

Chronological Changes in Terrestrial Insect Assemblages in the Arid Zone of Australia

CHRISTOPHER M. PALMER¹

Biodiversity Conservation Division, Northern Territory Department of Natural Resources, Environment, the Arts and Sport, PO Box 1120, Alice Springs NT 0871, Australia

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ABSTRACT Arid and semiarid environments are characterized by highly unpredictable and ‘pulsed’ availability of essential biological resources. The ‘boom and bust’ response of many vertebrates is commonly invoked for invertebrates and especially insects. This perception of the Australian arid zone is exacerbated by the lack of long-term surveys of insects identified at high levels of taxonomic resolution. From an 18 mo continuous survey of insects in central Australia I determine the phenology of many insect taxa, and clarify which climatic variables most influenced the activity of these taxa. Total abundance and taxon richness were higher in the warmer months and lower in the cooler months. Minimum temperature, rainfall during the survey month, and rainfall during the previous month had significant effects on phenology, demonstrating that there is pronounced and predictable activity of many species in the absence of rain, although rainfall has a marked effect on the activity of some species. Other species were more active or only active in the coolest months. These findings have implications for the most productive time for surveys in the Australian arid zone, the availability of insects as prey or pollinators, and for the potential effects of climate change.

KEY WORDS insects, climate, taxa, phenology, seasonality

Arid and semiarid environments are usually characterized by highly unpredictable and ‘pulsed’ availability of essential biological resources such as water and plant biomass, alternating between long periods of low availability and relatively short periods of very high availability triggered by rainfall events (Chesson et al. 2004, Schwinning and Sala 2004, Schwinning et al. 2004). This ‘pulsing’ of resources greatly affects ecosystem function and has a significant effect on the population dynamics of many animal species. In the arid zone of Australia, populations of rodents, reptiles, birds and frogs change rapidly after rain, with increases in abundance of many of these taxa coincident with the rapid increase in resource availability (James 1991a, Anonymous 1993, Reid et al. 1993, Dickman et al. 1999). Populations typically fall very quickly when drought returns. This ‘boom and bust’ scenario of vertebrate ecology is also commonly invoked for invertebrates and especially insects (e.g., Matthews 1976), so that arid zone landscapes are perceived as being quite sterile environments in the absence of rain. This perception is common in the Australian arid zone and is exacerbated by the lack of longer term surveys of insects identified at high levels of taxonomic resolution. For example, because of a historical absence of entomological expertise in central Australia many of the surveys that have been undertaken there

have been (1) ‘snap shot’ surveys of short duration targeting species for taxonomic research or for new locality and temporal records (e.g., Griffin 1979, Allsopp and Lloyd 1987), or (2) longer term surveys of invertebrates whose identifications are at high taxonomic ranks (often at ordinal level or at least reported at ordinal level) to indicate food availability for vertebrates (e.g., Read 1987, Gilfillan 2001). Other, more specific studies in the arid zone have examined the effects of climate on abundance, phenology and migration of pest species such as the Australian plague locust *Chortoicetes terminifera* (Walker) (e.g., Wright and Symmons 1987), the Australian bushfly *Musca vetustissima* (Walker) (e.g., Hughes et al. 1972), and the native budworm *Helicoverpa punctigera* (Wallengren) (e.g., Oertel et al. 1999). Another study reported the effects of precipitation on butterfly species diversity and migration Australia-wide (Dingle et al. 2000). There is consequently very little information on the climatic attributes that influence the presence and abundance of many other arid zone species, and whether seasonality is the dominant feature (or not) of the biology of these species. Such information has great potential to: (1) elucidate the effects of climate change on the arid zone invertebrate biota, (2) reveal when plant pollinators are present and clarify the environmental cues determining their presence, and (3) provide a more resolved picture of food availability for vertebrate predators.

¹ E-mail: christopher.palmer@nt.gov.au.

In this article, I report the results of an 18 mo-long continuous survey of insects in central Australia. I determine the phenology of different insect taxa, which climatic variables most influenced the activity of these taxa, and find out whether there was strong seasonality in insect assemblages. I relate this information to (1) the potential effects of climate change on the taxa studied, nominating suitable indicator taxa for monitoring change in phenology, (2) the availability of insects as a prey resource, (3) the importance of taxonomic resolution when identifying insects during surveys, and (4) a discussion of the optimal timing of surveys in central Australia.

Because of limited field resources available traps were concentrated by sampling one site more intensively rather than spatially replicating the field component at more than one site but with few traps. To offset this, greater effort was put into sorting and identification of material. An advantage of this approach was that a larger number of higher taxa were examined, giving a more complete picture of the overall effect climate was having on the biota at the survey site for the duration of the study. An additional advantage was that potential interactions between members of higher taxa (e.g., parasites and their hosts) could also be elucidated, as well as allowing examination of whether phenology is independent of phylogeny.

Materials and Methods

Study Site. The study site was located within the West MacDonnell National Park, 18.5 km west of Alice Springs in the southern Northern Territory. The habitat is alluvial flats with overstorey vegetation dominated by *Acacia kempeana* Mueller and *A. victoriae* Bentham (Mimosaceae), with *A. tetragonophylla* Mueller, *Eremophila longifolia* (Brown) Mueller (Myoporaceae), and *Senna artemisioides* (Caesalpiniaceae) also present. Species such as *Aristida contorta* Mueller, *Cenchrus ciliaris* L. (both Poaceae), and *Dioscorea paradoxus* (Brown) Ulbrich (Chenopodiaceae) dominate the groundcover layer. The study site has not been burned since at least the 1970s.

The climate of central Australia is characterized by extreme diurnal and within-year temperature differences. Average annual rainfall at Alice Springs Airport, 22.5 km south west of the study site, is 279.3 mm (Bureau of Meteorology 2009) although rainfall is generally temporally and spatially variable and unpredictable (Stafford-Smith and Morton 1990). Most precipitation is derived from a few concentrated falls, usually in the warmer months (Bureau of Meteorology 2009).

Sampling. Invertebrates were collected using two Townes style malaise traps and eight pitfall traps. The first malaise trap (−23.6978, 133.6948, altitude 598 m by GPS) was located 20 m west of a small creek. The second trap (altitude 593 m by GPS) was located 82 m south of trap one, 25 m west of the creek. The alignment of both traps was as consistent as possible with the recommendation of Stevens et al. (2007) to set up

traps in a north–south direction to optimize catches of Hymenoptera in the southern hemisphere, although precise orientation was dictated by topography and vegetation, and both traps were aligned in a north–west–southeast direction. The collecting bottles for both traps contained 98% ethanol.

Pitfall traps were arranged in two rows of four traps, each row approximately equidistant between the two malaise traps. The rows were 15 m apart. Each pitfall trap consisted of a 15 cm long sleeve of 90 mm PVC stormwater pipe sunk vertically into an augered hole in the soil. A 425 ml clear plastic cup of identical diameter was placed into the pipe and, if necessary, extra soil was added around the top of the pipe to ensure the lip of each cup was level with the soil surface. To help protect the specimens from the sun and prevent rain entering the cup, each pitfall trap was covered by a 20 cm² piece of 7 mm thick plywood, supported above the cup and anchored in the soil with a 10 cm galvanized nail at each corner. Each cup was filled with ≈100 ml of commercial antifreeze (Prestone, Danbury, CT) containing 93.6% ethylene glycol. The consistently good preservation of collected specimens meant that additional preservatives were not necessary.

All traps were installed on 27 September 2006 and removed on 27 March 2008. Within that period traps were emptied on the 27th day of every month (occasionally 1 d before or after) and refilled with ethanol (malaise traps) or antifreeze (pitfall traps). All traps were checked at least one other time during each month to ensure their integrity and to top up with ethanol when necessary. Traps were repaired or replaced as appropriate.

Opening the traps for 18 consecutive months meant that sampling of one 6-mo period (27 October to 27 March) was repeated the following year, allowing comparison of insect assemblages between the two periods. Because the effect(s) of climate on diversity, abundance and activity of insects was the focus of this study and not variability of insect assemblages between traps or between trap types, samples from all traps were combined in the analyses of each month.

Insect Sorting and Identification. Specimens were sorted to order before selected taxa were identified to family, genus, or species. The choice of taxon and the rank to which it was identified depended on: the availability of identification materials, time and financial resources, taxonomic expertise, and whether the taxon comprised a larger or smaller component of the trap samples, while ensuring a range of biologies was included. The groups chosen for study covered a broad taxonomic range, comprising holometabolous and hemimetabolous orders, winged and wingless species and a variety of life histories. The following taxa were identified to the indicated taxonomic rank using the following publications: butterflies (to species using Braby 2000); *Desmnozosteria* (Blattodea, to species using Mackerras 1966); Embioptera (to genus using Ross 1991); Hymenoptera (to family, excluding the Chalcidoidea and Mymarommatoidea, using Stevens et al. 2007); Sphecidae (to genus using Bohart and

Menke 1976, Pulawski 2009); Isoptera (to genus using Hill 1942, Watson and Gay 1991); Neuroptera (to genus or species using Aspöck and Aspöck 1984, 1986; Lambkin 1986a,b; New 1980, 1984, 1985a,b,c, 1988, 1991); and Thysanura (to genus using Paclt 1967). Once the termites were identified to genus it was apparent that very large numbers of the termitid *Drepanotermes* had been collected in the pitfall and malaise traps, and so to provide more ecological information on this highly abundant genus the alate, worker, and soldier castes were separated and scored as three separate 'taxa' for some analyses. Although the higher bee taxa are treated as either subfamilies in the Apidae (e.g., Stevens et al. 2007) or as families within the Apoidea (e.g., Michener 2000), the latter classification is used because identifying bees to family was more consistent with identifications of other taxa in this study. All specimens are held at the Museum and Art Gallery of the Northern Territory, Darwin.

Climate Data. Because of the spatial variation in precipitation, rainfall data used in this study were those recorded at the Parks and Wildlife Office at Simpsons Gap, 5 km southwest of the study site. Temperatures and relative humidity data used in this study were those recorded at the long-term weather station at Alice Springs Airport, and these data were obtained from the computer bank of the Australian Bureau of Meteorology.

Statistical Analyses. Statistica version 8 (StatSoft Inc., Tulsa, OK) and Statistix version 9 (Analytical Software, Tallahassee, FL) were used to calculate correlation coefficients. Several environmental variables could potentially influence the phenology of different species, and so the potential relationship between taxon presence and abundance was assessed in the context of: (1) rainfall during the survey month, (2) rainfall during the previous month, (3) average monthly minimum temperature, (4) average monthly maximum temperature, (5) average monthly minimum relative humidity, (6) average monthly maximum relative humidity, and (7) average monthly daylength.

Ordination analyses are commonly used to research the relations between organisms and their environment, and these were considered to be one of the most appropriate statistical methods for this study. To identify the appropriate constrained ordination to be used, a detrended correspondence analysis (DCA) was initially conducted, using CANOCO 4.5 (ter Braak and Šmilauer 2002), to assess whether the data were linearly or unimodally distributed as indicated by the eigenvalue (a measure of importance of the ordination axis) and the length of the gradient. Eigenvalues were low and gradient lengths short (<3.0) in all cases, indicating that species showed a linear response to environmental variables. This resulted in the application of a redundancy analysis (RDA).

The Forward Selection procedure was used to rank environmental variables for their overall importance in determining the abundance of taxa, to reduce collinearity among variables and to make sure that each variable made a statistically significant contribution to

the overall model. Marginal effects and conditional effects were assessed as part of the procedure. Marginal effects are a ranking of the individual environmental variables in order of the variance each explains singly, and are expressed as lambda-1 values (ter Braak and Šmilauer 2002). Conditional effects show the same variables in order of inclusion in the model, along with the additional variance each explains, expressed as lambda-A values (ter Braak and Šmilauer 2002). The overall significance of ordinations was assessed using 499 random Monte Carlo permutation tests. Redundancy analysis was carried out on monthly abundance of each taxon ($n = 18$ mo). For this analysis, the alate, worker, and soldier castes of the termite *Drepanotermes* were separated and scored as three separate 'taxa'. This made a total of 91 taxa for this analysis. Redundancy analysis was also used to determine (1) whether particular months comprised similar assemblages of insects (and therefore the presence of seasonality), and as a corollary of this (2) whether such months were subject to similar climatic conditions.

Results

Climate Data. A total of 251.2 mm of rain fell at Simpsons Gap during the 18 mo survey period; 188.7 mm fell from 1 January 2007–31 December 2007. This is well below the annual average. Most of the rain fell as relatively significant events lasting several days (Fig. 1). For example, 75.8 mm fell over 15 d in January 2007. Rainfall over the 6 mo period October 2006 to March 2007 was 147.1 mm, and rainfall over the corresponding period the following year (October 2007 to March 2008) was 83.8 mm (Fig. 1).

Lowest minimum temperature during the survey period was -2.5°C , and the minimum temperature fell below 0°C on 11 d. Highest temperature reached during the survey period was 42.3°C , and the temperature reached 40°C or above on 20 d. Mean minimum and maximum temperatures were coolest from June to August (Fig. 1), and highest mean minimum and maximum temperatures generally occurred from December to February in 2006/7 and 2007/8. Mean monthly minimum and maximum relative humidity were generally highest in the cooler months and during rainfall events (Fig. 1).

Specimens. There were 12,392 individual specimens identified to family, genus, or species during this study. Specimens were distributed in seven orders and 39 families. Contributing to this total were 6,211 Hymenoptera, 5,331 Isoptera, and 427 butterflies.

Overall Patterns of Arthropod Diversity and Abundance. Total monthly taxon richness and abundance (Fig. 2) were weakly correlated ($r = 0.516$; $P = 0.0282$). Total monthly taxon richness and abundance were moderately correlated with mean minimum temperature (diversity $r = 0.679$ $P = 0.002$; abundance $r = 0.786$ $P = 0.0001$) and mean maximum temperature (diversity $r = 0.710$ $P = 0.001$; abundance $r = 0.671$ $P = 0.0023$), but not with rainfall in the same or previous months, relative humidity or number of sunshine hours per month.

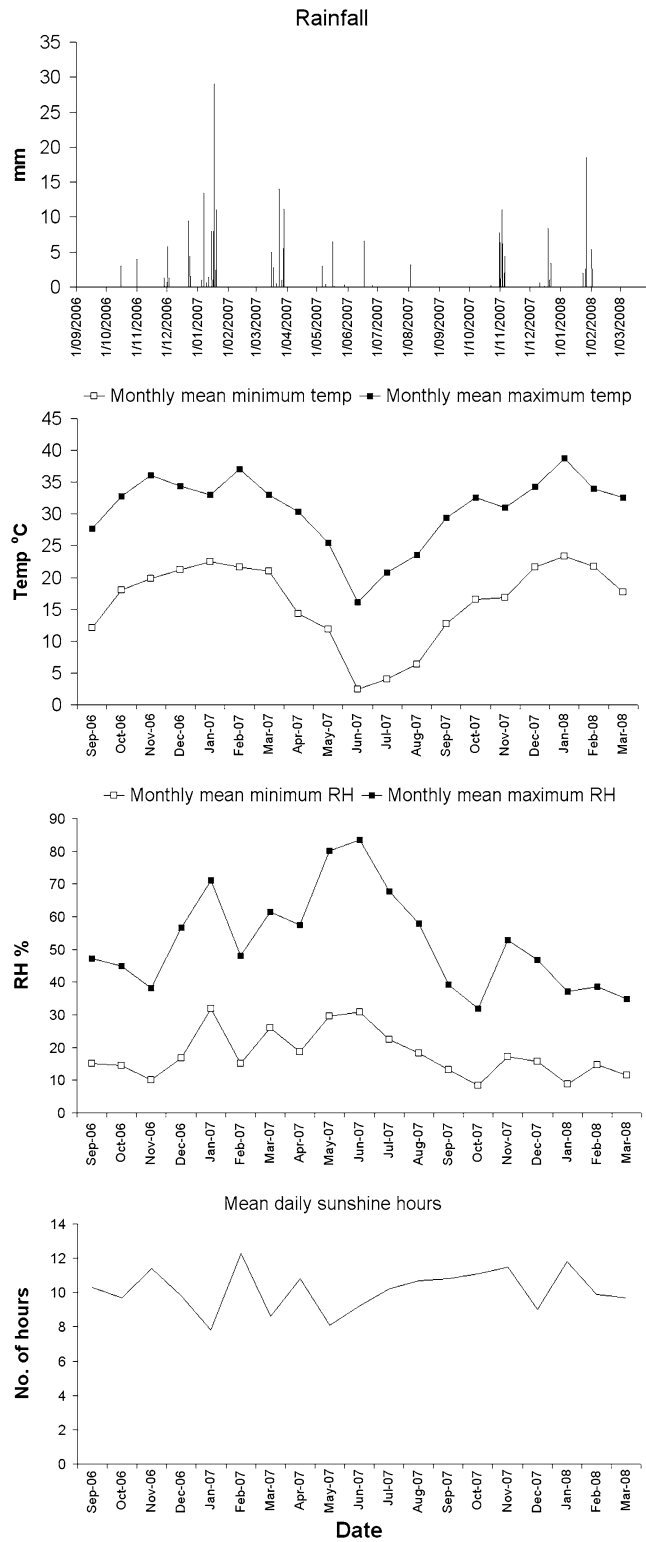


Fig. 1. Climate records for the survey period September 2006 to March 2008.

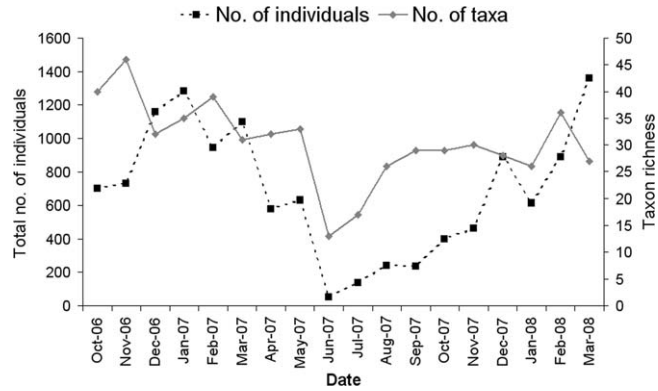


Fig. 2. Total abundance (number of individuals) and total diversity (number of taxa) of all identified specimens collected during the survey period.

The number of individuals was lowest in the austral winter (June to August) (Fig. 2). Numbers increased in spring and were highest in the warmest months. Abundance increased dramatically from November to December in both 2006 and 2007. Taxon richness followed a similar overall pattern, although there was no marked increase from November to December (Fig. 2). Taxon richness was generally higher during the period October 2006 to March 2007 compared with October 2007 to March 2008, and there was a ‘spike’ in taxon richness in February 2007 and February 2008. Both diversity and abundance were lowest in June.

Redundancy Analyses of Monthly Abundance, Taxon Diversity, and Climate. This produced a model that explained 51.7% of the total variation, with the first two axes explaining 45.4% of variation and the first axis explaining 33.3% of variation. Results of Monte Carlo permutation tests showed a highly significant relationship between taxon abundance and environmental variables (first canonical axis eigenvalue = 0.333, $F = 7.00$, $P = 0.002$; all canonical axes eigenvalue = 0.517, $F = 5.00$, $P = 0.002$; based on 499 permutations).

The highest marginal effects were associated with minimum temperature, maximum temperature and rainfall in the survey month (Table 1). The final model included three variables with significant conditional effects. After minimum temperature was selected in the final model, the conditional effects of rainfall in the survey month and rainfall in the previous month re-

mained significant (Table 1). Other variables, such as minimum and maximum relative humidity, maximum temperature, and daylength were ranked lower as conditional effects and were not significant. These last four variables were therefore excluded from the final model.

Monthly Assemblages. RDA of monthly diversity and abundance (Fig. 3) uncovered a ‘winter’ group of June to August 2007. Diversity and abundance in these months were determined by lowest mean minimum temperatures. January 2007 was well-separated from all other months and diversity and abundance were clearly influenced by rainfall during the survey month. December 2006 and December 2007 are very close on the ordination diagram, indicating that diversity and abundance were very similar. Mean minimum temperature had the greatest influence on this pair (Fig. 3).

Phenology of Different Taxa in Relation to Environmental Variables. Many taxa were strongly associated with mean monthly minimum temperature, rainfall during the survey month, or rainfall during the previous month (Fig. 4). Some taxa were influenced by both minimum temperature and rainfall, although in these cases the amount of contribution of each variable differed between taxa, as indicated by their relative positions on the ordination diagram. Examination of Fig. 4 and Table 2 indicates that several distinct groups of taxa can be identified based on their response to climatic cues.

Table 1. Results of ordinations by redundancy analysis showing the importance of environmental variables in explaining the phenology of 91 taxa as shown by their marginal and conditional effects

Variable	Marginal effects Lambda 1	Variable	Conditional effects Lambda A	F
Min temp	0.32	Min temp	0.32	7.66**
Max. temp	0.27	Rainfall survey month	0.12	3.23**
Rainfall survey month	0.19	Rainfall previous month	0.08	2.13*
Max. relative humidity	0.09	Max. relative humidity	0.05	1.60
Min. relative humidity	0.09	Min. relative humidity	0.04	1.31
Rainfall previous month	0.08	Max. temp	0.04	1.19
Day length	0.05	Day length	0.02	0.62

Significance levels * $P < 0.05$; ** $P < 0.01$.

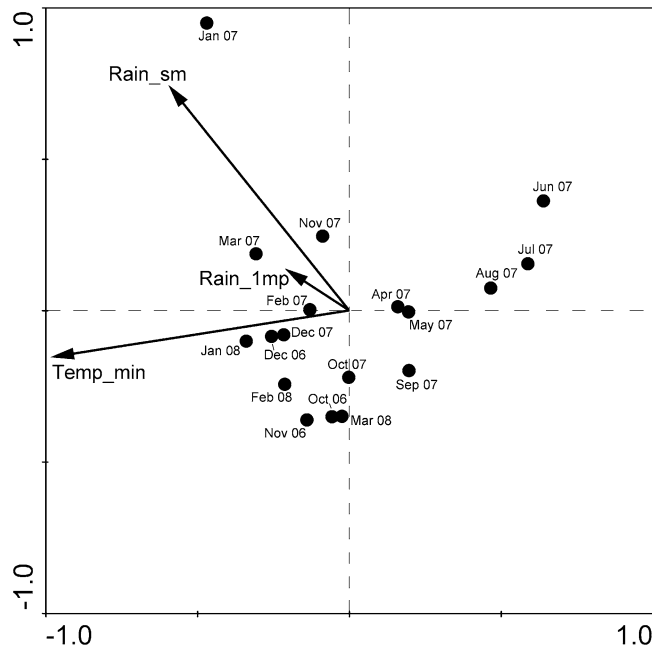


Fig. 3. Ordination (RDA) diagram showing the distribution of monthly abundance data ($n = 18$) in relation to environmental variables. Only the significant variables are shown. Arrows represent continuous environmental variables, and increasing arrow length represents a stronger correlation with environmental gradients. Environmental variable abbreviations: Rain_sm, rainfall during survey month; Rain_1mp, rainfall during previous month; Temp_min, monthly mean minimum temperature.

Rainfall-Dependent Taxa. Several taxa showed a distinct increase in abundance after rainfall, and a few taxa were collected only after rain. In almost all cases

abundance of these taxa was positively correlated with either rainfall in the current month (e.g., winged ants and winged termites) or rainfall in the previous month

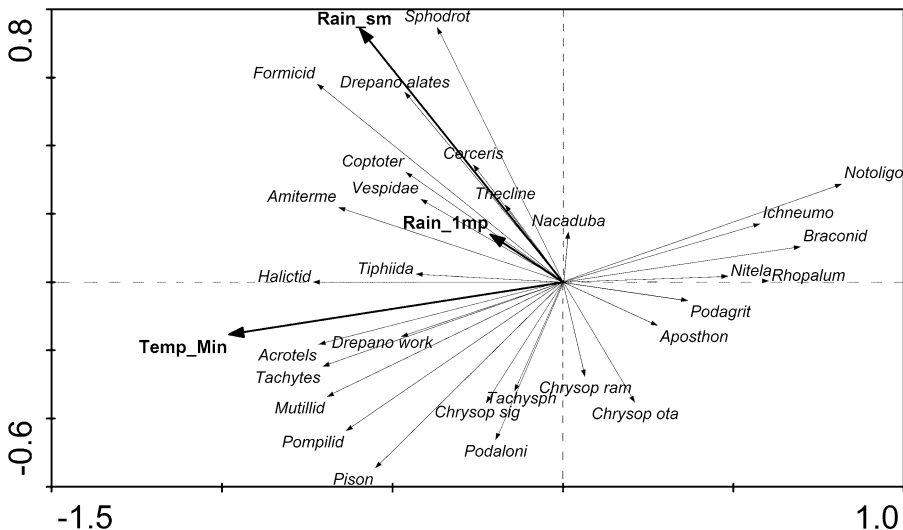


Fig. 4. Ordination (RDA) diagram showing the distribution of selected taxa in relation to environmental variables. Only the significant variables are shown. Arrows represent continuous environmental variables. Taxa shown are those selected for clarity on the diagram. See text for more details. Environmental variable abbreviations as for Fig. 3. Taxon abbreviations: Acrotels, *Acrotelsella*; Amiterme, *Amitermes*; Aposthon, *Aposthonia*; Braconid, Braconidae; Chrysop ota, *Chrysopa otalatis*; Chrysop ram, *Chrysopa ramburi*; Chrysop sig, *Chrysopa signata*; Coptoter, *Coptotermes alates*; Drepano alates, *Drepanotermes alates*; Drepano work, *Drepanotermes workers*; Formicid, Formicidae; Halictid, Halictidae; Ichneumo, Ichneumonidae; Mutillid, Mutillidae; Notoligo, *Notoligotoma*; Podagrit, *Podagritus*; Podaloni, *Podalonia*; Pompilid, Pompilidae; Sphodrot, *Sphodrotes*; Tachysph, *Tachysphex*; Tiphida, Tiphidae; Thecline, *Theclinesthes miskini*.

Table 2. Abundance of taxa identified for this study collected from Oct. 2006 to Mar. 2008

Taxon	2006			2007												2008		
	Oct	Nov	Dec	Jan	Feb	Mar	April	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar
Blattodea	1	1	0	2	3	0	0	0	0	0	0	0	2	0	4	0	0	0
Blattidae																		
<i>Desmozosteria</i>																		
Embioptera	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Notoligotomidae																		
<i>Notoligotoma</i>	0	0	0	0	0	0	0	0	0	0	1	7	0	0	0	0	0	0
Oligotomidae																		
<i>Aposthonia</i>																		
Hymenoptera																		
Bethyloidea																		
Bethyloidea	3	4	8	12	11	5	1	3	0	2	9	2	1	13	15	7	25	13
Braconidae	2	7	3	11	15	3	12	30	23	82	77	42	3	6	5	3	43	15
Chrysididae	3	8	3	2	1	0	0	0	0	0	1	2	3	1	0	1	1	2
Dryinidae	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	1	0
Evanioidea	2	11	3	4	6	3	2	0	0	0	2	2	1	1	2	2	3	2
Formicidae	15	14	76	395	13	70	14	15	5	3	4	9	3	47	35	111	87	9
Gasteruptionidae	12	10	8	21	13	0	5	2	0	2	8	5	3	2	3	1	8	1
Ichneumonidae	6	2	1	5	15	0	15	16	4	17	67	6	1	4	5	0	4	0
Megalyridae	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1
Mutillidae	241	156	210	50	178	116	109	69	1	2	3	4	74	94	121	66	64	71
Platygasteridae	0	6	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0
Pompilidae	185	227	152	48	34	25	20	17	0	3	3	14	77	46	56	55	40	42
Scelionidae	9	28	38	11	3	5	1	13	0	0	0	2	9	12	28	19	8	4
Sclerogibbidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Scoliidae	1	4	6	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Sphecidae																		
<i>Acanthostethus</i>	1	1	0	0	5	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Ammophila</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Arpactophilus</i>	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0
<i>Bembecinus</i>	0	1	0	0	9	0	0	0	0	0	0	0	0	1	0	0	2	0
<i>Bembix</i>	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cerceris</i>	0	0	0	1	4	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Larra</i>	8	6	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Liris</i>	5	4	27	1	2	1	0	1	0	0	0	0	3	3	5	6	8	0
<i>Lyroda</i>	0	0	0	0	1	0	0	0	0	0	0	0	4	5	2	0	0	0
<i>Nitela</i>	0	0	0	0	0	0	2	13	0	1	3	1	0	0	0	0	0	0
<i>Pison</i>	22	19	17	2	4	2	4	6	0	0	0	4	7	7	9	3	4	6
<i>Podagritus</i>	0	1	0	0	0	0	1	6	1	0	0	1	0	0	0	0	0	0
<i>Podalonia</i>	4	2	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
<i>Prionyx</i>	8	0	1	0	0	3	0	0	0	0	1	2	2	3	2	0	0	0
<i>Rhopalum</i>	0	0	0	0	0	0	9	14	0	11	4	11	0	0	0	0	0	0
<i>Sphex</i>	0	3	0	0	4	1	2	0	0	0	0	0	0	0	2	0	0	1
<i>Sphodrotes</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tachysphex</i>	8	9	5	3	4	1	2	9	1	0	2	7	0	0	2	0	7	3
<i>Tachytes</i>	35	75	20	25	24	4	5	5	0	0	0	0	5	17	31	17	72	5
Tiphidae	23	13	5	16	53	2	42	17	0	0	2	0	4	49	25	5	20	1
Vespidae	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Apoidea																		
Anthophoridae	9	11	3	2	5	0	2	2	0	0	0	0	0	2	0	0	0	2
Colletidae	6	11	9	5	17	9	8	2	0	1	0	1	5	5	0	5	20	6
Halictidae	24	19	22	65	23	9	1	6	0	0	1	10	12	15	11	5	85	17
Megachilidae	3	1	0	2	2	0	0	0	0	0	0	1	0	0	1	0	0	0
Stenotritidae	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
Isoptera																		
Rhinotermitidae																		
<i>Coptotermes alates</i>	13	2	0	39	0	0	0	0	0	0	0	0	3	0	0	1	8	0
Termitidae																		
<i>Amitermes alates</i>	1	1	49	74	0	1	0	0	0	0	0	0	0	0	45	69	47	0
<i>Drepanotermes alates</i>	0	0	0	194	0	0	0	0	0	0	0	0	0	0	0	9	60	0
<i>Drepanotermes soldiers</i>	3	5	18	10	7	74	12	21	1	0	3	7	8	13	48	8	17	96
<i>Drepanotermes workers</i>	22	35	443	230	280	731	270	184	8	1	28	73	142	99	411	186	198	1023
Lepidoptera																		
Hesperiidae																		
<i>Taractrocerana anomorpha</i> (Lower)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lycaenidae																		
<i>Famegana alsulus</i> (Herrich-Schäffer)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Lampides boeticus</i> (L.)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Nacaduba biocellata</i> (Felder & Felder)	1	0	1	18	136	1	17	145	1	1	5	3	1	0	0	1	15	0
<i>Theclinesstes albocincta</i> (Waterhouse)	0	2	0	4	13	2	1	8	2	2	1	1	0	0	0	0	0	0
<i>Theclinesstes miskini</i> (Lucas)	0	0	0	1	10	2	0	2	0	0	1	0	0	0	0	0	1	0
<i>Zizina labradus</i> (Godart)	2	0	0	2	0	0	0	5	1	0	1	2	0	1	0	2	6	0

Continued on following page

Table 2. Continued

Taxon	2006			2007									2008					
	Oct	Nov	Dec	Jan	Feb	Mar	April	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar
Nymphalidae																		
<i>Danaus chrysippus</i> (L.)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Junonia villida</i> (F.)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Pieridae																		
<i>Belenois java</i> (L.)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Neuroptera																		
Ascalaphidae																		
<i>Lobalasca</i>	1	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
<i>Megacmonotus</i>	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0
<i>Pseudencyoposis</i>	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Subpalasca</i>	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Suphalomitus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Larvae	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Berothidae																		
<i>Spermophorella</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
<i>Stenobiella</i>	2	0	1	5	1	1	2	3	1	5	7	9	12	6	6	6	3	5
Chrysopidae																		
<i>Chrysopa otalatis</i> Banks	1	1	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0
<i>Chrysopa ramburi</i> Schneider	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
<i>Chrysopa signata</i> Schneider	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1
<i>Italochrysa insignis</i> (Walker)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Larvae	0	0	0	0	1	0	2	2	0	0	0	0	0	1	0	0	1	0
Hemerobiidae																		
<i>Notiobiella</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mantispidae																		
<i>Theristria</i>	0	1	0	0	1	0	1	1	0	0	0	0	0	0	1	0	2	0
Myrmeleontidae																		
<i>Ceratoleon brevicornis</i> Esben-Petersen	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Compsoleon bembicidis</i> New	0	2	1	1	0	0	0	0	0	0	0	0	0	0	0	1	3	0
<i>Distoleon bistrigatus</i> (Rambur)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
<i>Distoplectron</i> sp. nr. <i>minor</i> Banks	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Froggattisca</i> sp. nr. <i>tipularia</i> (Gerstaecker)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Glenoleon berthoudi</i> Tillyard	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Glenoleon nigristriatus</i> New	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Glenoleon</i> sp. 1	1	0	0	0	0	0	0	0	0	0	0	0	3	1	0	0	0	0
<i>Heoclisis fundata</i> (Walker)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mossega</i> sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Myrmeleon croceicollis</i> Gerstaecker	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0
<i>Myrmeleon maculaclypeus</i> New	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Protoplectron eremiae</i> Tillyard	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Stenoleon grandithecus</i> New	0	0	0	0	0	0	3	1	0	0	0	0	0	0	0	0	0	1
<i>Xantholeon</i> sp. 1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Larvae	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Thysanura																		
Lepismatidae																		
<i>Acrotelsella</i>	10	16	18	16	37	18	8	8	3	1	3	3	6	5	8	20	21	29

Taxa are arranged alphabetically, other than the Apoidea (bees) which is presented as the last taxon in the Hymenoptera.

(e.g., several genera of Sphecidae, the wasp family Tiphiidae, the bee family Stenotritidae and two butterflies) (Table 3). Abundance of the lycaenid *Nacaduba biocellata* (Felder and Felder) was correlated with rainfall both in the previous month ($r = 0.457$) and 4 mo prior ($r = 0.493$).

Taxa More Active in the Cooler Months. This group includes those species most active in, or restricted to, the months of April to September 2007, which were subject to the lowest mean monthly minimum temperatures. This group includes the webspinners *Notoligotoma* (Notoligotomidae) and *Aposthonia*

(Oligotomidae), the wasp families Braconidae and Ichneumonidae, and the following genera of sphecid wasps: *Nitela*, *Podagritus*, and *Rhopalum* (Fig. 4).

Taxa More Common in the Warmer Months. This group includes species whose abundance was higher from October to March, when mean monthly minimum temperatures were highest. Abundance of these taxa was lower during the other months. This pattern was shown by the silverfish *Acrotelsella* (Lepismatidae), *Drepanotermes* workers, the wasp families Evaniidae, Scelionidae, Mutillidae, and Pompilidae, the bee family Colletidae, and the sphecid wasp genera *Tachytes* and *Pison*.

Table 3. Maximum cross-correlation coefficients of monthly rainfall and taxon abundance

Taxon	Maximum coefficient	Lag value (months)
Hymenoptera		
Formicidae alates	$r = 0.896$	0
Sphecidae		
<i>Acanthostethus</i>	$r = 0.725$	-1
<i>Bembecinus</i>	$r = 0.779$	-1
<i>Bembix</i>	$r = 0.787$	-1
<i>Cerceris</i>	$r = 0.800$	-1
<i>Sphex</i>	$r = 0.670$	-1
Stenotritidae	$r = 0.787$	-1
Tiphidae	$r = 0.718$	-1
Isoptera		
Rhinotermitidae		
<i>Coptotermes alates</i>	$r = 0.704$	0
Termitidae		
<i>Amitermes alates</i>	$r = 0.605$	0
<i>Drepanotermes alates</i>	$r = 0.758$	0
Lepidoptera		
Lycaenidae		
<i>Nacaduba biocellata</i>	$r = 0.493$	-4
<i>Theclinesthes albocincta</i>	$r = 0.564$	-1
<i>Theclinesthes miskini</i>	$r = 0.711$	-1

All correlations ($P < 0.05$). All taxa for which more than one individual was collected were tested. Taxa are arranged alphabetically.

‘Annual’ Taxa. This includes those species whose presence in the traps was separated by ~12 mo. This group includes several Neuroptera species, such as

Compsoleon bembicidis New, *Glenoleon* sp. 1, *Stenoleon grandithecus* New (all Myrmeleontidae) as well as myrmeleontid larvae, and *Lobalacsa* (Ascalaphidae). The abundance of all members of this group was low (see Table 2).

Patterns of Other Taxa. Members of the berothid lacewing genus *Stenobiella* were much less abundant in the first 9 mo period (16 individuals) from October 2006 to June 2007, compared with the second 9 mo period (59 individuals) from July 2007 to March 2008 (Table 2).

Frequency of Occurrence of New Species of Sphecidae and Neuroptera. A cumulative frequency plot of number of genera of Sphecidae with time shows that 18 mo of sampling easily represented the number of sphecid taxa collected, and that no new genera were collected after the first 7 mo of sampling (Fig. 5). The same plot with number of species of Neuroptera shows that 18 mo of collecting was almost certainly not sufficient to collect all the lacewings present at that site (Fig. 5). Both plots show that different species are active in spring (October, November), summer (December to February), and autumn (March, April). Both plots also show that no new species in either taxon was collected from May to November 2007.

Discussion

Monthly Assemblages. The separation of the winter assemblage (June to August) was because of the dis-

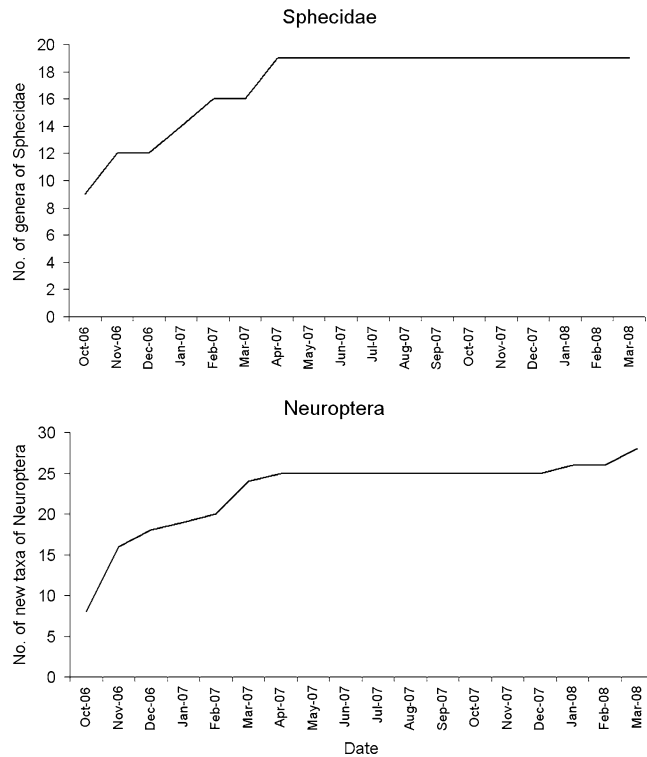


Fig. 5. Cumulative frequency plots of new species of sphecid wasps and Neuroptera collected during the survey period.

tinct fauna restricted to or most abundant in the cooler months. The deep separation of January 2007 from all other months based on abundance (Fig. 3) was because of the emergence of large numbers of winged ants and winged termites soon after heavy rain earlier in that month. The very similar assemblages of December 2006 and December 2007 were based on large numbers of *Drepanotermes* workers, as well as winged *Amitermes* termites and scelionid wasps.

Biology of Taxa. That heat drives the rate of growth and development in insects is well established, and so a rise in temperature within a favorable range will increase the rate of development (Gullan and Cranston 2005), leading to earlier emergence. Low moisture content of the air can also affect the physiology and thus the development, longevity, and oviposition of many insects (Gullan and Cranston 2005). Other climatic factors reported to influence the activity of some insects include humidity (e.g., Toshova et al. 2009), intensity and duration of sunshine (e.g., Patel et al. 2009), and lunar cycle (e.g., Tigar and Osborne 1999).

Many butterflies are active after rain, with development to adult accelerated as larvae take advantage of new growth of newly watered food plants. Adult *N. biocellata* and *Theclinesthes miskini* (Lucas) are distributed throughout much of Australia and can be extremely abundant and active most of the year (Braby 2000). The sporadically distributed inland form of *T. albocincta* is also active most of the year (Braby 2000). Termite alates are released from the parent colony at particular times of the year to found new colonies, and in Australia the main flight periods are late spring to early summer, and autumn (Watson and Gay 1991). Results of the current study show that alates of all species were released at the same time in response to rain. The maximum proportion of *Drepanotermes* soldiers to workers was 14.3% (mean 8.4%), although the proportion during the peak abundance of workers in March 2007 was 10.1%, and 9.4% in March 2008. *Drepanotermes* workers harvest grass and plant litter and carry it back to the nest for feeding (Watson and Gay 1991).

Members of the Hymenoptera have key roles in the functioning of natural and agricultural ecosystems: wasps are predominantly predators and parasites of many other insect and arthropod groups, and bees are some of the most important pollinators of flowering plants (Stevens et al. 2007). Most hymenopteran taxa were collected in greater numbers in the warmer months, indicating that predation, parasitism, and pollination occur throughout the year.

Winged males of the webspinner *Notoligotoma* were collected in June, July, and August, and members of the genus are known to be active during the first rains of the cold season (Ross 1991). Most species of Australian ascalaphid and berothid lacewings are restricted to drier areas (New 1991), although why the berothid *Stenobiella* was collected in much greater numbers during the second 9 mo period (July 2007–March 2008) is unknown.

When taken together, results demonstrate that for the fauna investigated in this study, seasonality is the most conspicuous feature of the phenology of insects in central Australia, but that rainfall has a pronounced effect on some taxa. Whether species are influenced by temperature or moisture is not determined phylogenetically, so that within higher taxa species respond to one or the other of these environmental cues or a combination of the two.

Availability of Insects as a Prey Resource. Results are similar to those of other studies conducted in the arid zone of Australia (e.g., Morton 1978, Read 1987, Gilfillan 2001), which show that overall insect abundance (and therefore food availability) is lowest in winter and higher in the warmer months. Such a pattern of availability is used by generalist insect feeding vertebrates such as *Pseudantechinus macdonnellensis* (Spencer), which occurs throughout central Australia and feeds on a large variety of invertebrates (Gilfillan 2001, Burwell et al. 2005). Results of the current study are probably of greatest significance when applied to predators with more specialized invertebrate diets, such as the arid zone scinid lizard *Ctenotus*. One study near Alice Springs showed that termites (including *Drepanotermes*) comprised the main part of the diet of many species in this genus, and especially so in March and April (James 1991b). The very high abundance of *Drepanotermes* workers collected during the current study indicates they are an important and predictable autumnal food source for many lizard species, and this is probably supplemented by the mass emergence of winged reproductives immediately after rain.

Optimal Timing of Surveys in Central Australia. There is a continual turnover of species from October to April (e.g., Fig. 5), and several taxa are more active or only active in the cooler months. Although June to August would be the least productive period for general collecting, both in terms of the numbers of taxa and individuals, to adequately sample diversity in central Australia any general survey should incorporate spring, summer, autumn, and winter. However, permits to undertake scientific research on invertebrates from June to August only are regularly issued by the Northern Territory Government Parks and Wildlife Division, indicating that many workers continue to undertake research and collection during this least productive time, presumably because of the more comfortable temperatures. Unless putatively winter-active taxa are sought, more effective collecting would almost certainly be obtained by shifting the period of study to spring or autumn.

The Importance of Taxonomic Resolution. Pooled monthly numbers of Sphecidae were weakly positively correlated with mean minimum temperature ($r = 0.5073$; $P = 0.0317$) and mean maximum temperature ($r = 0.5169$; $P = 0.0281$), but not with the other environmental variables, so that total abundance was higher in the warmer months. However, the relative abundance of five sphecid genera was correlated with rainfall (Table 3), and three genera (*Nitela*, *Podagrius*, *Rhopalum*) were most abundant in the cooler

months. This indicates that for the Sphecidae, investigating environmental determinants of activity and phenology at the family level is insufficient to explain the environmental determinants of these attributes at the generic level, further underlining the importance of examining large, preferably diverse, higher taxa at a high level of taxonomic resolution for such studies. This approach best accounts for the range of responses to environmental cues.

Although the abundance of each species of myrmecoleontid lacewings did not correlate with any environmental variable, the total abundance of the Myrmecoleontidae was weakly correlated with mean minimum temperature ($r = 0.4927$; $P = 0.0378$) and mean maximum temperature ($r = 0.4742$; $P = 0.0468$). This indicates that the abundance of individual species in the traps was low, but that a similar overall pattern was present.

Potential Effects of Climate Change. The 'best estimate' of climate change for central Australia is that by 2030 annual rainfall will decrease by between 2 and 10%, with a general decrease in rainfall across all seasons. Temperature will increase by between 0.6 and 1.5°C (Commonwealth Scientific and Industrial Research Organization [CSIRO] 2007). The best estimate projections for 2050 and 2070 are for even drier and hotter conditions (CSIRO 2007). It is likely that both rainfall variability and unpredictability will increase further with climate change, leading to larger rainfall events but longer dry periods between such events (Pickup 1998).

Although heat is generally the main driving force behind growth and development in insects (Gullan and Cranston 2005), moisture also has a significant role in many species such as herb-feeding Lepidoptera, the larvae of which use the rapidly responding vegetation that follows rain (Nielsen and Common 1991). The current study has shown that both temperature and rainfall influence insect activity, but which climatic factor is most influential varies between taxa. Longer periods between rain events in central Australia will most likely have a negative effect on rainfall-dependent taxa such as the butterfly *T. miskini* and the sphecid wasp *Bembecinus*. How long the immature stage of *T. miskini* can survive without rain is unknown, as is how an altered phenology because of increased variability of rain affects the ability of adult *Bembecinus* to locate their auchenorrhynchos hemipteran prey. Temperature-related earlier shifts in phenology have recently been detected for many invertebrates (e.g., Root et al. 2003) including butterflies (Roy and Sparks 2000).

Increasing climatic variability is also likely to disrupt other important regulators of animal community structure such as parasites; both by the variability itself as well as by the indirect and unpredictable variance in host dynamics in response to climate (Stireman et al. 2005). Most members of the Ichneumonidae and Braconidae parasitize the immature stages of their mainly endopterygote insect hosts (Stevens et al. 2007), which explains why in the current study the abundance of both families was greatest in winter,

before the emergence of adults of other orders. This synchronized phenology of host and parasite is unlikely to persist, as other studies (e.g., Stireman et al. 2005) have shown a decreased level of parasitism of Lepidoptera by Hymenoptera as climatic variability increases.

Indicator Taxa for Monitoring Change in Phenology. Parataxonomic sorting of specimens into morphospecies or other taxonomic unit to save time was avoided in this study, because (1) this approach is an unreliable method of detecting species or higher level taxa, and (2) the criteria for detecting taxa in this way are usually unspecified (Krell 2004). In the current study, all identifications were made to family, genus, or species. This approach allows other researchers in future assessments of the impacts of climate change on the phenologies of taxa in central Australia to: (1) identify the same taxa using the most appropriate method, and (2) use specified criteria for taxon discrimination (published keys and taxon descriptions if a nonspecialist of a particular group).

The most appropriate taxa for assessing impacts of climate change are those shown to have a phenology determined by one climatic factor, such as rainfall, including those reliably active at a particular time of year, demonstrating a dependence on temperature. Several taxa collected at Simpsons Gap during this study would be useful for monitoring likely changes in insect phenology because of climatic variability. Adult *Bembecinus* were collected only after rain, indicating that for this genus precipitation is the only driver of development leading to adult activity. Adults are large (≥ 10 mm) relative to other species of Hymenoptera, facilitating identification. Although the butterfly *N. biocellata* was present at Simpsons Gap throughout much of the survey period, it was collected in much greater abundance after more intensive rain (see Table 2). This species is one of only about forty butterflies known from central Australia and is easily identified. The species is also common and widely distributed across the southern two-thirds of the continent (Braby 2000).

Winged reproductives of termites in Australia are typically released at a particular time of the year (Watson and Gay 1991), and this also occurred during the current study. Large numbers of genus *Amitermes* were collected in December 2006–January 2007, and in December 2007–January 2008, indicating that temperature is the primary determinant of colony founding. The sphecid wasp *Rhopalum* was collected in good numbers only from April to September, suggesting that members of this genus are restricted to the cooler months. Long-term monitoring of both taxa at Simpsons Gap may demonstrate: (1) an earlier appearance of *Amitermes* alates, and (2) 'compression' of the phenology of *Rhopalum* to the coldest months, in a generally warming climate.

Future Research. In conclusion, this study has generated many insights relating to which aspects of climate influence the phenology of insect taxa in the Australian arid zone, incorporating a high level of taxonomic resolution across several orders. Of most

interest has been the discrimination of the group active during cool temperatures and the diversity of taxa active after rain. Only a continuous trapping methodology as used here can reveal the true phenologies of species and the presence of seasonality.

Future research should focus on increasing the number of study sites, even though it is extremely unlikely that spatial replication will help clarify the phenology of those taxa for which clear patterns were determined during the current study. However, increasing the number of sites will increase the number of known patterns, because any individual study site is core habitat for some species and marginal habitat for others, meaning that phenologies may become apparent at a second site for those taxa collected at low abundance at the first site. Future sampling could also be expanded beyond the 18 mo, with equivalent periods (e.g., October to March) sampled in several consecutive years.

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References Cited

- Allsopp, P. G., and R. J. Lloyd. 1987. New records of Scarabaeidae (Coleoptera) from central Australia. *Aust. Entomol. Mag.* 13: 71–76.
- Anonymous. 1993. Ecological patterns and processes of importance, pp. 133–148. *In* J.R.W. Reid, J. A. Kerle, and S. R. Morton (eds.), *Uluru Fauna: the distribution and abundance of vertebrate fauna of Uluru (Ayers Rock-Mount Olga) National Park, N.T. Australian National Parks and Wildlife Service, Canberra, Australia.*
- Aspöck, V. U., and H. Aspöck. 1984. Die Berthiden Australiens I: Neue spezie des genus *Stenobiella* Tillyard (Neuropteroidea: Planipennia: Berthidae). *Z. Arbeitsgem. Österr. Entomol.* 36: 17–32.
- Aspöck, V. U., and H. Aspöck. 1986. Die Berthiden Australiens III: Die genera *Spermophorella* Tillyard und *Quasispermophorella* n.g. (Neuropteroidea: Planipennia: Berthidae). *Z. Arbeitsgem. Österr. Entomol.* 38: 17–34.
- Bohart, R. M., and A. S. Menke. 1976. *Sphecid wasps of the world: a generic revision.* University of California Press, Berkeley, CA.
- Braby, M. F. 2000. *Butterflies of Australia: their identification, biology and distribution.* CSIRO Publishing, Melbourne, Australia.
- Bureau of Meteorology. 2009. Climate statistics for Australian locations. (http://www.bom.gov.au/climate/averages/tables/cw_015590.shtml).
- Burwell, C. R., F. Geiser, M. Barritt, K. May, and C. R. Pavey. 2005. Additional records of prey of the fat-tailed false antechinus *Pseudantechinus macdonnellensis* from central Australia. *Aust. Mammal.* 27: 227–229.
- Chesson, P., R.L.E. Gebauer, S. Schwinning, N. Huntly, K. Wiegand, M.S.K. Ernest, A. Sher, A. Novoplansky, and J. F. Weltzin. 2004. Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia* 141: 236–253.
- (CSIRO) Commonwealth Scientific and Industrial Research Organization. 2007. Climate change in Australia technical report. (<http://www.climatechangeinaustralia.gov.au/futureclimate.php>).
- Dickman, C. R., P. S. Mahon, P. Masters, and D. F. Gibson. 1999. Long-term dynamics of rodent populations in arid Australia: the influence of rainfall. *Wildl. Res.* 26: 389–403.
- Dingle, H., W. A. Rochester, and M. P. Zalucki. 2000. Relationships among climate, latitude and migration: Australian butterflies are not temperate-zone birds. *Oecologia* 124: 196–207.
- Gilfillan, S. L. 2001. An ecological study of a population of *Pseudantechinus macdonnellensis* (Marsupialia: Dasyuridae) in central Australia. I. Invertebrate food supply, diet and reproductive strategy. *Wildl. Res.* 28: 469–480.
- Griffin, G. F. 1979. Dragonfly (Odonata) records from central Australia. *Aust. Entomol. Mag.* 6: 75–77.
- Gullan, P. J., and P. S. Cranston. 2005. *The insects: an outline of entomology*, 3rd ed. Blackwell Publishing, Melbourne, Australia.
- Hill, G. F. 1942. Termites (Isoptera) from the Australian region. CSIR, Melbourne, Australia.
- Hughes, R. D., P. M. Greenham, M. Tyndale-Biscoe, and J. M. Walker. 1972. A synopsis of observations on the biology of the Australian bushfly (*Musca vetustissima* Walker). *J. Aust. Entomol. Soc.* 11: 311–331.
- James, C. D. 1991a. Population dynamics, demography, and life history of sympatric scincid lizards (*Ctenotus*) in central Australia. *Herpetologica* 47: 194–210.
- James, C. D. 1991b. Temporal variation in diets and trophic partitioning by coexisting lizards (*Ctenotus*: Scincidae) in central Australia. *Oecologia* 85: 553–561.
- Krell, F.-T. 2004. Parataxonomy vs. taxonomy in biodiversity studies: pitfalls and applicability of 'morphospecies' sorting. *Biodivers. Conserv.* 13: 795–812.
- Lambkin, K. J. 1986a. A revision of the Australian Mantispidae (Insecta: Neuroptera) with a contribution to the classification of the family I. General and Drepanicinae. *Aust. J. Zool. Suppl. Series.* 116: 1–142.
- Lambkin, K. J. 1986b. A revision of the Australian Mantispidae (Insecta: Neuroptera) with a contribution to the classification of the family II. Calomantispinae and Mantispinae. *Aust. J. Zool. Suppl. Series.* 117: 1–113.
- Mackerras, M. J. 1966. Australian Blattidae (Blattodea) IV. *Megazosteria*, gen. nov., and revision of the genus *Desmozosteria* Shelford. *Aust. J. Zool.* 14: 305–334.
- Matthews, E. G. 1976. *Insect ecology.* University of Queensland Press, Brisbane, Australia.
- Michener, C. D. 2000. *The bees of the world.* Johns Hopkins University Press, Baltimore, MD.
- Morton, S. R. 1978. An ecological study of *Sminthopsis crassicaudata* (Marsupialia: Dasyuridae) III. Reproduction and life history. *Aust. Wildl. Res.* 5: 183–211.
- New, T. R. 1980. A revision of the Australian Chrysopidae (Insecta: Neuroptera). *Aust. J. Zool. Suppl. Series.* 77: 1–143.
- New, T. R. 1984. Revision of the Australian Ascalaphidae (Insecta: Neuroptera). *Aust. J. Zool. Suppl. Series.* 100: 1–86.
- New, T. R. 1985a. A revision of the Australian Myrmeleontidae (Insecta: Neuroptera). I. Introduction, Myrmeleontini, Protoplectrini. *Aust. J. Zool. Suppl. Series* 104: 1–90.

- New, T. R. 1985b. A revision of the Australian Myrmeleontidae (Insecta: Neuroptera). II. Dendroleontini. Aust. J. Zool. Suppl. Series 105: 1–170.
- New, T. R. 1985c. A revision of the Australian Myrmeleontidae (Insecta: Neuroptera). III. Distoleontini and Acanthaclisinae. Aust. J. Zool. Suppl. Series 106: 1–159.
- New, T. R. 1988. A revision of the Australian Hemerobiidae (Insecta: Neuroptera). Invertebr. Taxon. 2: 339–411.
- New, T. R. 1991. Neuroptera (lacewings), pp. 525–542. In I. D. Naumann, P. B. Carne, J. F. Lawrence, E. S. Nielsen, J. P. Spradbery, R. W. Taylor, M. J. Whitten, and M. J. Littlejohn (eds.), The Insects of Australia, 2nd ed. Melbourne University Press, Melbourne, Australia.
- Nielsen, E. S., and I.F.B. Common. 1991. Lepidoptera (moths and butterflies), pp. 817–915. In I. D. Naumann, P. B. Carne, J. F. Lawrence, E. S. Nielsen, J. P. Spradbery, R. W. Taylor, M. J. Whitten, and M. J. Littlejohn (eds.), The Insects of Australia, 2nd ed. Melbourne University Press, Melbourne, Australia.
- Oertel, A., M. P. Zalucki, D. A. Maelzer, G. P. Fitt, and R. Sutherst. 1999. Size of the first spring generation of *Helicoverpa punctigera* (Wallengren) (Lepidoptera: Noctuidae) and winter rain in central Australia. Aust. J. Entomol. 38: 99–103.
- Paclt, J. 1967. Thysanura Fam. Lepidotrichidae, Maindroniidae, Lepismatidae. Genera Insectorum. 218: 1–86.
- Patel, P. V., M. F. Acharya, M. V. Gedia, and H. J. Vyas. 2009. Study on growing degree days and population dynamics of thrips, *Scirtothrips dorsalis* Hood (Thysanoptera: Thripidae) on castor. J. Agromet. 11: 79–82.
- Pickup, G. 1998. Desertification and climate change: the Australian perspective. Clim. Res. 11: 51–63.
- Pulawski, W. J. 2009. Catalogue of Sphecidae sensu lato (=Apoidea excluding Apidae). (http://research.calacademy.org/research/entomology/entomology_resources/hymenoptera/sphecidae/introduction.htm).
- Read, D. G. 1987. Diets of sympatric *Planigale gilesi* and *P. tenuirostris* (Marsupialia: Dasyuridae): relationships of season and body size. Austral. Mammal. 10: 11–21.
- Reid, J.R.W., J. A. Kerle, L. Baker, and K. R. Jones. 1993. Reptiles and frogs, pp. 58–68. In J.R.W. Reid, J. A. Kerle, and S. R. Morton (eds.), Uluru fauna: the distribution and abundance of vertebrate fauna of Uluru (Ayers Rock-Mount Olga) National Park, N.T. Australian National Parks and Wildlife Service, Canberra, Australia.
- Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature 421: 57–60.
- Ross, E. S. 1991. Embioptera: Embiidina (Embiids, web-spinners, foot-spinners), pp. 405–409. In I. D. Naumann, P. B. Carne, J. F. Lawrence, E. S. Nielsen, J. P. Spradbery, R. W. Taylor, M. J. Whitten, and M. J. Littlejohn (eds.), The Insects of Australia, 2nd ed. Melbourne University Press, Melbourne, Australia.
- Roy, D. B., and T. H. Sparks. 2000. Phenology of British butterflies and climate change. Global Change Biol. 6: 407–416.
- Schwinning, S., and O. E. Sala. 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. Oecologia 141: 211–220.
- Schwinning, S., O. E. Sala, M. E. Loik, and J. R. Ehleringer. 2004. Thresholds, memory, and seasonality: understanding pulse dynamics in arid/semi-arid ecosystems. Oecologia 141: 191–193.
- Stafford-Smith, D. M., and S. R. Morton. 1990. A framework for the ecology of arid Australia. J. Arid Environ. 18: 255–278.
- Stevens, N. B., C. J. Stephens, M. Iqbal, J. T. Jennings, J. La Salle, and A. D. Austin. 2007. What wasp is that? An interactive guide to the Australasian families of Hymenoptera. Australian Biological Resources Study, Canberra, Australia.
- Stireman, J. O., III, L. A. Dyer, D. H. Janzen, M. S. Singer, J. T. Lill, R. J. Marquis, R. E. Ricklefs, G. L. Gentry, W. Hallwachs, P. D. Coley, J. A. Barone, H. F. Greeney, H. Connahs, P. Barbosa, H. C. Morais, and I. R. Diniz. 2005. Climatic unpredictability and parasitism of caterpillars: implications of global warming. Proc. Nat. Acad. Sci. USA 102: 17384–17387.
- ter Braak, C.J.F., and P. Šmilauer. 2002. CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination, version 4.5. Microcomputer Power, Ithaca, NY.
- Tigar, B. J., and P. E. Osborne. 1999. The influence of the lunar cycle on ground-dwelling invertebrates in an Arabian desert. J. Arid Environ. 43: 171–182.
- Toshova, T. B., E. Csonka, M. A. Subchev, and M. Toth. 2009. The seasonal activity of flea beetles in Bulgaria. J. Pest Sci. 82: 295–303.
- Watson, J.A.L., and F. J. Gay. 1991. Isoptera (termites), pp. 330–347. In I. D. Naumann, P. B. Carne, J. F. Lawrence, E. S. Nielsen, J. P. Spradbery, R. W. Taylor, M. J. Whitten, and M. J. Littlejohn (eds.), The Insects of Australia, 2nd ed. Melbourne University Press, Melbourne, Australia.
- Wright, D. E., and P. M. Symmons. 1987. The development and control of the 1984 plague of the Australian plague locust, *Chortoicetes terminifera* (Walker). Crop Protection. 6: 13–19.

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