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## Geographic variation in the echolocation calls of *Vespadelus* spp. (Vespertilionidae) from New South Wales and Queensland, Australia

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We investigated the extent of geographic variation in the echolocation calls of five species of microchiropteran *Vespadelus* in eastern Australia. Bat calls were recorded with Anabat II detectors and computers, and analysed using Analook software. A single call parameter, characteristic frequency (the frequency at the end of the flattest part of the call), was used to document changes in echolocation calls over geographic distance. For *V. vulturnus* and *V. regulus*, changes in call frequency were abrupt and sizeable (up to 14 kHz), with two or three frequency groups present within each species. In *V. darlingtoni*, the changes in frequency were gradual across their range, with an isolated island population resembling the closest region on the mainland. One species examined here, *V. troughtoni*, had calls that were consistent throughout its range. Calls of *V. pumilus* were also consistent across geographic regions except for at one site (Chichester State Forest). At this site calls occupied only the upper end of the species frequency range. Body size, measured as forearm length for each species, was significantly smaller at inland sites, but did not vary with latitude or consistently with intraspecific call variation. Broad patterns and possible causes of geographic variation in call frequency are discussed. We conclude that confident identifications of *Vespadelus* calls from the geographic regions outlined in this paper will only be made with reference calls collected from the relevant regions.

**Key words:** bats, *Vespadelus*, search phase calls, geographic variation, Anabat

### INTRODUCTION

The identification of search phase echolocation calls of microchiropteran bats has proved extremely useful in the field identification of different species (O'Farrell *et al.*, 1999; Reinhold *et al.*, 2001b). However, identifications are hampered by intraspecific variation in calls (Thomas *et al.*, 1987; Barclay, 1999; Murray *et al.*, 2001), the extent of which is poorly documented for

most species. The calls of some species are known to vary by sex/age (Brigham *et al.*, 1989; see also Russo *et al.*, 2001), habitat (Schnitzler and Kalko, 1998) and geographic region (Murray *et al.*, 2001).

The extent of geographic variation continues to remain controversial. One example of geographic variation in the calls of the hoary bat *Lasiurus cinereus* from North America (Barclay *et al.*, 1999) was questioned recently on the basis that apparent

geographic differences may result if bats are recorded while using different components of the local environment (especially clutter) (O'Farrell *et al.*, 2000). Within Australian bat species, geographic variation in calls is acknowledged anecdotally, but there is little published evidence to support its existence. For example, the calls of *Miniopterus schreibersii* are consistent along the east coast of Australia, and only shift in frequency with a taxonomic change (Conole, 2000). Similarly, the calls of *Chalinolobus gouldii* show slight geographic variation, but are generally consistent within-species across Australia (Reinhold *et al.*, 2001a).

Clarifying the extent of geographic variation in the calls of different bat species remains a critical issue in improving confidence in the identification of bat species from their calls (Barclay, 1999; O'Farrell *et al.*, 1999). Our study aim was to describe geographic variation in the calls of bats from the genus *Vespadelus* (Vespertilionidae). To describe geographic differences we used an existing library of calls collected for various reasons, including the construction of a call identification key (Reinhold *et al.*, 2001b). The library contains only reference calls, which are calls from bats identified by methods other than call analysis, and where locality information is accurate.

*Vespadelus* are small bats weighing 3.5–6.5 g that hawk flying insects in forests and woodlands (Strahan, 1995). Within eastern Australia, five species of *Vespadelus* have been described (Kitchener *et al.*, 1987): the little forest bat *V. vulturnus*, the southern forest bat *V. regulus*, the large forest bat *Vespadelus darlingtoni*, the eastern cave bat *V. troughtoni* and the eastern forest bat *V. pumilus*. The core distribution of *V. vulturnus*, *V. regulus* and *V. darlingtoni* is temperate south-eastern Australia, *V. pumilus* is centred further to the north in the sub-tropics, while *V. troughtoni* ranges from

the sub-tropics to the tropics (Strahan, 1995). Up to three species co-occur at various locations throughout their range.

## MATERIALS AND METHODS

Calls of *V. vulturnus*, *V. regulus*, *V. darlingtoni*, *V. troughtoni* and *V. pumilus* were collected from Queensland and New South Wales (NSW) in eastern Australia (bounded by 19°21'S, 37°04'S, 159°08'E, 144°57'E). Calls from *V. darlingtoni* were also collected from Lord Howe Island, which is isolated by 500 km from the mid-north coast of NSW, on mainland Australia. It is the only extant species of bat on the island (McKean, 1975). There are no major barriers (e.g., large water bodies, significant mountain ranges) separating other localities. However, it is unknown whether there is any genetic structuring between localities that might be due to obscure barriers or historical events. More than 10 bioregions (Environment Australia, Canberra) are recognized in the study area, but these are not used to designate boundaries for differences in bat calls. Rather, because discontinuities in call frequency did not always match the recognized bioregions, indicative boundaries have been drawn to reflect observed differences in call frequency. Boundaries should not be interpreted as exact locations.

We recorded calls using the Anabat II bat detector and zero-crossings interface (ZCAIM; Titley Electronics, Ballina, NSW, Australia) connected to laptop computers. Methods of gathering reference calls included the following:

*Release calls:* After a bat is captured (usually by harp trap) and identified in-hand, it is released, sometimes with a piece of reflective tape (or sometimes a chemiluminescent tag) stuck to its belly fur. A spotlight is shone on the bat, and its call is recorded by a second person some distance away as it flies past, taking care to avoid recording calls from other flying bats. Alternatively, captured bats were released at dusk when ambient light levels were sufficient to follow released bats;

*Post-release calls:* If a species-specific colour of reflective tape is used for marking, a released bat may be recorded as it flies around through the night, and identified to species by shining a spotlight on its reflective tape;

*Capture calls:* A call can be recorded as a bat flies into a harp trap, trip line or mist net, and then the bat identified in-hand;

*Fly-out calls:* If the species occupying a roost is known, reference calls can be obtained by recording the dusk exit of the roost. This method was restricted

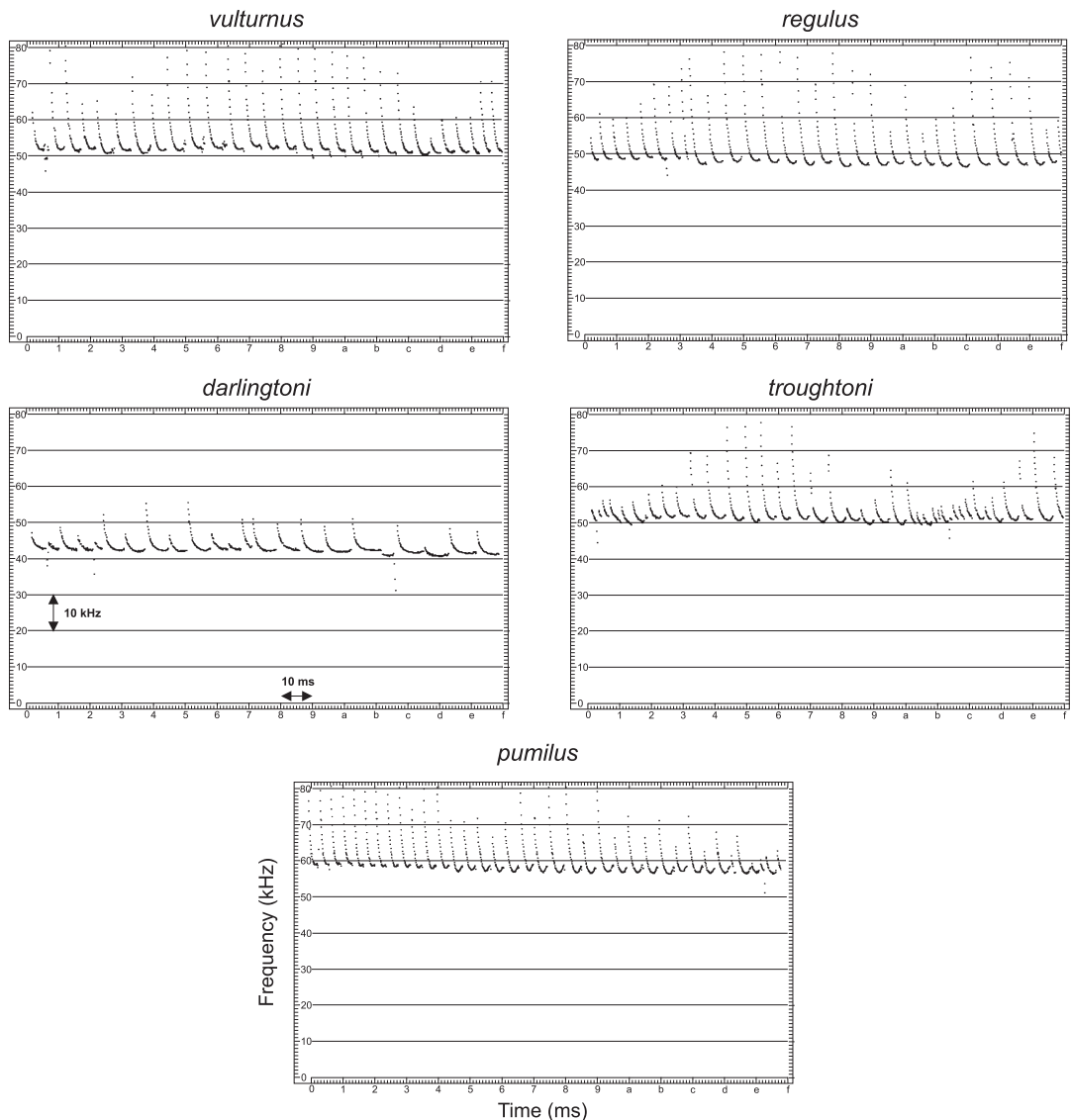


FIG. 1. Sample search-phase echolocation calls for five species of *Vespadelus* (*V. vulturnus*, *V. regulus*, *V. darlingtoni*, *V. troughtoni* and *V. pumilus*) from one geographic region (north-east NSW). Note that time between pulses has been compressed

to collecting calls from *V. troughtoni* as it left cave roosts. Detectors were positioned outside of caves and, where possible, individual flying bats were recorded;

*Other:* On Lord Howe Island, *V. darlingtoni* is the only extant bat, so its calls were recorded as it flew overhead, without relying on capturing individuals.

No attempt was made to exclude any age-class or sex when recording individuals. Reference calls thus represent the broad repertoire used by each species

at the different sites. However, some bias towards recording more males than females was evident as identification of captured bats sometimes relies on penis morphology (Parnaby, 1992), although with experience at certain sites, additional characteristics could be used.

Since the shape of *Vespadelus* calls are similar and only subtle differences occur between species that are not easy to quantify (Fig. 1 and Reinhold *et al.*, 2001b), only characteristic frequency (Fc) was used

to assess differences between regions.  $F_c$  is measured at the last point of the flattest part of a pulse.  $F_c$  is often similar to the minimum frequency of a call, but it varies less because it ignores down-sweeping tails that may occur at the end of a call.  $F_c$  was obtained in Analook (Version 4.8f, C. Corben) using 'Fc' in measurement mode.  $F_c$  is perhaps the single most important parameter for identification of bats using zero-crossings analysis (O'Farrell *et al.*, 2000; Reinhold *et al.*, 2001b). Other call parameters (e.g., time-related measures) are not reported because they are known to be strongly influenced by proximity to clutter (Kalko and Schnitzler, 1993; Obrist, 1995). For instance, steeper calls dominate when bats fly close to clutter. Other parameters such as maximum frequency are highly influenced by the proximity of the bat to the recording microphone and, because we could not control for these effects, they have little relevance in our field study.

Only search phase calls of a reasonable quality from known species were included in the analyses. Call quality was variable, but was usually high (i.e., not fragmentary) when bats had settled into

search phase. The first step in measuring  $F_c$  was to apply Analook's automatic filter (z-key) to quantitatively remove fragmentary pulses (especially echoes) out of a sequence. Sometimes additional editing was necessary to exclude non-search phase components, such as feeding buzzes, or calls that contained multiple individuals (e.g., roost exits).  $F_c$  was then averaged for remaining good quality pulses. Thus, a single value of  $F_c$  was calculated for each individual call sequence, which normally derived from a single bat. Occasionally bats released with light-tags or reflective tape may have been recorded a second time later in the evening. However, this was a rare event. On Lord Howe Island, multiple sequences from individual, unmarked *V. darlingtoni* are likely to have been recorded.

Forearm lengths from a sample of adult males of each species were measured with calipers (nearest 0.1 mm) to allow body size comparisons across the different geographic regions. Females are not included in the analysis as positive field identification of these species relies to a large extent on penis morphology (Parnaby, 1992).

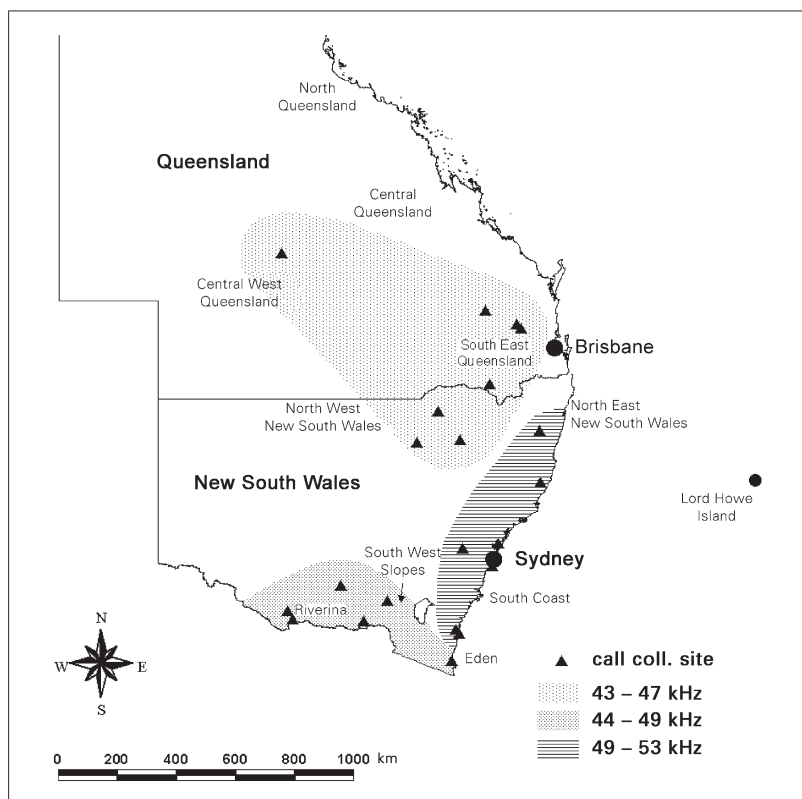


FIG. 2. *Vespudelus vulturnus* within Queensland and New South Wales, showing the geographical ranges of three frequency groups. Frequency boundaries are indicative. Place names mentioned in the text are also shown

ANOVA was used to detect geographic differences within each species. The Tukey-Kramer method was performed for post-hoc multiple comparison tests. Significance was determined at a level of 95%. A Kolmogorov-Smirnov test compared the frequency distribution of Fc's for *Vespadelus pumilus* from two geographic regions. These tests were performed using Statistica 5.5 (Statsoft Pacific).

## RESULTS

A total of 352 search phase call sequences from widespread sites in NSW and Queensland were analysed. This comprised 113 calls from *V. vulturnus*, 23 from *V. regulus*, 74 from *V. darlingtoni*, 78 from *V. troughtoni* and 64 from *V. pumilus*. Uneven sampling between different regions resulted in uneven sample sizes within species (see Fig. 8).

## Species Accounts

### *Vespadelus vulturnus*

This species showed a number of abrupt changes ( $F_{1, 76} = 42.5$ ,  $P < 0.001$ ) in Fc across its range (Figs. 2 and 8). The first frequency group includes Queensland and the north-west slopes and plains of New South Wales (note that in Queensland this species is not coastal as it can be in NSW). Another group, significantly higher in frequency, extends along eastern NSW, from the north down to the far south coast, between Narooma and Eden. The third frequency group, from Eden in the far south-east and extending across to the NSW Riverina is intermediate in frequency between the first two groups. This far south-eastern/south-western group is significantly different from the coastal

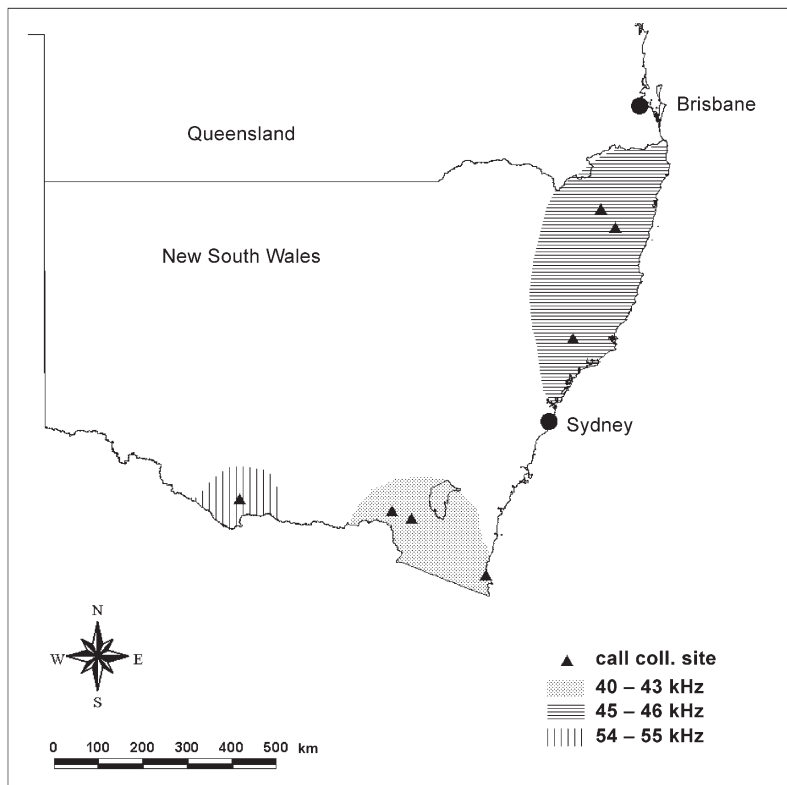


FIG. 3. *Vespadelus regulus* within New South Wales, showing the geographical ranges of three frequency groups. Frequency boundaries are indicative

group north of Eden, but is not significantly different from the Queensland/north-west group. A series of poor-quality calls from the south-west slopes shows *V. vulturinus* from this region calling at the same frequency as those from Eden in the south east corner of NSW.

### *Vespadelus regulus*

*Vespadelus regulus* from the NSW Riverina call significantly higher than those from further east ( $F_{1,19} = 107.1$ ,  $P < 0.001$ ; see also Fig. 8). This substantial shift of about 10 kHz in frequency occurs somewhere between the south-west slopes and the Riverina (Deniliquin) (Fig. 3). Although we only recorded two reference calls from the Riverina, an extensive collection of remote-recorded calls are consistent with the frequency reported here for *V. regulus*. [The identity of *V. regulus* from the Riverina was based on field identifications supplemented

with the morphological identification of a single specimen (Australian Museum Specimen No. M33477) by a taxonomic expert (H. Parnaby, pers. comm. 1997)]. A significant (but less marked) difference in frequency is also present between north-east and south-east NSW (Fig. 3). No calls were collected from the geographically intermediate Sydney Basin bioregion (Fig. 3). A greater number of calls could reveal overlap between these two groups.

### *Vespadelus darlingtoni*

There are gradual shifts in the call frequencies of *V. darlingtoni* between regions ( $F_{1,49} = 45.3$ ,  $P < 0.01$ ; Fig. 4). The trend is for frequencies to decrease from north to south, then rise again westwards of the south-east corner (Figs. 4 and 8). There are no sudden jumps in frequency between adjacent bioregions, as calls from intermediate bioregions are intermediate in frequency.

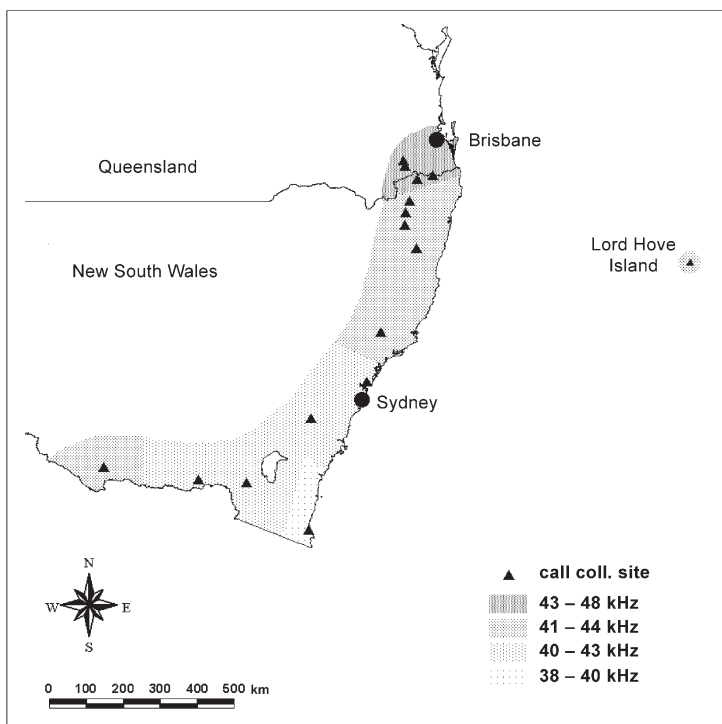


FIG. 4. *Vespadelus darlingtoni* within Queensland and New South Wales, showing the gradual frequency changes across geographic regions. Frequency boundaries are indicative



Calls from south-east Queensland are significantly higher in frequency than calls from the Sydney Basin, the South East Corner and the South West Slopes. Calls from north-east NSW and the Riverina are significantly higher than those from Eden. It is expected that the range of Fc from the Sydney Basin would increase with greater sample size. Calls from Lord Howe Island are consistent with those from northern NSW.

#### *Vespadelus trougtoni*

From the relatively extensive collection of reference calls gathered here ( $n = 78$ ), it can be concluded that the calls of this species are consistent over the range where we have recordings ( $F_{1, 78} = 0.71$ ,  $P \gg 0.05$ ; Figs. 5 and 8). The species also occurs in central and possibly southern NSW, but we did not record them from those locations.

#### *Vespadelus pumilus*

The Fc of this species ranges over 8 kHz, but there are no significant geographic differences ( $F_{1, 38} = 0.14$ ,  $P \gg 0.05$ ; Figs. 6 and 8). While recording calls at one site in NSW (Chichester State Forest), it was apparent that Fc differed from other collection localities. Closer inspection of this site reveals that the Fc has a higher mean ( $t = -3.93$ ,  $n = 32$ ,  $P < 0.001$ ) and a distribution skewed to the right compared to calls recorded at other sites in NSW (Kolmogorov-Smirnov test,  $n = 32$ ,  $P < 0.01$ ; Fig. 7).

#### Regional Forearm Length

Neither *V. pumilus* nor *V. trougtoni* displayed any significant regional differences in size (Table 1). For the remaining three species, measurements from the Riverina (south-west NSW) were significantly less

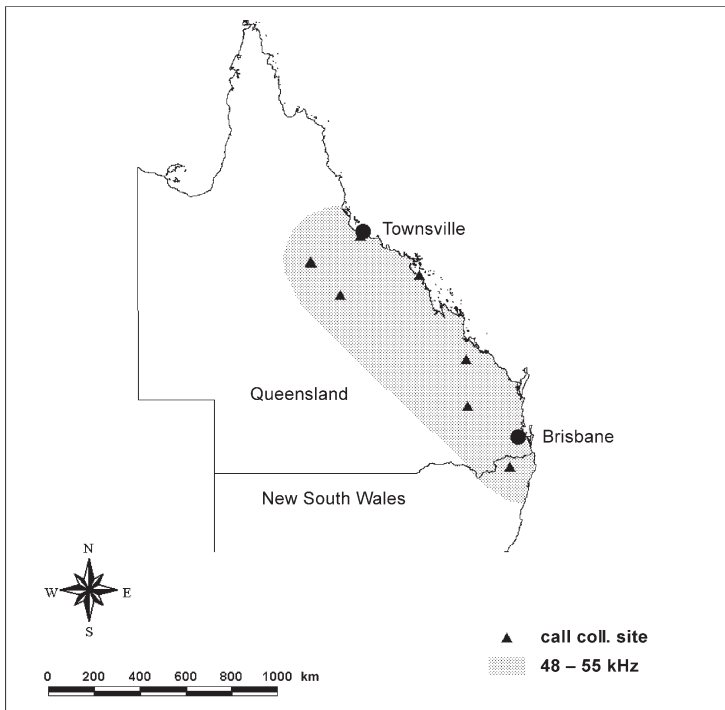


FIG. 5. *Vespadelus trougtoni* within Queensland and New South Wales, showing uniformity of frequency over the range of sites where we collected calls



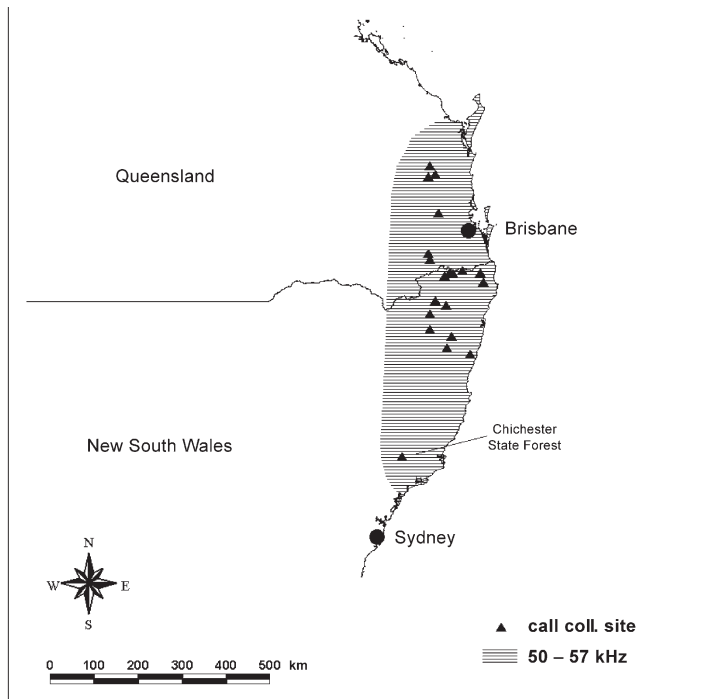


FIG. 6. *Vespadelus pumilus* within Queensland and New South Wales, showing uniformity of frequency over their range. Chichester State Forest is the most southern triangle shown on the map

than all other regions, except for *V. vulturinus* where both the Riverina and north-west NSW had the smallest forearm lengths. There were no differences in forearm lengths for any other region.

## DISCUSSION

Recently, the use of Anabat detectors (zero-crossings analysis) for describing bat call structure has been questioned (Fenton, 2000; Parsons *et al.*, 2000; Fenton *et al.*, 2001; but see Corben and Fellers, 2001). In comparison with time-expanded recorders, Anabat detectors were found to record narrower band-widths, due to lower values for maximum frequency and higher values for minimum frequency (Fenton *et al.*, 2001). Our study only presents data on the Fc of calls, which is the parameter most commonly used for discriminating species (Reinhold *et al.*, 2001b). This parameter is not

influenced by missing components of down-sweeping tails that determine minimum frequency. While it is clear that zero-crossing analysis systems provide limited (e.g., the strongest harmonic) and slightly different information to other systems, Anabat detectors remain one of the most widely used survey tools for bats. It is therefore important for the identification of bats in the field to describe the extent of geographic variation using Anabat detectors. As long as the detection system used is consistent, any observed differences will be real and they will require biological explanations.

There may also be some concern that the use of different recording techniques in different locations could have produced differences in call structure and possibly Fc. We consider this unlikely as only search-phase calls were analysed. Moreover, free-flight calls of *V. darlingtoni* on Lord Howe Island did not differ from release calls on

TABLE 1. Mean forearm lengths  $\pm$  SE (mm) with sample size in parentheses of male *Vespadelus* recorded across different geographic regions of New South Wales and Queensland. Forearm lengths at Chichester State Forest are shown only for *V. pumilus* (see text). Significance values were calculated using univariate ANOVA. Regional differences were identified using Tukey-Kramer post-hoc tests and are shown for the numbered regions. Abbreviations: a — species absent from region; n.a. — not available for that region

Region	Species			
	<i>vulturinus</i>	<i>pumilus</i>	<i>regulus</i>	<i>troughtoni</i> <i>darlingtoni</i>
1. Eden	27.8 $\pm$ 0.16 (21)	a	32.1 $\pm$ 0.31 (11)	34.7 $\pm$ 0.17 (26)
2. South Coast	27.6 $\pm$ 0.10 (38)	a	n.a.	34.7 $\pm$ 0.23 (13)
3. South-west slopes	28.1 $\pm$ 0.18 (26)	a	32.0 $\pm$ 0.14 (26)	34.7 $\pm$ 0.19 (36)
4. Riverina	26.7 $\pm$ 0.14 (27)	a	29.4 $\pm$ 0.18 (6)	32.5 $\pm$ 0.38 (5)
5. Sydney	28.0 $\pm$ 0.03 (3)	a	n.a.	n.a.
6. Chichester State Forest	n.a.	30.6 $\pm$ 0.14 (70)	n.a.	n.a.
7. North-east NSW	28.2 $\pm$ 0.15 (18)	30.3 $\pm$ 0.15 (31)	31.5 $\pm$ 0.12 (49)	34.7 $\pm$ 0.07 (166)
8. North-west NSW	27.0 $\pm$ 0.15 (31)	a	a	a
9. South-east Queensland	a	30.5 $\pm$ 0.13 (30)	a	n.a.
10. North-east Queensland	a	n.a.	a	a
F-test, P-value	13.3, <0.001	1.1, 0.351	19.1, <0.001	6.9, <0.01
Regional differences	4=8<1,2,3,5,7	nil	4<1,3,7	4<1,3,7

the adjacent mainland (see also Betts, 1998). Also, we found no variation in the calls of *V. trougtoni*, despite the fact that search-phase calls were recorded at both roost exits and after hand release.

Clarification of the extent of geographic variation is a key issue for the confident identification of bat calls to species level. Murray *et al.* (2001) found that geographic variation exists for seven species in the USA. However, variation was only slight and they recommended that species could be identified from broad geographic regions if a large sample of individuals (30–100) were recorded from a small region. Although our sample sizes were sometimes low, we still found substantial shifts in call frequency from one region to another among some species of Australian *Vespadelus*. The geographic variation within *Vespadelus* could explain the previously reported high variability in call frequency for certain species. An example is the Fc of *V. regulus* in Victoria, which ranges from 38–47 kHz (Duffy *et al.*, 2000). Calls from this species were pooled from a number of locations in Victoria (Duffy *et al.*, 2000).

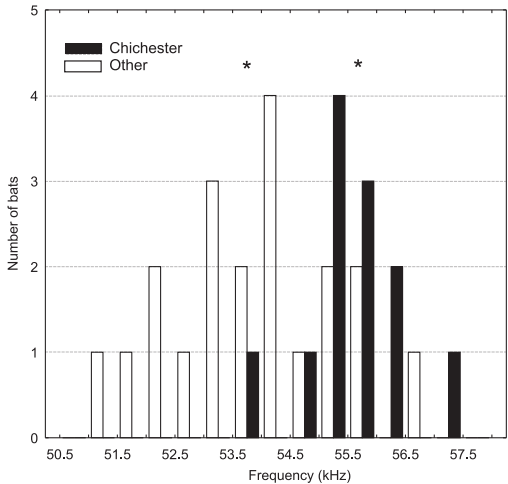


FIG. 7. Histogram of characteristic frequency for *V. pumilus* from Chichester State Forest and all other sites in New South Wales. \* — indicates the mean characteristic frequency for these two site groupings

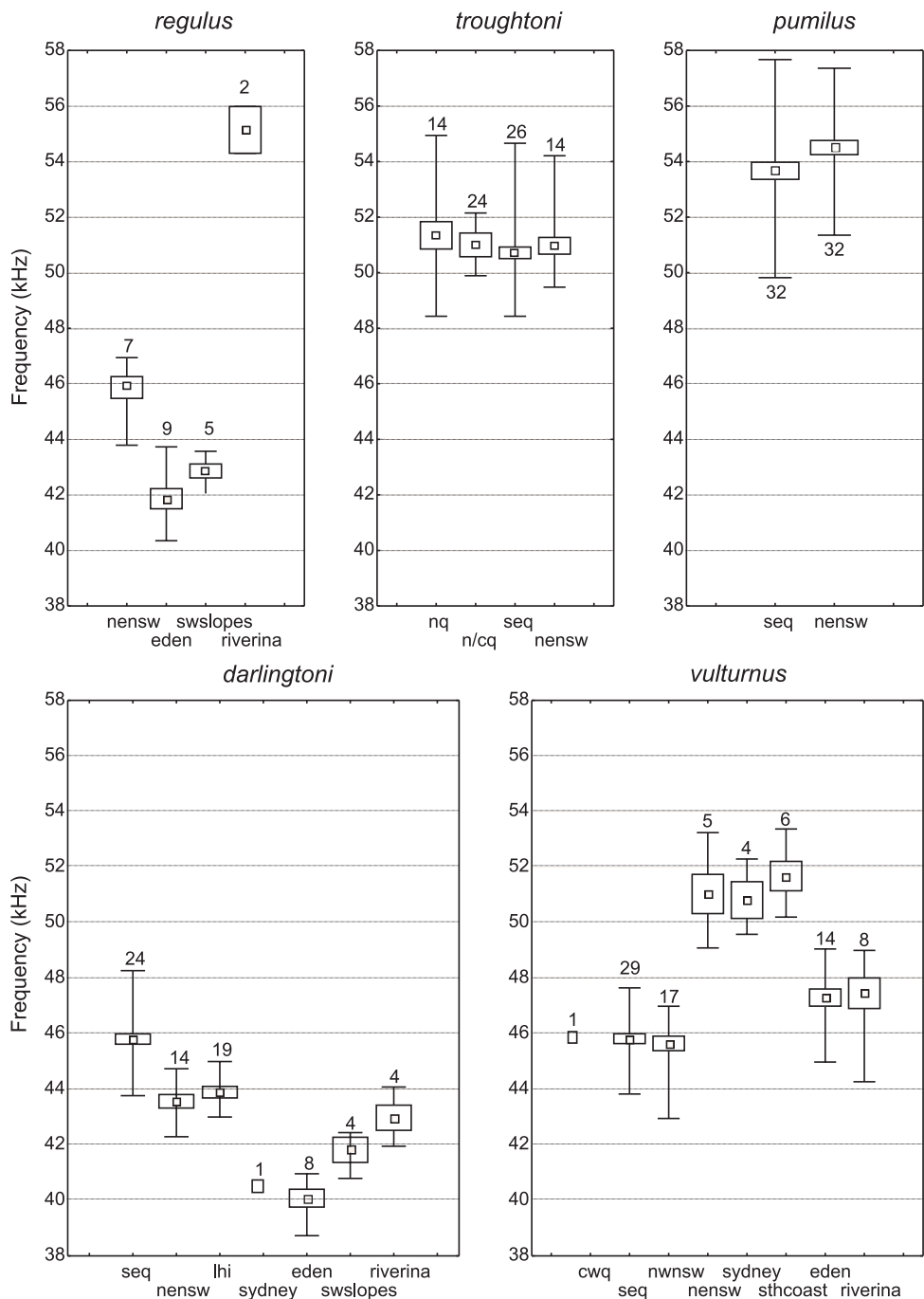


FIG. 8. Characteristic frequency ranges of *Vespadelus* (*V. darlingtoni*, *V. vulturnus*, *V. regulus*, *V. troughtoni* and *V. pumilus*) in each bioregion. Centre points are means, boxes are standard errors and whiskers are the maximum and minimum values. The number of bats contributing data is provided above the whiskers. nq — North Queensland; n/cq — North/Central Queensland; cnsw — Central west Queensland; seq — South-east Queensland; nensw — North-east NSW; nwnsw — North-west NSW; lhi — Lord Howe Island; sydney — Sydney Basin; sthcoast — South Coast; swslopes — South-west slopes; eden — Eden; riverina — Riverina

In our study, *V. regulus* calls at a mean of 42 kHz in south-eastern NSW, at 46 kHz in north-east NSW and at 55 kHz in western NSW. Such substantial frequency shifts are unlikely to be explained as a result of recording different parts of a species' repertoire in different places (O'Farrell *et al.*, 2000). This is because all calls were recorded in forest or woodland, especially on tracks or openings that are not heavily cluttered.

Unlike the small geographic variation found by Murray *et al.* (2001), we found both large frequency shifts as well as more gradual shifts. The larger species displayed gradual shifts (*V. darlingtoni*) or no variation in frequency (*V. troughtoni*). The smaller species varied between having large shifts (*V. vulturnus* and *V. regulus*) and minor shifts (*V. pumilus*). Another broad pattern was for calls of *V. vulturnus*, *V. regulus* and *V. darlingtoni* to have lower frequencies in southern/coastal NSW than further north. However, this was not entirely consistent for *V. vulturnus*, as its call frequency in the north-west was slightly lower than the far south coast of NSW.

The largest shift in frequency that we found was for *V. regulus* between the south-west slopes and the Riverina, south-western NSW. The boundary of this frequency shift is uncertain, lying somewhere between Kosciusko National Park and Deniliquin, perhaps near the boundary of the South West Slopes and Riverina bioregions. A Fc of 48.4 kHz was recorded for *V. regulus* from the western slopes of the Australian Alps (Herr, 1998), supporting this contention.

The call of *V. vulturnus* illustrates an abrupt change in frequency. The zone of frequency change is especially narrow between the coastal group and the far south/south-western group and occurs between Narooma and Eden. These two localities are only 100 km apart and are connected with

continuous forest, indicating that the species is not geographically isolated. In the north of their range, the north-western group seems to be separated from the coastal group by the Great Dividing Range/Macpherson Range.

More gradual changes in frequency were found in *V. darlingtoni*. Characteristic frequency in this species decreased with increasing latitude, but the changes between adjacent regions were relatively small. An isolated population of this species on Lord Howe Island did not differ from the adjacent mainland of northern NSW. At present it is not known how long this population has been isolated on the island. It is possible that it was accidentally introduced with early European settlers, although there is no evidence to support this. The earliest records are from the late 1800s (McKean, 1975).

Geographic variation in call frequency was not detected in *V. troughtoni* or *V. pumilus*. The frequency range of *V. pumilus* varied from 50–57 kHz, but such a broad range may not be found at the scale of a local site. For instance, we identified one site (Chichester State Forest), towards the southern edge of its distribution, where it consistently called at the higher end of its frequency range ( $\bar{x}$  = 56.0 kHz). It is possible that a more confined frequency range at this site could be related to the local species assemblage (see below). Local site variation was not detected within calls of *V. troughtoni*. Interestingly, this species probably has the most patchy distribution of all the *Vespadelus* in this study as it is the only one to roost in caves (Churchill, 1998). Thus, its presence is strongly associated with suitable geology. Yet, discontinuities in its distribution have not resulted in geographic variation in its calls.

Little is known about the causes behind the change in call frequency with geographic region. Possibilities include the presence

of cryptic species (Jones and van Parijs, 1993; Jones, 1997), morphological differences (Parsons, 1997), diet shifts and changes in local species assemblages. It is likely that these effects are interacting within the *Vespadelus* and various possibilities are put forward here as hypotheses to be tested.

First, differences in body size do not correspond with the changes in call frequency found here. Populations of species in semi-arid western NSW (Riverina and north-west NSW) consistently had smaller forearms than those towards the coast. A pattern for species to be smaller in semi-arid compared to mesic regions has been reported elsewhere (Lumsden and Bennett, 1995; Young and Ford, 1998), although small forearms are not found in *Vespadelus* from the largely dry South Australia (Queale, 1997). It is interesting to note that one of our inland (low rainfall) collection sites, the Riverina, could be considered mesic because it is a large inland river and wetland system surrounded by extensive semi-arid lands (Law and Anderson, 1999). We found no other regional differences in forearms, such as changes with latitude, indicating that body size is not likely to be an important influence on within species call variation in our study.

An alternative explanation is the possibility of cryptic species within the *Vespadelus* as abrupt changes in call frequency, such as those that occur in *V. vulturnus*, may reflect a species change. Given that no genetic analyses have been undertaken, the question of whether sudden shifts in frequency are also punctuated with taxonomic changes remains uncertain. Finding individuals of a 'single species' at zones of frequency change calling at distinct frequencies may also help to resolve this question.

Further alternative causes of geographic call variation could involve an interaction

between echolocation, diet and body size (Bogdanowicz *et al.*, 1999). Jones (1997) suggested that under certain circumstances, this complexity of causes may even lead to the evolution of cryptic species. For instance, selective pressures for acoustic divergence and speciation could involve the influence of call frequency on echo strength from acoustic targets of different sizes and thus prey selection (Jones, 1997). For the two cryptic species of *Pipistrellus pipistrellus* sensu lato in Europe (Jones and van Parijs, 1993), which call at different frequencies, it was predicted that the 55 kHz bats should eat smaller prey than 45 kHz bats. A study of their diet, found that their prey groups overlapped, although tiny chironomids (midges) dominated the diet of the 55 kHz bats and were less common in the 45 kHz bats (Barlow, 1997).

If call frequency is related to the size of prey, then it is possible that the high frequency used by *V. regulus* in western NSW (54–55 kHz) could be related to the superabundance of chironomids in the extensive wetlands along the Murray River (Maher and Carpenter, 1984; Law and Anderson, 1999). At a macro-scale, the lakes and rivers of this area are strikingly similar to the main feeding habitat of *P. pipistrellus* (55 kHz) in the United Kingdom (Vaughan *et al.*, 1997). If the utilization of small prey is indeed an important driver of geographic variation in call frequency, then we predict that bats of small body size (below some threshold, e.g., the body mass of *V. troughtoni* — 6 g) should display the greatest shifts. Detailed dietary studies are clearly required to investigate the extent of any dietary shifts.

Changes in bat assemblages from one region to another could also influence call frequency. One example is the abrupt frequency changes in calls of *V. vulturnus* in southern NSW. *Vespadelus vulturnus* co-occurs with *V. regulus* at Eden (Law and

Chidel, 2001), but *V. regulus* is absent or very rare from low altitudes further north (Mills *et al.*, 1996). Yet, the discovery of similar distributional limits for a cryptic species of *Antechinus*, a small, insectivorous marsupial, lends support to the existence of cryptic species within the *Vespadelus*. In the case of *Antechinus*, the recently described *A. agilis* is distributed in southern areas with a cooler, drier climate than *A. stuartii*, which is distributed further north (Sumner and Dickman, 1998). A narrow zone of sympatry for these two species occurs very close to the boundary separating 47 kHz bats of *V. vulturnus* at Eden from 52 kHz bats from the south coast.

Finally, the influence of diet on call frequency could interact with the influence of co-occurring species. At one study location (Chichester State Forest), we found an upwards shift in frequency of *V. pumilus* from an average of 53.9 kHz for other NSW sites to 55.6 kHz for Chichester. This bat is normally sympatric with a larger species, the little bentwing bat *Miniopterus australis*, whose call overlaps with the upper end of the *V. pumilus* frequency range (57–63 kHz — Reinhold *et al.*, 2001b). Extensive use of bat detectors and harp traps at Chichester State Forest (B. Law and M. Chidel, unpubl. data) revealed an absence of *M. australis* from this site. The absence of *M. australis* and an upward shift in mean frequency of *V. pumilus* may give the latter greater access to small-bodied prey. Diptera are an important component (37–44% of faecal pellets) of the diet of both species (Schulz, 2000). The upper restriction of call frequency in *V. pumilus* may not be widespread as *M. australis* is sympatric with *V. pumilus* throughout most of the latter's distribution. A shift in frequency at one site for *V. pumilus* also highlights the fact that geographic variation need not be restricted to isolated populations.

A practical outcome of understanding these patterns will be a better ability to discriminate between species that are currently thought to overlap in call characteristics. For instance, the calls of *V. pumilus* and *V. troughtoni* overlap extensively in Fc and cannot usually be separated when identifying calls using Anabat software (Reinhold *et al.*, 2001b). The calls of these species should be recorded where they occur in sympatry, because *V. pumilus* may shift its call frequency upwards in such sites. This would also provide a further test for the influence of larger co-occurring species such as *V. troughtoni* on call frequency for *V. pumilus*.

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