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Range expansion pattern of *Carabus granulatus* Linnaeus, 1758 (Coleoptera: Carabidae) in eastern North America and a new northern range record

Kaitlyn Fleming[1,*] and David V. Beresford[2]

[1]*Environmental and Life Sciences Department, Trent University, 1600 West Bank Drive, Peterborough, ON, K9L 0G2 Canada*
[2]*Biology Department, Trent University, 1600 West Bank Drive, Peterborough, ON, K9L 0G2 Canada*
E-mail addresses: kaitlynflemin@trentu.ca (K. Fleming), davidberesford@trentu.ca (D.V. Beresford)
**Corresponding author*

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Abstract

This paper reports the first record of *Carabus granulatus* L. from Moosonee, Ontario. The record extends the range of the species northward in Ontario by approximately 200 km. *Carabus granulatus* was first introduced into North America in 1890 from Europe. The historic area of *C. granulatus* in North America was plotted against year. The square root of area occupied by *C. granulatus* was linear over time ($R^2 = 0.96$, a type 1 expansion curve) a pattern associated with expansion driven by neighbourhood diffusion.

Key words: invasive species, neighborhood diffusion, radial expansion, distribution, ground beetle

Introduction

Carabus granulatus Linnaeus, 1758 is a European species that was originally introduced into North America in 1890 (Brown 1940; Lindroth 1956; Lindroth 1957). It is an invasive species in North America and has dispersed throughout Canada and several northern States in the United States (Brown 1940; Larson and Langor 1982; Bell et al. 2014).

Invasive species can be described by three types of expansion curves when invading a new region, based on the dispersal strategies employed: type 1 in which the range follows a linear expansion, type 2 is biphasic, the expansion beginning slowly and then entering a linear expansion at a faster rate than type 1, and type 3 in which expansions produce a convex curve, continuously increasing with time (Shigesada and Kawasaki 1997). When initially colonizing a new area, species disperse at a slower rate and as the population increases, the rate of dispersal and colonization of the surrounding area increases.

We examined records for *C. granulatus* (*C. g. forma typica* and *C. g. hibernicus*) to identify the dispersal pattern of *C. granulatus* as it expanded throughout eastern North America. The wings of *C. granulatus* are normally reduced and the species flightless but macropterous specimens are known from central Europe and flight records have been reported (Lindroth 1961; Erwin 2007).

Material and methods

We collected specimens using pitfall and pan traps which were deployed to survey the Carabidae and other terrestrial insects. Pitfall traps were constructed using 500 mL cups (plastic SOLO cups) half-filled with killing fluid of propylene glycol. The pan traps were constructed from 12oz plastic bowls and filled with killing fluid of soapy water three-quarters of the way full. Pitfall and pan traps were deployed for 24 and 48 hours (respectively) from 19 July 2015 to 28 July 2015 (Supplementary material Table S1). A separate survey was conducted between 2009 and 2014 in Northern Ontario using the same trapping methods. The Far North Terrestrial Biodiversity Project and the Natural Heritage Project sampled 531 locations across Northern Ontario (Ontario Biodiversity Council 2015). These sites were sampled and no *C. granulatus* were collected (Figure 1). Specimens were identified to species using published keys

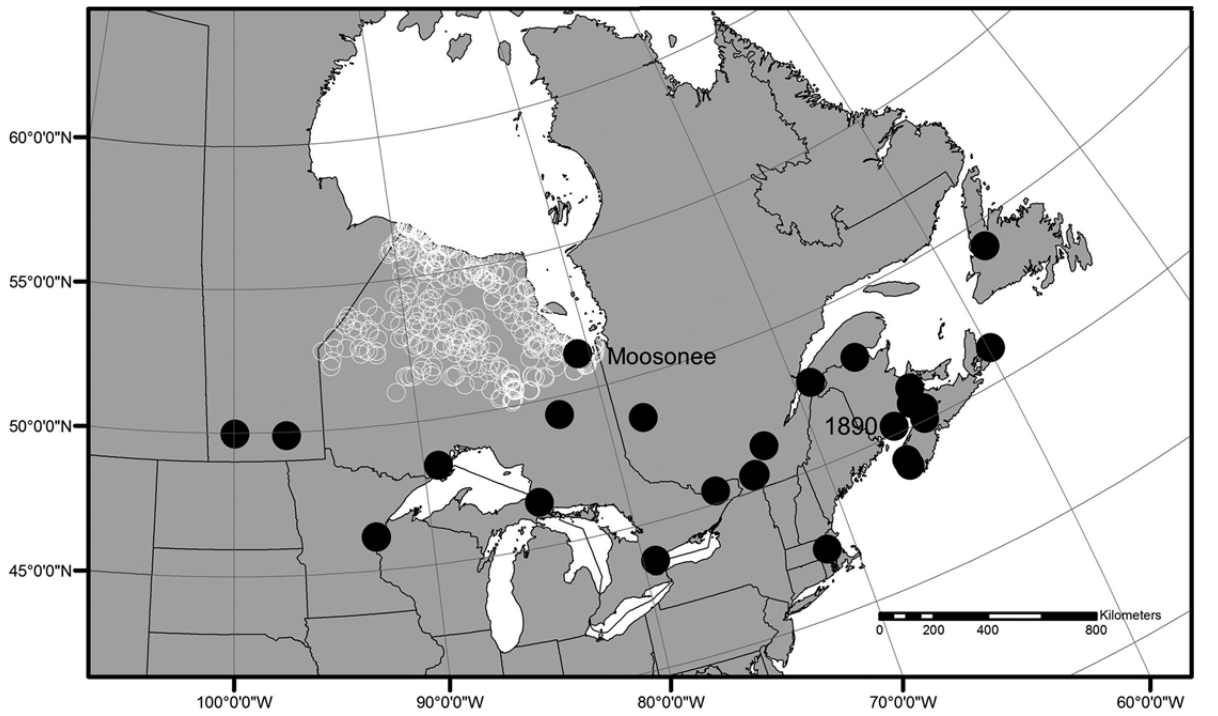

Figure 1. Map of Eastern half of Canada and Northeastern United States locations (Brown 1940; Lindroth 1961; Larson and Langor 1982; Pearce et al. 2002; Majka et al. 2006; Klimaszewski et al. 2012; Piascik 2013; Bell et al. 2014). Black circles denoting locations *C. granulatus* has been collected and used for the analysis (see details in the Supplementary material Table S2). Open, white circles are the 531 locations surveyed (Ontario Biodiversity Council 2015) at which no *C. granulatus* were collected. Map constructed using ARC GIS 10.4.1 for Desktop (Base map 2005, Lambert_Azimuthal_Equal_Area).

(Lindroth 1961; Bousquet 2010). All specimens are housed in the Entomology Collection at Trent University.

Historic collection data on *C. granulatus* were obtained from insect collections and institutions including the Canadian National Collection, Nova Scotia Museum, Nova Scotia Agricultural College, University of New Brunswick, the University of Manitoba and the Joyce Cook collection (Table S2). Specimen that fell within the expanding invasion region were excluded from the analyses. Collections located at Laurentian University and The Canadian Museum of Nature were checked and contained no *C. granulatus*.

Analysis

Previously documented sightings of *C. granulatus* were compiled from the published literature and museum collections (Table S2) and plotted on a map (Figure 1). For each year after the initial sighting, we determined the expansion area by drawing a polygon on the map using the reported sightings as the corners, to obtain the area (km^2) of each polygon (*Make A Topo Map* application Ontario Ministry of Natural Resources and Forestry 2015). We then plotted the square-root of the occupied area against time (years), and fitted a straight line using EXCEL (Skellam 1951; Shigesada and Kawasaki 1997). The analysis was conducted twice, once excluding the Winnipeg and Minneapolis locations, and once including these locations. It was unknown whether the documented sightings in Winnipeg and Minneapolis originated from the East coast expansion or the West, as there was a separate documented introduction in western North America. Therefore, the analysis of the east coast expansion was conducted twice.

Results and discussion

We caught 13 *Carabus granulatus* adults, 7 (3m and 4f) in 2011 (51.28º, −080.64º) and 6 (3m and 3f) in 2015 (ca. 51.2º, −080.22º) (Table S1; Figure 2). All specimen collected in Moosonee have short, rudimentary flightless (Lindroth 1961) hind-wings confirming Lindroth's observation of rudimentary wings among *C. granulatus* in North America. Between

Figure 2. Photograph of male *Carabus granulatus* (20 mm) collected Moosonee, July 2015 showing the bronze color and dull luster of the elytral carinae and tubercles typical of *C. granulatus*.

2009 and 2014, various locations across Northern Ontario were sampled and no *C. granulatus* were collected (Figure 1, locations denoted with open circles). Initially, the historic collection data were not included in the analyses. However, even after the inclusion of 12 additional data points, the results of the analyses did not change. From the initial introduction in 1890, the spread of *C. granulatus* was linear when plotted as square root of area over time for both analyses: with Winnipeg Manitoba and Minneapolis, Minnesota excluded ($\sqrt{}$area = 9.50x – 17924; R^2 = 0.95, Figure 3), and included ($\sqrt{}$area = 10.54x–19979; R^2 = 0.91, Figure 3). The invasion pattern was a type 1 expansion curve (Shigesada and Kawasaki 1997) which appears to have entered the saturation phase (Figure 3).

The range expansion of *C. granulatus* is consistent with neighbourhood diffusion outward from sources of introduction (type 1 curve). Based on reported collection records we could not identify an establishment phase. However, *C. granulatus* may have been present in North America at low levels prior to 1890. The model assumes that first detection is when the invasive species was first established. However, due to the large size of *C. granulatus*, the presence would be noted by entomologists.

Carabus granulatus has been found throughout much of Canada and some of the northern states of the U.S.A. (Lindroth 1961; Bell et al. 2014). Based on the European-wide distribution, which extends from the British Isles to the Pacific Ocean and throughout the boreal region to the middle of western Siberia to the north, we would expect that this species would be able to occupy both agricultural and wilderness regions

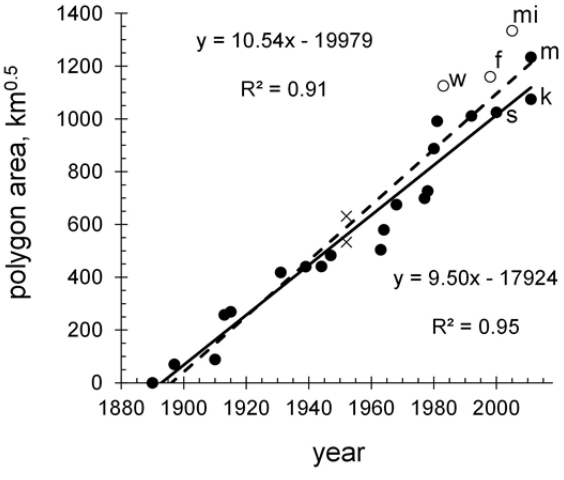

Figure 3. Locations where *C. granulatus* has been found in Eastern half of Canada and northeastern United States (see Supplementary material Table S2 for dates), since first reported at St. John New Brunswick in 1890 (Brown 1940). The solid line denotes the expansion of *C. granulatus* including Winnipeg, Manitoba (w) and Minneapolis, Minnesota (mi). The dashed line denotes the expansion of *C. granulatus* excluding Winnipeg, Manitoba (w) and Minneapolis, Minnesota (mi). The Toronto and Montreal occurrences are denoted with Xs. The empty circular marks represent the expansion of *C. granulatus* with the inclusion of both the Winnipeg and Minneapolis occurrences. The first initial of the locations where *C. granulatus* was collected were used to demark the differences between the polygon area (km^2) of the same location with and without the inclusion of Winnipeg and Minneapolis (w – Winnipeg, f – Forrest, s – Sault Ste. Marie, mi – Minneapolis, k – Kapuskasing, and m – Moosonee).

throughout Canada, excluding the Arctic (Lindroth and Bangsholt 1985). The presence of *C. granulatus* across all Canadian provinces is evidence that populations are consolidating (Bell et al. 2014).

The inclusion of the Winnipeg and Minneapolis locations in the analysis did not change the type of expansion *C. granulatus* exhibited (Figure 3). However, from the higher R^2 value when Winnipeg and Minneapolis were excluded (Figure 3) we argue that these two locations were not likely colonized from diffusion from the eastern expansion. It is more likely that Winnipeg and Minneapolis locations were part of the Western expansion of *C. granulatus* across North America. In support of this, Gandhi et al. (2011) conducted a long-term study of species turnover and succession of Coleoptera in Minnesota from 1980 to 2005. The area was sampled in 1981, 1982 and 2005 with *C. granulatus* only being collected in 2005 (Gandhi et al. 2011). The collection of *C. granulatus* in 2005 does not indicate the exact date *C. granulatus* first occurred in the area. In fact, *C. granulatus* could have appeared in that location in 1983, or it may have been present in 1981 and 1982 but if so it was in low numbers characteristic of an establishment phase and thus not collected. However, based on the rate expansion from St. John, New Brunswick, if *C. granulatus* was in the establishment phase in the Minneapolis area in the early 1980s, we would expect the number of *C. granulatus* collected in 2005 to be higher than 1 individual. If the Winnipeg occurrence in 1983 was part of the eastern expansion, this would indicate that the leading edge of the invasion front had surpassed the final four locations (Sault Ste. Marie, Minneapolis, Kapuskasing and Moosonee) all of which only have records of *C. granulatus* occurring in the 2000s. If this is the case, Sault Ste. Marie, Kapuskasing and Moosonee could indicate range infilling instead of range extensions.

The introductions in Toronto and Montreal were noted by Lindroth (1961) to be a separate introductions of *C. granulatus* and were thus not included in our expansion analysis. Of particular note is the timing of this occurrence with the expansion to Montreal also occurring as expected by the linear model (Figure 3). Although the Montreal occurrence was originally identified to the subspecies *forma typica,* there is no geographic separation of these two (former) subspecies such as occurs in its native Palearctic distributions. As well, with the delisting of the subspecies *hibernicus* (Bousquet 2012; GBIF 2016) it is possible that the Montreal location was part of the expansion. The Toronto sighting provides evidence of continued introductions via shipping from Europe into North America.

In the absence of long distance dispersal processes, an invasive species typically spreads through neighbourhood diffusion resulting in a constant rate of spread (a type 1 or type 2 curve) (Liebhold and Tobin 2008). Based on the relationship of the polygon area (km^2), *C. granulatus* likely spread by diffusion and not through long distance dispersal (Figure 3), aided by anthropogenic travel and the movement of goods such as lumber, produce and soil.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Details of surveys conducted in July 2011 and 2015 in Moosonee, Ontario.

Table S2. Historic records of *Carabus granulatus* in the Eastern half of Canada and Northeastern United States.

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