

# Geographical variation in calling song of the field cricket *Teleogryllus oceanicus*: the importance of spatial scale

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## Abstract

We compared calling songs of the field cricket *Teleogryllus oceanicus* from 15 sites within six regions of two continental areas, Oceania and Australia. The cricket was introduced to Hawaii, where it is subject to an acoustically orienting parasitoid fly not found elsewhere in its range. In a principal components analysis (PCA) of song from all populations combined, the first five components had eigenvalues greater than one, and collectively accounted for over 80% of the total variation. Means for all song components varied significantly among sites, and different components varied at the three levels of analysis (continent, region and site). The principal way in which sites differed was along a gradient in increasing song length, pulse duration and intervals between song elements. Crickets from Oceania had a significantly greater variance in their song than Australian crickets, driven largely by the high variance in Hawaii. Geography explained a substantial amount of variation in song, despite the likelihood of serial bottlenecks having occurred as the species moved from island to island. Because female crickets appear not to focus on the short chirp as a component of mate choice, a lack of selection may allow this song component to vary more widely.

## Introduction

How do sexual signals vary? Signals used in reproduction show considerable intraspecific variation that can occur at a variety of scales. One of the most important sources of variation is geographical. Wilczynski & Ryan (1999, p. 235) state that, 'Among the different levels of variation observed, geographical variation provides the best material for disentangling the myriad factors shaping the evolution and divergence of communication systems and for testing fundamental ideas about the evolution of behaviour'.

Divergence in signals among populations can lead to reproductive isolation and subsequent speciation, as has been suggested for *Drosophila willistoni* (Gleason &

Ritchie, 1998). After initial population divergence occurs in response to changes in signals, adaptation to local environmental conditions can cause further separation (Wilczynski & Ryan, 1999). Alternatively, if gene flow among populations is maintained, even rapidly evolving populations with different signals can resist differentiation; some populations of guppies, for example, show no signs of reproductive isolation, apparently because sneak matings restore gene flow when males from distant populations travel in search of females to fertilize (Magurran, 1998). Where gene flow prevents the evolution of geographical variation in genotypes, phenotypic plasticity may result (Thompson, 1999).

How does geographical separation reflect genetic divergence? In a study of sexual isolation and genetic differentiation in salamanders, Tilley *et al.* (1990) found that geographical distance was highly correlated with ethological isolation, suggesting that both reflect the gradual divergence of populations. This need not be the case, however. Evolutionary history can determine

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the time span over which variation can arise; for example, some populations of the European meadow grasshopper *Chorthippus parallelus* were confined to refugia during glaciation, whereas others diverged during subsequent range expansions (Tregenza *et al.*, 2000). The different histories of the various populations apparently caused distinctive patterns of divergence in song and morphology (Tregenza *et al.*, 2000). Even when sexual selection influences the evolution of sexual signals, this can be countered by natural selection in the form of predators or parasitoids, preventing the separation of populations (Endler, 1980; Zuk & Kolluru, 1998).

The field cricket *Teleogryllus oceanicus* presents a unique opportunity to examine geographical variation in a sexual signal. The cricket occurs over a wide geographical range, extending from northern coastal Australia to many of the Pacific islands. It has also been introduced to Hawaii at least as early as 1877 (Kevan, 1990). Only in Hawaii is it subject to an acoustically orienting parasitoid fly, the tachinid *Ormia ochracea* (tribe Orminii), which uses the calling song to find its host (Zuk *et al.*, 1993). Previous work has demonstrated that songs from unparasitized and parasitized crickets differ at a variety of scales ranging from within populations to inter-continental. Hawaiian *T. oceanicus* songs differ from those in two populations where the fly is absent, and among the three Hawaiian islands subject to the parasitoid, a significant portion of variation in temporal components of the song can be attributed to differences in prevalence of infestation with *O. ochracea* (Zuk *et al.*, 1993; Rotenberry *et al.*, 1996). Moreover, individuals found to harbour larvae had significantly different songs from those found to be parasite-free, with flies more commonly parasitizing crickets with longer trill-like long chirps given at the beginning of the song (Zuk *et al.*, 1998). Interestingly, although female crickets preferred calls with greater proportions of long chirp, variation in female preference functions did not match variation in call structure among nine Australian populations and two from Hawaii (Simmons *et al.*, in press). This known selective force occurring in a defined part of the range of the cricket allows us to examine geographical variation in calling song in the context of opposing selection between female choice and pressure from the fly. In addition, we have recorded calls from males in three island groups [Hawaii, Fiji and French Polynesia (we use 'Society', from the Society Islands within French Polynesia, in the tables and figures)] and at several sites clustered in distinct regions in Australia and can compare variation among islands with and without the parasitoid as well as variation between island and mainland populations. To what extent does geographical separation predict signal variation, given the forces operating within populations?

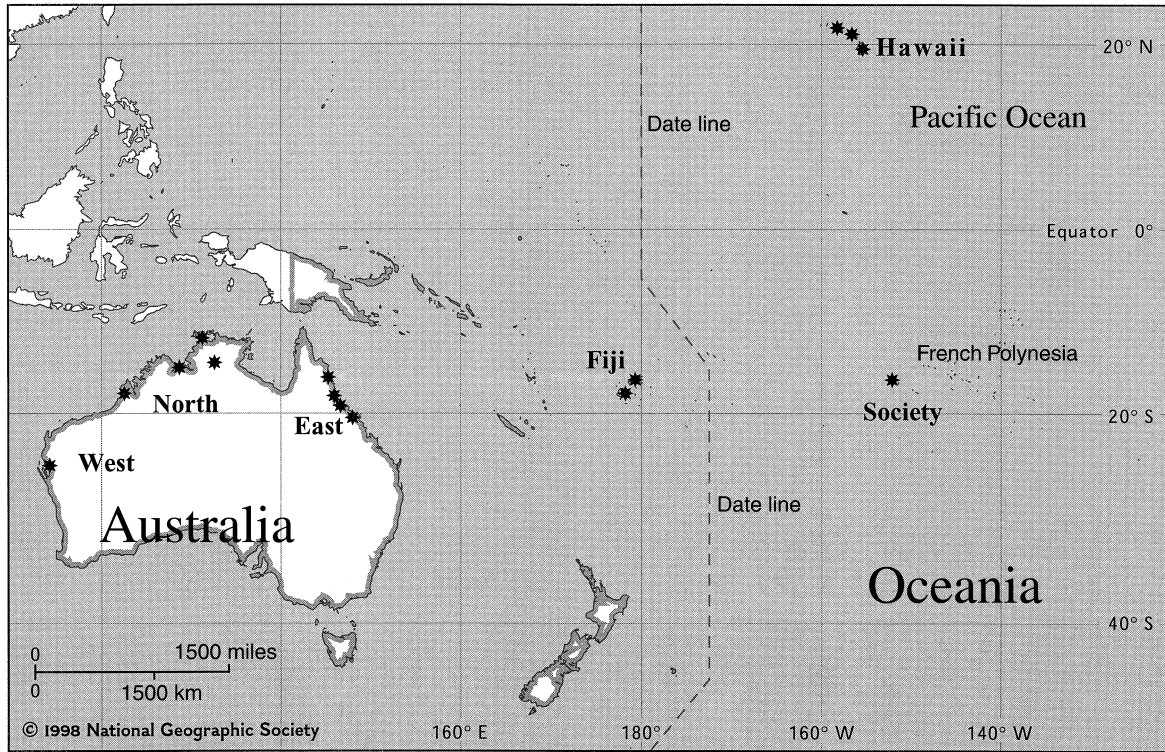
In this paper, we have three goals. First, we characterize geographical variation in song, both by constructing multivariate components that collapse the numerous song variables into units more amenable to statistical

analysis and by determining which individual song elements show geographical variation and which do not. Secondly, we compare variation at sites from the three island groups with the mainland sites, to see whether island populations show distinct patterns of variation because of their isolation. Within Australia, we examine both populations where gene flow probably occurred within recent history (e.g. along the Queensland coast) and populations which are more isolated from each other (e.g. Carnarvon in the west and Darwin in the north of the continent). Thirdly, we attempt to determine if variation in song is more canalized within the Hawaiian Islands than within two islands of Fiji or the island of Moorea in French Polynesia, as might be expected if the Hawaiian populations are experiencing strong selection from the parasitoid fly. We can also set this degree of variation in the context of variation observed within and among regions in Australia. The results have implications for understanding the relationships among genetic differentiation and geographical separation, and hence speciation, as well as for biogeography and the extent to which sexual selection can act on signals used in communication.

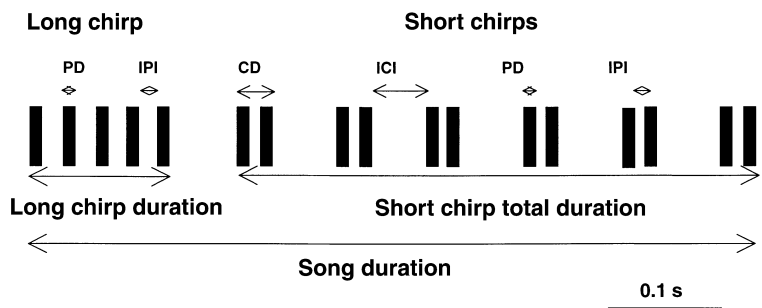
## Materials and methods

We recorded cricket song in the field between 1991 and 1996 in Australia, Fiji, Moorea and Hawaii (Fig. 1). Within Australia, *T. oceanicus* has a coastal distribution, extending north from Carnarvon in Western Australia and Rockhampton in north-east Queensland (Otte & Alexander, 1983). We sampled four populations from Queensland: Townsville, Ingham, Mission Beach and Cairns, with a distance of 110–123 km between populations. These were grouped into the East region. Two populations from the Northern Territory, Darwin and Katherine, and two from northern Western Australia, Kununurra and Broome, were grouped into the North region. The geographically distant population we recorded in Carnarvon, Western Australia (approximately 2440 km from the nearest other Australian sample), comprised the West region. We also recorded cricket song from the Hawaiian Islands of Hawaii, Oahu and Kauai; from the Fijian islands of Viti Levu and Vanua Levu; and from the Society Island of Moorea, near Tahiti. Each island archipelago was considered a region within Oceania. Each cricket was recorded for 30–60 s using a Sony Professional Walkman (New York, USA). The ambient temperature was noted during each recording session.

Songs were analysed using either a Kay DSP Digitizing Sona-Graph 5500 (Kay Elemetrics, NJ, USA) or the software package Canary<sup>TM</sup> 1.2 (Cornell Laboratory of Ornithology, Ithaca, NY, USA). Each song of *T. oceanicus* contains a 'long chirp' of three to eight pulses or wingstrokes followed by a series of 'short chirps' consisting of two pulses (Fig. 2; Zuk *et al.*, 1993, 1998; terminology after Otte, 1992). We measured the duration of



**Fig. 1** Map of locations where *Teleogyllus oceanicus* was recorded and collected. Locations are classified into two continents, Oceania and Australia; six regions within continents (east, north, and west within Australia; Society Islands, Fiji and Hawaii within Oceania); and a total of 15 sites within the regions (CARN, Carnarvon in West Australia; KUNN Kununurra, BROO Broome, DARW Darwin and KATH Katherine in North Australia; CAIR Cairns, INGH Ingham, MISS Mission Beach and TOWN Townsville in East Australia; HILO Hilo on the Big Island in Hawaii, KAUA Kauai in Hawaii, and OAHU Oahu in Hawaii; VANU Vanua Levu and VITI Viti Levu in Fiji; and MOOR Moorea in the Society Islands).



**Fig. 2** Stylized sonagram of *Teleogyllus oceanicus* song. PD = pulse duration, IPI = interpulse interval, CD = chirp duration, and ICI = interchirp interval. The horizontal axis is time, with the bar showing 0.1 s.

both types of chirps and their individual pulses, the duration of the portion of song containing short chirps, the number of pulses per short and long chirp, the carrier frequency, the interval between pulses in each chirp type, and the interval between the end of the short chirps and the beginning of the next long chirp. We also measured the duration of the song between the start of the long chirp and the end of the short chirps (song duration), as well as from the start of one long chirp to the start of the next (total song duration). We also calculated the per cent of song duration consisting of long chirp. Variables were

measured for seven to 10 songs for each cricket, and then averaged. All song variables were standardized for temperature by regressing each on the ambient temperature in the field measured at the time of the recording (Walker, 1975). Residuals from these regressions were used in subsequent analyses.

**Statistical analyses**

We used several approaches to assess song variation in a geographical context. We summarized major patterns of

covariation among the 18 song variables (represented by their temperature-independent residuals) with principal components analysis (PCA; Tabachnick & Fidell, 1996), which we performed on their correlation matrix. We retained all components with eigenvalues greater than one. We interpreted each component based on its correlations with the original variables (factor loadings). To improve the interpretability of the retained components, we performed a varimax rotation, which is an adjustment in factor loadings that seeks to maximize high correlations and minimize low ones, while still maintaining independence among the components. Each observation (individual song) has a score on each component, which is a weighted combination of that observation's value for each of the 18 song variables and the association of each variable with each component. We used these scores for further analyses.

We assessed differences in song structure (as defined by principal components) at several geographical scales by performing univariate and multivariate analysis of variance (ANOVA and MANOVA), and canonical discriminant function analysis (DFA). MANOVA indicates whether statistically significant differences exist among *a priori* defined groups, based on a number of variables considered simultaneously, whereas DFA indicates which variables in combination account most for those multivariate differences (Tabachnick & Fidell, 1996). DFAs were evaluated with prior probabilities of group membership assumed to be proportional to the number of observations in each group. We followed ANOVA of each component with a Duncan's multiple range test to evaluate *post hoc* differences among sites (Zar, 1984). We used nested hierarchical ANOVA applied to each song component to describe the amount of variance in each component associated with each level of geographical scale (Zar, 1984).

To estimate overall variance in song structure for any single site or combination of sites we calculated the determinant of a variance-covariance matrix derived from the scores on song principal components of all individuals recorded at the site(s) (Legendre & Legendre, 1983). We tested for differences in multivariate variances using the procedure outlined by Morrison (1976) for assessing homogeneity of variance-covariance matrices.

We used a simple cluster analysis to describe relationships among sites based on their geographical location and on the structure of the songs of crickets recorded at each site (Sneath & Sokal, 1973). Relationships between each pair of sites were quantified by Euclidean distances based on (1) latitude and longitude (geography), and (2) site averages on five song principal components (song). For convenience, and for consistency with previous analyses, we set the latitude and longitude of the Kununurra site to 0,0 (Rotenberry *et al.*, 1996). Clustering was performed using the centroid method (geography) and Ward's method (song) (Lance & Williams, 1967). We compared the overall similarity among sites based on song structure with geographical proximity of

sites using Mantel tests (Mantel, 1967; Douglas & Endler, 1982). In this case, the Mantel statistic evaluates whether the differences among sites based on song are associated with their differences based on the physical distances among them. The significance of a Mantel statistic was estimated using a randomization test implemented in PC-ORD Ver. 4.0 (McCune & Mefford, 1999).

The preceding analyses were performed with SAS Version 6.12 for a personal computer, using procedures FACTOR, GLM, DISCRIM and VARCOMP (SAS Institute, 1998).

## Results

### Patterns of song structure

The 18 song variables measured showed a variety of relationships. For example, song duration and total song length were highly correlated ( $r = 0.998$ ,  $n = 735$ ). As total song length is the sum of song duration and intersong interval, and intersong interval is not particularly correlated with any other variable, the implication is that almost all of the variation in total song is associated with variation in song duration. Furthermore, both song duration and total song length were highly correlated with short chirp total duration (both  $r > 0.967$ ,  $n = 735$ ), which was thus the principal source of variation in song length.

These and other patterns of correlation among the 18 song variables were best summarized by the PCA. The first five components had eigenvalues greater than one, and collectively they accounted for over 80% of the total variation in song variables (Table 1). The first principal component can be summarized as 'song length'. Increasing song length (song duration and total song) is associated with increasing number of short chirps per song and short chirp total duration. The latter two elements result in a lower long chirp/short chirp ratio and lower per cent long chirp within a song. This implies that increasing song length is mainly associated with increasing the short chirp component. The second song component captures variation in 'pulse duration'. Increasing duration of both the long and short chirp pulses are associated with increasing duration of the short chirp, but decreasing short chirp interpulse interval. As a result, duty cycle increases (more of the acoustic space is occupied by sound). The third component describes elements of 'Intervals'. Increasing long chirp interpulse interval and short chirp interchirp interval are associated with increasing intersong interval. As a result, duty cycle decreases. This occurs over increasingly lower frequencies. Component 4 is the 'long chirp' component, associated with increasing pulses per long chirp and long chirp duration. This relationship yields an increasing long chirp/short chirp ratio and higher per cent long chirp. Component 5, on the other hand, is the 'short chirp' component, with increasing pulses per short chirp and

**Table 1** Principal components analysis (PCA) of calling song variables measured on 735 *Teleogryllus oceanicus*. Main entries are factor loadings (correlation between components and original variables). Loadings less than 0.5 (which account for less than 25% of the variance of an original variable) are denoted by ‘-’.

Variable description	Principal component				
	1 (Song length)	2 (Pulse duration)	3 (Intervals)	4 (Long chirp)	5 (Short chirp)
Pulses per long chirp	-	-	-	0.94	-
Long chirp duration	-	-	-	0.93	-
Long chirp pulse duration	-	0.86	-	-	-
Long chirp interpulse interval	-	-	0.66	-	-
Pulses per short chirp	-	-	-	-	0.88
Short chirp duration	-	0.61	-	-	0.68
Short chirp pulse duration	-	0.94	-	-	-
Short chirp interchirp interval	-	-	0.80	-	-
Short chirp interpulse interval	-	-0.52	-	-	-
Short chirps per song	0.97	-	-	-	-
Song duration	0.89	-	-	-	-
Total song	0.88	-	-	-	-
Short chirp total duration	0.95	-	-	-	-
Long chirp:short chirp ratio	-0.81	-	-	0.50	-
Percent long chirp	-0.82	-	-	0.54	-
Intersong interval	-	-	0.69	-	-
Carrier frequency	-	-	-0.59	-	-
Duty cycle	-	0.75	-0.53	-	-
Total variance (%)	28.2	16.4	15.9	15.0	8.1
Cumulative percentage total variance	28.2	44.6	60.5	75.5	83.6

short chirp duration. Note that the ‘long chirp’ and ‘short chirp’ components express variation in these song elements largely independent of both each other and song length (component 1).

Patterns of covariation detected by PCA of this geographically extensive sample were similar to those observed previously in a much smaller Hawaiian data set ( $n = 132$ ; Zuk *et al.*, 1998). As before, the principal component of song variation among individuals is song length, with the same six variables showing high ( $|r| > 0.8$ ) factor loadings in both analyses. Likewise, the second component of this analysis is similar to the second of the previous one, in that both had high loadings for long and short chirp pulse duration, and short chirp duration. The remaining components are also similar, although a few additional variables had sufficiently large factor loadings (perhaps because of the much larger sample size) to be added to the current analysis.

### Variation in song components

Means for song components varied significantly among sites (all  $P < 0.001$  for overall models), although in different ways (Table 2; Fig. 3). The total amount of variation in each principal component explained by a hierarchical model varied from 11.3% for the short chirp up to 55.3% for the intervals. The remaining components had around 30% of their variances explained by the

hierarchical model (28.7% for song length, 33.1% for pulse duration, 32.7% for long chirp).

Significant between-continent differences in the long chirp and short chirp components accounted for 27.9 and 7.9% of the total variation in each, respectively (Table 2). All six Oceania sites had higher mean scores on component 4 than the nine Australia sites, and, except for Hilo, all Oceania sites had lower scores than Australia on component 5 (Fig. 3). No other individual component differed significantly between continents, although pulse duration neared significance (14.9% of total variation,  $P = 0.064$ ).

A significant proportion of variation in components 1 (song length; 19.6%) and 3 (intervals; 41.4%) was associated with differences among regions within continents (Table 2). For example, on component 3 the four sites in Australia East (Ingham, Townsville, Cairns, Mission Beach) had negative means, whereas the five sites in the other two regions had positive values (Fig. 3). Likewise, the three Hawaiian sites (Kauai, Hilo, and Oahu) differed significantly from the other regions in Oceania on component 1.

### Variation among sites, regions and continents

To compare the variation in song components among sites, regions and continents, we used discriminant analysis. First, note the highly significant heterogeneity among the 15 sites (four canonical axes with  $P$ -values

**Table 2** Hierarchical analysis of variation in song components. In partitioning variance (variance component), Continent is considered a fixed effect, region and site are random effects.

Component	d.f.	SS	MS	F	P	Variance component	Variance (%)
1 – Song length							
Continent	1	64.7	64.73	3.06	0.155	0.093	8.3
Continent (region)	4	84.7	21.18	18.34	<b>&lt;0.001</b>	0.219	19.6
Region (site)	9	10.4	1.15	1.45	0.162	0.009	0.8
Error	717	569.7	0.79			0.795	71.3
Total	731	729.6					
2 – Pulse duration							
Continent	1	67.9	67.93	6.46	0.064	0.168	14.9
Continent (region)	4	42.0	10.51	1.16	0.389	0.000	0.0
Region (site)	9	81.4	9.05	11.96	<b>&lt;0.001</b>	0.206	18.2
Error	717	542.3	0.76			0.756	66.9
Total	731	733.6					
3 – Intervals							
Continent	1	6.6	6.62	0.12	0.750	0.000	0.0
Continent (region)	4	227.9	56.98	8.37	<b>0.004</b>	0.536	41.4
Region (site)	9	61.3	6.81	11.28	<b>&lt;0.001</b>	0.154	11.9
Error	717	432.5	0.60			0.603	46.7
Total	731	728.3					
4 – Long chirp							
Continent	1	110.7	110.68	54.86	<b>0.002</b>	0.339	27.9
Continent (region)	4	8.1	2.02	0.64	0.648	0.000	0.0
Region (site)	9	28.4	3.16	3.87	<b>&lt;0.001</b>	0.058	4.8
Error	717	585.5	0.82			0.817	67.3
Total	731	732.7					
5 – Short chirp							
Continent	1	30.1	30.14	10.97	<b>0.030</b>	0.083	7.9
Continent (region)	4	11.0	2.75	1.16	0.391	0.001	0.1
Region (site)	9	21.4	2.37	2.54	<b>0.007</b>	0.036	3.4
Error	717	671.2	0.94			0.936	88.7
Total	731	733.7					

Bold denotes  $P < 0.05$ .

<0.001; Table 3). Sites differ along a gradient in increasing song length, pulse duration and intervals, and this canonical variate accounts for 58.4% of the differences among sites (Fig. 4). The second canonical variate, with a canonical  $R^2$  of 33.9%, further separates sites along a gradient of increasing intervals and long chirp component contrasted with decreasing short chirp and song length. Although statistically significant, the third and fourth canonical axes account for a relatively small amount of variation, and they are not shown.

Considering the first two axes simultaneously, some geographical structure becomes evident (Fig. 4). For example, the Oceania sites all lie to the upper left of the Australian ones in canonical space. Likewise, north and east Australian sites are distinctly separated along the first canonical axis. The appearance of geographical structure in an analysis not specifically designed to detect or enhance it foreshadows its role in accounting for song variation.

More explicit consideration of geography reveals the details of differences among the continents and regions (Table 3). Crickets from the oceanic islands differed from those from mainland Australia principally by having shorter songs and shorter pulse duration, longer long chirp elements, and shorter short chirps (Table 3, Fig. 3). Among the regions within Oceania, the first canonical variate separated the Hawaiian archipelago from Fiji and Society, with Hawaiian crickets having shorter songs and shorter intervals within songs. Although statistically significant, the second canonical variate accounted for only about 2% of the differences among regions. Regions within Australia also differed significantly, varying principally along a gradient of increasing pulse duration and intervals. Significant variation occurred among sites within the north and east regions of Australia, and within the Hawaiian archipelago, although without obvious spatial patterning.

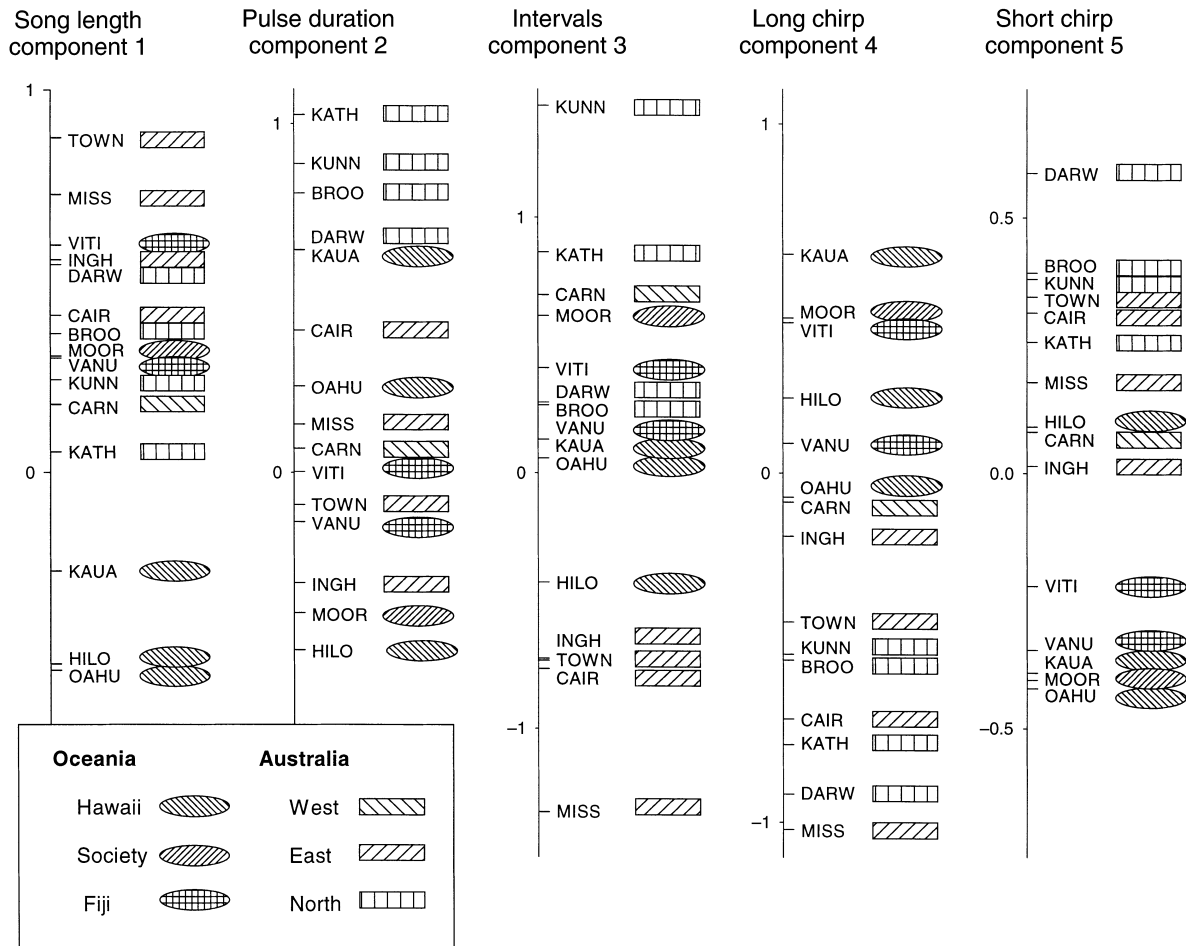


Fig. 3 Site means for each of five song principal components. See Table 1 for interpretation of components and Fig. 1 for explanation of site codes.

**Multivariate variance in song components**

Not only did means of song components vary among sites, so did multivariate variances (Table 4). For example, Oceania had a substantially and significantly greater variance among individuals in their song than did Australia. The high variance in Oceania was driven largely by the high variance shown by the Hawaiian islands, which in turn was mainly a manifestation of the high variance shown by the sample from Hilo. Initially, we were concerned that the high Hilo variance may have been driven by an outlying sample from one of the 4 years in which it was surveyed. However, a component-by-component ANOVA of songs grouped by Hawaiian island and by year (seven samples) revealed no differences in the Hilo population.

**Cluster analysis**

Cluster analysis of sites based on their physical proximity clearly captured the geographical hierarchy of our

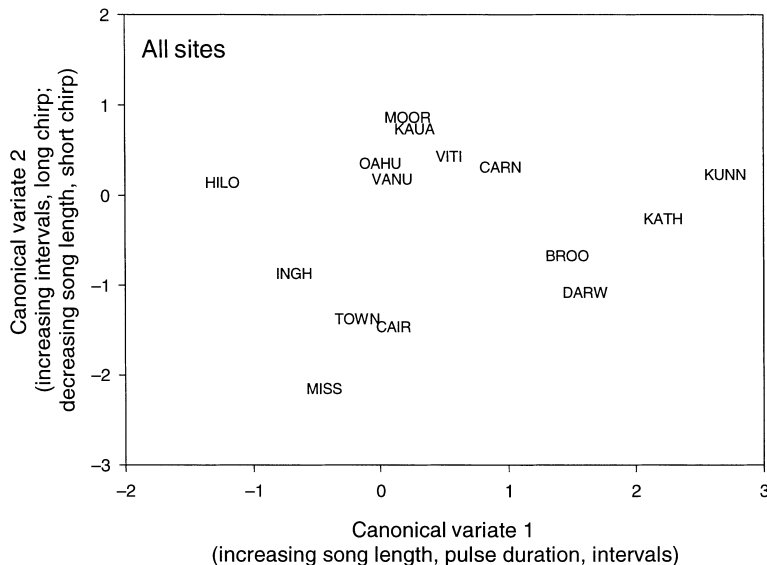
sampling design (Fig. 5). The dendrogram illustrates how regions within Oceania are more widely dispersed than those within Australia by coalescence of the three regions in Oceania at a greater distance than those of Australia. It is also clear that sites have a similar level of dispersal within regions.

Structure also appears in the pattern of clustering of sites based on similarity of song components (Fig. 5). Most notably, sites in the east Australia region (CAIR, MISS, INGH and TOWN) cluster together and are distinct from all other sites and regions. Likewise, both north Australia and Hawaii regions form distinct clusters, and the Fiji sites are very similar to each other. Interestingly, the two most geographically disjunct sites, Carnarvon on the west coast of Australia and Moorea in the eastern central Pacific Ocean (96° longitude apart), have crickets with very similar songs, and similar to those from the Fiji sites.

Despite distortion provided by the high similarity between Carnarvon in Australia and the distant ocean islands, the geographical signal in song similarities comes

**Table 3** Discriminant function analysis (DFA) comparing continents, regions within continents, and sites within regions.

Comparison and level	Canonical axis	Canonical correlation	Significance level	Canonical loadings for song principal components				
				1 Song length	2 Pulse duration	3 Intervals	4 Long chirp	5 Short chirp
Australia vs. Oceania	1	0.618	<0.001	0.49	0.49	–	–0.62	0.33
Three regions within Oceania	1	0.514	<0.001	0.78	–	0.70	–	–
	2	0.156	0.017	0.40	0.54	–0.54	–0.31	–
Three sites within Hawaii	1	0.571	<0.001	–	0.70	0.51	–	–0.36
	2	0.196	0.009	0.35	–	–	0.91	–
Two sites within Fiji	1	0.342	0.060	0.48	–	0.57	0.61	–
Three regions within Australia	1	0.788	<0.001	–	0.70	0.88	–	–
	2	0.422	<0.001	–	–0.41	0.42	0.51	–
Four sites within East	1	0.677	<0.001	–	–0.50	0.45	0.68	–
	2	0.418	0.003	–	0.73	0.46	–	–
	3	0.248	0.118	–	–	–	–	–
Four sites within North	1	0.550	<0.001	–	–	0.96	–	–
	2	0.213	0.407	–	–	–	–	–
	3	0.168	0.369	–	–	–	–	–
Among 15 sites	1	0.764	<0.001	0.33	0.58	0.68	–	–
	2	0.583	<0.001	–0.39	–	0.59	0.62	–0.32
	3	0.380	<0.001	0.85	–0.37	–	–	–
	4	0.285	<0.001	–	0.67	–0.41	–	–0.55
	5	0.153	0.072	–	–	–	–	–

**Fig. 4** Site means on canonical discriminant axes based on song structure for five principal components. See Table 1 for interpretation of components and Fig. 1 for explanation of site codes.

through clearly. The standardized Mantel statistic comparing all 15 sites based on similarities of song components vs. the physical distances among them was 0.331 ( $P = 0.004$  based on 1000 randomizations). If Carnarvon is deleted, the new Mantel statistic is 0.458 ( $P < 0.001$ ). In other words, knowing how far apart two

sites are tells us a significant amount about how similar their songs are.

Geographical proximity and degree of song similarity remains consistent within Australia as well; the Mantel statistic is 0.523 ( $P = 0.011$ ). Unfortunately, the same test for sites within Oceania is statistically weaker; with

**Table 4** Multivariate variances of calling song components arranged by geographical hierarchy. Values are determinants of variance–covariance matrices of five principal components. See Table 1 for site codes.

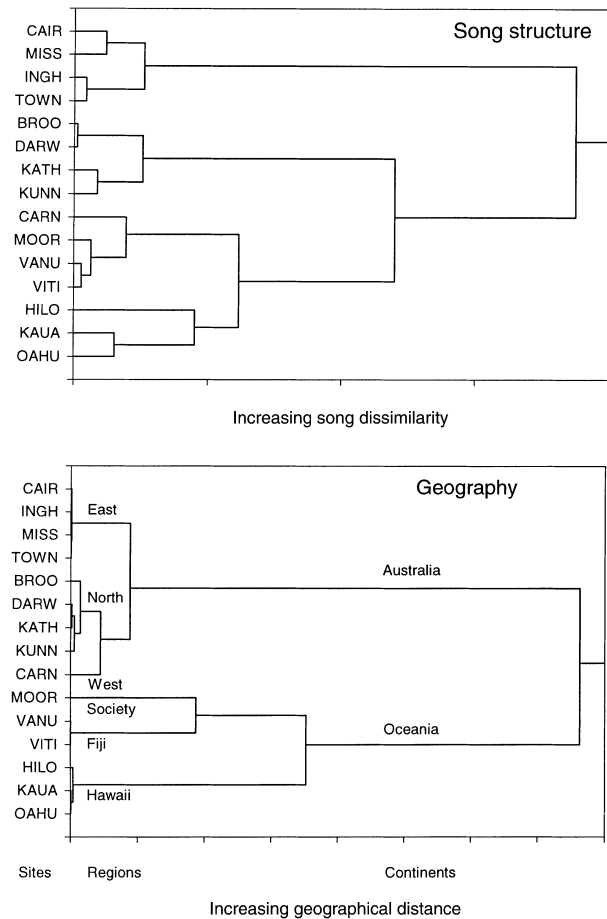
Continent		Region		Site	
Australia	0.2511	West	0.0045	CARN	0.0045
				KUNN	0.4837
	North	0.0836	BROO	0.0006	
			DARW	0.0244	
			KATH	0.0005	
	East	0.0315	CAIR	0.0160	
			INGH	0.0031	
			MISS	0.0024	
			TOWN	0.0077	
Oceania	0.6309	Hawaii	0.7318	HILU	0.6494
				KAUA	0.0448
				OAHU	0.0930
	Fiji	0.1180	VANU	0.1156	
			VITI	0.0127	
	Society	0.0108	MOOR	0.0108	

only six sites there are fewer possible permutations of the data (less than the 1000 randomizations employed in our other tests). Regardless, within Oceania the Mantel statistic is 0.341, marginally not significant ( $P < 0.064$ ).

**Discussion**

Geography explains much of the variation in song among populations of *T. oceanicus*, despite the inevitable bottlenecks and establishment of new populations that must have occurred as the species spread across its range. Although differential selection and genetic drift probably shifted song elements in different localities, it is striking to see the overall geographical fidelity among populations in their signal characteristics. It is important to note that between-population variation in call structure is genetically based, having persisted for five generations of common-garden rearing of two populations, Cairns and Oahu (L.W. Simmons, unpublished data), which means that the variation we observe is not the result of short-term phenotypic plasticity. Varying selection in different locations may be insufficient to counteract the influence of geography.

Our analyses suggest that the scale at which variation is evaluated is important, and that populations from, for example, oceanic islands all share characteristics that are not shared with continental Australian populations, even after the physical distance between populations is taken into account. This finding also implies that other studies of signal variation might do well to examine different levels of variation, such as might occur in distinct habitat types. As in previous studies, we again found that songs from the parasitized Hawaiian *Teleogryllus* populations are distinct. Furthermore, the three Hawaiian Island



**Fig. 5** Dendrograms showing relationships among sites based on cluster analysis of geographical locations [latitude and longitude, scaled from KUNN (Kunnunura) arbitrarily set to 0,0] and relationships among sites based on cluster analysis of mean song structure using principal components analysis (PCA). Scale on horizontal axis is arbitrary in the song dendrogram, and is in units of degrees squared in the geography dendrogram. See Fig. 1 for explanation of site codes.

populations are less similar to each other than the two Fiji islands are to each other, suggesting that simply being on an island, and even being part of an island chain, does not alone account for similarities among populations. Perhaps different levels of parasitism on the Hawaiian Islands have exerted different levels of selection on the crickets occurring there (Rotenberry *et al.*, 1996). Although we do not know the source of *T. oceanicus* in Hawaii, it seems unlikely that separate introductions from different places were made to each of the three islands where the cricket is found. A more plausible explanation is that selection has acted differently on each of the islands since the time the crickets came to Hawaii. The earliest record of the species is 1877 (Kevan, 1990), suggesting that it either arrived with colonizing Polynesian

sians approximately 1500 years ago or was brought on ships from the Pacific during the 19th century. In either case, because *T. oceanicus* breeds year-round and has a generation time of approximately 3 months, sufficient time has passed to allow divergent song evolution on the three islands. The prevalence of the fly differs among the Hawaiian islands as well, and prevalence alone explains a significant amount of variation in song (Rotenberry *et al.*, 1996).

Is it possible to break down the song into components that are more and less likely to vary with geography? *Teleogryllus* song contains a long chirp and a short chirp, and the long chirp appeared to be the focus of selection by the parasitoid fly in a previous analysis (Zuk *et al.*, 1998). A significant part of variation in the component associated with this part of the song was explained by geographical variation. Interestingly, island populations have consistently more long chirp in their songs than mainland crickets. In general, females prefer songs with more long chirp (Simmons *et al.*, in press), probably because the long chirp is the part of the song that is necessary for calling song recognition (Hennig & Weber, 1997). Islands are generally characterized by reduced predation pressure that results in the loss of behavioural and morphological traits that would otherwise serve in predator avoidance (Carlquist, 1974; Whittaker, 1999). One reason for the greater long chirp on Oceanic islands might be the generally lower predation pressure experienced by these island populations. Certainly morphological variation between Australia and Oceanic islands conforms with a second general characteristic of island forms; *T. oceanicus* from the island of Hawaii and from Moorea are significantly smaller than those from continental Australia (Zuk *et al.*, 1993).

In contrast, the short chirp portion of the song showed the largest geographical influence, as might be expected if selection differs at a small scale and acts on populations within each site. Female crickets appear not to focus on the short chirp portion of the song (Henig & Weber, 1997), and it is possible that a lack of selection allows the short chirp to vary more widely because of random genetic drift.

Hawaiian cricket song was more variable both among islands and within each population, and in general, Oceania was more variable than Australia. Such increased variability of ecologically important traits is a common characteristic of island populations (MacArthur & Wilson, 1967). Several factors may affect this kind of song variability. Differing habitat structure might make different elements of the song easier to locate in the various populations, as has been suggested for birds (Wiley, 1991; Bradbury & Vehrencamp, 1998). This is probably not the case in *T. oceanicus*, because the crickets are almost always found in fairly homogeneous disturbed grassy areas, with relatively little variation in three-dimensional structure. Unlike some other cricket species, *T. oceanicus* males do not construct burrows from which

to call, and instead use shallow scrapes in the ground or call from beneath leaf litter or grass clippings.

In addition, cricket calls may be affected by the presence of acoustic competitors, other species which produce sounds that could potentially interfere with detection of the signal sent by *T. oceanicus* (Walker, 1983; Otte, 1992). Reduced competition is also thought to shape evolution on islands (MacArthur & Wilson, 1967; Carlquist, 1974). Although, we have not formally compared the number of singing insects and other acoustically signalling organisms, some generalizations are possible. In Hawaii, *T. oceanicus* was introduced after the native insect fauna evolved. The native crickets are quite species-rich (Otte, 1994), but all are considerably smaller than *T. oceanicus* and hence do not call in the same frequency range. Furthermore, they are not generally found in disturbed areas and at low elevations, as is *T. oceanicus* (Otte, 1994). In contrast, Australia contains numerous species in the same subfamily as *T. oceanicus*, Gryllinae, at least some of which co-occur with it (Otte & Alexander, 1983). The other oceanic islands where we recorded *T. oceanicus* may contain a few species similar to *T. oceanicus*, such as the short-tailed cricket, *Anurogryllus muticus*, in Moorea (Lee & Loher, 1996), but do not have the species diversity of Australia. These patterns of acoustic competition could have resulted in a kind of competitive release (MacArthur & Wilson, 1967) in Hawaii and, to a lesser degree, in the rest of Oceania, and contributed to the increased variability seen in these two groups relative to Australia. Hawaiian *T. oceanicus* may be more variable simply because they are not constrained by the presence of similar acoustically signalling species.

Our findings have implications for the likelihood of reproductive isolation occurring among isolated populations. Ecological models of speciation suggest that divergent selection in different environments causes reproductive isolation and subsequent speciation (Schluter, 2001). In our case, the fidelity of songs to their geographical origins could work against their divergence, allowing populations of *T. oceanicus* to maintain their ability to interbreed. Perhaps the ability of the *Teleogryllus* to live in a wide range of habitats, as mentioned above, precludes specialization and hence divergent selection. The complex nature of female preference functions in this species (Simmons *et al.*, in press) also argues against a simplistic means of population separation.

Having determined the hierarchical relationships in song among populations of *T. oceanicus*, a logical next step will be to determine whether these relationships are associated with genetic differences among the populations. The Hawaiian populations may have come from any of the Pacific islands or (less likely) from Australia, and it would be interesting to see how their songs compare with those of their closest relatives. Knowledge of the genetic relationships among and the genetic

variation between populations should help direct study of the possible selective agents acting on each of the populations.

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