikal at depths of 1.5-100 m.

DISCUSSION. The insect living at the greatest depth in water must live in a freshwater habitat, since no insects live in the ocean depths (Norris 1991). The deepest lakes in the world are Lake Baikal (1,620 m) (Kozhov 1963) and Lake Tanganyika, located in Central Africa (1,400 m) (Cole 1983). Lake Tanganyika is a tropical lake with no temperature-induced turnover of oxygen rich water and is considered anaerobic below 200 m (Cole 1983). Lake Baikal is a temperate lake with seasonal turnover of water. Oxygen levels approach saturation down to 500 m, and then drop to 10 mg/l (Kozhov 1963) becoming more depleted toward the bottom; within the bottom layers of ooze, there is no oxygen (Linevich 1971). *S. koschowi* can be found in the abyssal zone, which is greater than 500 m. The zone is composed of silt/clay ooze, and the temperature is about 3.4-3.6°C throughout the year. Kozhov 1963 reported that *S. koschowi* larvae are big (12-20 mm) and bright-red colored with rudimentary eyes. The body color indicates that hemoglobin is present, allowing the insect to survive periods without oxygen. Hemoglobin is a respiratory pigment that can store oxygen (Eriksen & al. 1984). Among aquatic insects, only certain larval chironomids possess hemoglobin (Armitage & al. 1995). Kozhov 1963 published a well documented biological monograph about Lake Baikal that includes over 200 years of work by over 1,000 scientists. Of the insect orders mentioned, Plecoptera (stoneflies), Trichoptera (caddisflies), Ephemeroptera (mayflies), Diptera (flies, midges, mosquitoes), Odonata (dragon and damsel flies), Coleoptera (beetles) and Hemiptera (true bugs), all live in open bays and gulfs of Lake Baikal. The bays and gulfs of Lake Baikal are small bodies of water connected to the open lake by a broad channel. Their depth rarely exceeds 4.5-5 m, but they can be influenced by Lake Baikal's open waters during inshore winds (Kozhov 1963). Only chironomid midges (Diptera) inhabit the open waters of Lake Baikal. Based on present knowledge, *Sergentia koschowi* is the insect adapted to the deepest fresh waters, and the only possibility for another record would be an unknown species from the same lake.

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Chapter 20. Least oxygen dependent

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ABSTRACT. Apneustic insects (those with closed tracheal systems) rely solely on dissolved oxygen (O) and show the least O dependence. Midges (Diptera Chironomidae) are common and widespread apneustic aquatic insects and are often the only insects to occur in low O habitats such as profundal sediments in highly productive lakes. The midge *Chironomus plumosus* (Linnaeus 1758) typifies least O dependence and is declared champion.

INTRODUCTION. Insects, like other multicellular animals, require O for efficient cellular metabolism. Insects obtain O from their environments and convey it to cells in many ways, and hence have adapted to nearly all terrestrial and aquatic habitats. Morphological, physiological, behavioral adaptations of insect respiration must be examined to understand how insects can survive in a wide array of O environments. This chapter discusses how insects have adapted to low-O environments, identifies the insect group that has most successfully adapted and names a representative from this group as champion.

METHODS AND RESULTS

The candidates. Two groups of insects that have successfully invaded low O environments are endoparasitic and aquatic insects. These insects have developed a wide array of strategies to obtain O from their respective environments. These respiratory strategies can be grouped into 2 general categories:

1. Insects obtaining O from atmospheric sources, either through a direct connection with the atmosphere or indirectly through an intermediate source;
2. Insects relying solely on dissolved O of a particular microhabitat.

The insects requiring the lowest O concentrations and demonstrating the least dependence on atmospheric O (i.e., insects in the second category) are apneustic, meaning the tracheal system is closed with no functional spiracles. These insects generally obtain O by diffusion of O through the body cuticle into the tracheae where O comes out of solution and can be more readily transported as a gas to the areas of need.

Apneustic endoparasites. Examples of apneustic endoparasites include the larval forms of a number of parasitic Hymenoptera (e.g., Braconidae, Ichneumonidae) and parasitic Diptera, such as the Cryptochetidae which parasitize scale insects (Borror & al. 1989). The spiracles of these endoparasites remain closed and non-functional until larvae mature and are ready to leave the host. Until that time, apneustic endoparasites are strictly dependent upon cuticular diffusion of O, either dissolved or gaseous, from host O supplies. Braconidae facilitate gas exchange by everting their hindgut to form a caudal vesicle that then functions as an additional surface for cuticular diffusion of O from host tissues (Chapman 1982). In the case of Cryptochetidae, one species, *Cryptochaetum iceryae* (Williston 1888), possesses 2 long caudal filaments containing tracheae which become entangled with the tracheae of its host. Atmospheric O diffuses from the host tracheae into the tracheae contained in the caudal filaments of the parasite (Thorpe 1930).

Apneustic aquatic insects. Differences between terrestrial and aquatic environments, in terms of O availability, are striking. Approximately 20% of atmospheric air is composed of O whereas water, even when saturated, contains less than 0.4% (by mass) of free O. Therefore insect respiration, utilizing dissolved O in water, requires that far more water be processed for an equal amount of O. Additionally, because water weighs more than air of equal volume, more energy must be expended by aquatic insects in moving water past respiratory surfaces than expended by atmospheric breathers. In response to the intrinsic difficulties involved with aquatic respiration, aquatic insects have evolved a variety of morphological, physiological, phenological and behavioral adaptations enabling them to become widespread in aquatic habitats with variable supplies of dissolved O (Eriksen & al. 1996). Gas exchange in aquatic insects with closed respiratory systems requires that O be absorbed through the cuticle of the insect's body wall. In insects with a membranous, highly permeable cuticle and a high surface/volume ratio, diffusion of O through general body wall is sufficient in providing O. Respiration is strictly cutaneous in many of the smaller worm-shaped Diptera larvae, including Chironomidae, Ceratopogonidae, Simuliidae, Chaoboridae, as well as gill-less Trichoptera and Plecoptera larvae. In insects without these morphological attributes, cutaneous respiration is supplemented by tracheal gills (thin, highly permeable, tracheated outgrowths of body wall).

The champion. The dipteran family Chironomidae is widespread and abundant in extremely low O environments where other insects would quickly die or enter anoxybiosis. Although many chironomids are tolerant of low O conditions, the species *Chironomus plumosus* perhaps best typifies least O dependence. This well studied species is a common and abundant inhabitant of oxygen depleted lake sediments.

DISCUSSION. Chironomidae are often the only insects found in lake sediments of the profundal zone where hypoxic (O concentrations less than 3 mg l^{-1}) and even anoxic conditions sometimes occur (Pinder 1995). The chironomids inhabiting lake sediments are there throughout most of their larval and pupal stages. The pupae, just prior to eclosion, rise to the surface where the adults emerge. The terrestrial adult stage is relatively short-lived with mating constituting the activity of primary biological importance. The larvae, which pass through four larval instars, occur on the bottom sediments at population densities sometimes numbering thousands m^{-2}. Chironomids, occurring in sediments of high organic matter and very low oxygen content, have been uniquely successful in exploiting these environments as a result of behavioral and physiological adaptations. The larvae and pupae of most species occurring in low oxygen sediments construct burrows and fixed tubes of sediments held together with silky secretions. Tube and burrow dwellers are able to ventilate their tubes with fresh water by dorsoventral undulations of the body, thereby facilitating gas exchange during times of low ambient oxygen. In *Chironomus dorsalis* Meigen 1818, tube height above the sediment bed has been shown to be dependent on O concentrations, with larvae extending the tubes above the sediment bed as O concentrations at the sediment bed level decrease (Konstantinov 1971). Other species, such as *C. plumosus*, construct burrows within the sediments which are interconnected and ventilated in a mutualistic effort (Jonasson & Kristiansen 1967). The undulations, in addition to ventilating the tubes and burrows, draw in food from nearby organic sediments, thereby reducing activities related to food gathering. During periods of anoxia, chironomid larvae become inactive and some species are able to survive for extended periods of time. In a laboratory study of resistance to anoxia, Nagell & Landahl 1978 found that *C. plumosus* survived anoxic conditions about twice as long as *C. anthracinus* Zetterstedt 1860. The corresponding LT_{50} values were ~205 and ~100 days. In addition to the aforementioned behavioral adaptations, many of the tube- and burrow-dwelling Chironomidae that appear bright red (e.g., Chironominae) possess hemoglobins which play a vital physiological role in increasing respiratory efficiency. The hemoglobins found in Chironomidae have a very high affinity for O, unlike vertebrate hemoglobins, and serve as a temporary store for O absorbed through the cuticle until it is needed for metabolism. Walshe 1950 determined that hemoglobin present in *C. plumosus* is capable of storing O sufficient to meet the metabolic needs of the resting larva for ~9 minutes. Hemoglobin is also considered vital in the transport of O to the various tissues. Typically, Chironomidae in tubes or substrate burrows alternate periods of ventilation movements, causing the hemoglobin to become saturated, with periods of feeding or rest when O stored in the hemoglobin is released and used for metabolism.

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Chapter 21. Most heat tolerant

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ABSTRACT. Desert-dwelling, scavenger ants are among the most thermophilic insects yet identified. Of these desert ants, *Cataglyphis bicolor* (Fabricius 1793) (Hymenoptera Formicidae), an inhabitant of the Sahara desert, is identified as the most thermotolerant. At least 3 genera of desert dwelling ants, *Cataglyphis*, *Ocymyrmex*, and *Melophorus*, from the Sahara, Namib and Australian deserts, respectively, are known to forage in surface temperatures above 60°C. Current literature supports *Cataglyphis* as the most thermotolerant of these genera, with a critical thermal maximum of 55.1 ± 1.1°C recorded for *C. bicolor.*

INTRODUCTION. This chapter attempts to identify the insect which is naturally occurring and active at the highest temperature. Highest temperature is considered in 2 ways, with both interpretations influencing the selection of a champion. First, it is the *ambient temperature* in which the insect naturally lives and completes its life cycle. Second, it is *heat tolerance*, often measured as the Critical Thermal Maximum (CTM), that the insect can physiologically withstand in an active state (i.e., not egg or diapause). To determine CTM, organisms at their acclimation temperature are heated at a constant rate until they lose the ability to escape the increasing temperature by locomotion but are not killed. The temperature at which this endpoint occurs is recorded as the CTM (Moulton & al. 1993). The scope of search was limited to active life cycles to give it more ecological relevance. There are many instances, for example, of extraordinary tolerances in specific stages. One such example, a fly larva (*Polypedilum*) from NG and UG, can withstand a temperature of 102°C for 60 s and still metamorphose successfully (Hinton 1960). While this thermotolerance is remarkable and may contain scientific discoveries yet unrevealed, it would probably never be encountered in a natural ecosystem.

METHODS. Secondary literature, solicitation over the Entomo-L Listserv, and queries of faculty at the UF Entomology & Nematology Department provided the initial candidates. A subsequent literature search of Biological Abstracts and Zoological Record narrowed the focus.

RESULTS. There are at least 3 genera of ants, all desert scavengers, and each from a different desert around the world, that forage for the corpses of insects and other arthropods which have succumbed to the heat stress of their desert environment (Gehring & Wehner 1995). These genera include *Cataglyphis* Foerster 1850 (Formicinae) in North Africa, *Ocymyrmex* Emery 1886 (Myrmicinae) of South Africa, and *Melophorus* Lubbock 1883 (Formicinae) of AU (Heinrich 1993). Among these thermophilic ants, *Cataglyphis* seems to emerge as the premier thermophile. It lives in the Sahara Desert and forages at a body temperature well above 50°C with surface temperatures of up to 70°C (Wehner & al. 1992). In laboratory tests, the critical thermal maxima were measured at 53.6 ± 0.8°C (SD?, SE?) for *C. bombycina* and 55.1 ± 1.1°C for *C. bicolor* (Gehring & Wehner 1995). Although the other genera mentioned may forage at similar environmental temperatures, they are apparently not quite as thermotolerant. In lab tests, for example, the Namib Desert ant *Ocymyrmex barbiger* entered a heat coma in only 25 seconds when placed in a 55°C environment, whereas 5 *Cataglyphis* species exhibited symptoms after 10-25 minutes (Marsh 1985b). Perhaps the most serious challenger to *C. bicolor* is *Melophorus bagoti* Lubbock 1883 from the central AU desert. Greenaway 1981 reported that *M. bagoti* survived in lab tests for 1 h @ 54°C. In fact, the ants do not even emerge to forage in their desert environment until surface temperature is a blistering 56°C. Aquatic insects, principally those present in hot springs, were also examined. The physiological challenges presented by aquatic habitats are very different from those of terrestrial habitats, particularly with respect to thermoregulation. Due to the moderating effect of the heat capacity of water, aquatic insects must accept body temperatures equal to that of the pool. This limits the hot spring temperature they can accept. Pennak 1978 reported the upper limit for aquatic insects in an active state @ ~50°C. Ward 1992 compiled a list of active aquatic insects occurring in hot springs at temperatures in excess of 40°C, the most thermophilic being *Chironomus* sp. affinis *tentans* Fabricius 1805 (Diptera Chironomidae) @ 49°C. A variety of other insects were considered, including the desert cicada *Diceroprocta apache* (Davis 1921) (Homoptera Cicadidae), beetles such as desert tenebrionids and cicindellids, termites, and social bees and wasps. All fell short of the accomplishments of the desert scavenging ants.

DISCUSSION. No animal is known to live and carry out its complete life cycle at a temperature over 50°C (Schmidt-Nielsen 1990). It is probable, then, that desert scavenger ants are foraging at temperatures at or near the limit of animal potential. In field studies, it has been determined that these ants forage within a narrow internal heat band very near to their thermal maximum. As a typical case in point, the foraging activity of *C. bombycina* is compressed to a width of just 7°C (46.5°C to 53.6°C) (Wehner & al. 1992). They will forage until their body temperature reaches the CTM, at which time they must seek refuge. Failure to find respite from the heat in critical seconds will result in becoming a heat casualty themselves. One can assume that this small insect with a mean body mass of 9.7 mg would within seconds have a body temperature close to that of the environment, which often exceeds their CTM (Heinrich 1993). There are basically 3 characteristics that adapt these thermophilic ants to exploit the hottest deserts of the world at the hottest times of the day. First, the ants are quite speedy, which minimizes sun exposure and may contribute to convective cooling. Wehner & al. 1992 clocked *C. fortis* and *C. bombycina* at 1 m/s, which approaches the top speed of *Onymacris plana* Peringuey 1886, the Namib Desert tenebrionid which is possibly the fastest running arthropod ever recorded (Heinrich 1993). In addition, there is a direct correlation between running speed and surface temperature (Marsh 1985a). Second, their long legs elevate them above the hot substrate. Temperatures 4 mm above the ground (which is roughly "ant height") are some 6 to 7°C cooler than at the surface (Gehring & Wehner 1995). Third, they possess a foraging behavior of pausing on the stalks of dry vegetation where the lower temperatures can off-load excess body heat. On the hottest days, ~75% of their foraging time is spent in thermal refuges (Wehner & al. 1992). Desert ants occupy a specific ecological niche and risk thermal death with each foraging expedition. In the case of *C. bombycina* in the Sahara desert, foraging activity is limited to a small thermal window in the full midday summer sun. As other desert ants retreat to underground burrows at surface temperatures of 35 to 45°C, *C. bombycina* is only starting its foraging activity (Wehner & al. 1992). It is near this same temperature that a lizard predator, genus *Acanthodactylus* Fitzinger 1814 (Lacertidae) [Cfr. genus *Acanthodactylus* Escalera 1914 (Tenebrionidae)], also retreats underground. Ants experimentally released on the desert floor at temperatures lower than the natural foraging temperature fell victim to predation, often within 5 minutes. The narrow foraging window of *C. bombycina*, then, is defined by predation pressure at the low extreme and its CTM at the other (Wehner & al. 1992). By pushing their thermal limits to the extreme, they occupy a specialized ecological niche; effectively reducing competition from other, less thermotolerant, ants and neatly evading predation by desert vertebrates which must burrow to escape the intense heat. This incredible adaptation to exposure to high temperatures exhibited by desert scavenger ants may be linked to Heat Shock Protein (HSP) synthesis. Although the mechanisms are not fully understood, HSP studies conducted by Gehring & Wehner 1995 on *C. bombycina* and *C. bicolor* indicate the increased HSP synthesis observed in these species confers increased thermotolerance.

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Chapter 22. Most saline tolerant

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ABSTRACT. Brine fly larvae, *Ephydrella marshalli* (Diptera Ephydridae), show remarkable powers of osmoregulation in withstanding salinities up to 5,848 mOsm/l under laboratory conditions (sea water is 1,197 mOsm/l). Larvae of a long-legged fly, *Hydrophorus plumbeus* (Diptera Dolichopodidae), are second to *E. marshalli*, as they withstand osmotic concentrations as great as 5,650 mOsm/l.

INTRODUCTION. I define the most saline tolerant insect as the one capable of withstanding the strongest salinity for at least 24 h. The scope of my search was not limited to larvae, although larvae hold first and second prizes for saline tolerance.

METHODS. CD-ROM versions of Biological Abstracts and AGRICOLA 1986-1995 were searched and proved very helpful. Additional resources included personal communications with scientists, secondary literature, Entomo-L Listserv.

RESULTS. *Ephydrella marshalli* Bock 1987 larvae collected from commercial salt works lagoons on Port Phillip Bay, Victoria, AU have survived several days in hypersaline NaCl media of 5,848 mOsm/l (Marshall & al. 1995). This was determined by an experiment designed to find out whether ephydrid larvae could produce hypo- and hyperosmotic rectal fluids in response to changes in the external environmental salinity. *E. marshalli* larvae have the ability to regulate the composition of body fluid to compensate for fluctuating external salinities; K concentration in the flies' rectal fluid rises as the salinity of the external medium increases. Salinity tolerance of *E. marshalli* is nearly matched by larvae of yet another fly: the dolichopodid *Hydrophorus plumbeus* Aldrich 1911. Herbst & Bradley 1988 investigated the osmoregulation of *H. plumbeus* larvae they collected from Mono Lake, US-CA, and found that they, like *E. marshalli*, are able to osmoregulate over a wide range of salinities. These larvae survived exposure to concentrations as great as 5,650 mOsm/l for 7 d.

DISCUSSION. Diptera, or true flies, are a large order of endopterygote (= holometabolous) Neoptera. In aquatic species, only the larval and pupal stages live in the water, the adults, with very few exceptions, being terrestrial (Williams & Feltmate 1992). The family Ephydridae includes shore flies and brine flies which usually inhabit littoral zones, margins of lotic and lentic habitats, saline lakes and pools, salt marshes, crude petroleum pools, and hot springs (Williams & Feltmate 1992). Dolichopodids are known to have colonized at least the periphery of the marine environment and inland saline waters, as well as margins of ponds, lakes rivers and streams (Williams & Feltmate 1992). The salt water mosquito *Aedes detritus* (Haliday 1833) has also been noted for its high salinity tolerance (Beadle 1939), although not as high as either *E. marshalli* or *H. plumbeus*. Its method of osmoregulation is very similar to that of other dipterans; reabsorptive and secretory cells are arranged in parallel in an ileum-like area in *Ephydrella* larvae (Marshall & Wright 1973), and arranged in series in *Aedes* larvae (Askura 1973). Marshall & al. 1995 speculate "that since saline water ephydrid larvae have greater salinity tolerances than saline water mosquito larvae, the parallel arrangement of cell types... similar to those arranged serially in mosquito larvae, may be an inherently more efficient osmoregulatory system."

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Chapter 23. Most toxic insect venom

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ABSTRACT. Insects in the order Hymenoptera were recorded as early as the 26th century BC as possessing a venom toxic to vertebrates. Harvester ants in the genus *Pogonomyrmex* (**Figure 1**) have the most toxic venom based on mice LD_{50} values, with *P. maricopa* venom being the most toxic. LD_{50} for this sp. is 0.12 mg/Kg injected intravenously in mice, equivalent to 12 stings killing a 2 Kg rat. A *Pogonomyrmex* sp. sting produces intense pain in humans that lasts up to 4 h.

Figure 1. Adult ☿ of *Pogonomyrmex* sp. Photo courtesty of J.O. Schmidt.

INTRODUCTION. A venom is a toxin that is injected into another organism using a specialized apparatus attached to a venom-producing gland. It may be used to immobilize or kill prey and/or to defend the delivering organism against attack by predators. Venomous insects are known from the orders Lepidoptera, Hemiptera, Hymenoptera (Blum 1981). The method of delivery may be active, such as the sting apparatus of Hymenoptera (bees and wasps), and the mouthparts of Hemiptera (stylets), or passive such as the modified setae in some lepidopteran larvae (caterpillars) that are broken on contact and pierce the outer surface of the receiving organism. Schmidt 1982 proposed that some insects in the orders Diptera, Neuroptera and Coleoptera also possess oral venoms, but there is a problem with whether this constitutes a true venom or is a digestive fluid that is ejected. The biological activity of the venom can be classified as neurotoxic, hemolytic, digestive, hemorrhagic and algogenic (pain-producing). Venoms are chemically described as consisting of alkaloids, terpenes, polysaccharides, biogenic amines (such as histamine), organic acids (formic acid), and amino acids, but the majority are peptides and proteins (Schmidt 1986a; Blum 1981). The first record of human death attributed to envenomation by a wasp or hornet was that of King Menes of Egypt in the 26th century B.C. (Waddell 1930). Toxicity of venoms is difficult to quantify in an unbiased manner and will vary among target species. It is also confounded by responses to the venom that are due to immune system disorders (such as hypersensitivity and allergies). For this reason, morbidity and mortality data may not be the best comparative method to classify venom toxicity (Schmidt 1986b). I will base my selection of the species of insect with the most toxic venom to vertebrates based on LD_{50} values using mice as the test organism.

METHODS. Subscribing to the Entomo-L Listserv and posting a general inquiry about insect venoms was the most profitable first step in obtaining information about venomous insect species. Personal interviews with UF and USDA-ARS staff provided often colorful information on people's "favorite" stinging bug. A wire story ("Killer Caterpillars," *Gainesville Sun*, 1996-I-16) apparently was widely distributed in newspapers and generated some discussion on the bulletin board. Searches on the WebLUIS Search System for information on literature in the UF libraries retrieved some secondary literature such as the book by Blum 1981. Primary literature was identified using references obtained through Entomo-L replies and also by searching the AGRICOLA, Current Contents, and MEDLINE databases available at UF.

RESULTS. There were numerous insects suggested for the most toxic insect from personal interviews and the Entomo-L bulletin board replies, many of which were based on personal experience and descriptions of the reaction to being envenomed. Insects suggested included harvester ants (*Pogonomyrmex* Mayr 1868, Hymenoptera Formicidae), bees (Hymenoptera Apidae), yellowjackets and hornets (*Vespula* Thomson 1869, *Dolichovespula* Rohwer 1916; Hymenoptera Vespidae), velvet ants (Mutillidae), puss caterpillars [*Megalopyge opercularis* (J.E. Smith 1797), Megalopygidae], slug caterpillars [*Sibene stimulea* (Clemens 1860), Limacodidae], giant silkworm moth caterpillars (genus *Lonomia* Walker 1855; *Automeris io* Fabricius 1775, Saturniidae) and assassin bugs (genus *Rasahus* Amyot & Serville 1843, Reduviidae). However unpleasant the experience of being "stung" by ants, bees, wasps and assassin bugs is, it is difficult to quantify pain responses objectively. Likewise, the perception of the toxicity or danger may be artificially inflated when death of humans or other vertebrates is the result of envenomation (Schmidt 1986b). LD_{50} values provide an unbiased method of comparing insect venoms. Hymenopteran insects possess the most toxic venoms that have been characterized (Schmidt 1990; J.O. Schmidt personal communication). **Table 1** lists the LD_{50} values for some of these insects that are known to most people, such as the honey bee, paper wasp, yellowjacket, velvet ant and harvester ants. The most toxic venom is found in a species of harvester ant, *Pogonomyrmex maricopa* Wheeler 1914 with a mouse LD_{50} value of 0.12 mg/Kg (Schmidt & al. 1989; J.O. Schmidt personal communication). Schmidt 1986a states that for a 2 Kg mammal only 12 stings are required to reach the LD_{50} dose. Other species of *Pogonomyrmex* also produce venoms with low LD_{50} values when compared with other Hymenoptera (**Table 1**).

Table 1. LD_{50} (mg/Kg) in mice for toxins found in Hymenoptera. * Average of 20 spp. tested.

f	sp	common name	LD_{50}	reference
Apidae	*Apis mellifera* Linnaeus 1758	honey bee	2.8	Schmidt 1990
Mutillidae	*Dasymutilla klugii* (Gray 1832)	velvet ant	71	Schmidt & al. 1980
Vespidae	*Polistes canadensis* (Linnaeus 1758)	paper wasp	2.4	Schmidt 1990
Vespidae	*Vespula squamosa* (Drury 1770)	yellowjacket	3.5	Schmidt & al. 1980
Formicidae	*Pogonomyrmex* Mayr 1868 *	harvester ants	0.66	Schmidt 1990
Formicidae	*P. maricopa* Wheeler 1914	harvester ant	0.12	Schmidt & al. 1989

DISCUSSION. Comparing LD_{50} values of a test organism (in this case, mice) can be a useful tool to objectively assess the toxicity of insect venoms; however, this method has its limitations. The values obtained in mice reveal a relative toxicity scale for different toxins in mice only. They do not reflect how the same toxins would rank for another species (such as humans). For example, the LD_{50} value of *P. maricopa* venom against a lizard, *Phrynosoma cornutum* (Harlan 1825) (Phrynosomatidae) which is a predator of *P. maricopa*, was much higher than in mice (162 mg/Kg). When one other lizard, *Sceloporus jarrovii* Cope 1875 (Phrynosomatidae) was tested, the venom had an LD_{50} value of 28 mg/Kg. These results suggest that *P. cornutum* has evolved resistance to the harvester ant venoms and can exploit the ants as a food resource (Schmidt & al. 1989). In another species of harvester ant, *P. badius* (Latreille 1802) there were high levels of an enzyme, phospholipase A2, which is also present in honey bee and wasp venoms (Schmidt & Blum 1978a). Although cross-reactivity to honey bee and wasp venoms may be involved in the response of humans to *Pogonomyrmex* envenomation, in those cases that have been studied cross-reactions to vespid and formicid venoms have not been found (Schmidt 1986b). Interestingly, the venom of *P. badius* is not particularly lethal against larval insects (Schmidt & Blum 1978b). Since harvester ants are non-predatory, it suggests that their venom has evolved from being used in prey capture as in other ant spp. (Schmidt 1986a), to defense against vertebrates; hence their power against humans and other vertebrates.

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Chapter 24. Loudest

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ABSTRACT. The African cicada *Brevisana brevis* (Homoptera Cicadidae) produces a calling song with a mean sound pressure level (SPLm) of 106.7 decibels (dB) @ a distance of 50cm. 2 species of North American cicadas, *Megatibicen pronotalis walkeri* (Metcalf 1955) (= *Tibicen walkeri* Metcalf 1955) and *M. resh* (Haldeman 1852) [= *Tibicen resh* (Haldeman 1852)], produce an alarm call with SPLm of 105.9 dB @50cm. *B. brevis* is likely the loudest insect species on record. Cicada songs are species-specific and play a vital role in communication, reproduction and possibly defense.

INTRODUCTION. In the context of this chapter, "loudest insect" is defined as the insect species capable of producing the most intense sound within the range audible to normal human hearing (20Hz-20KHz). Loudness will be quantified by SPL in dB produced by a single insect measured @ a distance of 50cm using a reference value of 20 N/m^2. The greatest published sample SPLm for a sp. will determine the champion. The biological significance of the sound production is discussed.

METHODS. Initial candidates were provided through personal communications, an Internet search for the "loudest insect" using Yahoo!, and posting a request for help on the Entomo-L Listserv. CD-ROM versions of CAB Abstracts 1985-97 and AGRICOLA 1970-97 were searched to obtain other candidates and SPL measurements. Secondary literature was used to interpret and equalize SPL values obtained. SPL values were standardized sensu Peterson 1967.

RESULTS. The Entomo-L Bulletin Board was the most productive source of potential candidates providing numerous species from the orders Orthoptera and Homoptera. Suggested orthopteran species include a large field cricket from Malaysia, *Tarbinskiellus portentosus* (Lichtenstein 1796) [=*Brachytrupes portentosus* (Lichtenstein 1796) = *Gryllus (Acheta) achatinus* Stoll 1813], the bladder grasshopper *Bullacris membracioides* (Walker 1870), an acridid, *Circotettix rabula* Rehn & Hebard 1906, and the European mole cricket *Gryllotalpa vineae* Bennet-Clark 1970 registering 96 dB @ 50cm (Bennet-Clark 1970), the highest recorded SPL for these contestants. Homopteran contenders include ♂ cicadas of family Cicadidae. The range of SPLm for samples of calls from the 68 species considered is 69.1-106.7 dB (Sanborn & Phillips 1995; Villet 1987; Young 1990). A maximum SPL (SPLM) of 108.9 dB was measured in an alarm call produced by *Megatibicen pronotalis walkeri* (Sanborn & Phillips 1995). SPLm/M for the 6 finalists are presented **in Table 1**.

Table 1. Sound pressure levels (SPL) for the 6 loudest insect spp. finalists. **S**, song type: A, alarm; C, call. **SPLm*/M**, mean/max SPL.
* dB re 20 N/m^2 measured @ 50 cm (sample size). ** Adjusted to 50 cm from 20 cm.

sp	**S**	**SPLm*/M**	**reference**
Brevisana brevis (Walker 1850)	C	106.7(10)/107.5	Villet 1987
Pycna semiclara (Germar 1834)	C	106.2(11)/108.0	Villet 1987
Diceroprocta apache (Davis 1921)	C	106.2(8)/107.9	Sanborn & Phillips 1995
Megatibicen pronotalis walkeri (Metcalf 1955)	A	105.9(8)/108.9	Sanborn & Phillips 1995
Megatibicen resh (Haldeman 1852)	A	105.9(9)/107.2	Sanborn & Phillips 1995
Cyclochila australasiae (Donovan 1805)**	C	105.7(8)/107.8	Young 1990

Most ♂ cicadas produce an alarm call and calling song that vary in SPL. I award the loudest insect record to *Brevisana brevis* (Homoptera Cicadidae) for a calling song SPLm of 106.7 dB (Villet 1987). *Megatibicen pronotalis walkeri* and *M. resh* deserve honorable mention for sharing the highest mean alarm call SPL of 105.9 dB (Sanborn & Phillips 1995).

DISCUSSION. Sound is produced by cicadas when muscles buckle the tymbals, rib-strengthened chitinous membranes located on the dorsolateral surfaces of the 1st abdominal segment (Sanborn & Phillips 1995). Sound pulse is modified by several body components and radiated through the tympana (Young 1990; Young & Bennet-Clark 1995). Sanborn & Phillips (1995) found that SPL for both calling songs and alarm calls of 59 spp. of North American cicadas correlate directly with insect body M (R^2 = 0.325 and 0.451, respectively). Dry M of *Brevisana brevis* is ~0.3 g. *Tacua speciosa* (Illiger 1800) and *Megapomponia imperatoria* (Westwood 1842) [=*Pomponia imperatoria* (Westwood 1842)], SE Asian cicadas, have dry M of ~1.5 and 2.0 g, respectively. Anecdotal accounts of songs of *M. imperatoria* suggest they are deafening. It is likely that *B. brevis* holds the record only because of a lack of investigation in SE Asia (Villet, pers. com.). Most ♂ cicadas attract mates with their calling song (Sanborn & Phillips 1995) giving larger ♂♂ a competitive advantage in sexual selection. The calling song also stimulates aggregation of conspecific ♂♂ (Simmons & al. 1971); when ♂♂ are in close proximity, it may repel, resulting in minimum distance between individuals (Doolan 1981). Smith & Langley 1978 examined the immediate and short-term effects of the ♂ desert cicada *Diceroprocta apache* alarm song on prey handling ability of an aggressive generalist predator, the southern grasshopper mouse *Onychomys torridus*. While the irritating call was not sufficient to deter attacks, increased handling time reduced predatory efficiency and enhanced the probability of the insect's escape. The noise produced by cicadas could be interpreted as an advertisement for predators. At close range, the painfully intense sounds can also have a repellant effect on bird predators. Simmons & al. 1971 theorize the coexistence of different frequencies of songs produced during the simultaneous emergence of acoustically isolated sympatric cicadas may jam the hearing of predators better than one species by itself.

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Chapter 25. Greatest host specificity

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ABSTRACT. Fig wasps (Hymenoptera Agaonidae) show incredible host specificity which is essential to their survival in an obligate mutualism with figs. Hybrids do not occur in figs and fruit not pollinated is often aborted. A mistake by a wasp entering the wrong syconium (receptacle with multiple flowers) and ovipositing will likely cause the demise of its brood. The fig likewise will fail to produce seed and propagate. Figs have evolved intricate entrances and chemical cues which select their specific pollinators. *Blastophaga psenes* (Linnaeus 1758) is typical of the agaonids, the insect group showing the greatest host specificity.

INTRODUCTION. Host specificity is common among many insects during all stages of their life cycles. Often though, stages of the same insect are not specific to the same host or the same stage of one host. A larva may well derive its nourishment from the leaves of a plant and its adult stage survive on the nectar from the plant's flowers. This chapter attempts to determine the insect group and designate a representative species whose complete life cycle is most dependent on one stage of a single host (i.e., the greatest host specificity).

METHODS. Professors and colleagues were asked to nominate candidates and the Internet searched for pertinent information. Secondary literature on insect life cycles, parasitoids, and symbiosis were reviewed. Primary literature was obtained from references in the secondary literature and by searching AGRICOLA, Biological Abstracts and CAB Abstracts 1986-1997.

RESULTS. Mutualism is a mutually beneficial association between different kinds of organisms (i.e., a symbiosis in which both partners gain fitness. Often it is obligate so that each organism's existence is dependent on the other). Insects involved in an obligate mutualism are often extremely host specific as is the case with fig wasps, yucca moths, and fungus-culturing ants. The 884-odd species of *Ficus* Tournefort ex Linnaeus 1753, some sspp. and many varieties, constitute the most distinctive of the widespread gg. of tropical plants (Hill 1967; Janzen 1979). For the pollination of their flowers, figs are dependent upon Hymenoptera Chalcidoidea of family Agaonidae (fig wasps). Correct pollen transfer is essential because hybrids are not viable. For the propagation of their kind, fig wasps are dependent upon figs ovaries, in which their larvae develop. ♂♂ never leave the syconium (multiple flowers embedded in a hollow fleshy receptacle), dying after mating with ♀♀ and cutting an exit hole for them. ♀♀ do not feed in adult stage and have only a few days at most to find a receptive syconium of a like fig. Pollinating fig wasps are species-specific to their host, although in some instances the fig or the wasp may have developed into distinct subspecies (Wiebes 1979). One of the best-documented cases of a species of fig needing its distinct pollinator is that of the edible fig (Ramirez 1970). *Blastophaga psenes* is the pollinator of the edible fig (*Ficus carica* Linnaeus 1753) and will serve as the representative of the family Agaonidae which displays the greatest host specificity. There are ~40 spp. of *Yucca* Linnaeus 1753 which are pollinated exclusively and obligately by yucca moths (Lepidoptera ex Incurvariidae) in 2 closely related genera (genus *Tegeticula* Zeller 1873; genus *Parategeticula* Davis 1967, Lepidoptera Prodoxidae) containing a total of 4 species. 2 of these 4 spp are host specific, another pollinates 2 spp of *Yucca*, while the 4th is now known to actually be a complex of spp. whose members exhibit high, but not complete, host specificity (Addicott & al. 1990). Fungus-culturing ants (Formicidae Attini) with a normal garden, never culture an alien fungus or an alien part of the normal fungus garden of a different genus of attine. Occasionally the ants will accept a part of the garden of another ant sp. in the same genus but will eventually discard it if its own mycelium (mass of interconnected fungus hyphae) is in ample supply. Tests in Trinidad in 1934-35 showed variable results with workers of several different genera not only feeding upon, but also tending to fungus from outside their genus (Weber 1979).

DISCUSSION. It has been shown that agaonids from different varieties of the same fig species are often morphologically indistinguishable, although it is strongly felt that they must be biologically distinct (i.e. sibling species). An extreme case was found in Hong Kong where the agaonids from the closely related species *Ficus pyriformis* Hooker & Arnott 1837, *F. variolosa* Lindley ex Bentham 1842 and *F. erecta* Thunberg 1786 [= *F. erecta* var. *beecheyana* (Hooker & Arnott 1888)] were not separable on morphological grounds. A complication in this case was that there was considerable ecological and phenological difference between the respective plants and their fig crops. It was possible, but unlikely, that all 3 *Ficus* spp were being pollinated by different populations of the same wasp species. The final opinion was that most probably there were 3 sibling spp of *Blastophaga* Gravenhorst 1829 involved (Hill 1967). A supposedly shared wasp, *Pegoscapus mexicanus* (Ashmead 1904) [= *Secundeisenia (Eiseniella) mexicana* (Ashmead 1904)] of *F. aurea* Nuttall 1846 and *F. citrifolia* Miller 1768 in south US-FL, has recently been separated into 2 spp, *Pegoscapus jimenezi* (Grandi 1919) and *P. assuetus* (Grandi 1938) (Bronstein 1989). There are a few reports in the literature of one sp of fig being inhabited by 2 agaonid wasps. The best documented is *F. tuerckheimii* Standley 1917 which is always pollinated by 2 spp of *Pegoscapus* [*Pegoscapus carlosi* (Ramirez 1970) = *Blastophaga carlosi* Ramirez 1970; *P. mariae* Ramirez 1970 = *B. mariae* Ramirez 1970] in both CR and MX. These 2 wasps apparently never attempt to enter any other related figs (Ramirez 1970). Bronstein 1987 tried to determine the mechanism which isolates the common neotropical fig *Ficus pertusa* Linnaeus filius 1782 from its sympatric congener *F. tuerckheimii* and 2 rarer *Ficus* spp at one site in CR. In general, only the correct pollinator converged on each *F. pertusa* tree, even when syconia of other spp were available and all the pollinator spp were present. The evidence suggests the existence of species-specific recognition of flowering fig trees by their pollinator wasps. It appears that a species-specific, volatile chemical attractant is released briefly from *F. pertusa* trees when the florets are mature enough to be pollinated. Fig culture was established in GR as early as the 9th century B.C. by the process of caprification. This process is designed to secure the pollination of the cultivated fig (*Ficus carica*), which produces only ♀ flowers. It consists of suspending figs of the ♂ form of the wild fig (caprifig) in the cultivated trees to provide pollen via the emerging ♀ wasps, *Blastophaga psenes*. In US-CA the production of edible figs with viable seeds failed until the correct pollinator (*B. psenes*) was introduced in 1889 after many failed attempts with other *Blastophaga* spp. (Ramirez 1970).

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Chapter 26. Largest parasitoid brood

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ABSTRACT. The largest parasitoid broods are produced by polyembryonic parasitoids in the genus *Copidosoma* Ratzenburg 1844 (Hymenoptera Encyrtidae). The largest broods reported in the literature are for *Copidosoma floridanum*. This cosmopolitan wasp is an obligate egg-larval parasitoid of moths in the subfamily Plusiinae (Noctuidae). Broods for this species commonly exceed 2E3 wasps/host. The largest brood reported is 3,055 individuals. The runner-up is another encyrtid *Copidosoma (=Berecyntus) bakeri* (Howard 1898) which produces broods exceeding 1.5E3. Polyembryonic wasps reported in other ff. (Dryinidae, Platygasteridae, Braconidae) produce broods much smaller than this.

INTRODUCTION. A parasitoid brood consists of the individuals that hatch from a single egg or clutch of eggs laid by one parasitoid in a single host. Polyembryony is the development of multiple embryos due to the mitotic division of a single egg (Ode & Strand 1995). The largest parasitoid broods are produced by polyembryonic parasitoids. This chapter discusses some of the characteristic features of the polyembryonic parasitoids, identifies the insect group that has been reported with the largest parasitoid broods and names a representative from this group as champion.

METHODS & RESULTS

The candidates. All candidates for the largest parasitoid brood are polyembryonic parasitoids. Polyembryony has evolved in 4 ff. of parasitic Hymenoptera: Braconidae, Platygasteridae, Drynidae, Encyrtidae (Strand & al. 1991). Parasitoids reported to have the largest broods belong to Encyrtidae. The total number and sex ratio of embryos in a brood are highly variable both within and between species and are influenced by various factors (Leiby 1926; Walter & Clarke 1992). Some of those factors are host species, fertilization, developmental time of the host, temperatures within the host larvae, size of the parasitized host, the host Juvenile Hormone (JH) & ecdysteroid titers, host-egg age, host encounter rates (Leiby 1926; Nenon 1978; Strand & al. 1991; Ode & Strand 1995).

The champion. The largest broods reported in the literature (Ode & Strand 1995) are for *Copidosoma floridanum* (Ashmead 1900). Like all polyembryonic encyrtids, this wasp is an obligate egg-larval parasitoid of moths in the subfamily Plusiinae (Lepidoptera Noctuidae). In Florida it is usually found in the cabbage looper *Trichoplusia ni* (Hübner 1803) or *Pseudoplusia includens* (Walker 1858) (Strand, personal communication). The largest brood in the literature was displayed in a scatter plot and was ca. 2,750 individuals (Ode & Strand 1995). Dr. Strand confirmed that the real datum was 2,796 individuals. Two other larger broods (2,941 and the largest 3,055) have never been included in any paper as part of a data set (Strand, personal communication). Broods reported by Ode & Strand 1995 were counted as all emerged wasps plus dead offspring remaining in the mummy. The record of 3,055 was counted similarly and the dead offspring accounted for less than 2% of this brood (Strand, personal communication). The brood of 2,941 was just total emerged adults (Strand, personal communication). *C. floridanum* oviposit in the egg of the host, and progeny complete their development in the final (5th) instar of the host (Strand 1989). ♀♀ produce ♀ or ♂ broods by laying one egg per host (♂ or ♀), and mixed broods by laying 2 eggs (always one ♂ and one ♀) (Strand 1989; Ode & Strand 1995). On average, mixed broods are larger than single-egg broods, although single-sex ♀ broods can be as large as any two-egg mixed brood (Strand, personal communication). The 2,796 and 3,055 broods were all ♀ and almost certainly derived from a single egg (Strand, personal communication). The 2,941 brood was both ♂ and ♀ and thus arose from one ♂ and one ♀ egg (Strand, personal communication). ♀ and mixed broods decrease in size with increasing host-egg age, and the body sizes of ♀ and ♂ broods are negatively correlated with clutch size (Ode & Strand 1995). Some authors have found polymorphism in the larvae of polyembryonic parasitoids. *C. floridanum* larvae that develop from the multiple embryos can be divided into either precocious larvae that never become adult, or reproductive larvae that develop into reproductive adults (Ode & Strand 1995). Grbic & al 1992, and Ode & Strand 1995 believe that this polymorphism in *C. floridanum* is related to the host-egg age affecting the sex ratio of the broods. Multiparasitized host of *C. floridanum* produce either a brood of *C. floridanum* or die without any parasitoid emergence. However, Strand & al. 1990 found no direct evidence that physical attack by *C. floridanum* precocious larvae killed the other parasitoid. Cruz & al. 1990 found that precocious larvae of the encyrtid parasitoid *Copidosomopsis tanytmemus* Caltagirone 1985 may themselves be polymorphic and believe that larval polymorphism is related to the efficacy of polyembryonic species as parasitoids. Cruz 1981 demonstrated that the precocious larvae of genus *Pentalitomastix* Eady 1960 constitute a defender morph, eliminating other internal parasites that would otherwise compete with their normal sibs. The morphology, development and growth of *C. floridanum* have been investigated in relation to the development of its host, the noctuid *Trichoplusia ni*. Development of the parasitoid is synchronized with that of its host (Strand 1989; Baehrecke & Strand 1990).

DISCUSSION. Polyembryonic wasps in other ff. produce smaller broods than *C. floridanum*. For example the mean number of the braconid *Macrocentrus grandii* Goidanich 1937 per brood on parasitized *Ostrinia nubilalis* Hübner 1796 larvae is 39.8 (Orr & al. 1994). Platygastrid broods produce as many as 18 individuals; some drynid broods have as many as 60 young developing from a single egg (Borror & al. 1989). The 2nd largest parasitoid brood reported in literature (2,500) was for *Copidosoma truncatellum* (Dalman 1820), a parasite of cabbage looper (Leiby 1926). *Copidosoma truncatellum* was recently synonimized with *C. floridanum* by Noyes 1988 (Brit. mus.). *Litomastix truncatellus* (Dalman 1820) and *Paracopidosomopsis truncatellus* (or *floridanus*) Girault 1916 were used in the old literature and are also almost certainly *C. floridanum* (Strand, pers. com.). *Copidosoma* (=*Berecyntus*) *bakeri* is the apparent runner-up to *C. floridanum*, producing broods as large as 1,511 (Snow 1925). High rates of parasitism by polyembryonic spp. are not always desirable since they can increase crop damage and complicate control recommendations. This was the case of *Euxoa (Chorizagrotis) auxiliaris* Grote 1873 parasitized by *C. bakeri*. Parasitized larvae feed more and longer than unparasitized larvae (Byers & al. 1993). Parasitized larvae also grow considerably larger than unparasitized larvae and may have a supernumerary instar. Larger hosts supported larger broods of *C. bakeri* and apparently a successful strategy of *C. bakeri* is to prolong host development so as to maximize an acquired resource (Byers & al. 1993).

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Chapter 27. Largest swarm

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ABSTRACT. The desert locust *Schistocerca gregaria* (Forskål 1775) forms the largest swarms. In early 1954, a swarm that invaded Kenya covered an area of 200 Km^2. The estimated density was 5E7 individuals per Km^2 giving a total number of 1E10 locusts in that swarm.

INTRO. I define a swarm as a large, coherent group of flying insects.

METHODS. Secondary literature, solicitation over Entomo-L Listserv, BEE-L bulletin board, and interviews with staff at the UF Entomology & Nematology Dept. provided the initial candidates. Searching CD-ROM versions of Biological Abstracts & AGRICOLA yielded additional info.

RESULTS. The largest swarms reported in the literature are of migrating insects. Locusts in the desert, mosquitoes in the Arctic and tropics, and butterflies, moths, beetles, bugs and dragonflies, almost everywhere have been seen in mass flights, often involving millions of insects all traveling in the same general direction at the same time (Eisner & Wilson 1977). The most commonly reported measure of a swarm is the area it covers. When *Melanoplus spretus* (Walsh 1866), the rocky mountain grasshopper, periodically migrated to the valleys of the northern Rocky Mountain region, the swarms extended to a height of 1.5 Km and covered up to 330,000 Km^2, an area larger than Colorado. However numbers of insects were only referred to as myriads or immense (Riley & al. 1878, 1880). The book of Exodus mentions swarms of gnats attacking people and their animals followed by a swarm of locusts that ate what was left and blanketed the country in darkness for 3 days. The period is uncertain, but is deduced to have been about 1470 BC (Bimson 1981). Hoyte 1993 suggested that the area affected be interpreted as the Nile delta including the district of Goshen. Again, there was no specific information about the number of insects in the swarm. The first steps towards the quantitative assessment of the swarms were taken by Gunn & al. 1948. Air and ground reconnaissance were used to establish and maintain contact with *Schistocerca gregaria* (Forskål 1775) swarms and to assess their area, and objective photographic methods were introduced to estimate densities and numbers of locust in these swarms. Direct determination of density in settled locust swarms provided figures that were roughly similar for several different swarms and averaged 5E7 individuals per Km^2. These area-density figures were broadly consistent with photographic data on density of locusts in flying swarms. In early 1954, air reconnaissance observations registered 50 swarms that invaded Kenya. They covered a total area of ~1,000 Km^2 and rose to 1,000-1,500 m a.g.l., with the largest swarm covering 200 Km^2, ~1E10 locusts. The total number of individuals in the 50 swarms was estimated at 5E10 locusts, weighing ~1E8 Kg (Rainey 1954, 1989; COPR 1982).

DISCUSSION. Swarms of Desert Locust have been recorded somewhere or other in every year since 1860 (Rainey 1963); however, the longest plague period lasted from 1950-1962, and during this period the largest swarm was recorded. Rainey 1954 calculated that of a well-packed swarm observed in East Africa contained 5E7 locusts per Km^2. At such rates, a swarm of 100 Km^2 could contain over 5E9 locusts, but not all would be flying at once. Often some will settle while others take off, so that the swarm, however uniform it looks at any moment, is really progressing in a rolling motion with one part constantly replacing the other in the air as the whole body of the swarm moves forward (Baron 1972). Plentiful information about *S. gregaria* swarms exists because this insect has great economic importance in Africa and many countries are interested in estimates of their number and densities for timing the control measures. *M. spretus* was also a very important pest in the last century, but it cannot be made champion, because the largest swarm reported is only referred to as formed by myriads or immense insect numbers covering the sky (Riley & al 1880). For other insect spp. the swarms have been reported as millions or tens of millions individuals with no specific information as to densities or areas covered (Eisner & Wilson 1977).

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Chapter 28. Most spectacular batesian mimicry

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ABSTRACT. The swallowtail butterfly *Papilio dardanus* Brown 1776 occurs throughout most of Africa. While ♂♂ maintain a typical swallowtail appearance, ♀♀ occur in over 30 different mimetic forms that clearly resemble various spp. of 2 danaid gg.

INTRODUCTION. Batesian mimicry involves a palatable, unprotected sp. (the mimic) that closely resembles an unpalatable or protected sp. (the model) (Devries 1987). This theory was first presented in 1861 by H.W. Bates in his attempt to explain the similar appearance and behavior of otherwise unrelated Central American butterfly spp. (Devries 1987). The larvae of these model butterflies eat plants that contain noxious substances which pass, either altered or unaltered, to the adult stage (Sheppard 1962). Such chemicals make the model undesirable to predators. The mimics lack these substances in their bodies making them quite edible. True batesian mimicry is parasitic in nature with the model deriving no benefit and possible harm (Devries 1987). The mimics don't share the models nasty taste or painful sting, just its appearance and behavior. Thus, models may be harmed by being mistaken for palatable mimics and should evolve to rid themselves of these relationships (Devries 1987). Since its conception, batesian mimicry has been the subject of great debate and countless papers. C. Darwin, although accepting batesian mimicry, viewed it as accidental with the mimic looking similar enough to the unrelated model to allow it slight protection (Clarke & Sheppard 1960a). The theory is often misrepresented and confused with its counterpart, mullerian mimicry. In this case the model is not defined, and several unpalatable spp. share warning colors or patterns to evade predation. Batesian relationships are found in many insect orders. This chapter identifies the most spectacular example.

METHODS. Primary literature was obtained from sources listed in secondary literature. Secondary literature was gathered from several texts on the subject, as well as from books on insect ecology, specific insect orders, and geographical regions. Additional primary literature was located by computer search of AGRICOLA.

RESULTS. Many relationships involving what were once thought to be batesian mimicry are being reevaluated. The most common example, the Viceroy butterfly (*Limenitis archippus* Cramer 1775), once thought to mimic the Monarch [*Danaus plexippus* (Linnaeus 1758)], has through further investigation proven to be as distasteful to birds as the Monarch (Ritland & Brower 1991). Thus, the Monarch and Viceroy are mullerian mimics. That such a disparity could go unnoticed for so long shows to what extent mimicry needs to be studied. However, after sidestepping this non-batesian example in every text and article reviewed, several pure batesian examples stand out. In Borneo the grasshopper *Leptoderes ornatipennis* Serville 1838 (= *Condylodera tricondyloides* Westwood 1841) resembles tiger beetles so closely in appearance and mode of running that for years it was placed with them in museum collections (Wickler 1968). The grasshopper benefits from the tiger beetle's reputation for aggression. However, beetles and grasshoppers do develop differently. During its juvenile stage, this grasshopper lives in flowers with another tiger beetle, *Collyris sarawakensis* J. Thomson 1857, which it closely resembles in size and color (Wickler 1968). *L. ornatipennis* is a batesian mimic with 2 partners, and several such batesian relationships are known. However, a butterfly from Africa appears to be more spectacular. *Papilio dardanus* is a swallowtail with more than 30 mimetic morphs. The similarities between the mimetic morphs & their models are just as remarkable as that of the grasshopper & its beetles.

DISCUSSION. *Papilio dardanus* has a highly specialized batesian mimetic relationship with model species in the gg. *Danaus* Kluk 1802 and *Amauris* Hübner 1816 (Lepidoptera Danaidae). Caterpillars of the model butterflies feed on distasteful plants such as milkweed and pass the chemicals to the adult, making them distasteful to predators-namely, birds and monkeys (Sheppard 1962). The ♂♂ and ♀♀ of these model gg. are similar; however, the species vary greatly in appearance. The mimic, *P. dardanus* contains some 8 races (or sspp.) in MG, the Comoro Islands and the southern 67% of Africa (Sheppard 1962). The races are distributed so that only races *antinorii*, *meriones*, and *humboldti* are completely isolated from other races. All other races hybridize at the edges of their respective ranges (Sheppard 1962). The races are distinguished by black markings on ♂ wings and ♂ genital armature morphology (Clarke & Sheppard 1960b). Color pattern in ♂♂ is always black and yellow, and differs only in detail from race to race (Clarke & Sheppard 1960a). ♂♂ have a typical swallowtail appearance and are readily eaten by birds. ♀♀ are highly polymorphic, making this a spectacular mimicry. Only in the isolated races of *meriones* (on MG), and *humboldti* (Comoro Islands) are the ♀♀ monomorphic and nonmimetic (Clarke & Sheppard 1963). Throughout the Ethiopian region can be found model spp. of gg. *Danaus* and *Amauris* each with its own mimic (morph), or in most cases, several morphs. *Amauris niavius* (Linnaeus 1758) is an example of a model sp. It is mimicked by 10 different morphs throughout Africa. For example, the morph *hippocoon* mimics *A. niavius* in western Africa (Clarke & Sheppard 1960a). *Amauris echeria* (Stoll 1790) has 13 morphs mimicking it throughout Africa (Price 1984). The success of a mimic's relationship to its model can be judged by color patterns, using a scale developed by Sheppard 1962. This scale plots a butterfly mimics relative fitness against its color pattern, with the color scale ranging 0-5. A *P. dardanus* morph with a number 3 color pattern would have the greatest fitness. Primary factors influencing fitness of these color patterns would be abundance of the model and levels of predation (Clarke & Sheppard 1960a). Mimics falling into the color ranges above or below 3 will suffer decreased advantages because they appear less like the model (Sheppard 1962). Each *dardanus* mimic has a specific host and cannot be found in any region without this host, but the morphs can be shared among races. For example, 4 races (*dardanus*, *cenea*, *tibullus*, *meseres*) in eastern Africa share 31 morphs, however, no one morph is found in all 9 races (Wickler 1968). How successful and common each morph is appears to be based on its model's abundance and its ability to closely match the model's color patterns and behavior. When a species develops many mimetic morphs in an area, such as *P. dardanus* has done throughout Africa, the ratio of each mimetic morph to the individuals of the model is reduced, improving the rate at which predators learn to avoid the color pattern.

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Chapter 29. Greatest bioluminescence

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ABSTRACT. There are a few studies that report the brightness of bioluminescent insects. *Pyrophorus noctilucus* (Linnaeus 1758) (Coleoptera Elateridae) is not only one of the largest bioluminescent insects, but it has also been reported as having the greatest surface brightness, 45 millilamberts. The research on insect luminescence has placed a greater emphasis on flash patterns and wavelengths of emission, than on quantifying insect brightness.

INTRODUCTION. Many organisms have been described as bioluminescent. Some animal luminescence can be attributed to infection by luminous bacteria, while other animals have evolved luminous organs (Harvey 1952). Insects with luminous organs occur in Collembola, Hemiptera, Coleoptera and Diptera. Insect bioluminescence has evolved to allow insects to signal mates of the same species at night (Coblentz 1912). Flash patterns and wavelengths of maximum light emitted have been studied. This research has shown that these characteristics of insect light are diagnostically important because they are unique to each species studied (Lloyd 1978). These characteristics of insect luminescence can be used to distinguish bioluminous insect spp. from each other in the field more effectively than comparisons of surface brightness. The insect with the brightest bioluminescence is discussed in this report. Surface brightness, or flux emitted per unit area of light organ, is measured in *lamberts* (Seliger & McElroy 1965). One *lambert* is equal to one lumen per cm^2 of a perfectly diffusing surface. A *lumen* is the flux emitted per unit solid angle by a point source of one *candela*. Many studies have measured the intensity of emitted insect light in *candelas*, rather than the surface brightness of insect light organs. Luminous intensity is found by determining how many insects it takes to give the same light density as the flame of a standard sperm candle (Coblentz 1912). These measurements cannot be accurately converted to units of surface brightness because measurements of luminous areas are not reported.

METHODS. Dr. J.E. Lloyd and Dr. S. Wing were useful resources. I consulted them to determine how to approach my literature search. WebLUIS Search System and CAB Abstracts searches revealed references on Coleoptera taxonomy, and on bioluminescence emission studies. Physical chemistry and physics text books were used to interpret the numerical data and the units of measure.

RESULTS. Dr. Lloyd and Dr. Wing both suggested that the brightest insect was a Coleoptera. My review of the literature found that the brightest insect is the very large *Pyrophorus noctilucus* (Coleoptera Elateridae), with a brightness of 45 millilamberts (Harvey & Stevens 1928). This measurement was made by comparing the light of the insect with that made by a calibrated Macbeth illuminator, and by measuring the area of the insect light organ. This insect is also known as the Jamaican Click Beetle and the "Cucujo" beetle of the West Indies. Supporting evidence reported by Nicol 1978, names *Pyrophorus* as having the greatest number of photons emitted per unit area per unit of time, 7E-4 photons cm^{-2} s^{-1}. These measurements were taken with a calibrated photometer. This record of photon emission does not name a species.

DISCUSSION. The literature search revealed that more attention has been given to determining the wavelength of an insect's maximum emission, and to recording the flash pattern, than to quantifying surface brightness. Flash patterns and emission spectra can be used to distinguish species from each other. These bioluminescent signals attract animals of the same species to each other for mating (Lloyd 1978). Brightness not only varies between members of the same species, but can also vary for an individual insect with environment and therefore, is not a good diagnostic marker (Harvey & Stevens 1928). Coblentz 1912 named *Photinus pyralis* (Linnaeus 1767) as having the greatest recorded light density, 1/50 that of a sperm candle. He used a photograph taken with a spectrograph and a photographic plate that was most sensitive at 590 nm and did not report any measurements of the area of the light organs. Experiments on flash intensity reported by Harvey 1952 name *Pyractomena borealis* (Randall 1828) (Coleoptera Lampyridae) as having the greatest recorded light density, 9/50 the light of a standard sperm candle, but he did not give the area of the light organ. These two reports give no data that can be converted into units of brightness. The human eye is most sensitive to light at a wavelength of 540 nm (Coblentz 1912). Light emitted at other wavelengths requires more quanta for the human eye to record the same brightness. For example, *Pyrophorus noctilucus* gives a maximum light emission at 538-540 nm and *Photinus pyralis* at 567 nm. Most of the experiments found in the literature use the human eye and a candle to estimate relative intensities. Instruments that can measure photon emissions at different wavelengths would give less biased results.

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Chapter 30. Largest

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ABSTRACT. The largest living insect species, by virtue of having the greatest visible body mass and probably weight, are the giant scarabs, *Goliathus goliatus* Linnaeus 1771, *G. regius* Klug 1835, *Megasoma elephas* (Fabricius 1775), *M. actaeon* (Linnaeus 1758), and the immense cerambycid *Titanus giganteus* Linnaeus 1771. No clear winner can be declared on the basis of objective data, the candidates being nearly equal in this regard, but a visual comparison of all of them, side by side and scaled to maximum known size, may convince one otherwise. The heaviest weight reliably reported for any insect is 71 grams for the protected giant weta, *Deinacrida heteracantha*. For the purposes of this chapter, "largest insect" shall mean the species whose largest representatives have the greatest body mass. Weight data could more clearly define the winners, were it available with adequate documentation, and if taken in conjunction with corresponding body measurements. Such is not the case, however, and length-to-width-to-thickness measurements, taking into account exoskeleton density and visible body volume are the criterion used to separate these 5 beetles from amongst other competitive candidates.

INTRODUCTION. Insects come in a variety of sizes. Since an insects skeleton is on the outside of its body, the mechanics of support and growth are such that the animal is limited to a relatively small size. This small size enables insects to live in places that would not be available to other animals. The key is chitin, a light but structurally superior substance that composes the majority of the body wall and exoskeleton. This, combined with the internal muscle attachments that give insects proportionally better leverage and strength, enable insects to move or lift weights many times their own weight. Therefore, carrying their own body weight is a minor problem.

METHODS. Discussions with collectors and professionals, first-hand measurements of very large specimens, searches of primary and secondary literature and website articles - none have provided comparative evidence favoring one insect over all of the others. Several sources do offer reliable maximum body lengths. First-hand dry weight and linear measurements of 6 to 10 large specimens of each of the 5 giant beetle species were collected. Subsequent comparison of this variety of measurements was helpful to ascertain whether the proportions of giant specimens might change somewhat as the upper limits of size were reached. Except for slight incremental horn development of the scarabs, this was generally not the case. From the recorded data, graphic images were scaled to simulate the maximum size for each chosen beetle species so they could at least be compared visually. Dry weight data was considered only as evidence for the peripheral discussion on the relevance of weight in comparing potential winners.

RESULTS. Until further relevant data is available, 5 beetle species are likely co-title holders for Largest Insect. Beetles were selected due to their obvious density and greater measurable bulk. Though a gravid specimen of the cricket-like giant weta, *Deinacrida heteracantha* White 1842, of NZ had a reported weight of 71 g (Moffett 1991), weight data is lacking for nearly all of the beetles and extreme measurements of *Deinacrida* indicate it is smaller in bulk. Obviously, a maximum *Titanus* is compelling in comparison of top views, but there is yet no evidence that one of 167 mm has a measurably greater volume than the giant scarabs.

DISCUSSION. Perhaps few other popular subjects discussed among entomologists, amateur and professional alike, have engendered such interest and generated such a plethora of opinions, all claiming at least some supporting data, as that of the "largest/heaviest/bulkiest" insect. Gilbert J. Arrow 1951, in his analysis of the form and function of horn development of giant beetles, unequivocally states that the elephant beetles (*Megasoma actaeon* and *Megasoma elephas*) are the largest and bulkiest of all insects. H.E. Jacques 1951, author of *How to Know the Beetles*, concurs that "*Megasoma actaeon* Linne from South America, is likely the largest and heaviest beetle known." Ross H. Arnett 1968 states in a footnote to the Scarabaeidae chapter of his *The Beetles of the United States*, "This family [Scarabaeidae] includes the Goliath beetle, *G. goliathus* [sic] L. from Africa, probably the largest insect known." and "The tribe Goliathini, which contains the largest of all insects, *Goliathus goliathus* [sic] Drury 1770, from West Africa..." Patrick Bleuzen 1994, who personally captured the largest known specimen of *Titanus giganteus* Linnaeus 1771 in GF, writes of *Titanus*, "it is certainly the most bulky of all insects." Unfortunately, maximum sizes are universally expressed as a maximum total body length or, much less frequently, as an isolated weight. Single linear measurements are given in Endrötti's 1985 *Dynastinae of the World*, Lachaume's 1983 *Beetles of the World*, Vol. 3, Goliathini 1, and Bleuzen's 1994 *Beetles of the World*, Vol. 21, Prioninae. Bleuzen even comments about the unfortunate stretching of specimens to attain unrealistic sizes (further emphasizing the deficiencies of dependence on a maximum body measurement). Other close contenders, such as *Megasoma mars* (Reiche 1852), a glossy black giant from equatorial BR, and the beautiful East African *Goliathus orientalis* Moser 1909, which may reach a BL of over 105 mm, were excluded because neither has ever been claimed by specialists to be a contender for largest insect and, more importantly, no specimens of competitive size could be documented. If weight alone were the only consideration here and none of the beetles exceeded their projected maximum live weights, the all-time, *conditional* winner of "heaviest insect" would have to be bestowed on a lone gravid giant weta specimen from NZ. Finally, to avoid the unintentional errors of many popular writers, every attempt has been made to exclude hearsay data from this discussion. Several exceptional linear measurements were reported in the course of this research which, were they credible, could have tilted the decision in favor of nearly any one of the top five beetle species. Needless to say, documentation of still larger specimens than those quoted herein is expected and welcomed. After all, many of the linear maxes accepted for this comparison are beyond the limits published in sources quoted above.

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ADDENDUM, 2022-IX-20. The title of world's most massive (=heaviest) insect has many contenders, the most frequently cited of which is the *Goliathus goliatus* larva, with a reported mass of **115 g** and a maximum BL of **115 mm**. Two orthopteran contenders for the largest and heaviest extant adult insect are the world's largest bush cricket, *Arachnacris tenuipes* Giebel 1861 (Tettigoniidae Mecopodinae Mecopodini; WS **275** mm, BL **150** mm) and the world's largest grasshopper, a.k.a. the giant red-winged grasshopper, *Tropidacris cristata* (Linnaeus 1758) (Romaleidae Romaleinae Tropidacrini; WS **240** mm, BL **145** mm). The largest (and possibly heaviest) adult insect species of all times is the griffinfly †*Meganeuropsis permiana* Carpenter 1939 (†Meganisoptera †Meganeuridae), with a WS of **710 mm** and a BL of **430 mm**. The closest contenders are: †*Meganeura monyi* (Brongniart 1884) [= †*Dictyoneura monyi* (Brongniart 1884)] (†Meganisoptera †Meganeuridae), WS 700 mm, estimated total mass of up to **138 g** (Cannell 2018); the world's largest palaeodictyopteran, †*Mazothairos enormis* Kukalová-Peck & Richardson 1983 (†Palaeodictyoptera †Homoiopteridae), WS **560** mm; †*Homoioptera gigantea* Agus 1902 (†Palaeodictyoptera †Homoiopteridae), WS **400** mm; the world's largest titanopteran, †*Gigatitan vulgaris* Sharov 1968 (†Titanoptera †Gigatitanidae), WS **400** mm; the world's largest lacewing, †*Makarkinia adamsi* Martins-Neto 1997 (Neuroptera †Kalligrammatidae), WS **> 320** mm; †*Clatrotitan andersoni* McKeown 1937 (†Titanoptera †Mesotitanidae), WS **> 276** mm.

NOTES

Weight problems (Cfr. Figures 1-2)

Weight is sometimes offered as a criterion for largest, and the "heaviest insect" has been cautiously identified by several popular authors, notably Wood (1982) in *The Guinness Book of Animal Facts & Feats*, and McQuitty & Mound 1994 in *Megabugs*. Figures such as 100 g for *Goliathus* (sp. not specified) versus a mere 35 g for *Megasoma elephas* (McQuitty & Mound) are interesting of themselves, but have no comparative value whatever. Was the decimal misplaced, 35 g to 3.5 oz? Or, more probably, was 35 g misquoted as 3.5 oz and the unknown *Goliathus*, in fact, weighed 35 g? Neither length nor width, let alone feeding condition, was given for the above-quoted *Megasoma* weight. An average-sized living specimen of *M. actaeon* measuring 103 mm was reported to weigh 36 g (Beebe 1944). By a straight math comparison, that equals ~47 grams for a maximum *M. actaeon*. A large living *Goliathus goliatus* of ~100 mm TBL was recently reported to weigh 42 g (C. Campbell, personal communication). The same extrapolation of data applied to *actaeon* would produce a figure of ~45 g for a living 110 mm *Goliathus*. Considering the voracious feeding habits of *Megasoma* (Hovore, personal communication), giant specimens may vary widely in live weight within the same species and same length. Both *Megasoma* and the longer-horned *Dynastes hercules* have been observed in captivity to consume nearly an entire avocado in one day, ingesting both pulp and juice. *Goliathus*, a fruit and sap feeder, may consume comparable quantities of food, while *Titanus*, on the other hand, is not known to feed as an adult and, therefore, may never bulk up as the scarabs can [1]. A fair comparison, if it were possible to perform at all, might be to record live weight, under controlled conditions, of a series of starved specimens of all 3 genera. Linear measurements representing several widths plus the thickness, in addition to TBL of each test specimen, must accompany any relevant weight data. But *Goliathus* is heavier, isn't it? Given that dry weights of *Goliathus* are not greater than *Titanus* or *Megasoma*, and given that *Goliathus* is not visibly greater in bulk, there is yet no reason to believe that *Goliathus* is the heaviest insect or that it would necessarily outweigh a giant *Megasoma,* certainly not 3× over. The lack of relevant comparative data has spawned some academic speculation among collectors, the argument being when comparing *Goliathus* vs. *Megasoma,* that *Goliathus* should be heavier by virtue of its thicker exoskeleton and legs, coupled with less air space underneath the elytra. But if this is true, then dry weight comparisons should support this contention. As yet they do not. Of the data collected for this study and mathematically incremented up to the maximum size for dry-weight comparison, *Megasoma* was often the heavier beetle by a few grams [2]. Of course this point is by no means conclusive, given the range of data surveyed and the unknown factors bearing on total weight of living and preserved individuals of both genera, but it does nevertheless point to the need for better data collection on which to base a conclusion. Weight data has been and may remain inconclusive to decide a winner among earth's largest living insects.

[1] This remains to be seen, as one of the heaviest dry specimens measured for this writing was a 155 mm *Titanus*. The one exception among *Goliathus* was the weight of a relatively fresh 105+ mm specimen of *G. goliatus*, which probably was not dried out yet. All other specimens examined had been preserved for many years.

[2] In fact, the heaviest dry weight recorded by this author was for a 120 mm *M. actaeon* at 27.6 grams.

Maximum total body lengths in mm (TBL) (Cfr. Figure 5)

Maximum TBL of the giant weta and ♂ specimens of the world's bulkiest beetles, including horns and mandibles, accepted from reliable sources are:

Deinacrida heteracantha White 1842: The cricket-like giant weta of Little Barrier Island, NZ – 85; 110 including ovipositor. Legspan > 7"
Titanus giganteus Linnaeus 1771: Equatorial BR, GF – 167
Megasoma elephas elephas: (Fabricius 1775): The elephant beetle, from southern MX to South America – 137
Megasoma actaeon (Linnaeus 1758): Northern and Equatorial South America (2 sspp: *M. a. actaeon*, *M. a. janus*) – 135
Goliathus goliatus Linnaeus 1771: The goliath beetle (Central & W-Central Africa), and the less common *G. regius* Klug 1835 (CI, NG) – 110 [3]

[3] An inquiry to one author of Sakai & Sagai 1998 regarding their published record of **115 mm** *G. regius* remains unanswered. That figure is herein taken as a typo.

Length problems

A length is a length – Not. Differences in preparing specimens for study - not maintaining the body/head/horn alignment with the central axis of the body, raising or lowering of the head/horn, stretching the thorax or head forward beyond its natural position and unnaturally bending body segments out of position - any of these and, especially, combinations of these methods can greatly affect the total length of a specimen, making a relevant comparison of 2 specimens *of the same species* which are the same measured length, impossible. Visit any insect exhibition and you may see *Titanus* which have gained a "neck" by pulling the head forward out of the thorax. Therefore, a select variety of measurements was taken for all specimens examined by the author.

Measuring beetles 101 (Cfr. Figure 3). Angling of head and/or thorax, especially vertically, can significantly alter linear measurement, creating unrealistic size estimate. Width measurements of humeral region and pronotum should always be taken into consideration since they will not change, unless the specimen has been crushed.

Open wide (Cfr. Figure 4). Mandible tips are broken off in many *Titanus* specimens; the mandibles set at varying angles, making linear measurements of TBL inaccurate for precise comparison of specimens. Should the giant of them all, at 167 mm, have incomplete mandibles, its TBL may actually be closer to 170 mm.

Extra millimeters. The posterior abdominal segments of several species of large ♀ Prioninae are sometimes distended apically to aid oviposition. That *Titanus* ♀♀ could reach a length of 170+ or even 220+ mm in this condition has been contended as an explanation for its more outlandish size estimates. Photographic evidence (which cannot be reproduced here) indicates extension of the abdomen of *Titanus* ♀♀ of 0 to 12%. The largest known ♀ *Titanus* measures 150 mm to the tip of the elytra, so 12% extension would theoretically increase that length to 168 mm.

Horns: bigger beetles = bigger horns. Gilbert J. Arrow 1951 discusses the existence and utility for the incremental development of horns on the thorax and heads of the ♂♂ of certain large scarab beetles, mostly of the subfamily Dynastinae, and the similar development of giant mandibles for large stag and long-horn beetles. The common theme is that horn development is greater for larger specimens, sometimes attaining grotesque proportions in giants.

Titanus sizes (Cfr. Figures 6, 7, 9)

The Rev. J.G. Wood wrote in his book, *Insects Abroad* (1874), of a 9-inch *Titanus* which he had before him on his desk as he wrote his chapter on the Prioninae. No doubt, this single reference is the historical basis for much, if not all, of the speculation about the size of this huge insect. Obviously, if Wood's comment referred to the body length of *Titanus,* and the existence of such monsters could be proven, we would have an extremely short discussion about the "world's largest insect." Rev. Wood goes on to comment conservatively about other measurements of large insects. For him, *Goliathus* tops out at "4.25 inches and its breadth exactly 2 inches" (< 108 × 52 mm), easily within the accepted limit. *Megasoma* is reported as reaching five inches long and a width of two inches. Of *Titanus* he writes, "being the largest insect in existence, measuring **nine inches** in length, and being very wide and thick of body... I should very much like to have it engraved, but it is so large that no space would be found for it even if a whole page were given up to it." The print format of the book is 4×6"; perhaps the most logical conclusion is that he referred to the total length, including outstretched antenna (interesting in itself, as the antenna of *Titanus*, having a very rigid pedicel, does not easily bend forward); or that the figure is merely a typo and he meant to write "six" rather than "nine" inches. Tropical biologist Frank Hovore has stated that the average size of *Titanus* is about 135 mm and specimens exceeding 150 mm are considered rare where it is most commonly collected in the steamy rainforests of French Guiana and Brazil. Runts of 90-100 mm are known, giving *Titanus* an impressive size range, characteristic of many giant beetle species. Adults live for ~3-4 weeks and are not known to feed. Capable and willing to snap a standard lead pencil or ballpoint pen in two with a single bite or to shatter a plastic ruler carelessly held too close for a field measurement, *Titanus* is feisty quarry for the lucky collector. When pursued too closely, specimens have been known to turn and approach a collector, antenna waving and jaws snapping ominously. ♀♀ are smaller than ♂♂ and seldom collected, as they are not attracted to the elaborate 2000W light traps used to entice the ♂♂. Little is known of life history of *Titanus* and what natural enemies it may have in nature.

Giant Weta (Cfr. Figure 8)

Deinacrida heteracantha White 1842. The endangered giant weta of Little Barrier Island, NZ, is reliably credited with a maximum weight of 71 grams. The image at far left of **Figure 8** was "fattened" to simulate a gravid ♀ with a body over 85mm long, excluding ovipositor. To its right is what may be the smallest of the five "largest" insects included in this discussion (*Megasoma e. elephas*, illustrated to scale at a TBL of 137mm).

Photo gallery (Figures 1-9)

Figures 1-2. Popular West Coast exhibitor Phil Mays weighs in with two of his heavy-weights, two of the heaviest insects weighted dry for this comparison. Such comparisons provide peripheral evidence indicating the relative bulk and density of giant insect exoskeletons.

Figure 3. *Goliathus goliatus* Linnaeus 1771 ♂, Los Angeles County Museum of Natural History.

Figure 4.
The *Titanus* at right is from the Rosser Garrison collection.

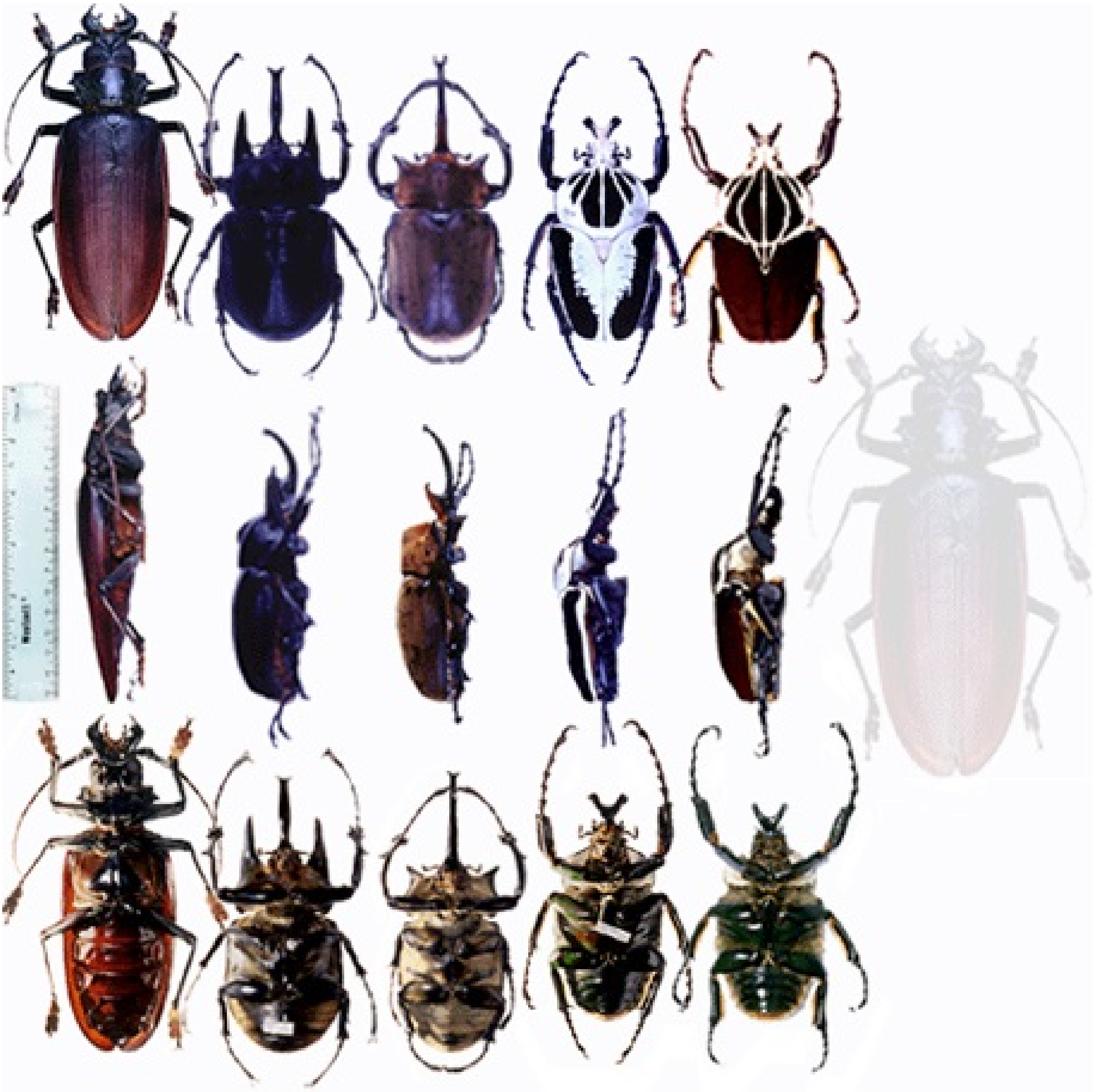

Figure 5. Dorsal, lateral and ventral aspects of the 5 bulkiest insects in the world, compared to a 150 mm (6") scale at left. Images are graphically sized representations of the 5 spp. at their **maximum known sizes in mm**. Scale was achieved by comparing widths first, then BL. From left to right:

1. ***Titanus giganteus*** Linnaeus 1771 : French Guyana, Brazil. **167**
2. ***Megasoma actaeon*** (Linnaeus 1758) : Columbia, Ecuador, Peru, Brazil. **135**
3. ***Megasoma elephas*** (Fabricius 1775) : Mexico through Venezuela. **137**
4. ***Goliathus regius*** Klug 1835 : Ghana, Ivory Coast. **110**
5. ***Goliathus goliatus*** Linnaeus 1771 : Equatorial Africa, central and east. **110**

Ghosted to the right of the documented sizes, also to scale, is the mythical **228.6 mm** (9") *Titanus giganteus* of popular lore.

Figure 6.

Figure 7. *Titanus* on display. The average museum drawer for insects will hold anywhere from dozens to hundreds of specimens, but not if it's filled with *Titanus* & co. *Macrodontia cervicornis* ♂♂, which sometimes measure over 160 mm, in the bottom right corner. This fine series was collected by permit along the Route de Belizon (GF) by Mr. Frank Hovore, who has studied living specimens of several of the giants mentioned in this chapter.

Figure 9.

Elytra of *T. giganteus* from F. Hovore's collection. Bite marks found on elytrae of some specimens could have been made by large bats during the beetle's nocturnal flights.

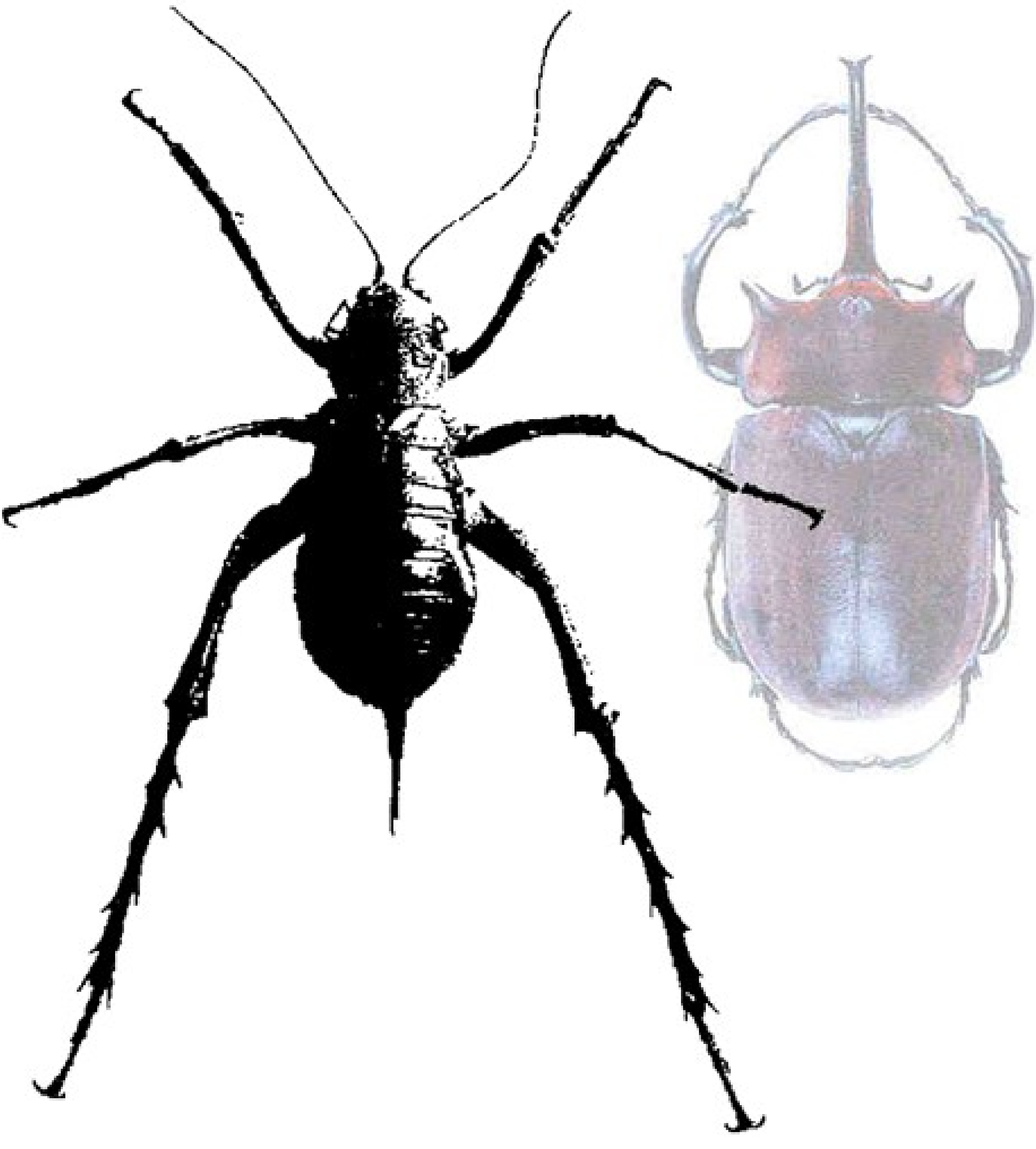

Figure 8. Weta composite based on a b&w plate in *The Insects of Australia and New Zealand*, by R.J. Tillyard 1926. According to Dr. Mary IcIntyre, weights up to 43 g are reached and maintained by adult ♀ wetas after weeks of accumulating eggs following their final molt. When eggs are not released through normal oviposition, such as the case of captive specimens like the 71 gram example, egg accumulation continues and can result in weights far in excess of 43 g. Without eggs, an average adult *Deinacrida heteracantha* would weigh ~19 g.

Chapter 31. Largest blood meal

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Editor's note: Ticks are not insects, so strictly speaking this chapter doesn't belong here. The chapter's author reported that she could not find an insect champion, and I decided that including the chapter might stimulate someone to write a replacement chapter that succeeded in naming one. - T.J. Walker, 2001-X-24.

ABSTRACT. The methods used to determine the size of blood meals are varied and controversial, and published data on largest blood meal is scarce. One source stated that the tick *Hyalomma asiaticum* Schülze & Schlottke 1929 takes a blood meal with a volume exceeding 8.00 ml. However, there are no publications stating that this is the largest blood meal taken by an arthropod species.

INTRODUCTION. Knowing the amount of blood taken in by a particular vector is important epidemiologically. It is known that many pathogens are found inside red blood cells and therefore enter a vector during blood meals. Species that accrue more red blood cells during individual feedings could increase their chances of becoming infected with pathogens (Rechav & al. 1994). Finding the species that takes the largest blood meal is a very complicated matter, especially among ticks. Ticks concentrate blood meals by excreting waste products and lymph back into the host animal through salivary glands while still feeding on the animal. This can make accurate determination of amount of blood meal very difficult (Sauer & al. 1995).

METHODS. Professors and graduate students were asked to propose candidates, these candidates were then researched using library search services and materials suggested by professors.

RESULTS. All nominations centered on one group of Arthropoda: ticks of the genus *Amblyomma* Koch 1844. Several species from this genus were suggested to have the largest blood meal-namely, *Amblyomma variegatum* Fabricius 1794, *A. tuberculatum* Marx 1894, *A. hebraeum* Koch 1844, *A. maculatum* Koch 1844. These spp have been studied in detail for their ability to transmit diseases, and persons queried usually had a favorite for the largest blood meal. The consensus was that *A. variegatum* took the largest blood meal; professors suggested that it could take in as much as 3 ml at one feeding, however no one could provide documentation. Dr. Sekouba Bengaly (personal comm.) suggested that between *A. variegatum* and *A. hebraeum*, the former produced the largest egg mass after engorgement. Yet, there was no documentation of a correlation between blood meal size and egg mass size. While researching the *Amblyomma* spp., another candidate was found. Sauer & al. 1995 stated that *Hyalomma asiaticum* ♀♀ can take extremely large blood meals. Eventually I located studies comparing plasma volumes (Vp), average blood volume imbibed (Vbm), and blood volume equivalents (Vbe). Of the ticks compared, discussions centered on only 3 candidates, *Amblyomma americanum* Linnaeus 1758, *A. maculatum*, *A. hebraeum*. *A. americanum* from one study had a Vbe of 0.806 ml (Koch & Sauer 1984) and in another study its Vbm was 0.740 ml (Sauer & Hair 1972). *A. maculatum* on the other hand showed a Vbe of 2.344 ml (Koch & Sauer 1984). In a more recent study, *A. hebraeum* had a Vp of 1.780 ml (Rechav & al. 1994). There was no research suggesting an avg. blood meal amount for either *A. variegatum* or *A. tuberculatum*. Sonenshine 1991 reported that Balashov 1972 found *H. asiaticum* to take a Vbe of 8.856 ml.

DISCUSSION. I could not find one source, primary literature or otherwise, that stated which tick took the largest blood meal; however, many studies dealt with the amount of blood taken by certain tick vectors. The primary method of determining the volume of blood ingested is by weighing pre-fed ticks and then weighing the same ticks after a blood meal (Rechav & al. 1994). This method is not very accurate because ticks not only ingest blood, but they also take in some non-blood tissue. They also inject waste materials into the host as they are feeding (Koch & Sauer 1984). Difficulties arise when trying to determine the rates at which different species ingest non-blood tissue or the rate at which waste is injected by individual species. Another method of blood volume determination is a colorimetric analysis, in which ticks are homogenized and a hematin compound added to the homogenization. The hematin binds to all red blood cells and the remaining hematin is washed away. Spectrophotometric analysis compares the solution to known amounts of the hematin compound to give an estimate of the total number of red blood cells present in the homogenization. This method is also very controversial, due to physiological differences among tick species; such as, varying rates of metabolism. Some species may start breaking down blood cells more quickly than others, even before removal from the host. A final method described is the use of different isotopes as blood markers in order to determine the degree of concentration of red blood cells by certain tick species (Rechav & al. 1994). There are many tick species not mentioned, primarily because they were too small for consideration. Of course there may be more Ixodid ticks, such as *A. variegatum* and *A. tuberculatum*, on which no published data is recorded. This does not suggest that other ticks do not potentially take the "largest blood meal"; these ticks have just not been studied in this respect. Among the candidates that I investigated, the literature suggests that *Hyalomma asiaticum* had the largest blood meal followed by *Amblyomma maculatum*. However, "due to varied analytical methods" the comparability of the determined blood volumes is questionable. Even though these studies were not all done using the same analysis, the difference in methods could not feasibly cause a discrepancy of 6.6 ml between the winner and the runner-up. This large of a difference between 1st and 2nd place suggests that *H. asiaticum* is the winner of the title "largest blood meal".

ACKNOWLEDGMENTS. I thank Dr. Jerry Butler and Dr. Harvey Cromroy from UF, and Dr. Sekouba Bengaly, visiting from Laboratoire Central Veterinaire in Mali, West Africa, for their interest and suggestions for this project.

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Chapter 32. Largest lepidopteran wing span

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ABSTRACT. *Thysania agrippina* (Cramer 1776) (Noctuoidea Erebidae Erebinae Thermesiini), the white witch moth, has the largest reported wing span (WS) of any lepidopteran. This neotropical species is reported to attain WS of up to 280 mm. While all books on Lepidoptera and entomology consulted award this status to *T. agrippina*, no supporting documentation from the primary literature was located. In wing area, some species of Saturniid moths from southern Asia surpass *T. agrippina*.

INTRODUCTION. Although the vast majority of Lepidoptera species are small and obscure, many species are admired for their size and color patterns by entomologists and non-entomologists alike. Some species of especially spectacular size occur in the moth families Saturniidae (giant silk moths), Sphingidae (sphinx moths), and Noctuidae (owlet moths), and in the butterfly family Papilionidae (swallowtails). This chapter investigates which lepidopteran has the maximum WS.

METHODS. To find candidate species, I consulted UF entomologists, general textbooks on entomology and various books on Lepidoptera. Literature searches of BioAbstracts 1982-1997 and AGRICOLA 1970-1997 were unproductive. In addition, I examined Lemaire's 1980 & 1988 monographs of new world Saturniidae which include maximum WSs for these taxa. Also, I looked up *Thysania* and *agrippina* in the index to the *Journal of the Lepidopterist's Society*.

RESULTS. While the moth families Saturniidae and Sphingidae may be the most famous for containing many species of spectacular size, the record holder is actually a South American member of the family Erebidae. All pertinent references consulted agreed that *T. agrippina* has the largest WS of any lepidopteran in the world. Metcalf & Flint 1951 gave their source as lepidopteran authority W.T.M. Forbes, while other authors neglected to state the source of their information. The measurements for the *T. agrippina* wing span vary slightly among different references. Folson 1906 and Metcalf & Flint 1951 reported a WS of 11 inches. Frost 1959 reported *T. agrippina* spreads 280 mm, Richards & Davies 1960 stated its WS is up to 280 mm, and Moucha 1966 gave a slightly smaller measurement of 270 mm. I measured the 2 specimens in the Lepidoptera research collection at the Florida State Collection of Arthropods housed in the Division of Plant Industry's Doyle Conner Building, and tip to tip measurements are 260 mm and 266 mm. However, these specimens were not spread in the standard position for Lepidoptera. The lower margin of the forewing was not raised to a 90° angle with the body, such that the tip to tip measurements are larger than they would be for a normally spread specimen. None of the cited references provided information as to how the wings were spread for the specimens upon which their claims are based.

DISCUSSION. There does not appear to be any controversy in the literature over *T. agrippina*'s status as the champion for the largest lepidopteran WS. However, all references I located lack specific information from the primary literature to validate this claim. Consequently, it is likely this claim originates from personal communication with lepidopterists (such as Forbes, noted above) and no supporting measurements have been published in primary literature sources. The only primary literature claim, Wiltshire 1959, stated "and Brazil indeed has the species with the largest wing-span in the world (the Noctuid moth *T. agrippina*)". However, since this reference gave neither a measurement nor a citation it at best can not be regarded as any more reliable than the other references. It is also possible all the reports are copied from the earliest report by Folson 1906, since 270 mm and 280 mm could be rounded down or up after being converted from 11 inches. A deficiency in all the references is a failure to state the position of the wings for the specimens used to derive the reported measurements. Has the reader to assume the specimens were spread in the typical Lepidoptera format, with the lower forewing margin perpendicular to the body? In addition, the references fail to provide collection data or what collections house the specimens from which their WS measurements were derived. Folson 1906 went as far as to claim *T. agrippina* is the largest living insect. However, in this case it is not clear how "largest" is defined. This claim is not repeated in any of the later references I consulted. The longest and heaviest insects are subjects of other chapters in this book. *T. agrippina* apparently holds its WS record by a decisive margin over other candidate lepidopterans. The apparent 2nd place maximum WS record holder is the saturniid *Attacus caesar* Maassen 1873 from PH. This species is reported to have a WS of 10 inches by Folson 1906 and 255 mm by Frost 1959. A SE asian saturniid, *Attacus atlas* (Linnaeus 1758), is "among the largest moths in the world" (Heppner & al. 1989). The *A. atlas* WS is reported to be 9.5" (241 mm) by Folson 1906 and up to 240 mm by Frost 1959 and by Richards & Davies 1960. Based on Lemaire's 1980, 1988 monographs, the largest WSs among the new world Saturniidae are only 190 mm, for *Arsenura sylla hercules* (Walker 1855) and *Caio championi* (Druce 1886). According to Parsons 1984, the maximum WS of a butterfly is found in the birdwing (Papilionidae) *Ornithoptera (Straatmana) alexandrae* (Rothschild 1907): ♀♀ of this uncommon sp., occupying a restricted range in PG, can attain WS>250 mm. *T. agrippina* apparently does not hold a record for the largest lepidopteran in terms of wing surface area. Moucha 1966 mentions that certain Saturniids from south Asia, including *Attacus atlas* and *Coscinocera hercules* have greater wing surface areas than *T. agrippina*.

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ADDENDUM, 2000-III-30. Since the original version of this chapter was placed on the Web, 2 collectors have come forward with additional information: **1**, Peter Brink provided a photograph of a *T. agrippina* specimen from CR measuring 286 mm tip to tip (**Figure 1**). **2**, Howard Romack has provided a photo of a *T. agrippina* specimen from BR measuring 298 mm (**Figure 2**). Because the 2 specimens are spread at different angles, the measurements can not be directly compared. In the CR specimen the lower margin of the forewing is ~6° below a line perpendicular to the body, while in the BR specimen the lower forewing margin is ~15° below the perpendicular (based on measurements from the dx side of the specimen). After enlarging the photographs of the 2 specimens, I estimated the distance from the base of the lower margin of the forewing to the tip of the wing to be 146.2 mm and 147.7 mm for the specimens from CR and BR, respectively. In addition, for the CR specimen a line from the base of the forewing to the wing tip forms a ~65° angle with a line parallel to the midline of the body, thus the distance from the body to the tip on one side is ~146.2 sin 65≅132.5 mm. Had the BR specimen had the wings raised to the equivalent position as the CR specimen, the length of the same distance would be ~147.7 sin 65≅133.9 mm. Consequently, if the BR specimen's wings raised at equivalent angles to the CR specimen, it would be ~1.4mm longer on each side (neglecting a possible slight difference in body widths which would be difficult to estimate from the photos), with a total WS of ~289 mm. Howard Romack (personal communication, 2000) raised the point that in nature *T. agrippina* rests with its forewings at lower angles than on his spread specimen, so WS of the moth in its natural resting posture is even larger than the reports given for spread specimens.

ACKNOWLEDGMENT. I gratefully acknowledge P. Brink and H. Romack for contacting me with their info on *T. agrippina* WS, and for providing me with photographs of their largest specimens.

EDITOR'S NOTE, 2005-III-01. In a 2004-I-13 e-mail, Peter Lillywhite, of Museum Victoria, AU, informed me of a large *Attacus atlas* collected in 1922 in Java. This specimen had a WS of 262 mm (**Figure 3**), which makes the atlas moth the lepidopteran species with the second largest documented WS.

ADDENDUM, 2022-IX-20. The Hercules moth *Coscinocera hercules* (Miskin 1876) (Saturniidae Saturniinae Attacini), endemic to PG and northern AU, is the lepidopteran with the largest wing surface area (300 cm^2) and a reported WS of 270 mm (Kästner 1973; Flindt 2006; Foottit & Adler 2009).

Figure 1.
Peter Brink's *Thysania agrippina* from Costa Rica.

Figure 2.
Howard Romack's *Thysania agrippina* from Brazil.

Figure 3.
Attacus atlas with 262 mm WS, collected in Java in 1922. Photo courtesy of Peter Lillywhite.

Chapter 33. Longest

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ABSTRACT. Using any criterion of measurement, certain walking sticks (ordo Phasmida) are the longest insects on earth. Of the phasmids, the champion is a ♀ *Phobaeticus serratipes* (Gray 1835) [=*Pharnacia serratipes* (Gray 1835) = *Pharnacia maxima* Kirby 1904] that measured 555 mm (nearly 22 inches) from extended fore tarsi to extended rear tarsi.

INTRODUCTION. The world's longest insect is indisputably from ordo Phasmida (stick insects). In fact, 2 different Phasmida specimens have been identified as the longest insect on record. Length determination for both of these insects has been made in 2 ways. The first, by measurement of the insect's body length (BL), excluding the length of the legs. The second, by incorporating the insect's BL and extended leg L from the terminal end of the fore tarsi to the terminal end of the rear tarsi (Bragg 1995). Employing the latter method reveals that there is one definitive winner.

METHODS. Secondary literature was examined: general entomology as well as natural history and biological texts were researched in order to determine candidates for "longest" insect. Additionally, entomology professors at UF were consulted. It was determined that ordo Phasmida contained all possible candidates.

RESULTS. Study of the primary literature revealed 2 candidates for longest insect. Of these 2, a *Phobaeticus serratipes* (Gray 1835) [=*Pharnacia serratipes* (Gray 1835) = *Pharnacia maxima* Kirby 1904] from the Malay Peninsula is the champion (Seow-Choen 1995). The 2nd candidate was a specimen of *Phobaeticus kirbyi* (Brunner von Wattenwyl 1907) [= *Pharnacia kirbyi* (Brunner von Wattenwyl 1907)] from Borneo. Although, misidentified for many years, this insect was the record holder before the discovery of the Western Malaysian specimen.

DISCUSSION. The specimen originally identified as the longest insect on record held that distinction for nearly a century. This walking stick was identified by Kirby in 1896 as *Pharnacia serratipes*. Eight years later, Kirby identified the same specimen as *Pharnacia maxima* (Bragg 1995). However when Bragg 1995 examined the insect, he concluded that it was actually *Pharnacia kirbyi*, as described by Brunner in 1907. Bragg measured this 99 year old walking stick and determined that it had an overall length, including legs, of 546 mm, which indeed made it the longest insect on record. However, a more recent discovery of an even longer specimen was made by Seow-Choen 1995. The insect was discovered alive soon after it molted to adulthood. Measurement of the insect after some time in captivity determined that the insect had an overall length of 555 mm (nearly 22 inches). The species of stick insects that reach the incredible lengths recorded here are primarily found in Indonesia. It is possible that there are other living specimens which may surpass the length of the present record holder. However, until a new candidate is identified, the clear winner for longest insect is *Phobaeticus serratipes* at 555 mm.

ACKNOWLEDGMENTS. I would like to thank Dr. Walker for his invaluable information and research assistance.

ADDENDUM, 2022-IX-20. On 2016-V-05, the Chinese state media Xinhua announced that a new species informally named *Phryganistria chinensis* was discovered in Liuzhou, Guangxi autonomous region of China. The discoverer Zhao Li, at the Insect Museum of West China in Chengdu, had found the original specimen in 2014, a ♀ with 624 mm TBL; as of 2022, it has not been formally described. In 2017-VIII, one of the offspring attained 640 mm in BL, and has been listed in the *Guinness World Records* as the "longest insect".

Phobaeticus kirbyi Brunner Von Wattenwyl 1907 [= *Pharnacia kirbyi* (Brunner Von Wattenwyl 1907)] is a very long stick insect native to Borneo. The holotype deposited at the NHM in London measures 328 mm excluding legs and 546 mm including legs. This made it the second-longest known insect in terms of BL, behind *Phobaeticus chani* Bragg 2008 with 357 mm. Both *P. chani* and *P. serratipes* exceed it in TBL with legs extended. However, recent specimens of *P. kirbyi* have only reached 283 mm in BL.

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Chapter 34. Longest adult life

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ABSTRACT. A queen ant *Lasius niger* (Hymenoptera Formicidae) has the longest recorded adult life of any insect: 28.75 years in captivity.

INTRODUCTION. The aim of this chapter is to identify the insect species with the longest adult life, i.e. the one with the longest period from adult emergence to death.

METHODS. To find candidates I looked in general entomology textbooks and asked professors and fellow graduate students in UF Entomology & Nematol. dept. The 2 candidates selected were investigated using standard library methods: AGRICOLA, CAB Abstracts and secondary literature.

RESULTS. The 2 candidates for the champion were queen ants (Hymenoptera Formicidae): *Lasius niger* (Linnaeus 1758), with a maximum recorded longevity of 28.75 years in captivity (Kutter & Stumper 1969), and *Pogonomyrmex salinus* Olsen 1934 (= *Pogonomyrmex occidentalis owyheei* Cole 1938), with a maximum estimated longevity of 30 years in the field (Porter & Jorgenson 1988). In the case of *P. salinus*, ☿☿ live only 1 or 2 years but colonies themselves live for several decades. Queens live as long as the colony.

DISCUSSION. Kutter & Stumper 1969 indicate that *L. niger* queens have lived from 18-29 years based on individuals in laboratory colonies. On the other hand, Porter & Jorgensen 1988 estimated that *P. salinus* queens lived from 14-30 years in the field, based on their studies and those of Sharp & Barr 1960. Kutter & Stumper 1969 state that ☿☿ can live 7-8 years but queens can live almost 30 years. They report that a queen of *L. niger* was held in captivity by Hermann Appel for 28.75 years. The estimates for *P. salinus* by Porter & Jorgenson 1988 were based on the survival of colony mounds in the Raft River Valley, Idaho. Such mounds were checked by Sharp & Barr 1960 during a 2-year period (1956-58) and by Porter & Jorgenson 1988 during a 3-year period (1977-80) and 6 years later (1986). In each case the researchers determined whether the mounds remained active or the colonies had perished. The latter researchers estimated average longevity of colonies by dividing the "mound years" of observation by the number of colony deaths. For example, Sharp & Barr had 121 mound years of observations in 6 plots vegetated with shadscale and recorded 4 colony deaths. This is the basis for Porter & Jorgenson's max estimate of 30 years for average colony longevity. The weakness of this estimate is that colony mortality during the 2-year monitoring period may have been unusually low. The max estimate of longevity based on 3 years of monitoring was 15 years (Porter & Jorgensen's Plots A & B). Ant colonies are apparently very long-lived once they became established. Colonies with one queen can live 5-30 years (Tschinkel 1987; Chew 1987), but most do not survive nearly as long in the field due to the rigor of competition, predation, pathogens and habitat change. Because mature queens might be replaced by young queens after they die, the longevity of individual queens in field colonies is uncertain (Lavigne 1969).

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Chapter 35. Longest regularly repeated migration

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ABSTRACT. Every autumn the eastern North American population of monarch butterflies, *Danaus plexippus* (Linnaeus 1758) (Lepidoptera Danaidae), migrates from as far north as southern Canada to overwintering sites in Central MX. This journey may cover 4,000 Km or more for some individuals and take as long as 75 days. The following spring these same individuals remigrate to the southern US to produce the first of 2 to 4 successive generations that repopulate their summer range.

INTRODUCTION. Almost every author who has written about insect migration has defined the term to suit his particular theory. C.G. Johnson 1969 divided insect migration into 3 classes of complexity. He placed monarchs in Class III defined as "Emigration to hibernation or aestivation sites and return flights by the same individuals after imaginal diapause." 17 years later L.R. Taylor 1986 described 4 kinds of migration, 2 of which he applied to the movements of insects. He described *dynamic migration* as one-way single migration actively initiated by the insect but dependent for the most part on wind or tides with no navigation or directional control by the individual. The vast majority of migrating insects falls into this category, and the desert locust, *Schistocerca gregaria* (Forskål 1775) holds the record for longest distance traveled (Tipping 1995). Taylor's homeostatic migration is two-way migration which may take advantage of wind but is directed by the navigational ability of the insect and includes a return to the point of origin by the same individual or its progeny. The distinguishing characteristic of Taylor's homeostatic and Johnson's Class III migration is that the insect directs its travel to a predetermined destination. This type of navigation is usually associated with mammals, birds, fishes, reptiles and amphibians that live long enough as adults to make at least one round trip, and is rarely observed in insects. Homeostatic migration is a valid topic for this book because it is distinctly different from dynamic migration.

METHODS. Discussion with my colleague Chris Tipping first confirmed my choice of the champion homeostatic migrating insect. I searched AGRICOLA & WebLUIS Search System for primary literature. A posting to Entomo-L Listserv led to website *Monarch Watch*, a valuable resource.

RESULTS. Almost all the homeostatic migrating insects are lepidopterans. Their flights range from a few kilometers up and down the side of a mountain to hundreds of Km across continents (Williams 1930; Urquhart 1960; Johnson 1969; Baker 1978). None of the other lepidopterans are close runners up to the records for monarchs. In 1937, F.A. Urquhart began marking monarchs with wing tags to study migration, and from 1952 to 1976 more than 3,000 volunteers in his Insect Migration Association participated in the study (Urquhart & Urquhart 1977). L.P. Brower 1996 reported flights of over 3,600 Km based on his own extensive research and overwhelming circumstantial evidence. The longest documented one-way record for a monarch is 1,870 miles (3,009 Km). This butterfly was tagged 1957-IX-18 in Highland Creek, Ontario, CA, and recaptured 1958-I-25 in Estacion Catorce, San Luis Potosi, MX (Urquhart 1960). Monarch Watch lists the longest known flight as 2,880 miles (4,635 Km) tagged in Brighton, Ontario, CA, 1988-IX-10 and recaptured 1989-IV-08 in Austin, US-TX. This butterfly is assumed to have overwintered in MX and been recaptured after remigration. It is important to remember that these insects are unlikely to have flown in straight lines from the point of tagging to recapture. They must make navigational corrections for unfavorable winds, fly over or around obstacles, and follow uneven coastlines. Consequently, they probably traveled much farther.

DISCUSSION. Special physiological adaptations of the south flying fall generation make these annual journeys possible. First, they are in reproductive diapause and do not sexually mature until just before the spring migration. Thus, they conserve energy required for egg development and can fly great distances without heavy eggs. Second, they have large fat reserves, which give them longer life span than the summer generations. As they fly south, they nectar from flowers to provide energy for the migration. During overwintering, the fat is conserved until they reach sexual maturity and begin the spring migration. At this time of year there are few nectar sources available and the stored fat must be utilized for the return trip (Urquhart & Urquhart 1977). Both ♂♂ and ♀♀ return to the southern US in spring to mate, lay eggs, and die. A third physiological adaptation is a lowered metabolic rate after they reach overwintering sites. This is accomplished as they hang in dense, quiescent clusters in the cool, high altitude Oymal fir forest of the Neovolcanic Belt Mountains in Central MX from mid-XI to mid-III (Brower 1996). Finally, this migration could not occur without sophisticated innate navigational ability. Behavioral and physiological experimental evidence both gives clues about monarch navigation. Researchers at Kansas University tested the monarch's ability to orient themselves by the direction of sunlight. By holding butterflies of the September generation in the dark for 6 h they caused a "clock shift." When these individuals were released they flew a mean heading that was 75° clockwise from the direction of the controls thus demonstrating a Sun compass in monarch butterflies (Perez & al. 1997). On cloudy or overcast days monarchs still find their way, though they are not known to fly after dark (Schmidt-Koenig 1979); therefore, there must be a "back up" system. Monarch adults contain magnetic particles, which may be part of a geomagnetic detection system though this is as yet unproven (Jungreis 1987).

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Chapter 36. Most polyandrous

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ABSTRACT. Polyandry refers to a ♀ mating with more than one ♂. Although more common in eusocial Hymenoptera, polyandry is widespread across various taxa. *Apis dorsata* (Hymenoptera Apidae) is here named as the most polyandrous insect because it has been recorded to mate up to 53 times, each with a different male. A blue milkweed beetle, *Chrysochus cobaltinus* (Coleoptera Chrysomelidae) ♀ has recorded up to 60 matings, though some of these were multiple matings with the same ♂.

INTRODUCTION. Mating is a process that has important evolutionary consequences. There are 3 types of mating: in *polyandry* a ♀ copulates with more than one ♂; in *multiple mating* a ♀ mate repeatedly with the same ♂; and in *prolonged mating* a ♀ copulates for a long time with a particular mate (Choe 1997). Some species may show both polyandry and polygyny (some ♂♂ copulate with more than one ♀ in a breeding season). Frequency of mating may be influenced by food quality, as was reported with burying beetles (Trumbo & Eggert 1994). This chapter aims to find the most polyandrous insect, defined as the ♀ insect with the highest number of matings with different ♂♂ reported in scientific literature.

METHODS. Primary literature was found mainly by searching Biological Abstracts and CAB Abstracts, and querying the Entomo-L Listserv. Secondary literature was found in books at Marston Science Library. Entomology professors and USDA researchers gave me good advice on where to find information.

RESULTS. In primary literature, authors usually reported whether a species has single or multiple mates, and some specified proportions of multiple matings. Page 1986 reported mating frequencies of 98 spp. Those with greatest number of matings were *Apis mellifera* Linnaeus 1758 (up to 20×), *Apis cerana* Fabricius 1793 (up to 30×), *Atta sexdens* (Linnaeus 1758) (up to 8×), *Vespula maculifrons* (Buysson 1905), *Vespula squamosa* (Drury 1770) (up to 10×). Moritz & al. 1995 reported that *Apis dorsata* Fabricius 1793 ♀♀ mated with as many as 53 mates. Dickinson 1997 indicated that *Chrysochus cobaltinus* LeConte 1857 (Coleoptera Chrysomelidae Eumollinae) ♀ mated up to 60× but not necessarily with different ♂♂.

DISCUSSION. Currently the most polyandrous species are eusocial Hymenoptera, but records may change in the next few years. Numerous and profound studies on polyandry have been completed recently, and the results are becoming available (Croizer & Pamilo 1996). Studies on *C. cobaltinus* marked individuals have shown that ♂♂ and ♀♀ mate with multiple partners in field, and often remate with the same individuals (Dickinson 1997). Single mating is certainly the case for honeybee ♂♂, because they lose their genitalia after mating (Croizer & Pamilo 1996). Polyandry in *Apis dorsata* was determined using single locus genetic markers. 3 DNA microsatellite loci with a total of 27 alleles provided sufficient genetic variability to classify the ☿☿, deducing their genotype from father drones and queen mothers. The statistical procedure used to estimate the actual and effective number of matings is conservative, and may underestimate these parameters. Patrilines were biased due to the small ☿ sample size which ranged from 18 to 41. Mating estimates ranged from 16 to 53 (mean 30.17 ± 5.98 SE). For the largest sample, the best fitting estimate of the number of matings was 53, with 95% confidence limits of 37 to 96 (Moritz & al. 1995). Since ♂♂ of polyandrous species on average mate more often than ♂♂ of monandrous species, not only is their total ejaculate greater, but the rate at which they are able to produce sperm and accessory substances is greater (Svard & Wiklund 1988). Cryptic ♀ choice may occur if ♀♀ bias sperm storage in favor of ♂♂ with preferred phenotypes or by refusing to mate (Dickinson 1997). The ♀ defines polyandrous behavior once copulation has begun (Thornhill & Alcock 1983). The evolution of polyandry in social hymenopteran queens may be caused by colony level selection, either because polyandry affects the distribution of non-functional diploid ♂♂ in colonies (the load hypothesis) or because it increases the genetic diversity of the ☿ force (the diversity hypothesis) (Pamilo 1991). Artificially inseminated queens with semen from one drone opposed to equal amounts of mixed semen from several drones, showed that mixed patriline results in a group of advantages in performance of honeybee ☿☿, resulting in higher comb building, storage of honey and pollen and brood rearing. This might have promoted the evolution of polyandry in honeybee queens (Fuchs & Shade 1994). Parasites and pathogens have been proposed as selective agents involved in maintaining genetic variability in populations and promoting polyandry in eusocial Hymenoptera (Shykoff & Schmidt 1996). By these facts and although *C. cobaltinus* mated up to 60 times, *Apis dorsata* is considered the most polyandrous insect.

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Chapter 37. Shortest reproductive life

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ABSTRACT. Many insects spend the majority of their lives in the immature stages of development. Although there are several species among many groups of insects that exist for only a few days as adults, the shortest adult reproductive life belongs to the ♀ of the mayfly *Dolania americana* which lives for < 5 minutes after its final molt. During this brief window, the insect mates and lays her eggs.

INTRODUCTION. Reproductive life can be defined in several ways due to the enormous variety of insect reproductive strategies. In this chapter, reproductive life is defined as the time from final molt until death in the stage where mating and egg laying occur, under natural conditions. Using this definition, I searched for the insect with the shortest reproductive life.

METHODS. A computer search of Biological Abstracts was employed to initially search for candidate insects in primary literature. This led to other sources cited in those publications.

RESULTS. Several groups of insects can be characterized by their short reproductive life. The order Ephemeroptera has even been named based on this trait. (*ephemera* means short-lived). Among this group, few spp. live > 48 h as adults, and most do not even have functional mouthparts. I have named the mayfly *Dolania americana* Edmund & Traver 1959 (Ephemeroptera Behningiidae) the shortest lived among Ephemeroptera with ♀♀ typically living for < 5 minutes (Sweeny & Vannote 1982).

DISCUSSION. In the search for the most ephemeral insect, 3 groups of what may be considered short-lived adults were found. Those whose adult life is typically measured in days, such as the Hessian fly with a span of ~4 days (Bergh & al. 1990) and the parasitic wasp *Acmopolynema hervali* Gomes 1848 which lives as an adult for 3 days or less (Boas & Andrade 1991). The next group is of those insects whose reproductive existence is measured in hours. Examples of this group are numerous and contain such species as the wasp *Trichogrammatoidea bactrae* Nagaraja 1979 which lives about 28 h (Hutchison & al. 1990), the moth *Thaumetopoea pityocampa* (Denis & Schiffermüller 1776) (Schmidt & al. 1990) and the mayflies *Ephoron virgo* (Olivier 1791) (Kureck & Fontes 1996) and *Ephemera nadinae* McCafferty & Edmunds 1973 (Balasubramanian & al. 1973) each of which lives ~24 h, and the gall midges of the genus *Rhopalomyia* Rübsaamen 1892 which emerge as adult in the morning and are dead by midday (Jones & al. 1986). But the champions are the insects whose reproductive lives are measured in minutes. *Dolania americana*, in which ♀♀ typically live < 5 minutes, is the shortest lived of these, and is therefore the insect with the shortest reproductive life (Sweeney & Vannote 1982). During this time, to reproduce, they must find a mate, copulate, and lay their eggs back into the water from which they so recently emerged. Although it is difficult to envision an insect that might live as an adult for an even shorter period than *D. americana*, such an organism may exist. However, since life expectancies (especially such brief ones) are rarely studied in natural conditions, it is unlikely that there are records of any competitors to this mayfly's title.

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Chapter 38. Smallest adult

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ABSTRACT. Based on overall length, the smallest adult insect is a parasitic wasp, *Dicopomorpha echmepterygis* Mockford 1997 (Hymenoptera Mymaridae). ♂♂ of this species are blind and wingless; BL=139 µm. This species recently replaced *Megaphragma caribea* Delvare 1993 (Hymenoptera Trichogrammatidae) (BL=170 µm*) as the smallest adult insect.

* Latest BLs of *M. caribea* from Colombia (181-224 µm) are slightly greater than the measurement provided by Delvare 1993 (Polilov 2017b).

INTRODUCTION. The intent of this chapter is to identify the smallest adult insect. For holometabolous insects, an adult insect is defined as an individual that has emerged from pupa and/or is capable of reproduction. Insects which undergo hemimetabolous or ametabolous development are considered adults when growth / molting ceases or when they become sexually mature.

METHODS. A preliminary review of secondary literature and advice from expert entomologists in Coleoptera and parasitic Hymenoptera yielded several candidates. In particular, the Entomo-L Listserv and the Internet proved to be very useful. AGRICOLA was used to investigate primary literature of the candidates.

RESULTS. Obviously, wasps that parasitize eggs of other insects are quite small. Wasps of the egg-parasitic family Mymaridae not only represent some of the smallest known Hymenoptera, but are also among the smallest of all insects. A mymarid, *Dicopomorpha echmepterygis*, holds the record as smallest adult insect. The ♂♂ of this minute wasp are wingless and measure as little as 139 µm in BL. ♀♀ of this species are ~40% larger than the ♂♂.

DISCUSSION. Mockford 1997 described *Dicopomorpha echmepterygis*, and its discovery displaced a trichogrammatid sp., *Megaphragma caribea*, as smallest adult insect (Delvare 1993). At 170 µm in BL, *M. caribea* is only about 20% longer than *D. echmepterygis*. Adult feather-winged beetles in the family Ptiliidae also rival the small size of both species of parasitic wasps described above. Some feather-winged beetles measure as small as 250 µm in length (Borror & White 1970). Mockford 1997 provided a complete physical description as well as a brief biological observation of *D. echmepterygis*. When parasitized by *D. echmepterygis*, an egg of its psocid host, *Echmepteryx hageni* (Psocoptera Lepidopsocidae), typically yields 1-3 ♂♂ and a ♀ of the parasite. The ♂ of *D. echmepterygis* is blind and wingless but possesses long legs that it uses to attach itself to a ♀ wasp that is emerging from the egg of its host. The diminutive ♂♂ of *D. echmepterygis* require less nourishment to develop and are relegated to perform their primary responsibility, mating. On the other hand, vigorous ♀♀ of this species are winged and possess compound eyes suited to aid in dispersal (Mockford 1997). Mockford 1997 also suggests that the great degree of sexual dimorphism in this species may be attributed to the limited nutritional value provided by the egg of the psocid host. Diminutive ♂♂ such as those of *D. echmepterygis* may often be overlooked by researchers (Mockford 1997). Tiny ♂ wasps that parasitize eggs in families such as Mymaridae and Trichogrammatidae may be present in species with ♀♀ that are thought to reproduce parthenogenetically. Therefore, ♂♂ smaller than those of *D. echmepterygis* may exist among parasitic wasps, especially those that parasitize eggs of other insects.

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ADDENDUM, 2022-IX-20. *Kikiki huna* Huber & Beardsley 2000 (Hymenoptera Mymaridae) from US-HI, CR, Nagarcoil and Trinidad, is the smallest flying insect known as of 2022 (BL=150 µm). The monotypic genus *Kikiki* is a close relative of wasps in another monotypic genus, *Tinkerbella,* in which *Tinkerbella nana* Huber & Noyes 2013 from CR is at 250 µm in BL. *Scydosella musawasensis* Hall 1999 (Coleoptera Ptiliidae) is regarded as the smallest free-living (i.e. non-parasitic) insect, as well as the smallest beetle. This monotypic genus of featherwing beetles was first discovered in NI, and described in 1999 by W.E. Hall of US-NE Univ. State Museum. Initial discovery consisted of very few specimens, and exact measurements were not conclusive; the generally accepted size was BL=300 µm. On 2015-II-08, A.A. Polilov of the Lomonosov Moscow State Univ. collected 85 specimens in Chicaque N.P. (CO) on a layer of fungus on which they feed: BL 325-352 µm, average BL of all specimens 338 µm. The currently recognized world's smallest fly is *Megapropodiphora arnoldi* Brown 2018 (Diptera Phoridae), described from a single limuloid ♀ from a site near Manaus (BR), BL=395 µm, slightly smaller than another phorid parasitoid fly, *Euryplatea nanaknihali* Brown 2012, from TH (BL=400 µm).

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Chapter 39. Fastest runner

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ABSTRACT. Australian tiger beetles, genus *Rivacindela* Brouerius Van Nidek 1973 (Coleoptera Cicindelidae) are the fastest running insects known. The fastest, *Rivacindela hudsoni* (Sumlin 1997) [= Cicindela *(Rivacindela) hudsoni* Sumlin 1997], can run 2.5 m/s (5.6 mph).

INTRODUCTION. Throughout time, races have been run in order to decide who or what is the fastest of its kind. Yet there has never been a race to determine the fastest insect in the world. Recently scientists studying movement and defense have published data on how fast some insects can run. Which insect is judged the fastest may depend on whether speed is measured in absolute terms (e.g. meters per second, m/s) or in relative terms (e.g. body lengths per second, bl/s). This chapter will decide that question and name a champion.

METHODS. I gathered information from professors and colleagues at UF about possible candidates. To confirm these candidates and to find additional candidates I searched Biological Abstracts and CAB Abstracts databases for relevant articles. ISI Web of Knowledge was later used to search for articles that cited the articles that I had already obtained. I gathered other possible candidates through posting on Entomo-L Listserv. Finally, I attempted to contact authors of relevant papers through e-mail.

The criteria established to determine the fastest insect are set as follows:

- **A**. At least 5 speed measurement runs must have occurred.
- **B**. The top speed of the insect must be within a plausible range compared to the multiple test runs.
- **C**. The methods and results must be published in a refereed journal.

RESULTS. I narrowed the field to 3 contenders for the fastest land insect:

1. The American cockroach *Periplaneta americana* (Linnaeus 1758)
2. The Australian tiger beetle *Rivacindela hudsoni* (Sumlin 1997)
3. The Australian tiger beetle *Rivacindela eburneola* (Sumlin 1997)

Young (1998) named *P. americana* the current record holder with a maximum speed recorded at 1.5 m/s (3.4 mph). Full & Tu 1991 measured this speed using a specially designed pressure sensitive plate inserted into the roach's raceway. A computer recorded the pressure and time of each footfall, from the first footfall to the last, as the roach crossed the 10.7 cm plate. They also used high-speed cameras to measure time and movement over the set distance. Kamoun & Hogenhout 1996 reported that both *R. hudsoni* and *R. eburneola* were faster than *P. americana,* with maximum recorded speeds of 2.49 m/s (5.57 mph) and 1.86 m/s (4.16 mph). *R. eburneola* has a greater relative speed (171 bl/s) than both *P. americana* (50 bl/s) and *R. hudsoni* (120 bl/s). Kamoun & Hogenhout 1996 originally derived the speeds of the tiger beetles by measuring the time and distance the beetles moved when disturbed. The speeds were later reconfirmed for a few of the species of Australian tiger beetles, including *R. eburneola,* by using video imaging. *R. hudsoni* was not reconfirmed, but the method used to measure its speed was verified (Kamoun 1999).

DISCUSSION. Many insects travel at great speeds for their own insect order but did not fall within the criteria established. One example is that Adams 1999 observed a tiger moth caterpillar, *Apantesis vittata* Fabricius 1787, that he recorded traveling at 3.13 mph (1.4 m/s) over a table top. However, the measurement was made only once and never published. The insects that were reviewed for this paper have some physiological modifications to their style of movement. *P. americana* was able to increase its speed to 1.5 m/s by running on its 2 hind legs (Full & Tu 1991). While it is known that most tiger beetles flee their potential predators through flight, for some tiger beetles flight is a waste of valuable energy and even a possible hazard to reproducing, since their natural habitat is isolated and food is scarce. Natural selection has helped to fix this problem by increasing their ground speed to the point where wings aren't needed. These tiger beetles evolved into a form with only vestigial wings and/or fused elytra. A few of the many species studied from the genus *Rivacindela* have vestigial or deformed wings, including the two speedsters *R. hudsoni* and *R. eburneola* (Kamoun & Hogenhout 1996). The final question now is which measurement of speed to use for the selection of the fastest runner: relative or absolute? If relative speed is the choice, the fastest running insect is *R. eburneola*. To convert its relative speed into human terms, a 6-foot man would move about 1,026 fps or ~0.2 miles per second or 720 mph. This speed almost breaks the sound barrier at sea level (732 mph) and would seem to clearly indicate a winner. Nonetheless, I decided that absolute speed would be the deciding factor for fastest land insect. The reasoning came from human contests for fastest land vehicle (763.035 mph; Young 1998); here size of the vehicle did not matter, only its absolute speed. In addition, for the fastest land animal size was not considered, again only its top speed (cheetah, 70 mph; Young 1998). Therefore, by this criterion the tiger beetle *R. hudsoni* is the fastest running insect.

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Chapter 40. Largest eggs

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ABSTRACT. The largest insect eggs are those of carpenter bees (Xylocopini). The eggs of many species remain to be measured, but *Xylocopa auripennis* Lepeletier 1841 produced the largest egg reported thus far: 16.5 mm in length (L) and 3.0 mm in diameter (∅).

INTRODUCTION. Chapter 7 of UFBIR reviews the smallest eggs of insects. In order to complete this topic, the present chapter is a bibliographical review of the largest insect eggs.

METHODS. The following bibliographical databases were consulted for reports of measurements of the eggs of Xylocopini (carpenter bees): Biological Abstracts from 1927, Zoological Record from 1900, Apicultural Abstracts from 1966, Entomology Abstracts from 1969, Review of Applied Entomology Series A from 1913. For data on egg size in other insects, Hinton's 1981 3-volume *Biology of Insect Eggs* and references therein were consulted.

RESULTS. After surveying the "egg capacity" of insects and the number and size of eggs in Hymenoptera, Iwata 1964 concluded that giant eggs were found only in subsocial Hymenoptera and that Xylocopini (carpenter bees) produced the largest insect eggs in absolute terms. However, Iwata gave no measurements for eggs other than for those of Hymenoptera, leaving uncertain how thoroughly he had reviewed egg size in other orders. Anderson 1972a, 1972b lists representative egg dimensions for 21 species in 12 orders of hemimetabolous insects and 35 spp. in 8 orders of holometabolous insects. The longest eggs he lists for Hemimetabola are 6-8 mm, for *Locusta migratoria* (Linnaeus 1758) (Orthoptera); the largest eggs he lists for Holometabola are 3.75 mm L × 0.85 mm ∅, for *Chalicodoma muraria* (Hymenoptera). Because Anderson did not report any measurements of carpenter bee eggs, it is evident that he may have missed the largest eggs in other orders as well. However, unable to find any evidence to the contrary, I assumed that Iwata 1964 was correct and confined my further efforts to researching the sizes of Xylocopini eggs. **Table 1** lists all the Xylocopini species with published data on egg size. The eggs of *Xylocopa auripennis* are largest, because they have the greatest ∅ (3.0 mm) and a L (16.5 mm) that is equaled only by *X. latipes*. However, Iwata 1964 derived the egg dimensions for *X. latipes* (16.5 × 2.6 mm) from measurements of a "near-mature ovarian egg" and suggested that future field observations may prove that *X. latipes* deposits the largest eggs.

DISCUSSION. Data on egg size are scarce. In order to complete the search for the largest egg, it will be necessary to measure adequate samples of the eggs of the largest Xylocopini spp.: *Xylocopa fimbriata*, Fabricius 1804, *X. flavorufa* (DeGeer 1778), *X. frontalis* (Olivier 1789), *X. latipes* (Drury 1773), *X. nigrita* (Fabricius 1775), *X. tenuiscapa* Westwood 1840, *X. torrida* (Westwood 1838), *X. tranquebarica* (Fabricius 1804) (*X. flavorufa* and *X. nigrita* are included because they are polytypic spp., making it desirable to supplement the existing data). This chapter seeks to identify the insect eggs that are largest in absolute size, but it is worth noting that Iwata & Sakagami 1966 also attempted to determine which carpenter bees produced the largest eggs relative to the ♀ size. To do that they calculated an *egg index* by dividing the L of the largest mature oocyte (**EL**) by the maximum distance between outer rims of ♀ tegulae (**TD**): egg index = **EL/TD**. As can be seen in **Table 1**, *X. tranquebarorum* has the largest egg index (2.00). However, the insect that produces the largest eggs relative to ♀ size is probably not a carpenter bee. Sexual ♀♀ of some aphids produce a single large egg that overwinters and the following spring produces a stem mother, whose success partly depends on her size - for example: *Daktulosphaira vitifoliae* (Fitch 1855) [(= *Phylloxera vastatrix* Planchon 1868)], *Pemphigus betae* Doane 1900 (Iwata 1964; Whitham 1979).

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Table 1. Published measurements of eggs of Xylocopini. EI, egg index = EL/TD.

***Xylocopa* sp.**	**L**	**∅**	**EI**	**reference**
X. appendiculata Smith 1852	12.5	2.5	1.38	Iwata 1964; Iwata & Sakagami 1966
X. auripennis Lepeletier 1841	16.5	3.0	1.72	Iwata 1964; Iwata & Sakagami 1966
X. bombylans (Fabricius 1775)	9.0			Houston 1992
X. flavorufa (DeGeer 1778)	13.0	2.5		Anzenberger 1977; Eardley 1983
X. imitator Smith 1854	10.0	2.3		Anzenberger 1977; Eardley 1983
X. iris (Christ 1791)	8.0			Bonelli 1967; Pagliano & Nobile 1993
X. latipes (Drury 1773)	16.5	2.6	1.38	Iwata 1964; Iwata & Sakagami 1966
X. nigrita (Fabricius 1775)	15.0	2.7		Anzenberger 1977; Eardley 1983
X. olivieri Lepeletier 1841	7.2	1.7	1.09	Rozen & Özbek 2003
X. sulcatipes Maa 1970	11.0	2.2		Gerling & al. 1983; Maa 1970; Stark & al. 1990
X. tranquebarorum (Swederus 1787)	13.0			Maeta & al. 1985
X. tranquebarorum (Swederus 1787)	15.7	2.9	2.00	Iwata 1964; Iwata & Sakagami 1966
X. violacea (Linnaeus 1758)	12.0			Janvier 1977
X. violacea (Linnaeus 1758)	11.3	2.4	1.31	Vicidomini 1996

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