

# Unexpected niche expansion in a forest-floor ant (Hymenoptera: Formicidae)

● BERNHARD SEIFERT, PATRICK FIEDLER & ROLAND SCHULTZ

**Abstract.** *Temnothorax crassispinus* (KARAVAJEV, 1926) is an extremely abundant ant constructing its nest on or near to the woodland floor of eastern Central Europe. The observed diurnal foraging ranges are very low in the small-sized and short-legged workers of *Temnothorax* species: they do not exceed three meters even on ideally smooth surfaces and there was no suggestion for *T. crassispinus* ever to climb higher than 1.5 m above ground. Catches of workers in branch eclectors and window traps in five mature *Pinus sylvestris* stands near Torgau (Saxony, Germany) would translate into minimum walking distances between 11 and 20 m if these workers originated from nests at forest floor. Two possible explanations are presented: there is an extremely long-range nocturnal foraging to the tree canopies or the foraging range is normal but the ants have their nests in the canopies. An argumentation based on (a) the relative size of the worker population of *T. crassispinus* on the forest-floor, (b) on species-specific behavior during trap contacts and (c) on the foraging range on smooth surfaces relative to the other species caught in the traps showed that canopy nesting was by far the most probable explanation. The findings are discussed in the context of all Central European canopy studies performed in 19 sites with populations of *T. crassispinus* on the forest floor. The data show the reported niche-expansion to be a rare phenomenon which is explained by absence of the specialized canopy ants *T. corticalis* (SCHENCK, 1852) and *T. affinis* (MAYR, 1855).

**Zusammenfassung.** Die Schmalbrustameise *Temnothorax crassispinus* (KARAVAJEV, 1926) ist eine extrem häufige Ameise, die ihr Nest auf oder nahe dem Waldboden im östlichen Mitteleuropa anlegt. Außendienstarbeiter der kleinen und kurzbeinigen *Temnothorax*-Arten entfernen sich bei der Futtersuche auch auf Oberflächen geringsten Raumwiderstandes nicht mehr als drei Meter vom Nest und es gibt keine Hinweise, dass *T. crassispinus* jemals höher als 1,5 m über den Boden klettert. Fänge von Arbeitern in Asteklektoren und Fensterfallen in fünf reifen *Pinus sylvestris* Beständen nahe Torgau (Sachsen, Deutschland) würden Laufdistanzen von mindestens 11 bis 20 m ergeben, wenn diese Arbeiter aus Nestern am Waldboden stammen. Zwei mögliche Erklärungen werden vorgestellt: die Reichweite einer nächtlichen Nahrungssuche zu den Baumkronen ist extrem erhöht oder die Reichweite ist normal, aber die Ameisen haben ihre Nester in die Baumkronen verlegt. Eine Argumentation basierend auf (a) der relativen Größe der Arbeiterpopulation von *T. crassispinus* am Waldboden, (b) dem artspezifischen Verhalten während des Fallenkontakts und (c) dem Nahrungssuchebereich auf glatten Oberflächen relativ zu den anderen, in den Fallen gefangenen Arten zeigt, dass die Anlage von Baumkronennestern die mit Abstand wahrscheinlichste Erklärung ist. Die Funde werden im Kontext aller mitteleuropäischen Baumkronenstudien an 19 Standorten mit *T. crassispinus*-Populationen am Waldboden diskutiert. Die Daten zeigen, dass die dargestellte Nischenerweiterung ein seltenes Phänomen ist, welches durch die lokale Abwesenheit der spezialisierten Baumkronenameisen *T. corticalis* (SCHENCK, 1852) und *T. affinis* (MAYR, 1855) erklärt wird.

**Key words.** *Temnothorax*, niche expansion, ecological release, ecology, tree canopy, Germany, Palearctic Region.

*No matter how many instances of white swans we may have observed, this does not justify the conclusion that all swans are white.*  
KARL POPPER

## Introduction

### The “established” knowledge on an ant species and an unexpected finding

The West Palearctic Myrmicine ant *Temnothorax crassispinus* (KARAVAJEV, 1926) is widely distributed in continental-temperate to continental-submeridional deciduous and pine forests of Europe from about 49°E (Volga River) to 11°E (Central Germany, Austria). It has repeatedly been subject of scientific studies during the last two decades (SEIFERT 1995, RADCHENKO 2000, TÍCHA 2002, STRÄTZ & HEINZE 2004, PUSCH *et al.* 2006a, 2006b, FOKUHL *et al.* 2012, MITRUS 2013). Nests of this small ant are constructed in any microspace on forest floor: dead wood, hollow acorns, nuts or galls, occasionally also leaf and needle litter or snail shells – provided these patches are not too moist and too shady. More rarely nests are situated up to 30 cm above ground surface in the bark of basal tree stems or in dead wood (SEIFERT 2007). Nest populations are small: they average 40 workers in summer and 80 workers in autumn nests (STRÄTZ & HEINZE 2004). Despite the small nest populations, *T. crassispinus* is a highly abundant species of the forest floor – most probably having there a big ecological impact. According to an unpublished long-term study of the senior author, the mean and maximum density on 24 positive Central European woodland test plots was 69 and 410 nests / 100 m<sup>2</sup> and STRÄTZ & HEINZE (2004) recorded as much as 8.6 nests/m<sup>2</sup> for smaller patches of 25 m<sup>2</sup>. Workers forage in litter, cleft spaces of top soil, wood and bark, on free surfaces and forest-floor vegetation usually not higher than 80 cm above ground. As an exception within 33 years of observation time, the senior au-

thor once caught a forager on a tree stem about 150 cm above ground. This experience is in agreement with the recent findings of FOKUHL *et al.* (2012) who determined the mean and maximum foraging distance of *T. crassispinus* on the bottom of *Fagus* forests as 52 cm and 162 cm. According to these authors, the nutrition spectrum is wide: *T. crassispinus* feeds on dead or living small insects such as Collembola, Diptera larvae, imagines of Sternorrhyncha and Nepticulidae (Lepidoptera). Dropped-off honey dew, nectar of forest floor plants or crushed nuts are further food sources and there is considerable myrmecochory and elaiosome feeding with *Chelidonium majus*, *Luzula luzuloides*, *Moehringia trinervia*, *Senecio vulgaris*, *Taraxacum officinale* and *Viola riviana*. All information gathered so far provided no suggestion of occasional foraging of *T. crassispinus* at heights above 1.5 m: it was not listed among the 51 species of the Central European ant fauna observed to forage regularly or occasionally in tree canopies (SEIFERT 2008) and other investigators having much experience with this species (J. Heinze, A. Schulz - pers. comm.) have no observations for foraging above the 1.5 m level.

Against the background of this long history of experience, the following finding appeared as a big surprise. During canopy investigations in nine forest stands situated within 12 km ENE and 10 km W of Torgau/Germany (Saxony), conducted in 2000-2001, workers of *T. crassispinus* were found in branch eclectors and window traps on seven trees in five remote forest stands (FIEDLER 2012). The branch eclectors were mounted at branches of average-sized *Pinus sylvestris* trees in the centre of canopies 14-17 meters above forest floor while the window-traps were positioned in the lower part of the canopies between 11 and 14 meters height. A total of nine *T. crassispinus* workers have been caught in the five sites together with the following species: 30 workers of *Lasius platythorax* Seifert 1991, 24 of *Formica fusca* LINNAEUS, 1758, 16 of *Lasius fuliginosus* LATREILLE, 1798, 11 of *Myrmica ruginodis* NYLANDER, 1846 and two of *Myrmica scabrinodis* NYLANDER, 1846. While the canopy catches of the other ant species are more or less in agreement with existing knowledge on foraging behavior (SEIFERT 2007, 2008), the unexpected finding of *T. crassispinus* foragers raised questions

of what they might really indicate. Here, we consider and discuss the case within the context of canopy investigations in 19 Central European sites in which populations of *Temnothorax crassispinus* were present at the forest floor.

## Material and Methods

We considered all available canopy investigations performed in sites for which populations of *Temnothorax crassispinus* could be found at the forest floor – altogether a total of 19 Central European sites. The material included both our own collections and samples of other working groups sent to Senckenberg Museum für Naturkunde (SMN) Görlitz with the request for species determination (see Table 1). After pre-sorting, all possibly critical ant determinations were checked by the senior author. As methods of ant collecting were applied: investigation of fallen trees between October and March, active climbing of the collector, bait traps, branch eclectors, window traps, canopy crane survey and canopy fogging with pyrethrum (for details see BARSIG & SIMON 1995, FLOREN 2008, HORCHLER & MORAWETZ 2008, ARNDT &

HIELSCHER 2009). The following table gives some details of the considered investigations.

## Results and Discussion

### Canopy nesting or extreme expansion of foraging range?

In the following we discuss all thinkable explanations for the unexpected trap catches in the five pine stands near Torgau.

#### Explanation (a): Contamination by predatory ants.

SEIFERT (1990) reported that predatory ants with a wide foraging range spanning over several habitats, *Formica rufa* group ants in particular, can contaminate pitfall trap contents with ant species not living in that particular habitat spot. The prey carried in the mandibles is usually released when the predatory ants fall into the catching liquid. This explanation can be clearly rejected in our case. Firstly, all the possible predators *L. platythorax*, *L. fuliginosus*, *F. fusca* and *M. ruginodis* shown to forage in the pine canopies of

**Tab. 1.** Tree canopy investigations in 19 sites with *Temnothorax crassispinus* present at the forest floor. Investigation methods: BAIT – bait traps, BREC – branch eclectors, CLIMB – climbing on trees, CRANE – canopy crane survey, FALL – investigation of fallen trees between October and March, FOGG – canopy fogging with Pyrethrum, WITR – Window traps. In brackets are given the numbers of trees and/or traps. If there was more than one site in a study area, the given coordinates are a compromise.

Site [°N,°E, in decimal format]; year; collector	number of investigated trees	METHOD tree genus	height zone [m]
Löbau [51.09, 14.69]; 1982; B. SEIFERT/SMN Görlitz	1	CLIMB: <i>Quercus</i> (1)	5–18
Meissen [51.14, 13.51]; 1982; B. SEIFERT/SMN Görlitz	6	CLIMB: <i>Quercus</i> (2)	3–8
Daubitz [51.40,14.88]; 1984, 1993, 2010; B. SEIFERT/SMN Görlitz	5	FALL: <i>Quercus</i> (3) <i>Pinus</i> (2)	5–26
Kreba [51.35,14.64]; 2004; B. SEIFERT/SMN Görlitz	3	FALL: <i>Pinus</i> (3)	12–21
Gröditz [51.21, 14.64]; 2009; B. SEIFERT/SMN Görlitz	1	CLIMB: <i>Quercus</i> (1)	3–7
Leipzig [51.37, 12.30]; 2003; B. SEIFERT/SMN Görlitz	8	CRANE: <i>Quercus</i> (5), <i>Tilia</i> (2), <i>Robinia</i> (1)	16–32
Leipzig [51.37, 12.30]; 2002–2003; FH Bernburg (see ARNDT & HIELSCHER 2009)	37	WITR (50), BREC (46): <i>Quercus</i> , <i>Acer</i> , <i>Fraxinus</i> , <i>Tilia</i>	20–27
Torgau [51.59, 12.86], 7 sites; 2000–2001; A. JÄKEL/ TU Dresden	56	WITR (56), BREC (112): <i>Pinus</i>	11–17
Białowieża [52.70, 23.86]; 2002–2004; A. FLOREN/ University of Würzburg	42	FOGG (42): <i>Quercus</i>	10–35
Neuburg [48.74, 11.28] 3 sites; 2007–2011; A. GRUPPE/ TU München	40	BREC (40), BAIT (530): <i>Quercus</i>	3–28

the five sites have their nests on forest floor or in the basalmost part of the tree stems. If catching a *Temnothorax* on ground or at tree base, the predator will immediately retrieve the booty to the nest to save it – there will not be a useless and dangerous prey transport up into the tree canopy. Secondly, predation of *Temnothorax* workers by these four ant species is extremely rare and over all species less frequent than one in a thousand retrieved prey items according to long-term observations of the senior author. This is in contradiction to the observed 10% ratio of the *T. crassispinus* workers within the total ant number caught in the canopies.

#### Explanation (b): Contamination during replacement of collecting tubes in the field.

Each trap contained two collecting vessels. When replacing trap contents, one of these was immediately closed and replaced by another vessel already above in the canopy. The second one was closed in the canopy, roped down, opened again and poured into a clean glass vessel without being in contact with the ground surface. The glass vessel was then closed and transported to the laboratory. There was no time and no way for contamination with ground-foraging ants and we reject this explanation.

#### Explanation (c): Contamination during sorting in the laboratory.

The process of sorting taxonomic groups in the laboratory did not allow confusing contents of canopy traps and soil-based pitfall traps. If there was ever some accidental sorting error then only among the tree traps. This cannot affect our general conclusion and it is extremely unlikely that sorting errors occurred so often with vessels containing only very few ants.

#### Explanation (d): The foragers climbed up into the tree canopy from their ground nests.

The mean and maximum foraging distances of 0.5 and 1.6 meters reported by FOKUHL *et al.* (2012) in experiments with baits of seeds and the fact that no field student has ever observed a *T. crassispinus* worker to climb higher than 1.5 m above ground makes this explanation unlikely. The shortest distance a worker would have to walk from a forest-floor

nest to finally fall into the branch eleanor or window trap varied between 11 and 20 m (in case of the window traps she also would have to walk down the rope!). However, the idea that there is unknown nocturnal foraging of (possibly starving) colonies up into the canopies and that foraging distances on the strongly structured forest-floor surface cannot be directly translated into those on the comparably smooth and nutrient-poor surface of a *Pinus* stem cannot be easily dismissed. As there are no observations of *T. crassispinus* workers in habitats with big parts of ground surface being smooth, a direct answer to this question is not possible. The senior author observed 44 prey retrievals in the similarly-sized and similarly-shaped congeners *Temnothorax nigriceps* (MAYR, 1855) and *T. unifasciatus* (LATREILLE, 1798) in a habitat with large portions of bare and smooth basalt rock in the 1980ties. All prey transport occurred over a distance of less than two meters. There was one exceptional 3-m run of a returning *T. nigriceps* (apparently without prey) over a smooth basalt rock. These observations suggest diurnal foraging of *Temnothorax* over smooth surfaces longer than 5 meters to be most unlikely. The maximum foraging distances of the other ground-dwelling ant species also caught in the canopy traps of the Torgau study are much larger: they range on smooth ground between 35 m in *Myrmica*, 50 m in *Lasius* and 100 m in *Formica* (BRAUNE 1974, SEIFERT 2007).

Another argument against explanation (d) is that *T. crassispinus* formed as much as 10% of all ants captured in the canopy traps. In soil traps, *Temnothorax* ants are caught disproportionately rarely. According to direct observations of ant behavior at pitfall traps (Seifert 1990), the percentage of *T. crassispinus* workers falling into a trap was only 0.6% among 175 observed trap contacts - i.e., they are very shy and cautious! This ratio differed by  $p < 0.0001$  in a  $X^2$  test from the 19-108fold higher figures in other ants: 65% *Formica rufa*, 25% in *Formica cinerea*, 22% in *Myrmica rubra* and 10% in *Lasius niger* (SEIFERT 1990). Is it possible that *T. crassispinus* may achieve a 10% canopy share if the sources of the catches are ground nests? Multiplying nest density data of ants recorded in 9 test plots in *Pinus* forests of Saxony with average nest populations gives us an idea of the relative worker force of the differ-

ent species (unpublished data, file available on request). According to these data, the worker population of *T. crassispinus* was only 1.8% of all ant nests found on forest floor given an average nest density of 59.1 nests/100 m<sup>2</sup> and a mean worker population of 60 per nest (STRÄTZ & HEINZE 2004). Modifying the data in order to favor explanation (d), let us assume that the *T. crassispinus* population at the 5 Torgau sites has been 3fold stronger (180 nests/100 m<sup>2</sup>), that the mean foraging range is 50% of the much faster-walking, larger ants of the other genera (in reality it is perhaps 15%, see above) and that the catching percentage is only 5fold smaller than in the other genera (instead of 19-108fold as found at pitfall traps), we would end at final catching number of 0.54% of all ants. The conclusion is: even under these “manipulated” assumptions it is very difficult to believe that 10% of canopy catches can be explained by climbing up from the forest floor.

#### Explanation (e): The ants had their nests in the canopies

This is the most probable explanation. Here, the question of long-term persistence and, in particular, of survival after hibernation in the weather-exposed tree crowns may be of importance. The potency of *T. crassispinus* to survive the cold winter temperatures at the ground of continental Ukrainian steppe forests should be a pre-adaptation to allow hibernation of nests in tree canopies the comparably winter-mild Sachsen. Final evidence for the suggested canopy nesting *T. crassispinus* can only be given by direct nest findings. One of us (PF) is currently attending a tree-climbing course.

#### The Torgau study within the context of all canopy investigations

Accepting canopy nesting of *T. crassispinus* as the most probable interpretation, one may ask if this is only a regional or a general phenomenon. The answer is that it is obviously a rare regional or local phenomenon (Tab. 2). The Torgau study included seven sites with 56 trees and canopy nesting was indicated here for 71% of the sites. The other nine studies considered twelve sites with 142 investigated trees but an indication of canopy nesting occurred in only one site in the floodplain forest of the upper Danube



**Tab. 2.** Tree canopy investigations of ants in 19 Central European sites with populations of *Temnothorax crassispinus* present at the forest floor.

Site	n trees	height zone [m]	ant species	total number of all ants [nests /workers]	total number of <i>Temnothorax</i> [nests/workers]	<i>T. crassispinus</i> /height [m]
Daubitz 1984, 1993, 2010	5	5–26	4	37 nests	32 nests <i>T. corticalis</i>	0
Kreba 2004	3	12–21	0	0	0	0
Löbau 1982	1	5–18	1	1 nest	0	0
Meissen 1982	6	3–8	2	20 nests	19 nests <i>T. affinis</i>	0
Gröditz 2009	1	3–7	3	10 nests	8 nests <i>T. affinis</i> and <i>corticalis</i>	0
Leipzig 2003	8	16–32	4	22 nests	9 nests <i>T. corticalis</i> and <i>affinis</i>	0
Leipzig 2002–2003	37	20–27	7	570 workers	59 workers <i>T. corticalis</i> and <i>affinis</i>	0
Torgau, 7 sites; 2000–2001	56	11–17	6	91 workers	9 workers <i>T. crassispinus</i> only	9 workers at 5 sites 11–17 m
Białowieża, 3 sites; 2002–2004	42	10–35	10	2915 workers	486 workers <i>T. corticalis</i>	0
Neuburg, 3 sites; 2007–2011	40	3–28	22	6310 workers	270 workers <i>T. affinis</i> and <i>corticalis</i> , 2 workers <i>T. crassispinus</i>	2 workers at 1 site 10.5 m, 12.9 m

(Neuburg). Here, two single workers were collected in bait traps 10.5 and 12.9 m above ground - the argumentation why this indicates canopy nesting is the same as given above. Summarizing the data in Table 2, we can conclude that there is no indication so far for canopy nesting of *T. crassispinus* on some 6000 km<sup>2</sup> of the district Dresden (sites Daubitz, Kreba, Löbau, Gröditz, Meissen) despite this ant is everywhere extremely abundant on forest floor. The data also indicate strong competitive exclusion by the specialized canopy species *T. corticalis* (SCHENCK 1852) and *T. affinis* (MAYR 1855): when these are present in a site or region, canopy nesting of *T. crassispinus* is excluded - or nearly excluded as in the Neuburg case. In contrast, they were absent just from the Torgau region where we have the strongest signal for canopy nesting of *T. crassispinus*. The reasons for the absence of competitors in this region are not clear. Pest management against *Dendrolimus pini* (LINNAEUS, 1758) and *Panolis flammea* (DENIS & SCHIFFERMÜLLER, 1775) might well have contributed to this absence but, as a matter of fact, insecticide treatment was not performed in most parts of the study area for at least 30 years prior to the study.

### The ecological interpretation

11.4% of the 176 Central European ant species belong to the genus *Temnothorax* (SEIFERT 2007, plus unpublished new records since then) but they form 40% of the 15 species nesting in tree canopies (account in SEIFERT 2008, plus *T. crassispinus*). This significantly higher per-

centage ( $p=0.027$  in a  $X^2$  test according to SOKAL & ROHLF 1995) is explained by particular preadaptations of *Temnothorax* ants to canopy nesting in temperate and meridional forests (for details see SEIFERT 2008). Firstly, they are adapted to the lack of nesting space in tree canopies - the small *Temnothorax* populations require a total cavity volume of only 0.5–2 cm<sup>3</sup>. Secondly, all *Temnothorax* - regardless if soil-dwelling, arboreal, open-land or woodland species - nest always very close to the substrate surface and, unlike other ants, they perform no or only minute diurnal or seasonal vertical movements. This makes them physiologically preadapted to the strong annual and daily temperature amplitudes in tree canopies. Another preadaptation to canopy nesting is the low sensitivity to desiccation of environment. Nest populations are encapsulated in a microspace with solid, more or less waterproof walls and having a connection with the environment only by a single entrance 1 mm in diameter. This prevents moisture loss and it seems that the ingestion of morning dew by a number of foragers is sufficient to meet the colonies' water requirements.

All these preadaptations are given also in *T. crassispinus*. From this point of view, the reported niche expansion appears less surprising. As a continental species, which is exposed to dry and hot summers as well as cold winters in the S Russian steppe forests, *T. crassispinus* should be a better canopy colonizer than its parapatric sibling species *T. nylanderi* (FÖRSTER, 1850) the range of which is influenced by Atlantic climate. *T. crassispinus*

are frequent on forest floor of the *Pinus* stands around Torgau and it is remarkable that ground- and canopy-nesting occurs syntopically. There are no nest density data available for the forest floor of the Torgau sites in the years 2000/2001 and the habitats have changed in the time since then. There was in particular an increased shading of forest floor due to massive upgrowth of the neophytic tree *Prunus serotina* in the bush layer and understory. This probably explains the subaverage density of 31.8 nests/100 m<sup>2</sup> forest-floor found in one of these stands during a census in 2012.

We apply here the terminus “niche expansion” without deciding if this is a constant, long-term phenomenon or some sort of temporal, opportunistic behavior allowed by genetically fixed preadaptations. The terminus would also apply if our conclusion on canopy nesting was wrong and if there was “only” an extreme extension of the foraging range of a ground-foraging ant into the canopy. A space temporarily free of competitors, here canopies without the specialized arboreal ants *T. corticalis* and *T. affinis*, is likely to have caused an ecological release in *T. crassispinus*. A long-term extension of the niche by canopy nesting probably requires a genetically mediated ethological change and it would be interesting to investigate if the spatio-ecological separation would lead to reduced gene flow between the floor and canopy populations. The supposed case of intraspecific niche segregation seems to be the only known example within independently living *Temnothorax* or *Lepthorax* ants. Among Formicoxenine

ants, the permanent slave hunter *Myrmoxenus ravouxi* (ANDRÉ, 1896) uses the nest sites of four ground nesting and one arboreal *Temnothorax* host species (MARTZ 2007, SEIFERT 2007).

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