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The 'waterfall spectacle' of *Libellula quadrimaculata*-aggregations (Odonata: Libellulidae)

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Abstract. A hitherto unknown swarming flight behaviour of *Libellula quadrimaculata* that included spectacular waterfall-like manoeuvres was observed and photographically documented in May and June 2015 in the steppes of the Kazakh Uplands. This unusual flight behaviour was connected to communal roosting aggregation. It is analysed and compared with common hypotheses and literature on communal roosting and swarm dynamics in Odonata and other animals.

Further key words. Dragonfly, Anisoptera, Korgalzhyn State Nature Reserve, Kazakhstan, Central Asia, mass occurrence, selfish herd theory

Introduction

The holarctic dragonfly *Libellula quadrimaculata* Linnaeaus, 1758 is known as a facultative migratory species *sensu* Corbet (1999: 418) within its Palaearctic range – however amazingly not in the Nearctic (cf. May 2013) – and is renowned for its spectacular periodic swarming migrations (e.g., Hagen 1861; Cornelius 1865: 270; Blasius 1883; Kolosov 1915; Bartenev 1919; Kiauta 1964; Burton 1996; Corbet 1999: 418). Reports in old chronicles on migrating swarms and related mass occurrences of dragonflies in which most probably *L. quadrimaculata* was involved go back to the late Middle Ages (Köppen 1871; Kuwert 1873). Such mass migrations occur in varying densities at more or less regular intervals with a mean period of ten years (Dumont & Hinnekint 1973; Haritonov & Popova 2011). Migrating *L. quadrimaculata* sometimes reach epic masses, estimated to comprise millions or even billions of individuals (Cornelius 1862). Due to the general complexity of the phenomenon of mass migration in Odonata and the methodological difficulties involved in properly recording and documenting such large-scale events, it seems unsurprising that the majority of articles dealing with this behaviour of *L. quadrimaculata* are anecdotal (Schröter 2011: 215). Thus only few recent publications provide well-founded data, allowing a detailed analysis and discussion of the causal background of geographical, climatic, ecological, and physiological interrelations associated with the phenomenon. More detailed descriptions of mass migration of this species in Central Europe as well as in the West-Siberian Plain are provided by Dumont & Hinnekint (1973), Burton (1996), and Haritonov & Popova (2011), respectively, the latter including long term data of population dynamics of the species.

Libellula quadrimaculata migrates during the day and roosts nocturnally in dense aggregations. Communal roosting is therefore a particularly remarkable partial aspect of migration in this species (Hagen 1861: 151; Kuwert 1873; Dumont & Hinnekint 1973). It appears notable, however, that none of the articles mentioned above, including the more recent ones, provide any photographic evidence. Hitherto neither migrating swarms nor mass gatherings of *L. quadrimaculata* have been filmed or photographically documented. Here we report on the swarming flight behaviour at a communal roosting site in the Kazakh steppe including spectacular internal-swarm waterfall-like flight manoeuvres that were filmed and photographically documented for the fist time.

Study area and methods

Data were collected from 30-v- till 14-vi-2015 at the Korgalzhyn State Nature Reserve, Aqmola district, in north central Kazakhstan by MK, partly with help from A. Koshkin.

The Korgalzhyn State Nature Reserve, a Ramsar wetland of international importance, is well known especially for the large shallow saline Lake Tengiz and together with the Naurzum Nature reserve in 2008 became the first Kazakh UNESCO World heritage site. The area is situated in the transition zone of dry steppes and semi-deserts of the Kazakh Uplands and has a harsh continental climate. The mean annual precipitation amounts to less than 300 mm, the winters are very cold with mean annual temperature in January of -17°C and summers hot with mean annual temperature in July of +21°C, incl. strong diurnal fluctuations (Berg 1952; Franz 1973; Lydolph 1977; Gusev & Chimshidova 1990).

Observations were made in the proximity to Karazhar field station (50°28’28.41”N, 69°32’33.46”E, 310 m a.s.l.) which was located on a peninsula between two large freshwater lakes, Sultankeldy and Esej (Fig. 1). The field station was surrounded by *Artemisia*-steppe with many different grass species and weeds. During the observation period the weather was generally hot by day (maximum temperature 35°C), with moderately strong winds in the afternoons and two thunderstorms. Details of the records, particularly the timing of the events, were either noted immediately after the observations or obtained from data on multiple photographs and video films taken during these two weeks. The number of individuals was estimated by analysis of photographs using a dot counting software (DotCount v1.2. Copyright: 2006–2015 Martin Reuter).

Results

The ‘waterfall spectacle’ was observed on 13-vi-2015 around sunset between 21:00 and 21:30 h QYZT (UTC + 6 h). That evening, the air was absolutely still and the sky was clear. Approximately 30 to 40 minutes before sunset, the dragonflies, previously distributed across large areas, started to congregate in swarms above potential night roosts such as tall shrubs, buildings, and reed vegetation, as they had done previously on calm evenings (Fig. 2).

Figure 1. Aerial view of the study site with Karazhar field station. Korgalzhyn State Nature Reserve, Aqmola district, Kazakhstan. Light blue colour indicates open fresh water and dark green shallow lakes and pools surrounded by reed beds. Salt lakes appear white and steppe vegetation is brown. Image copyright: 2016 DigitalGlobe/2016 Google

Figure 2. Detail view of a swarm of *Libellula quadrimaculata*. Korgalzhyn State Nature Reserve, Aqmola district, Kazakhstan (13-vi-2015). Photo: MK

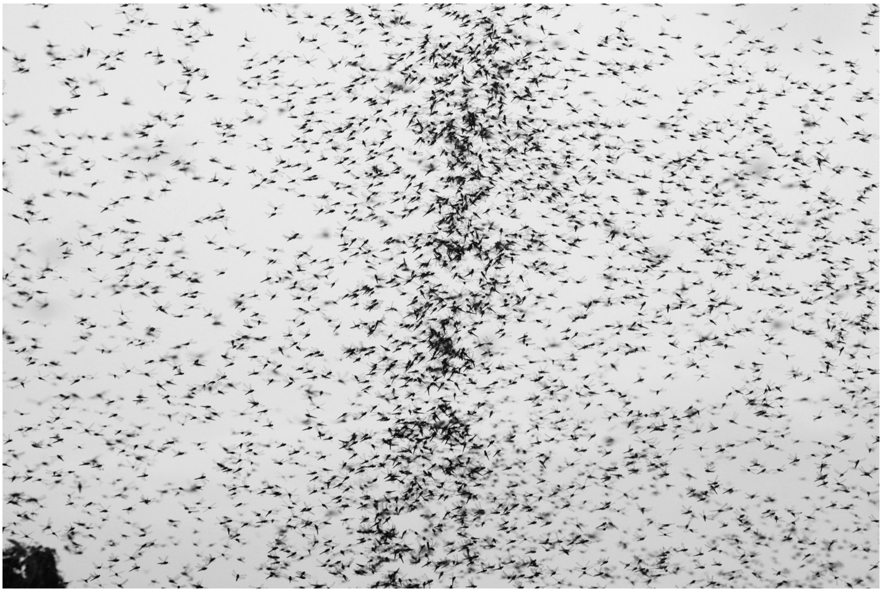

Figure 3. The 'waterfall spectacle', a specific flight manoeuvre performed by a swarm of *Libellula quadrimaculata* giving the impression of falling water. Korgalzhyn State Nature Reserve, Aqmola district, Kazakhstan (13-vi-2015). Photo: MK

However, in this instance the dragonflies in each of these swarms started to form dense columns three to five metres high above the ground, each consisting of 1 000–2 000 individuals. Then some of the uppermost individuals in each column started to drop down, taking along some of the ones below them. At the same time other individuals which previously remained hovering within or outside the column immediately replaced them, giving the swarm a fluidity that conveyed an impression of falling water (Fig. 3; see also video sequence by Koshkin 2015). Some individuals interrupted their plunge before they hit the vegetation, whereas others actually fell into shrubs or grass, resuming their flight seconds later. This spectacle continued for 20–30 minutes, accompanied by a loud noise of whirring wings of the dragonflies bumping into each other or caught in the vegetation. The same spectacle was previously noticed in the area by A. Koshkin (pers. comm.) four days before the event described here took place. Despite an annual mass emergence of *Libellula quadrimaculata* in the region, particularly in the proximity to Karazhar field station where some of the reserve’s staff are based annually throughout spring and summer, to the best of our knowledge, there are no previous records of such behaviour of this or any other species of dragonflies in the region.

On days with no or only moderate wind, the dragonflies were mainly on the wing, hunting in steppe during mornings and evenings, and perching on vegetation during the hottest part of the day. However, on days with a strong northerly wind they were seen moving with the wind. During thunderstorms they sought shelter in the vegetation. In the evenings the dragonflies congregated at night roosts, i.e., in shrubs, on buildings or in reeds (Fig. 4).

The number of dragonflies on one of the photo documents was estimated at a minimum of 2 560 individuals captured within single field of view of a 300 mm photo lens. Considering that dragonflies around the observer when the photo was taken were at a similar density and also evidence from other photos taken from the same spot, we extrapolated this number across the suitable area around Karazhar but excluding reed beds and open water. This resulted in an estimate of a minimum of 32 500 individuals within a 300 m zone around the field station (*ca* 0.002 km^2) at any time, or a minimum of 16 250 000 individuals per 1 km^2.

Figure 4. Aggregations of *Libellula quadrimaculata* at communal roosting sites. Korgalzhyn State Nature Reserve, Aqmola district, Kazakhstan (13-vi-2015). Photo: MK

Discussion

The mechanism and the adaptive value of the 'waterfall spectacle' in the context of swarm behaviour appear puzzling. To our current knowledge it can neither be explained by nor brought in accordance to any general hypothesis on collective animal behaviour (e.g., Emlen 1952; Brodie 1976; Pomeroy & Heppner 1992; Gueron et al. 1996; Beauchamp 1999; Bouffanais 2016). For a further understanding of causality and as an attempt to approach to this remarkable behaviour it appears reasonable to compare this phenomenon with case studies on other Odonata species that exhibit mass aggregations.

On the occasion of a mass emergence with subsequent migration of *Aeshna affinis* Vander Linden, 1820 in Kyrgyzstan, a neighbouring country in the south of Kazakhstan, Schröter (2011: 210) observed thousands of densely flying individuals, forming a compact bubble with »disctinctly jerking and dancing flight style, with a minimum space kept between individuals«. This behaviour of forming several extremely crowded nuclei within the bubble in principle showed certain similarities with the flight modus exhibited in the 'waterfall spectacle' but lacked the striking conveyer-belt-like downward flow of the 'waterfall'. The same applies to brief situations when different swarms collided and the internal organisation of them temporarily collapsed (Schröter 2011: 211). It is therefore possible that the 'waterfall spectacle' represents a kind of temporal system-crash within the self-organisation of the swarm with respect to the parameters of individual separation, cohesion, and alignment (Reynolds 1987).

Even though swarms of *L. quadrimaculata* were highly mobile in the study area and were regularly seen moving in one direction suggesting migration, we have no clear evidence that the swarms really left the area, exhibiting true target-orientated large-scale migration.

Libellula quadrimaculata is very common in the area and exhibits mass emergence regularly (Kazenas & Baizhanov 2009; MK unpubl.). According to long-term observations at Lake Chany, Novosibirsk district, Russia, the numbers of this species experience strong annual fluctuations in response to local water cycles, with numbers peaking one to two years after the lakes had reached their maximum level (Haritonov & Popova 2011). This shallow lake with brackish water and extensive reed beds is located in the forest-steppe region of southern Russia, very close to the border to Kazakhstan and is likely to provide similar conditions for breeding *L. quadrimaculata*. Thus, abundances and mass aggregations as recorded here could be considered normal for the steppe region of Korgalzhyn State Nature Reserve. *Libellula quadrimaculata* is a typical spring species *sensu* Corbet (1999: 245) whose larvae overwinter in the final stadium and exhibit synchronised emergence in early spring (Maier & Wildermuth 1992; Wildermuth 1994). Regarding mass emergence of this species several authors emphasised the relationship between the synchronous mass emergence in *L. quadrimaculata* and a pronounced cold–hot sequence of weather conditions during May (Fraenkel 1932; Dumont & Hinnekint 1973). Such a temperature regime is typical for spring in regions with strong continental climate as occurs in the vast Eurasian steppe belt. In spring the temperature of the predominantly shallow and structurally monotonic water bodies of these areas rises rapidly resulting in considerably synchronised emergence even of typical summer species with a prolonged emergence period elsewhere such as, e.g., *Aeshna* species (Peters 1985; Dyatlova & Kalkman 2008). It has therefore been assumed that the tendency to highly synchronised emergence might be generalized to Odonata in areas with pronounced continental climate with a sudden transition between cold winter and warm spring (Schröter 2011: 226). Moreover, Dumont & Hinnekint (1973) pointed out that the probability of incidents such as swarming migration and other mass occurrences being witnessed most probably correlates with human population density. The human population density of Kazakhstan and adjacent Central Asian countries is amongst the lowest in the world with an accordingly low number of odonatologists (cf. Schröter & Borisov 2012: 273 f.). Considering this there is a striking number of detailed studies of swarming in Odonata carried out in Central Asia (Peters 1985; Schröter 2011; Haritonov & Popova 2011; this study) and similar cases of documented mass roostings in continental Eastern Europe, e.g., Dyatlova & Kalkman (2008); this suggests that such observations are not coincidental but rather reflect a genuine correlation between climatic conditions and mass occurrences resulting from highly synchronised emergence.

The flight activities and aggregations of *L. quadrimaculata* observed around Karazhar field station can be classified as flight 'type 2' *sensu* Cor-

BET (1999: 383 ff). within the functional typology of spatial displacement in Odonata. This flight type covers commuting intrahabitat movements, i.e., daily activities between roosting sites and foraging or reproduction sites (cf. SCHRÖTER 2011: 219). However, migration (flight type 4) of these swarms cannot be excluded and could occur later in the season.

The swarming behaviour in dragonflies is basically analogous to that of other animal aggregations such as fish or birds. An often discussed functional aspect of swarming is the anti-predatory effect as ‘predator confusion’ (MILINSKI & HELLER 1978), the ‘encounter dilution’ in the sense of the ‘selfish herd theory’ (cf. HAMILTON 1971; WATERHEAD 1983). Analysis of communal roosting behaviour in dragonflies (MILLER 1989; SWITZER & GRETHER 2000), as well as group oviposition (MARTENS 1989; 1996: 97), support this anti-predatory hypothesis also for dragonfly gatherings. This effect might be interrelated with true social aggregative behaviour i.e., individuals prefer to perch as close as possible to conspecifics due to ‘spaced-out gregariousness’ (cf. KRAUSE et al. 1992; see also GRASSÉ 1932). This suggests that the ‘waterfall spectacle’ may also be a by-product of the anti-predatory functional level of aggregating behaviour of Odonata. However, it appears puzzling that the ‘waterfall spectacle’ has obviously not regularly been seen over the years and was not recorded every evening during the period of observation of roosting aggregations. If it would have an anti-predatory function one would rather expect obligate performance.

As to mass communal roosting and mass migration further studies applying modern experimental methods on *L. quadrimaculata* or other odonate species may provide further insight into this phenomenon. The central and eastern parts of the Eurasian steppe belt seem to be ideal as study areas, not only for climatic reasons. Central Europe nowadays no longer has the potential for exceptionally strong mass abundances of *L. quadrimaculata*. The majority of records of mass occurrences of this species are historical (RICHTER 1863; CORNELIUS 1862; FRAENKEL 1932), dating back to times before the systematic destruction of the larval habitats of the species, i.e., drainage and large-scale conversion of marshes, alluvial areas and shallow lakes during 19th and 20th century. It is therefore hoped that in the future at least in the vastness of Central Asia *L. quadrimaculata* will continue to find a stage to perform its enigmactic ‘waterfall spectacle’.

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