Baltic J. Coleopterol. 8(2) 2008
ISSN 1407 - 8619

Body size differentiation in selected carabid species inhabiting Puszcza Piska forest stands disturbed by the hurricane

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Garbalińska P., Skłodowski J. 2008. Body size differentiation in selected carabid species inhabiting Puszcza Piska forest stands disturbed by the hurricane. *Baltic J. Coleopterol., 8(2): 101 - 114.*

Intraspecific differentiation in body size was investigated for *Carabus arcensis*, *C. violaceus* and *Pterostichus niger* populations inhabiting pine forests disturbed by the hurricane in July 2002 and left "untouched" as an experimental area ("Szast Reference Forest"; Pisz Forest District, NE Poland). Non-affected control stands were established in Maskulińskie Forest District (NE Poland). Beetles were sampled using pitfall traps. The hurricane contributed to significant reduction in both *C. arcensis* and *C. violaceus* mean body length. However, an opposite trend was observed for *P. niger* which increased considerably in body size in disturbed stands compared to control ones. The most pronounced changes were observed in 2007. Differences in habitat preferences and food resources utilization of *C. arcensis*, *C. violaceus* and *P. niger* are discussed.

Key words: body length, body size, *Carabus arcensis*, *Carabus violaceus*, disturbance, hurricane, intraspecific differentiation, *Pterostichus niger*

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** Financial support of project 5041003040015 founded by Rector of Warsaw University of Life Sciences*

INTRODUCTION

Body size considerably determines many aspects of life history i.e. reproduction rate, dispersal, resource utilization, energetical balance or competition (Brandl and Topp 1985, Magura *et al*. 2006, Sota *et al*. 2000, Šustek 1987). Modification in body size among particular species individuals may be also interpreted as indicator of ecosystem state (McGeoch 1998, Niemi and McDonald 2004).

Body size differentiation induced by environmental changes has been frequently observed in ground beetle (Coleoptera: Carabidae) assemblages. These beetles are commonly used in zooindicative monitoring studies as they are ecologically diverse, taxonomically well known and may be easily sampled using pitfall traps (Bouget 2005, Ings and Hartley 1999, Poole *et al*. 2003, Schwerk and Szyszko 2007a, 2007b, Skłodowski 1995, 1997, 2007, Szyszko 1983, 1990, Szyszko *et al*. 2000, 2006). Szyszko (1983, 1990, see also Schwerk and

Szyszko 2007a, 2007b, Szyszko *et al*. 2000) was the first to hypothesize that human-created disturbances as clear-cuts decrease the mean individual biomass (MIB) in carabid assemblages by up to 75%. Also Skłodowski observed carabids' MIB decline following clear-cutting (1995, 1997, 2002, 2006), gap-felling (2002), as well as soil preparation, fertilization, acidification or alkalization (1995, 1997). Reduction in mean body size was reported for assemblages inhabiting forest ecosystems under urbanization pressure (Grandchamp *et al*. 2000, Magura *et al*. 2004, 2006, Niemelä *et al*. 2002). A significant decrease in MIB was noticed in forest stands subjected to natural disturbances i.e. fires (Skłodowski 1997) and hurricane (Skłodowski 2007b, Skłodowski and Garbalińska 2007a, 2007b, 2007c, Skłodowski and Zdzioch 2005a, 2005b, 2006).

Regardless of whether the disturbance was natural or anthropogenic a similar pattern was observed: disturbed ecosystems were colonized by small-sized open-habitat and eurytopic species, whereas large forest species (including *Carabus* Linnaeus, 1758 representatives) declined in abundance or even diminished (Bouget 2005, du Bus de Warnaffe and Lebrum 2004, Grandchamp *et al*. 2000, Koivula *et al*. 2002, Magura *et al*. 2006, Niemelä *et al*. 2002, 2007, Skłodowski 2002, 2006, 2007b, Skłodowski and Garbalińska 2007a, 2007b, 2007c, Skłodowski and Zdzioch 2005a, 2005b, 2006, Szyszko 1983, Šustek 1987). However, some of the authors cited (Brandl and Topp 1985, Grandchamp *et al*. 2000, Magura *et al*. 2004, 2006, Niemelä *et al*. 2002) have used literature data on particular species mean body size instead of measuring or weighting the carabids caught [as Szyszko (1983) and Skłodowski (1995, 1997, 2002, 2006, 2007b) did], thus disregarding the aspect of intraspecific body size differentiation among local populations.

It seems therefore interesting to verify, whether the hurricane-caused disturbance of forest ecosystem may also contribute to modification in particular species mean body size. In our study the following hypotheses were investigated: (i) the hurricane-caused disturbance of forest stand induces changes in the mean body size of particular forest carabid species, (ii) changes in the mean body size may vary depending on particular species biology.

MATERIAL AND METHODS

Study area

Carabid beetles sampling was carried out in "Szast" Reference Forest (Pisz Forest District) which is 445-ha remnant of pine forest disturbed by the hurricane on July 2002 and set aside without any human interference as an experimental area (hereafter referred to as "P" site). Since spring 2003 the post-hurricane stands have been investigated by the Department of Forest Protection and Ecology of Warsaw University of Life Sciences. Control areas have been established in non-affected Maskulińskie Forest District (hereafter referred to as "M" site). Both post-hurricane and control study plots were localized in fresh coniferous forest and comprised stands in five different age classes: class I (20-40 years old), class II (40-50 years old), class III (50-60 years old), class IV (60-80 years old) and class V (above 80 years old). Forest stands in each of the age classes distinguished have been investigated in three recapitulation, making a total of 30 study plots in the two districts.

Carabids sampling

Beetles were sampled using modified pitfall traps. Each trap consisted of 0.5 l glass jar (10 cm in diameter) set into the ground up to its upper edge and filled with 100 ml 70% ethylene glycol as killing and storing agent. A plastic funnel (12 cm in diameter) was put on each of the jars to extend the trap's catching range and to prevent small vertebrates from being caught. Additionally each of the traps was covered with a roof (wooden square 20 cm x 20 cm placed approximately 5 cm above each trap) protecting from the rainfall and litterfall. On each of the study plot 5 pitfall traps were installed from the beginning of May till the end of October and emptied every 6 weeks.

Data analysis

All carabid beetles caught were subsequently identified to the species level and measured with an accuracy of 0,5 mm, where the "body length" was defined as the distance from the front margin of mandibles to the apical part of the elytrae. Three forest large zoophages, namely: *Carabus arcensis* Herbst 1784, *C. violaceus* Linnaeus 1758 and *Pterostichus niger* (Schaller 1783) were chosen for further investigation as they had been caught on all post-hurricane and control plots numerously enough for statistical analysis. For each of these species the mean body length and the median value of body length were calculated for years 2003 – 2007 following the disturbance. Statistical analysis was conducted using Statistica package [Statistica; StatSoft, Inc. (1997)]. The data obtained were tested for normality of distribution with the Shapiro-Wilk's test. As the data distribution was aberrant from the normal distribution type, non-parametric Mann-Whitney U test was applied to assess differences between study plots investigated.

RESULTS

Altogether, the body length of 3919 *Carabus arcensis*, 1096 *C. violaceus* and 711 *Pterostichus niger* representatives was analyzed.

In years 2003 – 2007 a decline in *C. arcensis* mean body length was observed both in post-hurricane and control stands (Fig. 1). More pronounced differences concerned control populations, nevertheless in disturbed stands a reduction from 18,37 – 18,25 mm (years 2003 – 2005) to 18,08 mm in 2007 was also significant ($p < 0,005$-$0,001$). Almost every year *C. arcensis* representatives inhabiting „P" plots were smaller compared to those from control ones (Fig. 1). In 2004 the difference reached 0,44 mm ($p < 0,001$), whereas in 2007 – 0,06 mm ($p < 0,05$).

The decreasing body length pattern in *C. arcensis* "P" populations was confirmed by differences observed between the mean and the median value of body length. The differences recorded appeared to be positive, nevertheless

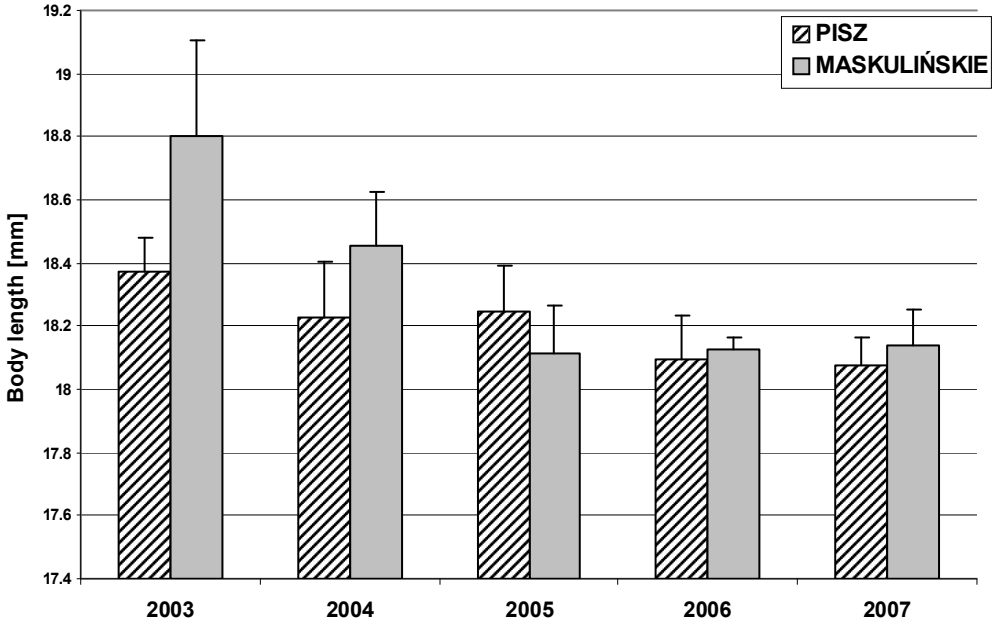

Fig. 1. The mean body length for *Carabus arcensis* individuals inhabiting post-hurricane (Pisz) and control (Maskulińskie) stands in years 2003-2007.

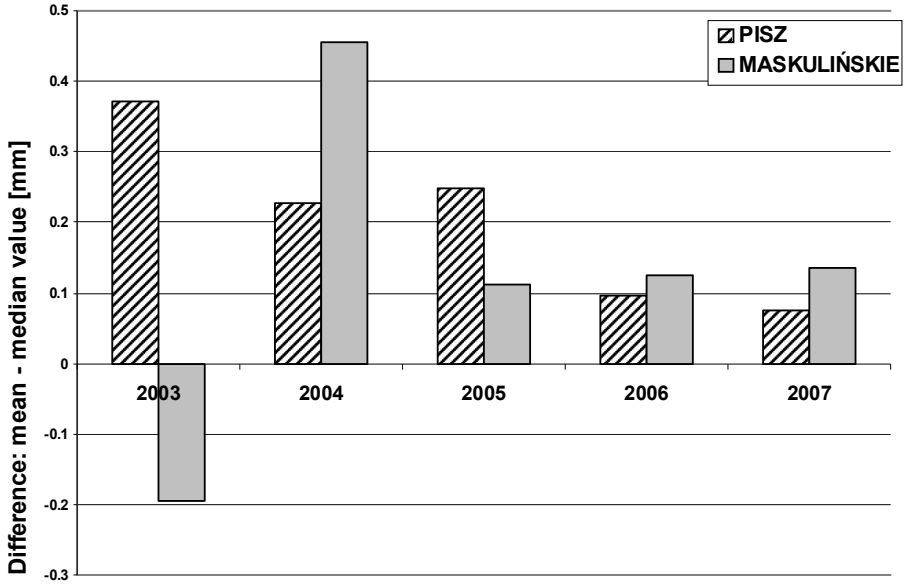

Fig. 2. The differences between the mean body length and the median value of body length for *Carabus arcensis* individuals inhabiting post-hurricane (Pisz) and control (Maskulińskie) stands in years 2003-2007.

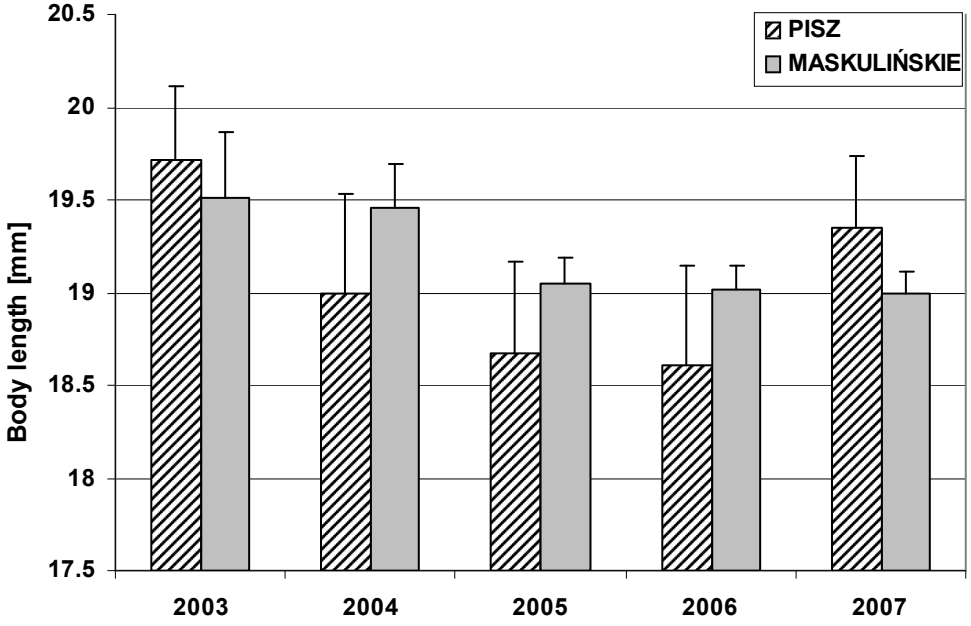

Fig. 3. The mean body length for *Pterostichus niger* individuals inhabiting post-hurricane (Pisz) and control (Maskulińskie) stands in years 2003-2007.

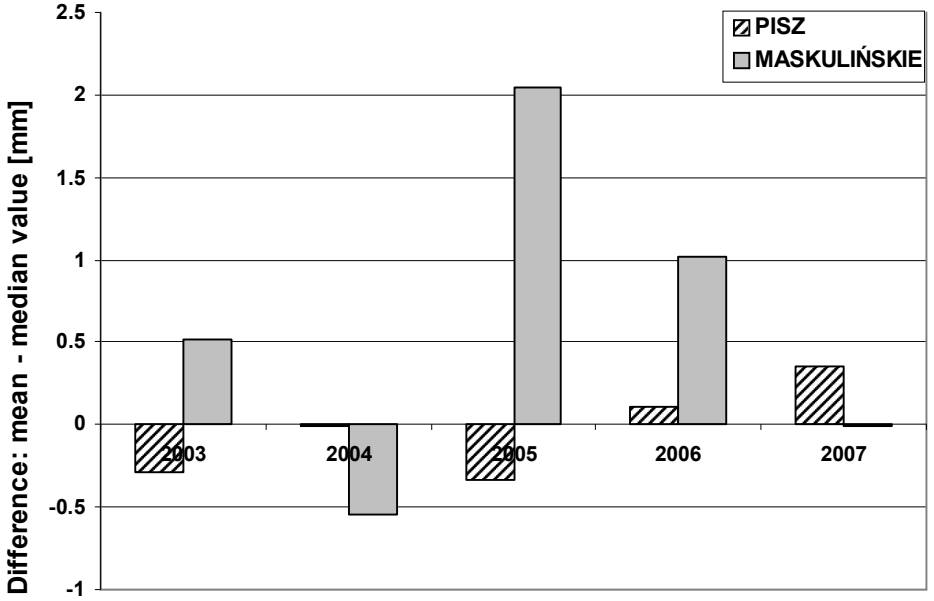

Fig. 4. The differences between the mean body length and the median value of body length for *Pterostichus niger* individuals inhabiting post-hurricane (Pisz) and control (Maskulińskie) stands in years 2003-2007.

systematically declined in the following years (Fig. 2) indicating an affinity to investing in smaller individuals after the disturbance.

The largest *P. niger* representatives were observed in disturbed stands one year after the hurricane (Fig. 3): 19,72 mm compared to 18,60 mm – 18,99 mm in years 2004 – 2006 ($p < 0,005$ – 0,001). In 2007 *P. niger* mean body length again increased to 19,35 mm, which was by 0,68 – 0,75 mm larger in comparison with "P" stands in 2005 – 2006 ($p < 0,005$ – 0,001) and by 0,36 mm ($p < 0,005$) larger than in control stands in 2007 (Fig. 3).

On control plots a considerable variation in the differences between *P. niger* mean body length and the median value of body length were recorded (Fig. 4). The data obtained for disturbed stands were significantly less variable and revealed a distinct trend towards positive, increasing values (Fig. 4) indicating a shift in mean body size towards larger individuals.

After the hurricane a gradual decline in *C. violaceus* mean body length was observed with the lowest value recorded in 2006 – 28,06 mm (Fig. 5). Mean body size of 28,60 mm recorded in "P" stands in 2007 was still significantly lower than 29,66 mm in 2003 ($p < 0,001$), 29,37 mm in 2004 ($p < 0,001$) and 28,93 mm in 2005 ($p < 0,05$). Even though in 2003 *C. violaceus* representatives were by 0,37 mm larger on disturbed plots compared to those from control area ($p < 0,005$), in the following years the situation has reversed in favour of control populations (Fig. 5). In 2006 the *C. violaceus* mean body length on "P" plots was by 0,83 mm reduced in comparison with "M" site ($p < 0,001$).

By the year 2005 the differences between the mean and the median value of body length recorded for *C. violaceus* individuals were similar at both study sites, nevertheless in the following years a distinct diversification between "P" and "M" populations could be observed (Fig. 6). In post-hurricane stands the difference between the

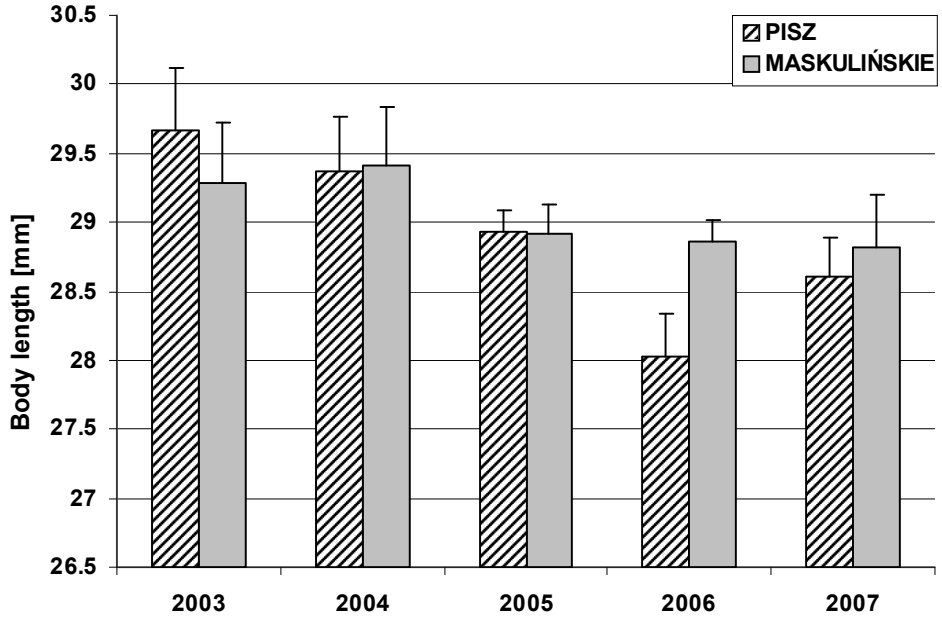

Fig. 5. The mean body length for *Carabus violaceus* individuals inhabiting post-hurricane (Pisz) and control (Maskulińskie) stands in years 2003-2007.

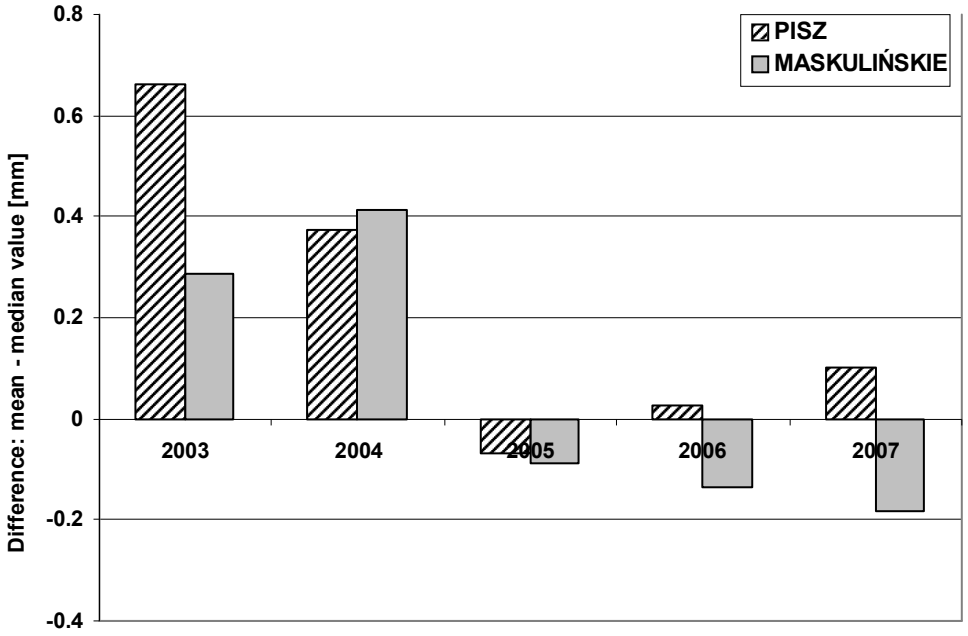

Fig. 6. The differences between the mean body length and the median value of body length for *Carabus violaceus* individuals inhabiting post-hurricane (Pisz) and control (Maskulińskie) stands in years 2003-2007.

mean and the median value of body length was positive indicating a shift in the *C. violaceus* mean body size towards larger individuals. On the other hand in control populations a gradual decrease in the difference between the mean and the median value of body length was recorded, which could be related to numerous appearance of small-sized individuals.

DISCUSSION

Results obtained are discussed below in order of the hypotheses put forward.

Hypothesis (i): The hurricane-caused disturbance of forest stand induces changes in the mean body size of particular forest carabid species

Hurricane-caused disturbance initiates a series of profound changes in forest ecosystem structure and function which afterwards influences all organisms inhabiting it (Bengtsson *et al*. 2000, Bouget 2005, Bouget and Duelli 2004, Chapin *et al*. 2002, Pickett and White 1985, Pickett *et al*. 1999, Skłodowski 2007a, Szwagrzyk 2000, Ulanova 2000). In Puszcza Piska forest the hurricane contributed to – among others – considerable reduction in the proportion of forest species – to 60%, European species – to 28% and large zoophages – to 47% (Skłodowski and Garbalińska 2007c). On the other hand carabids typical of early stages of forest ecosystem succession increased significantly in species richness and abundance. By the year 2007 the proportion of hemizoophages reached 33%, open-habitat species – 30%, eurytopic species – 11%, whereas macropterous species – 37%. Moreover, the share of xerophilous fauna in carabid assemblages markedly increased at the expense of hygrophilous species (42% *vs*. 10% respectively) indicating soil and litter layer desiccation in post-hurricane stands (Skłodowski and Garbalińska 2007c).

Modification in environmental condition should also contribute to changes in the mean body size of forest carabid species. According to the expectation, a clear tendency towards mean body length reduction was noticed for *C. arcensis* (Fig. 1) and *C. violaceus* (Fig. 5). A similar observation was made in years 2003-2006 for *P. niger*, however in 2007 this species seemed to have taken the strategy towards prevalence of large-sized individuals in population (Fig. 3).

Carabids body size to a large extent depends on habitat and food conditions of larval development (Luff 2005, Niemelä 1993, Schwerk and Szyszko 2006, Sota *et al*. 2000). Carabid larvae are weakly chitinised and less mobile compared to adults, thus they are particularly sensitive to habitat changes. This especially concerns large species with long larval period (Grandchamp *et al*. 2002, Magura *et al*. 2006, Turin *et al*. 2003).

Body size may be determined among others by climatic conditions (Sota *et al*. 2000) and vegetation type (Palmer 1994). Habitat fertility also matters. As reported by Skłodowski from Białowieża Primeval Forest (2005a, 2005b) species typical of fertile habitats grow bigger there compared to populations inhabiting poor habitats, whereas carabids characteristic of poor sites are larger there than at fertile sites. Furthermore, any habitat transformation such as induced by urbanization, contribute to the reduction in carabid body length, for instance in *C. nemoralis* populations as shown by Weller and Ganzhorn (2004).

In post-hurricane stands most of the trees are broken or overturned thus the soil and litter layer are exposed to intensive sun and wind activity. An increased microclimatic variability, e.g. daily and seasonal temperature variation or higher frequency of frosts (Bouget 2005, Bouget and Duelli 2004, Ulanova 2000) could be crucial for *C. violaceus* which overwinters as larvae. Moreover, reduced site humidity is also relevant as the presence and abundance of many forest carabids, among others – *C. violaceus* is conditioned by the moisture level of soil and litter layer (Pearce and Venier 2006, Sroka and Finch 2006, Turin *et al*. 2003).

Body size that larva can reach is largely dependent on its food resources quantity and quality (Luff 2005, Niemelä 1993, Schwerk and Szyszko 2006, Skłodowski 2005a, 2005b, Turin *et al*. 2003). Furthermore, larvae of many *Carabus* species cannot starve for more than just few days (Turin *et al*. 2003). Many authors pay attention that larger adults develop from larvae that grew in favourable feeding conditions (Sadler *et al*. 2006, Schwerk and Szyszko 2006).

In disturbed forest ecosystems the food resources for carabid larvae can be considerably limited (Grandchamp *et al*. 2000, Magura *et al*. 2006), e.g. Sławska and Sławski (2007) observed profound changes in assemblage structure and significant reduction in abundance of Collembola in post-hurricane stands. It may be therefore concluded that the decline in the mean body size of *C. arcensis*, *C. violaceus* and *P. niger* confirms the hypothesis (i) set. Moreover, the results obtained clearly suggest poor feeding situation for larval stages of species analyzed. It seems however essential, that response to the hurricane-induced changes in forest ecosystem may vary between particular carabid species.

Hypothesis (ii): Changes in the mean body size may vary depending on particular species biology

Differences between the mean body length and the median value of body length recorded (Fig. 2, 4, 6) suggest that particular species may show different patterns in body size adaptation to hurricane-induced habitat changes. A negative difference between the mean and the median value of body length indicates a prevalence of small-sized individuals in population, whereas a positive result characterizes population where large-sized individuals dominate. Any directive tendency towards either increase or decline in the difference between the mean and the median value of body length may reveal a non-random pattern in the species mean body size modification brought about by environmental changes.

This difference recorded for *C. arcensis* in control stands was to a large extent variable, whereas in case of post-hurricane populations a distinct trend towards positive but decreasing values was observed (Fig. 2). A shift in the mean body size in favour of smaller individuals could be then ascribed to the hurricane-caused changes to forest ecosystem.

An opposite trend was observed for *P. niger*. The difference between the mean and the median of body size recorded in post-hurricane stands increased with the time after the disturbance towards positive values (Fig. 4), thus indicating a shift in the mean body size towards larger individuals. In control stands no such trend could be distinguished.

For *C. violaceus* in both control and post-hurricane populations a decrease in the difference between the mean and the median value of body length was observed indicating the prevalence of small-sized individuals over large-sized ones. In disturbed stands however this trend seemed to be less pronounced in 2006 and 2007 (Fig. 6).

In Poland *C. arcensis* is commonly known as thermophilous species typical of old, light pine forests, however it also inhabits forest ecotones and open areas as pit-bogs and clear-cuts (Skłodowski 2002, Turin *et al*. 2003). Skłodowski (2001b, 2002) observed that this carabid beetle colonizes clear-cuts effectively and quite rapidly after clearance resulting in higher catchability there compared to adjacent stands. Of all species considered *C. arcensis* would be then most favoured by habitat conditions in post-hurricane stands. It is therefore not surprising that in years 2005-2007 it was significantly more abundant in canopy gaps compared to control area (Skłodowski 2007b, Skłodowski and Garbalińska 2007a, 2007b). However the systematic decline in its mean body size after the hurricane could seem quite unexpected.

The tendency towards *C. arcensis* body length reduction accompanied by its population

increase in disturbed stands might thus involve competitive interactions. Sota *et al*. (2000) observed *Carabus japonicus* body length decline in sympatry with *C. dehaanii*, whereas there was no such reduction in allopatric *C. japonicus* populations. Similarly, representatives of *C. albrechti* allopatric populations were larger than in populations sympatric with *C. insulicola* and other carabids. These authors also noticed that the body size ratio between particular species in an assemblage depends on the species number. The proportion between the largest and the smallest species increased with the number of species, whereas the size ratio between 2 species with adjacent body length showed an inverse trend and decline with the number of species (Sota *et al*. 2000). According to the authors cited these results could be ascribed to character displacement and character release – as morphological character (e.g. body length) of a species changes depending on the presence or absence of its competitors. Therefore the interspecific overlap in body size is almost absent or considerably limited even in species-rich assemblages and thus particular carabid species are able to coexist successfully. Also Brandl and Topp (1985) noticed, that the interspecific variation in body size of coexisting *Pterostichus* species is consistent with competition theory, at least in stable ecosystems that are rarely subjected to disturbances (e.g. moors).

Analogously, variation in body size could be also considered on a single species level in relation to intraspecific competition. Thus the reduction in *C. arcensis* mean body length could be interpreted as a result of its increased abundance and competitive interactions between its representatives in post-hurricane stands. Such assumption to some extent concerns also *C. violaceus*, however it gives no explanation for *P. niger* body length changes after the hurricane.

Particular species may reveal different patterns in hurricane-induced body size modification according to their diet requirements and food resources utilization. *P. niger* feeds on caterpillars, butterflies, spiders, mites, ants and beetles which are considerably less confined to moist habitats than slugs and earthworms – the major preys of *C. arcensis* and *C. violaceus* (Skłodowski 2002). Dense and diverse forest floor vegetation developing vigorously in sun-exposed canopy openings favours many phytophagous and anthophilous insets i.e. sawflies, butterflies, moths, beetles (especially Chrysomelidae and Curculionidae), aphids, bugs and hymenopterans (Bouget and Duelli 2004, Magura 2002), that *P. niger* can hunt for. On the other hand many earthworms tend to avoid soil and litter layer desiccation by migrating deep into the soil (Górny 1975), thus being less available for epigeic predators such as *C. arcensis* and *C. violaceus*.

Morphological differences among species analyzed are also worth considering. Both *C. arcensis* and *C. violaceus* are convex in shape and have smaller metatrochanters (they are "fast runners" according to Evans 1977), unlike the *P. niger*, which is considerably more flatten. Relatively flat body and well developed trochanters of the hind legs enable *P. niger* to penetrate the litter layer and narrow crevices under bark or under stones ("strong wedge-pusher" according to Evans 1977). In post-hurricane stands the moss cover, litter layer and soil profile remain almost intact (Bouget 2005, Bouget and Duelli 2004, Skłodowski 2007b, Skłodowski and Garbalińska 2007a, 2007b, 2007c, Skłodowski and Zdzioch 2005a, 2005b, 2006, Ulanova 2000). Litter layer is commonly known to be of vital importance for forest carabids as foraging and development site as well as a shelter from predators or unfavourable climatic conditions, e.g. drought, frost (Koivula *et al*. 1999, Niemelä and Halme 1992, Niemelä *et al*. 2007, Pihlaja *et al*. 2006, Poole *et al*. 2003, Skłodowski 2002, 2007b, Sroka and Finch 2006). Also hurricane-created coarse woody debris calls for attention as it provides wide range of microhabitats for saproxylic organisms (Bouget and Duelli 2004). Jabin *et al*. (2004) observed that dead or dying stumps, snags, logs, branches and uprooted trees lying on the ground attract great diversity of carabids' potential prey, such as millipedes, arachnids, isopods as well as larvae and adult insects – particularly on forest edges

and areas lacking canopy cover (thus also in canopy openings). Moreover, dead wood lying on the ground is often cracked and its bark is loose which make it accessible for some of the epigeic predators for both hunting as well as avoiding other predators or overwintering (Bouget and Duelli 2004, Skłodowski 2003). Apparently of all species investigated *P. niger* is the most effective in penetrating both the dry-out and dense litter layer as well as coarse woody debris in post-hurricane gaps. Skłodowski (2003) confirmed, that *P. niger* was amongst the carabids most numerously caught from decaying stem wood in Białowieża Primeval Forest.

In the light of results obtained the hypothesis (ii) seems to be confirmed. Patterns in body size modification in response to hurricane-caused disturbance are to a large extent conditioned by differences in species biology and ecology. These differences particularly concern both diet requirements as well as effectiveness in food resources and sheltering sites utilization in disturbed stands. Moreover, in case of *C. arcensis* the influence of intensified intraspecific competition could also be considered, as this species increased significantly in abundance in canopy openings. Both the litter layer and coarse woody debris provide large variety of sheltering and hunting microhabitats that seem to be most suitable for *P. niger*. Will this carabid beetle regard disturbed stands as optimal habitat worth "investing" in large individuals? Hopefully, the following years of our study on carabid assemblages inhabiting post-hurricane ecosystem will dispel these doubts.

CONCLUSIONS

1. Hurricane-induced habitat changes contributed to significant modifications in carabids body length – hypothesis (i): confirmed.

2. Patterns in body size change varied between particular species depending on their biology – hypothesis (ii): confirmed.

3. For both *C. arcensis* and *C. violaceus* populations inhabiting disturbed ecosystem a significant reduction in body size was observed. Such trend could be ascribed to hurricane-caused unfavourable habitat conditions. In case of *C. arcensis* intraspecific competition could also be considered in relation to its increased abundance in canopy openings.

4. A significant increase in *P. niger* mean body size observed in disturbed ecosystem indicates favourable conditions for its larvae development in canopy gaps. An assumption can be made that of all species analyzed *P. niger* is the most effective in utilizing food resources and sheltering microhabitats potentially available in post-hurricane stands. It particularly refers to its ability to penetrate the litter layer and coarse woody debris lying on the ground.

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Received: 28.09.2008.
Accepted: 01.12.2008.