Convergence and parallelism among cicadas of Argentina and the southwestern United States (Hemiptera: Cicadoidea)

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Cicadas of the genera *Derotettix* in Argentina and *Okanagodes* in the south-western United States resemble each other in colour, live on salt-tolerant plants (*Atriplex* spp. etc.), nearly match the colour of their respective host plants and produce songs above the range of avian hearing. The Argentine cicadas are smaller, but have nearly identical thermal limits for activity measured by the minimum temperature for flight (20–24 °C) and a body temperature at heat torpor (48–49 °C). The species shift activity from basking sites to shade at temperatures above 37 °C, although *O. gracilis* rises to a significantly higher temperature (40.7 °C) than its congener (38.2 °C) or *Derotettix* (37.2 °C). The thermal tolerances are the highest reported for cicada species. A third group using halophytes in Argentina (*Babras sonorivox*) has similar temperature tolerances and is cryptically coloured. The genera are convergent with respect to morphology, coloration, body size, behaviour, habitat choice and host plant selection. The similarities of thermal tolerances and their influence on behaviour can be viewed as parallelism because the underlying mechanisms are the same in all species studied.   © 2004 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2004, **83**, 281–288.

ADDITIONAL KEYWORDS: *Babras* – behaviour – *Derotettix* – *Okanagodes* – temperature – thermal responses.

INTRODUCTION

Animals that experience the same natural selective factors often arrive independently at similar biological solutions to environmental problems. This homoplasy can occur through several mechanisms. Convergence occurs when distantly related taxa evolve superficially similar characteristics through independent developmental pathways. Parallelism occurs when organisms evolve similar features through the independent alteration of shared developmental pathways, often in closely related organisms (Futuyma, 1998).

The exact definitions of convergence and parallelism are still a matter of debate (e.g. see summary in Weins, Chippindale & Hillis, 2003). Much of the confusion appears to be the result of the application of the definitions to specific problems. Convergence has been described as characteristics that arise from different antecedent states, have different mechanisms involved in the expression of the similar traits or occur in distantly related organisms (Weins *et al.*, 2003). By contrast, parallelism occurs when a trait evolves from the same antecedent state, uses the same mechanisms to express the trait and occurs in more closely related organisms (Weins *et al.*, 2003). We are interested here in how similar morphological, physiological and behavioural characteristics have evolved in cicadas that inhabit similar habitats. We consider convergence

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to produce similar structures or physiological adaptations through the alteration of independent developmental pathways in distantly related taxa. We will consider parallelism to produce similarities as a result of independent alterations of shared developmental pathways in more closely related taxa.

We examine several cicada species that inhabit similar habitats in Argentina and the southwestern United States to investigate convergence and parallelism in the cicadas. Higher classification of the cicadas has received little attention and is currently in a state of flux. Metcalf (1963a, b) listed three families. The next (and last published) bibliography of the Cicadoidea listed a total of six families (Duffels & van der Laan, 1985). Members of this study would have been classified into the families Tibicinidae and Tettigadidae. Duffels (1993) began the re-analysis of the higher taxonomy and stated that the monophyly of the Tettigadean lineage is suggested by the morphology but further phylogenetic analyses were necessary in the group to determine its validity.

The validity of the higher taxonomic divisions of the extant cicadas is currently being studied (Heath, 1999; Moulds, 1999). There have been between two and four families cited in papers discussing the higher taxonomy (Boulard, 1988, 1997; Moulds, 1990; Duffels, 1993; Chou *et al.*, 1997) since the publication of the last bibliography (Duffels & van der Laan, 1985). It appears now that extant cicadas comprise two families with all but two primitive Australian species classified within the Cicadidae. We will follow that convention with respect to the higher taxonomy of the cicadas discussed in this paper, assigning subfamily rank to what were family-level taxa in the last bibliography.

The species used in this study show different taxonomic affinities within the family Cicadidae. The genera *Okanagodes* and *Derotettix* are members of the subfamily Tibicininae and the tribes Tibicinini and Parnisini, respectively. By contrast, *Babras* is classified in the subfamily Tettigadinae (Metcalf, 1963b). The Tettigadean line (*Babras*) shows a number of common morphological characters with the Okanaganoid line (*Okanagodes*) (Heath M.S., 1983). However, they have probably been isolated since Cretaceous times (Heath M.S., 1983). The radiation of each of these groups began early in the Cenozoic (Heath M.S., 1983). Both lines are entirely temperate in distribution with no known tropical affinities (see location data in Metcalf, 1963b). *Derotettix* differs substantially from the other two genera. It appears to have affinities with some African genera (members of the tribe Parnisini are found across South America, Africa, India and Australia) and may have differentiated during Mesozoic times following the break up of Pangea (Heath M.S., 1983).

The major genera of the Tettigadinae (*Tettigades*) and the Okanaganoid cicadas (*Okanagana*) occupy similar niches in South and North America, respectively (Heath M.S., 1983). *Tettigades* is found in the southern boreal forest and the Patagonian steppe. *Okanagana* inhabits the northern boreal forest and the Great Basin steppes. *Babras* and *Okanagodes* appear to be derived taxa from the Tettigadean and Okanaganoid lineages, respectively, which have colonized *Atriplex* communities. *Derotettix* appears to have an independent evolutionary origin (based on morphological characters of the tribe Parnisini) but has also colonized the *Atriplex* communities of Argentina.

MATERIAL AND METHODS

North American cicadas were observed and captured in their native habitats from 1979 to 2001. *Okanagodes gracilis* Davis were collected in Pinal, Pima, Maricopa and Yavapai Counties, Arizona, Washington County, Utah, and Nye County, Nevada. *Okanagodes gracilis* var. *viridis* Davis was collected in Pinal, Pima and Gila Counties, Arizona. *Okanagodes terlingua* Davis were collected in Brewster County, Texas. Argentine cicadas were observed and experiments performed during December 1981, December 1986 to January 1987, January 1988 and January 1992. *Derotettix mendosensis* Berg were collected in La Rioja, Rio Negro and San Juan Provinces. *Derotettix wagneri* Distant were collected in Santiago del Estero Province. *Babras sonorivox* Jacobi were collected in La Rioja Province. General distributions of the species are shown in Figure 1. Observations were made as to habitat, host plant affiliations and behaviour at each collection site. Argentine habitat descriptions follow Cabrera (1971). *Okanagana bella* Davis and *Tettigades major* Torres are included as ancestral representatives of the Okanaganoid and Tettigadean lineages respectfully. *Okanagana bella* were collected between 1987 and 2001 across their range in Arizona, New Mexico, Colorado, Utah, Idaho, Wyoming, Montana and South Dakota. *Tettigades major* were collected in the Province of Mendoza during January 1987.

Thermal responses were determined using techniques designed by Heath (1967) and Heath & Wilkin (1970) that have been used in many other studies of the thermal responses of cicadas (see summary in Sanborn, 2002). Animals captured for experimentation were placed on ice in a cardboard container along with a plant sample and a damp paper towel during transport to the laboratory. Body temperatures were measured with a Physitemp Model BAT-12 digital thermocouple thermometer and a type MT 29/1 hypodermic copper/constantan micro-

probe sensitive to ± 0.1 °C, which had been calibrated with a National Institutes of Standards and Technology mercury thermometer. Cicadas were cooled to a torpid state and then tossed 1–2 m into the air until they made a controlled flight or landing. The minimum flight temperature represents the lowest body temperature of fully co-ordinated activity in a cicada. The body temperature range of full activity is determined by the minimum flight and heat torpor temperatures. The heat torpor temperature was determined by placing an animal in a cardboard container and placing this container under a heat lamp until movement stopped. The process is not lethal and animals regain motor control as they cool. Between these temperature extremes is the maximum voluntary tolerance or shade-seeking temperature. Animals were placed on a vertical surface under a heat lamp and their body temperature was recorded when the animal walked or flew from the heat source. This maximum voluntary tolerance temperature is a thermoregulatory temperature at which thermoregulation takes precedence over other behaviour (Heath, 1970). All temperatures were measured within 5 s of an animal performing the desired behaviour. Animals were orientated for insertion of the thermocouple by grasping only the wing tips to prevent heat transfer with the experimentor. Live mass was measured for each species with a triple beam balance sensitive to ± 5 mg.

Statistical analyses were performed using InStat 3 (Graphpad Software). Analysis of variance tests were performed to test for the equality of mean values between species. A Tukey–Kramer multiple comparison test was performed to determine which species had significantly different means for a variable if the ANOVA $P < 0.05$. A Student's t-test was performed to compare individual pairs of means. Results are presented as mean ± standard deviation.

RESULTS

All species studied inhabit relatively low-altitude sites with the potential to experience high ambient temperatures even though the species inhabit two distinct floristic provinces in Argentina and two different desert habitats in the USA (Table 1). The Argentine species inhabit the Monte and Chaco floristic provinces. The North American species inhabit the Sonoran Desert and Chihuahuan Desert. The Chaco is more of a subtropical thorn scrub habitat than the semi-arid Monte and North American desert habitats but the cicadas of this study were collected in the more arid woodlands of the southwestern portion of the Chaco floristic province. The habitats share plants of many genera, e.g. *Larrea*, *Opuntia*, *Acacia* and *Prosopis*, and are characterized by the presence of salt-tolerant plant species such as *Atriplex* spp. and *Allenrolfia* spp. in saline areas. These plants are used by the cicadas as
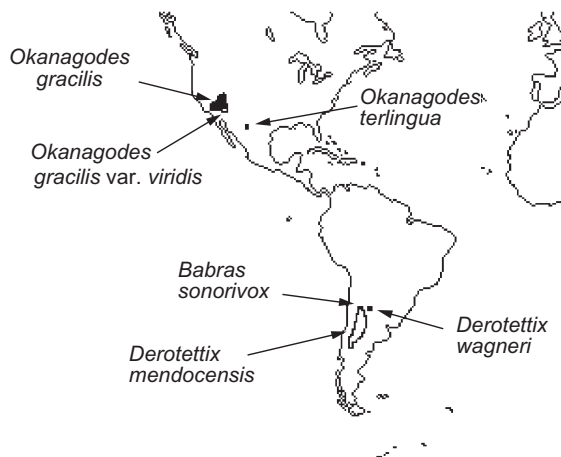
Figure 1. Distributions of the species compared in this study.

Table 1. Ecological characteristics of North and South American cicadas compared in this study. *Okanagana bella* and *Tettigades major* represent ancestral lineages

Species	Location	Altitude (m)	Host plant	Habitat – biotic province (no. of localities collected)
Derotettix mendosensis	Argentina	100–800	*Atriplex*	Salt Desert – Monte (10)
Derottetix wagneri	Argentina	200	*Allenrolfia*	Salt Flat – Chaco (1)
Okanagodes gracilis	N. America	0–900	*Atriplex*	Salt Desert – Sonoroan (15)
Okanagodes gracilis var. *viridis*	N. America	700–750	*Atriplex*	Salt Desert – Sonoroan (5)
Okanagodes terlingua	N. America	575–1050	*Atriplex*	Salt Desert – Chihuahuan (24)
Babras sonorivox	Argentina	200–800	*Atriplex*	Atriplex community – Chaco (2)
Okanagana bella	N. America	1825–3350	Various tree species	Western forest and woodland habitats (24)
Tettigades major	Argentina	0–1525	Various woody species	Patagonian (2)

host plants and the cicadas are cryptically coloured to match the host.

We found *D. mendosensis* in *Atriplex* communities in the Monte Biotic Province whereas *D. wagneri* occupied the shores of salt lakes and playas in the dry Chaco. *Babras sonorivox* was frequently found with *Derotettix* spp. *Okanagodes gracilis* was found in *Atriplex* communities of the Sonoran, Colorado and Mojave Deserts. *Okanagodes gracilis* var. *viridis* was found in the Sonoran Desert. *Okanagodes terlingua* was found in the *Atriplex* community in the Big Bend region of Texas, but may extend south in the Chihuahuan Desert of Mexico as some specimens were collected in sight of the Texas–Mexico border. The insects occupy similar latitudes and physiognomic regions in North and South America and are active during the warmest part of their respective summer seasons, i.e. June and July in North America and December and January in South America.

The thermal responses of the cicadas show many similarities as a whole (Table 2 and Fig. 2) despite minor statistical differences between individual groups. The minimum flight temperature shows some variability (ANOVA $F_{4,127} = 5.409$, $P < 0.0005$) between species, but minimum flight temperature appears to be related more to the morphology of the flight system than to habitat (Sanborn *et al.*, 2001). Shade seeking temperatures suggest the species are thermally tolerant. Shade seeking values across species are significantly different (ANOVA $F_{4,146} = 8.734$, $P < 0.0001$). Tukey–Kramer multiple comparison tests show significant differences between the shade seeking values determined for *D. mendosensis* and *O. gracilis* ($q = 7.896$, $P < 0.001$) and *O. gracilis* var. *viridis* ($q = 4.571$, $P < 0.01$) and for *O. gracilis* and *O. terlingua* ($q = 5.326$, $P < 0.01$). Heat torpor temperatures across all species are significantly different (ANOVA $F_{4,146} = 3.005$, $P = 0.0203$) but a Tukey–Kramer multiple comparison test shows a significant difference only between the heat torpor values determined for *D. mendosensis* and *O. terlingua* ($q = 4.699$, $P < 0.05$). Further analysis shows *D. menosensis* has a significantly higher heat torpor temperature than *O. terlingua* (one-tailed $t_{74} = 3.528$, $P = 0.0004$). *Okanagana bella* and *Tettigades major* have lower shade seeking and heat torpor values than the desert-adapted species.

The species also exhibit similarities in their physical characteristics (Table 3). Although the Argentine species are smaller than the North American species, all species are small cicadas (we have captured species which have a mass up to 5 g in nearby localities). Coloration patterns are again similar in that they have a light green or straw coloration, which makes the animals difficult to see on their host plants. The exception is *B. sonorivox*, which is a reddish brown colour char-

acteristic of the soil in its habitat. This is adaptive to *B. sonorivox* in that it sings from the ground. The altered coloration means the animal is still cryptically coloured in its environment. In addition, the *Derotettix* and *Okanagodes* species exhibit an enlarged clypeus (Fig. 3). The clypeus contains the pumping musculature used to obtain water and nutrients from the host plants.

Finally, the species exhibit similarities in several behavioural characteristics (Table 4). All species have relatively high-frequency songs. They all call from a similar perch height with the exception of *B. sonorivox*, which calls from the substrate. All species are active during the warmest part of the day and all but *B. sonorivox* simultaneously feed while they sing.
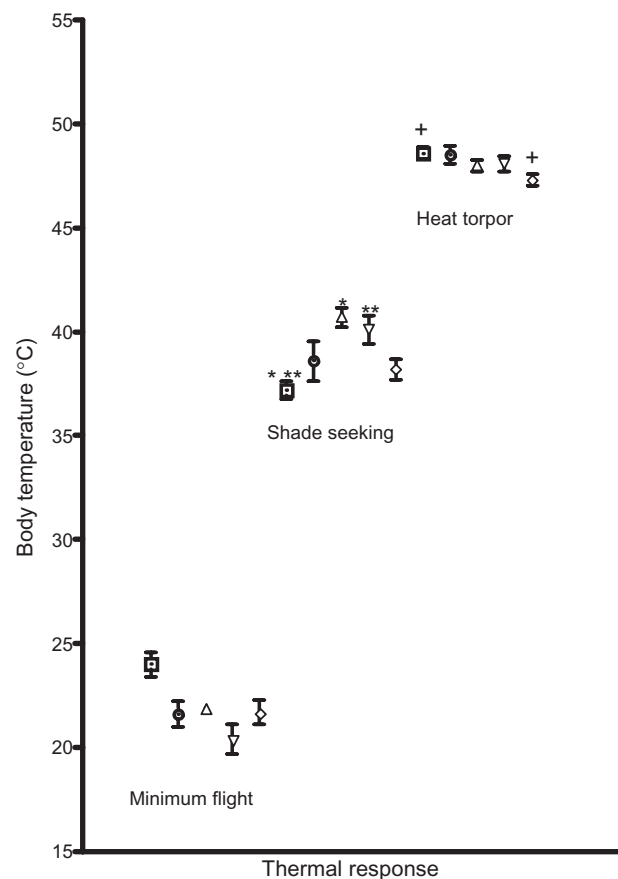
Figure 2. Relationship of thermal adaptation variables determined for the desert-adapted species used in this study. Symbols represent, from left to right: *Derotettix mendosensis* (□), *Babras sonorivox* (○), *Okanagodes gracilis* (△), *O. gracilis* var. *viridis* (▽) and *O. terlingua* (◇). *$P < 0.001$, **$P < 0.01$, +$P < 0.05$. No statistical analysis was performed on the minimum flight data as these values appear to be determined by the morphology of the flight system (Sanborn *et al.*, 2001).

Table 2. Temperature responses, a physiological characteristic, of cicadas (mean ±SD) used in this study. *Okanagana bella* and *Tettigades major* represent ancestral lineages

| Species	Location	Minimum flight (°C)	Shade seeking (°C)	Heat torpor (°C)
Derotettix mendosensis	Argentina	24.0 ± 4.0 (N = 45)	37.2 ± 2.8 (N = 42)	48.6 ± 1.7 (N = 44)
Okanagodes gracilis	North America	21.9 ± 1.6 (N = 45)	40.7 ± 3.2 (N = 47)	48.0 ± 1.9 (N = 46)
Okanagodes gracilis var. *viridis*	North America	20.4 ± 1.4 (N = 4)	40.1 ± 2.5 (N = 14)	48.1 ± 1.5 (N = 16)
Okanagodes terlingua	North America	21.7 ± 2.8 (N = 25)	38.2 ± 2.9 (N = 35)	47.3 ± 1.5 (N = 32)
Babras sonorivox	Argentina	21.6 ± 2.2 (N = 13)	38.6 ± 3.5 (N = 13)	48.5 ± 1.6 (N = 13)
Okanagana bella	North America	18.1 ± 2.1 (N = 72)	36.0 ± 2.6 (N = 70)	46.1 ± 1.4 (N = 72)
Tettigades major	Argentina	15.8 ± 2.1 (N = 12)	34.8 ± 3.2 (N = 12)	45.3 ± 2.5 (N = 12)

Table 3. Convergent and parallel physical characteristics (mean ± SD). *Okanagana bella* and *Tettigades major* represent ancestral lineages

Species	Location	Mass (mg)	Colour	Enlarged clypeus
Derotettix mendosensis	Argentina	95 ± 39 (N = 42)	Green/straw	Yes
Derottetix wagneri	Argentina	113 ± 6 (N = 3)	Green/straw	Yes
Okanagodes gracilis	North America	258 ± 74 (N = 74)	Green/straw	Yes
Okanagodes gracilis var. *viridis*	North America	243 ± 57 (N = 16)	Green	Yes
Okanagodes terlingua	North America	200 ± 47 (N = 53)	Green	Yes
Babras sonorivox	Argentina	107 ± 57 (N = 13)	Reddish brown	No
Okanagana bella	North America	554 ± 178 (N = 72)	Black	No
Tettigades major	Argentina	692 ± 187 (N = 12)	Black	No

Table 4. Behavioural characteristics exhibiting convergence and parallelism

Species	Location	Song	Sing and feed simultaneously	Diurnal activity	Perch height during activity
Derotettix mendosensis	Argentina	>10 kHz	Yes	Mid-day	0.5–1.5 m
Derotettix wagneri	Argentina	>10 kHz	Yes	Mid-day	0.5–1.0 m
Okanagodes gracilis	N. America	>10 kHz	Yes	Mid-day	0.5–1.5 m
Okanagodes gracilis var. *viridis*	N. America	>10 kHz	Yes	Mid-day	0.5–1.5 m
Okanagodes terlingua	N. America	>10 kHz	Yes	Mid-day	0.5–1.0 m
Babras sonorivox	Argentina	<10 kHz	No	Mid-day	0 m (sings from ground)
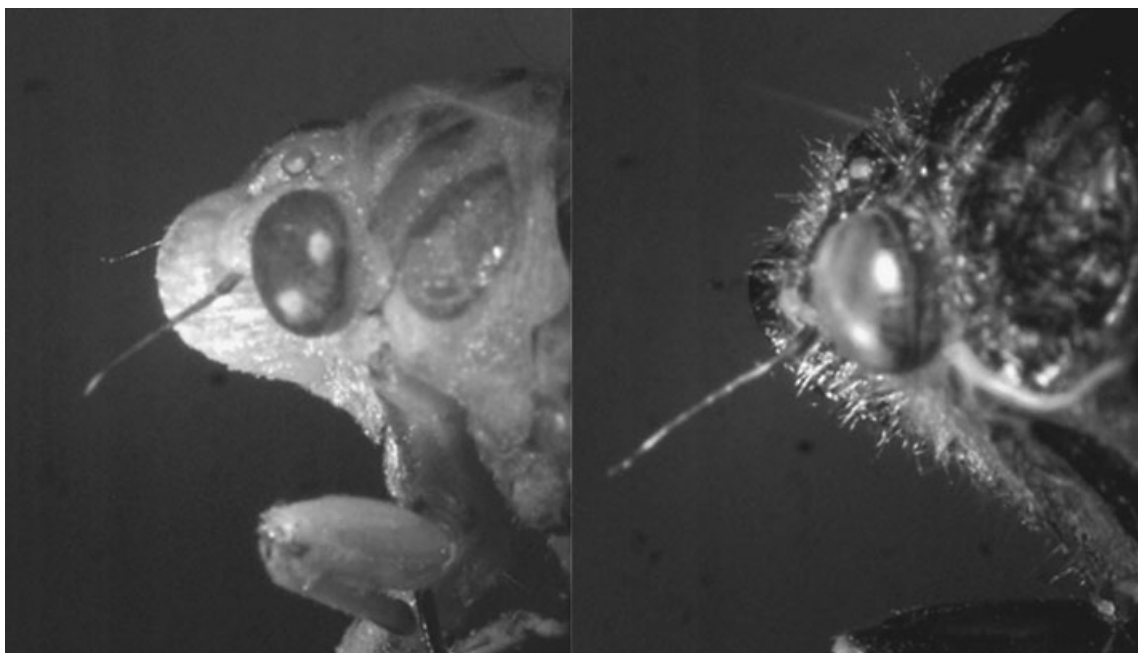
Figure 3. Side view of the clypeus of *Okanagodes gracilis* (left) and *Okanagana bella* (right). The expanded clypeus of the desert-adapted *O. gracilis* may be important in providing sufficient water for evaporative cooling.

DISCUSSION

The species studied show remarkable similarities in terms of habitat selection (Table 1). These habitats share many similarities with regard to plants and climate (Cabrera, 1971; Solbrig, 1976; Orians & Solbrig, 1977; Heath, J.E., 1983; MacMahon, 1988). All species are associated with *Atriplex* communities in both North and South America. These communities are found at approximately the same north and south latitudes and share general physiognomic characteristics even though they are geographically isolated from one another. The similarities in the habitats appear to have selected for convergence in similar physiological and morphological traits evolving in the different cicada lineages.

Analysis of the thermal responses shows interesting relationships between the species and their habitats (Table 2). The minimum flight temperature shows some variability but minimum flight temperature appears to be related more to the morphology of the flight system than to habitat (Sanborn *et al.*, 2001). Shade seeking temperatures are among the highest reported for cicadas (see summary in Sanborn, 2002) and are similar to the values reported from the Sonoran Desert species *Diceroprocta apache* (Davis) (Heath & Wilkin, 1970) and *Cacama valvata* (Uhler) (Heath, Wilkin & Heath, 1972). The smaller size of *D. mendosensis* may play a role in the lower shade seeking temperature as compared with *O. gracilis* and

O. gracilis var. *viridis* owing to an increased rate of heat exchange with smaller body size. Another possibility is that *D. mendosensis* behaviourally thermoregulates to a lower body temperature because it does not have the ability to cool evaporatively, as has been shown in *O. gracilis* (Sanborn, Heath & Heath, 1992), or because of its smaller size it may need to limit the use of evaporative cooling due to a small water reserve volume. Heat torpor data reported here are the highest reported for any cicada species. The environments inhabited by all the cicada species have the potential to experience extreme ambient temperatures with minimal shade opportunities. An elevated heat torpor temperature is essential if these animals are going to inhabit these environments and remain active during the day. No differences were seen in the thermal parameters of *O. gracilis* and the *O. gracilis* var. *viridis*. These data represent parallelism as the similar physiological mechanisms underlying thermal adaptation were altered independently in the various cicada lineages. The similar values obtained in the desert-adapted species contrasts the values determined for the representatives of the ancestral lineages (Table 2), further illustrating the parallelism.

All species show convergence in general size and exhibit cryptic body coloration. All species are relatively small cicadas, which may make it more difficult for a potential predator to find them in their host plants (based on the difficulty we experienced in finding specimens in their natural habitat). The *Derotettix*

and *Okanagodes* species all have green or straw-coloured bodies. This coloration pattern makes them very difficult to see on the *Atriplex* host plants. Although *B. sonorivox* does not have a green coloration, it does have cryptic coloration that provides protection from predators. *Babras sonorivox* has evolved cryptic coloration to match the ground rather than matching a host plant because they call from the ground rather than from a plant. Potential predators may use the acoustic signal produced by a male cicada to locate the calling animal (Soper, Shewell & Tyrrell, 1976). Cryptic coloration to the calling sites provides the greatest potential protection to the cicadas.

All species except *B. sonorivox* also exhibit an expanded clypeus. This may be the result of an enlarged musculature associated with the sucking mouthparts. *Okanagodes gracilis* has been shown to drink constantly during the day so that it may cool evaporatively (Sanborn *et al.*, 1992). The pumping musculature is necessary to provide the water for evaporative cooling in *O. gracilis*. The use of similar habitats by the other species studied may mean they also possess an evaporative cooling response and may need the expanded clypeus to facilitate water uptake. Evidence to support this hypothesis is shown in the simultaneous feeding and singing behaviour exhibited by all species except *B. sonorivox* (Table 4). *Babras sonorivox* differs from the other species in choice of calling site and therefore does not call simultaneously while feeding and may not need the enlarged clypeus to maintain water uptake while active.

Convergence and parallelism are also exhibited in these species' behavioural patterns (Table 4). The *Derotettix* and *Okanagodes* species show remarkable similarities in their behaviour. These animals all produce calling songs whose carrier frequency is greater than 10 kHz. This is probably more of a byproduct of the physics of the sound production system in animals of similar size (Bennet-Clark & Young, 1994) but is also a result of the convergence in body size observed. They also select similar perch heights in similar plants while calling during the hottest part of the day. The perch height selected may provide additional protective benefits along with the coloration patterns matching the host plants. By maintaining activity within the 0.5–1.5 m range, the cicadas can take advantage of some of the protective cover of the host plant. In addition, the selected calling sites permit use of the limited shade the host plants can offer, which can be used by the cicadas to regulate their body temperature and not overheat while they are calling. This type of vertical migration within a host plant has been shown to have thermoregulatory benefits (Sanborn *et al.*, 1992). The elevated thermal tolerances combined with the perch location means the cicadas can remain active while potential predators must retreat to shade to prevent thermal stress, as was described for the Sonoran Desert species *Diceroprocta apache* (Davis) (Heath & Wilkin, 1970).

The cicada genera *Derotettix* and *Okanagodes*, using salt-tolerant host plants in South and North American temperate habitats, show convergence in morphology, adaptive coloration, behaviour, habitat selection and host plant generic selection and parallelism in their responses to temperature. A South American genus, *Babras*, which may be distantly related to the North American taxa, occupies a different niche in the same habitat and exhibited parallelism in its thermal responses and convergence in host plant selection.

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REFERENCES

Bennet-Clark HC, Young D. 1994. The scaling of song frequencies in cicadas. *Journal of Experimental Biology* **191:** 291–294.

Boulard M. 1988. Taxonomie et nomenclature superieures des Cicadoidea. Histoire, problems et solutions. *Ecole Pratique des Hautes Etudes, Travaux du Laboratoire Biologie et Evolution des Insectes Hemipteroidea* **1:** 1–89.

Boulard M. 1997. Nomenclature et taxonomie supérieures des Cicadoidea ou vraies cigales. Histoire, problèmes et solutions (Rhynchota Homoptera Cicadomorpha). *Ecole Pratique des Hautes Etudes, Travaux du Laboratoire Biologie et Evolution des Insectes Hemipteroidea* **10:** 79–129.

Cabrera AL. 1971. Fitogeografia de la Republica Argentina. *Boletin de al Sociedad Argentina de Botánica* **14:** 1–42.

Chou I, Lei Z, Li L, Lu X, Yao W. 1997. *The Cicadidae of China (Homoptera: Cicadoidea). Ilustrataj Insect-Faunoj: 2.* Hong Kong: Tianze Eldoneio.

Duffels JP. 1993. The systematic position of *Moana expansa* (Homoptera: Cicadidae), with reference to sound organs and the higher classification of the Superfamily Cicadoidea. *Journal of Natural History* **27:** 1223–1237.

Duffels JP, van der Laan PA. 1985. *Catalogue of the Cicadoidea (Homoptera, Auchenorhyncha) 1956–1980.* Dordrect: Dr Dr W. Junk Publishers, Series Entomologica 34.

Futuyma DJ. 1998. *Evolutionary biology*, 3rd edn. Sunderland, MA: Sinauer Associates, Inc.

Heath JE. 1967. Temperature responses of the periodical '17-year' cicada, *Magicicada cassini* (Homoptera, Cicadidae). *American Midland Naturalist* **77:** 64–67.

Heath JE. 1970. Behavioral regulation of body temperature in poikilotherms. *Physiologist* **13:** 399–410.

Heath JE. 1983. The floristic provinces of Argentina and their relationships to those of the American Southwest. In: Mendez LFC, Bates LW, eds. *Brazil and Rio de la Plata, challenge and response*. Charleston: Eastern Illinois University Press, pp. 7–10.

Heath JE, Wilkin PJ. 1970. Temperature responses of the desert cicada, *Diceroprocta apache* (Homoptera, Cicadidae). *Physiological Zoology* **43:** 145–154.

Heath JE, Wilkin PJ, Heath MS. 1972. Temperature responses of the cactus dodger, *Cacama valvata* (Homoptera, Cicadidae). *Physiological Zoology* **45:** 238–246.

Heath MS. 1983. The semiarid regions of Argentina: a natural laboratory for the study of evolution. In: Mendez LFC, Bates LW, eds. *Brazil and Rio de la Plata, challenge and response*. Charleston: Eastern Illinois University Press, pp. 11–15.

Heath MS. 1999. 'A modest proposal': a new basis for revising the family and subfamily taxonomy of the Cicadoidea. In: *Abstracts of the 10th International Auchenorrhyncha Congress, 6–10 September, Cardiff, Wales.*

MacMahon JA. 1988. Warm deserts. In: Barbour MG, Billings WD, eds. *North American terrestrial vegetation*. Cambridge: Cambridge University Press, pp. 231–264.

Metcalf ZP. 1963a. General catalogue of the Homoptera, Fascicle VIII. Cicadoidea. Part 1. Cicadidae. Section I. Tibiceninae. *North Carolina. State College Contribution* **1502**: i–vii, 1–585.

Metcalf ZP. 1963b. General catalogue of the Homoptera, Fascicle VIII. Cicadoidea. Part 2. Tibicinidae. *North Carolina State College Contribution* **1564:** 1–492.

Moulds MS. 1990. *Australian cicadas.* Kensington: New South Wales University Press.

Moulds M. 1999. The higher classification of the Cicadoidea: a cladistic approach. *Abstracts of the 10th International Auchenorrhyncha Congress, 6–10 September, Cardiff, Wales.*

Orians GH, Solbrig OT. 1977. *Convergent evolution in warm deserts.* Stroudsberg, PA: Dowden, Hutchinson and Ross.

Sanborn AF. 2002. Cicada thermoregulation (Hemiptera, Cicadoidea). *Denisia* **4:** 455–470.

Sanborn AF, Heath JE, Heath MS. 1992. Thermoregulation and evaporative cooling in the cicada *Okanagodes gracilis* (Homoptera: Cicadidae). *Comparative Biochemistry and Physiology. A. Comparative Physiology* **102:** 751–757.

Sanborn AF, Perez LM, Valdes CG, Seepersaud AK. 2001. Wing morphology and minimum flight temperature in cicadas (Insecta: Homoptera: Cicadoidea). *The FASEB Journal* **15 (5, Part II):** A1106.

Solbrig OT. 1976. The origin and floristic affinities of the South American temperate desert and semiarid regions. In: Goodall DW, ed. *Evolution of desert biota*. Austin: University of Texas Press, pp. 7–50.

Soper RS, Shewell GE, Tyrrell D. 1976. *Colcondamyia auditrix* nov. sp. (Diptera: Sarcophagidae), a parasite which is attracted by the mating song of its host, *Okanagana rimosa* (Homoptera: Cicadidae). *Canadian Entomologist* **108:** 61–68.

Weins JJ, Chippindale PT, Hillis DM. 2003. When are phylogenetic analyses misled by convergence? A case study in Texas cave salamanders. *Systematic Biology* **52:** 501–514.