Rapid range expansion in *Lasius neglectus* (Hymenoptera, Formicidae) – an Asian invader swamps Europe

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With 5 tables

Abstract

After its first observation in Europe in 1974, *Lasius neglectus* Van Loon, Boomsma & Andrasfalvy 1990 has performed a rapid range expansion throughout the entire Mediterranean area and has reached Central Europe. The present range is delimited by 1° E and 75° E and by 36° N and 49° N with 38 sites known. Regarding colony structure, mating, mode of distribution, local dominance, pest status, and impact on local ant faunas, *neglectus* is comparable to *Linepithema humile* (Mayr 1868). *L. neglectus*, however, can establish permanent colonies in regions with mean January temperatures of −5 °C. Climatic barriers ending the northern expansion of *Linepithema* and preventing its long-term outdoor persistence in Central Europe and S Scandinavia will not stop *neglectus* that has the potency to develop into a most important pest species. Morphology, genetics, and zoogeography suggest a very recent separation of *neglectus* from *Lasius turcicus* Santschi 1921 with a most probable radiation centre in Asia Minor. The behavioural change from normal aerial mating to exclusively intranidal mating is considered as deciding step leading to complete reproductive isolation from *turcicus*. The obvious absence of *turcicus* from huge parts of *neglectus'* range is a further argument against considering the two as expression of intraspecific polymorphism. The loss of flight behaviour in queens is still not accompanied by significant morphological changes: wing load and development of flight muscles or fat tissue are comparable to well-flying and claustrally founding *Lasius* species.

Key words: morphometry, zoogeography, reproductive isolation, sister species, pest species.

Introduction

Lasius neglectus Van Loon, Boomsma & Andrasfalvy 1990 has been originally described from the city of Budapest. After the first discovery in about 1974, the ant became a pest species in gardens and parks of the city in the 1980ies. *L. neglectus* is the first European species of the subgenus *Lasius* s.str. known to form highly polygynous societies that can develop by repeated nest-fission into huge polycalic colonies. In the year 1988, the largest colony known from a suburb of Budapest was estimated to cover an area of 2 km^2. Within this area, *L. neglectus* almost exterminated any other ant species, caused problems in greenhouses and buildings, and exploited aphids on any available tree in huge masses, with thousands of workers running up and down the tree trunks. Only intranidal mating was observed so far in *L. neglectus*; the gynes apparently shed their wings immediately after copulation and stayed within the nest to become reproductive queens. Sometimes alates could be observed on soil surface but a clear nuptial flight was never observed during the period of 1974–1988. As only modes of dispersal in *L. neglectus* were considered passive human transport with plant material and ground movements during colony-fission (Van Loon et al. 1990).

Undoubtedly *Lasius* ants with such an extraordinary colony structure and such a strong impact on environment would have been noted by former European myrmecologists. However, no such phenomena were observed throughout the territory of Europe or elsewhere before the year 1974. As a consequence, we must consider this highly polycalic ant as new faunal element. The author received a lot of *L. neglectus* samples during revisionary work on Palaearctic *Lasius* species within the last decade. The collected data give evidence that *L. neglectus* invaded Europe from W Asia in an impressive range expansion during the last 25 years. The colonised geographic range is enormous and the rapid progress of *L. neglectus* together with its ability to displace local ant faunas is comparable to the

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performance of the famous Argentine ant *Linepithema humile* (Mayr 1868) that reached Europe by about 1895 and spread all over the Mediterraneans within 60 years (Way et al. 1997). However, there is one deciding difference: as it will be shown below, *L. neglectus* is able to survive cold winters. Climatic barriers that have ended the northern expansion of *Linepithema* will not stop *L. neglectus*. This paper aims to give information on taxonomy, zoogeography, and biology of *L. neglectus* – an ant that nobody can neglect anymore.

Methods and terminology of morphologic investigation

All measurements were made on mounted and dried specimens using a goniometer-type pin-holding device, permitting endless rotations around X, Y, and Z axes. A WILD M10 stereomicroscope equipped with a 1.6× planapochromatic objective was used at magnifications of 50–320×. The maximum possible magnification to keep a structure within the range of the ocular micrometer was used. A mean measuring error of ± 0.4 µm is given for small and well-defined structures, such as hair length, but may reach 4 µm for measures > 1700 µm with difficult positioning and high influence of air humidity. To avoid rounding errors, all measurements were recorded in µm even for characters for which a precision of ± 1 µm is impossible. In order to reduce irritating reflections of the cuticular surfaces and to get an improved visualization of the microsculpture, a plastic diffuser was positioned as close as possible to the specimen. Setae, also called pilosity or simply 'hairs', are differentiated from pubescence hairs in having a distinctly larger basal diameter. All seta counts (nSC, nHT, nOCC, nGU, nGEN) are restricted to standing setae projecting > 20 µm from the silhouette of cuticular surface as observed under use of transmitted-light.

CL – maximum cephalic length in median line; the head must be carefully tilted to the position with the true maximum. Excavations of occiput and/or clypeus reduce CL.
CW – maximum cephalic width; this is either across, behind, or before the eyes.
MaDe – number of dents on masticatory border of mandible. Data of both mandibles are averaged.
MH – mesosoma height measured perpendicular to the tangent of dorsal mesosoma profile from scutellum down to lower margin of mesopleuron (Seifert 1992).
ML – mesosoma length from caudalmost part of mesosoma (found either on median propodeum or caudal metapleuron) to steep frontal profile of pronotum as measured in lateral view (Seifert 1992).
MW – maximum mesosoma width before the tegulae
nGEN – number of setae projecting from genae. Counting is done with head in full face view. The bilateral number is halved.
nGU – number of setae on gula as seen in full profile. The bilateral number is halved.
nHT – setae number on extensor profile of hind tibia. The number of both tibiae is halved.
nOCC – setae number projecting from occipital margin frontad to caudal end of eye. Counting is done with head in full face view and in measuring position for CL. The bilateral number is halved.
nSC – setae number on dorsal plane of scape, counted with view on the small scape diameter. The number of both scapes is halved.
PDCL – pubescence distance on clypeus; mode of measuring as in Seifert (1992) or Seifert (1996).
PLF – mean length of pubescence hairs on head between the frontal carinae. 6 measurements in each individual are averaged
PNHL – maximum length of pronotal setae
SL – maximum straight line scape length excluding the articular condyle
GuHL – maximum length of setae on underside of head (gula)

Total queen fresh weight was estimated in specimens fixed in 70% ethanol for 2 years. Immediately after drying of body surface during short deposition on filter paper, weight was directly measured on a Kern 410 microbalance with an accuracy of ± 0.2 mg. The volume of head, mesosoma, gaster, and appendages (except for wings) was calculated by linear measurements and simple geometric calculations. In order to measure total wing area, the fore- and hindwings were drawn under use of a Wild projection system in a scale of 20:1. Wing area could then be inferred from the corresponding weight of the cut-out areas.

Results

Geographical range of *L. neglectus*

In the collection of the Staatliches Museum für Naturkunde Görlitz (SMNG) are now 40 samples of *L. neglectus* from 38 localities. These sites and the year of first discovery are given in lexicographic order:

Bulgaria: Albena/Black Sea coast, 1984
Czech Republic: Hnanice near Znoimo, 1997
France: Orange/Rhone, 1987; Port-Leucate/E Pyrenees, 1995; Toulouse, university campus, 1995; Toulouse, 1998.
Georgia: Pizunda/Black Sea coast, 1974; Sotchi/Black Sea coast 1984; Tiflis – 5 km E, 1985; Tiflis City, Botanical Garden, 1985.
Germany: Jena, Botanical Garden of the University, 1997
Greece: Rhodos: Rhodos City, 1983; Athens, Kifisia, 1988; Rhodos: Kolymbia, 1995
Hungary: Budapest, 1974; Debrecen, Botanical Garden, 1997
Italy: Volterra, 50 km SW of Firence, 1997
Kirghyztan: Tash Kumyr (41.50N,72.25E), 1998; Bishkek (formerly Frunze, 42.54N,74.38E), 1998.
Poland: Warszawa, Tamka Station, 1999.
Romania: Baile Herculeane, 1996
Spain: Barcellona City, 1990; Bellaterra/Barcelona, 1997; El Montanya, Aiguafreda/Barcelona, 1998
Turkey: Alanya, 1988; Beydag – 10 km SE, 1993; Bucak, 1988; Bulancak, 1989; Darende, 1989; Igdir – 10 km SE, 1993; Kabali – 5 km S,

1993; Kaymakei – 20 km SE, 1993; Konya, 1988; Koycegiz, 1996; Tuzluca – 10 km E, 1993; Van – 20 km E, 1989; Yalova, 1989; Ödemis – 20 km SE, 1993.

According to these data, *L. neglectus* was found within a huge range of 6100 km from Iberia to Central Asia (from 1° E to 75° E and from 36° N to 52° N). *Lasius turcicus* Santschi 1921, the species from which *L. neglectus* most probably has separated as own evolutionary line, is apparently restricted to the Aegean, Asia Minor, Syria, and the Iran where it is an abundant species (samples from 24 localities in the collection of the Staatliches Museum für Naturkunde Görlitz). Most remarkably and in contrast to *L. neglectus*, *L. turcicus* is not known from Bulgaria, Romania, Hungary, Czechia, Germany, Poland, Italy, France, and Spain. Considering the whole known range, the vertical distribution of *L. neglectus* varies between sea level and 1750 m (20 km ENE Van /Turkey), with 88% of the sites situated below 1000 m (arithmetic mean ± standard deviation for 26 sites with known altitude 418 ± 413 m). Restricting the consideration to Asia Minor and the Near East, *L. neglectus* had a significantly lower distribution with 625 ± 516 [50, 1750] meters (n = 12) than *L. turcicus* with 1214 ± 460 [50–1600] meters (n = 11) if tested in a nonparametric U test ($p < 0.01$). This difference is probably a byproduct of the higher affinity of *L. neglectus* to urban areas and of the strikingly different modes of queen dispersal.

Taxonomic position and morphologic discrimination from *turcicus*

The character combination of reduced mandibular dentition, short pronotal setae, thin lateral profile of petiole scale, and reduced scape pilosity is shared by six West and Central Palaearctic *Lasius* species: *brunneus* (Latreille 1798), *lasioides* (Emery 1869), *himalayanus* Forel 1917, *turcicus* Santschi 1921, *neglectus* Van Loon et al. 1990, and one undescribed species near to *lasioides* (Seifert, unpublished results). These species form a cluster of related species that is clearly different from species of the *alienus* or *niger* group. The failure to demonstrate a useful size-independent difference between the workers, the similar centering of geographic distribution to Asia Minor, and the possible explanation of size differences by differing epigenetic and nutritional factors within monogynous and polygynous colonies has led to a provisional synonymisation of *neglectus* with *turcicus* (Seifert 1992).

Investigations since then confirmed that absolute size remains the only useful criterion to distinguish the female castes. With the exception of small, initial colonies with nanitic workers, the discrimination of both species is possible by calculating nest means of worker cephalic length (CL) which does not exceed 840 µm in *neglectus* and is not lower than 850 µm in *turcicus*. Explicitely, the arithmetic mean, standard deviation, and upper and lower extremes were 797 ± 33 [661, 833] µm in 38 nest samples of *neglectus* and 904 ± 38 [859, 999] µm in 24 nest samples of *turcicus*. CL was 800 ± 42 [653, 893] µm in 155 individuals of *neglectus* and 890 ± 54 [809, 1043] µm in 96 individuals of *turcicus*.

The high similarity of workers in morphology and morphometrics is demonstrated if size-dependent variation produced by allometries is removed as described by Seifert (1992). A correction of data for the assumption of each worker having CL = 840 µm results in equal data for 7 characters (Tab. 1). Weak differences are exposed in nHT, PNHL/CL, and GuHL/CL which are significant for $p < 0.0001$ if tested in a **t** test.

Comparable to the situation in workers, only absolute size measures separate the queens, while body ratios and other characters fail (Tab. 2). One queen of *L. turcicus* from Turkey and 16 queens of *L. neglectus* from Spain, France, Hungary, Turkey, and Georgia were available for morphometric investigation. CL and MW of the *turcicus* queen are outside the 99.9% confidence

Table 1

Comparison of size-corrected characters of worker individuals of *Lasius neglectus* and *Lasius turcicus* calculated for the assumption of equal CL (= 840 µm). Upper line in heavy type arithmetic mean, lower line standard deviation, n = number of examined specimens.

	CL	CL/CW	SL/CL	PDCL	nSC	nHT	nOCC	nGU	GuHL/CL	PNHL/CL	MaDe	PLF
turcicus	**890**	**1.104**	**0.940**	**30.5**	**0.1**	**1.0**	**8.8**	**3.1**	**0.122**	**0.126**	**7.43**	**30.6**
(n = 96)	54	0.017	0.015	6.1	0.5	1.2	2.8	1.1	0.010	0.012	0.52	2.6
neglectus	**840**	**1.110**	**0.932**	**31.1**	**0.3**	**0.3**	**9.3**	**2.5**	**0.111**	**0.117**	**7.42**	**30.5**
(n = 97)	41	0.014	0.019	6.2	0.5	0.5	2.7	0.9	0.011	0.009	0.47	2.5

Table 2
Morphometric comparison of the queens of *Lasius neglectus* with the only available queen of *Lasius turcicus*. Characters of *turcicus* with a distance |value − mean|/SD > 3.09 are outside the 99.9% confidence limits of the *neglectus* normal distribution.

	turcicus n = 1	*neglectus* n = 16		distance
	value	mean SD	[min, max]	
CL	1301	1216 ± 24	[1181, 1268]	3.54***
CW	1439	1357 ± 36	[1282, 1403]	2.28
ML	2659	2538 ± 56	[2459, 2632]	2.16
MW	1842	1557 ± 62	[1439, 1668]	4.60****
CL/CW	0.904	0.897 ± 0.016	[0.881, 0.932]	0.44
SL/CL	0.846	0.865 ± 0.018	[0.835, 0.898]	1.06
SL/CW	0.764	0.776 ± 0.021	[0.736, 0.821]	0.57
MH/ML	0.526	0.498 ± 0.026	[0.469, 0.535]	1.08
PDCL	27.1	22.4 ± 6.0	[13.8, 37.8]	0.78
nHS	0.0	0.97 ± 1.49	[0.0, 6.0]	0.65
nHT	2.0	1.65 ± 2.33	[0.0, 9.5]	0.15
nOCC	17.5	12.15 ± 4.14	[2.5, 20.0]	1.29
nGU	4.5	5.94 ± 1.45	[3.0, 8.0]	0.99
GuHL	186	171 ± 15	[138, 183]	1.00
nGEN	3.0	2.41 ± 1.28	[0.5, 5.5]	0.46
MaDe	7.0	7.50 ± 0.62	[7.0, 9.0]	0.81

limits of the *neglectus* normal distribution with the difference in MW being large enough to believe in a reliable difference.

As a general rule within the genus *Lasius*, males are more difficult to distingish than female castes. In some closely related species they seem to be inseparable (Seifert 1988, 1992). From this point of view, it is remarkable to observe extreme size differences between the males of *L. turcicus* and *L. neglectus* (Tab. 3).

Species status of *neglectus*

The high similarity of female castes and preliminary genetic studies of S. Aron & J. J. Boomsma (pers. comm.) suggest conspecifity, i.e., *L. neglectus* could only represent a polygynous, intranidally mating morph of *turcicus*. However, the sum of present information has changed the view and a treatment of *neglectus* as bona species seems more adequate (Seifert 1996). The following arguments point in this direction:

(1) The mode of intranidal mating in *neglectus* should mean an effective reproductive isolation from *turcicus* the morphology of which suggests normal aerial mating.

(2) The males of *turcicus* and *neglectus* have extremely different morphometric data. It seems very doubtful if the tiny *neglectus* males can successfully participate in the high-altitude mating flights for which the 3.7fold weightier *turcicus* males are well-adapted.

(3) There seem to exist genital differences. In all studied *neglectus* males, the volsella is shorter than the sagitta while in the *turcicus* male the caudal tips of both structures reach equal level. In dorsal view, the sagitta of *neglectus* shows a distinctly widened, nodular apex; in *turcicus* it narrows continously towards the apex.

(4) The absence of *turcicus* from the Balkans and the Central and W Mediterraneans speaks

Table 3
Morphometric comparison of males of *Lasius neglectus* from Spain, Czechia, Hungary, and Turkey with the only available male of *Lasius turcicus*. Characters of *turcicus* with a distance |value − mean|/SD > 3.09 are outside the 99.9% confidence limits of the *neglectus* normal distribution.

	turcicus n = 1	*neglectus* n = 9		distance
	value	mean SD	[min, max]	
SL	670	472 ± 24	[434, 500]	8.25
ML	1796	1197 ± 87	[985, 1267]	6.89
CW	1021	733 ± 51	[631, 802]	5.65
CL	828	644 ± 50	[577, 711]	3.68
CL/ML	0.461	0.540 ± 0.048	[0.473, 0.631]	1.65

Table 4
Morphometric data of W European (west of 11° E) and Asian (east of 44° E) workers of *Lasius neglectus*. Upper, heavy-typed line arithmetic mean, lower line standard deviation, n = number of examined specimens. All means are equal for $p < 0.02$.

	CL	CL/CW	SL/CL	PDCL	nSC	nHT	nOCC	nGu	GuHL/CL	PNHL/CL
W European	**805**	**1.116**	**0.945**	**32.5**	**0.14**	**0.30**	**10.2**	**2.46**	**0.115**	**0.117**
(n = 22)	27	0.012	0.015	5.5	0.28	0.33	3.2	0.79	0.010	0.009
Asian	**802**	**1.125**	**0.939**	**31.1**	**0.03**	**0.39**	**9.3**	**2.22**	**0.111**	**0.115**
(n = 18)	19	0.013	0.012	6.4	0.12	0.40	2.3	0.94	0.010	0.006

against an interpretation of *neglectus* as intraspecific morph of *turcicus*.

To conclude, the weak differences in female caste morphology and the high genetic similarity are not necessarily arguments for conspecifity. Instead they suggest that *neglectus* has split off from *turcicus* only very recently. Thus we are witness of a process of a very rapid species divergence by a radical change in mating behaviour. The altered colony structure of the new entity, a new invention among European species of *Lasius* s. str., dramatically increased the competitive power and initiated a rapid range expansion.

Geographic variability

Lasius neglectus has a very constant external morphology throughout several thousand kilometers of its range (Tab. 4). W European samples (from Volterra, Toulouse, Port Leucate, Bellatera, and Aiguafereda) did not differ from Asian samples (from Tbilissi, E of Tbilissi, Tash Kumyr, and Bishkek). All evaluated characters were equal for $p < 0.02$ if tested in a **t** test.

Habitat, response to climate, and status as pest species

Huge polycalic colonies with a strong impact on the biotic environment, as described by Van Loon et al. (1990) for the city of Budapest, seem to be a frequent result if *neglectus* ever can settle down permanently. Observations made in the Tiflis Botanical garden and a suburb of Tiflis (B. Seifert), in Toulouse (L. Passera, pers. comm.), in the city of Volterra (G. Heller, pers. comm.), and near Aiguafreda (X. Espadaler, pers. comm.) are comparable to the situation studied in Budapest. The majority of the *neglectus* sites is characterised by a high degree of urbanization. City parks with trees and built-up areas with gardens are obviously the optimum habitats but strong populations were also observed in open, anthropogenically disturbed grassland outside of human settlements (dams of rivers and reservoirs) and light coniferous and deciduous woodland.

In Asia Minor, its putative radiation centre, *neglectus* was observed in natural steppe habitats (A. Schulz, pers. comm.). In the newly-colonised European ranges, distribution into natural or seminatural habitats proceeds very slowly as far as the sparse information indicates. The main reason should be the dependency of long-range dispersal from passive (anthropogenic) transport that significantly reduces the probability to found beach-heads in natural habitats. On the other hand, the well-adapted, saturated, and more stable ant communities of natural habitats could possibly longer resist the pressure of invading *neglectus* but this idea needs direct confirmation.

Expressed cold-hardiness of *Lasius neglectus* is indicated by climatic data that are available for 2 sites in Asia: the mean air temperature of the coldest month of the locality 20 km ENE Van (Turkey, 1800 m) and of Bishkek (Kyrghyztan, 760 m) is −4.4 °C and −5.5 °C (Walther & Lieth 1964). Hence *neglectus* is easily able to survive Central European or S Swedish winters and is expected to perform a farther range expansion to the north. For all sites with available climatic data, mean July temperatures vary between 19 °C and 30 °C and annual precipitations between 230 and 2000 mm (the latter achieved in the subtropical climate of the eastern Black Sea coast). In the cooler climate of Central and NW Europe, precipitations above 600 mm could limit the distribution. The futural development will show if this continental species can establish permanent populations in the Atlantic climate of NW France or S England. Big cities and urban areas with a low quotient of mean annual precipitation versus mean annual temperature in S Sweden should be the next localities where the species should appear in the north.

Table 5
Arithmetic means of morphometric data of 5 alate queens of *Lasius neglectus* and 5 alate queens of *Lasius psammophilus*. "Fresh weight" means liquid weight after 2 years of storage in 70% ethanol. Note the close agreement of the calculated total body volume obtained by linear measurements and simple geometric calculations with the fresh weight (physicalic density was in these specimens 0.95 g/cm).

	total fresh weight [mg]	total volume [mm^3]	head volume [mm^3]	mesoma volume [mm^3]	gaster volume [mm^3]	append. volume [mm^3]	total wing area [mm^2]
psammophilus	22.77	23.91	1.28	5.49	16.45	0.69	60.3
neglectus	15.24	15.42	0.78	3.07	11.10	0.47	32.4

L. neglectus may become an virtual pest species if huge polycalic colonies are built up. Situations as described for the city of Budapest are no exception. The species may occur as plague inside of houses, produces problems in greenhouses and gardens, and may even cause the death of trees by protection and fostering of Homoptera as observed by X. Espadaler (pers. comm.) in the Barcelona region. The extermination of resident ants and possible disturbance of whole biocoenotic systems is less dramatic from the view of species conservation as long as already disturbed urban areas are colonised but it could be disastrous if valuable natural habitats are affected.

Are single queens still capable of flight dispersal and claustral nest foundation?

Van Loon et al. (1990) and Espadaler (pers. comm.) assume exclusively intranidal mating and did never observe mating flights nor flight-dispersal of queens. As stated above, exclusive intranidal mating is also supported by male morphology. It might be asked if queens of *Lasius neglectus* have completely lost flight behaviour. Comparative investigation of five alate queens of *neglectus* and of five equivalent queens of *Lasius psammophilus*, a species with long range flight-dispersal and claustral colony foundation, did not provide morphological arguments for a loss of flight ability in *neglectus*. The wing load, i.e., the ratio of total fresh weight against total wing area, was 377 $\mu g/mm^2$ in *psammophilus* and 471 μg/mm in *neglectus* and in both species fully developed flight muscles comprised about 85% of mesosoma volume. Though the ratio of mesoma volume against total body volume is slightly smaller in *L. neglectus* (0.20) than in *psammophilus* (0.23), a dramatic reduction of physical flight ability is not expected from these data, the more since the well-flying queens of *Lasius brunneus* or *Lasius emarginatus* (Olivier 1792) have similar relative mesosoma volumes. Optical inspection of the dissected gaster showed strongly developed fat tissue in most of the *neglectus* queens indicating physical ability for claustral nest foundation.

A "mesosoma ratio" i.e., the ratio of queen mesosoma volume against worker mesosoma volume can be used to predict the potency of an ant queen for independent claustral nest foundation (Stille 1996). My own investigations could confirm this hypothesis in the ant genera *Lasius*, *Formica*, and *Leptothorax*, but not in *Myrmica*. In *Lasius*, claustrally-founding species have mesosoma ratios >20 (e.g. *psammophilus* 31.6, *flavus* 25.7, *niger* 24.1) and species with dependent colony foundation ratios <15 (*umbratus* 9.5, *mixtus* 8.6, *fuliginosus* 3.9, *carniolicus* 2.0). In *Lasius neglectus* and *turcicus* the mesosoma ratios are 25.1 and 24.0 respectively which clearly indicates a potency for independent colony foundation.

As a consequence, queens of *Lasius neglectus* still show the morpho-physiological adaptions for flight-dispersal and claustral colony foundation though the corresponding behavioural repertoire seems to be lost. However, a small fraction of *neglectus* queens could have maintained this behaviour as the recent finding near Znoimo in S Moravia/Czech Republic (leg. Seifert 1997) suggests. This site, a semi-natural, xerothermous grassland with *Calluna* on silicate rock, seems isolated and is not directly touched by human transport or traffic activities. It seems doubtful that *neglectus* has reached this most northern site known by ground movements after colony fission or anthropogenic transport. A most recent observation additionally suggests occasional flying of *neglectus*: alate males and queens were found trapped in a spider net at a house wall in Bishkek in July 2000.

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