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Variation in adult longevity in a polymorphic grasshopper species

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Abstract

Life-history theory suggests that the existence and persistence of phenotypic variation within species must be maintained through some advantage accruing to an individual following one developmental pathway over another. Here, we consider the adult lifespan of two highly differentiated male morphs and the female in the bladder grasshopper species *Bullacris membracioides* (Orthoptera: Pneumoroidea). Our results show that the adult longevity of small, uninflated males is twice that of both the larger inflated male and mature females. Uninflated males have a type II survivorship curve, whereas inflated males and adult females both have type I survivorship curves. This difference indicates that the latter two morphs die due to senescence, while the uninflated male does not. The longevity difference between the male morphs shows that while the volant inflated males have the ability to locate many females, they can do so only over a short term, whereas the flightless uninflated male has comparatively limited mobility, but twice as much time to search for mates. This lifespan extension may impart some reproductive advantage for the uninflated male in the longer term, allowing for more female encounters, and increasing its chances for reproduction.

Key words

lifespan, alternate phenotype, longevity, plasticity

Introduction

The presence of alternative male mating strategies within species is generally thought to represent individual optimization of mating opportunities in response to intrinsic or extrinsic factors. Oftentimes, the factors that determine an individual male's strategy relate to its ability to acquire resources, whether in the form of territory, nutrition, or mates (Eberle & Kappeler 2004, Hunt *et al.* 2004, Simmons & Kotiaho 2007). These plastic mating strategies provide males the opportunity to pass on their genes, even during periods when environmental factors may render them otherwise inferior to competing males in a single-strategy mating system (Leiser & Itzkowitz 2002, Lee 2005, Moczek 2008). Alternate behavioral mating tactics such as those exhibited by 'satellite' or 'sneaker' males have dramatic effects on individual life history, characterized by reallocation of energetic reserves (Jennings & Phillip 1992, Fraizer 1997, Bachman & Widemo 1999). By shifting energy expenditure away from such tasks as defending territory or procuring mates, males may extend their life span or increase sperm production (Simmons *et al.* 1999, Carlson *et al.* 2004). Such tactics represent a form of intrasexual competition, and can have profound effects on the fitness of individuals within a population.

Polyphenic males are an exaggerated form of alternative male tactic resulting in extreme variation in both behavior and mor-

phology. The bladder grasshoppers of southern Africa (Orthoptera: Pneumoroidea) are one such system where a clear discontinuous polyphenism results in two distinct male morphs exhibiting disparate mating strategies (Fig. 1) (Donelson & van Staaden 2005). The principal (most common) male strategy enjoins a large body (*ca* 51 mm), fully-developed flight wings allowing for long-range dispersal, a large inflated abdominal resonator to amplify acoustic advertisement signals, and phonotactic flight towards responsive females (Alexander & van Staaden 1989). The alternative strategy is characterized by a smaller male (*ca* 29 mm), lacking the conspicuous inflated abdomen, while retaining the micropterous wings and strong host-plant philopatry of nymphal stages. Rather than actively searching for females over great distances, they exhibit a satellite strategy in which they eavesdrop on the duet between females and inflated males and intercept the female prior to the arrival of the flighted male (Donelson & van Staaden 2005).

The absence of both dispersal and active mate-search behaviors may result in a substantial loss of mating opportunities for uninflated males. However, the persistence of the male polyphenism in multiple lineages within the Pneumoroidea (Donelson & van Staaden, submitted) suggests there is likely a compensatory mechanism that maintains the polyphenism in populations. We hypothesize that the lowered energetic costs of the uninflated male mating strategy led to an extended lifespan. When coupled with a density-dependent trigger, such an increase in lifespan could increase mating opportunities for uninflated males and compensate for the loss of potential mates in locations other than the nymphal host plant. In this paper, we analyze longevity data derived from lab-reared *Bullacris membracioides* to determine whether the uninflated male displays an extended lifespan in response to the polyphenic condition.

Materials and Methods

Over 100 *B. membracioides* nymphs were collected from a natural population at Inchanga (KwaZulu-Natal, South Africa) in January 2003. The collection time coincided with the emergence of young nymphs. The grasshoppers were individually captured from their food plant in a ~1-km² vegetated plot. The nymphs were raised to adulthood at Bowling Green State University (12:12 LD cycle, 23°C), grouped in 38-l glass aquaria (~50 individuals/tank), and fed an *ad libitum* diet of organic romaine lettuce, replaced every other day. Newly emerged adults (N = 30 inflated males, N = 13 uninflated males, N = 21 females) were identified daily and removed

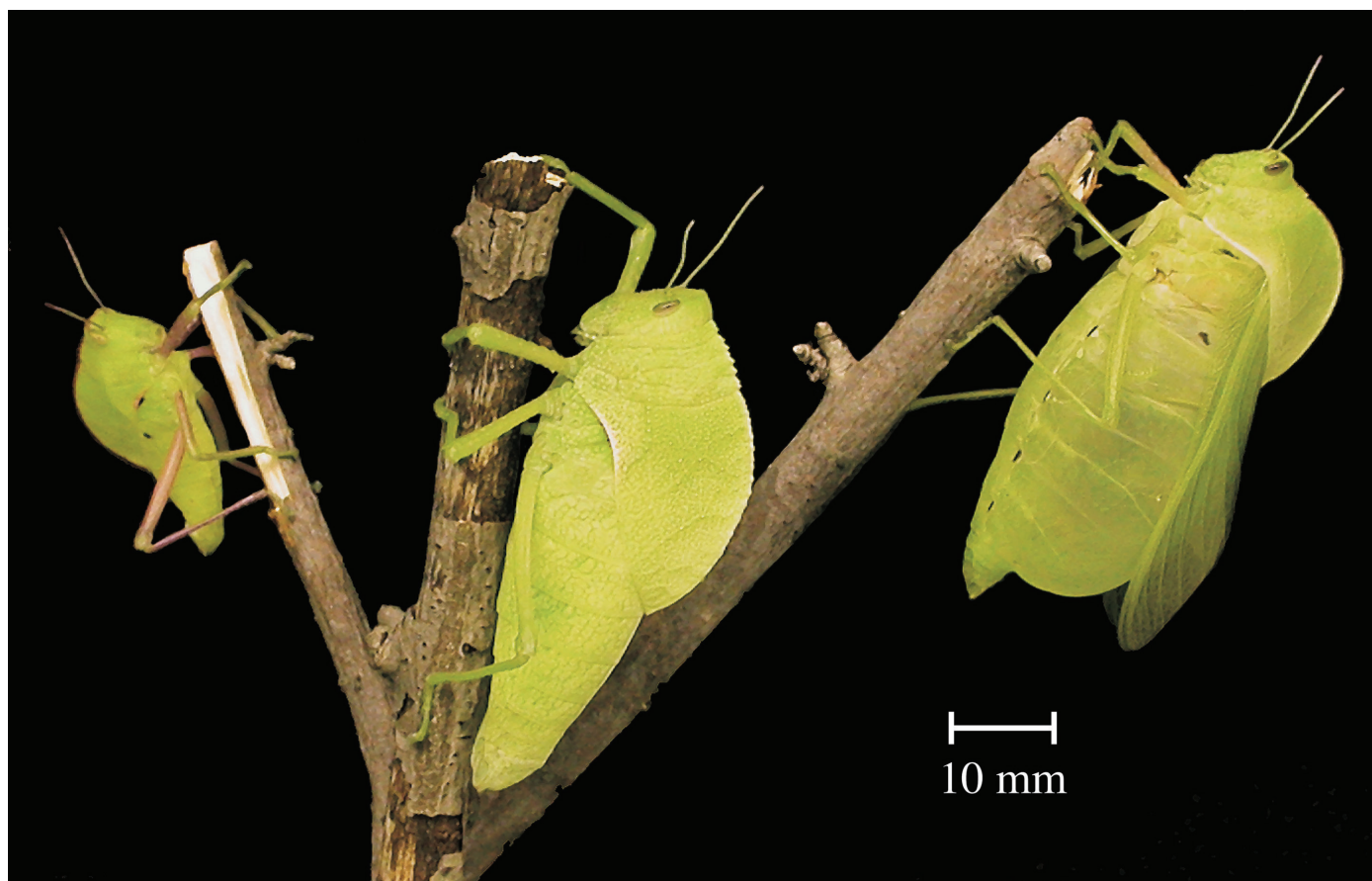


Fig. 1. Three adult forms of *B. membracioides* (from left to right) uninflated male, female, inflated male. See Plate VI.

from the nymphal tanks. Adult males were isolated in individual 1.9-l plastic aquaria to avoid intrasexual aggression. Mature females were removed from the nymph tanks and placed into a single 38-l communal tank. All grasshoppers were housed in the same location with identical diets, and without further chemical or acoustic isolation.

Inflated adult males were easily distinguishable from nymphal individuals due to the abdominal expansion and full flight wings which develop at the final molt. Mature uninflated males were differentiated from nymphs by more subtle but equally distinctive cues *viz.*, disproportionately long hind legs, and the development of purple coloration on mouthparts, femur, pronotal ridge, and antennal tips. Whereas nymphs and adults of both sexes are typically solitary, uninflated males are more gregarious, actively seeking proximity to others. Early development of these features meant that potential uninflated males could be identified well prior to the point of adult eclosion.

For this study, the dates of adult eclosion and death were recorded for each grasshopper that survived to maturity. To exclude the effects of high mortalities associated with adult eclosion, only individuals that survived a minimum of three days were included in the study. Statistical analysis was performed using JMP version 5.1 (SAS Institute, Cary, N.C.). A Kaplan-Meier log-ranks test was performed for each pair of adult types (inflated *vs* female, inflated *vs* uninflated, and female *vs* uninflated). This test compares the survivorship of each adult type to determine whether there is a difference in longevity. A Bonferroni correction was made to the experiment-wide alpha ($p = 0.05$) to account for each of the pairwise log-ranks tests ($p = 0.017$).

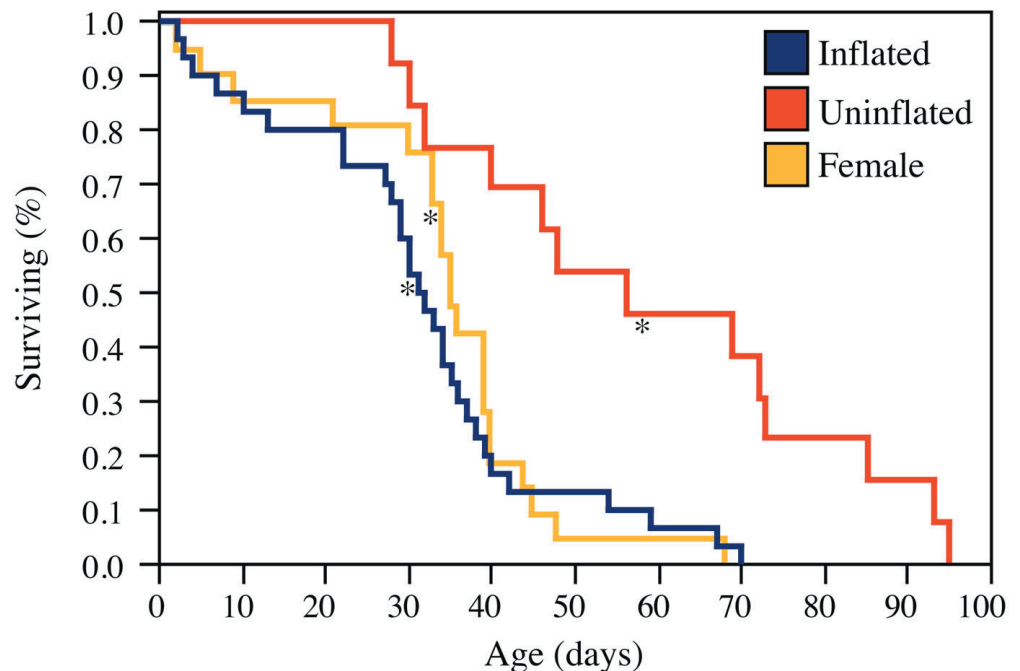
Results

The large, inflated males had a lifespan (mean \pm SD) of 31.2 ± 17.1 d with a median of 31.5 d. The uninflated males had an average lifespan of 59.0 ± 23.8 d, with a median of 56.0 d. The adult females had an average lifespan of 33.8 ± 14.8 d, with a median lifespan of 35.0 d.

The results of the Kaplan-Meier log-ranks survivorship test demonstrate that there is a significant difference between the survivorship of the inflated and uninflated males ($\chi^2 = 16.38$, $df = 1$, $p < 0.001$). The small, uninflated males show a constant rate of death (Fig. 2), indicative of a type-II survivorship. The inflated males follow a type-I survivorship, with an initial period of low mortality, followed by a high death rate occurring over a short time span. Comparison of the survivorship curves for both male types, reveals also that the uninflated males do not begin to die off until around day 30, coinciding with the point at which the inflated males begin dying in large numbers.

Analysis comparing uninflated male with adult female groups shows a significant difference in survivorship ($\chi^2 = 11.76$, $df = 1$, $p < 0.001$). Like the inflated male, the large adult female shows a type-I survivorship curve, with a sharp decline in survivorship also beginning at around day 30, though leveling off with a few remaining individuals at around day 49. There is no significant difference in the survivorship of inflated males and adult females ($\chi^2 = 0.45$, $df = 1$, $p = 0.502$), with both groups exhibiting similar type-I survivorship curves.

Fig. 2. Survivorship curves for the inflated males, uninflated males, and adult females. Mean lifespan for each survivorship line indicated by *.



Discussion

Our results indicate a twofold increase in adult longevity between uninflated males and both the inflated males and adult females, with the latter two groups displaying strikingly similar lifespans (Fig. 2). The type-II survivorship curve of the uninflated male shows no enhanced decline at any particular age, suggesting that death does not occur as a simple byproduct of senescence. In contrast, the much larger inflated males and adult females both exhibit survivorship curves with a precipitous increase in mortality after a similar initial period of high survivorship. The type-I survivorship curves of the large individuals (inflated males, females) suggest that their death rate is more directly associated with aging, leaving only a few individuals surviving after the steep decline. Additionally, the small males do not begin dying until after the steep decline of the other two morphs has been initiated. This delayed mortality may allow the uninflated males to be present throughout the entire adult lifespan of the females, potentially finding late-emerging females that the inflated males would miss.

The difference in lifespan between inflated and uninflated males reflects the behavioral and morphological specializations that characterize the morphs. These differences are important qualities that reveal functional effects of the polyphenism, as each morph exhibits unique mating tactics. The large inflated males are highly mobile, with the ability to locate potential mates across a relatively large geographic range. Their dispersive behavior provides them a larger pool of females from which to choose, though apparently with a limited amount of time in which to sample it. Conversely, uninflated males have access to a more limited number of similarly philopatric females, but have twice as much time in which to locate a mate.

The longevity difference between the large and small males raises several interesting issues regarding the relative cost and benefits of the alternative morphs. Inflated males have many significant costs associated with their mating tactic. Specifically, these large males must devote considerable energy expenditures to the inflation of the abdominal bladder, the development of flight wings and musculature (Reinhold 1999), and a courtship ritual (signaling, duetting, and flight) including the production of an acoustic signal capable of traveling several kilometers. Such costs are further com-

pounded when one considers cuticular water loss, which is likely much higher in inflated than uninflated males due to the presence of wings (Draney 1993) and an increase in cuticular surface area (Quinlan & Hadley 1993), without a corresponding increase in functional body volume from the inflated bladder. While these costs may not lead directly to a shorter lifespan in the large male, they are unavoidable expenditures with which the inflated male must contend in maintaining its strategy. They certainly contribute to the conspicuousness of the inflated morph. Adult eclosion is a prolonged process, with 2-3 h for inflation of the abdomen and expansion of the flight wings, and a further 24 h during which the inflating male is unable to evade predators or defend itself from the harassment of uninflated males (Donelson, pers. obs.). Moreover, the demands of acoustic signaling and flight heighten the predation risk of larger males, which perch in the open while calling and are clumsy fliers owing to the ungainly inflated abdomen.

The small uninflated males are able to alleviate the bulk of these costs. Philopatric behavior, loss of mate location displays and the associated morphological structures, allow these males to conserve energy and avoid circumstances that would expose them to predators. Moreover, the specific morphometrics of the uninflated morph create a relatively low surface area to volume ratio, which mitigates water loss. Such qualities are consistent with predictions relating to increased longevity in a wide range of taxa (Parsons 2007). Though not specifically tested here, the rate of predation on the uninflated male is expected to be lower than that on the inflated male, as small males do not actively advertise their position. Rather, these smaller males remain immobile during conspecific acoustic duets, moving only after the direction of the responding female is determined (Donelson & van Staaden 2005). This calculus of reduced expenditures, mating opportunities, and lifespan, represents a series of tradeoffs resulting in the maintenance of a genetically nonpredetermined polymorphism in *B. membracioides*, as well as several other dual-male pneumorid taxa (Donelson, in prep).

The observed variation in lifespan among adult pneumorid morphs provides indirect support for the notion that the uninflated phenotype is a response to environmental stresses. Females will lay

4-5 egg pods containing ~50 eggs each. The pods are laid up to 10 cm beneath the soil surface, under the canopy of the host plants (Alexander 1992). Hatching nymphs then take up residence on the plant, and all females and any uninflated males remain there while inflated males disperse. In situations where the likelihood of encountering mates in the surrounding area is low, uninflated males maximize their probability of encountering at least a single mate by remaining on their initial host plant and waiting for a female sibling to reach adult eclosion. This would be advantageous in isolated populations.

Hatching and development of pneumorid nymphs is the same, whether they become inflated or uninflated males. Therefore, neither male has a developmental advantage over the other one. The relative reproductive success of either male morph is currently unknown. However, because the polyphenism is not genetically predetermined, the success of either morph should not affect the presence of the other in future generations. Rather, both strategies provide advantages in mate location under particular environmental conditions, as presented in Gross (1998). Under high densities, a male would do better as an uninflated morph, whereas at low densities, long distance dispersal is presumably profitable.

The tradeoffs and adaptive value of male polyphenism in pneumorids are still rather poorly understood. We have suggested that the increased longevity observed in uninflated males has a positive influence on their reproductive success, compensating for the limits imposed by their dispersal ability. However, the possibility exists that extended lifespan is simply an indirect effect of the alternate tactic. Controlled experiments using lab-hatched animals are required to quantify the relative costs and benefits of male size polyphenism and the underlying conditions that favor these developmental pathways.

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