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On the biology of two species of ground-nesting eumenine wasps (Hymenoptera: Vespidae: Eumeninae) from the Charyn National Park, Kazakhstan

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Summary. Nine nests of *Jucancistrocerus* (*Eremodynerus*) *atrofasciatus* and 24 nests of *Odynerus* (*Odynerus*) *tristis* were observed in the same clay cliff in the Charyn River canyon near the Valley of Castles, Charyn National Park, Almaty Province of Kazakhstan. Both species used water from the Charyn River for nest construction. The wasps excavated nest burrows in a dense clay loam with a considerable amount of gravel and a predominance of loess and silt. The nests had entrance turrets made of mud; the provision was weevil larvae in the subfamily Hyperinae (Coleoptera: Curculionidae). The nests of *J. atrofasciatus* were burrowed out mainly in the vertical surface of the cliff and had laced and curved turrets opened downward. They contained 1–3 cells in one or two burrows (a linear-branched nest structure), separated within one burrow by simple partitions. The egg was suspended with a short thread to the cell wall at its inner end; the provision was 15–35 small weevil larvae. In two of the six studied cells, there were empty cocoons of a cuckoo wasp (Hymenoptera: Chrysididae). The nests of *O. tristis* were burrowed out mainly in the horizontal surface of small ledges, which were present on the cliff, and had solid and straight turrets opened upward. These nests contained 1–6 cells arranged mainly in a branched (sometimes linear-branched) manner. The provision was another species of Hyperinae, with 10 larvae stored per cell. A third of the studied nest cells of *O. tristis* were robbed by *Tetramorium armatum* (Hymenoptera: Formicidae). The ants penetrated to the sealed nests with the aid of tiny burrows made by themselves in lateral walls of the cells, as well as through narrow slits, sometimes occurring in the ground. *Odynerus tristis* nested earlier in spring than *J. atrofasciatus*. Two of the 13 observed prepupae of *O. tristis* hibernated for more than one year. Nests of *O. tristis* are typical of the genus *Odynerus*, while nests of *J. atrofasciatus* are quite similar to those of *Jucancistrocerus* (*Jucancistrocerus*) *caspicus*. The latter observation is consistent with the current treatment of *Eremodynerus*, which *J. atrofasciatus* belongs to, as a subgenus of *Jucancistrocerus* rather than a separate genus.

Résumé. Biologie de deux espèces d'Eumeninae (Hymenoptera : Vespidae) nidifiant dans le sol, du parc national Charyn, Kazakhstan. Neuf nids de *Jucancistrocerus* (*Eremodynerus*) *atrofasciatus* et 24 nids d'*Odynerus* (*Odynerus*) *tristis* ont été observés sur le même versant argileux du canyon de la rivière Charyn, près de la vallée des Châteaux, dans le parc national Charyn (province d'Almaty, Kazakhstan). Les deux espèces utilisaient l'eau de la rivière Charyn pour construire leur nid. Elles ont creusé des galeries dans un loam argileux dense, riche en gravier, où loess et limon dominent. Les guêpes ont façonné une cheminée de boue à l'entrée de leur nid et en approvisionnaient les cellules avec des charançons de la sous-famille des Hyperinae (Coleoptera : Curculionidae). Les nids de *J. atrofasciatus* étaient creusés principalement dans la paroi verticale du versant et présentaient des cheminées incurvées et ajourées, ouvertes vers le bas. Ils étaient formés d'une ou deux galeries (structure de nid linéaire ramifié) et renfermaient une à trois cellules séparées par de simples parois. Un œuf était suspendu par un court pédoncule à la paroi de l'extrémité interne de chaque cellule qui contenait 15 à 35 petites larves de charançons. Deux des six cellules étudiées contenaient des cocons vides d'une guêpe-coucou (Hymenoptera : Chrysididae). Les nids d'*O. tristis*, creusés surtout sur la surface horizontale de petites buttes présentes sur le versant, avaient des cheminées d'entrée en boue épaisse, ouvertes vers le haut. Les nids le plus souvent ramifiés (parfois linéaires ramifiés), contenaient une à six cellules approvisionnées de larves d'une autre espèce d'Hyperinae, à raison de dix larves par cellule. Un tiers des cellules d'*O. tristis* observées ont été attaquées par *Tetramorium armatum* (Hymenoptera : Formicidae). Les fourmis ont pénétré dans les nids obturés par d'étroites galeries percées dans les parois latérales des cellules, mais aussi à travers de minces fissures présentes parfois dans le sol. *Odynerus tristis* nidifie plus tôt au printemps que *J. atrofasciatus*. Par ailleurs, deux des 13 prénymphes d'*O. tristis* observées ont hiverné pendant plus d'un an. Les nids d'*O. tristis* sont typiques du genre *Odynerus*, tandis que ceux de *J. atrofasciatus* sont très semblables à ceux de *Jucancistrocerus* (*Jucancistrocerus*) *caspicus*. Cette dernière observation concorde avec le traitement actuel d'*Eremodynerus* – auquel appartient *J. atrofasciatus* – comme sous-genre de *Jucancistrocerus* plutôt que comme un genre distinct.

Keywords: *Jucancistrocerus atrofasciatus*; *Odynerus tristis*; nest structure; trophic relationships; brood parasites

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With more than 3900 described species worldwide, the subfamily Eumeninae (in the broad sense, including Raphiglossinae and Zethinae) is the largest in the family Vespidae (Luo et al. 2022) and at the same time the least studied. Dozens of new species are described every year (e.g. Lopes & Noll 2024; Nguyen et al. 2024; Qin et al. 2024; da Silva Cruz de Oliveira et al. 2025; Selis 2025; Cruciol et al. 2026), while few recent studies address the biology of these wasps (e.g. Pham et al. 2024; Du et al. 2025; Lopes & Melo 2025; Xie et al. 2025). Females of the eumenine wasps either nest in pre-existing cavities, excavate their own nest burrows in the ground (or rarely in wood), or construct aerial nests of mud or plant material (rarely combining them); the eumenines provision their nest cells with paralyzed larvae of phytophagous insects: moths and butterflies, beetles, or rarely sawflies (reviews by Spradbery 1973; Iwata 1976; Cowan 1991); meanwhile, adult wasps principally feed at flowers, where they consume nectar as the main source of carbohydrates (Mauss et al. 2019). The best-studied ecological group of the eumenine wasps is cavity-nesting species able to inhabit trap nests, while the ground-nesting group is the least studied (He et al. 2024). Further, many species are poorly known and rarely observed, confined to certain natural habitats and not tolerant of their changes. Protected areas can thus provide a good chance to find nests and to study the biology of rare ground-nesting eumenines (e.g. Fateryga & Ivanov 2013; Fateryga 2018; Fateryga et al. 2025).

The present contribution deals with two species of ground-nesting eumenine wasps observed in the Charyn National Park, Kazakhstan: *Jucancistrocerus* (*Eremodynerus*) *atrofasciatus* (Morawitz, 1885) and *Odynerus* (*Odynerus*) *tristis* (Blüthgen, 1939). *Jucancistrocerus atrofasciatus* is known from Iran, Kyrgyzstan, Kazakhstan, Mongolia, and China (Li et al. 2022), while *O. tristis* is distributed in Tajikistan, Kyrgyzstan, Kazakhstan, and China (Kurzenko 1977; Fateryga 2017). To the best of our knowledge, the biology has never been studied previously in either of these species. The purpose of the present contribution is to study the nesting site, nest structure, prey, and natural enemies of *J. atrofasciatus* and *O. tristis*.

Material and methods

Field research

Field observations were carried out in the Charyn River canyon near the Valley of Castles, Charyn National Park, Almaty Province of Kazakhstan (43.3483° N, 79.0768° E) on 13–17.V.2024. The locality was a part of the Toraygyr Mountains, the north-eastern spurs of the Trans-Ili Alatau Range of the Northern Tian Shan Mountains. The slopes of the canyon were covered with desert vegetation, and there were a few poplar trees (*Populus* sp., Salicaceae) along the river (Figure 1A). All wasp nests were found in a clay cliff a few meters from the river bank (Figure 1B). A careful examination of the surface of this cliff revealed 33 nests: nine of *J. atrofasciatus* and 24 of *O. tristis*. One nest of *J. atrofasciatus* was being provisioned by the female wasp, while the other 32 nests had already been left by their hosts. Some of these nests were old (evidently constructed by the wasps before 2024); others were either just sealed (sometimes incompletely) earlier that year or left unsealed. Wasp activity was also observed at their water-collecting site (Figure 1C) and at flowers around the nesting site. Photographs were taken with a Canon EOS RP digital camera (Canon Inc., Ōta, Tokyo, Japan) and a Sigma AF 105 mm f/2.8 macro lens (Sigma Corporation, Kawasaki, Kanagawa, Japan) (scale up to 1:1) or a Canon RF 35 mm F1.8 Macro IS STM lens.

Each nest was marked with four triangular pieces of red plastic set into the ground at equal distances from the entrance. The nests were excavated when we could be certain that they had been abandoned; the one with the active female was excavated after the wasp had sealed it. We excavated the nests with a small shovel and a knife; all nest cells were dissected at the nesting site, without removing the whole nests along with the surrounding soil. The nests had to be exposed by cutting the soil off layer by layer in a vertical plane perpendicular to the main cliff surface. Cutting was done with extreme care when approaching the approximate location of the nest, i.e. the crossing of imaginary lines between the pieces of red plastic used as markers. The excavated nests were documented with photographs and with diagrams drawn on graph paper at a scale of 1:1 using compasses, so all measurements were made directly in the field. The drawings of nests presented herein were made by tracing photographs and sketches on graph paper. A soil sample was collected from the nesting site for analysis of granulometric composition, specific gravity of the solid phase, physical fractions by the method of Rutkovsky, and granulometric classification using the system of Kachinsky (Vadyunina & Korchagina 1986). Preimaginal stages of the wasps found in the nest cells were placed in short glass tubes with cotton-wool stoppers, labelled with the nest and cell numbers, and kept in an unheated room until the emergence of adults. The prey (weevil larvae) and other associated insects extracted from the brood cells of the excavated nests were fixed in 96% ethanol. Any attempts to find conspecific but living weevil larvae in the surrounding vegetation (in order to rear imagines) failed.

Species identification

The prey and the associated insects were sent to the colleagues mentioned in the Acknowledgements section; the wasp reference material is kept in the collection of the first author. *Jucancistrocerus atrofasciatus* was identified by comparing our material with the type series of this species (three females and a male) in the collection of the Zoological Institute RAS (Saint Petersburg, Russia), as well as according to the key by Li et al. (2022). This species was described from the Alashan Range (Inner Mongolia, China) (Morawitz 1885). We studied a large series of females and males from Kazakhstan, Mongolia, and China, as well as a female from Iran in the abovementioned collection. There was a strong difference in the coloration of the specimens from Mongolia and China vs. those from Kazakhstan and Iran: the latter ones had less extended and lemon-yellow (or rarely orange-yellow) but not orange pattern of the body. At the same time, there were no evident structural differences (including those in the male genitalia) allowing description of a new species from Kazakhstan and Iran, so we provisionally consider it conspecific with the typical *J. atrofasciatus* from Mongolia and China. Besides, there are other eumenine-wasp species with a yellow pattern in Kazakhstan replaced further east in China by a more orange pattern, viz. *Pseudepipona herzi* (Morawitz,



Figure 1. Habitat of *Jucancistrocerus atrofasciatus* (Morawitz, 1885) and *Odynerus tristis* (Blüthgen, 1939) in the Charyn National Park. **A**, General view. **B**, Nesting site. **C**, Water-collecting site.

1885) (Fateryga & Proshchalykin 2022) and *P. kozhevnikovi* (Kostylev, 1927) (Fateryga 2022). *Jucancistrocerus* (*Eremodynerus*) *chotanensis* (Blüthgen, 1942), a closely related species described from Chotan (Xinjiang, China), has a coloration similar to *J. atrofasciatus* from Kazakhstan, according to its original description based on a single male (Blüthgen 1942), or to *J. atrofasciatus* from Mongolia and China, according to the description of a single female by Li et al. (2022). However, its punctation is different from any specimens of *J. atrofasciatus*, according to both descriptions. The holotype of *J. chotanensis* should be studied but it is deposited in the Museum für Naturkunde (Berlin, Germany) and unavailable to us.

As for *O. tristis*, it was described from a single female from Jagnob (Tajikistan) deposited in the Muséum d'Histoire Naturelle de Genève (Geneva, Switzerland) (Blüthgen 1939). The holotype was also unavailable to us, so we understand the identity of this species following Kurzenko (1977). The specimens from Kazakhstan correspond to the subspecies *O. tristis tianshanicus* Kurzenko 1977, with the type series examined in the Zoological Institute RAS. They differ from the typical *O. tristis* from Tajikistan mainly by a pure yellow (not pale yellow) pattern of the body. We do not support the necessity to recognize such cases of geographic variability as subspecies (e.g. Selis et al. 2024). Therefore, we consider both forms conspecific and merely belonging to *O. tristis*, without any subspecies within this species.

Results

Biology of Jucancistrocerus atrofasciatus

Besides one nesting female of *J. atrofasciatus*, another female was observed feeding at flowers of *Nitraria*

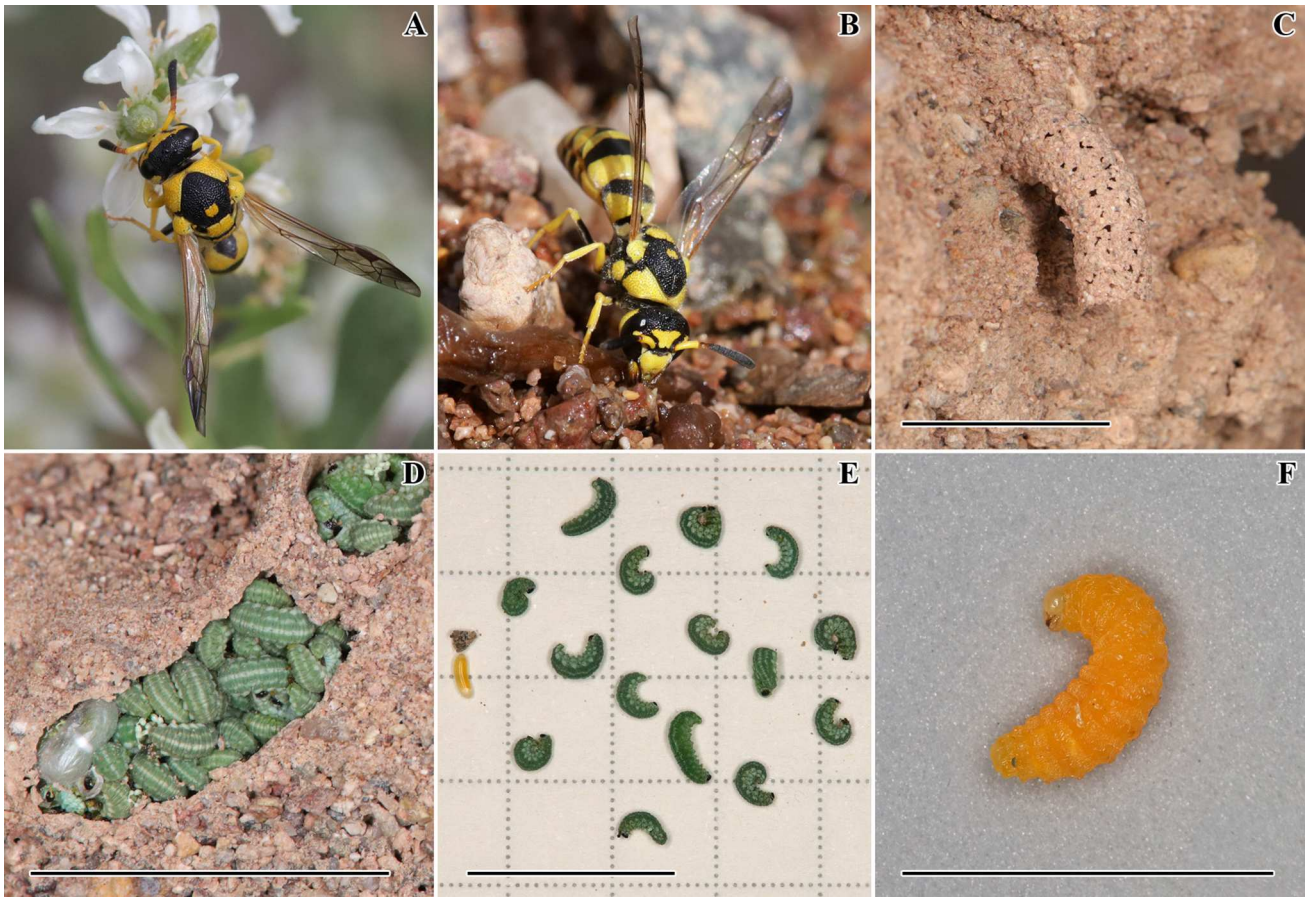

Figure 2. Biology of *Jucancistrocerus atrofasciatus* (Morawitz, 1885) in the Charyn National Park. **A**, Female feeding on *Nitraria schoberi* L. **B**, Water-collecting female. **C**, Nest turret. **D**, Dissected nest with weevil larvae stored as the provision in the cells and a cocoon of *Bathyplectes* sp. in the first cell. **E**, Provision and the wasp egg from the second cell of the same nest. **F**, Hibernating prepupa extracted from the nest cell. Scale bars (C–F) = 1 cm.

schoberi L. (Nitrariaceae) (Figure 2A) and numerous others were found at the water-collecting site at the Charyn River bank (Figure 1C), where they sucked water from wet sand (Figure 2B). This observation suggests that the females used water to moisten the dry ground during the nest construction. The nests of *J. atrofasciatus* were burrowed out mainly in the vertical surface of the clay cliff (rarely in small sub-horizontal ledges). The soil at the nesting site was a dense clay loam with a considerable amount of gravel and a predominance of loess and silt (Tables 1 and 2). All studied nests were recognized by a laced entrance turret made of mud (Figure 2C). The turret was 10–12 mm in length, curved and opened downward (except where it was incomplete or had been broken). The diameter of the nest burrows was 3–5 mm. Among the nine excavated nests, two were too old (and occupied by another unidentified hymenopteran species) to recognize their structure, while four had been abandoned by the wasps before starting the cells. The remaining three nests contained one, two, and three cells, respectively; however, the nest with three cells was also abandoned by the mother wasp, and it is likely that there could be more cells. This nest was 38 mm in length and had a linear-branched structure, i.e. the first inclined burrow contained two linearly arranged cells (1 and 2), while there was a secondary sub-horizontal burrow (Figure 3A). The cells (except the third one) were 9–10 mm in length and sealed with rather thin mud plugs; in the case of the first two cells, the plug of the first cell served as the bottom of the second one. The first cell in this nest contained an empty cocoon of *J. atrofasciatus* (the wasp had emerged earlier that year or even before). The cocoon was similar to that described previously for *Jucancistrocerus* (*Jucancistrocerus*) *caspicus* Giordani Soika, 1970 (Fateryga & Amolin 2014). The second cell contained an empty cocoon of an unidentified cuckoo-wasp species (Hymenoptera: Chrysididae); the nest with one cell was also old and contained a similar chrysidid cocoon.

The nest with two cells was the only nest with the mother wasp observed provisioning it. As it was dissected after the female had sealed it, its entrance turret (Figure 2C) was dismantled at that time (Figure 3B). The structure

Table 1. Granulometric composition of soil at the nesting site of *Jucancistrocerus atrofasciatus* (Morawitz, 1885) and *Odynerus tristis* (Blüthgen, 1939) from the Charyn National Park.

Granulometric composition, %						
> 10 mm	10–7 mm	7–5 mm	5–3 mm	3–1 mm	1–0.5 mm	< 0.5 mm
29.88	14.59	9.44	10.39	14.41	3.53	17.36

Table 2. Soil characteristics at the nesting site of *Jucancistrocerus atrofasciatus* (Morawitz, 1885) and *Odynerus tristis* (Blüthgen, 1939) from the Charyn National Park.

	Physical fraction content by Rutkovsky's method, %				
Specific gravity of the solid phase, g cm^{-3}	> 0.5 mm (sand)	0.5–0.05 mm (loess)	0.05–0.005 mm (silt)	< 0.005 mm (clay)	Granulometric class in Kachinsky's system
2.37	12.43	37.87	45.62	4.08	Dense clay loam

of this nest was somewhat unusual: the nest burrow (23 mm in length) was inclined and terminated by the first cell, while the second cell was excavated perpendicularly to it but not deeply enough, so that the plug of the second cell was in the first burrow but also on a lateral wall of this cell. The length of both cells was 10 mm. There was also a vestibular cell 1.5 mm in length, and a closing plug 8 mm in length in this nest (Figure 3B). The first cell contained the wasp larva and 35 rather small green weevil larvae stored as the provision (Figure 2D). The larvae apparently belonged to a single species of Hyperinae (Coleoptera: Curculionidae). It was impossible to identify them beyond the subfamily because their morphology did not correspond with certainty to any genus with described larvae (Ilya Zabaluyev, personal communication). Besides the provision, there was a cocoon of a parasitic wasp *Bathyplectes* sp. (Hymenoptera: Ichneumonidae) which had used one weevil larva as its host (Figure 2D). The second cell contained the wasp's egg and 15 weevil larvae of the same species (Figure 2E). The egg was 2.27 × 0.65 mm and attached by a short thread to the cell wall at its inner end. The larva from the first cell overwintered as a prepupa (Figure 2F) and an adult female of *J. atrofasciatus* emerged from it in 2025; the egg from the second cell was damaged by an accident.

Biology of Odynerus tristis

Just two females of *O. tristis* were observed at the water-collecting site at the Charyn River bank (Figure 1C), where they sucked water from wet sand (Figure 4A). This observation suggests that the females used water to moisten the dry ground during the nest construction, like *J. atrofasciatus*. The nests of *O. tristis* were burrowed out mainly in the horizontal surface of small ledges, which were present on the clay cliff (Figure 1A). Since the nests were made at the same place as those of *J. atrofasciatus*, the soil of the nesting site was also a dense clay loam with a considerable amount of gravel and a predominance

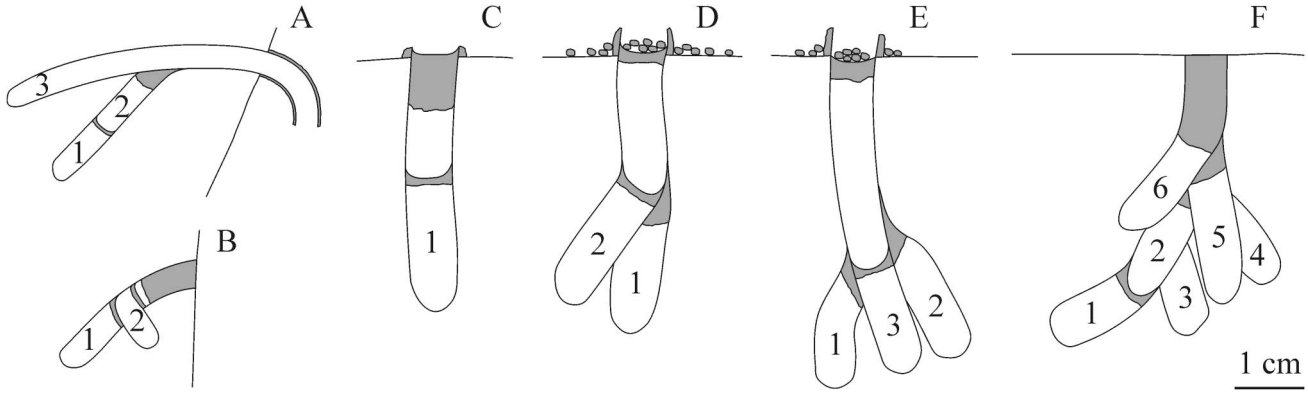

Figure 3. Schematic plans of nests of eumenine wasps from the Charyn National Park. **A, B**, *Jucancistrocerus atrofasciatus* (Morawitz, 1885): **A**, an open abandoned nest with three cells; **B,** a sealed nest with two cells. **C–F**, *Odynerus tristis* (Blüthgen, 1939): **C, F**, sealed nests with complete plugs; **D, E,** sealed nests with incomplete plugs; 1–6, cell numbers.

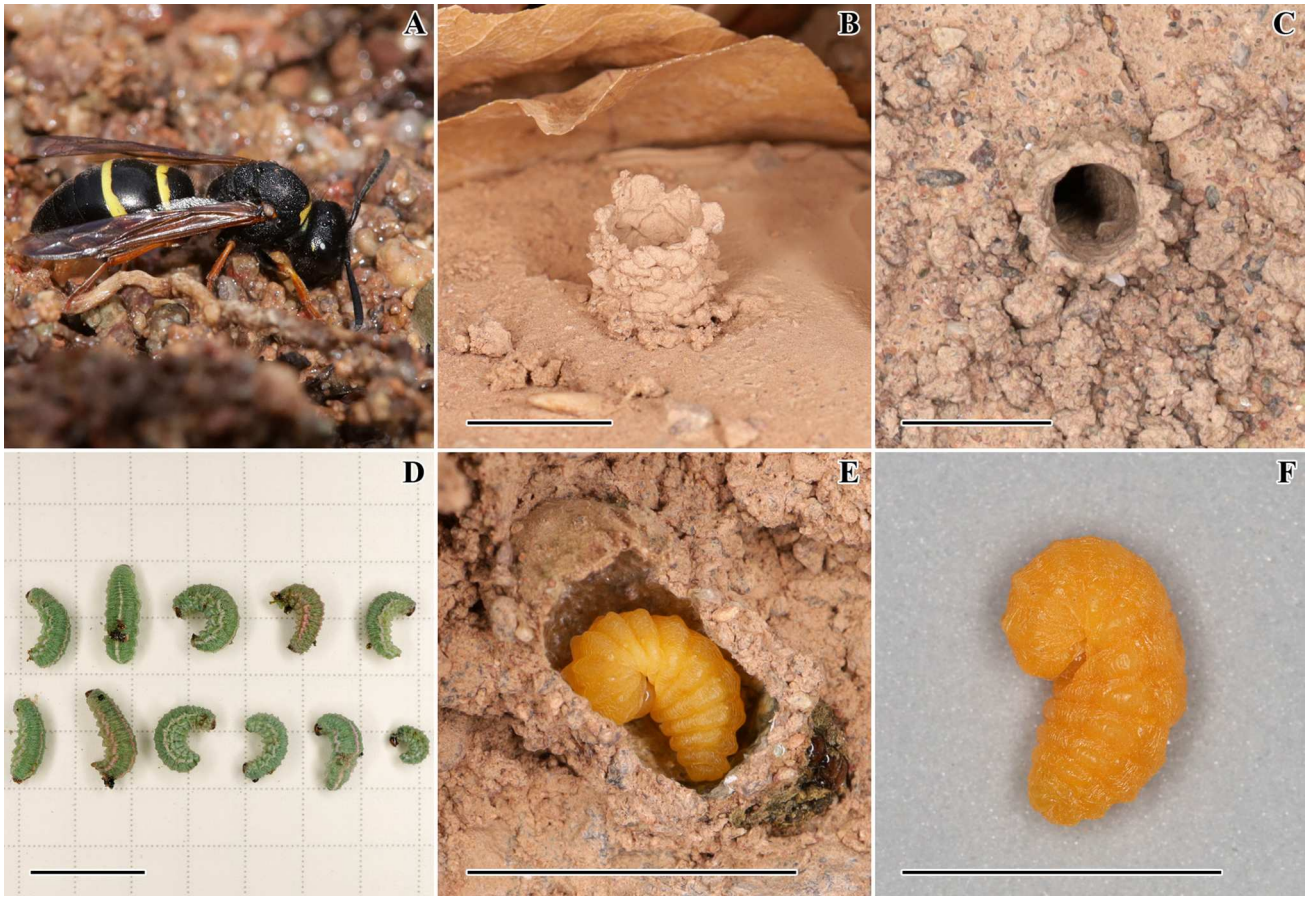

Figure 4. Biology of *Odynerus tristis* (Blüthgen, 1939) in the Charyn National Park. **A**, Water-collecting female. **B**, Nest turret in sub-lateral view. **C**, Another nest turret and dropped mud pellets, view from above. **D**, Provision from a nest cell. **E**, Prepupa in a cocoon. **F**, Another hibernating prepupa extracted from the nest cell. Scale bars (B–F) = 1 cm.

of loess and silt (Tables 1 and 2). The nest turrets of *O. tristis* were 4–8 mm in length, solid, straight, and opened upward (Figure 4B). Around the nest entrance, there were scattered mud pellets, which had obviously been dropped there by the female wasp during the burrowing process (Figure 4C). Table 3 contains the main parameters of the nests of this species. Among the 24 excavated nests, four were too old to recognize their structure and, besides, they were occupied by ants. Ten other nests had been abandoned by the wasps before starting the cells. The remaining 10 nests contained brood cells; however, two of these nests (with one and two cells) were also abandoned by the mother wasps, and there could probably be more cells. Most cells were sub-vertical and arranged in a branched manner; each one had its own mud plug (Figure 3C–E). However, two nests with six cells had two linearly arranged cells each (Figure 3F). A vestibular cell was present in all sealed nests (Figure 3C–E) except one (Figure 3F). The thickness of complete closing plugs in three nests was 3, 8, and 13 mm; other closing plugs had incompletely dismantled turrets (Figure 3D, E).

Among the 10 nests with cells, one was old (constructed by the wasp before 2024) and its three cells contained empty cocoons of *O. tristis*. The cocoons were

Table 3. Main parameters of the nests of *Odynerus tristis* (Blüthgen, 1939) from the Charyn National Park.

Parameter	*n*	Minimum–maximum	Median
Depth of the nest burrow (mm)	9	22–51	40
Width of the nest burrow (mm)	8	5.5–8	7
Number of cells per nest	10	1–6	2
Length of the brood cell (mm)	16	14–22.5	17.5
Length of the vestibular cell (mm)	5	1.5–27	9.5

similar to that described previously for *Odynerus* (*Odynerus*) *spinipes* (Linnaeus, 1758) (Fateryga 2021). The cells in the nine remaining nests contained either mature larvae of *O. tristis* spinning their cocoons or dead progeny with partially dried provision. This observation suggests that the nesting period of *O. tristis* occurred earlier in spring than that of *J. atrofasciatus*. There was a total of 24 cells in these nine nests, and eight cells (33%) were robbed by *Tetramorium armatum* Santschi, 1927 (Hymenoptera: Formicidae). In three of them, the ants killed and stole the wasp eggs, while they killed and consumed mature larvae in the other cells. The ants penetrated to the nests of *O. tristis* with the aid of tiny burrows made by themselves in lateral walls of the sealed cells, as well as through narrow slits, sometimes occurring in the ground. The provision of *O. tristis* was another species of weevils in the subfamily Hyperinae, with large green larvae, not conspecific to that used by *J. atrofasciatus* (Figure 4D). It was also impossible to identify them beyond the subfamily because they did not correspond with certainty to any genus with described larvae (Ilya Zabaluyev, personal communication). There were 10 weevil larvae in each of the three cells with the dead eggs. The remaining 16 cells contained successfully developed wasp larvae, although three of them were damaged by an accident; thus, 13 prepupae were obtained. Eleven of them overwintered (Figure 4E, F) and four females of *O. tristis* emerged in 2025 along with seven males. Two remaining prepupae did not pupate in 2025 but entered a second year of diapause. They were living at least until VI.2026, when the revised version of this paper was submitted.

Discussion

In the genus *Jucancistrocerus* Blüthgen, 1938, the biology was previously studied only for *J. caspicus* from the nominotypical subgenus (Fateryga & Amolin 2014). The latter species has nests generally similar to those of *J. atrofasciatus*. Females of *J. caspicus* nest in the vertical ground of clay cliffs, and the nests have linear-branched structure; the main burrow is sub-vertical, while secondary burrows are inclined to sub-horizontal. Each nest of *J. caspicus* has a curved entrance turret with a laced structure; the provision is weevil larvae, and the main natural enemy is a species of cuckoo wasps. There are a few differences observed between the habits of *J. atrofasciatus* and *J. caspicus*: the former species nests in dense clay loam, while the latter selects dense clay. The provision of *J. atrofasciatus* is rather small green larvae in the subfamily Hyperinae, while the provision of *J. caspicus* is very small and whitish larvae from different subfamilies. The partitions between the cells of the former species are simple, while the latter species constructs double partitions (Fateryga & Amolin 2014). However, certain behavioral conclusions may be preliminary due to a small number of informative nests of *J. atrofasciatus* in the present study. *Jucancistrocerus atrofasciatus* belongs to the subgenus *Eremodynerus* Blüthgen, 1939. This subgenus was initially described as a genus (Blüthgen 1939) but then reduced to the subgenus rank by Kurzenko (1982) after a thorough morphological study. However, the subgenus rank of *Eremodynerus* was recently questioned again by Luo et al. (2022), according to a phylogenetic reconstruction based on mitochondrial DNA. They showed that *Jucancistrocerus s. str.* was closely related to the genus *Ancistrocerus* Wesmael, 1836, while *Eremodynerus* was closely related to the genus *Parancistrocerus* Bequaert, 1925. A similarity between the nesting habits of *J. atrofasciatus* and *J. caspicus* (present contribution and Fateryga & Amolin 2014) is consistent with the treatment of *Eremodynerus* as a subgenus of *Jucancistrocerus* rather than a separate genus. The three differences between the abovementioned species are rather minor and not genus-level. On the other hand, the habits of both species of *Jucancistrocerus* strongly differ from those of both *Ancistrocerus* and *Parancistrocerus*. Species of *Ancistrocerus* nearly always hunt for lepidopteran larvae; most species of this genus nest in pre-existing cavities and divide them into cells with mud partitions, but seven species are known to construct aerial mud nests attached to stones (Iwata 1938; Blüthgen 1961; Krombein 1967; Spradbery 1973; Cowan 1991; Buck et al. 2008, etc.). Another species, *A. tuberculocephalus* (de Saussure, 1852), is able to enlarge and modify preexisting cavities (Cooper 1979). Species of *Parancistrocerus* also hunt for caterpillars and nest usually in pre-existing cavities (Iwata 1939; Bohart 1952; Krombein 1967; Buck et al. 2008, etc.), while *P. vagus* (Saussure, 1857) can also construct aerial mud nests (Evans 1978).

The nests of both species of *Jucancistrocerus* are the most similar to those of some ground-nesting species of *Antepipona* de Saussure, 1855, particularly *A. deflenda* (S.S. Saunders, 1853) and *A. orbitalis* (Herrich-Schäffer, 1839) (Móczár 1939), and *Stenodynerus* Saussure, 1863, particularly *S. microstictus* (Viereck, 1906) (Evans 1956; Hackney & Barrows 1977) and *S. papagorum* (Viereck, 1908) (Isely 1914; Evans 1970). These species nest in vertical ground surfaces and have a nest structure generally similar to that in the species of *Jucancistrocerus*, although *S. papagorum* can nest in horizontal ground surfaces as well (Evans 1970). A similar structure of the nests of *Jucancistrocerus* and the two other mentioned genera may reflect their common ancestry but could equally be convergent. A feature distinguishing the nests of *Jucancistrocerus* from those of *Antepipona* and *Stenodynerus* is the spatial orientation of consecutively constructed burrows. Judging by the figures published by Móczár (1939) and Hackney & Barrows (1977), secondary burrows in the

nests of *A. orbitalis* and *S. microstictus* branch down from the main one. In the nests of *J. atrofasciatus* and *J. caspicus*, secondary burrows branch rather sub-horizontally from the main one, which goes downward. Besides, species in the genera *Antepipona* and *Stenodynerus* usually hunt for lepidopteran larvae, although *S. papagorum* is reported to hunt beetle larvae as well (Evans 1970).

To the best of our knowledge, nests of 15 species of the genus *Odynerus* Latreille, 1802 were recorded previously (Ferton 1912; Nielsen 1932; Blüthgen 1941, 1961; Bristowe 1948; Grandi 1961; Madel 1964; Miotk 1979; Bohart et al. 1982; Schaber 1985; Castro 1992; Haeseler 1997; Mader 1999; Witt 2011; Fateryga 2013; Baldock et al. 2020, etc.). They excavate nest burrows in horizontal, vertical, or both horizontal and vertical ground surfaces and build one or several cells inside; cells are usually arranged in a branched (or linear-branched) manner. All species construct entrance turrets, which can be solid or laced, straight or curved, and open downward, sideward, or upward, sometimes even in the same species (e.g. Schaber 1985). At least 10 species with recorded prey hunt for weevil larvae in the subfamily Hyperinae, particularly the genus *Hypera* Germar, 1817 (e.g. Bristowe 1948; Grandi 1961; Madel 1964; Bohart et al. 1982; Schaber 1985; Fateryga 2013). We can speculate that larvae of Hyperinae represent a particularly accessible prey resource in open habitats. Our data on the nests of *O. tristis* are consistent with the previously reported observations on other species of the genus. However, it is worth mentioning that a closely related species *O. spinipes* constructs laced entrance turrets, which are usually curved and opened downward (e.g. Madel 1964; Miotk 1979; Mader 1999), while solid and straight turrets opening upward are more typical of another species, *O.* (*Odynerus*) *femoratus* de Saussure, 1856 (Fateryga 2013), which is less similar morphologically (Kurzenko 1977). The provision of *O. tristis* is also larvae in the subfamily Hyperinae but not the genus *Hypera*. In any case, species of both *Jucancistrocerus* and *Odynerus*, in their current treatments (Kurzenko 1982; Fateryga 2021), demonstrate similar nesting biology among the species within each genus. As for the observed two-year diapause of *O. tristis*, it is quite a common phenomenon in *Odynerus* and closely related genera, in which prepupae are known to be able to hibernate up to four years (e.g. Fateryga 2013, 2018; Fateryga & Ivanov 2013; Fateryga et al. 2025).

In our study, a third of the progeny of *O. tristis* was wasted due to the predation by *T. armatum* ants. Various species of ants were often reported previously as nest robbers of various eumenines (e.g. Cretin 1903; Isely 1914; Iwata 1953; Grissell 1975; Gess & Gess 1976; Krombein 1978; Barthélémy 2012; Fateryga et al. 2020; Catarineu et al. 2024). The impact of ants on the eumenine wasps may even be underappreciated because, unlike many other enemies, they often leave no evidence (such as cocoons, as in the case of cuckoo wasps) of their visit (Cowan 1991). Ants usually attack open nests during the provisioning stage and are able to steal the host egg, as well as the provision. Therefore, some adaptations evolved in some wasps to prevent ants from entering their nests, such as entrance turrets or rarely a temporary closure of the nest (Hacker 1918; Fateryga 2013; Fateryga & Ivanov 2013; Catarineu et al. 2024; Fateryga et al. 2025). However, sometimes ants can enter even a sealed nest (e.g. Cretin 1903; Isely 1914; Iwata 1953), and this was the case in our observations on *O. tristis*. In sealed cells, ants can consume not only the host egg and provision, but even mature larvae in incomplete cocoons. We can speculate that in all cases observed in our study, the ants detected the wasp nests due to their close proximity to the ant nests. Further, ants of apparently the same species occupied old nests of *O. tristis* for the purpose of their own nesting. A similar situation was previously observed, for example, by Iwata (1953) in the nests of *Eumenes fraterculus* Dalla Torre, 1894.

Jucancistrocerus atrofasciatus and *O. tristis* nest in the same place within the Charyn National Park and have similar habits. Both species excavate nest burrows with several cells, construct entrance turrets made of mud, and hunt for weevil larvae in the subfamily Hyperinae. However, we can speculate that some details of the biology of these co-occurring species help them in the differentiation of their ecological niches. First of all, *O. tristis* is a larger species, hunting for larger prey, and it nests earlier in spring than *J. atrofasciatus*. Further, nests of *O. tristis* are robbed by ants, while *J. atrofasciatus* was observed in our study to be parasitized by cuckoo wasps. Different natural enemies may correlate with somewhat different nest structure, particularly different entrance turrets, although this is speculative at least in relation to the cuckoo wasps. Furthermore, as it was recently shown by Fateryga et al. (2025), some co-occurring eumenine species with different nest entrances can be parasitized by the same species of cuckoo wasps. At the same time, several co-occurring species of cuckoo wasps with different strategies can have the same host (e.g. Wurdack et al. 2015).

Conclusion

Nests of *Jucancistrocerus atrofasciatus* and *Odynerus tristis* have been described for the first time. Both eumenine species nest in the same clay cliff in the Charyn National Park, use water for nest construction, excavate nests with branched or linear-branched structure, and hunt for weevil larvae in the same subfamily. However, the wasps demonstrate differentiated ecological niches due to different prey sizes, phenologies, natural enemies,

and entrance-turret structures, which may reflect different adaptive responses to vertical vs. horizontal nesting surfaces. Nests of *O. tristis* are typical of the genus *Odynerus* in its narrow circumscription (Fateryga 2021), while nests of *J. atrofasciatus* are quite similar to those of *J. caspicus*, from the nominotypical subgenus of *Jucancistrocerus* (Fateryga & Amolin 2014). The latter observation is consistent with the current treatment of *Eremodynerus*, which *J. atrofasciatus* belongs to, as a subgenus of *Jucancistrocerus* rather than a separate genus.

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