Alternate tactics in male bladder grasshoppers
Bullacris membracioides (Orthoptera: Pneumoridae)

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Summary

Bladder grasshoppers (Orthoptera, Pneumoridae) are a unique group of nocturnal, specialized herbivores, endemic to coastal regions of Southern Africa. Adult males are characterized by an inflated abdomen, which develops at the final molt, and a signaling system capable of producing high intensity calls detectable by conspecifics at distances of up to 2 km. Female response to male calls leads to reciprocal duetting and pair formation. We have found an alternative form to the dominant inflated male tactic in three pneumorid species. These alternate males are incapable of flight and lack the air-filled abdominal bladder used in long-range acoustic communication; but may be found in copula with mature females in the field. Here we address the issue of neoteny/paedogenesis in the alternate male by comparing the morphology of inflated and uninflated adult male *Bullacris membracioides* with that of ultimate and penultimate nymphal instars, to determine whether these forms follow a common developmental trajectory. We then compare the behavioral responsiveness of inflated and non-inflated morphs to conspecific advertisement calls, to ascertain whether alternate males have the potential to actively exploit the mate location system of duetting pairs. Morphometric analyses indicate that alternate males are a distinctly divergent form from the primary male developmental tactic. We conclude that males following the alternate tactic eavesdrop on the duets of inflated males and females to exploit the acoustic mate location system. This satellite tactic has potential impact on several aspects of pneumorid biology contributing to biasing sexual selection, sensory drive, and ultimately speciation events.

Keywords: alternative male, morphology, behavioral tactics, communication.

Introduction

The phenomenon of alternate male phenotypes encompasses significant behavioral, morphological, physiological, or developmental differences leading to the co-occurrence of multiple male phenotypes within a single species (Gross, 1996). Phenotypic plasticity, the differential expression of phenotypes of a single genotype in different environments or contexts, may be exhibited in one of two ways. Continuously varying phenotypes can be manifest in allometric size differences of structures or the type of tactics used in mate allocation (Thornhill & Alcock, 1983; Basolo, 1990; Andersson, 1994; Danforth & Desjardins, 1999). These traits have the potential to change over time, and a significant impact on mating success, whether by female choice or male-male competition. Discontinuous trait variations, in contrast, are non-overlapping alternative morphologies involving fixed and irreversible morphological and behavioral deviations of the individual from the predominant morph of the species (Alexander & van Staaden, 1989; Gross, 1996; Cook et al., 1997; Zera & Denno, 1997; Kotiaho & Tomkins, 2001). Distinct alternative variants have been well documented among Arthropods, including Arachnida (Heinemann & Uhl, 2000; Clark & Biesiadecki, 2002), Dermaptera (Tomkins, 1999; Forslund, 2003), Hymenoptera (Alcock, 1996; Cook et al., 1997; Danforth & Desjardins, 1999), and most widely in Coleoptera (Darwin, 1871; Emlen, 1997) and Orthoptera (Wagner et al., 1995; Hack, 1998).

Alternate male mating strategies capitalize on the reproductive efforts of their conspecifics established mating system. Satellite males may interfere with duetting pairs by interjecting extra components or overlapping the advertiser's call (signal jamming) to bring about a change in female preference, or by locating her first (Greenfield, 1994; Minckley et al., 1995; Bailey & Field, 2000). More rarely, satellite males may simply wait for an opportunity and make no sound at all (Cade, 1979). Whichever mechanism they employ, one may reasonably presume that the opportunities for such satellite behavior increase along with the separation distance between sender and receiver.

Bladder grasshoppers (Orthoptera, Pneumoridae) are nocturnal African endemics specialized for long-range acoustic communication (Dirsh, 1965). Adult males (Figure 1a) have an inflated abdominal bladder that functions as a resonating chamber, allowing for the production of an advertisement call with an effective transmission distance of ca. 2 km (van Staaden & Römer,
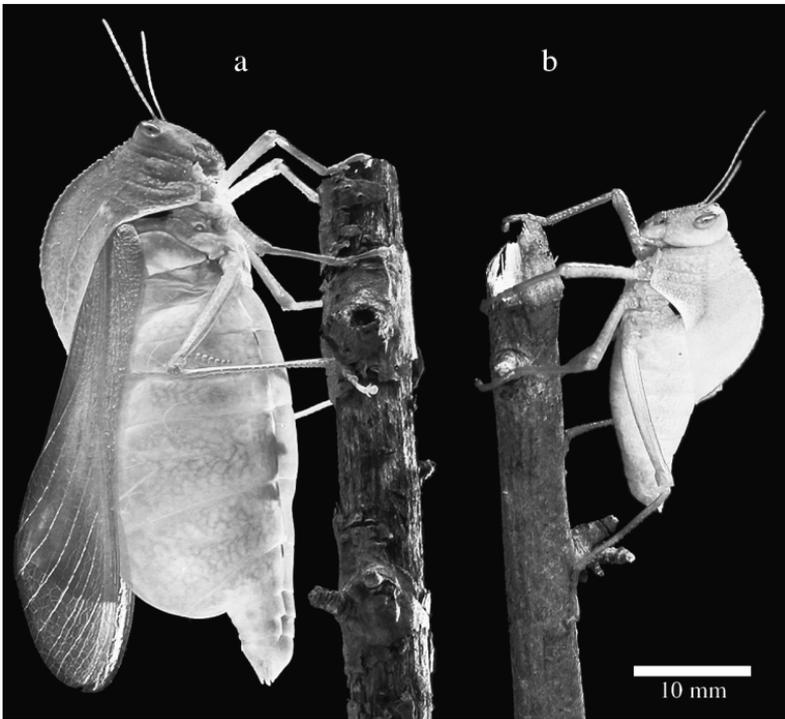
Figure 1. *Bullacris membracioides* primary male (a) and alternate male (b).

1997). Sexual pair formation occurs via reciprocal duetting whereby a male calls, receives an acoustic response from a receptive, stationary female, to whom he then orients and flies, repeating the procedure until the prospective female is located.

An alternate male morph (Figure 1b) was originally identified in *B. membracioides* from both field caught and laboratory raised individuals (Alexander & van Staaden, 1989). These alternate morphs lack both the stridulatory and abdominal machinery for producing advertisement calls, and that for flight; possessing only unexpanded micropterous wings (similar to those of adult females and all nymphs) recessed under the arched pronotum. This severely constrains the dispersal potential of alternate males, which consequently, are similarly restricted to the vicinity of their natal location as are the females. Tuning and sensitivity of hearing is, however, identical in alternate and primary males (van Staaden et al., 2003).

Unlike the majority of insect acoustic systems, pneumorid females show no phonotaxis, leaving the physical act of mate location entirely to the male.

The duet which develops between calling males and receptive females when his song reaches a sound pressure level of 65 dB (SPL, re 20 μPa) is her only contribution, and corresponds to a true communication distance of ca 50 m (van Staaden & Römer, 1998). The relatively large separation distance at the onset of female behavioral response, together with the discrepancy in active spaces of male and female sexual signals (2 km, and 50 m respectively; van Staaden & Römer, 1997) suggest significant opportunity for alternate males to exploit the duetting system of bladder grasshoppers.

To gain insight into the potential significance of alternate males as a selection pressure in the pneumorid communication system, we compared morphologies of primary and alternate males, conducted a behavioral comparison of both male morphs, and posed two questions. First, we tested the hypothesis that alternate male morphs follow a common developmental trajectory indicative of neoteny/paedogenesis. Secondly, we performed behavioral playback experiments to test the hypothesis that alternate morphs respond to conspecific acoustic signals in the same way as do primary males. As unintended receivers of the pair-formation duet, can alternate males locate a receptive female by capitalizing on the primary male's call?

Methods

Specimen acquisition and rearing

Bullacris membracioides nymphs were collected from a population approximately in the center of the species range, at Inchanga (KwaZulu-Natal, South Africa) in January 2003. The grasshoppers were individually captured by hand from natural stands of food plants. Nymphs were raised to adulthood in the lab (12:12 LD cycle), grouped in 37.85 l glass aquaria ($\sim$50 individuals/tank), and fed ad libitum on organically grown romaine lettuce. Newly emerged primary adult and alternate males (primary $N = 25$, alternate $N = 13$) were identified daily and placed individually into 1.89 l plastic aquaria. These males were maintained in physical, but not acoustic isolation, for a minimum of one week before being used in behavioral experiments. This provided sufficient time for the newly inflated abdomen of the primary male to harden and coincided with the onset of acoustic signaling.

Morphometrics

A total of 249 *B. membracioides* males were used for anatomical measurements. These included 153 inflated primary morphs, 56 uninflated alternate morphs, 29 final instar nymphs, and 11 nymphs in the penultimate larval instar. All nymphs were measured live and matured into primary males at their final molt. The majority of the adult material was well preserved in alcohol and exhibited negligible shrinkage. The remaining 23 specimens were dry, and came from archival collections in the Iziko Museums South African Museum (Cape Town) and the Transvaal Museum (Pretoria).

Measurements for morphometric comparisons were made to the nearest 0.01 mm using Fischer digital calipers. All were standard linear measurements and made on the left side for paired structures where possible. Body length (B) was measured from a point directly between the compound eyes to the tip of the abdomen. Antennal length (A) was measured from the antennal socket to the tip of the flagellum. Head width (H) was measured at the point directly behind the compound eyes anterior to the head articulation with the thorax. Pronotal length (Pr) was measured along the dorsal ridge from its beginning at the base of the head to its termination at the end of the thorax. Hind femur length (F) was measured from the proximal articulation with the base of the trochanter to the distal tibial articulation, and hind tibial length (T) was measured from the proximate articulation with the femur to the distal articulation with the tarsus. Estimates of measurement error were made for each anatomical structure (30 replicates) on single alternate and primary morph specimens to determine the measurement precision.

Behavioral experiments

Playback experiments were used to test the response of the two male morphs to conspecific social acoustic signals. Trials took place in a sound-dampened room beginning four hours into the dark cycle, from 2100 to 0200 hours, corresponding with the active time of calling in the field. We randomized the order in which individual males were tested, the sound type (male, female, or control), and the particular exemplar used, with the restriction that once selected, males were tested over three consecutive nights (one trial per night without repeat).

We constructed playback loops using SoundEdit 16 (Macromedia, U.S.A.) by editing original recordings of *B. membracioides* male and female calls
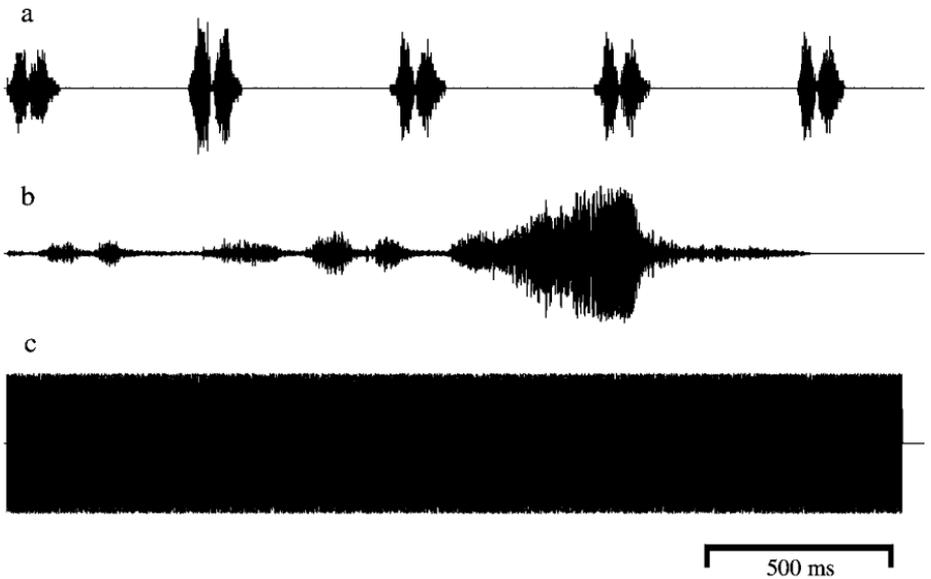
Figure 2. Oscillograms of representative acoustic stimuli. *Bullacris membracioides* inflated male advertisement call (a), adult female response (b), and white-noise control (c). Total duration of each call sample was 12 seconds after the addition of silence.

from conspecific populations. Calls of individuals not used in the behavioral experiments were recorded on a Marantz PMD430 using a Sennheiser MZW 66 unidirectional microphone, and digitized at a sample rate of 44 kHz and 16-bit precision. To reduce pseudoreplication in playback experiments, we created loops from each of four different primary males and adult females (Figure 2). Female response calls are highly variable in syllable number and were standardized to five syllables. Additionally, we created four white-noise stimuli; broadband, uniform, neutral signals, lacking meaningful temporal or frequency information, to serve as a form of control.

The test arena (Figure 3) was a 1.20×1.20 m frame of PVC piping with acoustically transparent cloth walls, and a floor lined with white fabric to facilitate video tracking. Because in preliminary playback experiments animals showed highly restricted mobility on flat surfaces, a four-armed elevated platform ($0.50 \times 0.50 \times 0.10$ m) of wooden dowel rods was positioned in the center of the arena to provide a structure on which grasshoppers would maneuver. The four arms of the platform converged on a central holding cage with transparent cloth walls ($0.10 \times 0.10 \times 0.10$ m), and a removable lid.
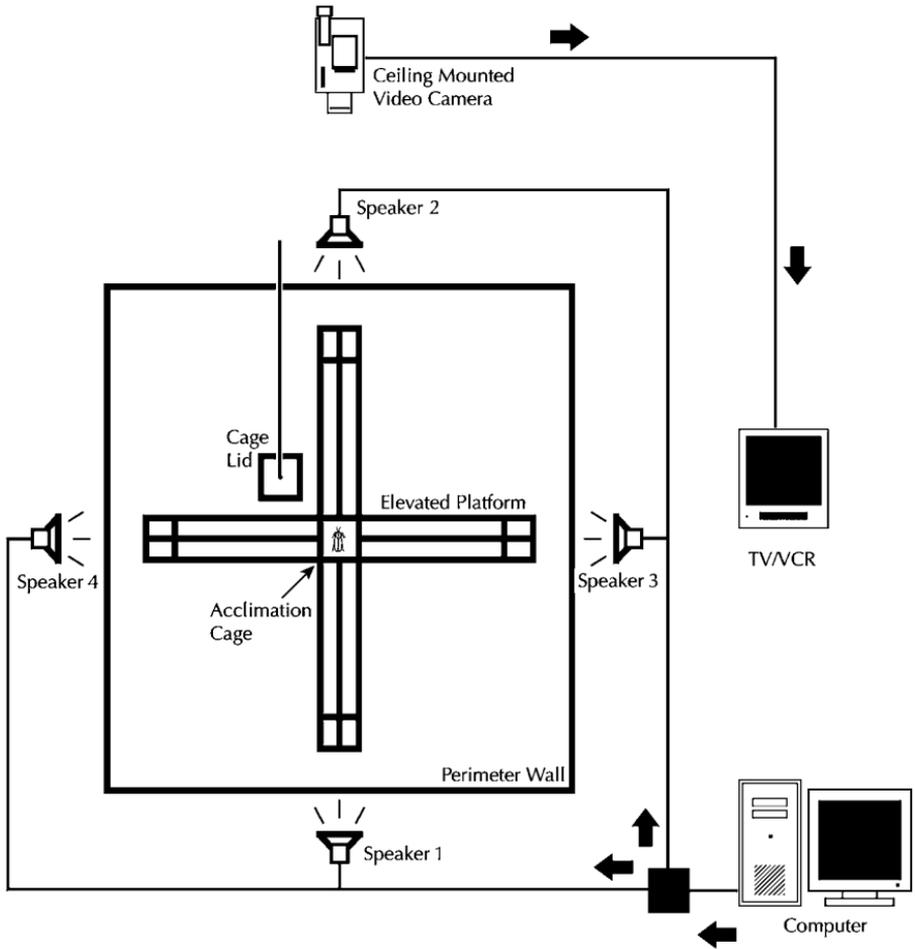
Figure 3. Arena setup for behavioral playback experiments.

Four RadioShack AMX-21 speakers were placed outside the arena, oriented to face the center, one at the end of each platform arm. A single speaker was randomly selected for each trial. In the adjoining room, a Macintosh G4 looped the signal, once every twelve seconds, for the duration of the trial. The acoustic stimulus was standardized to a playback intensity of 65 dB at the center of the holding cage.

Grasshoppers were acclimated in the holding cage for ten minutes before the start of a trial. Following one minute of stimulus playback, the lid of the holding cage was lifted by a microfilament-line from the adjoining room, and the animal allowed access to the platform while the acoustic stimulus

was played. Trials were run for a maximum of 20 minutes, and were ended if the animal did not leave the holding cage within twelve minutes, paused for ten minutes without moving, or left the platform.

Video tracking of the trial was accomplished using a camera (Sony DCR-TRV 140) with an infrared emitter, able to record at near zero lux, ceiling mounted directly over the arena. Trials were recorded via an Emerson TV/VCR and the precise position of the animal converted into X/Y coordinates at five-second intervals. These coordinates were analyzed using a customized Java applet from a public domain JavaGrinder library (http://caspar.bgsu.edu/~software/Java/Grinders.html). The applet analyzed the coordinate data and provided measures for vector direction and strength of vector movement.

Data analysis

To distinguish morph types and identify anatomical structures that predicted developmental outcomes, we employed multivariate analysis of variance (MANOVA) and Discriminant Function Analysis (DFA). DFA considers all measurements together, deriving linear combinations that maximize variation between groups and minimize variation within groups (Seal, 1964; Sokal & Rohlf, 1981; Norusis, 1988). The inclusion of the ultimate and penultimate nymphal stages allowed for a four-way DFA, which is of particular interest because it reveals the interaction of body characters as the animal develops.

The descriptive statistics for the playback experiments were compiled and analyzed using JMP 3.2.2 (SAS Inst. Inc.). Rayleigh circular statistics analyzed the overall angular direction of movement that the animals made over the course of individual trails. Because playback speakers were randomized, vector angles were zero-degree standardized to a uniform playback origin for comparative purposes. A second order analysis of the Rayleigh movement angles was performed using a further Java applet from the JavaGrinder library (see URL p. 9), which provided a grand mean angle and direction for each of the six trial combinations, and tested for significance of movement direction. A third custom Java applet (see URL p. 9) was implemented to perform a Watson-Williams test (parametric, two or more sample, second-order analysis) for equality of the grand angle means. This tested for both significant within-group variation in the direction of movement between sound types, and between-group difference of the primary and alternate males for same-sound combinations.

Table 1. Anatomical length measurements (Mean $\pm$ SE mm) for primary and alternate morphs of *B. membracioides* males.

Type	H	A*	Pr	F	T	B
Primary	6.39 ± 0.03	11.75 ± 0.17	21.34 ± 0.08	15.64 ± 0.05	16.98 ± 0.11	50.49 ± 0.23
N	201	45	200	199	64	161
Alternate	5.74 ± 0.05	11.56 ± 0.20	18.67 ± 0.14	15.13 ± 0.12	16.02 ± 0.20	29.69 ± 0.32
N	49	34	51	54	31	50

Abbreviations are: Head (H), Antennae (A), Pronotum (Pr), Femur (F), Tibia (T), and Body (B) length. Lengths were significantly different between the alternate and primary males for all structures except for antennal length (*) ($p = 0.46$). Level of significance (p): $0.01 < p \leqslant 0.05$.

Results

Morphometrics

Anatomical data summarized in Table 1 indicate that primary and alternate morphs differ significantly on all measures except antennal length ($p = 0.46$). Measurement error was low, ranging from 0.01-0.03 mm in the alternate, and from 0.01-0.02 mm in the primary male. Although the diverse sources of material and the way that they were preserved was initially a concern, two sources of evidence suggest that such variation is inconsequential for the present analysis. A Principle Components Analysis (data not shown) on measurements of the primary males revealed one contiguous cloud, with specimens of varying provenance (i.e. different populations, rearing procedures, and methods of preservation) randomly dispersed throughout. Moreover, the DFA (Figure 4) shows no overlap of morphs, indicating that variability within morphs is relatively low and between morphs is high. Since no category of individuals was strictly associated with any one of these variables, the present analysis is a conservative one.

The canonical centroid plot (Table 2; Figure 4) summarizes the direction and extent of developmental changes associated with late-stage nymphal growth and shows a pattern of development concordant with that of the primary male as well as the deviation made by the alternate morph. Of the six linear measurements, only the two hind limb measurements proved significant in differentiating nymphs from the alternate morph. Femur (F) and tibial length (T) are negatively correlated, such that as the transition from nymphal to alternate status occurs, femur length experiences greater growth relative to other body measures.
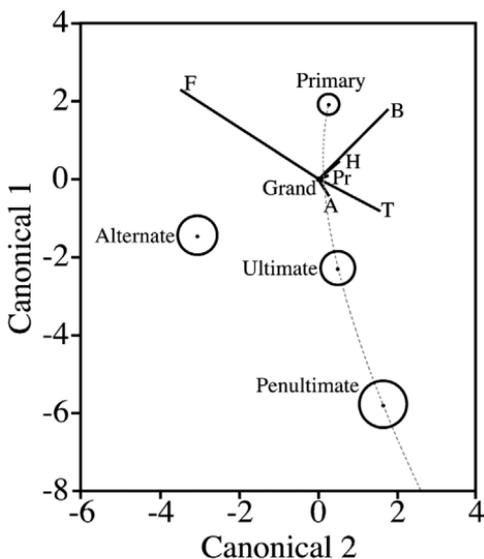
Figure 4. Canonical centroid plot illustrating the extent and direction of growth associated with changes in morph. Canonical axes 1 and 2 represent linear combinations of the original morphological measures plotted as vectors, which originate at a grand mean (Grand) and extend outward in a direction that imparts correlation. The length and direction of the vector lines indicate their ability to distinguish the body types. Positively correlated vectors face the same direction, negatively correlated in opposite directions, and uncorrelated vectors are orthogonal. The groupings of the data points for each morph type, represented as 95% confidence limit circles with a central multivariate mean, vary in size according to the sample size (small circle = large sample size), and are spatially separated by the most effective characters. Dotted line signifies primary male developmental trajectory. See Table 1 for abbreviations.

In the centroid plot, all of the morphological variables were simultaneously compared for the primary, alternate, ultimate, and penultimate nymphs. Canonical axis 1 is interpreted as the growth of the grasshoppers as they mature, whereas Canonical axis 2 is the differentiation of morph type. Because all individuals in the nymphal instar groups developed into primary adult males, the difference between these two nymphal morphs and the primary adult morph can be attributed to the normal development and maturation of structures. The nymph morphs and primary male line up vertically along the growth axis, with little horizontal deviation in the morph axis. The correlative differences between the three (penultimate, ultimate, and primary) are a result of body growth. This same developmental trend is not shared by the alternate male, whose developmental trajectory is largely determined by differential growth in femur length from the nymphs and body length from the

Table 2. Results of multivariate analysis of variance (MANOVA) and discriminant function analysis (DFA) to test for differentiation among *B. membracioides* males in four categories (viz., adults, alternates, penultimate, and ultimate instar nymphs).

	Value	df	F	p
Wilks' Lambda	0.055	18; 679.31	67.590	<0.0001
Eigenvector	**Eigenvalue**	**% Explained**	**Cum %**	**Canonical Corr**
Body	5.052	73.525	73.523	0.914
Femur	1.706	24.827	98.352	0.794
Pronotum	0.113	1.648	100.00	0.319
Head	$3.79e^{-16}$	0.000	100.00	0
Antenna	$2.69e^{-17}$	0.000	100.00	0
Tibia	$-1.29e^{-16}$	0.000	100.00	0

The MANOVA was highly significant (level of significance (p): $p \leqslant 0.0001$) for the Whole Model analysis, which was able to discriminate between the four morphs. Most of the variation in the DFA is explained by the first three variables. A centroid plot of this analysis is shown in Figure 4. Post hoc analyses with body and femur lengths removed yields similar results.

primary male. Based on Figure 4 we would predict that late instar individuals following an alternate morph trajectory would be shifted to the left of the ultimate/penultimate nymphs and below the adult alternate male.

Response to acoustic stimuli

Male bladder grasshoppers responded similarly to playback of acoustic stimuli under laboratory conditions independent of morph type. A second order Raleigh test (Figure 5) showed that the movements of both primary and alternate males were significantly toward the female stimulus (Primary $p = 0.012$, $N = 10$; Alternate $p = 0.008$, $N = 8$), and away from the white noise "control" stimulus (Primary $p \ll 0.001$, $N = 16$; Alternate $p = 0.010$, $N = 7$). Responses to the male call differed in that primary males had a highly significant movement ($p = 0.002$, $N = 15$) in a direction almost perpendicular to the stimulus, whereas alternate males remained essentially stationary ($p = 0.231$, $N = 7$).

There were no significant differences when comparing the alternate and primary grand mean angles of response to the male and female stimuli, but a significant difference ($p = 0.009$) was apparent in response to white noise
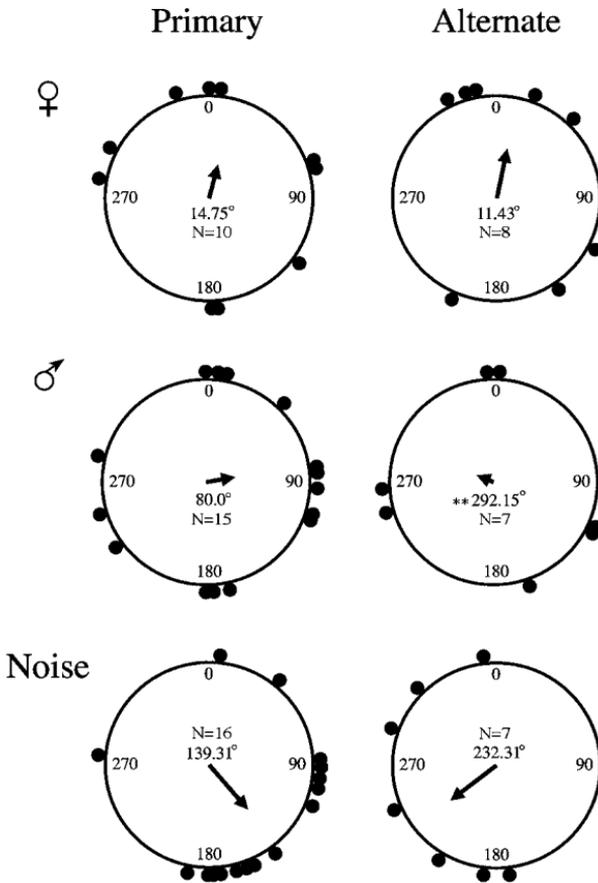
Primary   Alternate

Figure 5. Vector graphs of behavioral response of primary and alternate male morphs to playback of three sound stimuli (female, male, and noise). The direction of the central arrows indicate the grand mean angle of direction, arrow lengths indicate the strength of movement (long arrow = large distance). Filled circles represent individual trials. (**) indicates a non-significant movement ($p = 0.231$).

(Watson-Williams test; Table 3). The Watson-Williams test is not influenced by vector length, thus although alternate males do not move much in response to primary male signaling, when they do so, their overall angle of orientation is the same as that of primary males. Thus, whereas both morphs respond in a similar angular direction toward conspecific female signals and show an angular aversion to white noise, the particular direction of their aversion differs. Of the total 111 trials, 43% were rejected (45.3% in Primary, 38.8% in Alternate) due to no response, which was similar across the three sound stimuli.

Table 3. Testing the directional movement of morphs to conspecific and control sounds: Watson-Williams pair-wise comparisons for equality of angles.

	Stimulus	df	*F*	*p*
Alternate × Primary	Female × Female	1, 16	0.001	0.980
	Male × Male	1, 20	0.048	0.829
	Noise × Noise	1, 21	8.528	0.009

This analysis compared the alternate and primary males grand mean angles of response to the three stimulus types. The Watson-Williams test analyzes angular direction irrespective of vector length, which changed the alternate males grand mean angle of movement with respect to the male stimulus, pointing it in a direction that was not significantly different from the primary male. Level of significance (p): $0.01 < p \leqslant 0.05$.

Discussion

This work has shown that primary and alternate pneumorid males are two distinct morphs, and that the alternate male characteristics arise before late-stage nymphal development and adult eclosion. Furthermore, the two adult male morphs employ separate behavioral tactics to encounter females. Whereas large males use their wings and inflated abdomens in aggressive competition with other males over access to females, non-inflated alternate males adopt non-aggressive alternate behaviors to similar effect. Sneaking in this system requires first that an inflated male emit a call, second, that a female chooses to respond acoustically, and third, that the alternate male can localize the female before the flighted male arrives. Alternate males locating females are thus ultimately dependent on the calls of inflated males.

It may be insufficient to designate morph solely on the presence or absence of an inflated abdomen. If that were the case, then the alternate morph could be a simple case of developmental error that caused an improperly inflated abdomen. Although body length was the major component separating the two morphs, the DFA is robust enough to separate the four developmental stages with the body length component removed (data not shown). Indeed, when body length and all other characters were individually excluded from the DFA, the alternate and primary male were still well separated. Ad hoc analysis of the alternate and ultimate nymph measurements showed that the ultimate instar was statistically larger in head, body, and pronotal length, yet it was developmentally one stage behind the alternate, showing that the alternate is older, yet structurally smaller than the ultimate nymph. This indicates that the alternate morph is not simply a paedogenic individual in

which the genitalia have reached maturity in advance of adult eclosion, nor a neotenic individual in which juvenile characters persist in the adult, i.e. a primary male that underwent developmental error and did not inflate. Rather, the alternate is a clear divergence from what may be considered the 'normal' developmental trajectory of the nymphs, and deviates from the primary male not only in body size, but across multiple structures.

The alternate male is relatively rare in nature, with field captures at ca. 6% of all individuals taken. However, when we place large numbers of nymphs from these same populations in a small area under lab conditions, approximately 25% of the adult male population develops into alternates. Hence, the alternate male is not a laboratory artifact or developmental error. Indeed, in five independent instances, we have observed late-stage nymphal individuals showing all signs of the alternate phenotype inflate in a final molt (though to smaller size than other primary males) when physically and acoustically isolated from conspecifics. The crowding effect of high population density is an effective trigger for the alternate condition, suggesting that in areas with high population density, where long-range dispersal and communicative abilities are less feasible or assume lesser importance, some males may benefit from adopting an alternative mating tactic. These alternates subvert the usual inter-male competition and locate mates in ecological circumstances where competition might otherwise be too great to achieve success.

Our playback experiments have shown that the alternate is indeed capable of exploiting the sexual signaling system of conspecifics. Similarities in the auditory neurophysiology of primary and alternate males (van Staaden et al., 2003) result also in similar behavioral responses to female sexual signals; both primary and alternate males exhibit positive phonotaxis to female calls. However, their behavioral response to the male call differs. Whereas primary males choose to move upon hearing the calls of other inflated males, the alternate males remain stationary in this context. Both alternate and primary males react alike to white-noise, moving away from it, either because it is perceived as threatening or aversive, or as an adaptive response to avoid background noise that would mask potential female responses.

The rarity of the alternate pneumorid morph has made study of the natural history and behavior of these individuals difficult. Observations associated with this study revealed distinct behavioral differences exhibited by the alternate. Pneumorids normally behave cryptically, and are solitary insects. Alternate males are very social, by comparison, clinging onto the sides of

other nymphs in their vicinity. This behavior extends to when an alternate male encounters a primary male as well. Primary males are not aggressive to alternates as they are to other inflated males, preferring to avoid them as they do nymphs. Alternate males are, however, aggressive to primary males, causing damage to their wings and inflated abdomen. The more social behavior of the alternates may keep them in close proximity to male nymphs, which upon inflation could be damaged or killed to eliminate competition (pers. obs.). Likewise, the clingy behavior of the alternate can leave opportunities for interactions with feeding or nymphal females.

Within Pneumoridae, alternate phenotypes are not unique to *B. membracioides*, occurring also in *B. obliqua* (pers. obs.) and a third congener, *B. serrata* or *B. discolor* (from an image by A. Bannister in Skaife, 1979). Moreover, interesting parallels exist between male dimorphisms in *B. membracioides* and the phase state polymorphism of the swarming migratory locusts (Acrididae) of northern Africa (Bouaïchi et al., 1996; Roessingh et al., 1998; Bouaïchi & Simpson, 2003). In *Schistocerca gregaria*, two morphs (phases) vary in color, morphometry, and behavior. At low population densities, they are solitary, changing to a gregarious phase and aggregating in swarms when crowded (Uvarov, 1966; Roffey & Popov, 1968; Sword, 2003). This behavioral gregarization is stimulated primarily by physical contact, and secondarily by visual and chemical cues from conspecifics. Behavioral changes are the first manifestation of gregarization providing the feedback mechanisms driving changes in physical characters such as color, which accrue with successive molts as the nymph is transferred from solitarious to a gregarious condition (Despland & Simpson, 2000). Similarly, in *B. membracioides*, the first indication of the alternate condition occurs in nymphs that behave with uncharacteristic sociality. This is followed by distinct changes in coloration (reddening) of antennal tips, mouthparts, hind legs, and pronotal ridge, coinciding with a differentiation in the relative size of body structures. Given that the pneumorid lineage probably arose in the Jurassic (Flook & Rowell, 1997), this suggests either (i) parallel evolution of the alternate morphs in Pneumoridae and Acrididae, or (ii) that the phase shifting mechanism for producing alternate morphs is of a relatively ancient origin, prior to the divergence of these lineages in the early Cretaceous.

Acknowledgements

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