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The effects of population and landscape ecology on body size in orthopterans

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Abstract

Complex interactions between an individual's genotype and its environment determine characteristics such as body size. However, gene-environment interactions should not be seen as being restricted to individual ontogeny: the diversity of the local gene pool can be greatly influenced by habitat variables and population history (*e.g.*, landscape connectivity and propagule size). In this paper I use a model species, the bushcricket *Metrioptera roeseli*, and data from long-term experimental population introductions to examine individual body size as an indicator of the constraints placed on the gene pool by ecological variables following colonization of new environments. These broad-scale population-environment interactions are useful in understanding species ecology, species invasions and in managing successful reintroductions in conservation biology.

Key words

Metrioptera roeseli, body size, experiment, dispersal, colonisation, fragmentation, connectivity, propagule, survival, immune response, asymmetry, introduction, invasion

Introduction

During its development, an organism is exposed to stressors from the environment. These may be more challenging than the individual can cope with in producing an optimally-sized, symmetrical body (Thornhill & Møller 1998, Field & Yuval 1999). Additionally, the individual faces a constant barrage of disease-causing agents, against which it has to defend itself. A large part of the individual's ability to cope with such pressure from the environment is coded in its genetic make-up, but individuals also need access to required resources and to be able to allocate the necessary effort (Parsons 1990, Møller 1993, Schmid-Hempel 2003).

Genotypes derive from available genes within the local gene pool, and are thus dependent on local genetic diversity. Because of this, smaller more isolated populations are more likely to have a lower genetic diversity than larger more well-connected ones, a result being that individuals coming from smaller populations have an increased risk of being homozygous in many alleles (Mayr 1954). Increasing human impacts have reduced the amount of suitable habitat for species, resulting in populations becoming fragmented, and hence, isolated and effectively smaller (Fleishman *et al.* 2002). In landscapes where it is difficult for individuals to disperse into new suitable habitats, the risk of local population extinction increases because movement between local populations is impaired (Saunders *et al.* 1991). Thus small populations cannot supplement their membership through immigration, and there is an increased inbreeding risk, potentially lowering the fitness of the individuals in the population (Charlesworth & Charlesworth 1987, Hanski 1999). Even where new populations are founded through colonisations and recolonisations, the problem remains that the starting population will always be small and vulnerable to stochastic effects. Therefore a link exists between the likelihood of individuals within local populations being able to manufacture and maintain optimal body sizes and 1) landscape ecological parameters, which describe the composition of the landscape the organism inhabits, and 2) population parameters, which describe the size and history of the population.

In this paper I examine the link between an individual's body size and 1) the founding size of its population, 2) the composition of the landscape the population inhabits. I also look at the relationship between body size and other measures related to local genetic and environmental effects: 3) the symmetry of the individual and 4) its immune response to antigenic challenge. The focus organism in these studies is Roesel's bushcricket *Metrioptera roeseli*. This orthopteran (as many other insect species) is very useful for such studies, as it can be experimentally released into specific habitats, and individuals and populations can be monitored in both the short- and long-term. The bush-cricket can be regarded as a model organism for understanding ecological relationships and predicting the behavior of other similar-sized insects. As *M. roeseli* currently is expanding its distribution in Sweden and inhabits fragmented agricultural landscape, it is useful as a model species for looking at both ecological questions on small populations in fragmented landscapes and at questions on the ecology of invading species. The results presented here are a synthesis of my published (Berggren 2001, Berggren 2005) and unpublished data from continuously-running, long-term experimental studies. In this paper "propagule" refers to a group of individuals that are released into a new habitat island, and "propagule size" refers to the number of individuals released at that time.

The species.—Roesel's bush-cricket is a small species, 12-18 mm long (Bellmann 1985), and is common in south and central Europe, Finland, and Latvia. In Sweden the species is predominantly found in the southeast around Lake Mälaren and is currently undergoing a range expansion (Pettersson 1996, Berggren *et al.* 2001). Their preferred habitat is moist, ungrazed high-grass areas, where they feed on grass tissue, grass seeds and small insects (Marshall & Haes 1988). Eggs are laid in grass stems during summer and autumn and hatch in May, one or two years later (Ingrisch 1986), with the nymphs progressing through six instars before becoming adults (Marshall & Haes 1988). In Sweden adult males stridulate from July to October, and if the weather is warm or sunny they stridulate almost continuously during the day at this time. The song is characteristic, making the males of this species easy to survey. Most *M. roeseli* have short wings and cannot fly. However, a variable proportion of the population, but usually <1% is long-winged, and can make short flights (Vickery 1965). It is unknown if such individuals contribute to colonization of new habitats.

The long-term experiments

Study areas and introductions of bush-crickets.— In 1994 and 1995, one of five different propagule sizes (2, 4, 8, 16, and 32) consisting of even numbers of both sexes (*i.e.*, for propagule size 2, there was 1 male and 1 female) of *M. roeseli* was introduced onto each of 70 habitat islands in an area uninhabited by the species. All introduced bush-crickets were in their last nymphal stage, hence virginal, and were collected from the same source population. The experimental introductions were situated in agricultural landscapes in the counties of Uppsala and Stockholm, located in southeastern Sweden.

These habitat islands consisted of patches of ungrazed, semi-natural grasslands of varying sizes (264 - 8642 m^2) bordered by arable fields. Some of these habitat islands were connected to other suitable habitat patches (unoccupied by *M. roeseli*), whereas others were isolated by up to 85 m. The minimum distance between introductions was 2 km. The surrounding matrix consisted of arable fields, forests, and human settlements and included potential barriers such as creeks and roads (de Jong & Kindvall 1991, Kindvall & Ahlén 1992). The minimum distance from the edge of the current distribution of *M. roeseli* was 17 km (more details of the introductions are presented in Berggren 2001). The propagule sizes were distributed across these patches in a random order. There were no differences between the five propagule sizes regarding the landscape composition or structure they were released into (Berggren *et al.* 2001).

Landscape composition and population survival.— I produced digitized maps (1.5 × 1.5 km) centered on each of the introduction sites, based on land-use maps (scale 1:10000) and habitat mapping during field visits for monitoring population distribution. Areas of landscape elements (linear elements, amount of grassland) and isolation were calculated on the digitised maps (for more details see Berggren *et al.* 2001). To get information on population survival and growth, I surveyed a minimum of 30 ha around the introduction patch at the end of each reproductive season (*i.e.*, August and September) from 1994 to 2002. Each census was carried out by listening for stridulating males, mainly focusing on suitable habitat (details in Berggren 2001). As individuals dispersed during the years of the experiment, I increased the censused area up to 225 ha around the introduction patch.

Asymmetry and body size.— In 2002 I randomly selected 29 populations from different successfully colonising propagules. From the smallest propagule size (initial propagule 2 individuals) the one known surviving population was sampled. From the 4, 8, 16, and 32 initial propagule-size populations, 3, 5, 10, and 10 populations were sampled respectively. Individuals were caught by hand-netting. I caught a total of 609 animals, of these 576 were males and 33 females.

The bushcrickets were killed by freezing and then weighed with a Sartorious precision balance and measured on the same day using a microenhancer (× 10) with built-in ruler. In addition to the individuals' body weight and body length (measured from tip of head to end of abdomen, exclusive of ovipositor and cerci), three different traits were measured: maxillary palp length (distance from the maxilla-maxillary palp joint to the end of the maxillary palp); fore wing length (distance from the wing joint to the end of the radial sector); and hind tibia length (distance from the femur-tibia joint to the tibia-tarsus joint). Fluctuating asymmetry was measured for both sexes combined as the absolute value of the left-right difference for palps, wings, and femora (for more details see Berggren 2005).

The immune-response experiment.—For this experiment I collected a total of 370 males from 20 of the introduced populations in 2002. I collected individuals from populations descended from the three largest propagule sizes (4 populations from propagule size 8, and 8 populations each from propagule sizes 16 and 32) by hand-netting at the center of the initial introduction area. I used a standard protocol to provoke and assay immune defence by experimentally implanting a nylon monofilament under the individual's cuticula, exposed to the circulating haemolyph and positioned along the individual's length (see also Allander & Schmid-Hempel 2000, Rantala *et al.* 2000, Civantos *et al.* 2005).

On encountering this foreign body, the insect's immune system responds as if the object was biologically important: there is a synthesis of products 'toxic' to this invader, as well as haemocytes encapsulating the object. The response can then be measured as the degree of darkening (melanisation) and volume of cells attached to the removed filament. Individuals were weighed using a Sartorious precision balance and had their body length measured with a Peak micro enhancer (× 10) with built-in ruler. The nylon thread and the cells attached to the thread were carefully dissected out of the abdomen and fixed onto a microscopic slide after the bushcrickets were killed by freezing, 24 h after implantation [for more details see Berggren (in prep)]. The magnitude of the encapsulation response was measured using a combination of cell coverage and the degree of melanisation on the nylon filaments. High color values and a large area of cells indicate a strong immune response (Allander & Schmid-Hempel 2000).

Results and Discussion

Population variables and body size.—For mass and size traits, the sexes were analyzed separately: males (mean ± $s_{\bar{x}}$): mass 0.271±0.002 g, length 17.9 ± 0.05 mm, maxillary palp 4.24 ± 0.02 mm, tibia 13.6 ± 0.03 mm, wing 9.0 ± 0.07 mm. Females: mass 0.436 ± 0.007 g, length 23.1 ± 0.20 mm, maxillary palp 5.21 ± 0.10 mm, tibia 15.1 ± 0.11 mm, wing 7.4 ± 0.28 mm. Males from populations established from larger propagules (*i.e.*, larger numbers released at time of introduction) were heavier than males that originated from smaller propagules (stepwise regression F = 6.80, d.f. = 1, p = 0.019), Fig. 1. Females were also affected by propagule size, in that females from smaller initial propagules were shorter than females from larger propagules (stepwise regression F = 10.9, d.f. = 1, p = 0.029; Berggren 2005). This impact on body size from smaller initial populations may result from suboptimal growth performance due to a founder effect — with these populations likely to hold a lower relative genetic diversity. This consequence of propagule size may be further exacerbated as fewer individuals in the population means that females are less able to choose between males and/or mate with several partners.

Landscape variables and body size.— Males from more isolated populations weighed less than males from sites with greater habitat connectivity (stepwise regression F = 4.56, d.f. = 1, p = 0.048), Fig. 2. Females were also affected by isolation, with females from

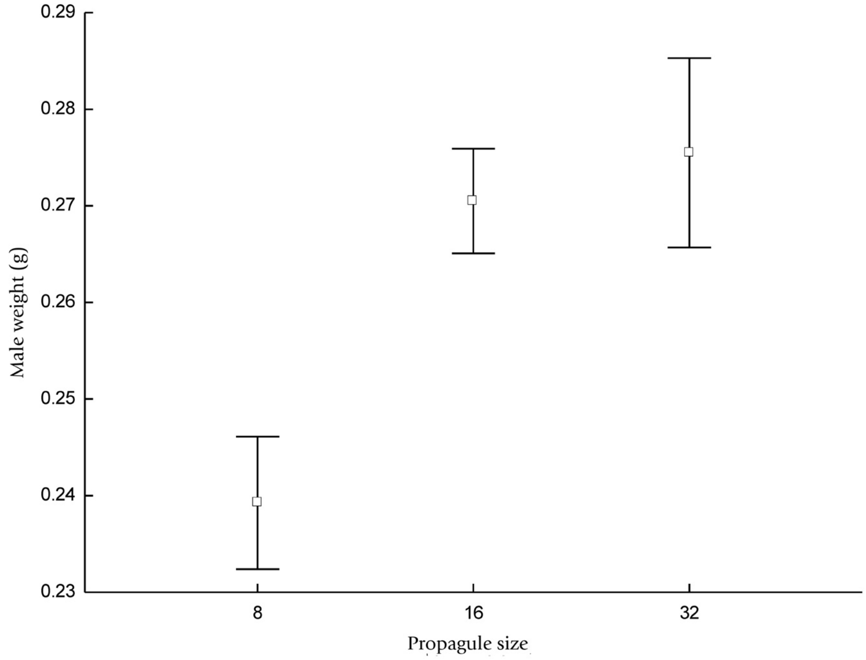

Fig. 1. The relationship between propagule size and weight of male *M. roeseli*. Data shown are means ± 1 $s_{\bar{x}}$.

more isolated populations being shorter than females from more well-connected sites (stepwise regression F = 24.0, d.f. = 1, p = 0.008; Berggren 2005). This was not a simple result of the amount of habitat, as there was no effect of available grassland on female or male body measurements.

Habitat isolation and low connectivity may influence body measurements in males and females by decreasing dispersal options and limiting areas available for foraging and mating in the initial population (Berggren 2001). Decreased connectivity reduces the availability of heterogenous habitat and thus, decreases the possibility of finding food, both locally and regionally, if conditions deteriorate (Kindvall 1996). This may affect individual survival directly (Schtickzelle & Baguette 2003) and indirectly, through a decreased population size and a lower chance of maintaining genetic diversity. Larger distances between individuals from poorly-connected patches mean an increase in mate-finding effort. This additional energy expenditure may limit other necessary activities in the life of the animal (foraging, predator avoidance) and decrease the number of mates to choose from (Gilpin & Soulé 1986). Isolation can also act through an increased mortality stemming from the risk of movement through nonpreferred habitat. This could further compound founder effects with a resulting higher risk of suboptimal trait sizes.

Asymmetry and body size.— For both sexes the asymmetry of wings and tibias in individuals was negatively correlated to their body

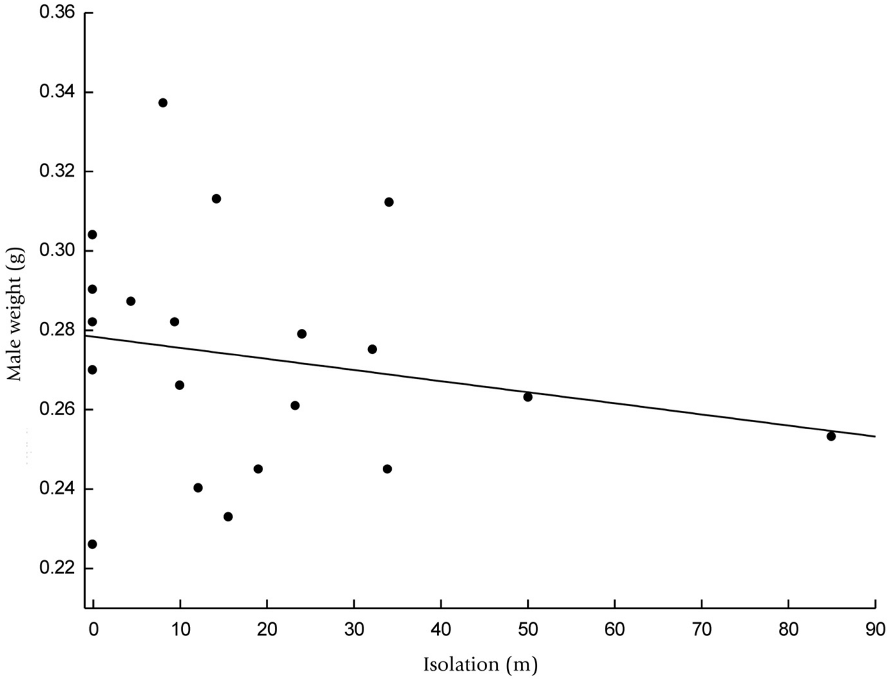

Fig. 2. The relationship between isolation of the introduction habitat and the mean weight of male *M. roeseli*. r = -0.202.

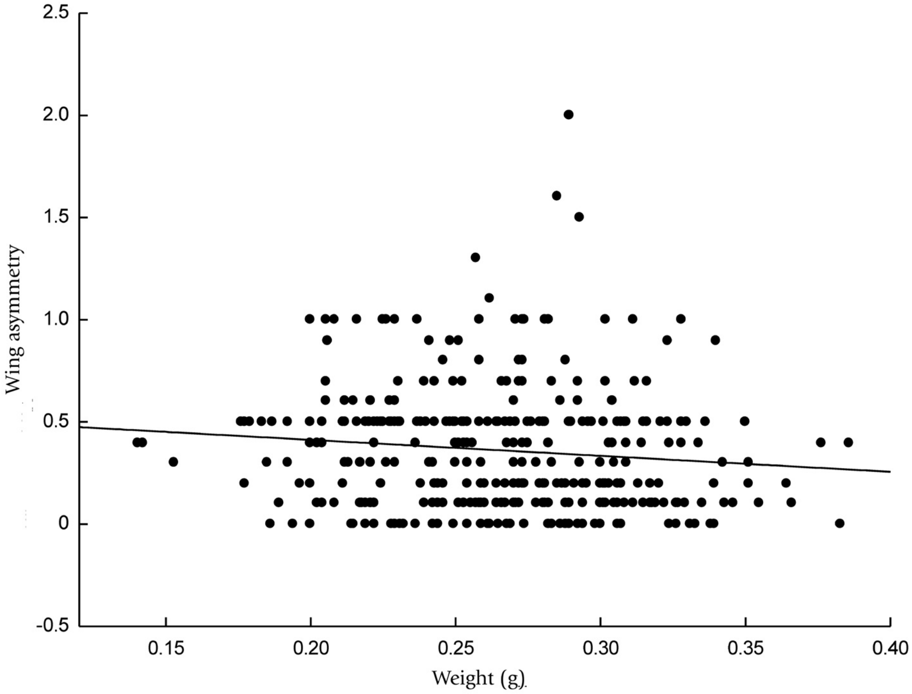

Fig. 3. Correlation between individual weight and degree of wing asymmetry (absolute value of the left-right difference) in individual *M. roeseli.*

weight and body length (Spearman rank correlation all p< 0.05, Berggren 2005), Fig. 3. Morphological traits were positively correlated in individuals (Spearman rank correlation all p< 0.0001) except the length of tibias and wings (r = 0.035, p = 0.47). Mean trait sizes ± $s_{\bar{x}}$ were (for both sexes): weight 0.279 ± 0.005 g; body length 18.1 ± 0.16 mm; maxillary palp 4.30 ± 0.08 mm; tibia 13.7 ± 0.05 mm; wing 8.9 ± 0.14 mm. The degree of asymmetry was: maxillary palp 0.13 ± 0.01 mm; tibia 0.14 ± 0.01 mm; wing 0.25 ± 0.02 mm, Berggren 2005).

Correlations between asymmetry and fitness indicators such as body size have been documented in other species (Bennett & Hoffmann 1998, Uetz & Smith 1999), and suggest that such fitness indicator traits are linked with a decreased ability of individuals to cope with environmental stressors and allocate resources for optimal growth. Asymmetry is associated with lower genetic diversity (Saccheri *et al*. 1998, Mpho *et al*. 2002), as well as being correlated with body measurements in this study. This provides additional support to the hypothesis that differences in body size between populations of differing population and landscape histories are in part, related to differences in available genes within the local gene pool.

Immune response and body size.— There was a negative relationship between the body size (mean weight 0.270±0.002g, mean body length 17.5±0.05 mm) of the individual and its immune response,

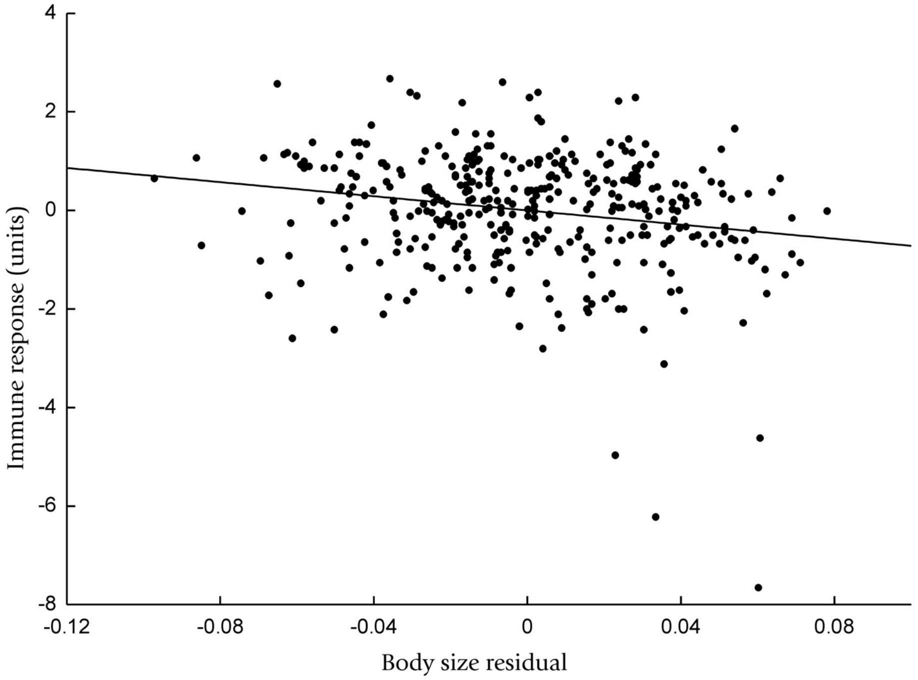

Fig. 4. Correlation between individual body size (residuals of length and weight) and degree of immune response (cell coverage and the degree of melanisation) to an inserted artificial parasite in individuals of *M. roeseli.*

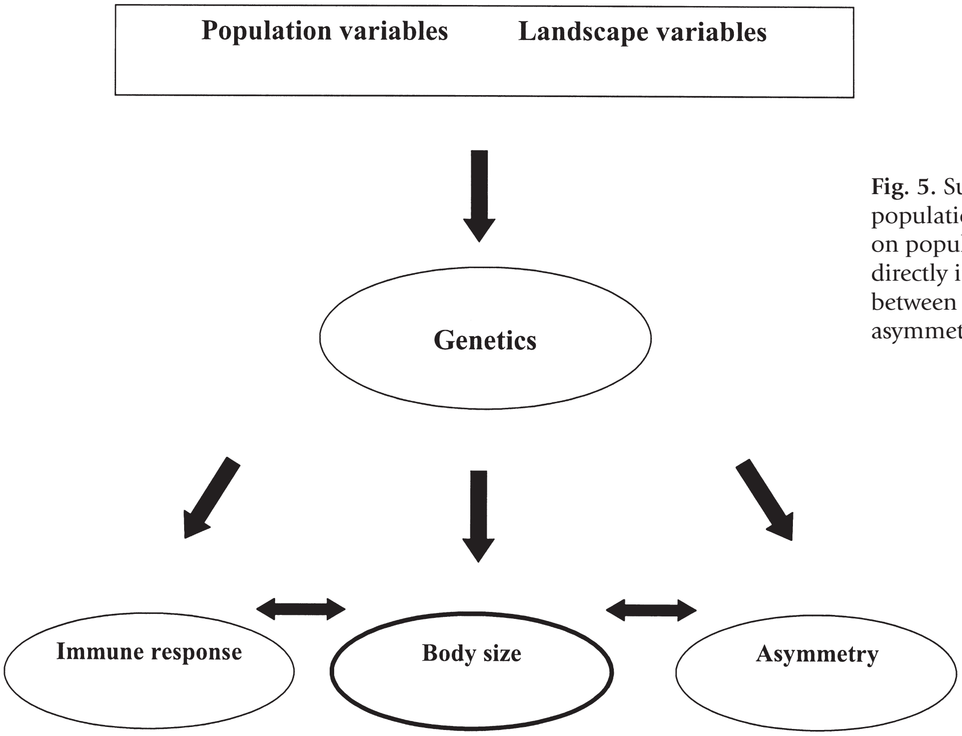

Fig. 5. Suggested functional links between population history and landscape variables on population and individual genetics, which directly influence body size (vertical) and between body size, immune function and asymmetry (horizontal).

with larger males showing a lower degree of melanisation of the cell-mediated immune response to the artificial parasite (using residuals of male length and weight from the data, linear regression r^2 adj $=0.140$, $N=369$, $p<0.001$), Fig.4. This indicates that there is some trade-off between resources put into body growth and resources put into immune defence in Roesel's bushcricket: *i.e.*, individuals that produced larger bodies showed a lower immune response (see also Rantala & Roff 2005). Such a trade-off between body growth and immune response is not unexpected, since substantial energy and nutritional demands are needed for maintenance and activation of the immune defence (Sheldon & Verhulst 1996). The negative relationship between size and encapsulation rate (immune response) in this species, supports the assumption that engaging this part of the immune defence is a costly process and it may be that males that have invested much in becoming large reduce their ability to produce an encapsulation response.

Implications for conservation biology.—Low genetic diversity in a population may influence an individual's morphology and asymmetry (Møller 1998): inbreeding has been seen to reduce body size (Fredrickson & Hedrick 2002). Small individuals often produce fewer offspring (Czesak & Fox 2003, Stauffer & Whitman 1997); thus, a general reduction in body size might further decrease the viability of a small population. A large body size and good immune response are often indicators of good condition (Thornhill & Møller 1998, Rantala *et al.* 2000). Therefore to understand what influences these attributes is valuable in conservation work, both with invading and naturally occurring populations.

My results show that initial population and environmental variables (*i.e.*, large propagules and well-connected landscapes) influence size of individuals, most probably by affecting genetic diversity. Larger individuals were more symmetrical, indicating that during their development they were better able to allocate resources to maintain optimal body growth and symmetry. For adults subjected to an immune challenge, additional effort spent in producing a large body may reduce their ability to defend themselves against diseases and parasites. Therefore there exists a vertical functional linkage of a population's history (*e.g.*, size of population and population growth) together with the landscape that the population inhabits (composition and structure of habitats), to population genetics and individual genetics (genetic diversity/degree of homozygosity), which directly influences individuals' body sizes. Additionally, there is a horizontal functional link between body size, immune function and asymmetry (Fig. 5).

These interactions are on different scales, from landscape ecology to individual physiology. Genetic diversity, which is at the very center of these connections, is primarily dealt with in conservation work through efforts aimed at maintaining or creating habitats and connectivity. From studies on *M. roeseli* there is an increasing body of evidence to suggest that such conservation work would also result in orthopterans producing and maintaining an optimal body size. While the resource trade-off between producing a large body and mounting an immune response will always be present, conservation work focusing on improving habitat connectivity might reduce the severity of this trade-off.

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