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NOTE

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Summary. Despite over 14,000 known species of ants on earth, a massive biomass, and their intrinsic social evolution, very little is known about how ants perceive their environment. In the face of such vast biodiversity, only about 50 species have been reported to use tools, which suggests unknown facets in myrmecological research. Herein, we report on a field observation where multiple *Tapinoma* workers restrained a large *Camponotus* worker for several hours without apparently inflicting injury. The *Tapinoma* workers used tools (stones) that were placed under the *Camponotus* worker, seemingly employing them as anchors against which they affixed themselves to restrain the seized ant. In addition, *Tapinoma* workers attached themselves to the head of the *Camponotu*s which seemed to blind it temporarily and restrict use of its mandibles. Such behaviour in ants demonstrates possible cognitive understanding of their environment and colony socio-adaptation.

Résumé. Utilisation d'un nouvel outil chez les fourmis *Tapinoma* sp. (Hymenoptera : Formicidae). Bien qu'il existe plus de 14000 espèces de fourmis sur Terre, que leur biomasse soit très importante et qu'elles aient évolué vers la socialité, on sait très peu de choses sur la façon dont les fourmis perçoivent leur environnement. Face à une biodiversité aussi vaste, seules une cinquantaine d'espèces environ sont connues pour utiliser des outils, ce qui suggère que de larges pans du comportement des fourmis restent inconnus. Nous rapportons ici une observation sur le terrain où plusieurs ouvrières de *Tapinoma* ont immobilisé une grande ouvrière de *Camponotus* pendant plusieurs heures, sans apparemment lui infliger de blessure. Les ouvrières de *Tapinoma* ont utilisé des outils (des pierres) qu'elles ont placés sous l'ouvrière de *Camponotus*, les utilisant apparemment comme des points d'ancrage sur lesquels elles se sont fixées pour immobiliser la fourmi saisie. De plus, les ouvrières de *Tapinoma* se sont attachées à la tête du *Camponotus*, ce qui semble l'aveugler temporairement et restreindre l'utilisation de ses mandibules. Un tel comportement chez les fourmis démontre une possible compréhension cognitive de leur environnement et de la socio-adaptation de la colonie.

Keywords: Myrmecology; behaviour; tools; *Camponotus*; Spain

Since the first report of chimpanzees *Pan troglodytes* (Blumenbach, 1776) using tools at the end of the 1960s (van Lawick-Goodall 1968), an increasing number of animals have been discovered to use tools, both vertebrates (birds, mammals, and fish) and invertebrates (arthropods and molluscs) (Bentley-Condit & Smith 2010). Within insects, ants are some of the few that have been shown to utilize tools. In fact, some ant species that use tools require highly complex understanding of the environment for their successful implementation (Zhou et al. 2020). Arthropods demonstrate a vast repertoire of behavioural and cognitive actions (Pfeffer & Wolf 2020), and certain cognitive flexibility is also involved in insect tool use (Maák et al. 2017), such as selective attention (Nityananda & Chittka 2015; de Bivort & van Swinderen 2016) and social learning behaviours (Sheehan & Tibbetts 2011; Alem et al. 2016; Loukola et al. 2017). These studies demonstrate that cognition is not restricted to animals with larger brains, but it is also present in insects such as ants (Czaczkes 2022). Indeed, Pierce (1986) in his review on insect tool use concluded that tool use is not related to intelligence, but rather to adaptations that compensate for morphological restrictions, and such adaptations are shaped by selection pressures and guided by evolutionary processes. In addition, personality traits are known to predict tool use behaviour in some ants (Maák et al. 2020)

Bentley-Condit & Smith's (2010) catalogue reports around 30 genera of insects and around 50 cases of tool use. All cases of ants using tools were in the subfamily

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Myrmicinae, which included species from the genus *Pogonomyrmex* Mayr, 1868, *Solenopsis* Westwood, 1840, *Novomessor* Emery, 1915 and *Aphaenogaster* Mayr, 1853 (Zhou et al. 2020; Richards 2022; see Módra et al. 2022). In 2017, Maák et al. published a notable study in which two *Aphaenogaster* species were shown to select appropriate tools in foraging for liquid foods, proving levels of flexibility in ant tool use. Additionally, ants which can use various debris to transport liquid food, and similar foraging examples are known from multiple ant species (see Lőrinczi et al. 2018; Módra et al. 2022).

Ant tools have been associated mostly with foraging strategies, which are particular responses to ecological pressures. Some ant species use stones for building, however these are not considered true tool use (St Amant & Horton, 2008). For example, *Tapinoma nigerrimum* (Nylander, 1856) has been shown to build walls to block other ants from gaining access to resources (Gómez-Durán 2012a). This species has also been reported to do nest plugging and soil or stone dropping, blocking the entrance of other nest colonies (Gómez-Durán 2012b). This behaviour has been rarely documented in other ant species, but some examples include *Dorymyrmex bicolor* Wheeler, 1906 (Möglich & Alpert 1979), *Tetramorium caespitum* (Linnaeus, 1758) (Lin 1964–1965; Schultz 1982), *Iridomyrmex purpureus* (Smith, 1858) (Höldobler 1986), and *Novomessor cockerelli* (André, 1893) (Gordon 1988). The aim of this behaviour is to block other competing ants from exiting their nests. In the Iberian Peninsula, there are nine described species of *Tapinoma* [*Tapinoma darioi* Seifert et al., 2017, *T. erraticum* (Latreille, 1798), *T. ibericum* Santschi, 1925, *T. madeirense* Forel, 1895, *T. magnum* Mayr, 1861, *T. melanocephalum* (Fabricius, 1793), *T. nigerrimum*, *T. simrothi* (Krausse, 1911), and *T. pygmaeum* (Dufour, 1857)] but to the best of our knowledge, there has been no other previous reporting of behaviour employing tools. To our knowledge, our study is the first documented case of tool use in *Tapinoma* workers, specifically their use of stones as tools to help restrain a large *Camponotus* worker for several hours.

Material and methods

Field observations

Field observations took place in Campo de Montiel County, Ciudad Real province (central Spain 38°85′N, 3°01′W, 750 m above sea level), on 26–27.III.2021. The observation was recorded with a cell phone, and several videos were taken on the behavioural event for a total duration of 38 min (34:40 on 26.III at 18:31–19:20, and 3:20 on 27.III at 08:43–08:49). A *Camponotus* Mayr, 1861 ant appeared seized by *Tapinoma* Förster, 1850 ants. Moreover, during the first day we also observed how the *Tapinoma* sp. workers (approximately 50–60 active ants) were apparently moving from one nest. We watched several *Tapinoma* sp. workers transferring several larvae (at least 3–4 larvae were observed). The movement of the ants on the trail was in both directions, and a nest was located roughly 4 m away from where the *Camponotus* worker was being seized. The nest was within the base of a rosemary bush (*Salvia rosmarinus* Spenn, 1835).

Molecular analysis of Tapinoma *workers and larvae*

Workers derive from queens and are, therefore, highly related to their sister colony workers (Jowers et al. 2013). Because of this close affiliation, using a maternally inherited gene fragment such as mitochondrial cytochrome oxidase I (COI) is sufficient for sequencing and species identification purposes. Thus, a single tissue sample was sufficient to represent the *Tapinoma* workers and the larvae transported by them. The primers were LCO and HCO (Folmer et al. 1994). Sequences were edited with Sequencher v5.4.6 (Gene Codes Corporation, Ann Arbor, MI, USA), and checked for potential contamination using GenBank's BLASTn search (Altschul et al. 1990). Blast searchers were conducted in Genbank and all matches up to 95% were included in the phylogenetic tree. In addition, we included all other *Tapinoma* species present in the Iberian Peninsula to infer phylogenetic relationships available in Genbank. Most species of *Tapinoma* ants have been sequenced and COI are available in Genbank; only one species was missing: *T. pygmaeum*. This species is found only in the Northeastern Iberian Peninsula (Espadaler & Garcia-Berthou 1997), and therefore it seems an unlikely candidate species. *Tapinoma erraticum* was used as outgroup. Sequences were aligned in Seaview v.4.2.11 (Gouy et al. 2010). Phylogenetic tree reconstructions for the three concatenated gene fragments were performed using maximum likelihood (ML) through RAxML v8.2.12 (Stamatakis 2014). ML searches were conducted under GTRGAMMA and support was assessed by using 1000 bootstrapped replicates. All phylogenetic analyses were performed in the CIPRES platform (Miller et al. 2010). The consensus tree was visualized and rooted using FigTree v1.4.4 (Rambaut 2018), and later prepared as a graphic with the software Inkscape v1.0.1 (http://www.inkscape.org). Uncorrected *p*-distances with partial deletion were computed in MEGA X (Kumar et al. 2018).

Results

Field observations

After closer observation, it was apparent that the *Tapinoma* workers were not aiming to predate on the *Camponotus* worker, but rather to restrain it. We observed (>30 times) actions in which the *Tapinoma* workers collected stones (Figure 1A, B) and deposited them under the *Camponotus* worker that was being restrained. The *Camponotus* worker was also fighting with the *Tapinoma* workers.

Meanwhile, we observed a few large larvae transported from an ant nest (Figure 2A). When the *Tapinoma* workers transitioned to using larger stones, the immobilization was more efficient. (Figure 2B). At first, we believed that the larvae could be *Camponotus* and that the *Tapinoma* were occupying its nest, but later molecular analysis revealed that they were *Tapinoma* larvae (see below). The following morning on our visit back to the site, the *Camponotus* worker was

Figure 1. *Tapinoma* worker carrying a stone (shown in yellow circles) placed under the seized *Camponotus* worker. **A,** Shows when the ant collects the stone. **B,** Shows when the stone is deposited under the *Camponotus* worker. This behaviour was seen multiple times from multiple ants (see supplementary materials).

still alive but exhausted (see supplementary materials). *Tapinoma* ants walked over the *Camponotus* worker but showed less aggression and did not use stones anymore to restrain it. Multiple *Tapinoma* were seen dead on the following day (videos are available in supplementary materials).

Tapinoma *sequence identification*

The closest Genbank blast of the sequenced *Tapinoma* worker (Genbank accession PQ789216) was to *Tapinoma magnum* from Italy (Sicily), isolate Tmag196 (Genbank accession KY426528) with a 96.16% match and 24 substitution difference. The results from the ML analyses, however, revealed an unsupported node of the *Tapinoma* sp. to any clade, as can be deduced from the high genetic divergence to any other *Tapinoma* in Genbank. *Tapinoma simrothi* and *T. madeirense* as well as a large clade of *T. cf. magnum* were excluded from the phylogenetic analyses as they proved to be highly divergent and not closely related to the *Tapinoma* sp. Genetic divergence between the *Tapinoma* sp. and *T. ibericum* was 5.8%, 5% to *T. hispanicum*, and 4.7% to all other remaining ingroup species. The clade divergence within *T. ibericum* was 1.6%, and within divergence in the *T. darioi* group was 1.8%, within *T. nigerrimum* it was 0.6% and 1.3% within *T. magnum* (Figure 3). Sequencing of the larvae revealed it to be identical to the *Tapinoma* sequence, and therefore this excludes the possibility that it was *Camponotus* sp.

Discussion

The field observation revealed multiple *Tapinoma* workers carrying stones and placing them near or under a *Camponotus* worker to restrain it for a prolonged period of time. While several ant species are known to carry or move stones (e.g. see introduction), these are often stone droppings to block nest entrances of other ant species (Möglich & Alpert 1979; Gordon 1988; Grasso et al. 2004). This behaviour has also been reported in *Tapinoma nigerrimum* from the Iberian Peninsula (Gómez-Durán 2012a). Yet, our field observation is different as no nest blocking was observed and, instead, the *Tapinoma* workers followed the *Camponotus* worker throughout the encounter. The sequencing of a *Tapinoma* worker and a larva transported by one of them recovered the same haplotype, matching an undescribed species of *Tapinoma* from the Iberian Peninsula, with its closest match (96.16%) to a *Tapinoma* sp. sequence from Italy.

While the exact function of this behaviour remains uncertain, we suggest that *Tapinoma* workers anchored themselves to the stones with their hind legs in order to restrain the *Camponotus* worker. This was observed often and when the *Camponotus* was surrounded by stones, it was immobilized by multiple *Tapinoma*. The tarsal claws of *Tapinoma* are likely suited to grip the rugged soil terrain and to anchor without the need of a stone; however, the *Camponotus* worker could pull strongly in response and the *Tapinoma* often lacked strength to counteract the force of such a pull (see supplementary materials). Pulling was possible but more strenuous for the restrained ant when the *Tapinoma* workers attached to a moderately heavy stone. In addition, we observed that occasionally, when many stones were present, the *Camponotus* worker seemed clumsy and destabilized. In accordance with our hypothesis that the subdued ant was indeed restrained was the fact that *Tapinoma* workers attached themselves to the head of *Camponotus* to possibly blind her temporarily and to prevent her from using her mandibles. Throughout this behaviour, the

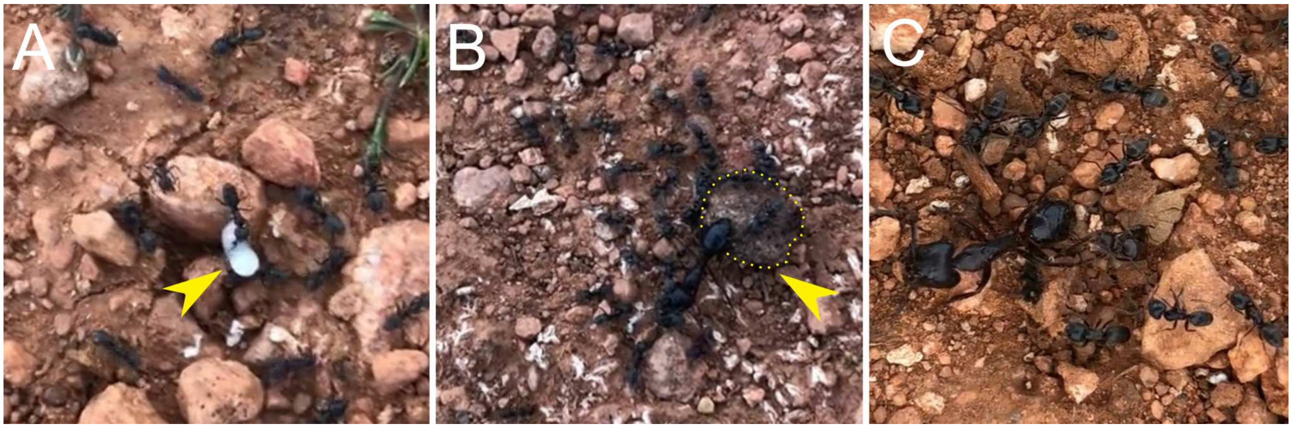

Figure 2. **A,** A *Tapinoma* worker transporting a larva (marked by yellow arrow). **B,** A larger stone (yellow arrow and delimited by yellow dots) used for *Tapinoma* nestmates to anchor and restrain the *Camponotus* worker. **C,** Close-up of *Camponotus* sp. and *Tapinoma* sp. the second day of the sighting (see supplementary materials)

movements of the *Camponotus* worker were much more erratic, with no apparent orientation. It became apparent that the *Tapinoma* workers did not intend to predate on the *Camponotus* worker, as it suffered no injuries or amputations, which would have been relatively feasible considering the high numbers of *Tapinoma* workers and the duration of the confrontation. Furthermore, the following morning on our visit back to the site, the *Camponotus* worker was still alive (Figure 2C) and *Tapinoma* workers walked over her without biting her. *Tapinoma* workers

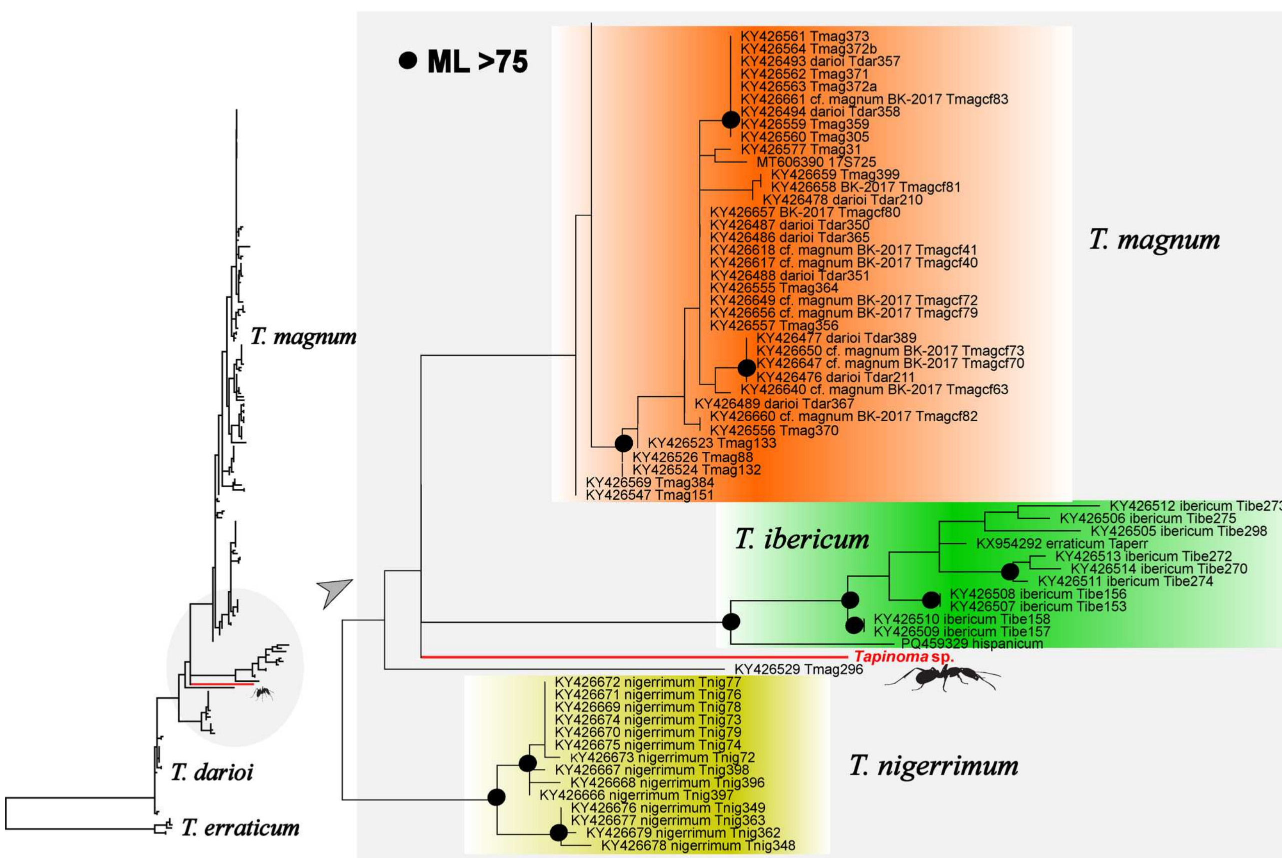

Figure 3. Maximum likelihood (ML) tree showing the closest phylogenetic relationships to the sequenced *Tapinoma* sp. (marked with a red branch and red writing and represented with an ant icon). Clades of interest have Genbank accession numbers (to the left) and voucher codes (to the right).

were seen removing dead *Tapinoma* nestmates on the following day.

Ant workers and colonies can show personalities (Pinter-Wollman 2012) and there is a relationship between individual and collective behaviour (Carere et al. 2018). In fact, there is a known association between personality traits and cognitive traits in ants. Consistent inter–individual behavioural variation has also been shown in ant species (e.g. Kuhbandner et al. 2014; Udino et al. 2017) and it might be a general characteristic of workers. Maák et al. (2020) conducted a series of experiments with *Aphaenogaster senilis* Mayr 1853 that showed that rather than worker task specialization, the involvement of workers with appropriate personalities ensured high efficiency in tool use. In our field observation, because only a minority of *Tapinoma* workers were seen transporting stones, it could suggest that this behaviour results from different personality traits at the colony level. It is interesting to notice that the size of the stones carried by the *Tapinoma* workers varied considerably. In addition, the following day, the *Camponotus* seemed exhausted and the *Tapinoma* had stopped the restraining and carrying of stones, and some individuals were seen on top of the *Camponotus*. Such behaviour might suggest individual complex cognitive traits in *Tapinoma*.

Because *Tapinoma* workers were seen transporting larvae, it seemed probable that *Tapinoma* workers were entering a *Camponotus* nest and taking their larvae for possible consumption. However, the sequence belonging to the larva revealed that it was not *Camponotus*, but instead it was *Tapinoma*. We do not know if the *Tapinoma* workers were moving nests and the *Camponotus* worker was restrained to avoid it releasing an alarm signal to recruit workers to forage the *Tapinoma* nest. However, in such a case, we would have expected the *Tapinoma* workers to kill the *Camponotus* worker immediately. There is no comparable report in the literature and only two reports have been documented of *Tapinoma* workers moving stones to build walls to block other ants getting access to resources or to block other ant's species nests. The following day, the stone-moving behaviour was absent, as the prey was much less mobile due to exhaustion from the encounter, suggesting that the stone moving was only necessary to help restrain the *Camponotus* worker, or the *Tapinoma* workers had habituated to the cues causing stone transport. Furthermore, the *Tapinoma* workers were no longer on the head of the *Camponotus* worker (see supplementary materials). Lack of time in the field prevented us from seeing the end of this encounter, and therefore, we cannot ascertain what happened to the *Camponotus* worker. Similarly, we can only infer the reason behind the use of the stones, as this behaviour seems novel.

The inclusion of all known *Tapinoma* species from the Iberian Peninsula in the phylogenetic analyses and the recovery of an unresolved position with no close association to any strongly supported clade suggests the distinct identity of this lineage (Figure 3). In fact, such results are further corroborated by the *p*-distances, where the genetic distances were over ~5% (or higher) to all other species, while the within-clade divergences of other species were low (<2%). Comparison to published genetic distance within the *Tapinoma nigerrimum* complex (Sheehan et al. 2011; Ruiz-Mena et al. 2024; Seifert et al. 2024) suggest that this species of *Tapinoma* is likely different. Sorting the taxonomic identity of this species is out of the scope of this study as it would require morphological data that is lacking and the possibility of an invasive species cannot be ruled out at this stage. Nevertheless, the phylogenetic data suggests that the biodiversity of ants in the Central Iberian Peninsula is likely higher than is currently known.

A short and fortunate encounter with a colony of ants has yielded unforeseen and novel insights into their social interactions and how their cognition perceives their environment (Zhou et al. 2020). We hope that this sighting will incite further research interest in the location of the sighting to fully understand this behaviour and to further conduct taxonomical work of this taxon.

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Supplemental data

Supplemental data for this article can be accessed here https://doi.org/10.1080/00379271.2025.2467429

References

Alem S, Perry CJ, Zhu X, Loukola OJ, Ingraham T, Søvik E, Chittka L. 2016. Associative mechanisms allow for social learning and cultural transmission of string pulling in an insect. PLoS Biology. 14:e1002564. doi:10.1371/journal.pbio.1002564.

Altschul SF, Gish W, Miller W, Myers EW, Lipman DJ. 1990. Basic local alignment search tool. Journal of Molecular Biology. 215:403–410. doi:10.1016/S0022-2836(05)80360-2.

Bentley-Condit V, Smith EO. 2010. Animal tool use: Current definitions and an updated comprehensive catalog. Behaviour. 147:185–232. doi:10.1163/000579509X12512865686555.

Carere C, Audebrand C, Rödel GH, d'Ettorre P. 2018. Individual behavioural type and group performance in *Formica fusca ants*. Behavioural Processes. 157:402–407. doi:10.1016/j.beproc.2018.07.009.

Czaczkes TJ. 2022. Advanced cognition in ants. Myrmecological News. 32:51–64.

De Bivort BL, van Swinderen B. 2016. Evidence for selective attention in the insect brain. Current Opinion in Insect Science. 15:9–15. doi:10.1016/j.cois.2016.02.007.

Espadaler X, Garcia-Berthou E. 1997. *Tapinoma pygmaeum* (Dufour, 1857) (Hymenoptera, Formicidae), not a rare species. Orsis (Organismes i Sistemes). 12:89–92.

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology. 3:294–299. doi:10.1093/bioinformatics/17.8.754.

Gómez-Durán JM. 2012a. http://historiasdehormigas.blogspot.com/2012/05/taponamiento-de-nido-por-tapinoma.html.

Gómez-Durán JM. 2012b. http://historiasdehormigas.blogspot.com/2012/06/nuevas-observaciones-sobre-el-uso-de.html.

Gordon DM. 1988. Nest-plugging: interference competition in desert ants (*Novomessor cockerelli* and *Pogonomyrmex barbatus*). Oecologia. 75:114–118. doi:10.1007/BF00378823.

Gouy M, Guindon S, Gascuel O. 2010. SeaView version 4: a multiplatform graphical user interface for sequence alignment and phylogenetic tree building. Molecular Biology. 27:221–224. doi:10.1038/nmeth.2109.

Grasso DA, Mori A, Giovannotti M, Le Moli F. 2004. Interspecific interference behaviours by workers of the harvesting ant *Messor capitatus* (Hymenoptera Formicidae). Ethology Ecology & Evolution. 16:197–207. doi:10.1080/08927014.2004.9522631.

Hölldobler B. 1986. Food robbing in ants, a form of interference competition. Oecologia. 69:12–15. doi:10.1007/BF00399031.

Jowers MJ, Leniaud L, Cerdá X, Alasaad S, Caut S, Amor F, Aron S, Boulay RR. 2013. Social and population structure in the ant *Cataglyphis emmae*: Adaptive mating strategies and dispersal. PLoS One. 8(9):e72941. doi:10.1371/journal.pone.0072941.

Kuhbandner S, Modlmeier AP, Foitzik S. 2014. Age and ovarian development are related to worker personality and task allocation in the ant *Leptothorax acervorum*. Current Zoology. 60:392–400. doi:10.1093/czoolo/60.3.392.

Kumar S, Stecher G, Li M, Knyaz C, Tamura K. 2018. MEGA X: molecular evolutionary genetics analysis across computing platforms. Molecular Biology and Evolution. 35:1547–1549. doi:10.1093/molbev/msy096.

Lin N. 1964–1965. The use of sand grains by the pavement ant, *Tetramorium caespitum*, while attacking Halictine bees. Bulletin of the Brooklyn Entomological Society. 59-60:30–34.

Lőrinczi G, Módra G, Juhasz O, Maák I. 2018. Which tool to use? Choice optimization in the tool-suing ant, *Aphenogaster subterranea*. Behavior Ecology. 29:1444–1452. doi:10.1093/beheco/ary110.

Loukola OJ, Perry CJ, Coscos L, Chittka L. 2017. Bumblebees show cognitive flexibility by improving on an observed complex behavior. Science. 355:833–836. doi:10.1126/science.aag2360.

Maák I, Lőrinczi G, Le Quinquis P, Módra G, Bovet D, Call J, d'Ettorre P. 2017. Tool selection during foraging in two species of funnel ants. Animal Behaviour. 123:207–216. doi:10.1016/j.anbehav.2016.11.005.

Maák I, Roelandt G, d'Ettorre P. 2020. A small number of workers with specific personality traits perform tool use in ants. eLife. 9:e61298. doi:10.7554/eLife.61298.

Miller MA, Pfeiffer W, Schwartz T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: 2010 Gateway computing environments workshop (GCE). New Orleans, LA, USA; p. 1–8.

Módra G, Maák I, Lőrincz Á, Lőrinczi G. 2022. Comparison of foraging tool use in two species of myrmicine ants (Hymenoptera: Formicidae). Insectes Sociaux. 69:5–12. doi:10.1007/s00040-021-00838-0.

Möglich MHJ, Alpert GD. 1979. Stone dropping by *Conomyrma bicolor* (Hymenoptera: Formicidae): a new technique of interference competition. Behavior Ecology and Sociobiology. 6:105–113. doi:10.1007/BF00292556.

Nityananda V, Chittka L. 2015. Modality-specific attention in foraging bumblebees. Royal Society Open Science. 2:150324. doi:10.1098/rsos.15032.

Pfeffer S, Wolf H. 2020. Arthropod spatial cognition. Animal Cognition. 23:1041–1049. doi:10.1007/s10071-020-01446-4.

Pierce JD Jr. 1986. A review of tool use in insects. The Florida Entomologist. 69:95–104. doi:10.2307/3494748.

Pinter-Wollman N. 2012. Personality in social insects: how does worker personality determine colony personality? Current Zoology. 58:580–588. doi:10.1093/czoolo/58.4.580.

Richards MH. 2022. Tool use by foraging ants. Insectes Sociaux. 69:1–2. doi:10.1007/s00040-022-00855-7.

Ruiz-Mena A, Mora P, Rico-Porras JM, Kaufmann B, Seifert B, Palomeque T, Lorite PA. 2024. Comparative analysis of Mitogenomes in species of the *Tapinoma nigerrimum* complex and other species of the genus *Tapinoma* (Formicidae, Dolichoderinae). Insects. 15:957. doi:10.3390/insects15120957.

Schultz GW. 1982. Soil-dropping behavior of the pavement ant, *Tetramorium caespitum* (L.) (Hymenoptera: Formicidae) against the Alkali Bee (Hymenoptera: Halictidae). Journal of Kansas Entomological Society. 55:277–282.

Seifert B, d'Eustacchio D, Kaufmann B, Centorame M, Lorite P, Modica MV. 2017. Four species within the supercolonial ants of the *Tapinoma nigerrimum* complex revealed by integrative taxonomy (Hymenoptera: Formicidae). Myrmecological News. 24:123–144.

Seifert B, Kaufmann B, Fraysse L. 2024. A taxonomic revision of the Palaearctic species of the ant genus *Tapinoma* Mayr 1861 (Hymenoptera: Formicidae). Zootaxa. 5435(1):1–74. doi:10.11646/zootaxa.5435.1.1.

Sheehan MJ, Tibbetts EA. 2011. Specialized face learning is associated with individual recognition in paper wasps. Science. 334:1272–1275. doi:10.1126/science.1211334.

St Amant R, Horton TE. 2008. Revisiting the definition of tool use. Animal Behaviour. 75:1199–1208. doi:10.1016/j.anbehav.2007.09.028.

Stamatakis A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics (Oxford, England). 30(9):1312–1313. doi:10.1093/bioinformatics/btu033.

Udino E, Perez M, Carere C, d'Ettorre P. 2017. Active explorer show low learning performance in a social insect. Current Zoology. 63:555–560. doi:10.1093/cz/zow101.

Van Lawick-Goodall J. 1968. The behaviour of free-living chimpanzees in the Gombe Stream Reserve. Animal Behaviour Monographs. 1(3):161–311, IN1–IN12. doi:10.1016/S0066-1856(68)80003-2.

Zhou A, Du Y, Chen J. 2020. Ants adjust their tool use strategy in response to foraging risk. Functional Ecology. 34:2524–2535. doi:10.1111/1365-2435.13671.