

Adaptation of the subimaginal life span of *Cloeon* (Ephemeroptera, Baetidae) in the arid areas of North Africa and the Canary Islands

TOMÁŠ SOLDÁN

Institute of Entomology, Czechoslovak Academy of Sciences,
Branišovská 31, 370 05 České Budějovice, Czechoslovakia

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Abstract. Substantial shortening of subimaginal life span occurs in *Cloeon saharense*, *C. cognatum* and *C. dipterum* populations living in arid areas of the North African Sahara. Subimagoes emerge immediately after sunset and this stage lasts only 8—10 hours until dawn, compared with 24 hrs in *C. cognatum* and *C. dipterum* populations in temperate humid areas. Adults mate only early in the morning. Although it resembles shortened emergence and swarming patterns of unspecialized (long-lived) genera in the tropics this phenomenon is considered as an adaptation to avoid extremely high day-time temperatures (30—40 °C) and low humidity (less than 10 % r.h.) in which subimagoes cannot survive. Shifting of the subimaginal stage to night-time period also minimizes exposure time to predators.

The subimaginal stage of the Ephemeroptera, an unique phenomenon within the recent insects, is mostly considered as a retained ancestral condition (HINTON, 1963; SCHAEFFER, 1975; KUKALOVA-PECK, 1978; SOLDÁN, 1981 and others). Apart from its evidently very important evolutionary significance (see MAIORANA, 1979) there are several presumably adaptive functions of this peculiar stage in the mayfly's life cycle. These are e.g. protection of pharate imago during emergence (hydrofuge surface), synchronization of mating flight, minimization of exposure time to predators, possibility of water loss before mating flight, etc. Moreover, in some species, at least in those with long-lived subimagoes, also gametogenesis is completed (SOLDÁN, 1981). The present short note describes substantial shortening of the subimaginal stage observed in some *Cloeon* species living in arid desert areas.

The observations and field experiments were conducted at the following localities in the Canary Islands and in North Africa (see Fig. 1): (1) reservoirs near Villafior, Tenerife, Canary Islands (Spain) and further localities of the island of Tenerife — see ALBA-TERCEDOR et al. (1986); (2) Oued Droh, Droh oasis; (3) Oued El Ham, Shott El Hodna; (4) reservoirs and pools in Touggourt; (5) pools (gueltas) in the Ahaggar Mts. (Algeria) — for further localities in Algeria see SOLDÁN & THOMAS (1983); (6) Bahr sur Seir, (eastern) El Qanatir el Qahiriya; (7) pools and reservoirs in Bawiti, Bahariya Oasis; (8) pools at Uyün Musa (Spring of Moses), Sinai (Egypt).

Subimagoes of *Cloeon dipterum* start to emerge from about one hour before sunset and their emergence is completely finished in 0.5—1 hour after sunset at the dry zone localities of the Canary Islands. There is almost no emergence in the afternoon and absolutely no subimagoes emerge in the evening. Subimagoes start to moult to adults about 1.5—1 hour before sunrise. Moulting to adults is completely finished during sunrise, mating flight follows immediately. Both males and females disappear (males dying, females resting in the vegetation) during at most 1—1.5 hour after sunrise (till 08.30 a.m. in July). Later or even afternoon (the Islands of Tenerife and Gran Canaria) mating flight occurs mostly only in the humid zone (cf. BRINCK & SHERER, 1961; MÜLLER-LIEBENAU, 1971) and seems to be independent on the weather.

Subimagoes of *Cloeon cognatum* at the localities of the humid and subarid zones in Algeria start to emerge shortly before sunset, imaginal moulting and mating flight are realized at the approximately the same time as those of *C. dipterum* on the Canary Islands.

Subimagoes of *C. cognatum* at the localities of the arid zone of Algeria, subimagoes of *C. saharensis* (localities No. 2–5) and those of *C. cognatum* in Egypt (localities No. 6–8) never emerged before sunset. They start to emerge at dusk, most of them emerge when it is completely dark (from 06.30–08.00 p.m. in September and October). The subimaginal stage of these populations lasts 8–10 hours maximally. Subimagoes moult to adults mostly at dawn before sunrise (from 04.30–06.30 a.m. in September and November) and start mating flight immediately. Mating flight is finished shortly (in at most 30 minutes) after sunrise. Female subimagoes seem to moult to adults a little earlier (0.5–1 hour) than those of males.

Field and laboratory experiments showed that the “switching on” mechanism of desert aquatic biotopes populations of the above species is starting dark night period and slight decrease of water temperature (1–3 °C). The larvae of *C. cognatum* from these biotopes usually die or emerge to

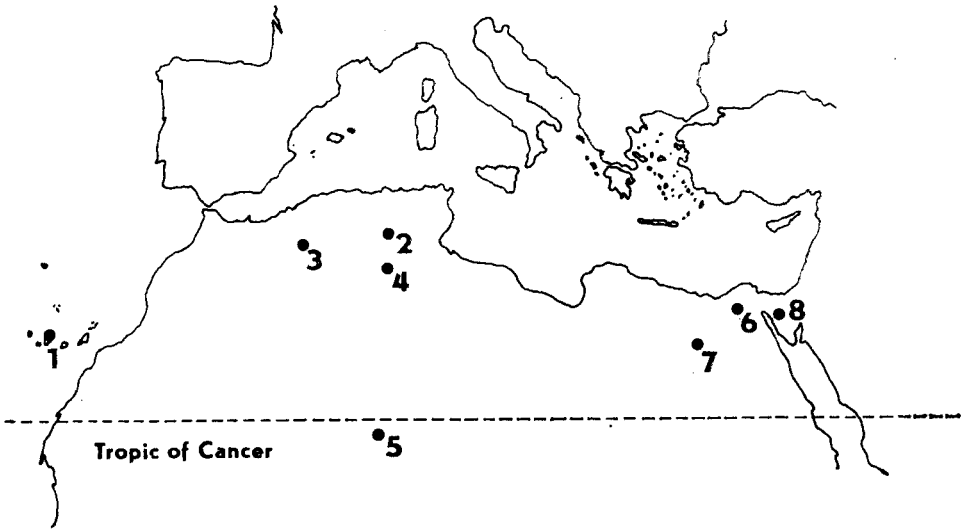


Fig. 1: Localities of occurrence of *Cloeon* subimagoes with substantially shortened subimaginal stage studied in the Sahara and Canary Islands (for names of localities see text).

subimagoes only exceptionally at the permanent light and constant water temperatures of 25°, 27° and 30 °C, respectively. The emergence of subimagoes is also lower (about 60–80 % of controls) at the conditions of alternating light-dark period but constant temperature. The subimagoes of *C. cognatum* never emerge during day in the Algerian Sahara and in Egypt. If forced to emerge under the laboratory conditions and then released in the field they die in about 15–30 min. On the other hand, the females of the ovoviviparous species *C. dipterum* (Canary Islands) and *C. cognatum* (Algeria, Egypt) can survive for at least several days at places with sufficient humidity. If unmated they are able to survive for 10–12 days in the laboratory. Females of probably oviparous *Cloeon saharensis* and males of all these species die immediately after mating flight and/or oviposition.

Although it is generally well known that populations of the same species at different latitudes show different moulting and mating flight patterns (see EDMUNDS et al., 1976 for some Nearctic species, and EDMUNDS & EDMUNDS, 1980 for mayflies in tropics) the relative length of subimaginal stage of the same species has not been studied so far in detail. As it is apparent from the above example of *Cloeon* species this question is worth of our attention.

While *C. saharensis* is probably endemic to arid areas, the two species *C. dipterum* and *C. cognatum* belong to the widespread West Palaearctic species occurring nearly all over the European continent. Their European populations show “normal” emergence pattern - subimagoes emerge nearly all day long with maximum emergence rate in early or late afternoon. Subimaginal stage lasts usually 16–18 hours, sometimes as long as 24 hrs. Shortening of this stage by at least half and its shifting to night hours in arid area populations of these species undoubtedly represent an ecological adaptation to extreme “desert” conditions, showing an unexpected plasticity of this

particular stage in mayflies. This adaptation tends to avoid unfavourable temperatures and humidity of these localities since mayfly subimagos are known to be very sensitive to these factors. Mayfly subimagos can survive and successfully moult to adult only at humidity of 60–90 % r.h. and can tolerate more easily relatively lower temperatures (preferably up to 20–25 °C). In arid and desert areas studied in Algeria and Egypt and to a certain extent also in arid (not exposed to precipitations) areas of the Canary Islands, daily temperatures usually reach 30–40 °C or more and the humidity is only 30–40 % r.h. or even down to 10 % r.h. (e.g. in the Ahaggar Mts. in Algeria). Such severe conditions cannot be tolerated by any mayfly subimago. On the other hand, much more favourable conditions at night (temperatures lower by 10 °C or even more and much higher humidity reaching at least up to 75 % r.h. near the water surface) are quite sufficient for subimaginal moulting. Although this adaptation is not so pronounced in *C. dipterum* on the Canary Islands mating flight of *C. cognatum* and *C. saharense* is realized during changing temperature (increase) and humidity (decrease) period round sunrise. Also the minimizing of predatory pressure of natural enemies with day activity (mostly dragonflies and insectivore birds) can be taken into account (SCHAEFER, 1975). Considerable shortening of the subimaginal stage enables to synchronize more effectively the moulting of imagoes immediately before mating flight. Although occurring in the Palaearctic region these features resemble, in some respect, the subimaginal stage life span of unspecialized (long-lived) mayfly genera in the tropics (EDMUNDS & EDMUNDS, 1980). However, contrary to most of these genera the subimagos of which moult late in the morning (08.00–12.00 a.m.), *Cloeon* subimagos moult much earlier. The emergence and moulting patterns of *Cloeon* species is comparable to that of some species of the lowland tropics where nights are relatively warm and most subimagos emerge during the first 1.5 hours of darkness and transform to the imaginal stage before 03.00 hr the next morning (EDMUNDS & EDMUNDS, 1980).

The above adaptation enables these three species of *Cloeon* (and probably applies to other species of *Cloeon* in arid areas of other biogeographic regions) to colonize extreme desert aquatic biotopes such as "gueltas" in the Ahaggar Mts. "foggaras" (desert wells) or "seguias" — temporary irrigation pools of date palm cultures in some oases in the Sahara (cf. SOLDÁN & THOMAS, 1983). This adaptation of subimaginal life span is, together with a relatively high tolerancy of larvae to lower oxygen content and slight salinity, responsible for apparent colonization success of *Cloeon* species in desert aquatic biotopes.

It also documents that temperate species of *Cloeon* (*C. dipterum*, *C. cognatum*) in dry subtropics have shifted to tropic behaviour. This phenomenon is noted for the first time. "Behavioral shifts" to temperate emergence and swarming habits were described in some tropical genera found in temperate regions (e.g. in *Dactylobaetis*, originally a Neotropical genus with extension to Idaho — EDMUNDS & EDMUNDS, 1980). On the other hand some other tropical genera (e.g. *Tricorythodes* and *Traverella*) retained their basically tropical emergence and swarming habits also in the areas of extension of their tropical distribution (EDMUNDS, 1948; HALL et al., 1975).

REFERENCES

- ALBA-TERCEDOR F. J., BÁEZ M. & SOLDÁN T. 1987: Nuevas citas de Efemerópteros de las Islas Canarias. *Eos, Madr.*, **62** (in press).
- BRINCK P. & SCHERER E. 1961: On the Ephemeroptera of the Azores and Madeira. *Bolm. Mus. Municip. Funchal*, **47** : 55–66.
- EDMUNDS G. F. 1948: A new genus of mayflies from western North America (Leptophlebiidae). *Proc. biol. Soc. Wash.*, **61** : 141–148.
- EDMUNDS G. F. & EDMUNDS CH. H. 1980: Predation, climate, and emergence and mating of mayflies. In: Flannagan J. F. & Marschal K. E. (eds): *Advances in Ephemeroptera biology*. Pp. 277–285, Plenum Press, New York, London.
- EDMUNDS G. F., JENSEN S. L. & BERNER L. 1976: *The mayflies of North and Central America*. x + 330 pp., Univ. Minnesota Press, Minneapolis.
- HALL R. J., BERNER L. & COOK E. F. 1975: Observations on the biology of *Tricorythodes atratus* Mc Dunnough (Ephemeroptera: Tricorythidae). *Proc. ent. Soc. Wash.*, **77**, : 34–49.
- HINTON H. E. 1963: The origin and function of the pupal stage. *Proc. ent. Soc. London*, **33** : 77–85.
- KUKALOVA-PECK J. 1978: Origin and evolution of insect wings and their relation to metamorphosis, as documented by the fossil records. *J. Morphol.*, **156** : 53–126.
- MATORANA V. C. 1979: Why do adult insects not moult? *J. Linn. Soc.*, **11** : 253–258.
- MÜLLER-LIEBENAU I., 1971: Ephemeroptera (Insecta) von den Kanarischen Inseln. *Gewäss. Abwäss.*, **50/51** : 7–40.
- SCHAEFER C. W. 1975: The mayfly subimago: a possible explanation. *Ann. ent. Soc. Am.*, **68** : 183.
- SOLDÁN T. 1981: Secondary sexual characters in mayfly larvae and their evolutionary significance (Ephemeroptera). *Acta ent. bohemoslov.*, **78** : 140–142.

SOLDÁN T. & THOMAS A. G. B. 1983: New and little-known species of mayflies (Ephemeroptera) from Algeria. *Acta ent. bohemoslov.*, **80** : 356—376.

Адаптация продолжительности субимагинальной жизни у видов *Cloeon* (Ephemeroptera, Baetidae) в аридных областях Северной Африки и Канарских островов

Вылет, брачный полет, пустыня, влажность, температура, адаптации к среде

Резюме. У популяций *Cloeon saharense*, *C. cognatum* и *C. dipterum*, живущих в аридных областях Северной Африки, было установлено значительное сокращение субимагинальной жизни. Субимаго вылетают непосредственно после захода солнца и эта стадия длится 8—10 часов до рассвета, в сравнении с 24 часами у популяций *C. cognatum* и *C. dipterum* в областях с умеренным и влажным климатом. Взрослые насекомые спариваются только рано утром. Хотя указанное сокращение периода вылета и роения похоже на таковое у неспециализированных (долгоживущих) тропических родов, в данном случае это явление рассматривается как адаптация позволяющая извечать чрезвычайно высокие температуры (30—40 °C) в течение дня и низкую относительную влажность воздуха (ниже 10%), в которой субимаго не выживает. Перенесение субимагинальной стадии в ночной период также снижает на минимум уязвимость со стороны predators.

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REVIEW

Fritz A. Popp: *BIOLOGIE DES LICHTS* (Grundlagen der ultraschwachen Zellstrahlung). 160 pp., 34 figs., 2 tables. Verlag Paul Parey, Berlin und Hamburg, 1984. Price DM 46.

The subject of the book is interaction between light and biological objects. Various kinds of radiation of a variable character and intensity have been affecting biological objects throughout their evolution on Earth. Some of the evolutionary theories take this fact into account, presuming that radiation may be one of the factors affecting the evolution of organisms. Some biophysicists have therefore focused their attention on the physical manifestations of living matter and possible interactions with physical fields. Many items of information bearing on these questions can be found in literature.

F. Popp has analysed the question of possible interaction between living tissues and light quanta (photons). Data in the literature and his own experimental findings are correlated with each other as well as with certain other (e.g. biochemical) processes. The book is divided into 17 chapters. Some hypotheses

of evolution and some biochemical and biophysical processes are discussed in the first three chapters. Radiation of light by cells, verified by the author, is discussed in the following chapters along with the possibility of explaining some processes by means of absorption of light quanta. The possibilities of generation and absorption of coherent radiation are examined. F. Popp suggests that this radiation may be the result of physiological processes, but he also considers the possibility of its being a kind of means of communication involved in the regulation of cell development. Development could then be explained as the result of a joint action of coherent and incoherent radiations, as progression toward a new balance between "order" and "chaos". There are references to 265 papers by 238 authors, and author and subject indexes.

The book offers an interesting view of some of the modern lines of research in biophysics. However, in some cases the author bases his conclusions on theories that have not yet been verified, and occasionally puts forward hypotheses which are not founded on firm experiments.

V. Brunnhofer