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Geographical variation in acoustic signals of the planthopper, *Nilaparvata bakeri* (Muir), in Asia: species recognition and sexual selection

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Populations of the planthopper *Nilaparvata bakeri* (Muir) were sampled from the Philippines (Luzon), Indonesia (Bali), India (Bihar) and Sri Lanka (Central Province) from the grass *Leersia hexandra* (Schwartz), and cultured in Cardiff. Low intensity vibratory signals produced by males and females during mate location and courtship were recorded and analysed. Obvious differences were found between male calling songs of insects from the Philippines and those from the other three areas. Smaller differences were detected between the Indonesian, Indian and Sri Lankan populations. Hybrids between Philippine and Indonesian, and Indonesian and Sri Lankan, insects were obtained freely in the laboratory. Male calls of F_1 hybrids were variable and intermediate between parentals. Mate choice experiments showed no significant assortative mating between the different populations. There was no indication of reproductive isolation and therefore of different biological species. The assumption that different male calling songs necessarily indicate the presence of different biological species is not confirmed in this example.

ADDITIONAL KEY WORDS:—Hybridization – *Leersia hexandra* – mate choice – speciation – specific mate recognition systems.

CONTENTS

INTRODUCTION

Acoustic signals in insects are widely regarded as good indicators of biological species status (Alexander, 1967). Among the Homoptera it has often been said that sympatric species of cicadas are easily distinguished by clear differences in their songs (Myers, 1929; Claridge, 1985a). Fewer data are available on the

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related leafhoppers and planthoppers which communicate primarily by damped vibratory signals transmitted through the plants on which they live (Claridge, 1985a, b). However, in some genera, species have been identified by-characteristics of both male and female calls. Sometimes they may differ apparently only in rates of repetition of pulses within the signals (Claridge, 1988). Two extreme sibling species, morphologically attributable to the brown planthopper, *Nilaparvata lugens* (Stål), have been recognized in this way (Claridge, den Hollander & Morgan, 1985b, 1988).

Paterson (1985) has advocated a recognition species concept in which species are primarily characterized by unique specific mate recognition systems (SMRS). In planthoppers the associated signals may often be primarily acoustic. An important prediction from Paterson's concept is that SMRSs will be maintained relatively invariant by stabilizing selection across the complete range of a species. Thus not only will there be little variation within populations, but also between spatially separated populations of the same species. That is geographical variation in SMRSs will be extremely limited. Such a prediction is useful because it can be tested. However, a major practical difficulty is that of determining what part of any signal functions as a SMRS. Often it has been assumed that the most constant features necessarily function in this way. Unfortunately this may obviously lead to circular arguments (Claridge, 1988, 1990). Thus in order to identify the relevant aspects of signals, there is no alternative to the experimental investigation of signal function, but this has rarely been done.

For the two host-associated sibling species of brown planthopper, both presently known as *N. lugens*, rates of repetition of pulses from the main sections of both the male and female calls have been demonstrated by playback and similar experiments to play a major role in species recognition (Claridge, den Hollander & Morgan, 1984, 1985b). However, populations of these same species from different parts of Asia and Australasia show geographical variation in just these characteristics (Claridge, den Hollander & Morgan, 1985a, 1988), clearly contrary to Paterson's prediction.

Here we describe geographical variation in calls of the related species, *N. bakeri*, from India, Sri Lanka, Indonesia and the Philippines and discuss the variation in the light of mate choice and hybridization experiments and in terms of the concept of specific mate recognition systems (Paterson, 1985).

Nilaparvata bakeri *populations studied*

Nilaparvata bakeri (Muir) (Fig. 1) is morphologically very closely related to *N. lugens* and differs most obviously in the structure of the male genitalia (Fig. 2) (Wilson & Claridge, 1991). It is widely sympatric with *N. lugens* through large areas of tropical and temperate Asia. In the Philippines it has been recorded as feeding and reproducing only on the grass *Leersia hexandra* Schwartz (Saxena, Velasco & Barrion, 1963). We have recorded it in the Philippines from the same grass together with the *Leersia*-feeding sibling species of *N. lugens* (Claridge & Morgan, 1987).

Saxena *et al.* (1983) recorded laboratory hybridization between *N. bakeri* and *N. lugens*. Despite many efforts using parental populations from a combination of

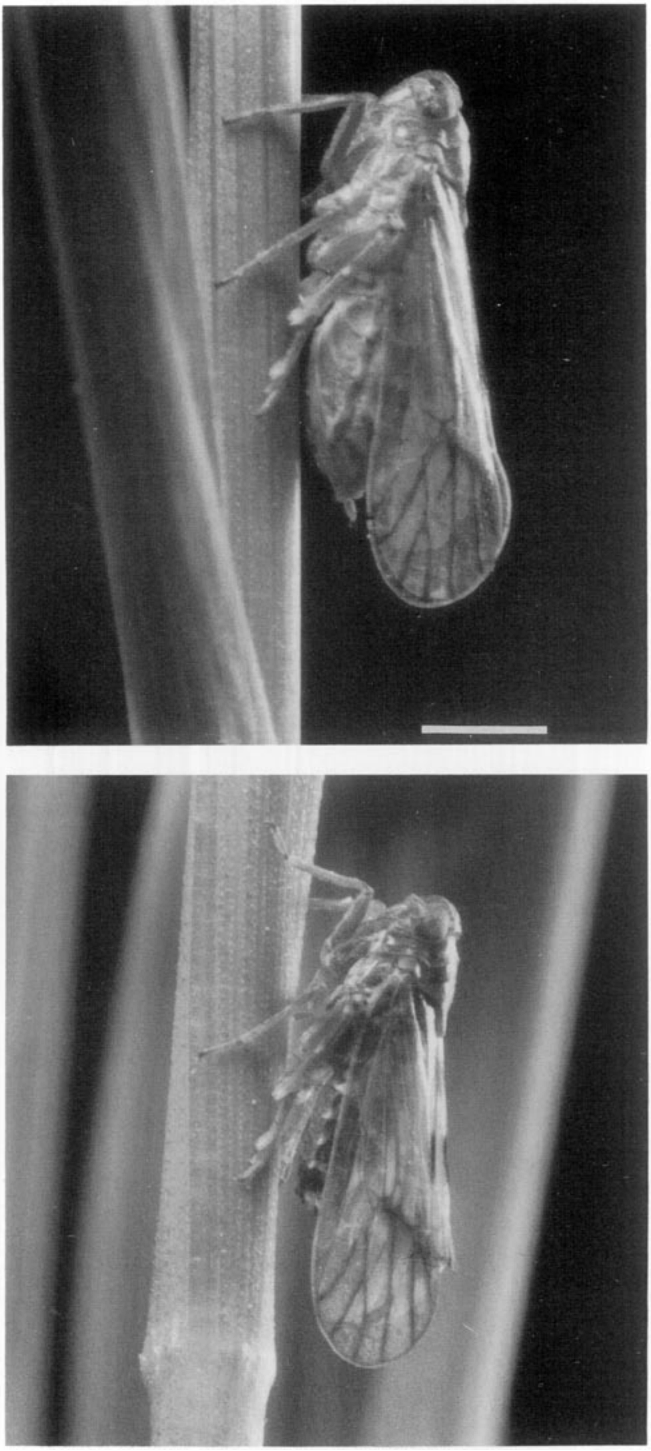

Figure 1. Adult macropterous male (top) and female (bottom) of *Nilaparvata bakeri* on stems of *Leersia hexandra*. Scale line = *c*. 1 mm.

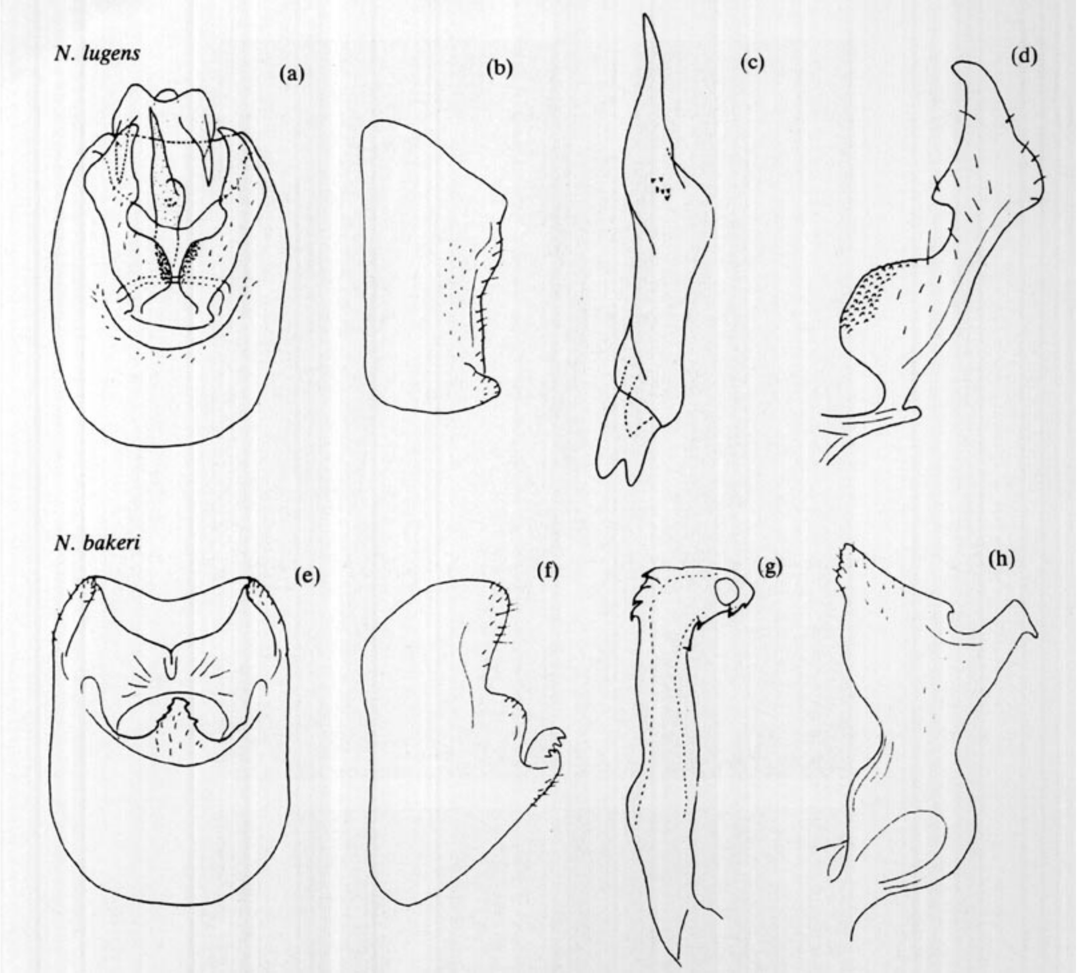

Figure 2. Male genitalia of *Nilaparvata lugens* (a–d) and *N. bakeri* (e–h), showing complete genital capsule in ventral view (a, e), pygofer in lateral view (b, f), aedeagus (c, g) and parameres (d, h). After Wilson & Claridge (1991).

different geographical regions and host plants, we have been unable to repeat these interspecific hybridizations. Indeed we have argued that the results of Saxena *et al.* must be regarded with suspicion because, unusually, their supposed hybrids showed no intermediate or divergent characters, but resembled only the female parental species (Claridge & Morgan, 1987). It is thus most likely that in these experiments the parental females had already been mated with their own species before the crosses were made.

We have collected samples of *N. bakeri* in the field on *L. hexandra* from widely separated regions of Asia—India (Sindri, Bihar, 23°60N, 86°88E), Sri Lanka (Kandy, Central Province, 7°18N, 80°43E), Indonesia (Ubud, Bali, 7°54S, 115°46E) and the Philippines (Rosalis, Pangasinan, Luzon, 15°35N, 120°38E). Populations of each have been maintained in continuous culture on growing *L. hexandra* plants in heated glasshouses at Cardiff.

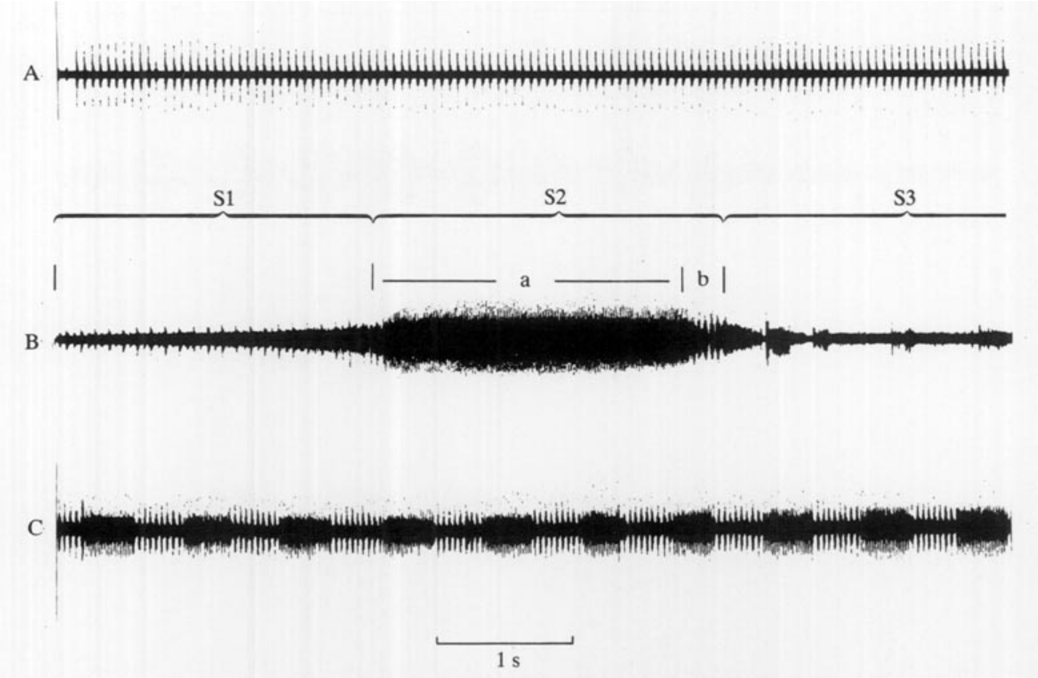

Figure 3. Oscillograms of acoustic signals of *N. bakeri* from Luzon, Philippines. A, female; B, male call with phases S1, S2, S3 and subdivisions S2a and S2b; C, male "aggressive" call.

ACOUSTIC SIGNALS

Males and females of *N. bakeri* exchange distinctive acoustic signals, or calling songs, as do those of *N. lugens* (Claridge *et al.*, 1985a, Claridge & Morgan, 1987). Calls were recorded and analysed as described previously for other species (Claridge, 1985b). The calls will be described separately for each of the geographically definable populations followed by comparisons between them.

Luzon (Philippines) populations

As in most planthoppers, the female call consists of a sequence of regularly repeated and similarly structured pulses which produce a drumming effect (Fig. 3A).

The male call (Fig. 3B) is more complicated: each repeated unit consists of three phases. The first (S1) includes a sequence of pulses building in amplitude and leading into the second (S2) and most distinctive phase. This itself is subdivided into a first part (S2a) consisting of rapidly and regularly repeated high-amplitude pulses followed by a second (S2b) consisting of more slowly repeated, complex, but clearly separable, groups of pulses. The third phase (S3) consists of a variable group of complex pulses of decreasing amplitude. This call structure is characteristic of the population from Luzon briefly described previously by us (Claridge & Morgan, 1987). We found no individual Luzon males that showed repetition of phase S2 in the sequence (S1–3) of calling.

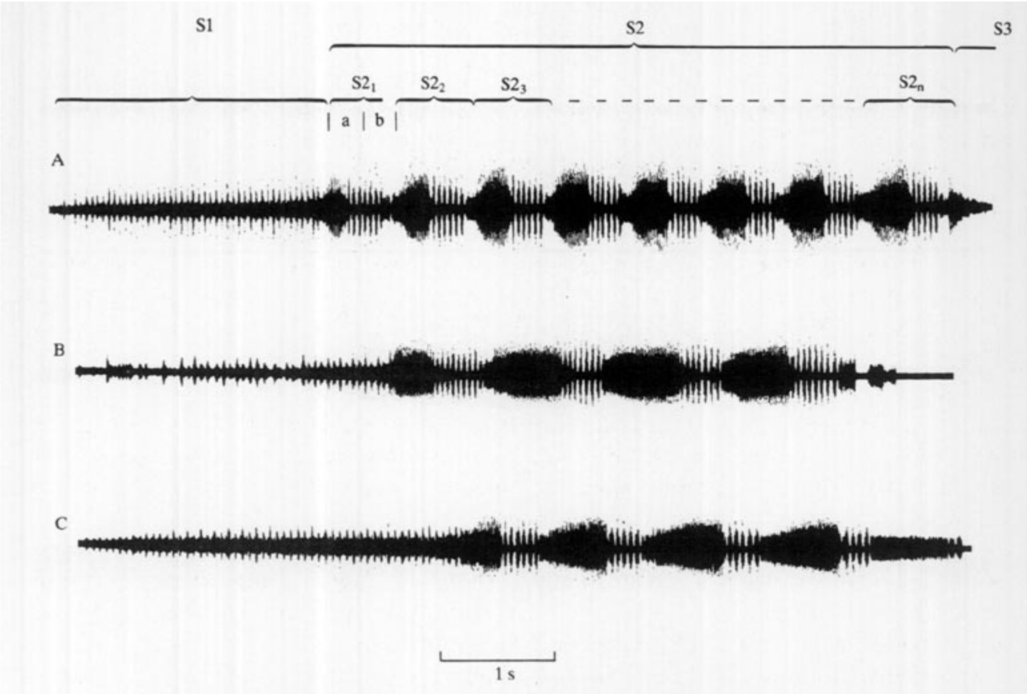

Figure 4. Oscillograms of male calling songs of *N. bakeri* from A, Bali (Indonesia), B, Kandy (Sri Lanka), and C, Sindri (India).

Males respond to the calling of other males by producing a characteristic acoustic sequence, quite distinct from the calling song (Fig. 3C). Ichikawa (1982) described aggressive interactions between males of *N. lugens* accompanied by similar calls. Our own observations with both *N. lugens* and *N. bakeri* indicate that sequences of such aggressive calling have the effect of disrupting mating exchanges of calling between a male and female, at least under laboratory conditions. These aggressive calls are not discussed further here, but they should not be confused with true calling signals.

Bali (Indonesia) populations

To the human ear the calls of male *N. bakeri* from Bali sound very different to those of Luzon insects (Fig. 4A). However, on analysis each sequence consisted of a similar introductory phase, S1, and a concluding S3, but included a repeated sequence of phases, $S2_{1,2,3-n}$, each resembling a single S2 from the Luzon calls. Thus, each S2 from Bali male calls consists of a first part, S2a, with rapidly and regularly repeated high amplitude pulses followed by the second part, S2b, consisting of more slowly repeated complex pulses. Thus the most obvious difference between the male calls of the two populations lies in the number of repetitions of S2 (1 from Luzon, 4–9 from Bali) and the relative lengths of each S2 phase.

Indian and Sri Lankan populations

The male calls of insects from Kandy (Sri Lanka) (Fig. 4B) and Sindri (India) (Fig. 4C) resembled each other closely. Like those from Bali, each complete sequence, S1–3, always included more than one repeat of S2.

Comparisons between populations

The Duncan procedure for comparison amongst means at the 5% level of significance was used to test all sets of acoustic data presented here (see Claridge *et al.*, 1985a, 1988). Full acoustic data for males from each sample are given in Appendix 1.

Calls of females from all of the populations consisted of sequences of regularly repeated drumming pulses. Simple counts of pulse repetition frequencies showed that only the Sindri population was significantly different from the other populations (Fig. 5). The biological significance of this difference, if any, is not known.

Three different characteristics of the calling sequences of the different male populations were measured and compared; (1) number of repetitions of S2 in each call; (2) lengths (s) of phases S1, S2 and S3, and of the subdivisions of S2, when present, and (3) PRFs of S1 and S2a and S2b.

(1) Repetitions of S2. This obvious feature separates the four populations studied into two groups, with the Luzon population clearly separated from the others (Fig. 6).

(2) Length of phases. Lengths of phases S1, S2, S2a, S2b and S3 were measured for the four populations studied. Significant differences were found between the Luzon population and those from Bali, Sindri and Kandy in length of S2.

(3) PRFs. PRFs of phases S1, S2a and S2b were compared for all populations. Significant differences were found for S2a between the Luzon, Bali and Sindri populations (Fig. 7). No difference was demonstrated between the Sindri and Kandy insects.

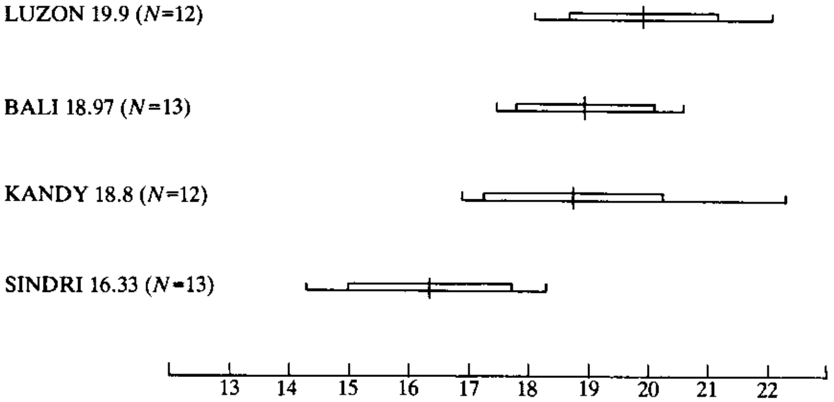

Figure 5. Pulse repetition frequencies of female calls of *N. bakeri*. Vertical line represents mean for each population, thick bar one standard deviation on either side of the mean, and thin bar total range.

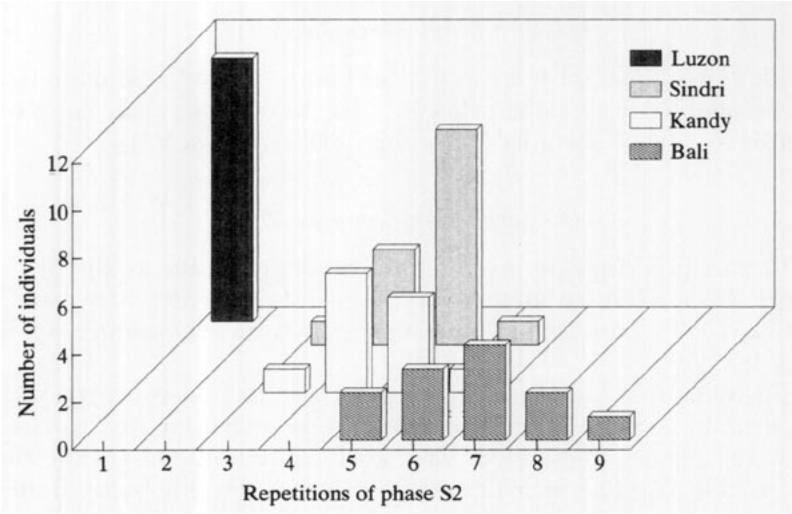

Figure 6. Histograms of repetitions of phase S2 for male calls of *N. bakeri*.

Conclusions

Male calls showed significant differences particularly in respect of repetitions of phase S2, PRF of S2a and length of repeated S2 phases. The Luzon population was the most obviously distinct. This was confirmed by multiple discriminant analysis in which six variables were used. Figure 8 shows the plot of canonical discriminant function 1 against function 2. Function 1 accounted for 96% of the variance and function 2 for 4%, together representing primarily the differences in repetition of phase S2 and PRF of S2a respectively.

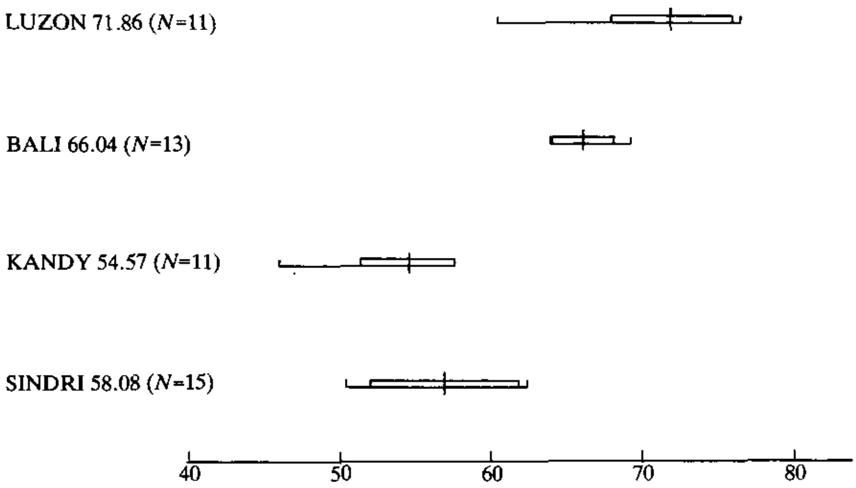

Figure 7. PRFs of phase S2a for male calls of *N. bakeri*. Conventions as in Fig. 5.

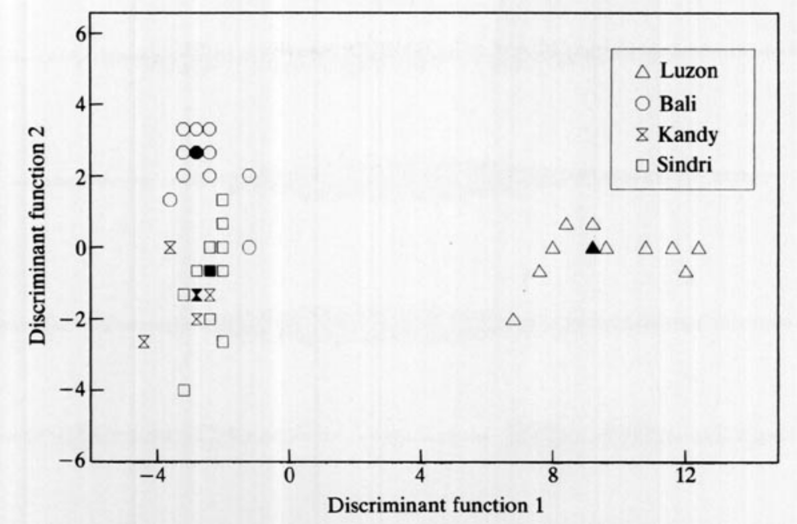

Figure 8. Canonical variate plots for eight characters of the male calls of *N. bakeri* from four allopatric populations. Centroids for each population are marked by a solid symbol.

HYBRIDIZATION

No difficulties were found in obtaining fertile F_1 hybrids in laboratory crosses between the Luzon and Bali populations and between the Bali and Kandy populations. There is no reason to expect that other possible crosses between the experimental populations would not have been equally successful. The acoustic signals of male F_1 hybrids between Luzon and Bali insects were very variable and intermediate between the parentals (Fig. 9). This was most obvious in the number of repetitions of phase S2 in individual courtship calls (Fig. 10). In some individuals the differentiation between the a and b part of each S2 unit appeared partially to break down. Remarkably, hybrids were not intermediate in PRF of the characteristic S2a phases, but were consistently lower than either parental population (Fig. 11) and significantly different to both.

Hybrids between the Bali and Kandy populations were intermediate in repetitions of phase S2.

MATE CHOICE EXPERIMENTS

Claridge *et al.* (1985a, b) have previously used mate choice experiments to demonstrate reproductive isolation between some populations of the *N. lugens* complex. Here mate choice experiments were done with the Luzon and Bali populations of *N. bakeri*.

Individual females from each of the test populations on a *Leersia* plant were presented with a choice of two males, one from their own and one from the other population. Matings were observed and confirmed as successful by subsequent dissection of the females and examination of the spermatheca for the presence of sperm. The average time of copulation was 2 min 23 s and varied between 1 min

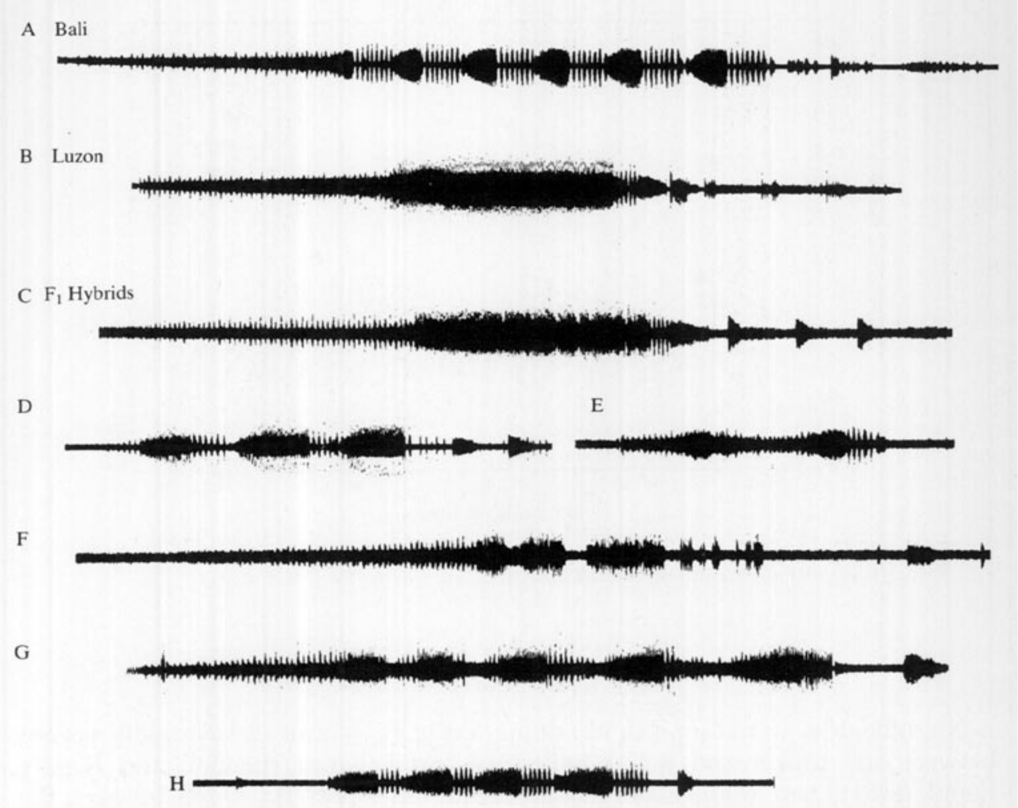

Figure 9. Oscillograms of male calls of parental *N. bakeri* from A, Bali, and B, Luzon, and C–H, hybrids between them.

2 s and 4 min 45 s. Experiments were terminated after 30 minutes if no matings had occurred. The results showed no significant preference for within population (homogametic) matings (Table 1). Any female usually mated with the first male that found and attempted to copulate with her. Normally males called first and the female then responded. The Bali males usually called first. Out of 32 trials in which males initiated calling, six were Luzon and 26 Bali. However, once the female responded then both males replied with apparently equal vigour.

Thus there is no evidence that the acoustic differences between the Luzon and Bali populations are adequate to produce reproductive isolation between them.

Table 1. Mate choice experiments with females of *N. bakeri* from Bali and Luzon and males from both populations

Female	*N*	Mated with Bali male	Sperm present	Mated with Luzon male	Sperm present
Bali	17	9	4	8	6
Luzon	20	10	7	10	9

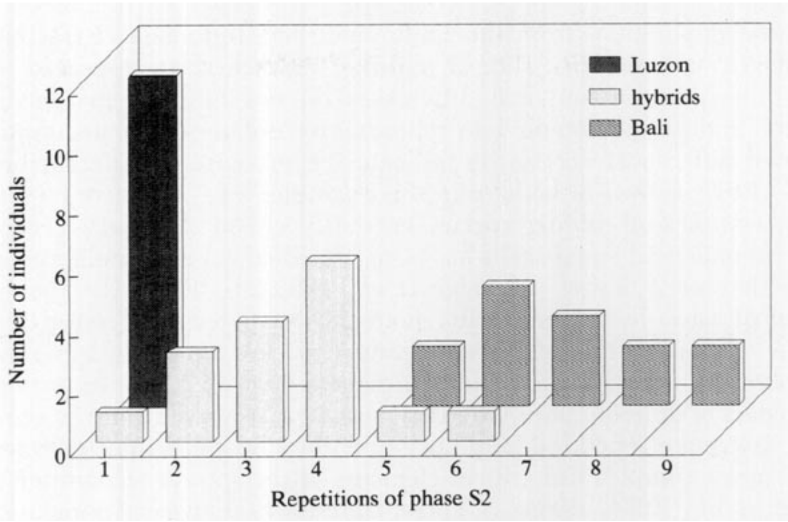

Figure 10. Histograms of repetitions of phase S2 in male calls of *N. bakeri* from Luzon and Bali, and hybrids between them.

DISCUSSION

It is widely assumed that distinctive male calling songs of insects that rely on such signal systems for mate recognition (e.g. grasshoppers, bush crickets, cicadas etc.), indicate reliably the limits of biological species. Male calling signals of the populations of *N. bakeri* from the Philippines, Indonesia and India described here, might suggest therefore that each represents a different biological species. Such a conclusion assumes that the observed call differences are sufficiently great to represent different specific mate recognition systems (SMRS), in Paterson's (1985) terminology.

Our hybridization experiments show that genetic differentiation between these allopatric populations of *N. bakeri* is not very great. Most importantly, mate choice experiments showed no preference for homogametic matings

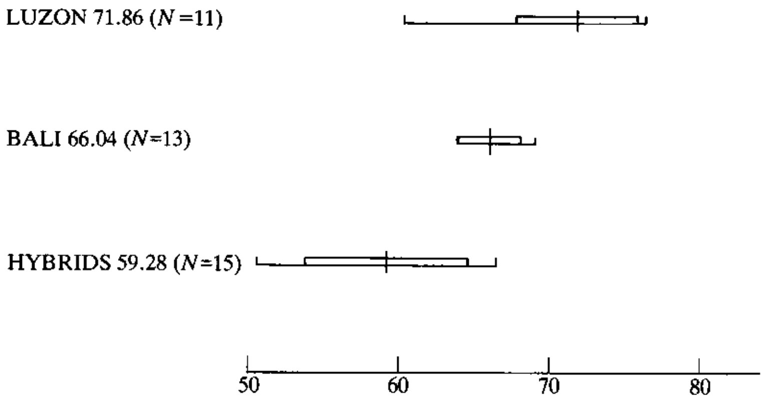

Figure 11. PRFs of phase S2a of male calls of *N. bakeri* from Luzon and Bali and hybrids between them. Conventions as in Fig. 5.

between the populations from the Philippines and Indonesia characterized by very different call patterns. Indeed matings between them appeared to be at random. Thus the obvious call differences do not function in specific mate recognition and provide no obvious reproductive isolation. The assumption that distinct call differences necessarily indicate the presence of different biological species is clearly shown to be false in this example.

In the complex of sibling species currently called *N. lugens*, geographical variation in male and female calls has been described across a similar geographic range to that of *N. bakeri* (Claridge *et al.*, 1985a, b, 1988). In these species geographical variation is primarily quantifiable in terms of pulse repetition frequencies of parts of the calls. These features are less obviously apparent to the human observer than are the major differences described here in patterning of call sequences of different populations of *N. bakeri*. However, there is very strong evidence that pulse repetition frequency of both male and female calls of species of the *N. lugens* complex are critical elements of the species recognition systems (Claridge *et al.*, 1984, 1985a). These differences between populations are responsible largely for observed levels of reproductive isolation. Thus, in the *N. lugens* complex there is little doubt that speciation has occurred and indeed is in progress by the allopatric evolution of divergent male and female call patterns. By contrast in *N. bakeri*, although allopatric song divergence is even more obvious to the human observer, there is no evidence of the accompanying evolution of significant levels of reproductive isolation and therefore of speciation.

The mechanisms by which rapid evolutionary divergence of mating signals may occur are subject to much controversy, but little experimental evidence. Several authors, including for example West Eberhard (1983, 1984), suggest that sexual selection may lead to the rapid divergence in allopatric populations of signals systems used in mating and courtship. If such divergent sexual selection affects features of the call systems important in specific mate recognition, then the rapid evolution of reproductive isolation, and thus speciation, is to be expected. Such processes could account for the observed pattern of speciation in the *N. lugens* group. However, in other circumstances divergent sexual selection might affect call characteristics not involved in specific mate recognition. This could lead to call divergence in allopatric populations, but to minimal levels of reproductive isolation. The divergent populations of *N. bakeri* show just such a pattern of variation and are therefore consistent with such a hypothesis.

Experimental studies on the evolution of reproductive isolation are few. However, recently de Winter (1992, and in Claridge & de Vrijer, 1993) has elegantly demonstrated the divergent evolution of pulse repetition frequency in the female call of a European planthopper, *Ribautodelphax imitans* (Ribaut), by artificial selection in the laboratory. After only ten generations of selection separately for high and low pulse repetition frequencies, he obtained populations with significantly different and non-overlapping PRFs. More important, these laboratory populations when brought together showed significant levels of reproductive isolation. Thus, these experiments show the possibility for the rapid evolution and divergence of specific mate recognition signals by selection, and therefore for rapid speciation in allopatric populations. Similar experiments with *N. lugens* and *N. bakeri* should enable the evolutionary hypotheses developed here to be tested.

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APPENDIX 1

Acoustic data for calls of individual male *N. bakeri*—numbers of repetitions of phase S2; lengths of phases (secs) S1, S2, $S2a_{1-4}$, $S2b_{1-4}$; and pulse repetition frequencies (/sec) for phases S1, S2a and S2b.

Population	Repetitions phase 2	S1	S2	S21a	S22a	S23a	S24a	S21b	S22b	S23b	S24b	PRF S1	PRF S2a	PRF S2b
Luzon														
1	1	2.19	2.66	2.27				0.39				17.20	61.11	15.36
2	1	2.89	3.91	3.41				0.50				17.20	67.22	16.00
3	1	1.25	2.66	2.34				0.31				19.20	73.33	19.20
4	1	3.13	3.05	2.66				0.39				18.80	72.14	15.36
5	1	2.50	3.13	2.81				0.31				21.60	77.00	19.20
6	1	1.72	2.50	2.13				0.38				21.60	73.35	18.67
7	1	8.44	3.05	2.58				0.47				19.00	73.35	17.07
8	1	5.31	2.73	2.34				0.39				18.40	73.35	17.92
9	1	2.81	3.13	3.13								19.20	73.35	
10	1	0.63	2.50	2.19				0.31				20.00	73.35	19.20
11	1	3.75	3.59	3.28				0.31				19.60	73.35	16.00
Bali														
1	5	1.39	6.03	0.39	0.62	0.62	0.70	0.54	0.46	0.54	0.46	16.80	66.33	12.93
2	7	8.20	6.19	0.15	0.46	0.46	0.46	0.54	0.39	0.39	0.39	18.00	66.00	14.78
3	7	1.24	7.43	0.31	0.39	0.39	0.46	0.31	0.43	0.39	0.39	18.00	61.38	25.86
4	7	3.40	8.04	0.31	0.46	0.46	0.54	0.46	0.46	0.46	0.43		64.35	8.62
5	8	3.09	7.73	0.31	0.31	0.39	0.39	0.46	0.39	0.46	0.39	17.60	64.35	15.08
6	6	3.56	6.34	0.23	0.39	0.46	0.46	0.46	0.50	0.50	0.50	17.20	69.30	17.24
7	5	1.70	5.41	0.54	0.54	0.54	0.54	0.46	0.46	0.46	0.46	17.60	66.83	15.08
8	6	4.64	7.73	0.34	0.54	0.54	0.54	0.54	0.46	0.46	0.39	17.12	64.35	11.08
9	9	7.12	10.21	0.23	0.46	0.39	0.39	0.46	0.54	0.50	0.46	16.80	64.35	15.08
10	8	9.90	11.76	0.46	0.54	0.54	0.54	0.54	0.46	0.46	0.39		67.82	14.78
11	6	3.09	6.81	0.34	0.54	0.54	0.54	0.54	0.54	0.46	0.46	19.00	67.32	16.62
12	6	2.78	6.81	0.23	0.46	0.46	0.46	0.54	0.46	0.39	0.31	16.80	67.32	11.08
13	9	3.09	7.73	0.39	0.46	0.46	0.46	0.39	0.39	0.39	0.39	19.00	69.30	23.27
Kandy														
1	4	1.87	5.03	0.36	0.58	0.58	0.58	0.72	0.58	0.50	0.58	20.00	57.50	8.35
2	5	4.60	4.60	0.29	0.43	0.50	0.58	0.36	0.50	0.43	0.43	18.00	55.20	13.91
3	4	5.46	4.60	0.36	0.58	0.58	0.58	0.58	0.50	0.58	0.65	16.00	52.90	13.91
4	3	6.90	5.46	0.29	0.58	0.72	0.72	0.65	0.58	0.65	0.72	16.00	46.00	
5	6	5.46	6.04	0.43	0.72	0.72	0.72	0.72	0.72	0.72	0.86	16.80	55.20	9.74
6	5	3.16	6.90	0.43	0.58	0.72	0.72	0.86	0.58	0.58	0.72	16.00	52.90	10.43

7	5	1.44	4.60	0.36	0.58	0.58	0.58	0.50	0.36	0.36	0.50	19.00	55.20	13.91
8	4	3.74	4.31	0.29	0.58	0.58	0.58	0.72	0.43	0.50	0.50	18.00	55.20	11.13
9	4	3.74	4.89	0.43	0.72	0.72	0.72	0.58	0.50	0.65	0.58	18.00	55.20	10.43
10	4	3.16	4.31	0.36	0.58	0.58	0.58	0.50	0.58	0.50	0.29	18.80	57.50	7.85
11	5	2.88	4.03	0.29	0.50	0.50	0.50	0.58	0.43	0.36	0.43	18.00	57.50	8.70
Sindri														
1	4	9.30	4.20	0.45	0.23	0.98	0.98	0.45	0.45	0.45	0.38	17.76	54.86	13.33
2	5	2.70	4.95	0.38	0.53	0.60	0.68	0.45	0.45	0.60	0.38	17.76	60.00	13.33
3	6	3.30	5.93	0.30	0.60	0.60	0.60	0.53	0.45	0.60	0.60	20.64	60.48	13.33
4	5	2.10	7.50	0.83	0.90	0.83	1.35	0.45	0.30	0.53	0.53	20.40	51.20	11.11
5	5	1.20	5.40	0.38	0.53	0.60	0.60	0.75	0.60	0.45	0.53	20.16	62.40	12.00
6	5	3.60	4.50	0.35	0.50	0.60	0.60	0.45	0.45	0.38	0.38	18.72	58.80	15.56
7	5	6.00	4.73	0.38	0.53	0.53	0.54	0.45	0.45	0.42	0.41	19.20	61.20	15.56
8	5	2.40	5.40	0.45	0.60	0.60	0.75	0.30	0.30	0.30	0.30	21.00	62.40	16.67
9	3	2.10	4.65	0.41	0.75	0.90	1.05	0.96	0.68	0.75		19.89	57.60	9.38
10	4	1.50	5.30	0.38	0.83	0.90	1.05	0.60	0.53	0.38	0.38	20.16	64.80	8.33
11	5	5.40	4.05	0.30	0.45	0.53	0.53	0.38	0.30	0.38	0.38	19.20	62.40	13.33
12	5	2.10	3.98	0.30	0.60	0.48	0.45	0.38	0.38	0.53	0.38	20.00	50.88	13.33
13	4	3.60	4.22	0.41	0.60	0.75	0.75	0.41	0.33	0.45	0.53	14.88	51.60	12.35
14	5	2.70	7.20	0.53	0.90	0.98	0.98	0.68	0.60	0.45	0.45	17.28	50.40	11.85
15	4	3.90	4.65	0.41	0.45	0.53	0.45	0.60	0.60	0.53	0.38	15.84	62.40	13.33
Hybrid Bali parental female														
1	4			0.50	0.50	0.50	0.58	0.29	0.22	0.36	0.43		63.63	27.83
2	5	7.19	6.33	0.50	0.79	0.86	0.86	0.43	0.43	0.36	0.43	14.00	57.96	16.23
3	3	1.73	5.46	0.50	0.58	0.50		0.65	1.37	0.86		21.00	69.00	15.46
4	2	0.50	4.10	0.79	0.79			1.65	1.15			16.00	55.20	6.65
5	3	0.58	4.89	0.79	0.93	0.86		0.43	0.36	0.58		16.00	50.60	13.91
6	4	1.73	4.17	0.36	0.79	0.86	0.79	0.29	0.36	0.29	0.36	17.20	51.98	13.91
7	2	2.01	3.36	0.58	0.58			1.01	1.21			17.00	55.20	9.94
8	2	0.86	2.43	0.36	0.50			1.22	0.35			16.00		4.09
9	4	1.73	6.40	0.36	0.50	0.50	0.50	0.72	0.93	1.73	1.15	16.00	55.20	
10	4	1.73	7.19	0.36	0.58	0.58	0.58	0.58	2.01	1.08	1.44	17.20	57.50	10.43
Hybrid Luzon parental female														
1	6	2.01	6.61	0.43	0.58	0.58	0.65	0.29	0.29	0.29	0.22	16.00	59.80	31.30
2	3	1.15	3.45	0.22	0.29	0.50		0.43	0.72	0.58		21.00	66.70	
3	3	0.43	2.44	0.50	0.50	0.58		0.29	0.29	0.22		16.00	59.80	20.87
4	4	2.73	3.59	0.29	0.36	0.43	0.29	0.29	0.29	0.22	0.43	20.00	64.40	17.39
5	4	1.01	3.74	0.29	0.50	0.50	0.50	0.36	0.36	0.58	0.22	20.00	62.10	19.48