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Alternative sexual tactics in male bladder grasshoppers (Orthoptera, Pneumoridae)

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Synopsis

Two contrasting male reproductive tactics occur amongst three ecologically categorised groups of the short-horned grasshoppers of the family Pneumoridae: forest, marginal and desert groups. On grounds not presented in this paper, the forest-living pneumorids are considered to be phyletically most primitive: males use only a single tactic and it is hence assumed to be the primary one. Here the male calls to, locates an answering female, and flies to her for mating. The alternative tactic involves no calling or flight and this tactic occurs in some marginal species together with the primary one whilst in some desert species the alternative tactic only is used. What little is known of the proximate and ultimate explanation is given. The distribution pattern of the use of male sexual pattern is correlated with geographical distribution and the alternative male tactic is tentatively associated with environmental instability, as envisaged in the original r-K selection theory. Other aspects of the biology that have been presented as r-K correlated are considered: body size, life cycles,

longevity, reproductive output, and complexity of social relationships are presented for the three pneumorid groups. Some of these features fit classical theory adequately but additional constraints must be invoked to account for patterns of vagility, reproductive output and social relationships. Discontinuities in time and space, general harshness of the environment and biotic pressure, whether of conspecifics, competitors or predators, need to be taken into account. Population pressures within the groups and patterns of predator activity are suggested as areas where important contraints may be acting and that require investigation.

1. Introduction

In the 1979 reprinting of Skaife's *African Insect Life* (1953), reference is made to two 'forms' of pneumorid male within a species – one in which the mature male flies and calls and the other that is capable of neither flight nor calling but mates with the flightless females nevertheless. No other record has been found of this subject in pneumorids but the difference in form was the basis for separating three genera (*Parabullacris*, *Pneumoracris* and *Paraphysemacris*) from other pneumorids to which they are very similar, *Bullacris*, *Peringueyarcris* and *Physemacris* respectively. The significance of this feature was emphasised further when it was used as the distinction between two subfamilies, Pneumorinae and Parabullacrinae (Dirsh 1975). The phenomenon of alternative male tactic is evident in a local species of pneumorid *Bullacris membracoides* and, though present work is far from complete, the topic is deemed worth reporting here because it is both within a species and across the family that the alternative male behaviour is shown. Taxonomic implications of some of the material in this paper will be presented elsewhere but here it is necessary to establish which of the two forms is the primary (plesiomorph) and which the 'alternative' (apomorph) one. Hence two topics that could illuminate this question are considered initially: the phylogeny and the present geographical distribution of the family.

2. Geographical and phylogenetic origins of Pneumoridae

Primarily confined to southern Africa, these short-horn grasshoppers occur along the coasts of South Africa, extending very little inland. They are found northward into East Africa, one species occurring as far north as the Sudan. On the west coast, the Orange River is the northern limit for collection of these insects, though males have been heard calling in

the Fish River Canyon (R.H. Watmough, personal communication).

On the phylogeny, two diametrically opposed views are possible (Dirsh 1965): the simplicity of wing venation, genitalia and lack of tympanum could be plesiomorphic from their early locustopsid ancestors or could be apomorphic from a later acridid form. For a variety of anatomical and ontogenetic reasons, the theory espoused here regards them as specialised acridoids that arose from tropical forms fairly recently, i.e. subsequent to the split of South America and Africa. The pneumorid radiation into South Africa, following the line of evergreen forest along the eastern shores, has resulted in a diversity of anatomy that has been recognised in the establishment of nine genera. Those species now living closest to the tropical area of origin seem to retain most of the primitive acridoid features, acceding to concepts propounded by Brundin (1972). These also show most clearly the fundamental pneumorid specialisations. For the purpose of this paper only these primary pneumorid features are relevant.

3. Primary pneumorid specializations

The tropical pneumorids are tree-living and this may account for three inter-related features: (a) There is a reduction of flight and saltation, the former being a feature quoted by Uvarov (1977) for life-forms of grasshoppers in African forest generally. As a result, predators can be avoided neither by flying nor jumping. (b) Crypsis is well-developed both morphologically and behaviourally, and (c) the male locates, contacts, and courts the female using highly specialised femero-abdominal stridulation and unspecialised flight mechanisms, both of which appear only during the final moult. The specialisation of the male sexual tactic also includes the feature that the behaviour is shown only at night, in contrast to the diurnal sexual behaviour of most other acridoids.

4. Definition of three pneumorid groups

The hypothesis that the evolutionary radiation of pneumorids has been from a tropical centre, south-eastward to the Cape and then westward along the Namaqualand coast provides not only a directive as to which strategy to regard as primary, but also assists in establishing the pneumorid groups as they are presented in this report.

Three groups are determined on their ecological distribution. The animals will be termed (a) 'forest' – those eating the leaves of large to
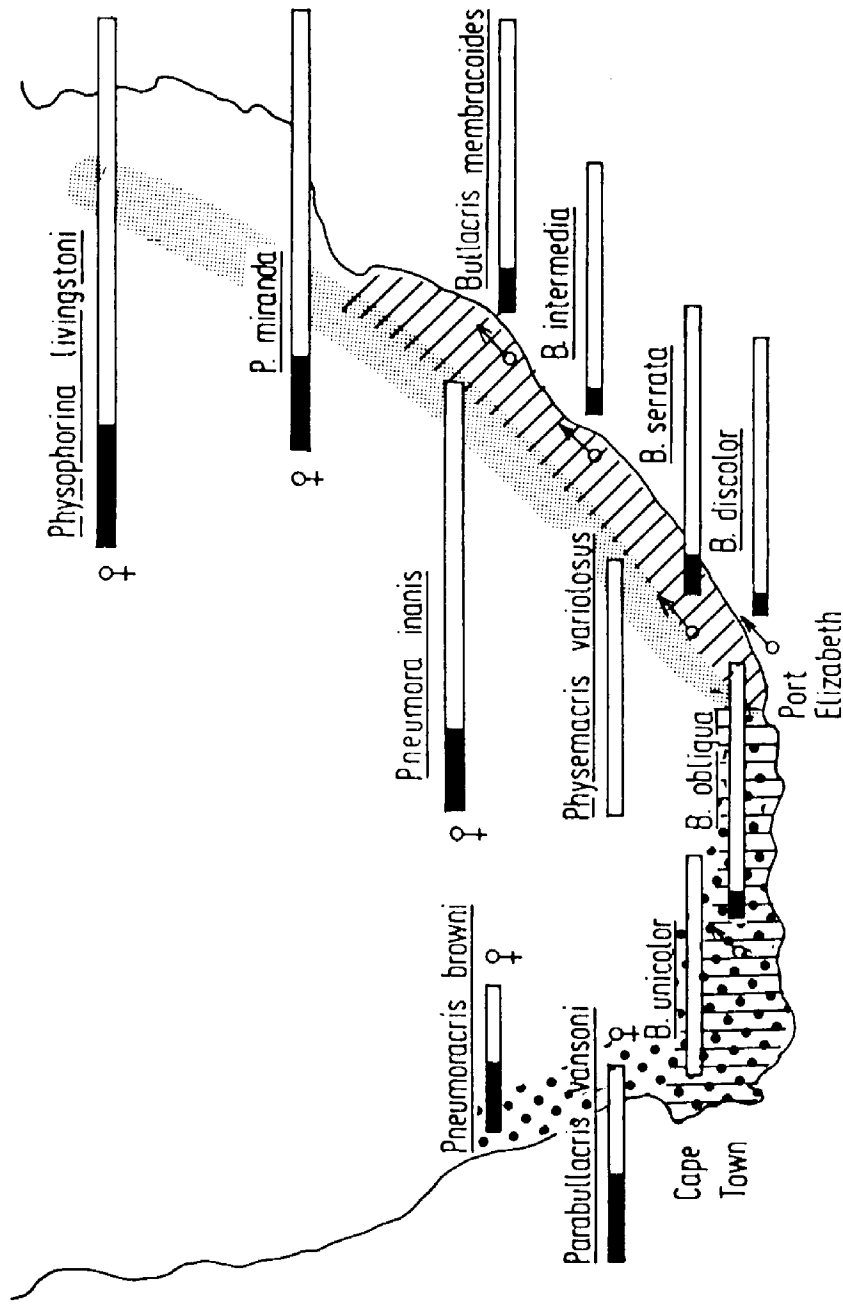
Figure 1. Representation of the geographical distribution of the pneumorid genera and species referred to in the text. Categorisation into three ecological groups is indicated by the background: forest = fine stipple; marginal = hatched; and desert = coarse stipple. Also represented are the mean body lengths of adult insects: the black area in each bar indicates the extent that the length of one sex exceeds the other, the larger sex is indicated by the symbol.

medium-sized evergreen trees, (b) 'marginal' – those eating leaves of shrubs and herbs on the perimeter of forests and adjacent grassland, and (c) 'desert' – those eating leaves of shrubs and herbs of the semi-desert regions.

The forest category comprises two genera that together show a geographical distribution closest to the hypothesised origin of the family. The genera are *Physophorina* and *Pneumora*, and they occur from as far north as pneumorids have been reliably recorded, south to the Hogsback and areas around Grahamstown (Fig. 1). The distinction between these forest species and the others is not geographically absolute, there being small areas of overlap. The differentiation is, however, both taxonomically acceptable (Dirsch 1965) and relevant to the general biology.

The deviation between the marginal and desert groups is neither as distinct as the previous nor as taxonomically authentic. The marginal group consists of *Bullacris membracoides* which is primarily a coastal species in Natal, Zululand and as far southward as Port St Johns. This group also includes *B. intermedia*, *B. serrata*, *B. discolor* and *B. obliqua* as well as *Physemacris sp.*: these occur in the Transkei and southwards around the tip of the Cape but do not occur in Namaqualand (Fig. 1).

The desert group is made up of two components. The one species, *B. unicolor*, occurs as far north along the west coast as Springbok, near the border of South Africa and occurs around the east coast as far as Port Elizabeth. The other component is more restricted geographically, and consists of two genera: *Parabullacris* and *Pneumoracris**. These are found living on shrubs and herbs in Namaqualand and are referred to here as neotenic species.

In this paper, where the forest group is referred to, most of the information on biology comes from a study of *Pneumora inanis* from the Bulwer area in Natal. The marginal group is represented by *Bullacris membracoides* studied at Inchanga, also in Natal. The desert group is least adequately covered and the information derives from investigation of *Bullacris unicolor* in the Springbok, Kamieskroon and Clanwilliam areas of Namaqualand, together with the sparse information gathered by Dirsh (1965) from previous collectors in these areas.

5. Comparison of the primary and alternative male tactic

Wing stubs in the primary male develop gradually beneath the pronotum during nymphal life but increase dramatically during the final moult so

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* It is possible that '*Parabullacris vansoni*' represents a neotenic form of *Bullacris unicolor* and '*Pneumoracris browni*' is the neotenic form of *Peringueyacris namaqua* (see Dirsh 1965).
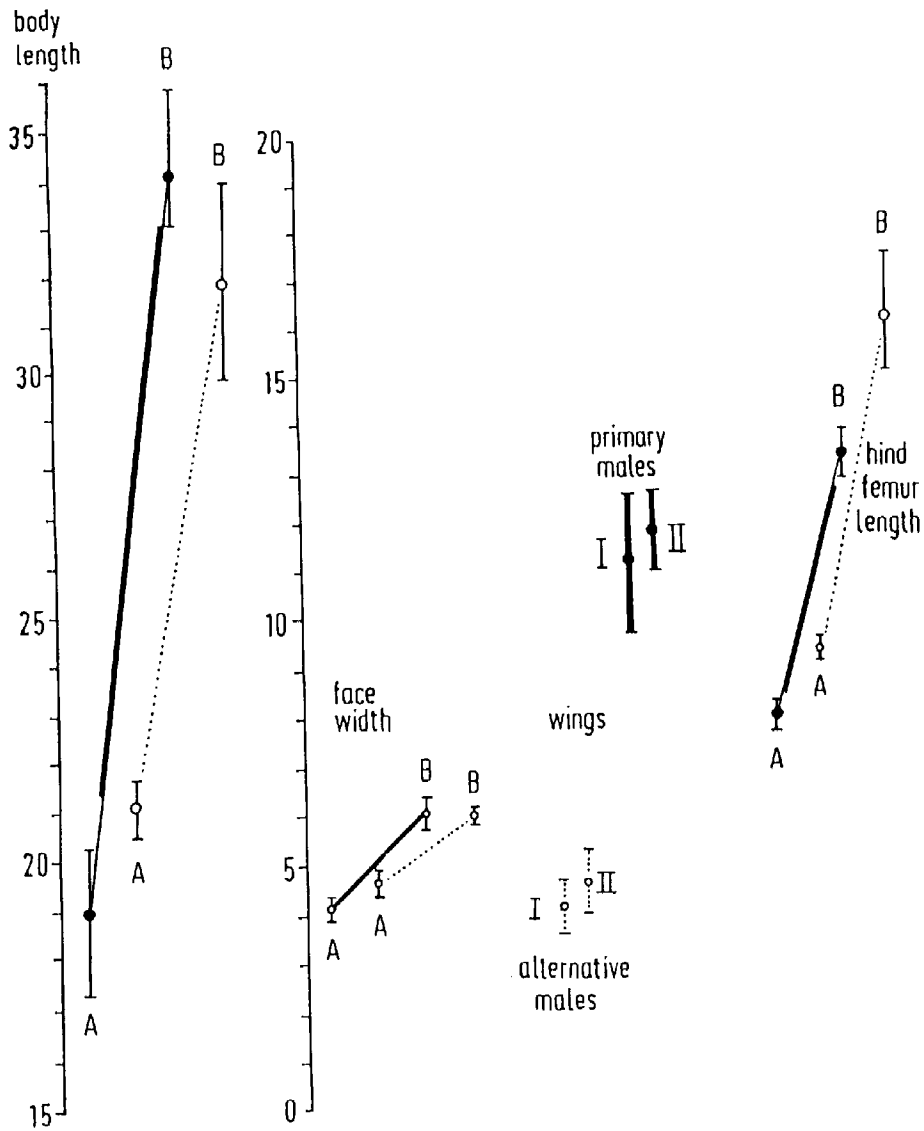
Figure 2. Dimensions of the final, sixth instar male nymph of *B. membracoides* that will moult to produce males (solid circles) and those of alternative males (open circles). The increases from fourth (A) to final (B) instar dimensions are shown for body length, face width and hind-femur length. Lengths of wings I and II are shown only for sixth instar primary and for alternative males. Dimension measurements are in mm, standard deviations are shown as bars.

that in the adult male the wings equal or exceed the abdominal length. In contrast, mature males using the alternative tactic look superficially like final sixth instar nymphs, with total body length and face width being within the primary nymphal range (Fig. 2). The wing stubs however are approximately half the length of those in primary sixth instar nymphs. This difference is not patent to the observer since nymphal wing stubs are hidden by the pronota in both forms. In the shed exuvia of the fourth instars of males that subsequently adopt the alternative tactic, this deviation in wing stub length can be recognised. Hence divergence of the pathways must occur before the fourth instar, at least in *B. membracoides*. Length of the hind femur in alternative males is greater than the corresponding 4th and 6th instar primaries, more so in the 6th but with greater variance (Fig. 2).

At the final moult the primary male expands not only the wings, but also six or seven of the abdominal segments, maintaining them in this inflated condition which acts to amplify both his own stridulatory call (so that it can be heard for a distance of up to one km) and also the rather faint reply of the flightless female that, for a human, is audible only metres away. On the third segment of the inflated abdomen the mature primary male has a row of striations against which a carina of denticles on the posterior femur is stridulated. In the final stage male nymph, as well as the alternative male, both the abdominal and femoral specialisations can be distinguished but it is only after the final (sixth) moult that they are developed fully. (In a single case, out of 14 alternative males, the animal moulted for a sixth time but without development of either wings adequate for flight or stridulatory apparatus).

Mature primary males call and fly to an answering female at species specific times during the night (van Son 1958). Mating occurs on the plant on which the female has matured. Alternative males remain on the plants on which they have matured, mate during the day with receptive females and will do so even with freshly moulted females that would not be answering the calls of flying males. Females sometimes reject males but do not appear to do so more for one form of male than the other.

Primary adult males, at least in the marginal group, are often competitive, fighting (sometimes to the death) when they meet, and calling at night. Towards the alternative males, the primary males appear to be neutral in that they do not attack them as is the case in other animal species where the 'sneaky-male strategy' arouses aggression in the primary males (Arak 1984). Like the primary males, the alternative males fight amongst each other, biting off legs and antennae and tearing holes in pronota and bodies, a behaviour that they do not extend to nymphs. Hence they recognise differences between themselves and nymphs.

6. Proximal causes of flightless adult males

Little progress has been made in identifying proximal causes for the production of flightless males. Certainly it is not a laboratory-induced artifact since six individuals have been found mating with mature females in the field in *B. membracoides*. Until recently the phenomenon was not documented, though casual notes on this behaviour were made in this laboratory in 1974. There are also no reliable assessments of population densities and proportions of one form to the other.

In the forest group there is no indication of alternative males at all. In the desert group two genera, *Parabullacris* and *Pneumoracris*, apparently produce *only* flightless adult males, so that here the effect appears to be genetically fixed and to have replaced the primary one. In the other component of the desert group, typified by *B. unicolor*, mating behaviour has been observed only in primary males.

In *B. membracoides* the primary males occur from October onwards with maximal catches at lights later in the season. The collections of alternative males have been from November to April, with a mid-season peak in January (Fig. 3). Thus it seemed possible that some aspect of crowding could act as a proximal cause for alternative male production. Preliminary experiments of crowding in *B. membracoides* males were equivocal in that these animals were already in their fifth instar with visible morphological differences when the experiments were run (Fig. 2).

Theoretically it seems that an effect of crowding could operate, possibly through a pheromonal emission of the same sort as that which elicits phase-change in locusts. *B. membracoides* (as adults and in all nymphal stages) projects its faecal pellet clear of its body by twisting its abdomen to one side and kicking vigorously with the hind leg of that side. This behaviour may be defensive. These insects rely heavily on crypsis, and as the black faecal pellets on bright green leaves do indeed serve as conspicuous indications of the presence of the defaecator (students used as 'potential pneumorid predators' soon learnt to use these signs). A more important adaptive feature of the faeces-kicking behaviour may lie in some effect of accumulation of faecal pheromones.

7. Functional causes

Functional explanations in terms of fecundity of the two forms are not available because in captivity observers have been unable to hatch pneumorid eggs from egg-pods fertilized by either primary or alternative males.
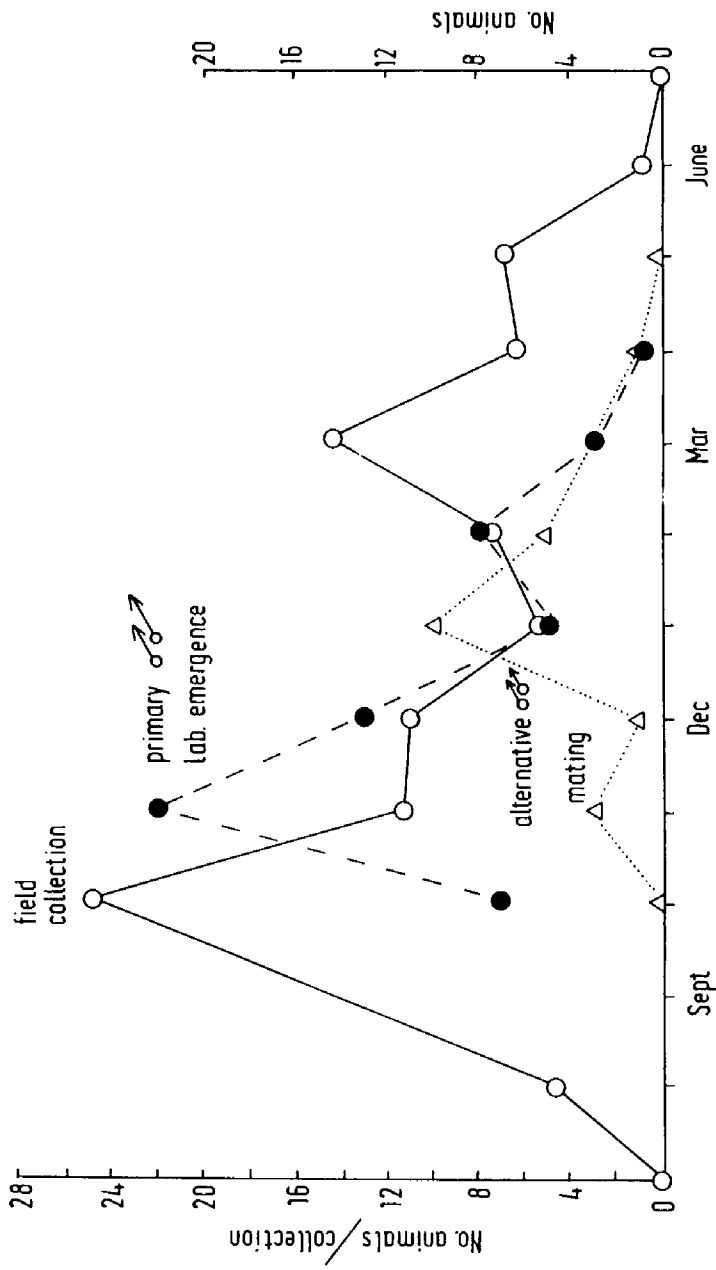
Figure 3. Distribution of *B. membracoides* throughout the season at Inchanga. Ordinate on the left: mean number of animals of any stage collected. Ordinate on the right: numbers of primary males moulting to adulthood in the laboratory and numbers of alternative males, either emerged in the laboratory or collected from the field and observed to be mating.

Ledger & Bannister (1979) suggest that the two forms of male pneumorid are explicable in terms of a division of labour: the flighted males serve to summon the females and flightless males to a common area where the females are mated by the flightless males. Three considerations mitigate against this as a functional explanation: (a) primary as well as alternative males are observed to mate with females, both in the field and in the laboratory, (b) neither alternative males nor females leave their food plants to move to another area for mating, (c) it is difficult to see how any increased fitness could accrue to the primary males to compensate for the cost of their investment in flight, a problem considered in depth by Thornhill & Alcock (1983), for insects with alternative male tactics.

Roff (1986) comments on the advantage to the flightless morphs of any insect species in saving developmental resources and energy by reducing wings and wing musculature. A further functional advantage where paedogenesis is involved is the omission of a moult. Moulting is hazardous in terms of both attacks from predators and accidents within the moulting process itself. In the present pneumorid studies, predation by ants was important in the laboratory cages during the hours of a moult only. A moulting pneumorid dislodged from its perch usually led to the death or deformation of the emerging insects. With the complex process of abdominal inflation as well as considerable wing expansion, the final moult for the primary male pneumorid involves more risks than do either the previous nymphal moults or the equivalent female moult to maturity: in a group of 12 pre-adult female moults there were no casualties whereas 41% of the 17 primary males attempting their final moult during the same period failed to survive. Intermoult intervals also show a time expenditure by the primary male one third above the female.

The main handicap for a flightless morph is usually accredited to its inability to disperse in order to obtain either food or mates. The ability of a species to colonise new areas must depend on female mobility (Horn & Rubenstein 1984), except in those unusual cases in which the male carries the female. The consideration of colonising new areas through flight is not relevant in the case of pneumorids since all females are flightless. In his review of wing dimorphism in insects, Roff (1986) concludes that non-dispersing and hence flightless morphs are likely to correlate with habitat stability.

The habitats of both the marginal and particularly the desert group of pneumorids are unstable in comparison with the forest habitat. The pneumorid male tactics therefore appear to be in direct contradiction to the suggestion by Roff. We believe that the phenomenon relates to r-K differences as defined initially by MacArthur & Wilson (1967).

8. Pneumorids and the classical gradient

There is a clear r-K gradient in pneumorid body size, largest in the most northerly of the forest group, smaller in the marginal and smallest in the desert group (Fig. 1). This pattern is repeated in life cycle and life
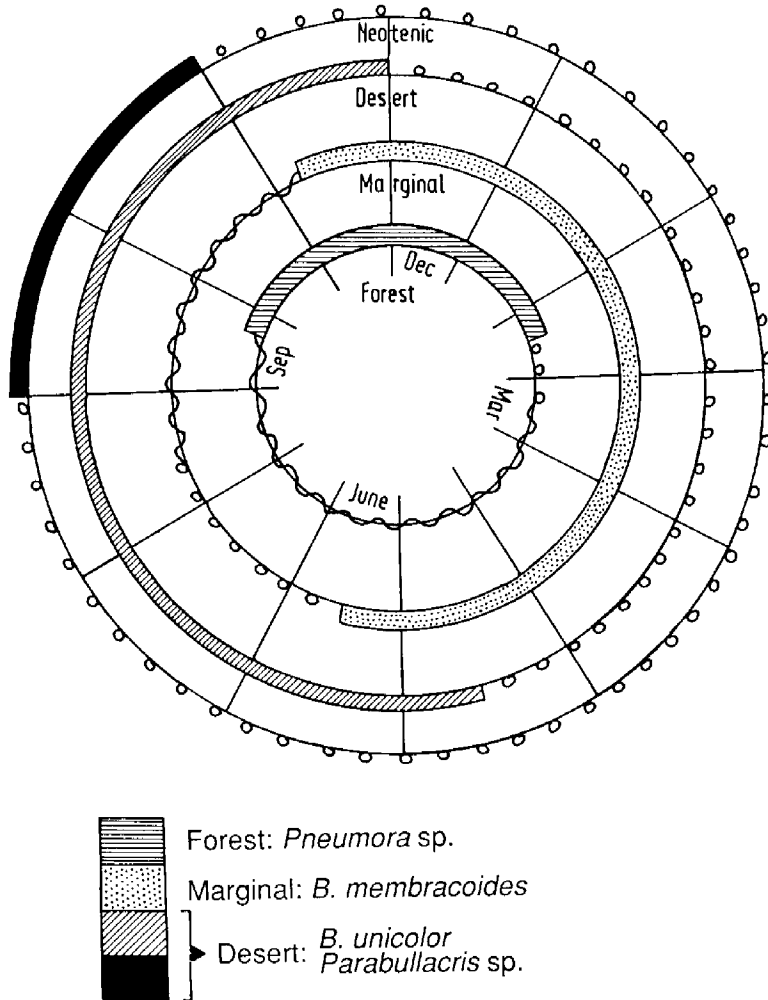

Forest: *Pneumora* sp.

Marginal: *B. membracoides*

Desert: *B. unicolor*
Parabullacris sp.

Figure 4. Distribution of life history stages of pneumorids throughout the year. The forest group, represented by *Pneumora* sp., is shown in fine hatching: marginal group, represented by *B. membracoides*, is shown as stippled and the two components of the desert group, are shown separately – *B. unicolor* in heavy hatching and the neotenic species, *Parabullacris* sp. is in black. The time during which the species is represented: (i) only by eggs is indicated by circles (ii) only by nymphs is shown by the wavey line. The rest of the time adults, nymphs and eggs are present.

span (Fig. 4). *P. inanis* of the forest group spends the entire year as a single generation, individuals existing as adults for as long as four and a half months, and spending the winter months as third or fourth instar nymphs. *B. membracoides*, representing the marginal species, is present for 10 months of the year as nymphs or adults, spending the most unfavourable months (June and July) in the egg envelopes. During these two months, growth of food plants is restricted and fires occur unpredictably over much of the area where the insects occur. In the remaining ten months, marginal pneumorids pass through at least two generations (Fig. 3), with individuals surviving as adults for a maximum duration of 2½ months. For 5½ months of the year *B. unicolor* in Namaqualand are present only as eggs; the duration of the egg interval is twice that of the marginal group. During the remaining 6½ months it is possible that several generations are completed. As the data are a compound of collection records it is possible that the period of 6½ months represents the picture over a number of years, in any one of which the insects were present only for a few months, depending on when the rains fell. *B. unicolor* collected in September 1982 had 4 nymphal instars represented, less than the 6 usual for the marginal and forest groups. In the case of the two genera of the desert habitat where mature males are flightless, nymphs and adults have been collected only during two months of the year [September and October (Fig. 4)]. Thus the life cycles of the desert group would correspond with an r-strategy in comparison with the K-strategy of the forest group and intermediate for the marginal group.

Only one oviposition has been observed in the desert group but the comparison of *P. inanis* and *B. membracoides* is possible and supports further the categorisation of the forest group as being K-strategist as opposed to the r-strategist marginal group. Thus *P. inanis* lays two egg pods per female, the eggs are 9.9 mm long and 75% fewer in number than in *B. membracoides* where a female lays three, four or even five egg pods, between 50 and 70% smaller than the pods of *P. inanis* and containing eggs with a mean length of 8.4 mm. The difference in egg size is emphasised by a specialisation that occurs in *Pneumora* sp. but not *B. membracoides*: a cap is present opposite the micropylar end of the egg, similar in appearance to structures in other insect eggs, which may facilitate hatching (Chapman 1969). Again it is the K-strategist in which the specialisation occurs.

A further behavioural feature in which the forest group shows the greatest specialisation is that of food plant acceptance. Table 1 summarises information for the number of known host plants for *P. inanis, B. membracoides* and *B. unicolor*. The last-mentioned is the most generalised feeder with three different host plant families and at least seven genera.

Table 1. Summary of the food-plant relationship of the three groups of pneumorids. The forest group is represented by *P.inanis*, marginal group by *B.membracoides* and desert group by *B.unicolor*.

Pneumorid group	Pneumorid food plants			
	Number of plant species	Total no.plant genera	Total no.plant families	No.plant genera per single area
Forest *(P. inanis)*	2	2	2	1
Marginal *(B. membracoides)*	7	3	1	3
Desert *(B. unicolor)*	7	7	3	7

So far the information available on general pneumorid biology fits in with Pianka's (1978) generalisations on r- and K-selection. In terms of intra- and inter-specific competition, however, the fit is more equivocal. The forest group, otherwise categorised as K-strategist, fails to show social relations characteristic of traditional K-strategists. There is no inter-male aggression or alternation of male calls in *P. inanis*, both of which occur in *B. membracoides*. This lack could have been predicted on the grounds that males in the forest group are smaller than the females (Fig. 1) as opposed to the case in *Bullacris* spp. where in general the male is the larger. In the paedomorphic desert species (*Parabullacris* spp. and *Pneumoracris* spp.), there is no apparent selection for larger size in the males and hence a lack of physical antagonism between males can be predicted. These matters are presently under investigation.

Nymphs and adult females of *B. membracoides*, as well as the males, react strongly toward each other, exhibiting mandibular threat displays, biting each other and stridulating. This behaviour serves to space out all individuals on the plants and is presumably an important component of their primary defence strategy i.e. crypsis. It is not evident in either *P. inanis* nor *B. unicolor*.

In interspecific interactions *B. membracoides* is again more specialized than *P. inanis*: both species have morphological camouflage, behaviourally they both exaggerate the effect by folding their legs close to the body and antennae onto the face, and both exhibit thanatosis (death feigning) when shaken from a bush. Only *B. membracoides* stridulates aggressively at a potential predator and will bite if provoked further. Adult females of this species are particularly aggressive, using a modification of the sexual call, made louder and more continuously than in sexual calling. This sound is made with modified tegmina and neither males nor immature stages can produce it.

9. Conclusion

The correlation of male mating tactic and general biology throughout the three ecological groups of pneumorids suggests that this family provides a clear example of the r-K-strategy gradient. The assumption on which this is based is that the habitat in Namaqualand provides the extreme in instability for pneumorids while that of the evergreen montane forests along the east coast provides the most stable environment. However two discrepancies suggest that this is too simplistic a view. Firstly the flightless condition prohibits dispersal, and vagility is usually associated with the r-strategy. Secondly the social interactions of forest and marginal groups are the reverse of what would have been predicted if the forest animals were to be regarded as K-strategists and the marginal species relatively r-strategist.

Holm (1989, this volume), draws up a matrix using four environmental restraints that include the classical r-K formulation based on environmental stability. Using this extended basis, he examines a sample of African insect life histories in the hope of deriving a more widely applicable generalisation than can be achieved by using stability alone.

Taking into account problems of scarcity of information and subjectivity of judgement concerning environmental parameters for pneumorid habitats, Table 2 presents the summary of such an analysis. Using Holm's (1989) terms, the habitats of the pneumorid groups are classified as follows: forest = continuous in space and time, predictable, benign and possibly biotically saturated; marginal = less continuous in space and time, less predictable, more adverse but biotically competitive; desert = least continuous in space and time, least predictable, most adverse and least biotically demanding. Pneumorid information for four of the columns match Holm's conclusions of which life-strategies could be expected when the species live under such combinations of restraints. A further two columns could well fit if information on the desert group continues along the same gradient as would be extrapolated from the forest and marginal groups. However four of the columns, a, g, h and j do not conform to Holm's finding for other insects. These columns cover essentially the topics of male vagility (represented by male flight) and environmental biotic pressures (represented by the intra- and inter-specific interactions).

The matter could be left with these two inconsistencies unresolved, as information on pneumorids is still incomplete and the problems may disappear with the collection of further facts. However in both cases speculation may serve to focus investigations. Flight in the case of the primary male occurs at night when the predators that have been observed to kill pneumorids (e.g. birds, mantids and spiders) are generally inactive.

Table 2. Extent to which information on the pneumorid groups is in agreement with their environmental restraints when these are categorised in terms of the four pairs of characteristics put forward by Holm in this volume. For the forest group the habitat characteristics: benign, stable continuous, predictable and biotically saturated. For the marginal group: less benign, discontinuous in space and time, less predictable and biotically less demanding. For the desert group: most adverse, most discontinuous in space and time, most unpredictable and biotically unsaturated. (xxx – well developed, xx – moderately developed, x – low, ? – indicates missing/inadequate information).

| | a | b | c | d | e | f | Specialisations | | | |
| | | | | | | | g | h | i | j |
F	Male flight	Body size	Life cycle	Life span	Fecund-ity	Food plant	Intra-specif. agro	Predator avoidance	Male courtship	Male: male interaction
F	xx	xxx	xxx	xxx	x	xxx	x?	x	xx	?x
M	x	xx	xx	xx	xx	xx	xx	xx	x	xx
D	x	x	x	?	?	x	?	?	?	?
Agree with Holm	No	Yes	Yes	as far as known	as far as known	Yes	?	?	as far as known	?

While there are likely to be other predators active at night in the forests (e.g. bats, genets, rodents), it is likely that in semi-desert regions the proportion of nocturnal predators is higher (the larger bodied predators finding it harder to avoid heat and desiccation during the day). It would seem worthwhile to assess the proportion of nocturnally versus diurnally hunting predators of pneumorids in the three different habitats.

Perhaps the information relevant to solving the second problem concerns population levels of these insects. It is feasible that the forest group is individually very sparse, so much so that intra- and interspecific responses are hardly called for. This would explain why sexual calling of both male and female is more highly elaborate, complex and flexible in *P. inanis* than in *B. membracoides*. If individuals are more spread-out within the forest habitat, this would obviate the necessity for inter- and intra-specific acoustic responses, but increase the need for sexual calling. Furthermore, in the forest group the cost of omitting the flying, calling male would be too high. Measures of population density will be more difficult to obtain in pneumorids than most groups, but they are surely high on the priority list for understanding the life-histories in this family.

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