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Morphological responses to disturbance in wing-polymorphic carabid species (Coleoptera: Carabidae) of managed urban grasslands

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A disturbance gradient comprising three intensities of management of grasslands in urban parks is used to study the responses of carabid beetles to disturbance. The three levels of disturbance are: mown, intermediate and meadow. GLM is used to analyze the response of two morphological traits to disturbance: body size, macroptery and wing length of brachypterous individuals. The proportion of macropterous individuals was greater in the populations of both disturbed and intermediate sites. Also wing-length of brachypterous individuals was longer in the disturbed and intermediate treatments. For body size, there was no change in mean body size for females, though males were larger in the disturbed and intermediate treatments. These males were similarly sized with females, whereas in the undisturbed treatment, there was strong sexual dimorphism for this trait. I conclude that disturbance results in changes that are important for population dynamics. There is a need for further study of species traits that are affected by disturbance, rather than just species assemblage effects.

Key words: Benign neglect, brachypterous, dispersal, disturbance, Lamarck, lawn, macropterous, semi-natural grasslands, sexual dimorphism, Wing-dimorphic, wing-polymorphic, urban

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INTRODUCTION

Urban Grasslands

Urban environments typically contain a wide variety of semi-natural grassland habitats. These vary from intensely managed lawns and amenity grasslands, through periodically cut habitats, such as roadside verges, to unmanaged grasslands. Lawns in urban parks are amongst the most intensely managed grasslands, generally being mown using tractor-drawn machinery on an approximately 2-week interval. Whilst the long history of this form of management has resulted in some species developing behaviour patterns to help them exploit the resultant lawn habitat, particularly birds of the thrush family

(*Turdus* spp) and starling (*Sturnus vulgaris*), it has also been criticized on ecological grounds for preventing plant species from completing their reproductive cycles. Thus the flora of lawns is dominated by species that colonize vegetatively and those which manage to flower and set seed very rapidly, such as white clover *Trifolium repens*.

Whilst the establishment and management of lawns has been traditionally favoured for reasons of ease and economy (Kendle & Forbes 1997), and a number of popular recreational activities require lawns, many municipalities are considering the adoption of alternative grassland management strategies. The potential economical and ecological benefits resulting from transferring to less intensive grassland management regimes are the main incentive for this change. The term benign-neglect has been applied to the termination of such habitat management regimes (Haila *et al.* 1989). For grasslands, however, the adoption of a less intensive management regime is generally preferable to the complete cessation of management. Mowing once or twice per year produces conditions favourable for many forbs and nectar-feeding insects, whereas cessation of management often results in a habitat that is both aesthetically and ecologically of poor quality.

Habitat management, such as mowing, represents a disturbance regime for at least some taxa (Grime 1979). In the case of mowing a lawn, the impact on different taxa will vary according to their mobility and scale of perception. For bird species of the lawn ecosystem, it is highly unlikely that mowing represents a disturbance, though for plant species, mowing represents a stress that impairs the growth of dominant species but improves growing conditions for shorter forbs in particular. For epigaeic arthropod assemblages, the disturbance of mowing is likely to represent a periodically repeated disturbance.

As well as representing a disturbance regime, mowing also maintains favourable habitat conditions for many sensitive taxa. This has been shown particularly well for nectar-feeding insects, such as the butterfly species *Melitaea cinxtia* (Hanski *et al.* 1995). For the less mobile epigaeic fauna, however, the influence of mowing is not clear. The primary objective of this study is to consider the influence of mowing and its cessation on the carabid assemblage of urban grasslands. The reason for this is to consider the influence of changes in management regime on biodiversity.

Wing morphology in carabids

Carabid beetles are one of a number of insect taxa in which wing morphology can vary considerably within the same species. Thus different individuals within the same population of the same species can have radically different dispersal ability. Species that exhibit two or more wing morphs, generally with a flight capable full-winged (macropterous) form and a reduced winged (brachypterous) form that is incapable of flight, have been referred to as dimorphic, which implies that there are simply two morphs: macropterous and brachypterous. However, in many instances, wing length appears to be a continuous variable, so I consider the term polymorphic to be more appropriate than dimorphic. In addition to wing morphology, there is also variation in development of the flight muscle, with some macropterous individuals being incapable of flight due to undeveloped flight muscles (Desender, Lindroth 1992). Lindroth (1992) also reports observations of individuals with reduced wings that attempt to fly, that clearly possess functional flight muscles. In the present study, flight muscles are not examined and wing morphology is the only measured indicator of potential flight ability.

Lindroth also observed that the proportions of macropterous and brachypterous individuals in populations of wing-polymorphic carabids could vary considerably between populations from the same geographical region. He used such wing morphology data to hypothesize on the colonization routes of carabid species in the Palaearctic region subsequent to the Würmian glacial period (Lindroth 1971?), and he also acknowledged that "environmental factors are likely to influence the distribution of different wing morphs in populations" (Lindroth 1992).

Both Lindroth (1992) and den Boer (1971) considered that the proportion of macropterous individuals in a population was indicative of the age and stability of the population. A stable and long established population should contain almost exclusively brachypterous individuals, as dispersal ability is not advantageous in these circumstances. By means of breeding experiments, Lindroth (1949) has shown that for *Pterostichus anthracinus,* macroptery is determined by a recessive gene, with macropterous individuals being homozygous recessive. If we assume, as Lindroth (1992) and den Boer did, that macropterous species are adapted for colonization, then a newly founded population will be composed of macropterous individuals and their progeny. In reality it is likely that some colonizers might be brachypterous individuals, as species that are entirely brachypterous are also capable of dispersal and colonization of new habitats. Clearly though, individuals that have functional wings in addition to strong legs are better adapted to disperse. Indeed if newly founded populations are composed entirely of homozygous recessive macropterous species, then that population will remain macropterous unless there is an inoculation of brachypterous individuals. The only other possibility for development to a wing-polymorphic population is if brachypterous individuals are produced as the result of a mutation. Thus in a newly founded population of a wing polymorphic species, the population should either 1) remain macropterous (homozygous recessive) or 2) acquire the brachyptery gene and produce a gradually increasing proportion of brachypterous individuals and eventually develope a brachypterous population with a small number of macropterous individuals. Being better adapted for dispersal, a proportion of these macropterous individuals will emigrate, further reducing the proportion of macropterous individuals in the population. This fraction of emigrating individuals should increase as the population size approaches its carrying capacity, as competition for resources increases the incentive to disperse. Thus an old, stable population is likely to be composed of almost entirely brachypterous individuals and correspondingly a less stable population should contain more macropterous individuals.

A number of more recent studies using carabids have suggested that when disturbance increases, the numbers of specialist, large bodied and poorly dispersing species decrease in abundance, whilst generalist, small bodied effective dispersers increase (Rushton *et al*. 1989, Blake *et al.* 1994, Niemelä *et al.* 2000 & Grandchamp *et al.* 2002).

In this study I compare the wing morphology ratios of wing-polymorphic species under three treatment regimes, 1) lawn - mown at c. 2 weekly intervals, 2) intermediate - mown at two weekly intervals until the previous season and thereafter not managed, 3) meadow - unmanaged for >10 years. Assuming that mowing constitutes a disturbance for epigaeic carabid populations of these habitats, I consider that this design represents a disturbance gradient with treatment (1) lawn as intensive disturbance, treatment (3) meadow as undisturbed and treatment (2) as intermediate. Treatment 3 should thus represent a stable population, treatment 1 an unstable population and treatment 2 an intermediate population. My hypothesis is that there should be a higher proportion of macropterous individuals in the lawn treatment, a small proportion in the meadow treatment and intermediate in the intermediate treatment. I will also compare the wing lengths of brachypterous specimens to see if there is any change in wing length along the disturbance gradient.

MATERIALS AND METHODS

Study sites

Five urban parks in the city of Helsinki were used for this study. Each site contained **(1)** an area of grassland that had been managed intensively (mown lawn) for many years previously (intense disturbance), **(2)** an area of formerly mown grassland that had been unmanaged for c. 10 years previously (unmanaged/minimal disturbance) and **(3)** an area of formerly mown grassland that had been mown until one year prior to the onset of this study but was subsequently left unmanaged (intermediate disturbance), except for the site Hertakannas Crematorium Park, in which there was no meadow treatment.

Study design

Sampling was performed using 140 plastic pitfall traps of 67mm diameter. Traps were placed 10 m apart in transects of 10 per treatment and contained propylene glycol (50% aqueous) as a preservative. Lids of 10 cm^2 were placed over the traps to prevent inundation. The traps were set on 7/5/2003, emptied monthly and maintained until 16/9/2003. The trapped carabid beetles were identified to species using Lindroth (1985, 1986).

Analyses

GLM

Wing morph was analyzed by means of generalized linear model (GLM) using the negative binomial distribution, as has been recommended for taxa with an aggregated distribution (Niemelä *et al.* 1992). The tested factors are macropterous vs. brachypterous for all carabid species and wing length of brachypterous individuals of wing polymorphic species, and with gender as a categorical variable. A randomized block design was employed, though it was incomplete due to the absence of one treatment from one site. A hierarchical design of trap nested in site was used. The statistical package R 1.7.1 was used for the statistical analyses.

RESULTS

The total catch consisted of 1902 carabid beetles, belonging to 40 species. The most abundant species were *Bembidion properans* (28.9% of total catch), *Pterostichus melanarius* (14.1%) and *Harpalus rufipes* (9.46%).

DISCUSSION

My previous paper on this study (Venn & Rokala 2005) considered the effects of disturbance, in this case mowing, on beetle size and flight at the species level. This was accomplished by categorizing species into five size classes and as flight capable, flightless or wing dimorphic. That study showed that, in accordance with Gray`s hypothesis that larger sized species should be predominant when disturbance is less intense, the smallest size class was more numerous in the most disturbed treatments and the largest size class was most numerous in the least disturbed treatments (Gray 1989). Also the proportion of flightless species decreased with increasing disturbance and the proportion of flight capable (pioneer) species increases, in accordance with Gray`s hypothesis, that the proportion of flight capable pioneer species should increase with increasing disturbance. Furthermore individuals of dimorphic species increased strongly with increasing disturbance, in keeping with the suggestion that wing dimorphism is an adaptation to overcome dispersal barriers.

In the present study, I have tested the same hypotheses but at the individual level, using the factors body size, wing morphology and length of wing fragments of individuals with reduced wings, in place of species values derived from the literature. This enables me to test the actual variation of wing morphology and body size within species. The results show that mean body size is unaffected by disturbance for females though male body size was considerably smaller in the undisturbed treatment (Fig. 1). This result is the opposite to the prediction of Gray`s hypothesis, whereby body size should decrease with increasing disturbance.

For wing morphology the results were in keeping with Gray`s hypothesis. The proportion of macropterous individuals was much less in the undisturbed meadow treatment (Fig. 2). For females the mean value was much smaller than for males, though the amount of variation was also much greater. Measurement of the wing fragments

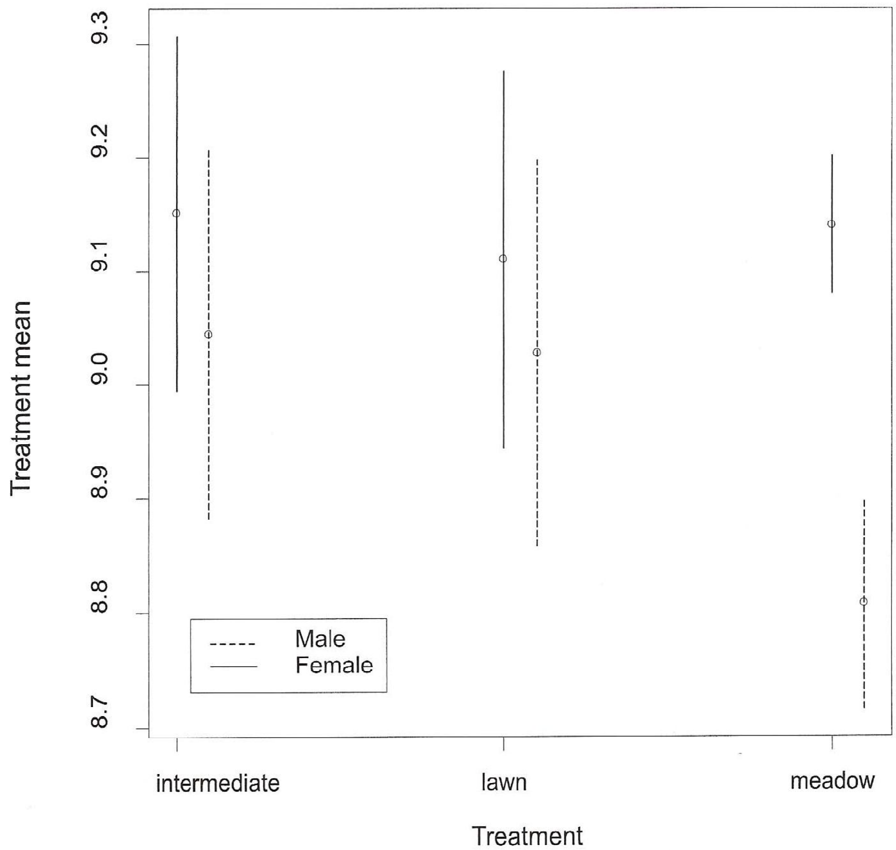

Fig. 1 Male body size is smaller at the meadow (unmanaged) sites than on both of the other treatments. There is no significant difference in female body size between the treatments, though the variation is markedly less in the meadow population, suggesting greater stability

of brachypterous individuals showed furthermore that the wings were smaller for individuals from the least disturbed treatment (Fig. 3). This is also in keeping with Gray's hypothesis, that flight ability should be more developed in individuals from more disturbed treatments. In this case males showed the greater difference in wing size between more and less disturbed treatments (Fig. 3).

For all three of these analyses there was no discernable difference between the most disturbed (lawn) treatment and intermediate (mown until previous season).

These results thus support the hypothesis that increased levels of disturbance result in increased investment in flight ability. The similarity in the results for the most disturbed treatment (lawn) and intermediate (undisturbed for one season) suggest that there is a delay of more than one year before any reduction in this adaptation to disturbance. It would be interesting to repeat the study in subsequent seasons in the same sites, to see whether there is evidence of a subsequent reduction in macroptery and wing size with time in subsequent seasons after the cessation of mowing and, if so, how rapidly this change

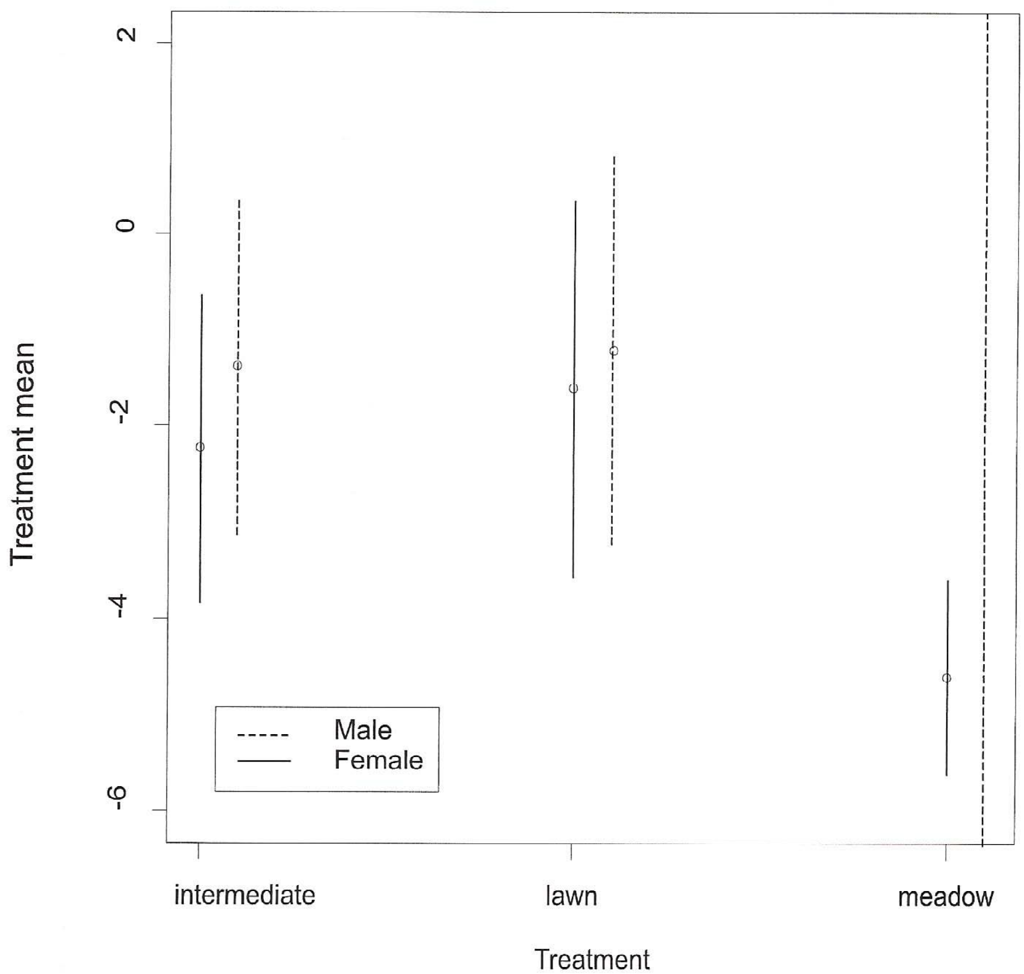

Fig. 2 Less macropterous individuals in meadow (unmanaged) populations, particularly females. In this case, the variation is greatest in the meadow treatment.

then spreads through the population. The morphology of individuals from the undisturbed meadow treatment should be regarded as the normal situation, and that of the other two treatments as the response to disturbance. Thus these results seem to also indicate that another affect of increasing disturbance is reduced sexual dimorphism in these traits, as there is considerable variation between the results for males and females for all three of the measured traits in the meadow treatment, and very little such variation from the two disturbed treatments.

These results appear to show that, for males in particular, there is a shift towards macroptery and larger body size as disturbance increases, presumably because smaller sized and brachypterous individuals are lost from the population. For the larger females, their body size is already sufficiently large to enable persistence

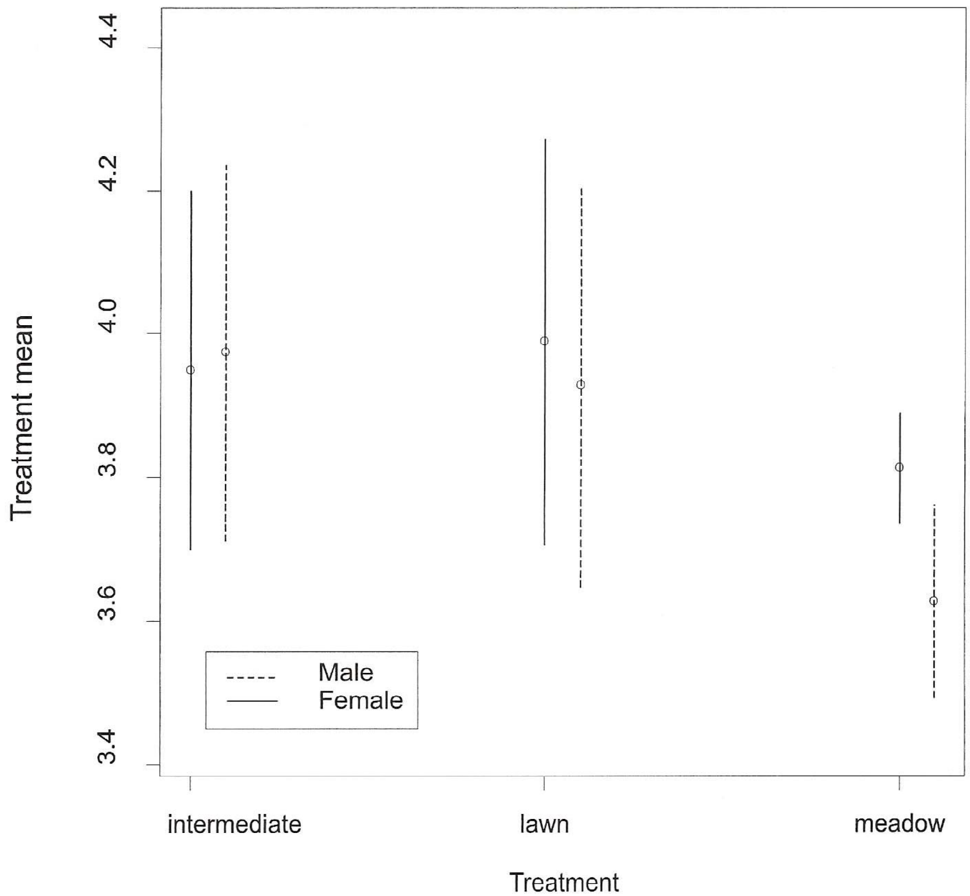

Fig. 3 Wing rudiments are smaller in individuals from meadow populations, particularly in males.

in a disturbed site, though disturbance results in a considerable reduction in the proportion of brachypterous individuals.

The increase in length of wing fragments of brachypterous individuals with increasing disturbance seems at first puzzling, as it is difficult to conceive of a longer non-functional wing conferring any kind of advantage to individuals in persisting in a disturbed site. This could suggest that there is continuous variation between brachyptery and macroptery, with increasing mean wing fragment length leading towards the production of macropterous individuals. However, such an explanation seems to be Lamarckian and to defy explanation in terms of natural selection.

I conclude that whilst disturbance effects on community composition are well documented for many taxa in a variety of disturbed habitats, this study shows that there are also complex effects on population dynamics, and traits affecting fitness. This suggests that, changes in species composition of communities is inadequate for assessing the ecological impacts of disturbance. There is clearly a need for the developement of other indicators for assessing the ecological impacts of disturbance. Genetic studies to elucidate the mechanisms behind the phenotypic responses observed in this study are also necessary, as there are many issues that are not resolvable on the basis of phenotype data.

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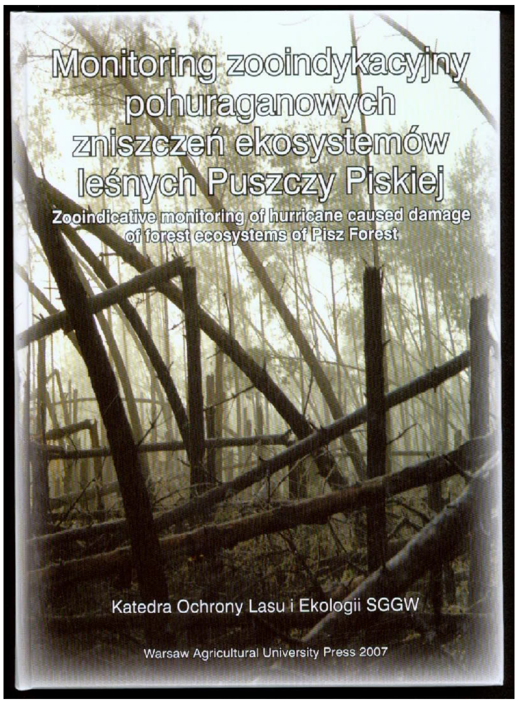

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