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Phenology and Sex Ratio of *Triturus cristatus* (Laurenti, 1768) (Amphibia: Salamandridae) at its Southern Range Limit

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Abstract: The great crested newt *Triturus cristatus* is a widespread species and there are numerous gaps in knowledge regarding its varying population characteristics at a regional level. This study provides new data on the seasonal activity and the sex ratio of the species from its southernmost distribution limit. For three consecutive years (2021–2023), we conducted monthly visits and set funnel traps in three ponds situated at 1360–1380 m a.s.l. in the Vrachanski Balkan Nature Park, Bulgaria. Traps were set in the evening and collected the following day. All captured newts were counted, sexed, photographed and released. Photographs of the ventral pattern were used for individual identification. The newt count was used to estimate the relative abundance and sex ratio across different ponds and years. We compared this data to existing unpublished data for the species across its range in Bulgaria. Our results revealed a clear temporal trend of decline of the relative abundance from spring to autumn for all years, confirming existing data on the species' phenology but with different patterns for adults, immatures and larvae. There was a slight male bias (1.24:1) overall but sex ratio differed across the three ponds and demonstrated clear monthly dynamics.

Key words: altitude, abundance, Bulgaria, distribution, newt, seasonality.

Introduction

The great crested newt *Triturus cristatus* (Laurenti, 1768) is one of the most widespread species of European amphibians, with its range extending from Scotland, Wales and western France to the Urals in the east, and in a north south direction – from the middle parts of Norway and Sweden to south-eastern France and north-western Bulgaria (Litvinchuk & Borkin 2009, Wielstra et al. 2014). In Bulgaria, *T. cristatus* occurs only in the north-western part of the country (up to ca. 1380 m above sea level), inhabiting all kinds of stagnant water bodies, preferring those of small area, shallow depth and without fish (Naumov et al. 2023). At the European level, *T. cristatus* is a strictly protected species (Appendix II of the Convention on the Conservation of European Wildlife and Natural Habitats, Bern, 1979) and, within the EU, it is among the species protected in the Natura 2000 network (Annex II of the Council Directive 92/43/EEC).

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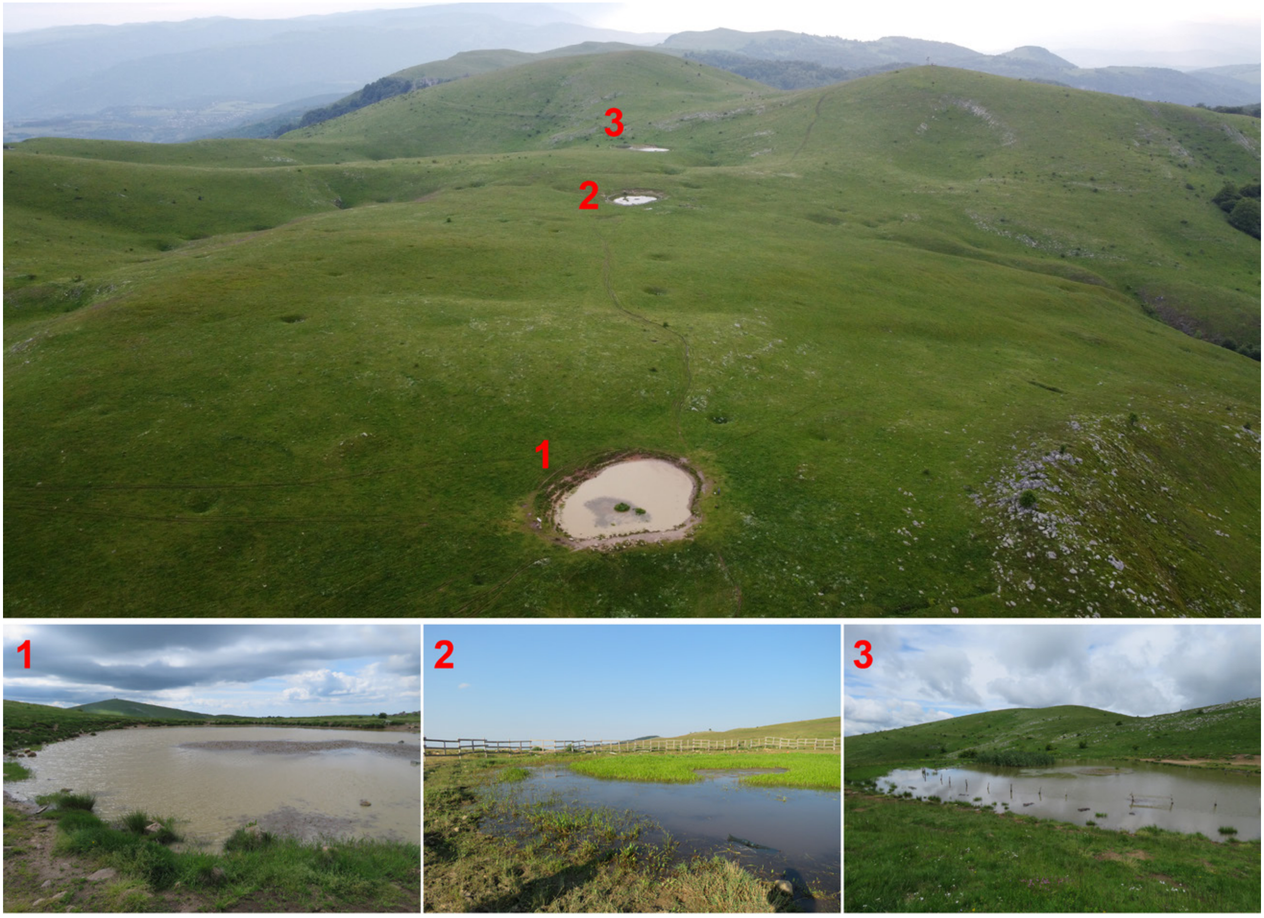

Fig. 1. View of the study area (from east to west; June 2023) with designations for the individual water bodies (1, 2 and 3 according to the main text) and a view of the same water bodies from a closer distance.

As could be expected given its large range, *T. cristatus* has been the subject of numerous studies in various aspects including phenology and population ecology (Arntzen 2003, Jehle et al. 2011, Fahrbach & Gerlach 2018). However, at the regional level, especially in the Balkan Peninsula, there are many gaps in knowledge. E. g., in Romania, a number of such studies have been conducted by Cicort-Lucaciu et al. (2009, 2010, 2011), Dobre et al. (2009), Bogdan et al. (2012), Covaciu-Marcov et al. (2023), etc., while, in Bulgaria, there are none at all. Given the high conservation status of the species, it is clear that research aimed at filling the lack of ecological information would not only have a scientific contribution but would also be beneficial for the conservation of the species.

The aim of the present study was to derive and analyse data on the seasonal activity and the sex ratio of *Triturus cristatus* in the southernmost part of its range. We expected to observe both inter- and intra-population level differences, with distinct phenology patterns for adults, immatures and larvae.

Materials and Methods

Study area

The study was conducted in three permanent ponds, situated at 1360–1380 m a.s.l. in the Vrachanski Balkan Nature Park (Stara Planina Mts., NW Bulgaria). Study area represents one of the southernmost known “points” of the general range of the species and, at the same time, one of those with the highest altitude (Wielstra et al. 2014, Naumov et al. 2023). The three ponds, hereafter referred to as Pond 1, Pond 2 and Pond 3, have been defined as separate localities of *T. cristatus* by Naumov et al. (2016, 2023), respectively as “Ochindol (3.7 km N)”, “Ochindol (3.8 km N)” and “Ochindol (3.9 km N)” = “Parshevitsa”]. The main ecological features of the studied ponds are the following (see also Fig. 1):

- surface area of ca. 1000 m^2 (Pond 1), 900 m^2 (Pond 2) and 1500 m^2 (Pond 3); maximum depth of ca. 1 m (for all of the three ponds);
- macrophyte coverage (relative to the pond

area) of below 10% (Pond 1 and Pond 3) or ca. 80% (Pond 2);

- access of domestic animals (horses) – free in Pond 1 and Pond 3 and impossible in Pond 2 (due to the presence of a fence);
- fish presence – established only in Pond 1; one fish species, *Carassius gibelio* (Bloch, 1782), which according to information received by local people, has been deliberately introduced in 2015–2016. Individuals of this fish species were captured in almost every one of a total of 24 trap-sessions during 2021–2023, while no fish were detected in the period 2009–2012 (seven trap-sessions).

The ponds are located in an almost straight line in the east-west direction. The distances between them [measured between their centroids based on satellite images (Google Earth Pro)] are as follows: 700 m (between Pond 1 and Pond 3), 425 m (between Pond 1 and Pond 2) and 265 m (between Pond 2 and Pond 3).

Sampling

For three consecutive years (2021–2023), the area was visited monthly (in almost all cases in the second half of the month) from April to November. At each visit and simultaneously in all three ponds, newts were captured with funnel traps (L70/H25/W25 cm, 0.5 cm mesh size; for more details, see Bock et al. 2009): 10 traps (in several cases 8 or 9) in each pond; average duration of exposure 18 hours (from late afternoon or evening to noon the next day). Water temperature was measured twice (at the time of set up and at the time of collection of the traps) at a depth of about 10 cm using a digital thermometer with a probe (resolution 0.1ºC). Caught newts were counted on site and categorised according to their ontogenetic stage [adults, immatures (both juvenile (age 1+) and subadult (age 2+) individuals, as it is not always possible to distinguish these stages correctly by external markings) or larvae] and sex (only in adults). All adults were photographed from the ventral side using a digital camera (resolution 180 dpi). After these procedures were completed, the newts were released. Thus, the results of the present study are based on 72 trapping sessions conducted in the same manner and distributed evenly across months, years, and ponds.

Data processing and analysis

We compared photographs of the unique ventral patterns of all captured individuals in order to identify recaptures. The HotSpotter v 1.0 (Crall et al. 2013) was used for software-assisted image recognition, as this method has been demonstrated to work well for amphibians (Burgstaller et al. 2021) and newts in particular (Naumov & Lukanov 2018, Lukanov 2022, Lukanov et al. 2022) and unlike other marking techniques such as toe-clipping, is non-invasive (Parris & McCarthy 2001). Suggested recaptures were always verified manually by the authors (for the full procedure, see Naumov & Lukanov 2018).

Relative abundance (Ab), calculated by the formula: $Ab = N/(T*H)$, where N is the number of captured newts, T is the number of traps, and H is the trap exposure time (with accuracy of ½ hour), was used as the main indicator for assessing newt activity. The sex ratio is represented by the number of captured males divided by the number of captured females (e.g., if 50 males and 40 females are caught, the ratio is given as 1.25:1). The water temperature is represented by an arithmetic mean of the measured values at the respective times of placing and collecting the traps.

Kruskal-Wallis test (Mann-Whitney test as a post hoc analysis) were used for comparison between ponds and between years based on the relative abundance of newts as well as when comparing ponds by water temperature. Mann-Kendall test was used for detecting monotonic time trends in the observed relative abundance and sex ratio, and Z-statistic – for calculating the probability of an observed proportion against a hypothetical proportion (0.5, i.e. 1:1) regarding sex ratio. All analyses were performed using PAST 4.07 (Hammer et al. 2001).

As "comparative material" in the discussion, we used our unpublished data and data provided by colleagues collected in the same manner (capture with funnel traps), both from ponds included in the present study (in 2009–2019) and in other ponds in NW Bulgaria (in 2008–2021). These data are presented in Appendix 2 but have not been statistically analysed due to the non-systematic nature of their collection.

Results

During the three years of the study, a total of 3467 individuals of *Triturus cristatus* were recorded; these were 1637 adults (including 40 recaptures), 484 immatures and 1346 larvae (Fig. 2; Appendix 1). The number of recaptures of adults was 9 in 2021 (2.18% of a total of 413 captured), 9 in 2022 (1.32% of a total of 681 captured) and 22 in 2023 (4.05% of a total of 543 captured). In all cases the animals were recaptured in the same pond. Only two individuals (from Pond 2) were caught a third time.

The relative abundance for adult newts ranged between 0.005 and 1.623, for immature newts be-

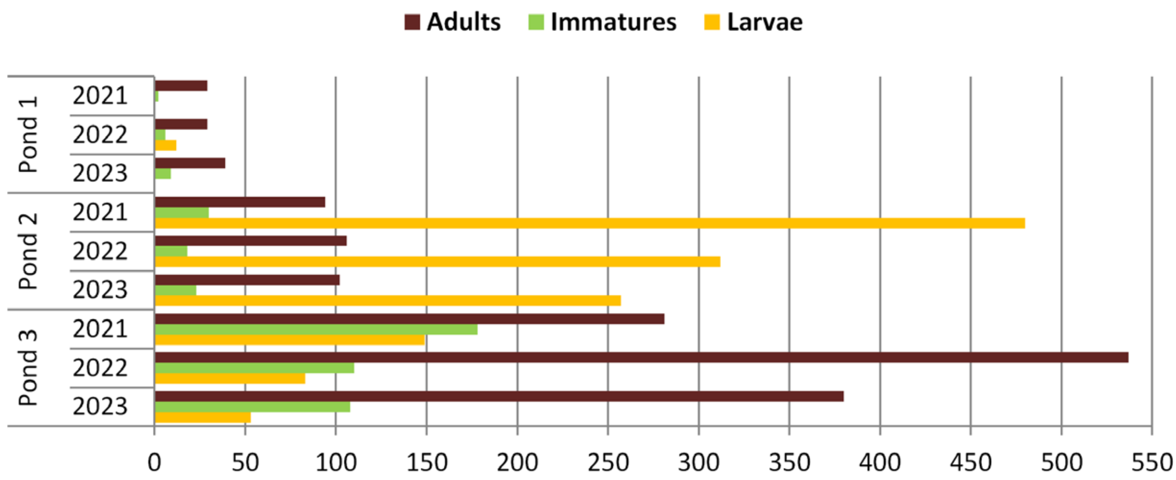

Fig. 2. Distribution of the number of *Triturus cristatus* caught by ponds and years (recaptures of adults are not included).

Table 1. Kruskal-Wallis test (H, *p*) for differences in the relative abundance of *Triturus cristatus* between 2021, 2022 and 2023.

	Adults		Immatures		Larvae	
	H	*p*	H	*p*	H	*p*
Pond 1	0.365	0.8173	1.260	0.3767	n/a	n/a
Pond 2	0.140	0.9323	0.114	0.9439	0.219	0.8927
Pond 3	1.140	0.5641	0.386	0.8237	0.635	0.6573
Overall	0.344	0.8397	0.938	0.6095	0.722	0.6666

tween 0.005 and 0.616, and for larvae between 0.006 and 1.450 (excluding trap sessions with a zero score for the respective age category), with no reliable differences between different years (Table 1). However, there were significant differences between ponds (Table 2), with adults and immatures having highest relative abundance in Pond 3, lower in Pond 2 and lowest in Pond 1, and in terms of larvae – highest in Pond 2, lower in Pond 3 and lowest in Pond 1 (in this pond larvae were recorded only in July and August 2022).

Phenology

Adults of *T. cristatus* were recorded every month from April to November but in varying numbers, as were immatures, while larvae were registered only from June to November. Adults showed a gradual decrease in abundance from spring to autumn and this trend was statistically significant for each of the studied ponds, while for immatures and larvae there was no reliable trend in monthly abundance fluctuations (Fig. 3, Table 3). Analysis of individual photographs of adults showed the greatest time gap between first and last capture to be about four months for males. One individual caught on 20.05, 14.07 and 16.09.2021 at Pond 2, and another on 26.04 and 11.08.2022 in Pond 3) and about three months for females (one individual caught on 21.04, 12.06. and 15.07.2023 in Pond 2, another on 15.07 and 13.10.2023 in Pond 2, and a third on 12.06 and 19.09.2023 in Pond 3). Regarding immatures, in Pond 3 (the pond with the largest number of records of immatures), a bimodal type of seasonal variation in abundance was observed, and in the other two ponds, a rather monomodal type. Regarding larvae, both Pond 2 and Pond 3 showed a well-marked monomodal pattern of seasonal variation in abundance, although the peaks were in different months.

The recorded pattern of seasonal variations in water temperature was such that a direct comparison with seasonal variations in *T. cristatus* abundance would obviously be meaningless (Fig. 3). No significant differences between individual ponds regarding water temperature were found (Kruskal-Wallis test: $H = 0.52$, $p = 0.7728$). The lowest water temperature values at which newts were found were 5.3ºC (October 14, 2021, Pond 2: 2 adults and 36 larvae) and 5.9ºC (November 16, 2023, Pond 3: 1 adult and 1 immature), and the lowest when there was no catch were 4.2 and 4.6ºC (respectively in Pond 1 and Pond 3, October 14, 2021).

Sex ratio

The established sex ratio of adult newts (excluding recaptures: 24 males and 16 females in total) in the entire sample was 1.24:1, and in individual ponds: 1.85:1 in Pond 1, 1.03:1 in Pond 2, and 1.26:1 in Pond 3. Deviations from the hypothesised sex ratio (1:1) were statistically significant for the sample as a whole ($Z = 4.276$, $p < 0.001$) as well as separately for Pond 1 ($Z = 2.9448$, $p = 0.003$) and Pond 3 (Z

Table 2. Kruskal-Wallis (H, *p*) and Mann-Whitney pairwise (U, *p*) tests for differences in the relative abundance of *Triturus cristatus* between ponds.

	Overall		Pond 1 vs. Pond 2		**Pond 1 vs. Pond 3**		**Pond 2 vs. Pond 3**	
	H	*p*	U	*p*	U	*p*	U	*p*
Adults	18.63	0.0001	155.5	0.0059	102.5	0.0001	166.0	0.0121
Immatures	23.37	0.0000	144.5	0.0018	81.0	0.0000	144.5	0.0031
Larvae	n/a	n/a	n/a	n/a	n/a	n/a	186.0	0.0265

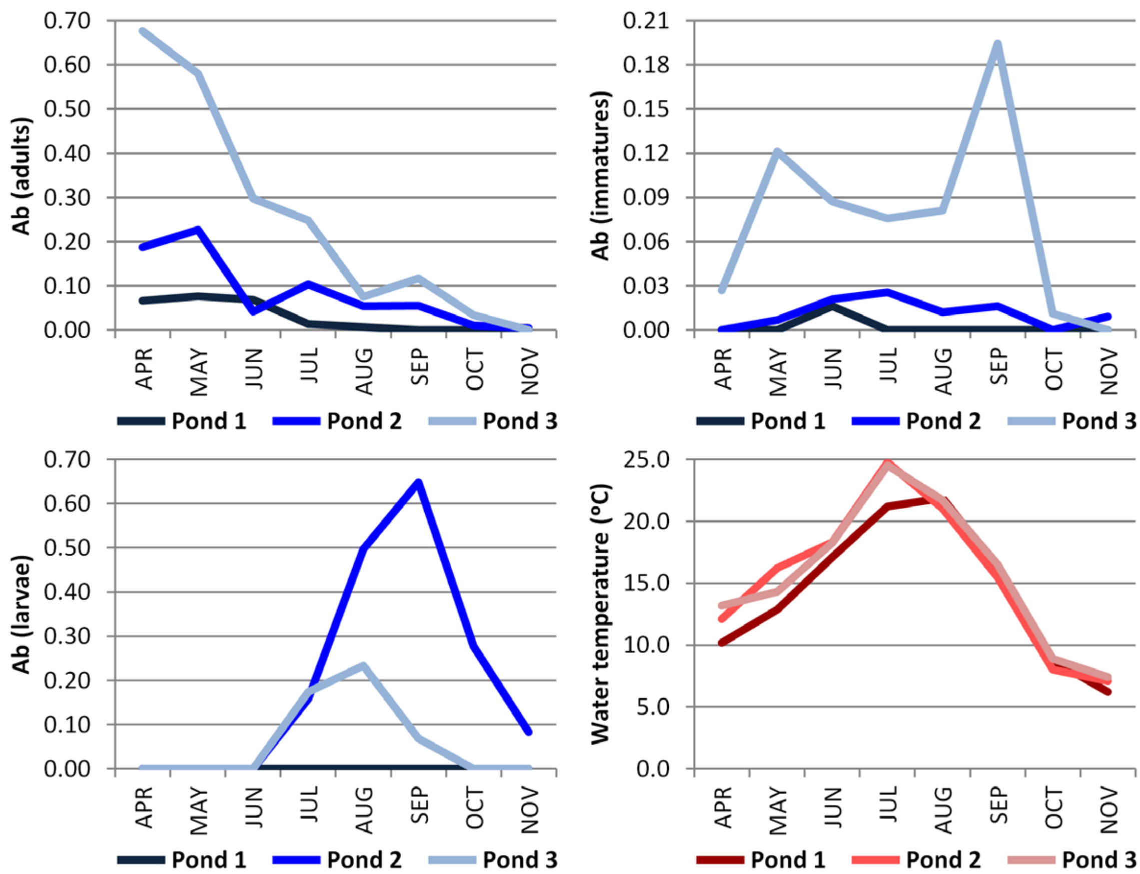

Fig. 3. Relative abundance (Ab) of *Triturus cristatus* and average water temperature in the studied ponds by month (based on median values derived from the three years).

Table 3. Mann-Kendall test (S, *p*) for detecting monotonic time trends in the relative abundance of *Triturus cristatus* in the study ponds.

	Adults		**Immatures**		**Larvae**	
	S	*p*	S	*p*	S	*p*
Pond 1	-21	0.0028	-3	0.3600	n/a	n/a
Pond 2	-18	0.0160	1	0.4520	13	0.0540
Pond 3	-26	0.0002	1	0.4520	2	0.4520
Overall	-22	0.0028	-3	0.3600	2	0.4520

= 3.987, $p < 0.001$), but not for Pond 2 ($Z = 0.229$, $p = 0.819$).

The registered sex ratio showed a distinct monthly-dynamics in each of the three study ponds. For Pond 2 and Pond 3, there was a statistically significant four-month trend from a peak in the number of males in April to a predominance of females in July (in both cases Mann-Kendal's S = -6, p = 0.042). This trend was not observed in Pond 1 (S = -2, p = 0.375), probably due to the small sample size for July (seven individuals) distorting the ratio estimate. An increase in the number of males over females was recorded in September; it was pronounced in Pond 3 and slightly pronounced in Pond 2, and for Pond 1 no data were available for this month. Statistically reliable deviations (Table 4) from the hypothetical sex ratio were found in April (with the highest reliability both in the aggregated data and in Ponds 2 and 3), May (in the aggregated data but not in the ponds separately), July (in the aggregated data and in Pond 2) and September (in the

Table 4. Results of the Z-test for deviation from the hypothesized proportion (0.5) in the sex ratio of *Triturus cristatus* adults in the study ponds by month (the test was applied only to the months in which there were more than 30 individuals caught).

	Pond 1		Pond 2		Pond 3		Overall	
	Z	*p*	Z	*p*	Z	*p*	Z	p
APR	n/a	n/a	|3.79|	0.0001	|4.51|	<< 0.001	|6.00|	<< 0.001
MAY	|1.89|	0.0583	|0.78|	0.4331	|1.46|	0.1431	|2.16|	0.0309
JUN	|1.36|	0.1750	n/a	n/a	|0.76|	0.4493	|0.60|	0.5503
JUL	n/a	n/a	|2.38|	0.0173	|1.82|	0.0681	|2.45|	0.0141
AUG	n/a	n/a	n/a	n/a	|0.60|	0.5494	|1.28|	0.2022
SEP	n/a	n/a	n/a	n/a	|2.89|	0.0038	|2.16|	0.0305
OCT	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
NOV	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a

aggregated data and in Pond 3). For June and August, no significant deviations from the hypothetical ratio were observed. For the autumn months, applying this test would not be informative because the small sample sizes.

Discussion

The results of the present work showed that the southernmost known population of *Triturus cristatus* is numerous and probably numbers several thousand individuals. At this stage, its size cannot be correctly determined due to the small number of recaptures (between 2 and 4% per year). The latter in itself means that the actual number of newts in the ponds is much higher than that of those captured, as funnel traps have been demonstrated to be rather efficient in large-bodied newts, with Arntzen & Zuiderwijk (2020) observing a trend for catchability to increase with body size (*Lissotriton* < *Ichthyosaura* < *Triturus*). E. g., in April 2022, nine traps caught 241 adults in Pond 3, and if we compare the pond area (ca. 1500 m^2) with the total area of nine traps (ca. 1.6 m^2), it becomes clear that only a small fraction of the newts in the water could have entered the traps during the exposure (16.5 hours).

Migrations of adult newts from one pond to another were not recorded but, given the small number of recaptures, it is highly likely that if such movements did occur, they would have gone undetected. In his study on *Triturus ivanbureschi* Arntzen et Wielstra, 2013, Lukanov (2022) established that out of over 500 individuals from two temporary ponds and recapture rate of over 50%, only 10 individuals were recaptured in a different pond the following year, thus suggesting a low percentage of newt inter-pond migration. On the other hand, since none of the three ponds dries up, there seems to be little reason for newts to move from one pond to another, especially since the distances between the ponds are not so small (265–700 m) as to suggest spontaneous movement of adult newts. Although the maximum recorded migration distance for *T. cristatus* is 1650 m (Haubrock & Altrichter 2016), Kovar et al. (2009) have established that the vast majority of adults migrate within 274–303 m from the home pond.

Our results showed significant differences between the three study ponds in terms of the relative abundance of *T. cristatus*. Pond 1 was characterised by the lowest abundance of each of the age categories, but mostly in terms of larvae (Fig. 3), the latter suggesting a very low reproduction success of the local population. In all likelihood, this is due to the presence of fish (which are absent in the other two ponds) as well as the extremely poor food base in this pond (Naumov et al. 2024). The introduction of *Carassius* species by local people for the purpose of recreational fishing is not an uncommon practice and has been reported before (e.g., Covaciu-Marcov et al. 2009). If data from the same pond before the introduction of fish are analysed, the maximum recorded value of the relative abundance of adults is calculated as 0.292, and of larvae – 0.115 (August, 2009; Appendix 2). In 2021–2023, the corresponding values were 0.120 and 0.048 (recorded values of the relative abundance of larvae in the other two ponds in August 2009 were 1.071 in Pond 2 and 0.044 in Pond 3, i.e. lower than the maximums recorded in 2021–2023 (1.450 in Pond 2 and 0.406 in Pond 3 in August, 2021). According to a number of authors, the presence of predatory/omnivorous fish in the water body has a negative impact on the newt population, mostly because the fish feed on the newt's eggs and/or larvae (e.g. Brana et al. 1996, Beebee & Griffiths 2000, Hartel et al. 2007). Still, it has to be noted that Cupsa et al. (2020) established the presence of both fish and newts in 21 out of their 54 study ponds from North-Western Romania, hypothesizing that when this co-occurrence is naturally evolved and not a recent event, negative consequences for the amphibians are at a minimum.

Considerably more difficult to explain is the difference found between Ponds 2 and 3. Pond 3 is used as a watering hole by horses introduced in the area and is under pollution pressure from their constant presence (unlike Pond 2, which has been fenced in for a long time). While the diversity of the food base in Pond 3 was lower (Naumov et al. 2024), the recorded relative abundance of adults and subadults in it was quite higher (Fig. 3). It is possible that this difference in abundance is only fictitious and may be due to a lower probability of newts entering the traps in Pond 2 than in Pond 3, as the former is almost entirely covered by abundant vegetation, which could physically limit newt movement. In Pond 3 the vegetation is sparse (only one "island" formed by bulrush and other aquatic plants), so there are no "barriers" and the newts likely swim longer distances, increasing the likelihood of entering a trap. Regarding the larvae, however, the abundance recorded in Pond 2 was significantly higher than in Pond 3, which could be due to one of the following three circumstances. First, the abundant vegetation in Pond 2 greatly facilitates the typical *T. cristatus* behaviour of wrapping individual eggs in leaves, which hides them from predators and protects against direct solar radiation (Arntzen 2003, Maletzky et al. 2007), while its absence from Pond 3 could mean lower chances of egg survival. Second, the constant presence of horses in Pond 3 could alter water parameters and it is possible that larvae and/or eggs are more sensitive to water contamination caused by horses than subadults and adults (Pond 2 is fenced and therefore protected). Third, the food base diversity is higher in Pond 2 than in Pond 3 (Naumov et al. 2024).

Phenology

Regarding the seasonal dynamics in the relative abundance of *T. cristatus* adults found in water, our results demonstrated a clear temporal trend of decline from spring to autumn, which is largely consistent with general knowledge of the species' phenology (Arntzen 2003 and references therein) and is mostly (but not only) a reflection of the duration of the breeding period. Maximum values of abundance were recorded in April and May, which means that the breeding period takes place mainly in these months (according to local people, in March in the study area there is usually a thick snow cover and the water bodies are still frozen), and for Ponds 2 and 3 in particular, probably continues into July. Such prolonged breeding periods are not unusual for *T. cristatus*. E.g., Kowalewski (1974) established the duration of the breeding period from 10–15 April to mid-June (data from central Poland, 200-400 m a.s.l.). Covaciu-Marcov et al. (2023) observed a duration of the breeding period from March to June with a peak in April (data from SW Romania, 900 m a.s.l.). Bogdan et al. (2012) recorded a peak of the breeding period at the beginning of May, but also noted that the water phase is quite extended (data from SW Romania, 430 m a.s.l.). The migration of adult newts from the water to dry land, as far as Ponds 2 and 3 are concerned, is apparently gradual and continues until November, while in Pond 1, the process is shorter and the mass exit from the water apparently happens before the middle of July (no newts were captured after August). In all probability, this period is site-specific – Blab & Blab (1981) established that adults left the ponds in the period from mid-July to mid-October, but mostly in August, von Bülow (2001) found that most adults left the water at the end of June.

Wenzel et al. (1995) suggested that the early emergence of adults on land could be due to a lack of food resources in the pond. This is also the most likely explanation in our case, since in Pond 1 the food base is many times poorer compared to the other two ponds (Naumov et al. 2024). Overwintering of *T. cristatus* adults in the study area undoubtedly takes place mainly on land, and only a small part of them overwinter in water, which can be judged by the low relative abundance recorded in the ponds in October and especially in November (the probable beginning of hibernation). The other observations in NW Bulgaria also show low values of relative abundance in October and November (Appendix 2). In all cases, however, male newts caught in the autumn had well-developed crests (unlike males caught in the summer months), which indicated that they were almost ready for the breeding season the following spring, thus they would not leave the pond but would hibernate in it. Von Bülow (2001) mentioned that the males caught in winter had well-developed crests. The same has been recorded by Lukanov et al. (2022) for the closely related *T. ivanbureschi*. There is no way to judge whether these newts stayed in the water during the entire active period or entered secondarily to overwinter there (autumn migrations to breeding ponds have been established, e. g., by Verrell & Halliday (1985) and Glandt (1986), and a year-round presence of adults in water was mentioned by Kowalewski (1974) and von Bülow

(2001). In other parts of the *T. cristatus* range, both similar (mainly on land) and a different type of overwintering have been registered. In southern Poland, Kowalewski (1974) found overwintering both on land and in water and, in the Ukrainian Carpathians, newts leave water bodies at the end of August and in September, migrating to wintering sites on land (Shcherbak & Shcherban 1980). According to Feldmann (1981), a large number of crested newts from NW Germany overwinters in water. For newt populations from the territory of former USSR, hibernation occurs on land but possibly also in unfrozen ponds with springs (Kuzmin 1999, based on a synopsis of publications).

Seasonal changes in the relative abundance of adult newts in the study ponds do not appear to depend directly on seasonal changes in water temperature. In general, we recorded newts at water temperatures between 5.3 and 25.7ºC; this is largely consistent with data from the Ukrainian Carpathians where newts were recorded in a temperature range between 5 and 28ºC (Shcherbak & Shcherban 1980).

On the other hand, water temperature undoubtedly has a significant effect on reproduction. According to Kowalewski (1974), spawning starts at a temperature of 10–12ºC, with the optimum temperature being between 15 and 20ºC, and Kuzmin (1999) has mentioned that breeding starts at a water temperature between 10 and 15ºC. In our study, there was no way to determine exactly when egg-laying begins (we did not search for eggs) nor exactly when the eggs hatch. The length of the larvae at hatching is only 0.9–1.1 cm (Arntzen 2003), which excludes the possibility of their retention in the used funnel traps (mesh size of 0.5 cm) but, for these reproduction stages, it can be estimated indirectly. The earliest appearance of larvae in the traps was recorded in June, meaning they probably hatched in May, as one month should be enough for the larvae to grow large enough to be retained in the traps. At that time, the recorded water temperature was between 11.3 and 17.4ºC (other observations from Bulgaria show registrations of larvae in the third part of May but in sites at a much lower altitude; see Appendix 2), and the first eggs were probably laid in April, when the recorded temperature of the water was between 4.7 and 17.2ºC. Egg development lasts about 20 days when the water temperature fluctuates between 4 and 17ºC (Kowalewski 1974). Arntzen (2003) mentioned that the length of the embryonic phase varied between 10 and 37 days depending on the temperature. Peaks in relative larval abundance were recorded in August and September (in Pond 3 and Pond 2, respectively), which could mean that during these months larvae have reached maximum body size (hence maximum probability of holding large numbers of larvae in the traps). This also clearly marks the completion of metamorphosis, since a sharp decrease in the abundance of larvae was observed afterwards. For immatures, the observed seasonal changes in abundance are more difficult to explain. Two peaks were recorded in Pond 3 (in May and September), and the high abundance in September could be linked to the peak in larval abundance in the previous month, i.e. the bulk of immatures caught in September consisted of juveniles that had recently completed metamorphosis (thus not yet out of the water). The May peak could be explained by immatures entering the water during the breeding season adult period, a phenomenon that has been observed by a number of authors, but its biological meaning is not well understood yet (Blab & Blab 1981, Verrell & Halliday 1985, Arntzen 2003 and references therein). In Pond 2, the recorded seasonal fluctuations in the abundance of immatures were less pronounced, with only one maximum in July, i.e. well before the peak of larval abundance but also after the end of the breeding period, which is difficult to interpret and perhaps reflects the effects of some local factors that remained unregistered during the study. It is interesting to note that the presence of immatures and larvae in November was observed only in Pond 2, which also suggests that the environmental conditions in this pond probably allow overwintering of larval newts. Shcherbak & Shcherban (1980) suggested overwintering in water of both larvae and juveniles in which metamorphosis occurred late, i.e. when it is already colder on land than in water. We had no registrations of larvae in the study area in April; however, according to other observations from Bulgaria, no larvae were also recorded in March and April (Appendix 2). This indicated that the individuals in the larval stage in late autumn had metamorphosed in winter (or in early spring) and, by mid-April, they were already juveniles (provided they have survived). According to Kowalewski (1974), larvae that had not metamorphosed by mid-November overwintered in the water and the metamorphosis of some of them occurred the following spring. However, the mortality rate in these larvae was high during the winter.

Sex ratio

Regarding the sex ratio of adult newts found in the water, our results demonstrated a slight overall male bias (1.24 : 1); however, the ratio recorded in the different ponds was not uniform. Again, Pond 1 was clearly distinguished from the other two ponds and its ratio of 1.85 : 1 deviated the most from the hypothetical ratio while, in Pond 2, it was the closest to the hypothetical (1.03 : 1). This could be interpreted as a reflection of anthropogenic influence in the study area: Pond 2 is slightly affected and practically retains its natural character, while Ponds 1 and 3 are under pressure (see above). A summary of other available data for *T. cristatus* from Bulgaria (Appendix 2) reveals that a total of 437 males and 439 females were registered, i.e. the sex ratio is practically 1 : 1. If only the relatively larger samples (n > 30) are considered separately, the ratio varies from 0.58 : 1 to 2.06 : 1, and specifically in the largest sample (n = 152) it is 0.65 : 1. It should be borne in mind that these data were not collected systematically, but can be seen rather as randomly collected, which makes them indicative of an overall characterization of the species in terms of sex ratio, at least on a regional level. In other parts of *T. cristatus* range, both similar and different sex ratios have been recorded. E.g., Arntzen & Teunis (1993) found a ratio of almost 1 : 1 (395 males vs. 389 females; data from NW France). Blab & Blab (1981) reported a male bias in a ratio of 1.6 : 1 (288 males vs. 176 females; data from W Germany). Meyer & Grosse (2007) registered a male bias in a ratio of 1.33 : 1 (786 males vs. 589 females; data from W Germany). Feldmann (1981) reported a females bias (697 males vs. 966 females, i.e. 0.72 : 1; data from NW Germany). Kühnel et al. (2001) found a female bias in 9 out of 10 samples with a size of more than 100 individuals (data from E Germany). Bogdan et al. (2012) recorded a female bias in a ratio of 39.80 : 60.19% (i.e. 0.66 : 1, based on 82 males and 124 females; data from SW Romania).

Our observations confirm the presence of distinct seasonal fluctuations in the sex ratio of aquatic adult newts and show a trend from a predominance of males in April to a predominance of females in summer. Similar fluctuations have also been recorded in a number of other studies, although most of them refer only to the breeding period. Based on long-term research in France, Arntzen (2002) established a trend for a male-biased sex ratio at the start of the aquatic season (late winter/early spring) and for a female bias toward the end of the aquatic season (early summer), suggesting that males mostly arrive and leave the breeding sites ahead of the females. For the Ukrainian Carpathians, Shcherbak & Shcherban (1980) also mention that in spring, males enter the water first, and females appear 2–3 days later. In a study in SW Romania at 900 m a.s.l., Dobre et al. (2009) found variation in sex ratios within 46 : 34, 50 : 39 and 16 : 23 [1.35 : 1, 1.28 : 1 and 0.70 : 1, respectively], in early, mid, and late April, respectively. In the same pond ten years later, Covaciu-Marcov et al. (2023) found sex ratios of 71 : 42, 72 : 89 and 63 : 87 [1.69 : 1, 0.81 : 1 and 0.72 : 1] in March, April and June, respectively. The biological meaning of this trend remains unclear, since males are generally expected to stay in the water longer (to increase mating opportunities) and females shorter (leaving ponds after egg laying) as found, e.g., by Verrell & Halliday (1985) in southern England. One of the possible reasons for the longer stay of the females in the water is that some of them will likely need to mate again after several weeks of oviposition to fertilise all of the ova, although sperm can be stored for up to a year (see Arntzen 2003 and references therein). Another hard-to-explain result of our observations is the second peak of male predominance recorded in September (albeit only in one pond, but the one with the largest sample). This could not be associated with either breeding (captured males had no developed crests) nor with hibernation (water temperature in September is still too high; Fig. 3). Jehle et al. (2011) hypothesised that males overwintered in water more often than females but explicitly stated that there was no evidence for this. Our results do not confirm this hypothesis since in November (i.e. the probable beginning of hibernation) four males and six females were recorded (in total) in the studied area; according to other data from NW Bulgaria for the same month (Appendix 2) – three males and three females. Research focusing on typically winter months is needed to clarify this question (see e.g. Lukanov et al. 2022). In conclusion, it can be stated that the seasonal activity and sex ratio of the southernmost populations of *Triturus cristatus* are similar to those reported from other parts of its range. In terms of conservation, the results of our study (and in particular the identified anthropogenic threats) should be taken into account when planning measures to maintain and improve the status of the species' populations at both local and national levels.

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Appendix 1. Number of *Triturus cristatus* caught in the study area in the period 2021–2023 (each row presents one trapping session, and the arrangement is by month, pond and exact date). TºC = water temperature; T = trap number; H = trap exposure time (with accuracy of ½ hour); Adults [M = number of males (number of recaptures if any); F = number of females (number of recaptures if any)].

	Pond	Date	TºC	T	H	Adults [M; F]	Immatures	Larvae
April	Pond 1	27.04.2021	4.7	10	20.5	-	-	-
		26.04.2022	15.5	8	16	10 [8; 2]	-	-
		21.04.2023	10.5	10	16.5	11 [8; 3]	-	-
	Pond 2	27.04.2021	8.6	10	21	18 [14; 4]	-	-
		26.04.2022	16.7	10	16.5	31 [19; 12]	-	-
		21.04.2023	11.2	10	16.5	41 [30; 11]	3	-
	Pond 3	27.04.2021	12.4	10	22	65 [31; 34]	1	-
		26.04.2022	17.2	9	16.5	241 [140; 101]	4	-
		21.04.2023	10.0	10	17	115 [87; 28]	7	-
May	Pond 1	20.05.2021	15.6	10	19.5	15 [8; 7]	-	-
		19.05.2022	11.3	10	15	13 [10 (2); 3]	2	-
		20.05.2023	11.8	10	16	7 [5; 2]	-	-
	Pond 2	20.05.2021	17.4	10	20	24 [16 (1); 8]	-	-
		19.05.2022	15.3	10	15	34 [9; 25 (1)]	1	-
		20.05.2023	16.1	10	16.5	38 [27 (1); 11 (1)]	7	-
	Pond 3	20.05.2021	16.9	10	20	105 [57; 48]	28	-
		19.05.2022	12.7	10	15.5	91 [33 (1); 58]	17	-
		20.05.2023	13.4	9	16.5	139 [92 (4); 47 (2)]	18	-
June	Pond 1	15.06.2021	14.3	10	19	13 [5 (1); 8]	2	-
		23.06.2022	21.2	10	18.5	7 [4; 3 (1)]	3	-
		12.06.2023	16.0	10	15	18 [14 (1); 4]	3	-
	Pond 2	15.06.2021	15.4	10	19	8 [2; 6]	4	-
		23.06.2022	21.8	10	18.5	5 [3; 2]	3	4
		12.06.2023	17.8	10	15	13 [4 (2); 9 (1)]	8	-
	Pond 3	15.06.2021	15.2	10	19.5	58 [28; 30 (1)]	17	-
		23.06.2022	22.2	9	18.5	29 [15; 14]	25	6
		12.06.2023	17.5	10	15.5	72 [42; 30 (4)]	10	-

Appendix 1. Continuation.

	Pond	Date	TºC	T	H	Adults [M; F]	Immatures	Larvae
July	Pond 1	14.07.2021	21.3	10	17	2 [2; 0]	-	-
July	Pond 1	15.07.2022	20.3	10	15	2 [0; 2]	-	4
July	Pond 1	15.07.2023	22.1	9	16	3 [3 (1); 0]	4	-
July	Pond 2	14.07.2021	24.9	10	17	21 [9 (1); 12 (1)]	12	27
July	Pond 2	15.07.2022	25.7	10	15.5	15 [4; 11]	4	29
July	Pond 2	15.07.2023	23.7	10	15.5	13 [3; 10 (1)]	2	1
July	Pond 3	14.07.2021	25.5	10	17.5	21 [9; 12]	5	60
July	Pond 3	15.07.2022	23.3	10	15.5	73 [31 (1); 42]	20	27
July	Pond 3	15.07.2023	24.8	10	14.5	36 [15 (2); 21]	11	-
August	Pond 1	12.08.2021	22.8	10	15.5	1 [1 (1); 0]	-	-
August	Pond 1	11.08.2022	19.8	10	16.5	-	1	8
August	Pond 1	18.08.2023	23.1	10	18.5	2 [1; 1]	-	-
August	Pond 2	12.08.2021	23.4	10	16	15 [4; 11]	7	232
August	Pond 2	11.08.2022	19.9	10	16.5	9 [4; 5]	2	82
August	Pond 2	18.08.2023	19.9	10	18	-	1	55
August	Pond 3	12.08.2021	21.9	10	16	12 [6; 6]	13	65
August	Pond 3	11.08.2022	21.0	10	17	44 [20 (2); 24 (1)]	19	37
August	Pond 3	18.08.2023	22.4	10	18	-	1	42
September	Pond 1	16.09.2021	18.2	10	18	-	-	-
September	Pond 1	17.09.2022	13.9	10	18.5	-	-	-
September	Pond 1	19.09.2023	16.7	10	18.5	-	2	-
September	Pond 2	16.09.2021	18.1	10	18	10 [6 (3); 4]	5	167
September	Pond 2	17.09.2022	14.6	10	18.5	13 [4; 9]	3	119
September	Pond 2	19.09.2023	13.9	10	18.5	1 [0; 1]	1	120
September	Pond 3	16.09.2021	19.2	10	18.5	21 [15; 6]	114	24
September	Pond 3	17.09.2022	14.2	10	19	51 [32; 19]	23	13
September	Pond 3	19.09.2023	16.3	10	18	21 [13; 8 (1)]	35	11
October	Pond 1	14.10.2021	4.2	10	19.5	-	-	-
October	Pond 1	20.10.2022	9.1	10	18	-	-	-
October	Pond 1	13.10.2023	13.1	10	17.5	-	-	-
October	Pond 2	14.10.2021	5.3	10	19	2 [1; 1]	-	36
October	Pond 2	20.10.2022	8.8	10	18	-	-	50
October	Pond 2	13.10.2023	10.0	10	17.5	2 [0; 2 (1)]	-	72
October	Pond 3	14.10.2021	4.6	10	19	-	-	-
October	Pond 3	20.10.2022	8.7	10	18	6 [3; 3]	2	-
October	Pond 3	13.10.2023	13.5	10	18	10 [7; 3]	26	-
November	Pond 1	12.11.2021	6.4	10	21	-	-	-
November	Pond 1	15.11.2022	6.2	10	20	-	-	-
November	Pond 1	16.11.2023	6.1	10	20.5	-	-	-
November	Pond 2	12.11.2021	7.4	10	21.5	2 [1; 1]	2	18
November	Pond 2	15.11.2022	8.1	10	20	-	5	28
November	Pond 2	16.11.2023	5.9	10	20.5	1 [1; 0]	1	9
November	Pond 3	12.11.2021	7.9	10	22	-	-	-
November	Pond 3	15.11.2022	8.4	10	20	7 [2; 5]	-	-
November	Pond 3	16.11.2023	6.1	10	20.5	-	-	-

Appendix 2. Other (unpublished) data on abundance and sex ratio of *Triturus cristatus* in Bulgaria (collected by the authors or provided by their colleagues in the period 2008-2021) [localities of "Ochindol (3.7 km N)", "Ochindol (3.8 km N)", and "Parshevitsa" are equal respectively to Pond 1, Pond 2, and Pond 3 in this study (for descriptions of the other localities see Naumov et al. 2023)]: TºC = water temperature; Adults [Ab] = number of adults [relative abundance]; SR = ratio between the number of males and females caught; Imm. [Ab] = number of immatures [relative abundance]; Lar. [Ab] = number of larvae [relative abundance].

Date	Altitude	Locality	TºC	Adults [Ab]	SR	Imm. [Ab]	Lar. [Ab]
March 26, 2011	234 m	Palilula	-	11 [0.098]	2.67:1	-	-
March 26, 2011	273 m	Stubel	-	5 [0.027]	1.50:1	-	-
March 27, 2021	234 m	Palilula	-	53 [0.303]	1.52:1	-	-
March 31, 2021	240 m	Deleyna	8.5	26 [0.218]	1.17:1	-	-
March 31, 2021	230 m	Kalenik	13.3	52 [0.437]	2.06:1	-	-
April 1, 2021	201 m	Tolovitsa	9.8	1 [0.008]	n/a	-	-
April 2, 2012	234 m	Palilula	11.7	6 [n/a]	n/a	-	-
April 2, 2012	273 m	Stubel	12.5	1 [n/a]	n/a	-	-
April 4, 2012	77 m	Gromshin	13.6	2 [0.006]	n/a	-	-
April 8, 2020	234 m	Palilula	-	19 [0.165]	3.75:1	-	-
April 11, 2012	1015 m	Ledenika	10.6	152 [0.306]	0.65:1	-	-
April 12, 2012	1380 m	Ochindol (3.7 km N)	2.7	8 [0.024]	1.00:1	-	-
April 12, 2012	1370 m	Ochindol (3.8 km N)	5.4	5 [0.014]	4.00:1	-	-
April 12, 2012	1360 m	Parshevitsa	5.4	23 [0.066]	0.28:1	-	-
April 13, 2021	102 m	Reselets	15.4	12 [0.073]	1.40:1	-	-
April 14, 2021	210 m	Borovan	12.2	13 [0.151]	12.00:1	1 [0.012]	-
April 14, 2021	40 m	Kriva Bara	12.5	1 [0.004]	n/a	-	-
April 18, 2020	234 m	Palilula	-	18 [0.143]	3.50:1	1 [0.008]	-
April 27, 2021	1015 m	Ledenika	15.9	39 [1.147]	0.77:1	-	-
April 28, 2021	370 m	Krapets (NW)	15.4	16 [0.103]	4.33:1	-	-
April 28, 2021	390 m	Krapets (W)	16.4	8 [0.074]	1.67:1	-	-
April 30, 2013	234 m	Palilula	-	1 [0.010]	n/a	-	-
May 1, 2013	234 m	Palilula	-	1 [0.013]	n/a	-	-
May 4, 2014	273 m	Stubel	-	3 [0.015]	n/a	-	-
May 7, 2021	290 m	Gara Oreshets (NW)	19.7	13 [0.084]	5.50:1	-	-
May 22, 2009	150 m	Montana	-	4 [n/a]	1.00:1	-	4 [n/a]
May 27, 2021	110 m	Erden	24.9	-	-	-	12 [0.071]
May 28, 2021	210 m	Slavotin (N)	21.5	2 [0.009]	1.00:1	-	-
May 28, 2021	220 m	Slavotin (SE)	23.5	-	-	-	5 [0.038]
June 17, 2021	580 m	Tipchenitsa	24.6	13 [0.111]	1.60:1	-	1 [0.009]
July 4, 2009	273 m	Stubel	-	-	-	5 [0.028]	-
July 6, 2008	234 m	Palilula	-	-	-	-	19 [0.365]
July 6, 2008	273 m	Stubel	-	3 [0.021]	n/a	1 [0.007]	30 [0.207]
July 6, 2019	1370 m	Ochindol (3.8 km N)	-	9 [0.083]	0.29:1	-	-
July 6, 2019	1360 m	Parshevitsa	-	19 [0.176]	0.27:1	-	-
July 9, 2012	1015 m	Ledenika	-	25 [n/a]	0.92:1	-	-
July 9, 2012	1380 m	Ochindol (3.7 km N)	22.6	10 [n/a]	0.67:1	-	-
July 9, 2012	1360 m	Parshevitsa	24.3	21 [n/a]	0.91:1	-	-
August 4, 2012	1380 m	Ochindol (3.7 km N)	20.4	26 [n/a]	0.73:1	-	1 [n/a]
August 4, 2012	1370 m	Ochindol (3.8 km N)	22.2	30 [n/a]	0.67:1	-	197 [n/a]
August 5, 2012	1380 m	Ochindol (3.7 km N)	18.3	12 [n/a]	0.50:1	-	-
August 5, 2012	1370 m	Ochindol (3.8 km N)	19.5	19 [n/a]	1.11:1	-	221 [n/a]
August 5, 2012	1360 m	Parshevitsa	19.7	22 [n/a]	0.57:1	-	118 [n/a]
August 5, 2018	1380 m	Ochindol (3.7 km N)	-	2 [0.018]	n/a	1 [0.009]	-
August 6, 2012	1380 m	Ochindol (3.7 km N)	-	20 [n/a]	0.54:1	-	1 [n/a]
August 6, 2012	1370 m	Ochindol (3.8 km N)	18.9	13 [n/a]	0.63:1	-	253 [n/a]

Appendix 2. Continuation.

August 6, 2012	1360 m	Parshevitsa	21.0	21 [n/a]	0.62:1	-	105 [n/a]
August 15, 2009	1380 m	Ochindol (3.7 km N)	-	38 [0.292]	0.58:1	1 [0.008]	15 [0.115]
August 15, 2009	1370 m	Ochindol (3.8 km N)	-	6 [0.043]	1.00:1	-	150 [1.071]
August 15, 2009	1360 m	Parshevitsa	-	21 [0.093]	0.75:1	-	10 [0.044]
October 6, 2011	1380 m	Ochindol (3.7 km N)	-	1 [0.004]	n/a	-	2 [0.008]
October 6, 2011	1370 m	Ochindol (3.8 km N)	-	11 [0.042]	0.83:1	21 [0.080]	1 [0.004]
October 6, 2011	1360 m	Parshevitsa	-	14 [0.050]	1.80:1	-	-
October 22, 2014	234 m	Palilula	-	16 [0.067]	0.78:1	-	-
October 22, 2014	273 m	Stubel	-	6 [0.021]	5.00:1	-	-
November 4, 2021	230 m	Kalenik	13.1	6 [0.032]	1.00:1	-	-
November 5, 2021	290 m	Gara Oreshets (NE)	13.1	-	-	-	2 [0.006]