

Determinants of Male Spacing Behaviour in *Panacanthus pallicornis* (Orthoptera: Tettigoniidae)

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Abstract

Panacanthus pallicornis is a neotropical species of katydid endemic to Colombia that inhabits premontane forests, and individuals are found in regenerating (RF) and dense forest (DF) habitats. Members of this species are made conspicuous by their colouration, remarkable defensive body thorns and the loud mating calls of the males. Through capture, marking, and recapture, we determined singing-site characteristics in two different natural habitats: an RF and a DF. Using nearest neighbour analysis, we found male distribution tends to uniformity in forest habitats, but in the RF, male distribution is more random. Males also showed preference for high singing sites and these were correlated with host plant height. Although host plants in DF were taller than those in the RF, male's perch preference was independent from the habitat; and in RF, males select lower perches. To investigate if male spacing was a function of the calling song, we manipulated two groups of males from a different population, one group deafened (tympanic membranes torn), and another control group with tympanic membranes intact. Insects were released from a single location in the two different zones of similar area. After a number of days we measured male displacement, and found that the deafened group distribution tended to aggregation, while the control group spread throughout the experimental zone with a random distribution. These results suggest that male spacing behaviour is one of the functions of the calling song. Based on a pre-established phylogenetic framework of the genus *Panacanthus*, we discuss some implications for the evolution of the calling song of *P. pallicornis* in both RF and DF.

Introduction

Acoustic signals produced by different animal species may vary as a result of environmental conditions: vegetation, the presence of another species, or population density (Riede 1996). Similarly, in an agonistic context, the distance between individuals is a factor that affects the production and reception of sound (Latimer & Schanral 1986). For this reason, in those species in which acoustic communication is impor-

tant, individual spatial distribution is of considerable ecological significance (Rohlf 1978; Southwood 1980) and can be an indirect tool to determine the relations between individuals and the environment (Ludwig & Reynolds 1988).

Acoustic communication is common in some species of Orthoptera, in which the male produces calling songs to attract a mate. Males can use acoustic signals to announce their presence to other males (Gwynne 1977). Spatial distribution of a single male

can be maintained by sound as other males react to it (Gerhardt & Huber 2002; Greenfield 2002). Thus, calling songs of the involved males results in rivalry and males establish space and territory. Calling songs have the function of long range communication (Robinson & Hall 2002) and therefore may convey information about a male's location (Latimer & Schantral 1986), which can be used by both female and male conspecifics.

In some Aridoidea habitat use depends on many biotic and abiotic factors such as vegetal structure, which influence other microclimatic factors (Anderson 1964; Joern 1982). Studies involving plant height, density and ground cover, indicate that all the aspects of the plant's assembly, affect the Aridoidea's community structure (Anderson 1964; Joern 1982). In this respect, few ecological studies have been performed on Tettigoniidae in tropical areas. A few studies have related the distribution of individuals and song production in some *Ensifera* spp., these, mostly, have been performed in temperate zones (Cade 1979; Meixner & Shaw 1979; Shaw et al. 1982; Greenfield 1983; Simmons 1988).

In this paper we study the distribution of singing males of *Panacanthus pallicornis* (Walker 1869) in their natural habitat. Our main hypothesis is that a function of the male's calling song is male spacing behaviour. If male spacing depends on calling song, a group of deafened males will distribute differently from a group of normal or intact males. Finally, as *P. pallicornis* inhabits in regenerating (open; RF) and dense forests (DF) which might have considerable effects in sound propagation, spatial distribution of males should be different in both environments.

Panacanthus pallicornis is a nocturnal species, inhabiting premontane forests (Montealegre-Z 1997). It is endemic to Colombia with a broad distribution in the Western Mountain range, especially on the natural reserve of Yotoco and forested areas of Bitaco (Montealegre-Z & Morris 2004). Males are robust and brachypterous, and present low vagility. They are very abundant and start singing at about 1800 h, performing continuously until approximately 0400; their calling song is the most conspicuous sound at night in their habitat (Chamorro-R et al. 2005). In the laboratory, adult males do not actively feed, consume less food than females, and exhibit high longevity (approx. 14 mo). In nature, males have been observed feeding on small fallen rotten flowers or debris accumulated by the drops of rain on the leaves.

Acoustic signals are given in bouts of several calls, during which male acoustic interactions occur in an

alternated chorus (Montealegre-Z & Morris 2004) (Fig. 1a, b). The spectrum of a call is complex with a dominant fundamental frequency (f_D) near 5 kHz and several higher harmonic components masked within a noisy band (usually 13–29 kHz) (Fig. 1c). Therefore, the calling song exhibits two components: a resonant part (the 5-kHz peak) and a non-resonant part (the 15–16-kHz band). The mean (\bar{x}) intensity of the song is approx. 97.6 dB at 10 cm dorsal (Montealegre-Z & Mason 2005). Sounds produced by resonance are also called pure tones, tonal or musical, and are said to have high-Q values (Bennet-Clark 1989). Q is the quality factor and measures a resonant system's internal to external damping (Prestwich & O'Sullivan 2005).

Methods

Study in Natural Populations

Study site

Field work was performed at several sites in the Vereda Chicoral (N03°33'59", W076°35'41"), Bitaco, La Cumbre, Valle del Cauca (Colombia). The zone encompasses altitudes between 1600 and 2100 m and is characterized as low montane humid forest and premontane humid forest. The average temperature varies between 14 and 19°C, and the average annual precipitation from 2000 to 3000 mm³, with 75–80% of relative humidity (IGAC 1996).

Spatial distribution of *P. pallicornis* males in natural populations was studied at four sites varying in plant cover: two disturbed RF and two (relatively cluttered) DF (RF I and II; and DF I and II). Size and vegetal cover of the sites were determined through the transect method (Matteuci & Colma 1982). RF exhibited more homogeneous vegetation because of the recurring introduction and use of ornamental plants (mostly Heliconiaceae and Marantaceae). RF I and II had extended areas of 5755 m² (with 62% of vegetal cover); and 18165 m² (44% with of vegetal cover), respectively. DF were secondary-growth fragments of wild plants, native in most cases. Both DF had a vegetal cover of 95%, but different areas, DF I = 6052 m², and DF II = 3859 m². Vegetation density was conspicuously lower in RF than in DF.

Mark – recapture

From 18 Oct. 2002 to 4 Mar. 2003, two to four samplings on successive nights were performed every 10 d in all four zones. In total every zone included seven sampling events, except for RF II which was

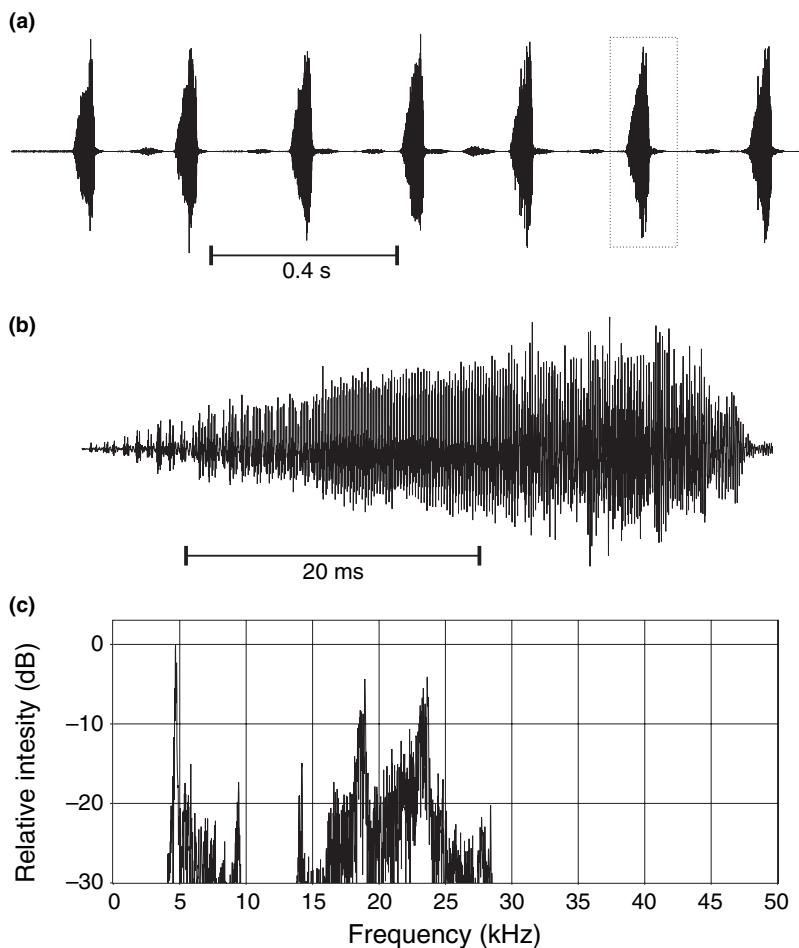


Fig. 1: Calling song features of *Panacanthus pallicornis*. (a) Sequence of seven songs. (b) High resolution of the sixth pulse shown in (a). (c) Spectrogram of the song in (b). Note the two components of the spectrum: the narrow-band peak at approx. 5 kHz (resonant part), and the broadband (non-resonant part) of approx. 15 kHz in width.

sampled only six times. Between 1830 and 0200 h, every singing male of *P. pallicornis* was captured, marked, and released back to its capture site. Pre-capture males were noted as recapture and released again to its last singing site (Southwood 1980). Each male was marked with Paper Mate's liquid paper (Cade 1979; Dixon & Cade 1986), a number was painted on the radial field of the left tegmina [which is acoustically damped to sound and do not effect in the sound radiated (Montealegre-Z 2005) and disappears from the animal cuticle after several weeks]. Numeration was consecutive for all captured males.

Every singing site (host plant or perch) and male position were marked with the corresponding male number and the capture or recapture date using a yellow plastic tape. Height of the male on the plant, as well as taxonomic information and height of the plant were noted. For recaptured males, displacement was measured from the previous capture location. Following marking, each male was returned to its capture site. Localization of individuals was facil-

tated by drawing a different map of male distribution every sampling date. A Lensitac compass and a 10-m tape rule decametre were used to map every zone using a pre-established method (Wyld & Manthey 2001).

Experimental Population

Study site

Experiments were conducted at Reserva Forestal Bosque de Yotoco. Forest preserve of low premontane humid forest ($N03^{\circ}52'$, $W76^{\circ}23'$; 1400–1600 m elevation) on the eastern slope of the western cordillera in the Departamento Valle, the village Yotoco is the nearest settlement. Annual rainfall is 1000–2000 mm³, and humidity ranges between 75% and 80% (Montealegre-Z & Morris 2004).

An improved version of the method proposed by Thiele & Bailey (1980) was used to study male spacing. A flat open area was divided into two square zones (45 × 45 m, Figs 2 and 3), separated by a

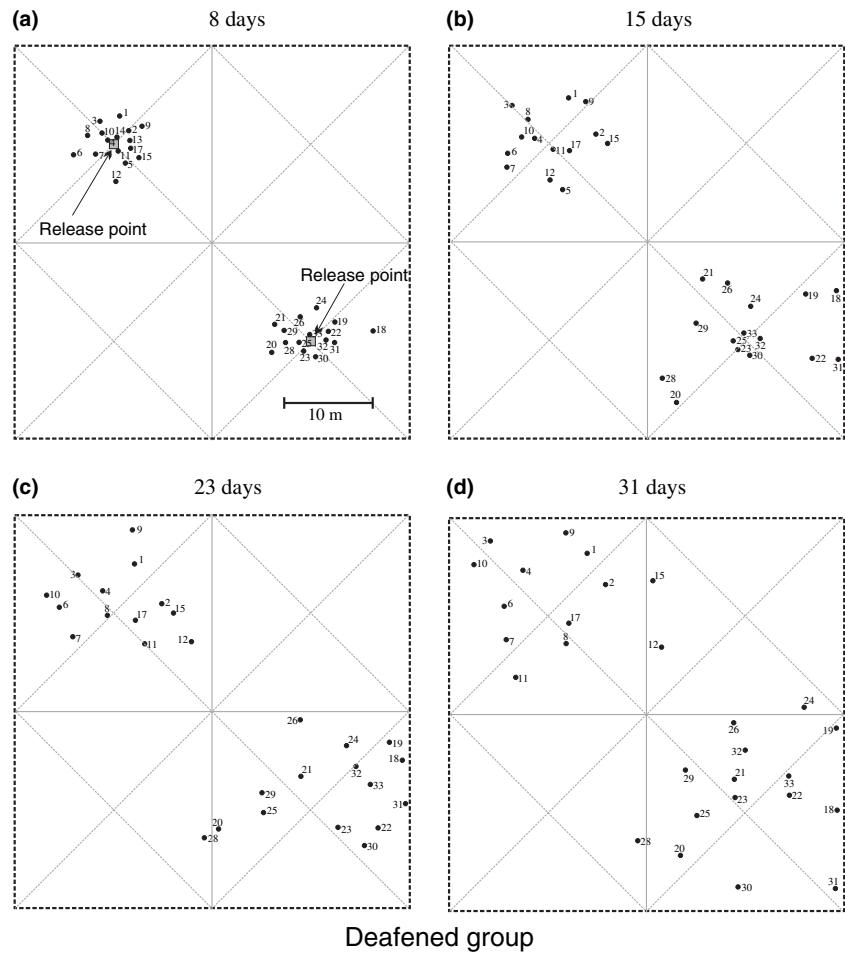


Fig. 2: Deafened males (experimental population). (a) Two groups, each of 16 and 17 males with their tympana torn, were released at the two locations indicated. (b-d) Inter-male distances and male movements measured and mapped over the following 4 wk. Six males went unrecovered during the experiment. Surrounding dashed line indicates mown periphery.

distance of 6 m. Both zones were similar in vegetal structure: growing forest with no plants higher than 1.2 m, dominated mostly by herbs and shrubs [e.g. *Codiaeum* sp. (Euphorbiaceae), *Abarema* sp. (Fabaceae)] dense enough that the plants' branches are intermingled.

Boundaries around each zone were created by cutting down some of the vegetation on the perimeter. Individuals were discouraged from dispersing beyond these experimental zones, and will probably not descend to ground and walk away as their body structure makes them poor jumpers (Montealegre-Z & Morris 2004). Every zone was divided into four quadrants with bisecting diagonals demarcated with thin plastic cords (Figs 2 and 3). The centres of the two adjacent quadrants were chosen as the release loci.

When applicable, experimental zones were first totally cleared of resident males by removing detected singers. A group of 33 males, in most cases collected from a different locale, was marked and all

four of each male's ear tympana torn with an entomological pin (No. 0). Specimens were finger-held under a microscope, legs extended, and pushed against a flat foam surface: this evoked grasping and biting of the substrate by the struggling insect. A pin tip bent to form a hook, and sterilized with heat was used to quickly pierce the two tympanic membranes of each foreleg. Marking consisted of a small number (see marking in natural populations), and a piece (4 × 4 mm) of reflective tape (8850 retro-reflective tape, 3M Co, distributed by Motion Lab Systems Inc., Baton Rouge, LA, USA) was placed on the pronotal metazona. The reflective tape permitted fast nocturnal localization of the specimen (torch-light reflects well from the tape) in the event a male was not locatable by sound (in case the process of tearing their tympanic membranes had affected the singing activity). Males were released, in two groups (of 17 and 16 individuals each), at each different loci. Individuals were mostly released in the foliage of the same plant.

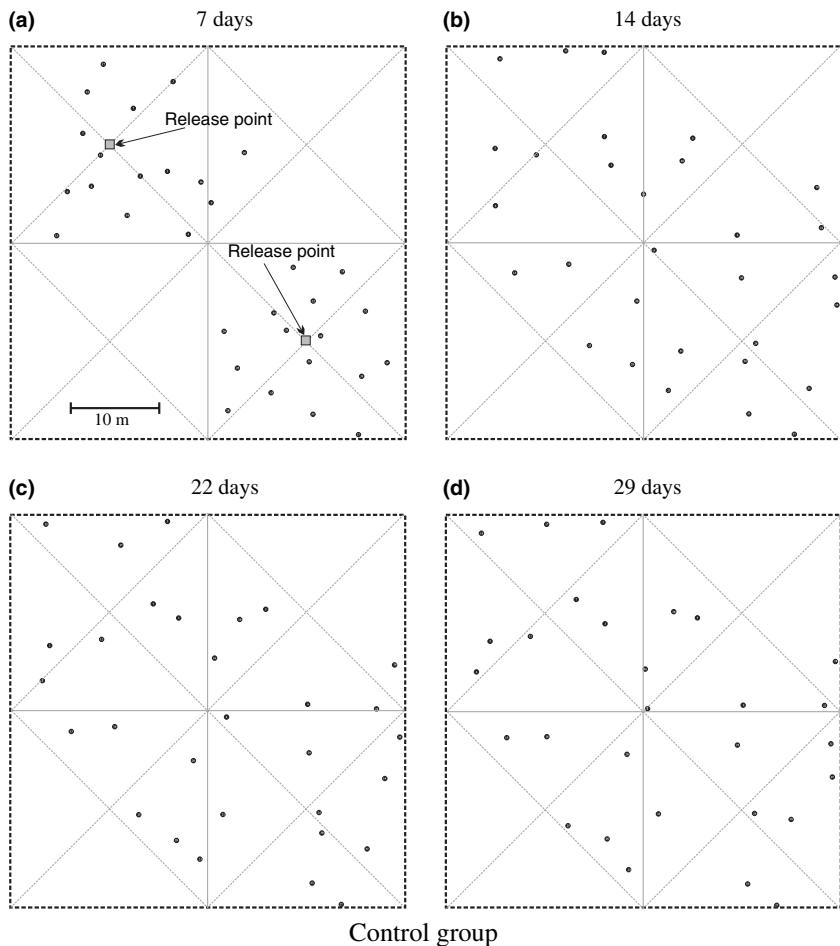


Fig. 3: Intact males (experimental population). (a) Two groups, each of 16 and 17 males with their tympana intact, were released at the two locations indicated. (b-d) Inter-male distances and male movements measured and mapped over the following 4 wk. Four males went unrecovered during the experiment. Surrounding dashed line indicates mown periphery.

Another group of 33 males was used as a control, they were similarly marked, but their tympana left intact. These males were released in another zone of similar vegetal structure and area, using the method explained before. Every 7 d each experimental zone was sampled at night. All singers were localized and identified and each perch marked by a stake. The next day from each release loci, using a compass and a 10-m tape rule, we obtained distances and bearings that helped us to construct a map (Figs 2 and 3). Inter-male nearest neighbour distances used were measured directly between stakes, but were also corroborated from the map.

The flat topography of both experimental zones, and the relative short plant substrate, permitted to approach the male distribution analysis in a two-dimensional model (see next). Maps of natural populations were only used for facilitating individual locations; they were not used in the analysis because the vegetation height and topography of the sampled zones causes a more complex spatial distribution of

individuals, which may require complicated mathematical models (Southwood 1980).

Statistical Analysis

Natural population

The general distribution of free-living males in RF and DF habitats was studied using classical nearest neighbour analysis (NNM) (Clark & Evans 1954). We took into consideration the later modifications by the same authors (Clark & Evans 1979) to account for three-dimensional sampling places. Each site was considered as a volume (using as height to calculate volume, the \bar{x} value of plant height). The Clark and Evan's index R represents the type of distribution, between regular and clumped, exhibited by a group of individuals. R establishes a test statistics to determine the type of distribution of a group of individuals with respect to each other; with values ranging from 0 to 2.1491. Values less than 1 indicate an aggregated population, values equal to 1 suggests

randomness, and those greater than 1 indicate a regular distribution. A significance test (two-tailed) was performed on the value of R under the hypothesis: *P. pallicornis* males exhibit a random distribution. For comparative purposes, R values for both types of habitat, and their respective replicates, were compared in a two-way ANOVA.

To detect any difference between nearest neighbour distances in both habitats, a two-factor ANOVA with repeated measures was conducted. To investigate any preference of males for a particular host plant species, a simple correlation was performed between the number of individuals and the number of host plant species occupied. The relationship between perch height and plant height was first analysed using ANCOVA. The model considered the perch height as dependent variable, type of habitat as factor, and the plant's height as covariate. The residuals of this analysis were then tested for normality. A regression analysis of perch height on plant height was then conducted. We also regressed perch height (measured from the top of the plant) on plant height. Male displacement over time was analysed using a two-factor ANOVA with repeated measures, nesting the two replicates of each environment (RF and DF), respectively. Non-parametric tests (e.g. chi-squared test) were conducted to study the relation between number and density of individuals and the type of habitat. We report the chi-squared value, df, and the appropriate p-value.

Experimental population

One problem arising with NNM is that R is biased by an edge effect. This is because individuals situated near the edge tend to have greater neighbour distances than those in the centre of the area under study: neighbours lying outside the plots are not considered (Fröhlich & Quednau 1995). Some authors have suggested corrections for this problem, and Fröhlich & Quednau (1995) point out the useful approach of Donnelly (1978). Donnelly found corrections for expectation and variance of nearest neighbour distances stemming from finite areas (for details, see Fröhlich & Quednau 1995). We based our analysis of experimental populations on Clark & Evans (1954) method, but also used Donnelly's (1978) correction.

The NNM requires a normal distribution of the data (Sokal & Rohlf 1969). There are some methods that may also provide information about spatial distribution, one of them is the I δ Morisita's Index of Dispersion (MID), which is relatively independent of

quadrant size (Brower & Zar 1984). MID was used by Thiele & Bailey (1980), and chosen for the present study. We divided each zone into four quadrants and monitored male distribution during all sampling dates as mentioned before. Details of calculations can be obtained from Thiele & Bailey (1980).

The purpose of using three different approaches for estimation of spatial distribution in our experimental population is simply to compliment the analysis carried out in natural populations, which might be, in certain ways, biased by the problems discussed before. It is not our intention to compare the statistical methods. All statistical analyses were performed using R software (v2.4.0, <http://www.r-project.org>).

Results

Natural Populations

Capture, marking, and recapture

One hundred and seventy-eight males were captured and marked during 31 sampling events (nights). Approximately 70% of the captures and recaptures were performed from one to three times. The number of individuals is affected by the type of the habitat ($\chi^2_{(3)} = 11.89$, $p < 0.01$), being higher in RF. However, male density was similar between the habitats ($\chi^2_{(3)} = 0.0008126$, $p > 0.05$), but (\bar{x}) density was higher in DF.

Spatial distribution in males of natural populations

R-values were significantly lower for the RF than for the DF habitats ($F_{(1,23)} = 82.05$, $p < 0.01$; see Table 1). A significant departure from randomness (in the direction of spatial uniformity), occurs in DF, while in RF male distribution tends to randomness. In only one of the measurements (DF I) a slight departure from regularity to randomness was observed (Table 1). The type of habitat did not show a significant effect ($F_{(2,992)} = 0.675$, $p > 0.05$), which suggests that the mean nearest neighbour distances were similar in RF and DF.

Vertical distribution

The total distribution ranges are illustrated in Table 2. The lowest observed heights chosen by *P. pallicornis* occurred in RF (0.3–4.50 m); while in DF males have a broader range (0.4–7.0 m). When comparing both habitats, the ANCOVA suggests that the covariate (plant height) significantly predicts male's perch height ($F_{(1)} = 213.914$, $p < 0.01$); the

Table 1: Analysis of mean nearest neighbour distances (NND) for individuals in two types of habitats of natural populations: a regenerating and a dense forest

Habitat	Date	Area (m ²)	n	Male density	Expected NND (m)	Observed NND (m)	R	c	p	Distribution
Regenerating forest I	18/10/2002	5755	48	0.00139	4.964	5.182*	1.044	0.121	>0.05	Random
	19/10/2002	5755	48	0.00139	4.964	5.225*	1.053	0.145	>0.05	Random
	20/10/2002	5755	48	0.00139	4.964	4.977*	1.003	0.007	>0.05	Random
	21/10/2002	5755	48	0.00139	4.964	4.977	1.003	0.007	>0.05	Random
	2/11/2002	5755	48	0.00139	4.964	5.026*	1.013	0.034	>0.05	Random
	3/11/2002	5755	48	0.00139	4.964	5.178	1.043	0.119	>0.05	Random
	4/11/2002	5755	48	0.00139	4.964	5.203*	1.048	0.133	>0.05	Random
Regenerating forest II	24/01/2003	18 161	62	0.00085	5.840	5.277*	0.9	0.265	>0.05	Random
	26/01/2003	18 161	62	0.00085	5.840	5.149*	0.88	0.325	>0.05	Random
	27/01/2003	18 161	62	0.00085	5.840	5.306*	0.92	0.224	>0.05	Random
	07/02/2003	18 161	62	0.00085	5.840	5.162*	0.88	0.319	>0.05	Random
	08/02/2003	18 161	62	0.00085	5.840	5.079	0.87	0.359	>0.05	Random
	10/02/2003	18 161	62	0.00085	5.840	5.302*	0.91	0.254	>0.05	Random
	16/11/2002	6052	45	0.00135	5.012	5.841*	1.164	1.641	<0.05	Regular
Dense forest I	17/11/2002	6052	45	0.00135	5.012	5.841*	1.164	1.641	<0.05	Regular
	30/11/2002	6052	45	0.00135	5.012	5.881*	1.172	1.72	<0.05	Regular
	01/12/2002	6052	45	0.00135	5.012	5.988*	1.194	1.935	<0.05	Regular
	18/01/2003	6052	45	0.00135	5.012	5.949*	1.186	1.856	<0.05	Regular
	20/01/2003	6052	45	0.00135	5.012	5.696	1.135	1.353	>0.05	Random, regular
	21/01/2003	6052	45	0.00135	5.012	5.502*	1.097	0.965	>0.05	Random
	04/03/2003	3859	30	0.00137	4.988	6.683	1.339	2.96	<0.05	Regular
Dense forest II	05/03/2003	3859	30	0.00137	4.988	6.606	1.323	2.825	<0.05	Regular
	07/03/2003	3859	30	0.00137	4.988	6.363*	1.275	2.401	<0.05	Regular
	18/03/2003	3859	30	0.00137	4.988	6.106*	1.223	1.951	<0.05	Regular
	19/03/2003	3859	30	0.00137	4.988	6.199*	1.242	2.114	<0.05	Regular
	20/03/2003	3859	30	0.00137	4.988	6.180*	1.238	2.081	<0.05	Regular
	21/03/2003	3859	30	0.00137	4.988	6.191*	1.240	2.100	<0.05	Regular

c, standardized normal variate; density, number of males/volume. Asterisk shows normally distributed data.

Table 2: Ranges for *Panacanthus pallicornis* male heights on host plants in a natural population pooled across all sampling days

Site	Perch height on host plants (m)				
	n	Mean	SD	Minimum	Maximum
Regenerating forest I	46	1.50	0.90	0.30	3.50
Regenerating forest II	56	1.82	1.82	0.30	4.50
Dense forest I	41	2.33	1.29	0.40	7.00
Dense forest II	27	2.93	0.98	1.50	5.00

residuals of this analysis behave normally ($K-S_{(171)} = 0.042$, $p > 0.05$). Male perch is therefore influenced by plant height; the taller the host plant, the higher the perch chosen by a male associated with the plant. There was a positive correlation between the host plant's height and the height of the male's perch ($R = 0.757$, $p < 0.01$). But, significant differences were found between the heights of the plants in both habitats: host plants in the forest are significantly higher than those in the RF ($t_{(68)} = -2.4$, $p < 0.05$; Fig. 4b). Also the heights of

perches in the forest were higher ($t_{(68)} = -5.45$, $p < 0.01$). To remove the effect of possible confounds (Field 2005), we obtained the residuals of the relation habitat–plant height, and those of habitat–perch height, and conducted a regression analysis with them. The regression is still highly significant ($F_{(1,1)} = 215.2$, $p << 0.01$). Therefore, a singing perch chosen by a male depends on the height of its host plant (Fig. 4). But there was an overall tendency in males from RF to perch at lower heights (Fig. 4a). A highly significant correlation also occurs between perch height (measured from the top of the tree) and plant height; i.e. on taller plants males withdraw further from the plant top (Fig. 4b).

Host plant type

There is a positive correlation between the number of males (nm) and the number of host plants (np) species occupied by males ($nm = 0.3 np$, $R^2 = 0.98$, $p < 0.05$). This suggests that males do not specialize on a particular plant species.

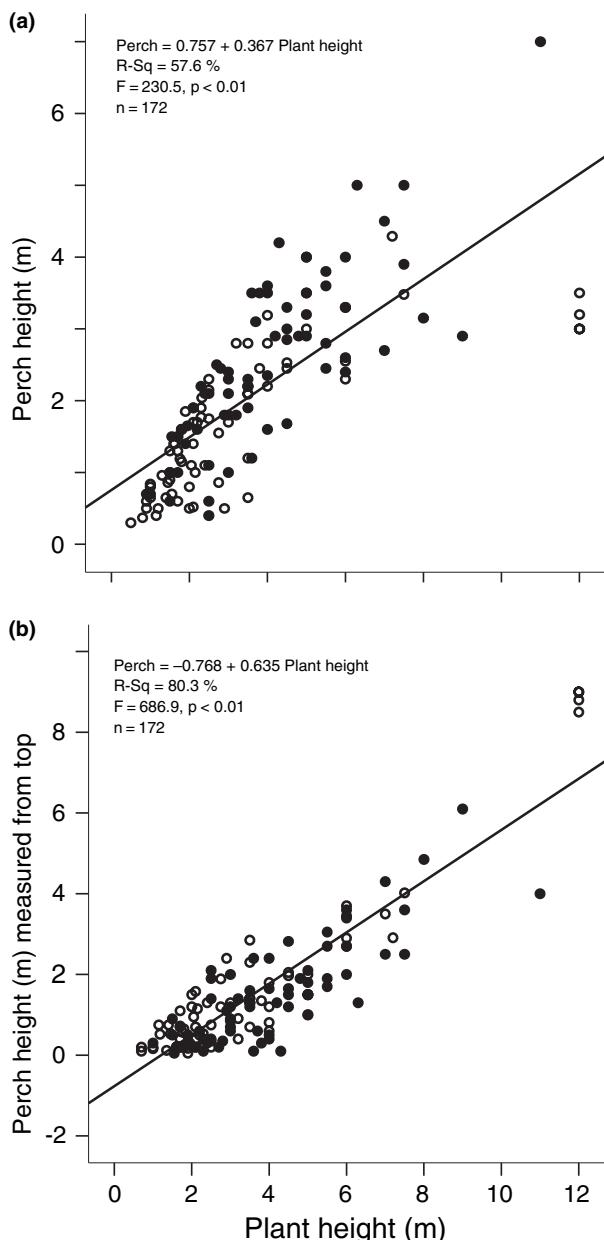


Fig. 4: A scatterplot showing the correlation between plant height and singing place chosen by males. (a) Regression of perch height (as measured from the ground) on plant height. Note that in regenerating forest (RF), males tend to perch at lower heights than in the forest. (b) Regression of perch height (as measured from the top of the plant) on plant height. The smoothing line is included only to emphasize the relationship between the two variables. Black circles represent dense forest (DF) specimens; open circles those of RF.

Displacement and singing site

Males exhibited some displacement from their original perches during several days of sampling ($F_{(3,922)} = 3.87, p < 0.01$). Their displacement was

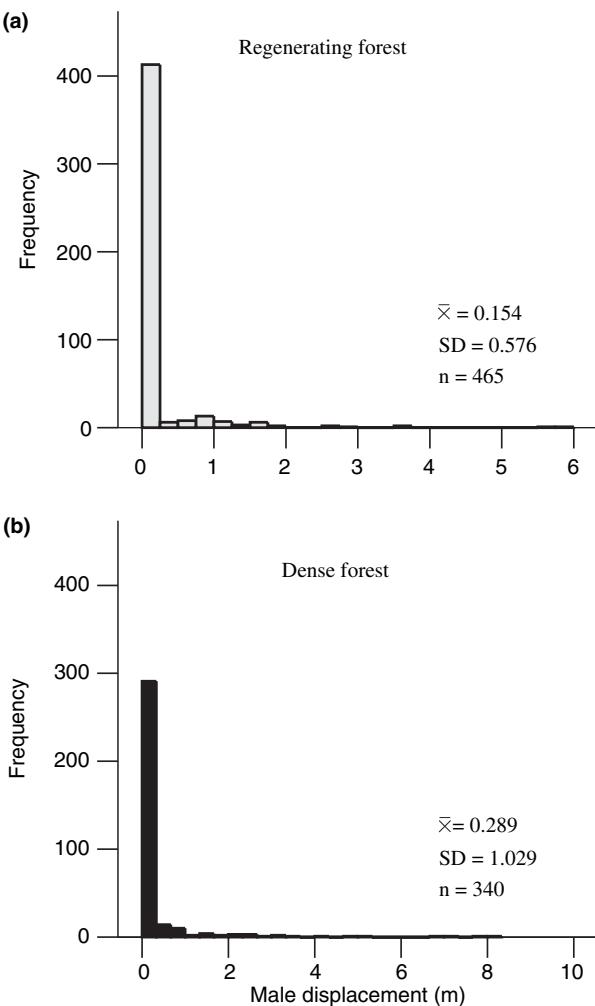


Fig. 5: Male displacement over time. The frequency distribution of male displacement in regenerating (a) and dense forests (b) pooled across all sampling dates. Note that male movements are strongly reduced in both groups.

similar between the replicates of each habitat ($F_{(3,922)} = 0.39, p > 0.05$), but different between habitats ($F_{(3,92)} = 3.50, p < 0.01$). In general, (\bar{x}) travelled distances were relatively short in both habitats ($DF = 0.28 \pm 0.05$; RF = 0.242 ± 0.04) (Fig. 5); and males of *P. pallicornis* exhibit a remarkable loyalty to their singing places.

Experimental Population

About 85–87% of the deafened specimens were later recaptured by making use of their loud calling to localize their position: this is consistent with singing activity being unaffected by the tearing of the tympanic membranes.

Clark & Evans (1954) NNM (original version)

Data obtained from experimental animals are presented in Table 3. The number of males released in each experimental site gradually changed across all days of sampling. Such a reduction in the number of individuals would have only a modest effect on the density. The control group was always associated with R-values > 1.7 , and male distribution departed significantly from the random expectation in the direction of regularity. Conversely, and except for the last day of sampling, the group of deafened males exhibited a random pattern of distribution (they retained some clumping from their original release). Thirty-one days after these males' initial release, the R-value increased to 1.7, suggesting a departure from randomness to uniformity (Table 3). After both 28 and 31 d post-release, it was still possible to distinguish both groups of deafened males (Fig. 2), while dispersion was faster and higher for the control group, making it impossible to distinguish between sub-groups after the second day of sampling (Fig. 3). Except for the last sampling event, (\bar{x}) nearest neighbour distances were significantly shorter for the group of deafened males (Fig. 6). Note that in Fig. 6, outliers and extremes are present, especially for the control groups (sampling event 4), indicating that the sampled population is not normal. Therefore, the box plots' whiskers do not extend to the minimum and maximum of the sample, but rather to the smallest and largest values within a reasonable distance from the end of the box.

Donnelly's (1978) correction to the NNM

Although Fig. 2 suggests that the group of deafened males exhibit some degree of clumping during all sampling events, calculation of the Clark–Evans index of dispersion did not support the hypothesis of clumping. Donnelly's (1978) correction for r_e and σ_{r_e} in finite areas more closely approached the mapped patterns (Figs 2 and 3), and yielded greater resolution than did Clark & Evans (1954) procedure. The control group exhibited change in the pattern of distribution from aggregated to regular to random. In contrast, the distribution pattern of the group of deafened males was consistently aggregated with a significant departure from randomness (Table 3).

Morisita's Index of Dispersion

The MID shows those males in the control group gradually dispersed, maintaining an aggregated

Table 3: Analysis of mean nearest neighbour distances (NND) in the two groups of the experimental population. Males of each group (deafened and control) were released in each experimental area at the same time on 16 Apr. 2001

Clark & Evans (1954) Method										Donnelly (1978) corrections for expectation and variance					
Treatment	Date	Area (m ²)	n	Density	Expected NND	Observed NND	R	c	p	Distribution	Expected NND	R	c	p	Distribution
Control	23/04/2001 (7 d)	2025	32	0.013	2.35 ± 0.85	4.07 ± 1.12*	1.74	-2.02	<0.05	Regular	4.34 ± 0.02	0.94	4.72	<<0.01	Aggregated
	30/04/2001 (14 d)	2025	30	0.012	2.40 ± 0.87	4.80 ± 1.29*	2.00	-2.76	<0.01	Regular	4.50 ± 0.01	1.07	-4.41	<<0.01	Regular
	08/05/2001 (22 d)	2025	30	0.012	2.40 ± 0.87	4.75 ± 1.40*	1.98	-2.70	<0.01	Regular	4.50 ± 0.01	1.05	-3.65	<<0.01	Regular
	14/05/2001 (28 d)	2025	29	0.012	2.42 ± 0.88	4.66 ± 1.06	1.92	-2.54	<0.01	Regular	4.58 ± 0.01	1.017	-1.07	>0.05	Random
	24/04/2001 (8 d)	2025	31	0.013	2.37 ± 0.86	1.58 ± 0.70	0.665	0.92	>0.05	Random	4.42 ± 0.06	0.36	45.66	<<0.01	Aggregated
	01/05/2001 (15 d)	2025	29	0.012	2.45 ± 0.89	2.28 ± 0.87*	0.94	0.17	>0.05	Random	4.67 ± 0.08	0.49	29.83	<<0.01	Aggregated
Deafened	09/05/2001 (23 d)	2025	27	0.011	2.48 ± 0.90	3.13 ± 1.08*	1.259	-0.71	>0.05	Random	4.77 ± 0.09	0.66	18.67	<<0.01	Aggregated
	17/05/2001 (31 d)	2025	27	0.011	2.48 ± 0.90	4.27 ± 1.77*	1.718	-1.98	<0.05	Regular	4.77 ± 0.09	0.89	5.72	<<0.01	Aggregated

c, standardized normal variate. Asterisk shows normally distributed data. Data analysed by standard and corrected version of Clark & Evans's method.

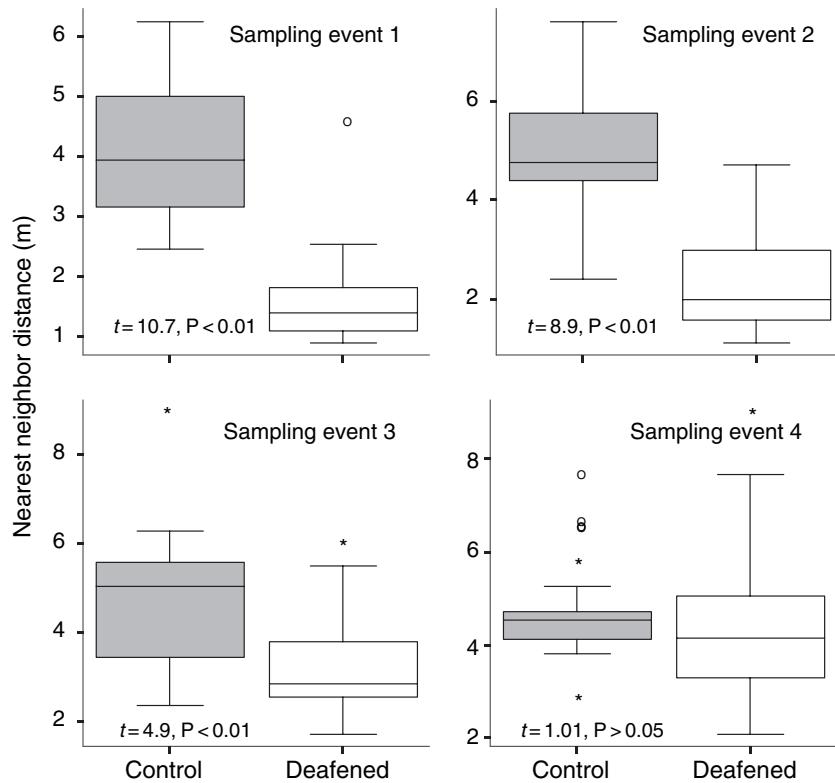


Fig. 6: Mean nearest neighbour distance in experimental animals. Inter-male distances were always significantly shorter in the group of males with mutilated tympana (except for the last sampling event). The line across the box shows where the sample is centred. Whiskers indicate the minimum and maximum data values; asterisks represent extreme values; and open circles represent outliers.

pattern over the first 7 d of sampling, while organizing randomly after 14 d post-release. The deafened group, however, exhibited a significant aggregated distribution across the sampling period, which contrasts with the regular pattern exhibited when the data were analysed with the NNM. However, this analysis agrees with the distribution pattern obtained by applying Donnelly's (1978) correction to the NNM (see Table 4), and also coincides with the patterns of distribution observed in natural populations of RF.

Discussion

Low Vagility and Host Plants

Although the spatial distribution of *P. pallicornis* males is not determined by host plant species, the availability of perches affects their distribution. Their sedentary behaviour, coupled with these insects' longevity, made this species especially suitable for our study.

Remarkable perch fidelity, as exhibited by *P. pallicornis* males (Fig. 5), has been observed in other katydids (Greenfield 1983) and some crickets (Mhatre & Balakrishnan 2006) and seems to offer some

Table 4: Analysis of male spatial distribution in experimental populations of *Panacanthus pallicornis* using the Morisita's Index of Dispersion

	Date	$I\delta$	F	p	Distribution
Control	23/04/2001 (7 d)	1.710	8.333	<< 0.01	Aggregated
	30/04/2001 (14 d)	0.984	0.844	> 0.05	Random
	08/05/2001 (22 d)	0.864	0.311	> 0.05	Random
	14/05/2001 (28 d)	0.837	0.517	> 0.05	Random
Deafened	24/04/2001 (8 d)	1.76	8.60	<< 0.01	Aggregated
	01/05/2001 (15 d)	2.07	11.02	<< 0.01	Aggregated
	09/05/2001 (23 d)	1.93	9.02	<< 0.01	Aggregated
	17/05/2001 (31 d)	1.55	5.77	< 0.01	Aggregated

advantages for a female in the choice of a mate. She could exercise a preference for a certain male of high quality and should be able to find him again for subsequent matings; but this is possible only if the male remains constant in his singing place (Mhatre & Balakrishnan 2006).

Spatial Distribution

Our results show that deafened experimental males could not regulate their distance from other singing males, which suggests that male spacing is one of

the functions of the calling song. Males depend on their neighbours' calling song to establish their singing places and inter-male distances as observed in *Mygalopsis marki* by Thiele & Bailey (1980).

We used three different approaches to study male distribution: NNM, a corrected version of the NNM for finite areas, and the MID. The analysis of experimental populations data using the original version of Clark & Evans (1954) NNM, and the corrected version of the same method (Donnelly 1978) (Table 3), implies biased results of the former method, as noted by other authors (Donnelly 1978; Thiele & Bailey 1980; Fröhlich & Quednau 1995). The corrected version of the NNM gives results more similar to the ones obtained in natural populations: the control group gradually adopted a random distribution. Some individuals of this group migrated, producing the significant clumping demonstrated in Table 3. Therefore, extreme values observed in the control group during sampling event 4, might have had an effect on p-values, creating the similar pattern of distribution between the control and the deafened groups observed in Fig. 6. The gradual regular pattern obtained for the deafened group might be an effect of scale not resolved by Clark & Evans (1954) NNM. For levels of aggregation and scale issues, see Campbell (1990) and Hill (1999).

The MID on the other hand, gave results similar to the ones obtained with the corrected version of the NNM and also supports our studies in RF of natural populations: random distribution.

Distributions of singers can result from plant distribution and/or song-mediated behaviour. The regularity of singers seen in DF could be the result of song-mediated spacing imposed upon an overabundance of usable perch plants. The randomness seen in RF could be the result of a lack of usable perch plants, meaning that males sing where they can and that these perches are randomly distributed. Thus spacing by song to produce regularity does not occur in RF because usable perch density is never achieved. Song is a potential basis for regular spacing, but it is never a basis for random spacing. It is probably plants and their positions that determine the random perching in RF. But in the DF it may be either plant positions or song responses or both that produce regularity.

But male spacing can be affected by another factor. If spatial distribution of *P. pallicornis* males is conditioned by the calling song, habitat characteristics (plant height and foliage) might affect sound propagation, and hence male distribution. Two important observations might support this idea: first,

this species does not depend on specific host plants, and second, both experimental zones represent a clear example of an open regenerating environment with no trees and dense vegetation, in which plants were organized in a more regular spatial pattern (different to the RF in natural habitats). This regularity of plant distribution suggests that the control group could have adopted a regular spatial distribution; nevertheless, they adopted a random pattern instead. Thus, there might not be considerable effect of the physical distribution of trees and branches on the distribution pattern adopted by males. But one ought to interpret these results with caution. The experimental population was monitored for only 30 d. Beyond this period, displacement of individuals might have changed again (Table 3). The experimental zones might have just given these males a substrate to sing from (distinct from places to oviposit, feed, gain refuge to escape diurnal predators, and so on).

When singing is reduced, other forms of communication should come along (Thiele & Bailey 1980; Riede 1987). Experimental deafened males conserved the aggregated pattern over 4 wk, slowly increasing (\bar{x}) inter-male distance (Figs 2 and 6). A deafened male could have detected the presence of other males by vibrations of the substratum (Thiele & Bailey 1980). Some of the acoustic signals might be picked in the form of vibration, as 85–87% of the deafened males were collected by their loud acoustic signals. Loud acoustic signals such as those of *P. pallicornis* will probably produce vibrations in plants within the sound field; collecting by their loud acoustic signals is almost a 'non-sequitur'. Additionally, dispersion of deafened males might occur also as an effect of the distribution of food resources.

Encounters or male fights in *P. pallicornis* were never observed, in either the experimental or the natural population, and males seem to avoid this mechanism. In this species, spacing seems to be established by an intensity-dependent factor or acoustic territory (Morris 1971). Nevertheless, the more random pattern in RF shows that there is an intensity threshold beyond which regular spacing by calling song does not occur (only at high densities does the song space singers).

Acoustic Space and Calling Song

Low frequency signals attenuate less than high frequency because for low frequencies, there are few large echo-producing objects in the signal path. As a

consequence the signal will be transmitted faithfully (Bennet-Clark 1998). Attenuation also increases with the distance of the sender and the receiver and their proximity to the ground (Wiley & Richards 1978). Factors such as temperature, humidity, wind speed, density of vegetation, foliage size, position of sender and receiver, and the carrier frequency of the sound, all determine the degree to which a sound signal is attenuated (Michelsen 1978; Wiley & Richards 1978; Römer & Lewald 1992).

Panacanthus pallicornis descends from an ancestor that used narrow-band calling songs at frequencies higher than 10 kHz (Montealegre-Z & Morris 2004). Based on the habitat of its closest extant relative, one can speculate on the likely acoustic environment of this ancestor. The extant relative, characterized by a higher number of plesiomorphic traits than *P. pallicornis*, is *Panacanthus cuspidatus*. This species inhabits rain forests in the Amazon basin (>29°C, and >90% of relative humidity), and males perch high up in the vegetation strata (5–15 m above the ground) where they sing at 11 kHz using a narrow-frequency band with few harmonic components (Montealegre-Z & Morris 2004). Males do not usually perch in forest clearings or at low heights in the vegetation (being difficult to hunt). The high-Q spectrum (at 11 kHz) of this species should be adapted to these conditions, for transmission in humid DF at some metres below the canopy. Conversely, males of *P. pallicornis* are well adapted to both RF and DF with lower temperature, and have evolved a calling song (with an f_D sharp peak at 5 kHz and a higher 12-kHz band component; Fig. 1) that is expected to transmit well in both environments, even if broadcasted from low heights. Prior to the settlement of humans, the primary forest formation of *P. pallicornis*' habitat would have had natural clearings (RF) that allowed these insects to exploit a different acoustic environment, and adapt the nature of their calling song to these conditions.

Pure tone signals (narrow frequency band) permit greater signal/noise ratios on the reception if emitter and receiver are tuned to the same frequency; and thus extend the range of effective transmission (Wiley & Richards 1978). Broad-spectrum signals, on the other hand, provide a means for the receptor to make binaural comparisons of many frequency components, and thus allow easier localization of the sound source (Konishi 1973a,b). But in contrast to pure tones, broadband signals have a disadvantage for long-range communication. Amplitude modulation patterns with broadband carriers are more effec-

tive in open habitats than are pure tones (Römer & Lewald 1992; Römer 1993).

If excess attenuation is in fact a problem for high frequency transmission, an insect must evolve behavioural strategies and make use of optimal positions in its environment for acoustic signalling (Römer & Lewald 1992). Such an optimal range to broadcast calls in a forest lies at least 1 or 2 m above the ground and somewhere below the canopy (Paul & Walker 1979; Römer & Lewald 1992). The vertical distribution of *P. pallicornis* males was significantly correlated to the plant's height, with a tendency to perch at low heights in RF (Fig. 4a). But in the woods, males were never found singing on or close to the canopy. However, there was strong correlation between perch height (measure from the top of the plant) with plant height. The higher was the perch the higher was the distance between plant top and perch. This observation suggests that males have an upper limit for acceptable perches, i.e. they do not get too far from the ground. This may be because of eavesdropping danger that increases with plant height (Paul & Walker 1979; Arak & Eiriksson 1992), better transmission of sound in lower vegetation levels (Latimer & Sippel 1987; Römer & Lewald 1992), and optimal distances (stem diameters) in relation to substrate signalling to approaching females (Morris et al. 1994). It might also involve avoiding cuckoldry by competitors (Thiele & Bailey 1980; Cade 1981; Campbell 1990).

The low frequency narrow peak at 5 kHz might have been selected for as an adaptation to singing at lower heights (relative to heights used by the species' ancestor) in both RF and DF. Tonal sounds at 5 kHz experience less loss of acoustic energy near the ground and few metres above the ground than higher frequencies (Römer & Lewald 1992). This effect can be observed in other singing insects. Most crickets, e.g. occupy low heights in the vegetation strata (usually close to the ground) and the vast majority use carriers in the range of 2–8 kHz, with a strong emphasis at 5 kHz (Walker & Moore 2002).

The information contained in the high-frequency component of a broadband song will not be available for the receiver except at very short distances (Latimer & Sippel 1987; Römer & Lewald 1992). Thus the 15–16-kHz band of *P. pallicornis*' calling song may function in male spacing, permitting other males to recognize the distance at which a conspecific is singing. This band might have appeared when an ancestor faced new challenging

environments. The harmonic vibrational modes of the sound generator changed to more non-resonant modes, and hence the other components of the stridulatory mechanism (tooth density, wing speed and tooth contact rate) (Montealegre-Z & Mason 2005). Lowering the f_D and masking the harmonic components might have been an adaptation for an environment acoustically less cluttered, which offered a variety of singing places and a lower average temperature. The temperature of the environment has some effect in the evolution of calling songs. For example, some lowland species of the genus *Uchuca*, use resonance in their calling songs (Montealegre-Z et al. 2003), but those inhabiting cloud forests exhibit calling songs with a more broadband nature (Braun 2002).

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