Dynamics of local expansion by an introduced species: Pterostichus melanarius III. (Coleoptera, Carabidae) in Alberta Canada.

Niemelä, J.

Blackwell

1999


http://hdl.handle.net/1975/313

Downloaded from Helda, University of Helsinki institutional repository.
This is an electronic reprint of the original article.
This reprint may differ from the original in pagination and typographic detail.
Please cite the original version.
Dynamics of local expansion by an introduced species: Pterostichus melanarius Ill. (Coleoptera, Carabidae) in Alberta, Canada

JARI NIEMELÄ and JOHN R. SPENCE* Department of Ecology and Systematics, PO Box 17, FIN-00014 University of Helsinki, Finland. E-mail: jari.niemela@helsinki.fi, *Department of Biological Sciences, CW405A, Biological Sciences Building, University of Alberta, Edmonton, Alberta, T6G 2E9 Canada

Abstract. A recently established population of Pterostichus melanarius Ill., a wing-dimorphic, introduced carabid beetle species, was studied over a 7-year period in Alberta, Canada. We monitored local colonization, and tested classical hypotheses about spatial and temporal changes in proportion of flight-wing morphs in the Carabidae. Between 1991 and 1997, a sizable population in a road verge (0.17 individuals/trap/day in 1991) expanded only slowly into an adjacent aspen-poplar forest: the catch of 0.005 ind./trap/day in the forest in 1997 was not significantly higher than that of 0.001 ind./trap/day in 1991. However, a significantly higher proportion of P. melanarius were macropterous, long-winged (LW) in the forest (80%) than in the road verge and at the forest edge (54%). This supports the hypothesis that newly established populations are characterized by a high proportion of LW individuals, and further indicates that dispersal from the road verge into the forest has taken place primarily through flight. The overall proportion of flightless, brachypterous individuals (SW) captured at the study site increased from 39% in 1991 and 1992 to 57% in 1997, supporting the hypothesis that the proportion of SW individuals will increase with time since establishment of a population. Captures of P. melanarius in the forest were patchy and concentrated in particular areas throughout the study. However, these bridgehead populations did not grow or expand obviously, suggesting that populations adapt to forest conditions or reach some threshold size before effective expansion.

Key words. Biological invasions, expansion, distribution, carabids, Canada.

INTRODUCTION

Expansion of species into new areas is assisted by humans through international trade, travel and landscape modification, bringing about homogenization and ‘Europeanization’ of biotas (Elton, 1958; Spence & Spence, 1988; Spence, 1990). For instance, nearly 2000 insect species of European origin have established in North America during the past 500 years (Niemelä & Mattson, 1996). One of the most successful epigaeic arthropod invaders from Europe, in terms of spread and abundance, is the wing-dimorphic carabid beetle Pterostichus melanarius Ill. (Niemelä et al., 1997).

P. melanarius was first recorded in Edmonton (Alberta, Canada), >1000 km from the nearest probable port of entry (Vancouver, British Columbia), in 1959 (Madge, 1959). After a remarkable local population build-up, it is today among the most common carabid species within 60–80 km of the Edmonton city centre (Niemelä & Spence, 1991). It is especially abundant in urban habitats and agricultural areas surrounding the city (Cárano et al. 1995). However, the species is also invading aspen-poplar forest habitats, and is the most numerous species in some forest areas (Niemelä & Spence, 1991). A survey of the distribution of the species around Edmonton suggested that P. melanarius populations expand into rural areas, first along road verges, and then more slowly colonize adjacent deciduous forest (Niemelä & Spence, 1991).

In this paper, we examine local expansion and changes in wing-length proportions of P. melanarius in a road verge and an adjacent aspen-poplar forest in central Alberta. In particular, we test the following hypotheses developed by Lindroth (1949): (1) If flight
is an important means of dispersal for early colonists, the proportion of long-winged individuals ought to be higher in newly founded populations ('parachute' effect), and (2) if the short-winged form is genetically dominant, the proportion of SW individuals should increase over time after a population is established. Based on these hypotheses and our previous observations we predicted that (1) if P. melanarius is expanding into the aspen forest from the adjacent road verge, numbers should be higher in the forest in 1997 than in 1991; (2) proportion of LW individuals should be higher in more distant areas of forest than in the road verge, if colonization of such new areas is mainly by flight; and (3) as the populations in both the road verge and in the forest grow older, the proportion of LW individuals decreases with time (Aukema et al. 1996). Although these propositions are widely accepted and used to interpret data about expanding insect species, they have not been tested for single populations of carabids or, to our knowledge, other insects.

MATERIALS AND METHODS

Phenology of P. melanarius in central Alberta

In central Alberta, activity of P. melanarius adults peaks in July/August with the emergence of new breeders (Niemelä et al., 1997). These beetles mate and lay eggs the same year. Larvae overwinter in the second or third instar, and development is completed the following summer (Aukema et al., 1996). In Alberta, few adults are captured early in the season (May to June), and we found no adults that overwintered twice during a 4-year field experiment, it appears that overwintering by adults is rare in our study area (Niemelä et al., 1997).

Field site and trapping design

This study was conducted at the George Lake Field Site, located some 75 km north of Edmonton (for habitat descriptions, see Niemelä et al., 1992). To our surprise, P. melanarius was common in 1990 in traps located in a grassy road verge of Provincial Highway 651 at George Lake (Niemelä & Spence, 1991). Some individuals were also found in the adjacent aspen-poplar (Populus tremuloides-P. balsamifera) forest. No representatives of this species had been encountered at George Lake during an extensive study of the ground-beetle assemblages in 1981–82 (Niemelä et al., 1992), or in previous work at the Field Site, although large collections had been made in these same spots. This apparent expansion of P. melanarius prompted us to study the local distribution of the species in more detail.

We established trap-lines in the ≈10 m wide, southern road verge of Highway 651 and up to 800 m into the adjacent aspen-poplar forest. In 1991, 11 lines, consisting of pairs of pitfall traps, located ≈2 m apart, were established parallel to the highway forming a regular trap grid. The first line was near the middle of the grassy road verge, and the second line was 5 m into the aspen-poplar forest. The next nine lines were spaced at 50 m intervals, proceeding northward into a large (>1800 ha) block of continuous mixed wood aspen forest. A pair of traps in each of these lines was located in the grassy road verge (≈5 m wide) of a narrow dirt road providing access to the George Lake field station and running perpendicular (N–S) to the highway. Another pair of traps was set 5 m into the forest from the dirt road. The remaining pairs of traps were set 50 m apart, perpendicular to the access road. Thus, a regular grid of pairs of traps was established. Because we expected few captures of P. melanarius in deep forest, traplines more than 400 m from the highway were separated by 100–150 m. The three first lines closest to highway 651 were established on May 20, and the remaining eight trap lines were established on 3 June. The total grid of 106 traps were in operation until 19 September and were checked seven times at bi-weekly intervals.

In 1992, the trap layout was similar to that in 1991 but lines 100 m, 200 m, 300 m, and 400 m from the highway 651 were not operated. A total of 66 traps were in operation from 10 May until 21 September; these were checked seven times.

In 1997, single traps were used, and no traps were placed in the verge of the field station access road. It was not possible to consistently locate the exact trap sites used in 1991 and 1992, and thus the 1997 data must be treated as representing different microsites than before, although general locations were similar. Five traps, set 50 m apart, were placed parallel to highway 651 in the middle of the grassy verge, and
another line was established 5 m into the forest. In addition, 15 parallel lines 50 m apart were set out in the forest north of the highway. The last trap line, located 800 m from the highway, was the same as in 1991 and 1992 but more trap lines were established in the zone 400-800 m from the highway. The 85 traps were operated from 3 July to 19 August to provide a regular grid that covered an area of 200 x 850 m.

The traps used were similar plastic cups (diameter 100 mm) each year, and they were partly filled with propylene glycol as a preservative, as described by Spence & Niemelä (1994). All carabids collected in the traps were counted and P. melanarius were identified, sexed and assessed for wing-length. As only fully winged individuals of P. melanarius are expected to be able to fly (van Huizen, 1980), beetles were divided into two wing-length classes: SW (short-winged, wings rudimentary, not reflexed at pterostigma) and LW (long-winged, flight wings reflected under the elytra).

RESULTS

Expansion of P. melanarius at George Lake

In all, 690 specimens of P. melanarius were captured during the 3 years of trapping, comprising 9% of the total carabid catch. The species was clearly most numerous in the grassy verge of highway 651, where 533 individuals were captured. Abundance of the species dropped rapidly towards the forest interior: 88 individuals were captured in the forest edge (5 m from the verge), 44 individuals in traps 50 m into the forest, and only 25 individuals in traps 100 m or more into the forest (Fig. 1a). Due to high variation in catch among traps these differences were only marginally significant (Table 1). The distribution of catches of P. melanarius varied somewhat over the years, as follows: 75-80% in the road verge, 7–17% in the forest edge (5 m from the verge), 4–11% in the forest interior 50 m from the highway, and 1–7% in the forest interior 100 m or more from the highway (Fig. 1b). Due to high variation in catch among traps these differences were only marginally significant (Table 1). The distribution of catches of P. melanarius varied somewhat over the years, as follows: 75–80% in the road verge, 7–17% in the forest edge, 4–11% in the forest interior 50 m from the highway, and 1–7% in the forest interior 100 m or more from the highway (Fig. 1b).

There was a weak, increasing trend in overall catch of P. melanarius during the period of the study from 1991 (0.022 individuals/trap/day) through 1992 (0.036) to 1997 (0.057), despite the removal of beetles through trapping (Fig. 1). However, the increase in catches of P. melanarius between the years was not statistically significant (Table 1).

Expansion of P. melanarius from the road verge into the forest has been slow over the 7-year period. In the forest interior (100 m or more from the highway), catches standardized by the trapping effort were not significantly higher in 1997 (0.005 ind./trap/day) than in 1991 (0.001) (t-test comparing same trap lines: t = 0.22, d.f. = 12, P = 0.83) (Fig. 1a).

Proportion of macropters in the forest

Over the study period, about half (55%) of P. melanarius captured were long-winged, but the proportion of macropters was significantly lower in the road verge and forest edge [up to 50 m from the verge (54%)] than further into the forest (80%) (Fisher's exact test, P < 0.001) (Fig. 2). Furthermore, each year there was a positive correlation between the proportion of long-winged P. melanarius and distance from the road verge (1991 Spearman r_s = 0.94; 1992 r_s = 0.87; 1997 r_s = 0.80; all P < 0.001).

In addition, the proportion of LW specimens decreased during the course of the study. In both 1991 and 1992, the overall proportion of LW individuals was 61%, while in 1997 it had dropped to 43%. The drop from 1991–92 to 1997 was significant in the road verge and forest edge (5–50 m) (t-test: 1991–92 t = 0.55, d.f. = 4, P = 0.61; 1991–97 t = 4.93, d.f. = 4, P = 0.008; 1992–97: t = 4.28, d.f. = 4, P = 0.013). Also in the forest interior, the proportion of LW individuals decreased somewhat (Fig. 1); in 1991–92, 78% (seven individuals) of the specimens collected further than 50 m from the road were long-winged, but in 1997, the proportion had dropped to 69% (11 individuals).

Correlation of P. melanarius and native species

A trap-wise analysis showed that the number of P. melanarius and the pooled number of the native species were positively correlated, although in 1992 the correlation was not statistically significant (1991 Spearman r_s = 0.37, n = 53, P < 0.01; 1992 r_s = 0.19, n = 33, ns; 1997 r_s = 0.29, n = 94, P < 0.01). There were also significant positive correlations in trap-wise occurrence between the subsequent years 1991 and 1992, both for P. melanarius (Spearman r_s = 0.79, n = 33, P < 0.001) and for the native species (Spearman r_s = 0.73, n = 33, P < 0.001) implying temporal constancy in spatial distribution. Data from 1997 were excluded from this analysis as the exact trap locations differed somewhat.

© 1999 Blackwell Science Ltd, Diversity and Distributions, 5, 121–127
Our predictions were more or less satisfied. We expected that *P. melanarius* was expanding into the aspen forest from the adjacent road verge. However, the expansion was slow, and catches were not higher in the forest in 1997 than in 1991–92. This is perplexing because the species is common in similar aspen–poplar forest within and near Edmonton (Niemelä & Spence, 1991, 1994), and a 4-year enclosure experiment at George Lake showed that *P. melanarius* can survive, reproduce and...
Table 1. Factorial ANOVA (trapping lines and years) on standardized catches in the verge, edge, 50 m into the forest, and 100–350 m into the forest during the 3 years of sampling (1991, 1992 and 1997)

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Line</td>
<td>3</td>
<td>0.27322</td>
<td>0.09107</td>
<td>4.40</td>
<td>0.0585</td>
</tr>
<tr>
<td>Year</td>
<td>2</td>
<td>0.07155</td>
<td>0.03578</td>
<td>1.73</td>
<td>0.2557</td>
</tr>
<tr>
<td>Error</td>
<td>6</td>
<td>0.12431</td>
<td>0.02072</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>11</td>
<td>0.46909</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

persists in this same forest (Niemelä et al., 1997). However, some of the experimental populations dropped to very low levels indicating that some microhabitats may be less favourable for *P. melanarius*.

We also predicted that the proportion of LW individuals should be higher in the forest than in the road verge because long-distance colonization would primarily involve flight. This prediction was supported by our data as virtually all individuals collected further than 50 m from the highway were long-winged. Colonization by flight has been suggested by Desender (1985, 1989) to be of primary importance in wing-dimorphic carabid species. *P. melanarius* is able to fly as individuals have been collected in light traps and flight intercept traps in Europe (van Huizen, 1980; Czechowski, 1989; Kadar & Szél, 1989), but we have no direct evidence for flight of this species in Alberta.

Third, as predicted, the proportion of LW specimens decreased as the populations at George Lake grew older and brachyptery gained dominance. Based on single-pair, cross-breeding experiments, Aukema et al. (1996) showed that wing dimorphism in *P. melanarius* is inherited in a simple Mendelian fashion with brachyptery being the dominant form. SW alleles are presumably brought into the forest population at George Lake by LW females that have copulated with SW males before flying to the forest to lay eggs. Furthermore, LW individuals may be lost from the population due to emigration (Desender, 1985, 1989; Desender et al., 1998).

The proportion of LW *P. melanarius* was lower in 1997 than in 1991–92 especially in the oldest populations in road verge and forest edge. This supports results by Aukema et al. (1996) who reported that the proportion of LW *P. melanarius* was 25–95% in recently established populations, but only 0.4–1.7% in old populations in the Netherlands and Belgium. However, even the lowest proportion (42%) LW specimens observed in the road verge at George Lake in 1997 is within the range of 25–95% macropters for young populations in Europe. Niemelä & Spence (1991) found no populations in Alberta where the proportion

![Fig. 2. Proportion (%) of long-winged individuals (i.e. probably able to fly) of *P. melanarius* in the trap-lines during the three study years (the scale is logarithmic). Note that in 1992 trap lines 100 m, 200 m, 300 m and 400 m from the verge were not in operation.](image-url)

of LW specimens approached levels characteristic of long-established European populations (<2%) reported by den Boer (1970) and Haeck (1971).

Spatial distribution of *P. melanarius* and the native species

Although negative interactions between indigenous and introduced species have been detected (Pimm & Gilpin, 1989; Coblentz, 1990), not all introductions lead to extinctions of indigenous species (Elton, 1958). Furthermore, it may be notoriously difficult to demonstrate such interactions and effects (Simberloff, 1981; Usher et al., 1992; Case, 1996). In the present study, catches of *P. melanarius* and the indigenous species were positively correlated, as has been found in surveys of other populations (Niemelä & Spence, 1991, 1994), and in a field experiment in the George Lake forest (Niemelä et al., 1997). This suggests, on the one hand, that *P. melanarius* does not have a strong and consistent negative effect on the occurrence of the indigenous species, and, on the other hand, that the indigenous species are not able to prevent *P. melanarius* from invading the forest.

Furthermore, we found a positive year-to-year correlation between catches for both the indigenous species and *P. melanarius*. This is not surprising for *P. melanarius*, as during all years most of the individuals were found along the road verge and the forest edge. However, the basis of high correlation between years is not clear for the indigenous species, although it indicates temporal consistency in the spatial distribution within the forest at George Lake. This finding is in accordance with the high predictability reported for soil communities in temperate forests (Bengtsson, 1994).

CONCLUSIONS

Lindroth's (1949) hypotheses about changes in wing-morph proportions were corroborated by our results. These results complement genetic studies on wing-length determination in *P. melanarius* (e.g. Aukema et al., 1996) and zoogeographical work on the distribution of the species in Canada (e.g. Spence & Spence, 1988; Niemelä & Spence, 1991), and provide additional support for the zoogeographical interpretations. For instance, our study supports previous findings that wing-morph proportions do provide a reasonable measure of age of a population for colonizing carabid species. Desender et al. (1998) showed that dispersal ability (measured as the wing length) of the saltmarsh carabid *Pogonus chalceus* individuals decreased with the age of the population, probably due to continuous emigration of winged individuals (see also Desender, 1985, 1989). Furthermore, it appears that the selective and genetic processes involved in changing wing-morph ratios are repeated locally, especially at habitat boundaries. Changes in wing-length proportions observed at George Lake imply that *P. melanarius* spreads by individuals walking from the road verge to the forest edge while longer distance movement to the forest interior is primarily by flight. As expected the overall proportion of short-winged specimens increased, especially in the road verge, during the 7-year study.

Our study shows that the local expansion of *P. melanarius* has been surprisingly slow from a substantial population in the road verge into aspen-poplar forest. It appears that several generations will be required before significant population build-up occurs in the forest. However, based on high forest populations elsewhere in similar forests and success of *P. melanarius* in enclosures at George Lake, we predict that the population in the forest will reach a level high enough for rapid population growth within the next few years. It is of interest to understand whether such changes are strictly a matter of population size per se, or whether local adaptation to new habitat conditions is also required.

ACKNOWLEDGMENTS

We thank K. Cryer, J. Hammond, A. Heming, A. Meyer and B. Spence for assistance with field work, and G. Ball and K. Desender for constructive comments on the manuscript. The work was supported by an NSERC Research Grant to JRS, and by a Killam Postdoctoral Fellowship and Academy of Finland grant (no. 39715) to JN.

REFERENCES


van Huizen, T.H.P (1980) Species of Carabidae (Coleoptera) in which the occurrence of dispersal by flight of individuals has been shown. *Entomologische Berichten, Amsterdam*, 4012, 166–168.