Acta Ethol (2005) 15: 35–44
DOI 10.1007/s10211-005-0107-7

ORIGINAL ARTICLE

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Can the acoustic adaptation hypothesis predict the structure of Australian birdsong?

Received: 15 September 2004 / Revised: 13 December 2004 / Accepted: 9 March 2005 / Published online: 5 April 2005
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Abstract The acoustic adaptation hypothesis (AAH) predicts that long-distance signals will be structured so as to maximize their transmission fidelity. Previous studies testing the hypothesis on birdsong have provided equivocal support. The best support comes from large-scale comparative studies and those studies where habitat is characterized as "open" versus "densely vegetated." In the first case, sufficient statistical power is present to detect even small effects on song structure, whereas in the later case the "effect size" of the habitat may be sufficiently large. Most studies have focused on Holarctic or Neotropical species, which may ultimately share a common evolutionary history. In this study, Australian birds were chosen for a phylogenetically independent test of key predictions of the AAH. Specifically, birds in open habitats were predicted to sing songs with higher frequencies, greater bandwidth, have a greater probability of having overtones, and be emitted at a quicker rate than birds inhabiting densely forested habitats. Acoustic measurements were made on commercially available recordings of 121 species of Australian birds from 41 different families. Analyses controlled for variation explained by body mass (using ANCOVA), and phylogeny (using genus pairs analyses). We found only modest support for the AAH. Our finding that birds in open habitats produced higher frequency vocalizations and greater bandwidth vocalizations is also consistent with hypotheses about signal structure facilitating auditory distance assessment. Forest birds may therefore rely on cues other than frequency-dependent attenuation for ranging.

Communicated by P. McGregor

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Keywords Acoustic adaptation hypothesis · Animal communication · Habitat acoustics

Introduction

Once emitted by a signaler, the structure of acoustic signals attenuates (loses amplitude) and degrades (loses fidelity) while traveling to a receiver (Bradbury and Vehrencamp 1998). For long-distance acoustic communication, signals must be transmitted from the signaler to the receiver with minimal or predictable (Naguib and Wiley 2001) attenuation and degradation. Morton (1975) suggested that structural differences in the habitat may influence sound transmission. For instance, sounds transmitted through forests are more affected by reverberation off leaves and tree trunks than sounds transmitted in the open (Richards and Wiley 1980; Waser and Brown 1986). In contrast, sounds transmitted across large open areas are subject to degradation by irregular amplitude fluctuations because of air turbulence from heat reflected off the open ground (Wiley and Richards 1978; Richards and Wiley 1980). Thus, the acoustic adaptation hypothesis (AAH) predicts systematic differences in the structure of long-distance acoustic signals transmitted through dense forests versus those transmitted through more open habitat (Morton 1975; Hansen 1979; Rothstein and Fleischer 1987; Wiley 1991).

Despite its intuitive appeal, and despite theoretical support (Brown and Handford 1996), there has not been consistent empirical support for the AAH. The best support has come from large-scale studies focusing on broad categories of habitat (e.g., dense forest vs open) for either a variety of species or a single oscine songbird found in a variety of habitats (Chapuis 1971; Morton 1975; Nottebohm 1975; Wasserman 1979; Ryan and Brenowitz 1985; Sorjonen 1986; Handford 1988; Wiley 1991; Tubaro and Segura 1994; Van Buskirk 1997). Studies that have focused on fewer species or tried to explain microstructural differences in long-distance signals have not consistently supported the AAH (Lemon et al. 1981; Rothstein and Fleischer 1987; Smith and Yu 1992; Date and Lemon 1993; Williams and

Slater 1993; Fotheringham et al. 1997; Daniel and Blumstein 1998; Naguib and Wiley 2001; but see Doutrelant and Lambrechts 2001). The majority of these studies focused on some or all of the same Holarctic or Neotropical birds (but see Chappuis 1971; Slabbekoorn and Smith 2001). Thus, the general applicability of the AAH is unknown.

If behavioral theory is to be generally useful, it must be predictive. We elected to evaluate key predictions of the AAH with Australian birds. Australia has several endemic passerine and nonpasserine families (Pizzey and Knight 1997) that include major radiations of whistlers (Pachycephalinae), honeyeaters (Meliphagidae), and scrubwrens (Pardalotidae), which have not been used in previous tests of the AAH. Thus, Australian birds can be used to provide an independent evaluation of the AAH.

Methods

We focused on songs and loud calls of species of Australian birds obtained from two commercially available CDs: the *Australian Bird Song Collection* (Horton 2000) and *Australian Bird Calls: Favourites* (Stewart 2000). The AAH applies specifically to long-distance territorial calls and songs. We used Pizzey and Knight (1997) and the recordings' written notes to determine whether vocalizations were long-distance territorial calls. In most cases, however, insufficient information about the precise function of these vocalizations was reported in the literature. We excluded obvious short-distance low-amplitude contact calls, but erred on the side of inclusion. As long as a vocalization is designed to function for more than a few meters it will be subjected to degradation and attenuation. Thus, its structure should reflect a history of selection to facilitate effective transmission. In contrast to our strategy, Wiley (1991) excluded from his analyses broad categories of calls that were not specifically long-distance territorial signals, which included all corvid vocalizations. By contrast, the corvid calls we included were not obviously short-range calls emitted around nests (e.g., copulatory or begging calls) for which we would expect different selective pressures to become important (Richards and Wiley 1980). Nonetheless, our results should be viewed as a conservative test of the effects of the environment on signal design.

For each species we created individual 16-bit, 44.1-kHz sound files containing the best quality recording (i.e., that with the greatest signal-to-noise ratio); all acoustic measurements were made on these sound files. Recordings were of variable quality and some species were excluded from analysis on the basis of poor recording quality. Our final data set consists of data on 121 species from 41 families. Unlike Wiley (1991), we did not focus specifically on oscine birds because the predictions of the AAH should be generally applicable to birds, not simply those that can learn their songs or those with complex syrinxes. Following Wiley, we assumed that there would be no systematic recording bias because the vocalizations were not recorded with our hypothesis in mind.

Acoustic measurements

We used Canary 1.2.4 (Charif et al. 1995) to make all measurements. A maximum of three songs or three 10-s segments of song (when song structure was not well defined) for a given species were analyzed. We attempted to analyze a species' most common song or call as described by Pizzey and Knight (1997). If the vocalizations on the recording did not obviously match Pizzey and Knight's description, then we used the most common vocalization in the recording.

From the waveform we calculated a spectrogram and spectrum for each bout of vocalizations. Spectrogram parameters were standardized: −120-dB clipping, 50% overlap, 1024-point fast Fourier transform. The same parameters were used to generate spectra averaged over the duration of each recording. Using the spectrum, we standardized spectrograms so that measurements were restricted to the range including −40 dB below peak amplitude. Acoustic measurements were taken from standardized window dimensions: 1 in.=200 ms, 2 kHz, and 4 μPa for the spectrograms and waveforms, respectively.

Frequency measurements were made on spectrograms and temporal measurements were made on waveforms (Fig. 1). We focused both on the entire song and on the acoustic elements (i.e., independent "traces" on the spectrogram) that made up each song because of a recent suggestion that they may evolve independently (Van Buskirk 1997). A single observer (A.C.T.) trained until measurements were consistent, and then measured the following acoustic characteristics across all three songs: highest frequency, lowest frequency, and the dominant frequency (the frequency where energy is most concentrated). For each of the three songs, she counted the number of acoustic elements and measured duration, interval between elements, bandwidth, highest, lowest, and dominant frequencies at the level of the song and at the level of acoustic elements within the song. As can be seen in Fig. 1, there is the opportunity for some subjective interpretation of the maximum and minimum frequencies as well as the starting and ending time. By varying the clipping level, it was possible to determine what was part of the song and what was not before making measurements −40 dB below peak amplitude. Reverberation clearly degraded a number of sounds; measurements by the single observer were consistent. Bandwidth was calculated by subtracting the minimum from the maximum frequency. These measurements were then averaged across a song (in the case of measures on elements) and then across all songs for each species. Additionally, each species' vocalization was scored as having either or both overtones (harmonic or otherwise) and repeated units (the same acoustic element that was repeated at least once).

Because body mass may explain variation in the frequencies a species can produce (Ryan and Brenowitz 1985; Wiley 1991), we obtained body masses for 85 of the species from two sources (Dunning 1993; Geffen and Yom-Tov 2000) and used mass as a covariate in subsequent analyses. We elected not to attempt to control for other possible factors that might explain variation in song such as the in-

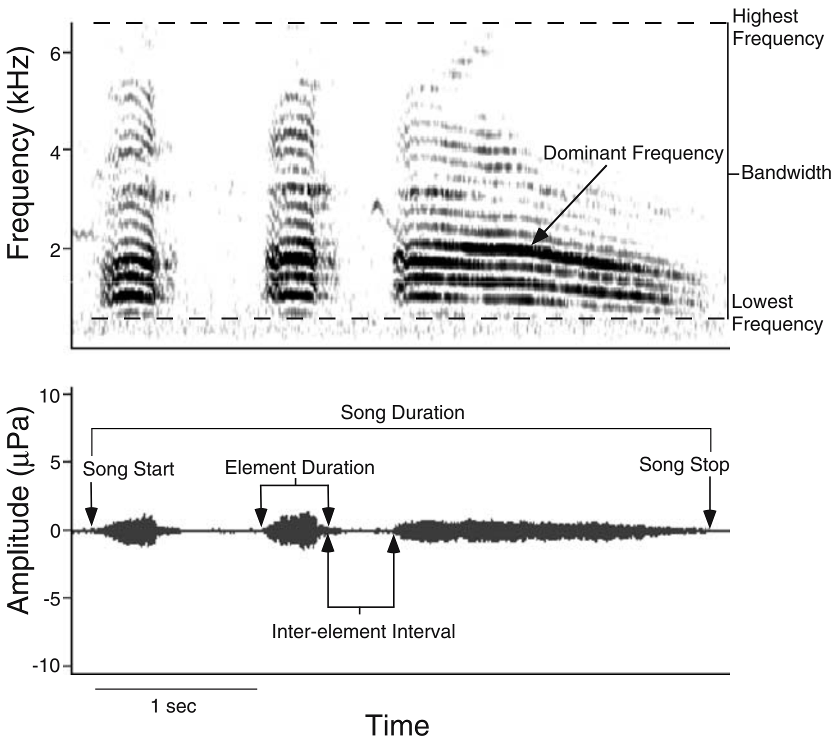

Fig. 1 Spectrogram and waveform of the vocalization of an Australian raven (*Corvus coronoides*; from Stewart 2000) illustrating quantitative acoustic measurements

tensity of sexual selection, beak size, community structure, and ambient noise (Catchpole and Slater 1995; Podos 2001; Slabbekoorn and Smith 2002).

We classified a species' habitat openness by the amount of vegetation as described in Pizzey and Knight (1997). The primary habitat for each species was initially classified in order of decreasing vegetation density as follows: dense forest, open forest or rainforest edge, scrubland, wetland or beach. For analysis, we defined dense forest as closed habitat, and scored as open habitat all other habitat types (sensu Wiley 1991). We did so because studies that found modest support for the AAH were those that similarly scored habitats as densely forested versus other. Strictly, the AAH should be with respect to the exact location of where the birds sing and not overall habitat type. Thus, our categorization of habitat type is overly conservative because it is less likely to lead to a significant effect.

Our final data sets varied based on the specific analysis and on the availability of body mass measurements. For analyses based on frequency data, we had 37 species from closed habitats and 48 species from open habitats. For analyses on the temporal or gross structure of calls, we had 54 species in closed habitat and 67 species in open habitat.

Phylogenetic analysis

Closely related species may share song types and habitat preferences, and this dependence may therefore confound our ability to study the effects of habitat on song characteristics. Thus, and in addition to analyses on species values, we conducted a series of phylogenetically corrected analyses. Unfortunately, there is no single accepted phylogeny containing all species of interest. Thus, we elected to use "genus pairs" (e.g., Beauchamp 1999; Maddison 2000) analysis to test the hypothesis of independent evolution of bird song structure in response to habitat openness. The key assumption in genus pairs analyses is that any difference between the pairs evolved independently and the differences are thus phylogenetically independent.

Genus pairs consisted of a species living in open habitat and a congener living in a closed habitat. There was no significant difference in the body masses of the genus pairs (Wilcoxon P=0.953) and we therefore did not "control" for body size. For genera with more than one species available in either closed or open habitats, we selected randomly one pair. We were able to extract 12 genus pairs (Table 1) and view this as powerful (because it is focused on the key factor—habitat openness), but conservative (because of the small sample size).

Statistical analysis

Specifically, we tested the following explicit and implicit predictions of the AAH:

> P1: Birds in the open would produce higher maximum frequencies when measured at the level of the song and at the level of the element than birds in the forest. This is because reverberation in the forest has a larger effect on the transmission of higher frequencies than lower frequencies and this should affect the entire song, as well as its components.

Table 1 Species used in this analysis and their classification according to habitat

Common name	Latin binomial	Family	Open/closed
Emu	*Dromaius novaehollandiae*	Struthionidae	Open
Orange-footed scrubfowl	*Megapodius reinwardt*	Megapidiidae	Closed
Plumed whistling duck	*Dendrocygna eytoni*	Anatidae	Open
Black swan	*Cygnus atratus*	Anatidae	Open
Great egret	*Ardea alba*	Arideidae	Open
Whistling kite	*Haliastur sphenurus*	Accipitridae	Open
Brolga	*Grus rubicundus*	Gruidae	Open
Black-winged stilt	*Himantopus himantopus*	Recurvirostridae	Open
Masked lapwing	*Vanellus miles*	Charadriidae	Open
Peaceful dove	*Geopelia striata*	Columbidae	Open
Diamond dove	*Geopelia cuneata*	Columbidae	Open
Emerald dove	*Chalcophaps indica*	Columbidae	Closed
Brown cuckoo-dove	*Macropygia amboinensis*	Columbidae	Closed
Wonga pigeon	*Leucosarcia melanoleuca*	Columbidae	Closed
Pied imperial pigeon	*Ducula bicolor*	Columbidae	Closed
Rose-crowned fruit-dove	*Ptilinopus regina*	Columbidae	Closed
Wompoo fruit-dove	*Ptilinopus magnificus*	Columbidae	Closed
Palm cockatoo	*Probosciger aterrimus*	Cacatuidae	Open
Red-tailed black-cockatoo	*Calyptorhynchus banksii*	Cacatuidae	Open
Galah	*Cacatua roseicapilla*	Cacatuidae	Open
Cockatiel	*Nymphicus hollandicus*	Cacatuidae	Open
Rainbow lorikeet	*Trichoglossus haematodus*	Psittacidae	Closed
Australian king parrot	*Alisterus scapularis*	Psittacidae	Closed
Crimson rosella	*Platycercus elegans*	Psittacidae	Closed
Red-rumped parrot	*Psephotus haematonotus*	Psittacidae	Open
Ground parrot	*Pezoporus wallicus*	Psittacidae	Open
Brush cuckoo	*Cacomantis variolosus*	Cuculidae	Closed
Fan-tailed cuckoo	*Cacomantis flabelliformis*	Cuculidae	Closed
Shining bronze cuckoo	*Chrysococcyx lucidus*	Cuculidae	Closed
Common koel	*Eudynamys scolopacea*	Centropodiae	Closed
Southern boobook	*Ninox novaseelandiae*	Strigidae	Closed
Tawny frogmouth	*Podargus strigoides*	Podargidae	Open
Laughing kookaburra	*Dacelo novaeguineae*	Halcyonidae	Open
Forest kingfisher	*Todiramphus macleayii*	Halcyonidae	Open
Rainbow bee-eater	*Merops ornatus*	Meropidae	Open
Noisy pitta	*Pitta versicolor*	Pittidae	Closed
Albert’s lyrebird	*Menura alberti*	Menuridae	Closed
Superb lyrebird	*Menura novaehollandiae*	Menuridae	Closed
Noisy Scrub-bird	***Atrichornis clamosus***	**Atrichornithidae**	**Open**
Rufous scrub-bird	***Atrichornis rufescens***	**Atrichornithidae**	**Closed**
White-throated treecreeper	*Cormobates leucophaeus*	Climacteridae	Closed
Super fairy-wren	*Malurus cyaneus*	Maluridae	Open
Red-browed pardalote	*Pardalotus rubricatus*	Pardalotidae	Open
Striated pardalote	*Pardalotus striatus*	Pardalotidae	Open
Pilotbird	*Pycnoptilus floccosus*	Pardalotidae	Closed
White-browed scrubwren	***Sericornis frontalis***	**Pardalotidae**	**Open**
Fernwren	*Oreoscopus gutturalis*	Pardalotidae	Closed
Yellow-throated scrubwren	***Sericornis citreogularis***	**Pardalotidae**	**Closed**
Large-billed scrubwren	*Sericornis magnirostris*	Pardalotidae	Closed
Western gerygone	*Gerygone fusca*	Pardalotidae	Open
Brown gerygone	***Gerygone mouki***	**Pardalotidae**	**Closed**
White-throated gerygone	***Gerygone olivacea***	**Pardalotidae**	**Open**
Inland thornbill	*Acanthiza apicalis*	Pardalotidae	Open
Brown thornbill	***Acanthiza pusilla***	**Pardalotidae**	**Closed**
Chestnut-rumped thornbill	***Acanthiza uropygialis***	**Pardalotidae**	**Open**

Table 1 (continued)

Common name	Latin binomial	Family	Open/closed
Little wattlebird	*Anthochaera chrysoptera*	Meliphagidae	Open
Red wattlebird	*Anthochaera carunculata*	Meliphagidae	Open
Helmeted friarbird	***Philemon buceroides***	**Meliphagidae**	**Closed**
Noisy friarbird	***Philemon corniculatus***	**Meliphagidae**	**Open**
Spiny-cheeked honeyeater	*Acanthagenys rufogularis*	Meliphagidae	Open
Blue-faced honeyeater	*Entomyzon cyanotis*	Meliphagidae	Open
Bell miner	***Manorina melanophrys***	**Meliphagidae**	**Closed**
Noisy miner	***Manorina melanocephala***	**Meliphagidae**	**Open**
Lewin's honeyeater	*Meliphaga lewinii*	Meliphagidae	Closed
Yellow-faced honeyeater	*Lichenostomus chrysops*	Meliphagidae	Open
Singing honeyeater	*Lichenostomus virescens*	Meliphagidae	Open
Varied honeyeater	*Lichenostomus versicolor*	Meliphagidae	Open
White-plumed honeyeater	*Lichenostomus penicillatus*	Meliphagidae	Open
White-throated honeyeater	*Melithreptus albogularis*	Meliphagidae	Open
Crescent honeyeater	*Phylidonyris pyrrhoptera*	Meliphagidae	Closed
Scarlet honeyeater	*Myzomela sanguinolenta*	Meliphagidae	Closed
Brown honeyeater	*Lichmera indistincta*	Meliphagidae	Open
Jacky Winter	*Microeca fascinans*	Petroicidae	Open
Eastern yellow Robin	*Eopsaltria australis*	Petroicidae	Closed
Hooded robin	*Melanodryas cucullata*	Petroicidae	Open
Grey-headed robin	*Heteromyias albispecularis*	Petroicidae	Closed
Northern scrub-robin	*Drymodes superciliaris*	Petroicidae	Closed
Chowchilla	*Orhonyx spaldingii*	Orthonychidae	Closed
Logrunner	*Orthonyx temminckii*	Orthonychidae	Closed
White-browed babbler	*Pomatostomus superciliosus*	Pomatostomidae	Open
Grey-crowned babbler	*Pomatostomus temporalis*	Pomatostomidae	Open
Chirruping wedgebill	*Psophodes cristatus*	Cinclosomatidae	Open
Chiming wedgebill	***Psophodes occidentalis***	**Cinclosomatidae**	**Open**
Eastern whipbird	***Psophodes olivaceus***	**Cinclosomatidae**	**Closed**
Crested bellbird	*Oreoica gutturalis*	Pachycephalidae	Open
Olive whistler	***Pachycephala olivacea***	**Pachycephalidae**	**Closed**
Golden whistler	*Pachycephala pectoralis*	Pachycephalidae	Closed
Rufous whistler	***Pachycephala rufiventris***	**Pachycephalidae**	**Open**
Little shrike-thrush	*Colluricincla megarhyncha*	Pachycephalidae	Closed
Bower's shrike-thrush	***Colluricincla boweri***	**Pachycephalidae**	**Closed**
Grey shrike-thrush	***Colluricincla harmonica***	**Pachycephalidae**	**Open**
Black-faced monarch	*Monarcha melanopsis*	Dicruridae	Closed
Restless flycatcher	*Myiagra inquieta*	Dicruridae	Open
Willie wagtail	***Rhipidura leucophrys***	**Dicruridae**	**Open**
Grey fantail	***Rhipidura fuliginosa***	**Dicruridae**	**Closed**
White-winged triller	*Lalage sueurii*	Campephagidae	Open
Yellow oriole	***Oriolus flavocinctus***	**Oriolidae**	**Closed**
Figbird	*Sphecotheres viridis*	Oriolidae	Closed
Olive-backed oriole	***Oriolus sagittatus***	**Oriolidae**	**Open**
Masked woodswallow	*Artamus personatus*	Artamidae	Open
Black butcherbird	***Cracticus quoyi***	**Artamidae**	**Closed**
Grey butcherbird	*Cracticus torquatus*	Artamidae	Closed
Pied butcherbird	***Cracticus nigrogularis***	**Artamidae**	**Open**
Australian magpie	*Gymnorhina tibicen*	Artamidae	Open
Magpie-lark	*Grallina cyanoleuca*	Artamidae	Open
Pied currawong	*Strepera graculina*	Artamidae	Closed
Victoria's riflebird	*Ptilotis victoriae*	Paradisaeidae	Closed
Australian raven	*Corvus coronoides*	Corvidae	Open
Little crow	*Corvus bennetti*	Corvidae	Open
Apostlebird	*Struthidea cinerea*	Corcoracidae	Open

Table 1 (continued)

Common name	Latin binomial	Family	Open/closed
White-winged chough	*Corcorax melanorhamphos*	Corcoracidae	Open
Spotted catbird	*Ailuroedus melanotis*	Ptilonorhynchidae	Closed
Tooth-billed bowerbird	*Scenopoeetes dentirostris*	Ptilonorhynchidae	Closed
Green catbird	*Ailuroedus crassirostris*	Ptilonorhynchidae	Closed
Golden bowerbird	*Prionodura newtoniana*	Ptilonorhynchidae	Closed
Satin bowerbird	*Ptilonornynchus violaceus*	Ptilonorhynchidae	Closed
Zebra finch	*Taeniopygia guttata*	Fringilidae	Open
Mistletoebird	*Dicaeum hirundinaceum*	Dicaeidae	Open
Clamorous reed-warbler	*Acrocephalus stentoreus*	Sylviidae	Open
Rufous songlark	*Cinclorhampus mathewsi*	Sylviidae	Open
Silvereye	*Zosterops lateralis*	Zosteropidae	Open

Species used in genus pairs analysis are highlighted in bold

P2: Birds in the open would produce higher dominant frequencies when measured at the level of the song and at the level of the element than birds in the forest.

P3: There would be no effect of habitat on the lowest frequency when measured at the level of the song and at the level of the element because habitat, per se, has no systematic effect on low frequencies.

P4: Birds in the open would have greater bandwidth (maximum − minimum frequency) when measured at the level of the song and at the level of the element than birds in the forest.

P5: Birds in the open would vocalize at faster rates when measured by examining element duration, the interval between elements, the number of elements produced per second, and the number of acoustically unique elements per song than birds in the forest. In the open, the absence of reverberation permits rapidly paced repeated units (Richards and Wiley 1980). Reverberation in the forest, which will be most pronounced on elements at the same frequency (Richards and Wiley 1980), will degrade rapidly repeated song.

P6: Birds in the open would have shorter songs than birds in the forest. Although not precisely predicted by the AAH, we believe that this follows because of the degradational constraints associated with singing in forests that prevents complex songs with many parts. Reverberation may select for slowly paced and redundant song. By contrast, birds singing in open habitats can get their message across quickly and accurately.

P7: Wiley (1991) specifically said that there is no reason to expect harmonics to be influenced by habitat because long-distance signals should have most of their energy at any single moment concentrated in one frequency. However, because we included all loud calls and songs, we predicted that overtones, and therefore higher frequency acoustic components, would be more common in birds that lived in open habitat compared to birds in the forest because calls with overtones would become relatively more degraded than calls in the open.

P8: Finally, and related to prediction 5, the presence of repeated units would be more common in birds that lived in open habitats compared to birds in the forest because reverberation in the forest would degrade repeated units that were repeated quickly.

All statistical analyses were conducted in SPSS-10 (SPSS 2000). We used ANCOVA to test for habitat effects confounded by body mass (i.e., frequency measurements), Mann–Whitney *U* tests to compare temporal aspects, and chi-square tests to evaluate hypotheses based on frequencies (presence of repeated units and overtones). Analyses on genus pairs used Wilcoxon signed rank tests for continuous variables and McNemar tests for counts.

All tests were two-tailed and the alpha was set at 0.05. The effect size of the acoustic environment is typically small (Daniel and Blumstein 1998). Thus, and so as to not make type II errors, we therefore interpret P values <0.1 as suggestive. The data used to test predictions 1–4 are highly correlated within each data set (i.e., species, genus pairs). A Bonferroni correction would suggest that only P values <0.006 (0.05/8 comparisons within a data set) should be interpreted as significant. The four variables used to evaluate prediction 5 were also highly correlated. A Bonferroni correction would suggest that only P values <0.013 (0.05/4 comparisons within a data set) should be interpreted as significant.

Results

Our analyses of the acoustic structure of Australian bird song were not entirely consistent with the predictions of the AAH (Figs. 2, 3; Tables 2, 3, 4). Specifically, we found limited support for prediction 1: when all species were considered, birds in the open produced songs and elements with higher frequencies (Fig. 2). However, this result was not strongly supported by genus pairs analyses (Fig. 2). We found no strong support for prediction 2: when measured at the level of the song, and when examining all species, the dominant frequency was higher for species found in open habitats. However, this effect disappeared when a Bonferonni correction was used. Prediction 3 was supported: however examined, there was no effect of habitat on the lowest frequency (Fig. 2). Prediction 4 was supported when the entire song was considered: birds in the open had

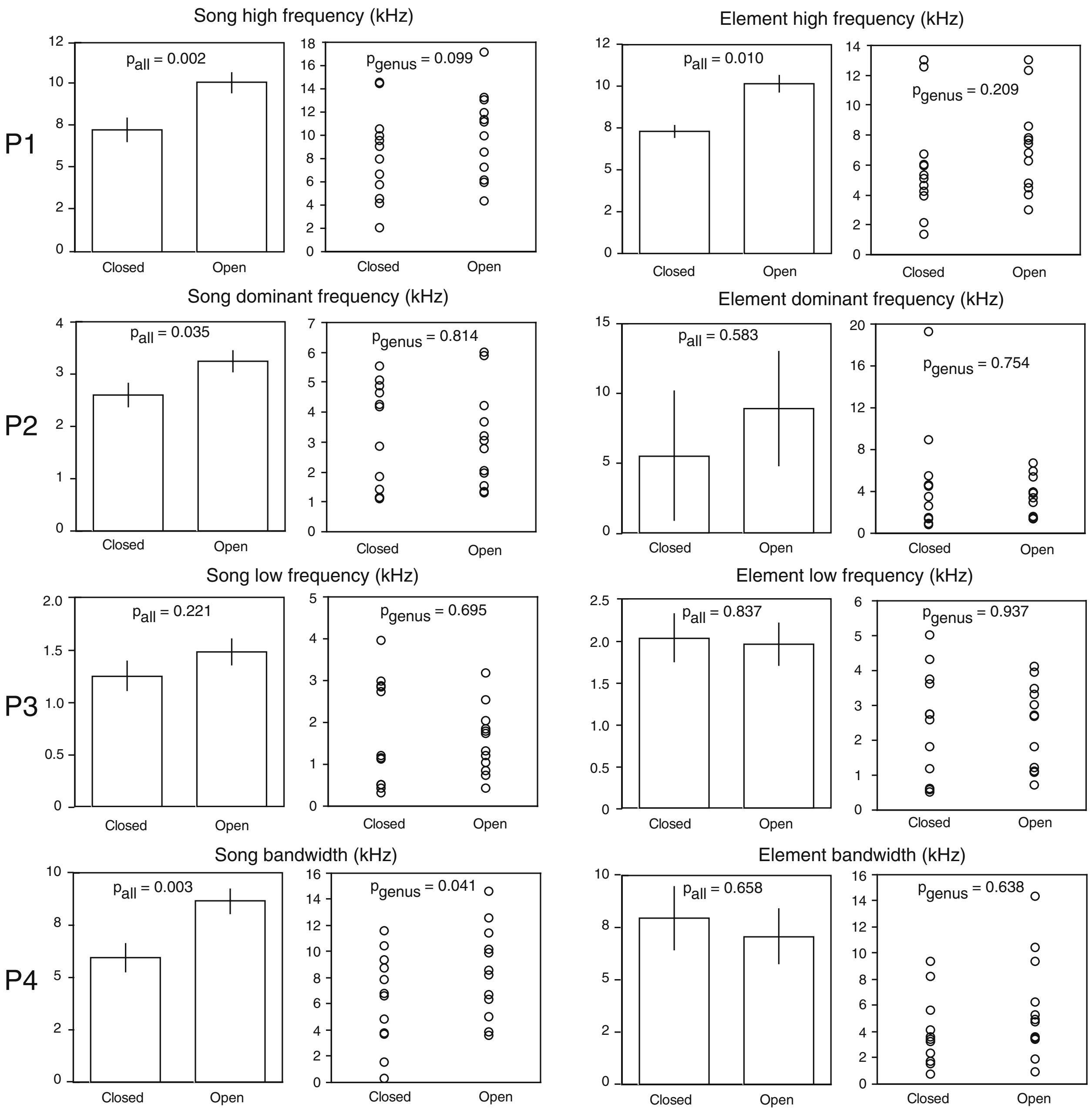

Fig. 2 Average (±SE), or the species values in the genus pairs analysis, of frequency measurements made on a subset of Australian birds that are predominantly found in dense forest habitat (*Closed*) or open habitat (*Open*). P_{all} is the *P* value reporting the effect of habitat openness from ANCOVA analyses after accounting for variation explained by body size. P_{genus} is the *P* value from the Wilcoxon matched pairs signed rank genus pairs analyses. *P1–P4* refer to predictions being tested (see text for details)

songs with greater bandwidth, but the genus-pair result did not support the prediction when a more rigorous Bonferroni correction was used. Prediction 5 was supported when species, but not genus pairs, were analyzed. Birds in the open emitted more elements per second and produced elements of shorter duration (Fig. 3). However, there were no differences in the number of elements per song, or in the inter-element interval. Song duration was highly variable, but its variation was not explained by habitat type (Fig. 3), thus refuting prediction 6. Prediction 7 was supported: there was an association between habitat openness and the presence of overtones (P_{all}=0.003, Table 2; P_{genus}=0.012, Table 4). A post hoc chi-square test suggested that birds in dense forest habitats were significantly less likely to have calls with overtones (P<0.05). Whereas the likelihood of having repeated units was not significantly different in the species analyses (P=0.717, Table 3), in the genus pairs analysis birds in closed habitats were more, not less, likely to have vocalizations with repeated units (P=0.025, Table 4). Thus, prediction 8 was not supported.

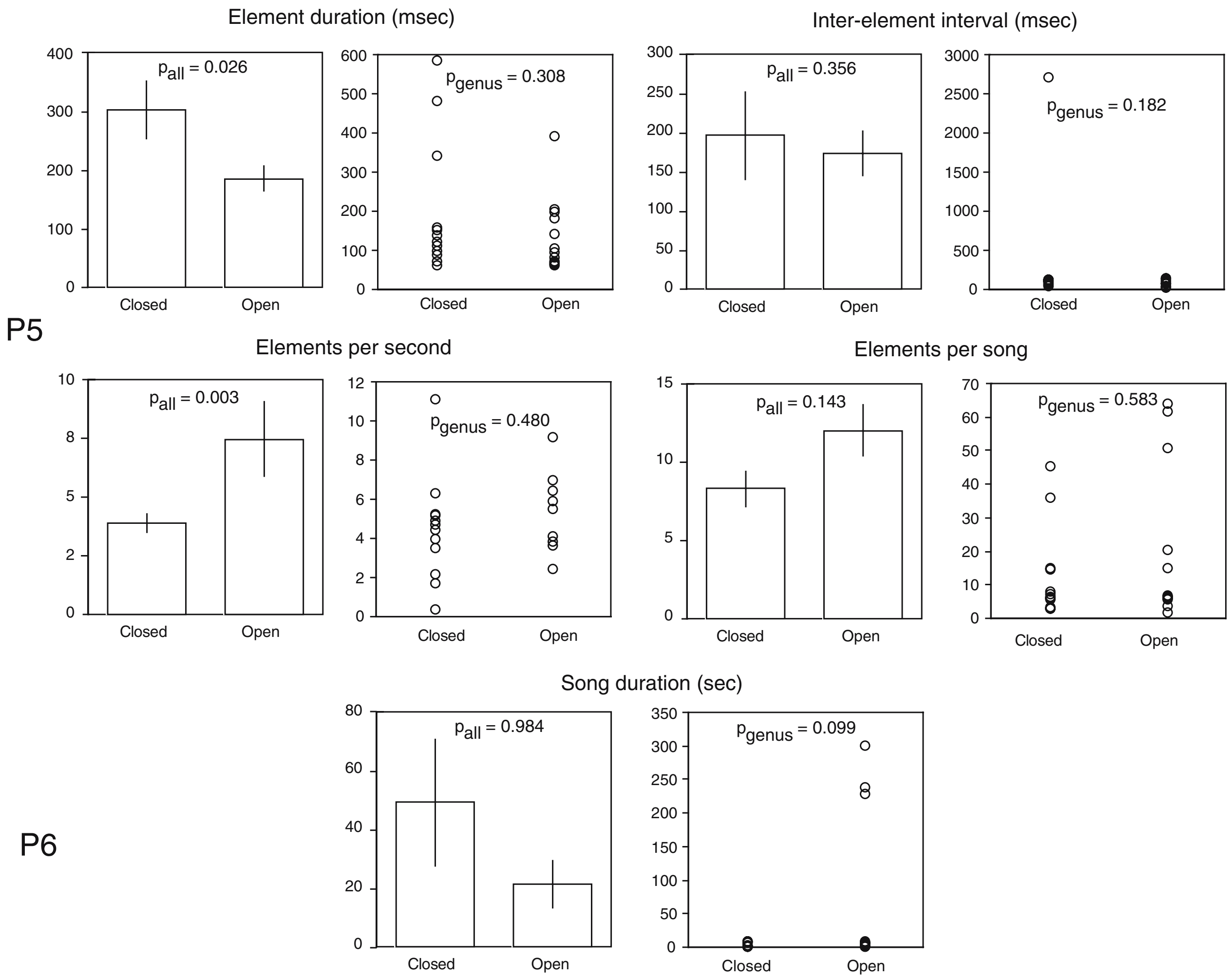

Fig. 3 Average (±SE), or the species values in the genus pairs analysis, of temporal measurements made on a subset of Australian birds which are predominantly found in dense closed forest habitat (*Closed*) or more open habitat (*Open*). P_{all} is the *P* value reporting the effect of habitat openness from Mann–Whitney *U* tests, and P_{genus} is the *P* value from the Wilcoxon matched pairs signed rank genus-pairs analysis. *P5* and *P6* refer to prediction being tested

Discussion

Our test of some predictions of the acoustic adaptation hypothesis using Australian bird song provided only limited support for the AAH. Australian birds living in open habitats produced higher frequency songs with greater bandwidth and were more likely to have overtones than those inhabiting dense forest. However, a genus pairs analyses suggests that this may not be an evolutionary consequence of acoustic adaptation to these different habitats.

Evidence for selection having acted on temporal characteristics is also unconvincing because most relationships were found only in the analyses based on species, rather than analyses based on the more conservative genus pairs. Vocalizations of dense forest birds were longer, emitted at a slower rate, and were more—not less—likely to contain repeated units, but again, these results were not strongly supported by the genus pairs analyses. Reverberation, which is expected in dense forest environments, selects for slower paced vocalizations, which are most likely to reduce ambiguity in light of expected degradation (Morton 1975; Hansen 1979; Wiley 1991), but this effect seems to be weaker than the frequency effect. Repetition, in this context, may have evolved as a method to increase efficacy (Guilford and Dawkins 1991).

Wiley (1991) focused on the song-learning oscines and reported a consistent effect of habitat openness on the rate at which elements were emitted. It is possible that oscines

Table 2 The presence of overtones as a function of whether the species were found in dense forest or in open habitat

Habitat	Overtones	
	No	Yes
Closed	24	30
Open	12	55

Table 3 The presence of repeated units as a function of whether the species were found in dense forest or in open habitat

Habitat	Repeated units	
	No	Yes
Closed	27	27
Open	36	31

Table 4 Presence of repeated units and overtones in each of the 24 species that made up the genus pairs as a function of whether they lived in the dense forest or in open habitat

Closed	Open	Repeated units		Overtones	
		Closed	Open	Closed	Open
Atrichornis rufescens	*Atrichornis clamosus*	1	0	1	1
Sericornis citreogularis	*Sericornis frontalis*	1	0	1	1
Gerygone mouki	*Gerygone olivacea*	1	0	0	1
Acanthiza pusilla	*Acanthiza uropygialis*	1	0	1	1
Philemon buceriodes	*Philemon corniculatus*	0	0	1	1
Manorina melanophrys	*Manorina melanocephala*	0	0	1	1
Psophodes olivaceus	*Psophodes occindentalis*	0	0	1	1
Pachycephala olivacea	*Pachycephala rufiventris*	0	0	0	1
Colluricincla boweri	*Colluricincla harmonica*	1	1	0	1
Rhipidura fuliginosa	*Rhipidura leucophrys*	0	0	1	1
Oriolus flavocinctus	*Oriolus sagittatus*	0	0	0	1
Cracticus quoyi	*Cracticus nigrogularis*	1	0	0	1

are generally able to learn to modify this rate based on habitat (e.g., Hunter and Krebs 1979), whereas it is more difficult to have an evolutionary response to modify rate (which would be required in species that do not learn their vocalizations). It is also possible that non-oscines repeat units because of their simpler syrinx. Although not discussed here because of the small sample sizes, we also conducted analyses restricted to those species that may learn their vocalizations (parrots, cockatoos, oscines). In this reduced data set we found similar evidence that habitat-influenced bandwidth, but not temporal components.

The observation that birds in open habitats produced higher frequency and greater bandwidth songs, which were more likely to contain overtones, is also consistent with hypotheses about signal structure facilitating auditory distance assessment (Naguib and Wiley 2001). Thus, there is ample opportunity for birds in relatively open habitats to use frequency-dependent attenuation to estimate the distance to the signaler. Because of the limited bandwidth and reduced likelihood of having overtones, forest birds must therefore rely on other cues. Although absolute amplitude may be a problematic cue for ranging (Naguib and Wiley 2001), reverberation may generally be an important cue forest birds use to estimate distance (Richards and Wiley 1980; Morton 1986).

In conclusion, our results provide only limited support for the hypothesis that birds living in densely forested habitats have experienced directional selection against producing high-frequency vocalizations. Importantly, we found no support for the hypothesis that the habitat effected temporal characteristics of song. Playback studies are required to determine whether in fact song from open habitats is better transmitted in the open than in closed habitat. Results from previous playback studies testing the AAH are equivocal (e.g., Lemon et al. 1981; Fotheringham et al. 1997; Daniel and Blumstein 1998). Nonetheless, our results suggest that, for at least birds, the AAH can generally explain differences in bandwidth.

Acknowledgements We thank Janice Daniel, Doug Nelson, and two anonymous reviewers for constructive comments on a previous version of this manuscript. We thank the UCLA Division of Life Sciences and the Lida Scott Brown Endowment for support of this research.

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