# SHIFT IN THE STRUCTURE OF *Lasius flavus* (HYMENOPTERA, FORMICIDAE) NEST COMPLEXES UNDER THE INFLUENCE OF ANTHROPOGENIC FACTORS

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## ABSTRACT

The structure of five *Lasius flavus* Fabricius, 1781 (yellow meadow ant) nest complexes with 33 to 211 nest mounds exposed to the anthropogenic impact of varying intensity was studied in 2001 and 2014 from four locations in Crimea. The study areas can be arranged in order of increasing intensity of anthropogenic impact as follows: the Chatyr-Dag Mountain (no impact, two nest complexes), arboretum near Simferopol city (low-intensity impact, moderate grazing, one nest complex), the outskirts of Kurtsy village (high-intensity impact, intensive grazing, ne nest complex), and Gagarinsky Park (critical level of intensity, draining, one nest complex). In 2001, mound measurements were taken from all nest complexes, divided into squares of 20 × 20 m. In 2014, mound measurements were taken from three out of five locations, namely the Chatyr-Dag Mountain (one nest complex), Kurtsy village, and Gagarinsky Park). In 2014, the nest complex in Gagarinsky Park was found to no longer exist. Other nest complexes underwent significant changes. Small nest mounds either disappeared or grew in size. The total nest volume did not change significantly or slightly increased. Therefore, this study concluded that grazing did not affect the ability of nest complexes to grow. The lowering of the groundwater table was found to be a critical factor. Nest complexes on the Chatyr-Dag plateau turned out to be 100 years of age, and other nest complexes were at the age of 40 to 80 years.

**Key words***:* *Lasius flavus*, nest complexes, anthropogenic factors, Formicidae

## ABSTRAK

Struktur lima kompleks sarang spesies *Lasius flavus* Fabricius, 1781 (semut rumput kuning) dengan 33 ke 211 busut yang terdedah kepada kesan antropogenik dengan intensiti berbeza-beza dari 2001 dan 2014 dari empat lokasi di Crimea telah dikaji. Kawasan kajian yang terlibat merupakan kawasan yang terkesan dengan aktiviti antropogenik iaitu Gunung Chatyr-Dag (tiada impak, dua kompleks sarang), taman botani berdekatan bandar Simferopol (impak intensiti rendah, padang ragut sederhana, satu kompleks sarang), perkampungan pendalaman Kurtsy (intensiti tinggi, padang rumput aktif, satu kompleks sarang) dan Taman Gagarinsky (intensiti kritikal, kering dan kosong, satu kompleks sarang). Pada tahun 2001, ukuran busut telah diambil dari kesemua kompleks sarang dan dibahagikan kepada empat segi sama iaitu 20 × 20 m. Kemudiannya, pada 2014 ukuran busut diambil tiga dari lima lokasi iaitu Gunung Chatyr-Dag, pendalaman perkampungan Kurtsy dan Taman Gagarinsky. Walaubagaimana pun pada 2014, sarang di Taman Gagarinsky didapati tidak lagi wujud, manakala kompleks sarang lain mengalami perubahan signifikan. Didapati busut kecil sama ada hilang atau bertambah saiznya. Keluasan sarang didapati tidak berubah secara signifikan atau sedikit bertambah. Oleh itu, aktiviti meragut tidak memberikan kesan ke atas kemampuan sarang untuk berkembang. Penurunan air bawah tanah juga didapati memainkan faktor kritikal. Kompleks sarang di dataran tinggi Chatyr-Dag berusia 100 tahun dan lain-lain di antara umur 40 ke 80 tahun.

**Kata kunci***:* *Lasius flavus*, sarang kompleks, antropogenik, Formicidae

## INTRODUCTION

Ants serve as a convenient model for studying the impact of anthropogenic factors on zoocenoses. Some studies are devoted to the study of the species diversity of ants on man-made phytocenoses (for example, oil palm plantations (Syarifah et al. 2016), others are related to the study of ants as bioindicators of forest restoration (Mustafa 2018). Most studies using ants as model organisms to study anthropogenic influences deal with changes over time in ant species richness in urban ecosystems (Pećarević et al. 2010; Ślipiński et al. 2012). Some studies focus on urban parks and green spaces, areas containing many different species of ants, as shown by studies concerned with large cities, such as Tokyo (Yamaguchi 2004), Warsaw (Trigos-Peral et al. 2020), Sofia (Antonova & Penev 2006), and Kyiv (Ihnatiuk & Stukalyuk 2015; Radchenko et al. 2019). Not only the above studies compared species richness of ants in different habitats, but they also examined factors affecting the distribution and abundance of ant species. Of those, the major factor was found to be the availability of nesting sites, which was crucial to dendrobiont species, such as *Lasius fuliginosus* (Latreille); and also for red wood ants. In Europe, high-density urban areas were found to be dominated by one or two ant species, typically *Lasius niger* (Linnaeus) (Ślipiński et al. 2012; Putyatina et al. 2018; Vepsäläinen et al. 2008).

Besides species diversity, the research on adaptive behavior of ant communities exposed to anthropogenic stressors should focus on the structure of ant populations. Some ant species can build nest complexes in anthropogenic landscapes. From this perspective, differences in resistance of ant nests to anthropogenic disturbances depending on the ant species is an acute topic in myrmecological research. Some studies showed that in urban forests, the nest complexes of red wood ants tend to degrade (Stukalyuk 2017a), which manifests in the loss of interaction between parent and satellite colonies. Furthermore, large colonies red wood ants may break up into several smaller nests (Zakharov & Kalinin 2007). The opposite is also possible where smaller nests may merge into a larger one (Zakharov 2015). There are also evidences on migration of red wood ants between habitats in response to artificial recreation (Stukalyuk 2017b). In our opinion, red wood ants are not suitable for monitoring the impact of anthropogenic disturbances because they live mainly in forest ecosystems. Genus *Lasius*, on the other hand, is more suited to this research. Ant species (*L. flavus*) that belong to genus *Lasius* can form a polycalic supercolony with hundreds of connected nests.

One of the species in the genus *Lasius* is *Lasius flavus* Fabricius, 1781, commonly known as the yellow meadow ant. *L. flavus* is a geobiont ant species that can be found throughout the Palaearctic region (Radchenko 2016). In Asia, the natural range of this species includes the territories of Asia Minor (Turkey), China, Korea, Iran, the Asian part of Russia (Siberia, Ural), the Far East, Kyrgyzstan, Turkmenistan, Kazakhstan and Japan, but this species of ants is absent in Malaysia.

In the southern part of the overall distribution, in the Crimea specifically, this species can be encountered in mountain habitats. *L. flavus* constructs nest mounds primarily in moist habitats, such as meadows and pastures near ponds. The nest complex of *L. flavus* can consist of hundreds of connected nests (Marikovsky 1965). Each nest normally has up to 10 thousand workers (Odum & Pontin 1961), whereas some large nests that grow 1 meter in diameter can comprise 60 to 100 thousand workers (Czechowski et al. 2012). All nests in the nest complex are connected by underground passages and galleries. Due to this, hundreds of nests can coexist locally within a relatively small habitat, and the overall high density of those mounds can be rather high. *L. flavus* forage underground, where they farm root aphids for food (Waloff & Blackith 1962). In this way, yellow meadow ants can avoid competition with other species of ants that forage above the ground.

The biology of *L. flavus* has been studied in detail by Pontin and Odum, whose classic works became a reference for many future scholars (Pontin 1961, 1963, 1969; Odum & Pontin 1961). Other studies focused on dimensional differentiation of nests in nest complexes (Ehrle et al. 2017), on interactions with other ant species (Marikovsky 1965; Rosengren 1986), and on trophobiosis with aphids (Depa & Wegierek 2011). Single studies discussed polygyny in *L. flavus* colonies (Boomsma et al. 1993; Steinmeyer et al. 2012). Although many topics about ants have been addressed in the past, the issue regarding the stability of the nest complex in the anthropogenic environment remains unresolved.

The purpose of this study was to compare the intensity levels of anthropogenic impacts on the structural parameters (size and number of nest mounds) of various *L. flavus* nest complexes. Anthropogenic factors included intensive cattle grazing and changes in soil moisture regime (draining of marshy areas). The stability of the nest complex was measured using parameters, such as nest size, density of mounds per unit area, and the shape of the nest mound. It was hypothesized that nest complexes consisting of small nest mounds with low-dense aggregation will be less resistant to anthropogenic impacts.

## MATERIALS AND METHODS

### Sampling Location

The study was conducted in the Crimean peninsula in May 2001 and May 2014 in four locations (Figure 1).

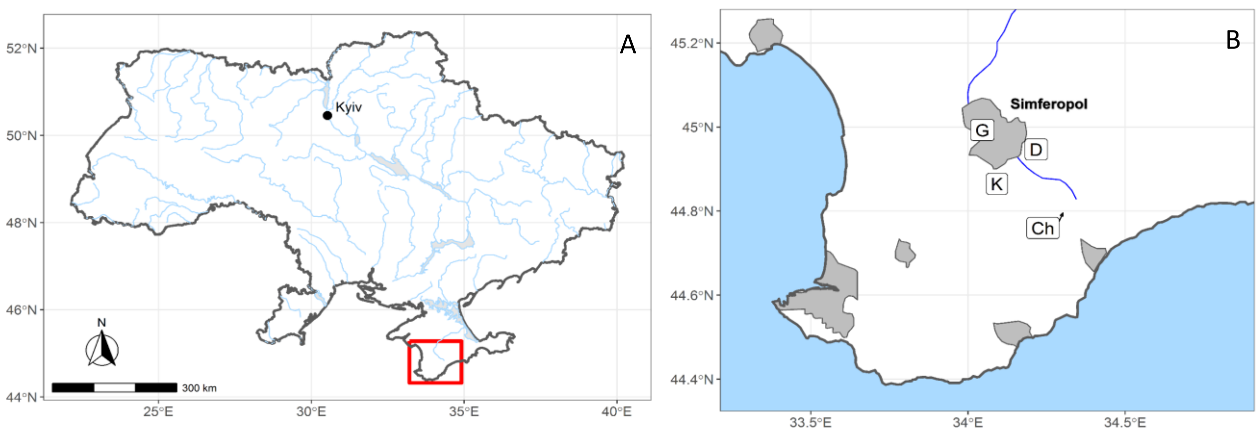


Figure 1. Research areas. A) Crimean Peninsula (Ukraine) and B) research site (Simferopol district)

The examined nest complexes of *L. flavus* were located at the following sites: the center of the Simferopol city (Gagarinsky Park); the outskirts of the Simferopol city (arboretum and the Kurtsy village); and the lower plateau slopes of the Chatyr-Dag Mountain, a mountainous massif in the Southern Ridge of the Crimean Mountains. The first three research sites are located in the foothills of the Crimean Mountains (300-400 m above sea level), whereas the Chatyr-Dag is 900-1100 m above sea level.

There were five nest complexes monitored in 2001, of which two were found on the lower plateau of the Chatyr-Dag Mountain, and other nest complexes were located in the foothills. The number of nests in each nest complex is given in Table. 1. The territory of each complex was divided into squares of 20 × 20 m (400 $m^2$), and the number of nests per square was counted. In 2014, all nest complexes except one on the lower mountain plateau were re-checked.

Table 1. Characteristics of nest complexes of *Lasius flavus*

| **Location** | **Geographical coordinates** | | **Number of nest mounds per nest complex** | **Number of squares 20 × 20 m per nest complex** |
|---|---|---|---|---|
| | **Northern latitude** | **Eastern longitude** | | |
| Gagarinsky Park, 2001 | 44.963980 | 34.097551 | 108 | 6 |
| Gagarinsky Park, 2014 | 44.963980 | 34.097551 | 0 | 6 |
| Kurtsy, 2001 | 44.892586 | 34.140614 | 229 | 3 |
| Kurtsy, 2014 | 44.892586 | 34.140614 | 113 | 3 |
| Arboretum, 2001 | 44.924455 | 34.166733 | 211 | 1 |
| Chatyr-Dag, lower plateau, 2001 | 44.795509<br>44.797960 | 34.301772<br>34.320011 | 73 (1st complex);<br>33 (2nd complex) | 1 (1st complex);<br>1 (2nd complex) |
| Chatyr-Dag, lower plateau, 2014 | 44.795509 | 34.301772 | 54 (1st complex) | 1 (1st complex) |

Nest complexes on all sites were seen within meadow habitats. The first nest complex of the Chatyr-Dag Mountain was found at the bottom of the karst funnel, and the second nest complex was detected on the lower plateau slope. The nest complex in the arboretum was seen along the mouth of a stream, in the Kurtsy village in the pasture, and in the Gagarinsky Park in the wet meadow, where woody plants were detected.

All locations examined were exposed to anthropogenic impacts of different origin and intensity. Nest complex on the lower plateau slope, for example, was in close proximity to the tourist trail. Area around the nest complex in the arboretum was near the Simferopol reservoir, where small groups of ruminants were grazed (1 to 5 goats per day). The intensity of grazing on the outskirts of Kurtsy has been very high (50-100 sheep per day) since 2005, which caused trampling of vegetation and damage to nest mounds. Before 2005, grazing groups were much smaller. Therefore, the nest complex found on that site was exposed to both low (in 2001) and high intensity levels (in 2014) of anthropogenic impact. Finally, there were efforts to reconstruct the Gagarinsky Park in 2010, which involved draining of the marshy area, where the ant colonies lived. Given the fact that increased water content in soil (Marikovsky 1965) is crucial for the existence of hyphrophilic *L. flavus* species (Marikovsky 1965), draining was labeled as the most destructive anthropogenic factor. Therefore, research sites can be arranged in order of increasing intensity of anthropogenic impact as follows: the Chatyr-Dag Mountain (no impact), arboretum (low intensity of impact), Kurtsy village (high intensity of impact), and Gagarinsky Park (critical intensity of impact).

**Mound Characteristics**

The following mound characteristics were measured: height, diameter (in centimeters, cm), and volume. Mound diameter was expressed as the average of the two variables, namely circumferences at the narrower and widest parts of the mound. Mound volume was computed using the cone volume formula, as seen in Equation 1:

$$\mathbf{V = 1/3H\pi R^2}\text{-----------(1)}$$

Where *r* is equal to *d/2*, and the height-to-diameter ratio is a generalized indicator of the shape of the mound.

Other measurements taken for each nest complex included the mound count, total volume (or capacity) of the nest complex, average mound height, and average mound diameter. To link morphometric profile of mounds with the level of anthropogenic impact, an additional parameter was found, namely the degree of habitat's anthropogenic transformation. This measure was determined through comparing the target location with habitats untouched by human activity, and it was estimated in points.

The quantitative data, such as height, diameter, and volume, were divided into three classes to estimate the mound size, namely small, medium, and large. Class boundaries were determined using the k-means method. The results are given in Table 2.

Table 2. Size-based classes of mounds based on morphometric parameters of height, diameter, volume, and shape of the nest

| Size of nest | Height (cm) | Diameter (cm) | Volume ($cm^3$) | Shape |
|---|---|---|---|---|
| Small | 3.00-19.30 | 22.00-49.94 | 50.27-732.21 | 0.07-0.35 |
| Medium | 19.30-31.43 | 49.94-73.45 | 732.21-1476.56 | 0.35-0.52 |
| Large | 31.43-57.00 | 73.45-140.00 | 1476.56-3078.76 | 0.52-1.05 |

Note: Class boundaries

Morphometric parameters of mounds were compared in two contexts: location and time period/years. Besides geographical disunity, the location-based comparison reflects the influence of different anthropogenic activity intensities. The comparison based on time period focuses on changes over time regarding the structure (i.e., number of nest mounds per square, total volume, and mound density) of the entire nest complex and its single parts/squares. The mound density was expressed as the ratio between the sums of all mound bases per square and the total square area multiplied by 100%, as shown in Equation 2:

**Mound density = sum (pi*d/2)*100/4e6**-------------------------(2)

Where *d* is the base diameter.

**Statistical Analysis**
The significance of differences between morphometric data sets was measured using statistical tests. All computations were done using the R software package (https://cran.r-project.org). The multiple comparison of the mean between groups was carried out by employing procedures, such as the one-way analysis of variance (R function: Aov) and Tukey test (R function: Tukey HSD), in R. The distribution of morphometric data was visualized using the R's boxplot function.

## RESULTS

Based on mound dimensions, *L. flavus* nests can be divided into 5 size-based classes, as shown in Table 3. Data on the number of nest mounds from each class are given in Table 6.

Table 3. Distribution quantities obtained for morphometric parameters of *Lasius flavus* nest mounds

| Quantile | Height (cm) | Diameter (cm) | Volume ($cm^3$) | Shape |
|---|---|---|---|---|
| 0%(min) | 3 | 22 | 50.27 | 0.07 |
| 25% | 16 | 43 | 356.05 | 0.3 |
| 50% | 21 | 53 | 578.05 | 0.38 |
| 75% | 29 | 73 | 1047.2 | 0.48 |
| 100%(max) | 57 | 140 | 3078.76 | 1.05 |

Table 3 presents morphometric variables, specifically diameter, height, volume, and shape, at different quantiles of the distribution. As can be seen, the largest *L. flavus* nest mounds in the studied area were more than 50 cm in height and nearly 1.5 m in diameter. However, the amount of such mounds was insignificant (Table 6). Although the oldest mounds (quantile range, 75% to 100%) were the largest mounds in the nest complex, younger mounds (quantile range, 25% to 50%) made up the majority of the overall volume. A considerable portion of nest mounds belongs to the category to medium-size mounds (Table 2). For example, the nest complex in Gagarinsky Park had 108 nest mounds in 2001, of which 45 were medium-sized (Table 6). In Kurtsy, there were 54 out of 229 medium-sized mounds in 2001 and 55 out of 113 medium-sized mounds in 2014. The arboretum was characterized by the presence of 85 out of 211 medium-sized nest mounds. In regards to the Chatyr-Dag Mountain, the first nest complex comprised 15 out of 73 medium-class mounds in 2001 and 10 out of 54 medium-class mounds in 2014. The second nest complex had five out of 33 medium-class mounds in 2001. The number of large (d3) nest mounds is significantly lower as compared to small (d1) and medium-sized (d2) ones in all nest complexes, except for the mountainous location. The youngest nests are likely to belong to class I (small mounds).

The spatial form of the mounds changes with age. For instance, younger mounds tend to be flat and gain shape in later years. The shape of the mounds in this study varied from flat (quantiles 0.01 and 25%) to hemispherical and conical (quantile range, 50% to 100%). This proves that flat nest mounds acquired a conical or hemispherical shape as they grew.

The comparison of *L. flavus* nest complexes between locations revealed a significant difference in the capacity of nest complexes, as shown in Table 4. For example, the nest complex on the mountain plateau slope had 2 times less nest mounds than that at the bottom of the karst funnel, but the total volume of the nest complex was higher. The average height of nest mounds was similar between the above two nest complexes, yet mounds on the lower plateau slope were larger in diameter compared to the flatter ones at the bottom of the karst funnel (Figure 2 & Table 4). This indicates that old conical mounds gradually turn into hemispherical ones as their growth slows down. The nest complex from the bottom of the karst funnel is younger than that from the plateau slope, as evidenced by the significant increase in mound height recorded in 2014.

Table 4. Main statistical indicators describing nest complexes of *Lasius flavus* in all locations examined

| **Location** | **Year** | **Id complex** | **Number of nest mounds per nest complex** | **Sum_v (cm3/1000)** | **Avg heigth (cm)** | **Std.err heigth (cm)** | **Avg diameter (cm)** | **Std.err diameter (cm)** | **Intensity of antropogenic Impact** |
|---|---|---|---|---|---|---|---|---|---|
| Chatyr-Dag | 2001 | 1 | 73 | 93.06 | 30.23 | 1.08 | 78.82 | 1.56 | 0 |
| Chatyr-Dag | 2001 | 2 | 33 | *52.82* | 31.45 | 1.23 | **95.06** | 3.15 | 0 |
| Chatyr-Dag | 2014 | 1 | 54 | 96.67 | **38.46** | 1.01 | 87.80 | 2.28 | 0 |
| Arboretum | 2001 | 1 | 211 | **138.76** | 23.09 | 0.60 | 51.87 | 1.03 | 1 |
| Gagarinsky Park | 2001 | 1 | 108 | 60.56 | 19.43 | 0.65 | 52.52 | 1.43 | 3 |
| Kurtsy | 2001 | 1 | 229 | 84.38 | *15.50* | 0.39 | *44.48* | 0.64 | 2 |
| Kurtsy | 2014 | 1 | 113 | 101.02 | 25.33 | 0.69 | 65.07 | 1.30 | 2 |

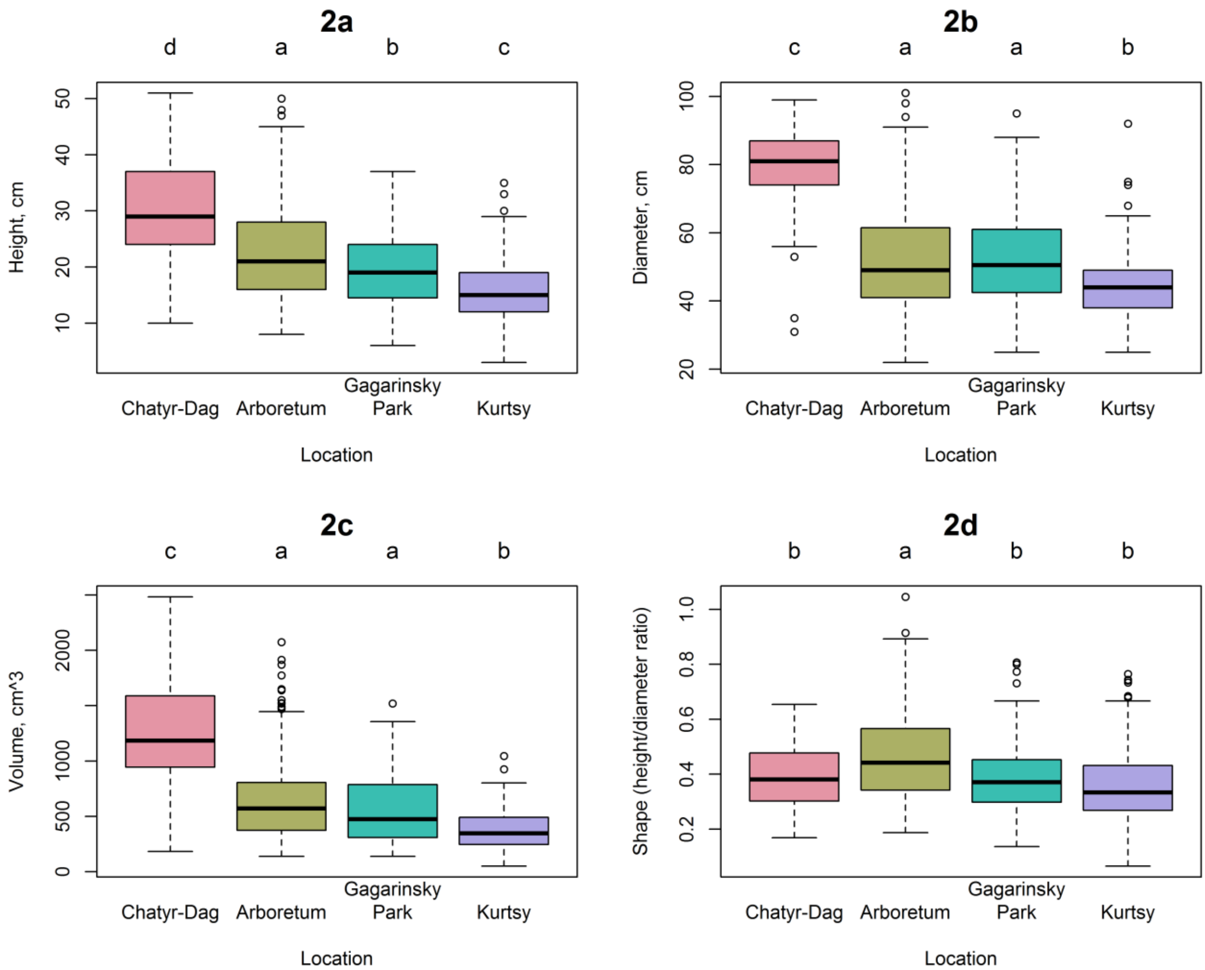


Figure 2. Morphometric comparison of nest complexes between four locations in 2001: 2a) by height, 2b) by diameter; 2c) by total volume and 2d) by height-to-diameter ratio

The significant differences in data sets between locations were recorded for all morphometric parameters, with a few exceptions (Figure 2). There were no significant differences in the average mound diameter and the total volume between nest complexes in the arboretum and Gagarinsky Park (Figure 2b, c). There were no significant differences in the height-to-diameter ratio between locations except for the arboretum (Figure 2d). In the phase of growth, the nest complex grows higher, whereas the increase in diameter indicates the beginning of the stabilization phase.

The nest complex in the arboretum was found to be larger in volume than that at the bottom of the karst funnel. This was achieved due to the three times higher number of nest mounds. The height and diameter of those nest mounds, however, were smaller. Thus, itcan be suggested that this nest complex was younger compared to that within the Chatyr-Dag plateau's area. The nest complex on the outskirts of Kurtsy had even smaller nests as compared to that found in the arboretum (Figure 3). Figure 3 presents the results of morphometric comparison of nest complexes in the Chatyr-Dag and Kurtsy for 2001 and 2014.

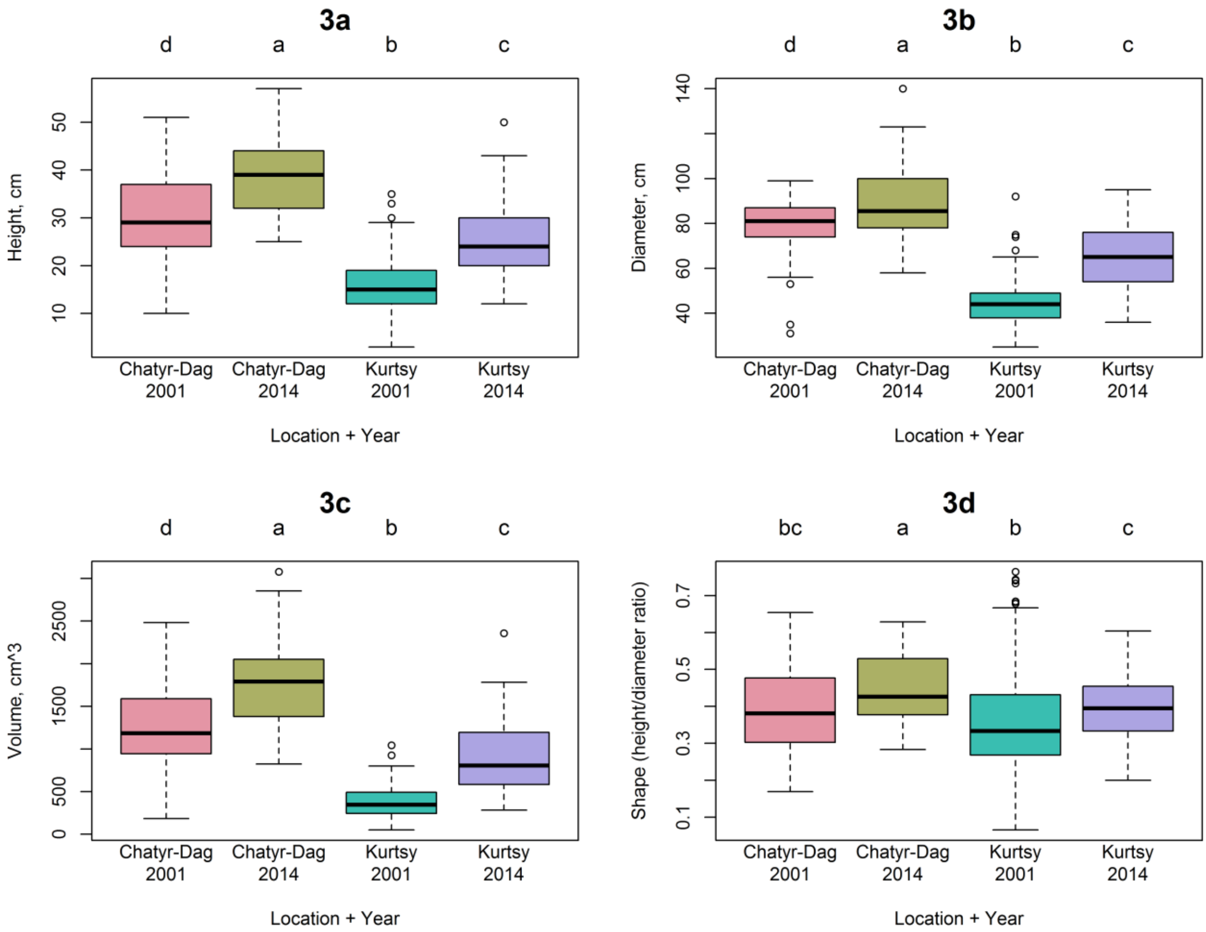


Figure 3. Comparison of nest complexes in Chatyr-Dag (first nest complex) region and Kurtsy village between 2001 and 2014: 3a) by height, 3b) by diameter, 3c) by total volume and 3d) by height-to-diameter ratio

Note: Letters on top of boxplots are based on the results of pairwise comparison and indicate the presence or absence of statistically significant differences between the two group means.

As can be seen from Figure 3, mound dimensions, such as height, diameter and volume, changed over a 10-year period. There were no significant differences in the shape of the mound because this parameter is allometric and less prone to change than metric measurements.

The comparison of comparable data regarding the number of mounds per nest complex showed that the total volume of the nest complex in the arboretum was greater than that in Kurtsy. The second visit to nest sites in 2014 showed that the number of mounds in the nest complex on the outskirts of Kurtsy decreased by half, and other mounds increased in size (1.6 times in average height and 1.5 times in diameter). Therefore, the total volume of the nest complex grew 1.2 times. Finally, the nest complex in the Gagarinsky Park had the least amount of mounds and thus the smallest volume. The nest mounds themselves, however, were slightly larger as compared to those in Kurtsy. Based on data recorded in 2001, the oldest nest complex with the largest mounds was the nest complex on the lower plateau slope of the Chatyr-Dag Mountain, followed by nest complexes in the arboretum, Gagarinsky Park, and Kurtsy. By 2014, the Kurtsy's nest complex became larger in volume, and the nest complex in Gagarinsky

Park was found to no longer exist. According to 2014 data, the number of nest mounds decreased in all nest complexes examined, but their size and volume showed an upward trend. As the mounds count can greatly fluctuate, it does not reflect the nest complex stability. The dimensions of the mound, however, are suitable for detecting transition of the nest complex to stabilization phase. The results of the study revealed that mounds typically grow in size when exposed to non-critical anthropogenic disturbances. Thus, even intensive grazing did not affect the growth of nest complexes.

In the nest complexes of *L. flavus*, nests may not be distributed within one single square. Some nest structures can occupy 2 to 6 squares of 20 × 20 m. Hence, the number of nest mounds and the sum of nest volumes per square may vary between squares (Table 5).

Table 5. Morphometric profile of *Lasius flavus* nest mounds within the examined squares (400 $m^2$)

| **Location** | **year** | **Id complex** | **Id square** | **Count** | **sum_v ($cm^3$/1000)** | **Coverage (%)** |
|---|---|---|---|---|---|---|
| Chatyr-Dag | 2001 | 1 | 1 | 73 | 93.062 | 0.226 |
| Chatyr-Dag | 2001 | 2 | 1 | 33 | 52.818 | 0.123 |
| Chatyr-Dag | 2014 | 1 | 1 | 54 | 96.666 | 0.186 |
| Arboretum | 2001 | 1 | 1 | **211** | **138.755** | **0.430** |
| Gagarinsky Park | 2001 | 1 | 1 | 14 | *4.085* | *0.021* |
| Gagarinsky Park | 2001 | 1 | 2 | *13* | 5.187 | 0.024 |
| Gagarinsky Park | 2001 | 1 | 3 | *13* | 6.503 | 0.027 |
| Gagarinsky Park | 2001 | 1 | 4 | 14 | 7.429 | 0.028 |
| Gagarinsky Park | 2001 | 1 | 5 | *13* | 8.891 | 0.030 |
| Gagarinsky Park | 2001 | 1 | 6 | 41 | 28.465 | 0.093 |
| Kurtsy | 2001 | 1 | 1 | 112 | 30.696 | 0.175 |
| Kurtsy | 2001 | 1 | 2 | 76 | 32.855 | 0.149 |
| Kurtsy | 2001 | 1 | 3 | 41 | 20.827 | 0.076 |
| Kurtsy | 2014 | 1 | 1 | 60 | 54.940 | 0.155 |
| Kurtsy | 2014 | 1 | 2 | 34 | 26.707 | 0.083 |
| Kurtsy | 2014 | 1 | 3 | 19 | 19.374 | 0.051 |

Due to differences in the volume of the mound between squares, the mound density can vary within the same complex. The maximum mound density was recorded in Chatyr-Dag and arboretum, where they were concentrated within one single square. In the arboretum, nest mounds covered twice the territory of the square in Chatyr-Dag due to the greater number of mounds. In regards to mound density and total volume, the Kurtsy's nest complex with its three squares occupied an intermediate position. For instance, this nest complex had the total mound volume per square and mound density per square in 2001 lower that other nest complexes. In 2014, the total mound volume increased in all nest complexes except for one in Gagarinsky Park. At the same time, there was a decrease in the total mound density, which we associate with a decrease in the number of mounds.

In Kurtsy, the volume of small mounds increased significantly (by 1.8 times) due to growth. Other squares in this complex either did not change, or slightly lessened their volume. The reduction of nests in 2014 resulted in lower mound density per square. A similar trend was noted in 2014 for Chatyr-Dag. In Gagarinsky Park, mound density was the lowest (0.120 to

0.430%) among nest complexes in 2001, which means that all mounds were located far from each other. In 2014, this nest complex was no longer there. From this it follows that high density of mounds ensures the survival of the nest complex exposed to anthropogenic impact, such as grazing. The nests are interconnected by underground passages so that ants can travel from areas with high mound density to areas with low mound density.

As can be seen from Table 6, the nest complex on the lower plateau of Chatyr-Dag was dominated by large nest mounds (h3, d3, and v2-v3). The total number of nest mounds in this nest complex dropped from 73 in 2001 to 54 in 2014. Nest complexes in Gagarinsky Park and Kurtsy were dominated by small, asymmetrical mounds. Over the period of 13 years, small nest mounds in the Kurtsy's nest complex either disappeared (h1, d1, v1, r1) or grew to become medium size (h2-h3, d2-d3, v2-v3, r2-r3). In 2001, around 50% of nest mounds found in the arboretum were medium sized, whereas large mounds accounted for 15% of the nest complex. The predominance of larger nest mounds can be explained by the fact this nest complex was located within the zone of small anthropogenic impact. As it can be seen from the above, all mounds in nest complexes compared varies in size. Besides high density nesting, the condition for the stability of the nest complex is that nest mounds should belong to the second and third dimensional classes. It can be assumed that larger mounds have higher grazing resistance than smaller ones.

In spite of the decrease in the total number of nest mounds in the nest complex on the lower plateau of Chatyr-Dag, the amount of large (v3, Table 6) mounds increased from 23 in 2001 to 36 in 2014. All large nest mounds were concentrated within the same square. In the arboretum in 2001, large nest mounds made up around 5% of the total number (11 out of 211). However, every single one was found within the same square. In Kurtsy, there were no large mounds in 2001; the first large mounds were detected in 2014 in each square examined. There were 7 large mounds within the first square, 1 within second, and 4 within third. The nest complex in Gagarinsky Park occupied 7 squares, but there was only 1 large nest mound detected. Therefore, the number of large mounds and mound density determine the ability of *L. flavus* nest complex to withstand anthropogenic disturbances. Anthropogenic resistance depends upon the presence of large nest mounds rather than the total number of mounds in the nest complex. Since large mounds can be considered the oldest in the nest complex and they normally concentrate within one square, it can be assumed that *L. flavus* nest complexes begin with a group of closely located nests.

Table 6. Distribution of morphometric classes of *Lasius flavus* nest mounds depending on location and time period/year

| **Location** | **year** | **Id complex** | **Number of nest mounds** | **h1** | **h2** | **h3** | **d1** | **d2** | **d3** | **r1** | **r2** | **r3** | **v1** | **v2** | **v3** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Chatyr-Dag | 2001 | 1 | 73 | 9 | 34 | 30 | 2 | 15 | **56** | 30 | 35 | 8 | 8 | 42 | 23 |
| Chatyr-Dag | 2001 | 2 | 33 | 3 | *10* | 20 | *0* | *5* | 28 | 17 | *16* | *0* | 3 | *7* | 23 |
| Chatyr-Dag | 2014 | 1 | 54 | *0* | 11 | **43** | *0* | 10 | 44 | *8* | 31 | 15 | *0* | 18 | **36** |
| Arboretum | 2001 | 1 | 211 | 89 | **86** | 36 | 10<br>8 | **85** | 18 | 55 | **86** | **70** | 151 | 49 | 11 |
| Gagarinsky Park | 2001 | 1 | 108 | 56 | 46 | 6 | 50 | 45 | 13 | 46 | 46 | 16 | 77 | 30 | 1 |
| Kurtsy | 2001 | 1 | 229 | **172** | 55 | *2* | **17**<br>**2** | 54 | *3* | **126** | 72 | 31 | **222** | *7* | *0* |
| Kurtsy | 2014 | 1 | 113 | 23 | 65 | 25 | 18 | 55 | 40 | 35 | 66 | 12 | 49 | **52** | 12 |

**Note:** Height classes were designated as h1, h2, and h3, which correspond to small, medium, and large mound sizes, and coincide with mound diameter d1, d2, d3, etc.

## DISCUSSION

**Habitats of *L. flavus*.**
In Crimea, *L. flavus* occupies intrazonal habitats, such as mountain meadows and meadows in the foothills (Radchenko 2016; Stukalyuk & Radchenko 2011). This species prefers to build nest complexes in open habitats, where the amount of insolation is enough to favor brood development (Vele & Holusa 2017). *L. flavus* is able to form large aggregations of nest mounds, which makes it difficult to graze farm animals and harvest hay (Radchenko 2016). Note that some plant species can grow on top of anthills and that these species can differ from the surrounding vegetation (Dauber et al. 2006; Woodell 1974) due to the presence of nitrogen in *L. flavus* nests (Bierbaß et al. 2015). *L. flavus* visits numerous aphid colonies that feed on plant roots. In Poland, for example, *L. flavus* were found to feed on up to 14 aphid species (Depa & Wegierek 2011). In England, there were up to 3000 aphids per nest (Pontin 1978). The diet of *L. flavus* consists primarily of carbohydrate excreta. The life cycles of their nest complexes are rather long, at least 30 years (Pontin 1978). We found out that over the period of 13 years, the structure of *L. flavus* nest complexes can undergo significant changes, from complete disappearance (Gagarinsky Park) to increase in mound density and mound dimensions (other nest complexes).

**The Structure of Nest Complexes of *L. flavus*.**
*Lasius flavus* belongs to ant species capable of creating nest complexes at very high densities, up to 52 nests per 100 $m^2$ (Dostál et al. 2005). There are also evidences showing that *L. flavus* can build single nests or mounds (Marikovsky 1965). Nest complexes discovered in this study have a relatively low mound density (Chatyr-Dag: 18.2 and 8.2 nests per 100 $m^2$ in the first and second nest complexes, respectively; Kurtsy: 19.1 nests per 100 $m^2$; Gagarinsky Park: 4.5 nests per 100 $m^2$). The only exception was the nest complex in the arboretum with the mound density of 52.7 nests per 100 $m^2$, which coincided with that in the study by Dostál et al. Mound densities identified in this study are within the normal range for *L. flavus*, which is 1 to 35 nest mounds per 100 $m^2$ (Doncaster 1981). Seifert (2017) reports a maximum density of nest mounds for *L. flavus* of 103.4 per 100 $m^2$ for grassland habitats in Central Europe, with a density of nest mounds in this habitat ranging from 34.8 to 103.4 per 100 $m^2$. In other habitats of Central Europe, the density of nest mounds is not so high: from 12.2 to 35.9 per 100 $m^2$ in peat bogs, 13.5 to 34.6 in woodlands. Our data on the density of nest mounds per 100 $m^2$ is comparable to most of Seifert's data. The exception was the pasture lands of Central Europe, where the maximum density of nest mounds per 100 $m^2$ can be 2 times higher than in Crimean habitats.

High mound densities are linked to high abundance (average, 1.082 ± 0.047 workers per 1 $m^2$) of *L. flavus* workers amongst the local ant assemblages (Boomsma & Van Loon 1982), which makes this species dominant in some habitats (Doncaster 1981). On the other hand, we believe that nests can only be interconnected when there are at least 4 nest mounds per 100 $m^2$, as in Gagarinsky Park. The lower mound density is associated with single mounds that are located too far apart to be connected by underground passages. Perhaps, a colony begins with the union of such initially divided nests. Workers from different colonies are hostile to each other and to winged males and queens (Steinmeyer et al. 2012), whereas workers within the colony avoid aggression.

*Lasius flavus* is not a strictly monogynous species; large colonies can have 2 and more queens per nest. This form of co-existence is called oligogyny (Boomsma et al. 1993). Newer papers report polydomy and confirm data from Boomsma et al. 1993 regarding the percentage of monogynous and polygynous colonies in the nest complex of *L. flavus* (Steinmeyer et al. 2012). Furthermore, the founding of new *L. flavus* colonies normally occurs through pleometrosis, that is, by a group of queens (Pontin 1960).

*Lasius flavus* queens can re-colonize nest mounds after the nuptial flight or by workers from neighboring nests even if the population is dying. This ensures the survival of the nest complex. In our study, the percentage of abandoned nests in all nest complexes did not exceed the value of the statistical error (up to 1-2%). In other words, the majority of nests performed their functions. Other studies indicate a larger percentage of abandoned nests in the colony – 28% (Steinmeyer et al. 2012), but, apparently, data on active and abandoned ant nests can vary greatly for different colonies and different locations.

*Lasius flavus* nests can be classified based on age and volume (Dlussky 1981). Young nest mounds are those with a volume of 1 to 11 $dm^3$. The volume of medium-aged nest mounds varies from 12 to 44 $dm^3$. Nest mounds larger than 44 $dm^3$ are considered mature. Among 5 colonies (nest complexes) examined, those located in the Crimean Mountains consisted mainly of mature nests, whereas that in arboretum was of middle age. Ant colonies from Kurtsy and Gagarinsky Park can be considered as young. Our data proved that young nest mounds make up the largest and the most vulnerable group of nests in young colonies. As the colony grows, some nest mounds become larger and other mounds end up destroyed by grazing or other causes. In addition, nest mounds of all size-based classes can disappear completely when the groundwater level changes, as happened in Gagarinsky Park. Our suggestions regarding the age of nest complexes are in line with the Dlussky's classification. According to some reports, *L. flavus* nest mounds that are 30 cm high and 1 m in diameter can be 80 to 90 years old (Harlov 1960). The average annual growth increment for *L. flavus* mounds is 1 liter (Harlov 1960). Nest complexes on the Chatyr-Dag plateau can be up to 100 years of age, since they contain nest mounds of appropriate sizes (42 cm high and 100-120 cm in diameter, sometimes up to140 cm in diameter). Nest complex in the arboretum is slightly younger (60-70 years) since it has large mounds 60-80 cm in diameter. Nest complexes from Kurtsy and Gagarinsky Park with mounds 40-60 cm in diameter are unlikely to be older than 40 years. According to the literature, the age of some nest mounds in England can reach 164 years (King 1981). This author developed an original technique to assess the history and age of meadows and pastures based on the age of *L. flavus* nest mounds. Small nest mounds were found to grow first in height, and then is diameter (Waloff & Blackith 1962).

The ratio between nest mounds of different ages and sizes is an important marker. Other studies report that 50% of mounds were young and small, 38% were of middle age and medium size, and 12% were large and mature (Ehrle et al. 2017). These data are consistent with our study where all nest complexes examined were young except for those on the Chatyr-Dag plateau. The population of one small nest usually does not exceed 2-3 thousand workers, medium-sized nest 5 thousand, and large nest 10 thousand (Odum & Pontin 1961). According to some reports, large nest can have somewhere from 50 to 100 thousand workers (Czechowski et al. 2012; Radchenko 2016). Therefore, they can help maintain the colony when population of small nests dies. In addition, large nests have larger forage areas compared to small ones (Waloff & Blackith 1962).

**Anthropogenic Impact on the Structure of Nest Complexes of *L. flavus* and Other Ant Species**.

Besides anthropogenic disturbances, one of the most important destructive factors affecting nest complexes of *L. flavus* is the influence of other ant species, such as *Formica sanguinea*, *F. exsecta* (Marikovsky 1965), *F. truncorum* (Rosengren 1986), and *F. pratensis* (in the Crimean Mountains, Stukalyuk & Radchenko 2011). On the other hand, *L. flavus* can also encounter negative consequences of its competition with *L. niger* (Pontin 1961). According to some reports, the disappearance or decrease in the abundance of *L. niger* was coincident with the increase in abundance of *L. flavus* (Pontin 1961, 1963; Rosengren 1986). Some studies report a similar negative effect of *Myrmica scabrinodis,* which manifested in the increased production of winged queens (Pontin 1969). Since *L. niger,* the main competitor of *L. flavus*, is not common in Crimea (Radchenko 2016), *L. flavus* colonies can enjoy the riches of nature without the risk of competition. Therefore, the major factor limiting the growth of *L. flavus* colonies is anthropogenic impact.

Seifert (2017) reports that the *L. flavus* nest complex with 437 nest mounds was found in the pasture with intensive sheep grazing in Germany. Nest complexes discovered by us in the Crimea were two to three times smaller. Our data also showed that grazing practices did not limit the growth of colonies but rather influenced the change of dimensional characteristics of mounds. They became larger, whereas small mounds disappeared. Another critical factor is the lowering of the groundwater level. Nevertheless, the size of *L. flavus* colonies is not limited to hundreds of nests. There are evidences that a single *L. flavus* nest complex in Siberia can contain even thousands of those (Marikovsky 1965).

## CONCLUSION

Among anthropogenic factors grazing does not affect the viability of nesting complexes. Over a period of 14 years, the nests of average size class in 4 complexes out of 5 moved from 1 size class in terms of height and diameter to the next classes, i. e. enlarged. This is one of the protective mechanisms of viability of ant nesting complexes. Lowering the groundwater level is a fatal factor that leads to the death of the entire nesting complex. The density of nests less than 5 per 100 $m^2$ is a sign of the existence of nests separately from each other, greater - a sign of existence as a nesting complex. The density of nests 52 per 100 $m^2$ is a sign of the maximum level of density of nests in the complexes of ants *L. flavus* in the discovered habitats of Crimean peninsula.

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