

THE EXPANSION OF *CROCOTHEMIS ERYTHRAEA* (BRULLÉ, 1832) IN GERMANY – AN INDICATOR OF CLIMATIC CHANGES¹

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(Dedication : Prof. B. Kiauta, whom I had promised a paper on Crocthemis for a long time, on his 70th birthday)

ABSTRACT

In this paper a detailed account of the northward expansion of *Crocothemis erythraea* in Germany is presented. While only a few decades ago the species was rare even in southern Germany, it is now found in nearly every federal state, in most of them autochthonous. The species conquered Germany from south to north, parallel to climatic changes in the country; similar expansions of this species are registered also in other European countries, as well as northward expansions of other southern species. The main reason for this range expansion are climatic changes, some consequences of which are discussed.

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INTRODUCTION

The Scarlet Darter (*Crocothemis erythraea*) (Brullé, 1832) (see Fig. 1) is called in German "Feuerlibelle", meaning "fire dragonfly" because of the intensive red colour of the male's body and the upper parts of the eyes (the female is olive green or brownish). The scientific species name "erythraea" also refers to the red colour (Greek "erythros" means red, see Fliedner, 1997). The range of this Orthetrum-sized libellulid covers the mediterranean (Brullé described specimens from Greece) and the whole of Africa, from there stretching eastwards via Afghanistan to India (Tsuda, 1991). It belongs now to the German odonatofauna (Müller & Schorr, 2001).

In Germany it was discovered for the first time already in 1918 in the federal state of Brandenburg, near Berlin, Northern Germany, by Bollow (1919), but in the following decades it was registered only very rarely. According to Schiemenz (1953), during the first half of the last century the original area of this species was still restricted to Southern Europe, from where it flew only occasionally to Middle Europe (Belgium, Vienna, Munich, Baden), but it never established autochthonous populations there. Also Robert (1959) described its range in Europe in that time span as "Italy, Spain, Greece and southern France", from where it would fly "in hot summers" to southern Germany, Belgium, Hungary and Switzerland, but "only single specimens". Without doubt it is a mediterranean element, and as such it was classified by St. Quentin (1960).

Dumont (1967) still postulated that individuals observed in the north originated from big populations in the Camargue, Southern France, and had followed the rivers as guiding lines.

Consequently the species was generally regarded as a "wanderer" and classified as an "invading species" from the south: Jurzitza (1978) called her "Wanderlibelle" ("wandering dragonfly" or "travelling dragonfly") and in his book he showed a photograph of a male which had reached Karlsruhe in southern Germany in the hot summer of 1976. Lohmann (1980) in his "Odonate fauna list of the German Federal Republic" also spoke of an "invasive species" and "wandering species", to be met with in Germany only in climatically favoured regions with high water temperatures in summer, and he classified the species as a "Vermehrungsgast" (a "guest sometimes reproducing"), as already a very few populations were known then from Baden-Württemberg.

A few years later Dreyer (1986) and Bellmann (1987) still classified *Crocothemis erythraea* as a species belonging to the

Mediterranean, entering northern countries occasionally with warm air streams, but they also pointed out that the species was already autochthonous since several years in the climatically favoured Rhine valley of the southern German federal state of Baden-Württemberg.

In the following decades the species dramatically expanded its range northwards in Germany and also up to higher altitudes. This range expansion is analysed here in detail, being a model also for other European countries as well as other mediterranean species expanding their range to the north.

CROCOTHEMIS ERYTHRAEA IN GERMANY – AN ONGOING “SUCCESS-STORY”

BIOLOGY AND ECOLOGY OF THE SPECIES – A SHORT INTRODUCTION

The following description is based on Robert (1959), Ott (1988), Sternberg (1989), Schorr (1990), Burbach (1998) and Sternberg & Höppner (2000).

Crocothemis erythraea is a medium sized libellulid and because of its intensive red colour (males) very striking when present at a water body or nearby, where it perches on the ground or in the vegetation.

In general the species prefers habitats (standing waters, in the mediterranean also running waters) with open zones at the shoreline, like sand- and gravel pits, but it occurs also at lakes with reeds and emerse vegetation (where the males often fly fast and with some “hovering stops” over the *Nymphaea*- or *Potamogeton*-zones and return to the reed-banks for perching). In the south it is very abundant in rice fields. It has been regarded as a “lowland species”, but meanwhile it is found also at altitudes higher than 1600 meters a.s.l. in the Alps (Landmann, 1984) and even up to 2.000 meters a.s.l. in Spain (Anselin & Hoste 1996). In Germany it was found first of all at low altitudes only, but later on also higher up: in Bavaria it emerged even at a small garden pond (Bönisch in Burbach (1998) at an altitude of 550 meters a.s.l.. The species has a preference for clear water with good transparency (see Ott 1988), which may be the reason for its preference in northern Germany for *Leucorrhinia caudalis*-waters (Mauersberger, 2003). Fish are not problematic if there is enough water vegetation and if the number of carp (which cause turbidity and by this a reduction of submerse vegetation) and of grass carp (which reduce the submerged vegetation directly, thus increasing predation pressure by other fish upon dragonfly larvae) is not too high (Ott, 1993).

The males appear rather early in the morning at the water, a dependence on high temperatures could not be verified (Ott, 1988), but at hot temperatures the males tend to take up the so called "obelisk-position" (thermoregulation - or is it threat display ?). The males are aggressive against conspecific males and also against other species of similar size. Pairing – generally lasting only a few seconds during flight, with a tendency to finish it while seated – takes place mostly near the water, but was also observed in some cases away from the water. Males show a typical threat display behaviour against other *Crocothemis*-males, but a real territorial behaviour (as described by Falchetti & Utzeri, 1974 or Sternberg, 1989) is not the general behaviour - maybe only at low densities (different strategies ?). The female lays eggs guarded by its male, but sometimes alone (e.g. when the guarding male pursued another male and then lost its female).

By marking individuals in Germany a high site fidelity to the particular habitat (a gravel pit) was detected. After about 10 days of maturing, juveniles returned to the water where they had emerged. In the Camargue Aguesse (1959) also carried out marking experiments, but he could not register site fidelity in this wetland, so the type of biotope or the general density of the species in a habitat may have an influence. The minimum life span of *Crocothemis erythraea* is about 29-32 days (Ott, 1988).

The phenology in Germany lasts from May until September, with main activity from June to August, but pairing activity was occasionally observed even in September.

The larvae – oval and without dorsal spines – are found in standing water bodies of different sizes (always containing vegetation), even sometimes in brackish water, where they seem to prefer the shallow and warmer zones down to a depth of 50 cm; they are univoltine, but in the mediterranean and in warmer climates also bivoltine (Heidemann & Seidenbusch, 1993, Sternberg & Höppner, 2000). Exuviae are generally found close to the water in the vegetation.

CROCOTHEMIS ERYTHRAEA IN GERMANY: CONQUERING GERMANY IN A FEW DECADES

Here the continuous expansion of the species in Germany is documented, using 10-years time spans and referring to the German federal states (see Fig. 2).

FROM THE SEVENTIES OF THE LAST CENTURY TO PRESENT TIME

Before 1970

As mentioned above, *Crocothemis erythraea* was discovered already in 1918 in Brandenburg (Brodowin in the Mark Brandenburg, north-east of Berlin, Bollow 1919) and then near Konstanz by Rosenbohm (1922), in Bavaria in the Osterseen area in 1952 and 1954 (Burbach 1998), by Jurzitza (1963) near Karlsruhe in Baden-Württemberg, and then in Rhineland-Palatinate in 1967 (Friedrich et al., 1976). Always only single specimens were found, no autochthonous population was ever registered.

Between 1971 and 1979

In the seventies the species was again observed in Bavaria near Munich by Bilek (1978) and also again in Baden-Württemberg at several localities (Heidemann, 1977; Lohmann, 1980), as well as in Rhineland-Palatinate (Friedrich et al. 1976, Weitzel 1978). In this decade Heidemann (1977) for the first time in Germany reported reproduction of *C. erythraea* in Baden-Württemberg in several years (1974-76). Lohmann (1980), when reviewing the up to then existing literature from western Germany, mentioned only Heidemann's observations of indigenous populations; in eastern Germany (GDR, German Democratic Republic) the species was not found at all during this decade (Donath, 1984). A single specimen was registered in 1977 (Kikillus & Weitzel, 1981) near Cologne in Northrhine-Westfalia, this being the sixth federal state with a record.

Between 1980 and 1989

During the next decade the species expanded its range in southern Germany, mainly in the two southern federal states of Baden-Württemberg and Rhineland-Palatinate. According to Buchwald et al. (1984), the species had become autochthonous in Baden-Württemberg in "several waters and during several years in the Rhine valley". In Rhineland-Palatinate the number of sightings increased significantly (Niehuis 1984), and finally *C. erythraea* was found being autochthonous near Ludwigshafen for the first time for this federal state by Ott (1988), where it continued to reproduce from 1985 onwards (Ott 1990; unpubl. data). No data are available for Hessen, but without doubt the species was present also in this federal

state, for the same biotope types exist there at similar altitude as in Rhineland-Palatinate. In the Saarland the species was registered for the first time in 1986 (Röhlinger 1988) and became indigenous from 1990 onwards (Trockur & Didion, 1994). In Northrhine-Westfalia in 1989 another single male was noticed by Schmidt (1990), which was the second record for this federal state.

Between 1990 and 1999

During this decade the populations in the Saarland and in Northrhine-Westfalia became indigenous and also much more numerous (see the compilation in Ott 1996, 2000, and in Rudolph, 1998; Bauhus, 2001). In Northrhine-Westfalia the first record of a reproducing population had been made in 1995 near Dortmund by Bauhus (1996). In Rhineland-Palatinate the species left the Rhine-valley (ca. 95 meters a.s.l.) and colonised also higher altitudes in the Palatinate (ca. 300 meters a.s.l., Ott, 2000). First confirmed records came now also from Hessen, where the species without doubt was also indigenous then in some areas (e.g. in the Rhine valley). After its "rediscovery" in 1991 in Bavaria – where the species had not been registered in the previous decade – the number of observation sites increased from single ones to several dozens (Burbach, 1998; e.g. in the Danube valley and near Freising), some of them also with autochthonous populations. After its long absence from Brandenburg since 1918, *Crocothemis erythraea* was registered there again in 1995 by Günther (see the addendum in Mauersberger, 2003), and in Saxony it was recorded as new for this federal state in 1997 (and again in 1998, see Xylander, 2005).

From 2000 to present time (2006)

The number and sizes of populations in the southern federal states showed further increase, e.g. in the Saarland *Crocothemis erythraea* is known now from more than 50 sites, being autochthonous in more than 20 out of these (Trockur, pers. comm. 2006). In Baden-Württemberg an ongoing increase of population numbers was stated as well as colonisation of areas known from previous investigations as definitely uninhabited (Hunger et al., 2006): so a real expansion could be documented by these data. These new populations inhabit also regions at higher altitudes (up to 700 meters a.s.l.) outside the Rhine-valley. The same happened in Bavaria: also in this state the species "climbed" up to higher altitudes, i.e. distinctly over 700 meters (Voith, pers. comm. 2005).

Some more observations came from Saxony, where only two observation sites did exist until 2004, and autochthony was not verified (Xylander, 2005), but in 2005 and 2006 the numbers of observations increased again (Xylander, pers. comm. 2006). In the southern parts of Lower Saxony *Crocothemis erythraea* finally became a new member of the federal fauna in 2000 and was continuously observed in the following years (Lohr, 2003), in 2006 it was one of the most abundant dragonflies at some gravel pits near the river Weser (Lohr, pers. comm. 2006) and it is also now autochthonous in many waters. In 2001 the species was recorded in Thuringia for the first time by Mey (2003), as well as for Saxony-Anhalt in 2003 (Heidecke & Lindemann, 2004; Buttstedt & Zimmermann, 2005). In both federal states it is now also indigenous. Also in 2003 the first observation in Mecklenburg-Vorpommern was made by Mauersberger (2003), the northernmost observation ($53^{\circ}4' \text{ N}$) up to that date – yet this was topped in 2006 by Frank (2006), who found the species near Schönberg ($53^{\circ} 51' \text{ N}$); another observation was mentioned by Ritter (pers. comm. 2006) for the eastern part of the federal state. In Brandenburg the number of sightings increased (e.g. Donath, 2003), and also in this federal state the species is now indigenous (Schneider et al., 2005), having flourishing populations with some thousands of emerging individuals. Beutler & Beutler (2005) found 170 exuviae along 10 meters of shoreline and from that number calculated a total population of > 5000 individuals. Presently the species is known from more than 30 localities (Beutler, 2006, and pers. comm. 2006). In 2006 it was finally registered for the first time for Bremen (ARLT 2006) and also in northern Lower-Saxony (Jödicke, 2006: $53^{\circ} 22' \text{ N}$ (Friesland), Finch, pers. comm. 2006: $53,18^{\circ} \text{ N}$ (Hahn-Lemden)), the two latter observations being made at nearly the same latitude as the one in Mecklenburg-Vorpommern.

Actually, records of *C. erythraea* are missing from only three northern German federal states, but very probably it is already present there, as it has reached and even transgressed the geographical latitude of these states, namely Berlin and Hamburg and even Schleswig-Holstein.

During this present decade for the first time in Germany a probable second generation of this species – generally being univoltine in the north – was observed in Hessen and southern Lower Saxony in the hot summer of 2003 at shallow waters (Horn, 2003; Böhm, 2004).

Table 1. Distribution and expansion of the Scarlet Darter (*Crocothemis erythraea*) in the German federal states (o = observation(s) of single individuals, ● = indigenous populations, ▲ = increasing / expanding, in (): probably; see text for details)

German federal state	< 1970	1971-1979	1980-1989	1990-1999	2000-2006
Baden-Württemberg (BW)	O	●	●▲	●▲	●▲
Bavaria (BY)	O	O	O	●▲	●▲
Rhineland-Palatinate (RP)	O	O	●▲	●▲	●▲
Saarland (SL)			O	●▲	●▲
Hessen (HE)			(O)	O (●)	●
Thuringia (TH)					●
Saxony (SN)				O	O
Saxony-Anhalt (ST)					●
Northrhine-Westfalia (NW)		O	O	●	●▲
Lower Saxony (NI)					●
Brandenburg (BB)	O			O	●▲
Bremen (HB)					O
Hamburg (HH)					(O)
Schleswig-Holstein (SH)					(O)
Mecklenburg-Vorpommern (MV)					O
Berlin (BE)					(O)

CROCOTHEMIS ERYTHRAEA EXPANDING IN THE REST OF EUROPE

Not only in Germany, but also in other Central and Middle European countries *Crocothemis erythraea* expanded its range in the recent decades. Only a few examples are presented here, as a detailed review will be published later (Ott, 2007). Already in the 18th century the species was known from Austria, where it had populations near Vienna, but in the 19th century it expanded its range in all Austrian federal states and is now, except for Tyrol, autochthonous. There it occurs even up to an altitude of 1,640 m a.s.l., and the highest breeding population was found at 570 m a.s.l. (Raab et al., 2006). In Switzerland it was indigenous only in very few cases in former times, but from 1980 onwards the number of populations increased continuously, combined with range expansion. It was registered up to 2090 meters a.s.l. and breeding populations were confirmed as high as 663 meters a.s.l. (Wildermuth et al., 2005). In The Netherlands only 3 individuals had been recorded in 1959, 1967 and 1968, respectively, but in 1993 a whole population was discovered in the southern part of that country, and in the following years several additional populations

were established with an increasing tendency (NVL, 2002). Meanwhile *C. erythraea* has reached the UK, where it was first seen in 1995 and now has also established the first population (Smallshire & Swash, 2004).

Already these few examples show that range expansion of this species is a general process in Europe and not limited to Germany (and some of the above named authors also mention the climatic changes as a reason for this, see below).

DISCUSSION

Ways of expansion – a clear sign ?

As shown before, the species colonised the whole of Germany in about four decades, starting in the southern Rhine-valley and proceeding step by step to the north. At a first glance the species seems to have followed the rivers, at least it was found first of all in the river valleys – from where it expanded into adjacent regions and ascended from low altitudes to higher ones. Dumont (1967) supposed the species to use the large rivers as “corridors” or “guiding lines”, entering Germany via the gate of Burgundy (junction of the rivers Saône and Rhine) and/or the river Mosel and then continuing down the river Rhine.

However, as the species needed nearly 80 years to proceed to areas more northerly than its first observation site in Germany (Bollow, 1919), this assumption sounds a bit too simple or generalising.

From comparing the map (Fig. 2) with Table 1 we may conclude that the species moved northwards on a rather “broad front”. If it had strictly followed only the rivers as expansion corridors, it should have been expected to conquer the northern German federal states beginning at the lower course of the Rhine, from there heading eastwards through the lowlands of the northern federal states. But this was obviously not the case, as the species was not discovered on this route via Hannover, Braunschweig *etc.* (especially along this route in Lower Saxony the “observation intensity of GdO-members” is very high, so it certainly would have been discovered). It was found, on the contrary, in that thoroughly investigated region for the first time as late as 2005 in the area of Celle (Clausnitzer, 2005).

So we may rather assume that *Crocothemis erythraea* obviously passed through the central German low mountain region as a whole and arrived simultaneously in several federal states of the north in

the mid nineties (see here also Fig. 3). We may also plausibly consider the populations of the northern federal states being of different origin. Populations *e.g.* in the north-eastern federal state of Brandenburg, possibly have been established by animals having proceeded on the route via Austria, Hungary, through the gate of Hungary (Danube valley near Hainburg/Vienna) and through the Czech Republic and Poland – this assumption is supported by the fact that also in these countries the species was rediscovered and expanding around the mid nineties (Czekaj, 1994; Mocek, 1998; Bernard, 2000). At the moment genetic analyses of different populations are carried out (Ott & Sanchez Guillén, in prep.) to decide on the question, whether the northern *Crocothemis*-populations are of homogenous or different origin.

THE EXPANSION OF *CROCOTHEMIS ERYTHRAEA* IN GERMANY – WAS THE SPECIES ONLY OVERLOOKED OR IS THE EXPANSION A RESULT OF NEWLY CREATED WATERS?

The period before its expansion

It is hard to assess the real situation of the species during the decades before and after its first discovery in Germany in 1918. On one hand, of course less investigations than at present have been carried out on the whole in that phase, but on the other hand it has to be mentioned that especially in those particular regions where the species was found much later, several thorough odonatological investigations have been performed even in these first decades of the last century (*e.g.* Rhine-valley, see the compilation in Lohmann, 1980, or Niehuis, 1984). Moreover, in Germany Odonatology has a long tradition, leading to the detection of other very rare and much more cryptic species in this period (*e.g.* *C. hylas*, *O. curtisii*).

So we may conclude that in this time span *Crocothemis erythraea* very probably was not at all present or at the most in very small numbers, in any case there were no noticeable populations.

The period during its expansion

In Germany we saw a strong increase in the number of odonatologists during the last three decades: in the seventies there were only a few dozens, in the early eighties, when the GdO (German Odonatological Society, see: www.libellula.org) has been founded, there were about 100, and presently the GdO comprises more than 500 members, this number being a reliable indicator of the general "odonatological activity".

Also in the eighties environmental issues and nature protection became more and more important in Germany; the federal states started mapping and monitoring programmes, most often including Odonata – in the same period other private initiatives started to document the distribution of dragonflies (e.g. Niehuis, 1984 for Rhineland-Palatinate).

Without doubt our detailed knowledge of the species distribution as well as the density of observations increased enormously during this period, though already at the beginning of the expansion of *C. erythraea* the number of odonatologists had been pretty high. Moreover, the species is of such a striking appearance that even amateurs or beginners in odonatology do recognise it immediately when present at a water. In addition, in a lot of areas we do have reliable data for the situation before its expansion or intrusion into these previously unsettled areas; so it is rather impossible that this striking species – in particular an indigenous population – has been overlooked during this time (see the increase of faunistic literature during the second half of the last century in Schorr (1990) as another “indicator” of high odonatological activity).

Another aspect may be the increase of the number of water bodies in Germany. In particular garden ponds were created in huge numbers, and along the rivers the number of gravel pits increased – the latter function as good and typical *Crocothemis erythraea*-habitats, if not used too intensively for fishing or recreation purposes. In total Germany's land surface is presently covered by 2, 3% of different waters (BFN, 1997, 2004; BFS, 2006) with an increasing tendency during the last decades. Consequently in the beginning of the expansion this was assumed to be the main reason, as no other factor could be recognised then (e.g. Ott, 1988).

From old and historic maps it is easily seen that already in former times a big number of waters existed, in general more natural waters existed in those times (running waters with morphodynamic; less exploitation of land !), and today the species is present in waters, which do exist already since decades. In addition, the increasing creation of garden ponds and exploitation of gravel pits along the rivers during the decades after WW 2nd was occurring more or less simultaneously all over Germany and not at first in the south and then moving northwards.

Finally there is no good reason, why the number of waters should have been a limiting factor during the first half of the last century and why those which already existed for a long time should not have been populated earlier. As shown before, the species colonised Germany

continuously from south to north, but being a vigorous flier and with regard to its ability to cross higher altitudes and to reproduce also in small water bodies, colonisation should have happened much quicker: so the creation of new waters can't be the (only) reason for the documented way of expansion of *Crocothemis erythraea*.

ANOTHER REASON FOR THE EXPANSION: CLIMATIC CHANGE

At the beginning of the nineties of the last century the problem of climatic changes and the first registered effects on flora and fauna became a theme in science (e.g. Gates, 1993; BFN, 1995; Graves & Reavey, 1996). For dragonflies – and in particular for *Crocothemis erythraea* – this theme was mentioned for the first time by Ott (1996 a) at the SIO-conference in Essen, where it was discussed controversially, as many odonatologists interpreted the first steps of its expansion in Germany as a normal oscillation which they expected to stop soon.

But the expansion of *Crocothemis erythraea* continued and similar processes were shown also for several other species of Mediterranean origin in Germany, all over Europe, the United States and Japan (Ott, 1996 b, 2000, 2001, 2007; Parmesan & Yoke, 2003; Hickling et al., 2005). In this context it must be pointed out that – with only very few exceptions – other species, in particular those with a typical Euro-Siberian distribution, did not expand their range.

So today the well documented range expansion of southern dragonfly species to the north is accepted as a fact (e.g. Hickling et al., 2006).

If species with a previous distribution restricted to warmer southern areas extend their range to northern areas, the reason may be (or should be) related to temperature. Looking at the history of its expansion, *Crocothemis erythraea* first of all populated the warmer regions in the Rhine valley (according to its bio-climatic envelope as a mediterranean species) and then spread to the north and up to higher altitudes.

Parallel to this process we had in Germany an increase of temperature: the warmer regions (e.g. Rhine valley) became even warmer and colder regions also became warmer, a still continuing phenomenon.

From 1988 onwards, in Germany the mean temperature of every single year except 1996 exceeded the long-term medium temperature of 8,3°C. (period: 1961-1990): in 1994 it was 9,7°C, in 2000 it was even



Fig. 1. Male Scarlet Darter (*Crocothemis erythraea*) (Brullé, 1832)
(Pescara, Italy, 2006)

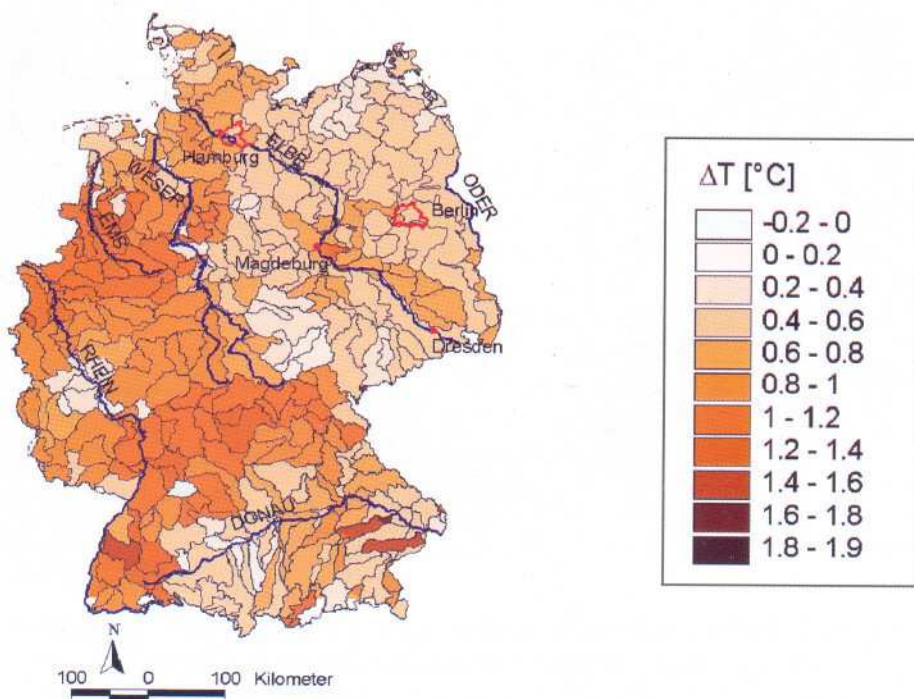


Fig. 3: Change of mean temperature in Germany from 1901-1998
(data source: DWD; Fig. prepared by F. Badeck)

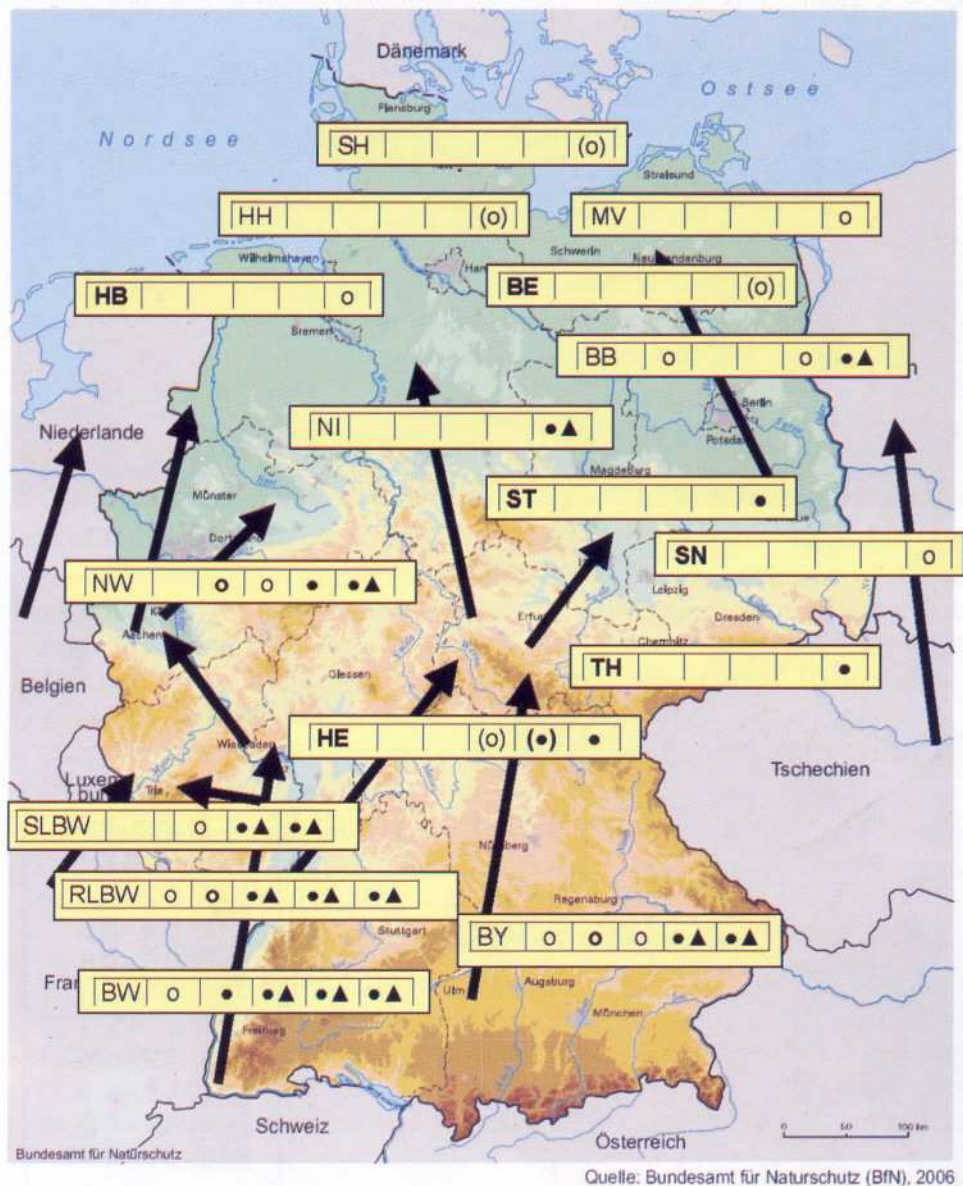


Fig. 2: Expansion of the Scarlet Darter (*Crocotthemis erythraea*) in Germany (codes for the federal states see Table 1)
 — arrows indicate the known or possible ways of expansion

9,9°C, and in 2003 again 9,4°C. In 2003 the duration of sunshine in Germany reached the extremely high amount of 2014 hours, which is 32% more than medium duration (DWD 2000-2004). In addition we are experiencing an increasing number of so called "summer days" and "hot days", and a decreasing number of "cold days" and "frost days" (DWD, 2004, see also Rapp & Schönwiese, 1996).

These data given here for Germany as a whole of course vary in the single federal states, but the general increase is found everywhere. For example, for Rhineland-Palatinate an increase of about one degree was shown already by Ott (1996 b) for various climatic stations, and this process continued in the recent years (Am, 2006).

The increase of the mean temperature in Germany from 1991-1998 is shown in the following figure and here we see that the previously demonstrated ways of expansion of *Crocothemis erythraea* reflects very well the trend in the temperature increase in the different areas or federal states.

So expansion of *Crocothemis erythraea* reflects the change of the abiotic climatic conditions in Germany, and this is in concordance with a lot of other investigations and results stating obvious changes in plant and animal phenology (e.g. earlier breeding of birds, earlier flowering of trees etc., e.g. Walther et al., 2002; Parmesan & Yohe 2003; Root et al., 2003; Leuschner & Schipka, 2004; Schröder et al., 2005) related to climatic changes, although in detail some questions of course remain as yet unanswered (see below) as well as some controversial discussions on the species level (e.g. Schmidt, 2004).

Still remaining is the important question, whether the species reacts to key factor "temperature" (or another one ?) via the adult stage, the larval stage or via both of them, and also the question whether it is influenced by a combination of several factors – and, moreover, whether the northern populations are already adapted in any way (e.g. differing body sizes and behaviour of the adults, differing behaviour of the larvae (ice-avoiding strategy), altered physiology).

Various possibilities may be considered as key factors:

- increase of mean temperature per annum (for the species in general)
- increase of mean summer temperature, influencing activity period of the adults (for the adult stage – higher activity and mobility)
- increase of water temperature (for the larval stage – lower mortality)

- increase of the sunshine duration during summer (for the adult stage – higher activity and mobility)
- increase of so called “summer days” and “hot days” (for the adult stage – higher activity and mobility) or
- decrease of so called “frost days” (for the larval stage – lower mortality)

As the mean air temperature increased during the last decades, the water temperatures-especially in shallow waters-must have risen as well (unfortunately there are no long term data e.g. from gravel pits in Rhineland-Palatinate, available; Wendling, pers. comm. 2006), so that a combination of these two factors might be effective. According to Lohmann (1980) the species is “depending on high water temperatures in summer”, but he did not give any proof or reference for this.

A “non freezing over” of the waters, as postulated by Jurzitza (2000), is obviously not an essential factor: larvae of the species survive unharmed a freezing over of the waters, as shown by Ott (1988: *C. erythraea* emerged after the water bore an ice cover as thick as 30 cm in the previous winter) and also emphasised by Burbach (1998). It goes without saying that long periods of higher temperature definitely increase the species` mobility (as in most other odonata / insects) and its ability to expand its range by colonising new waters.

OUTLOOK

Consequences for the biotopes

As shown before, *Crocothemis erythraea* has invaded a lot of waters and also different biotope types, mainly sand- and gravel-pits of different successional stages, but also alluvial waters, ponds, lakes with a rich reed and submersed vegetation, and obviously even moorland biotopes (Ott, 2007; Wildermuth, 2006; Jödicke, 2006). As no experiments have been carried out up to now, it is unclear whether the larvae of *C. erythraea* do have a negative impact on other larvae in the water, either by direct predation or indirectly via the food chain. But as they do co-exist with a lot of other dragonfly species over a long time span (Ott, 1990; Ott, 2007) it is more probable that they occupy their special niche within the whole coenosis, exerting no severe and direct effect on other (protected) Odonata species. However, a decline of another species (*Orthetrum cancellatum*) during an increase of *Crocothemis erythraea* at a water has been reported (Lohr, pers. comm. 2006).

The appearance of *Crocothemis erythraea* may indicate altered conditions in the waters, in particular if it settles in an untypical biotope like moorland bogs, and here it should be considered a disturbance indicator revealing some negative impact (e.g. decrease of typical moorland species like *Aeshna juncea*, *Somatochlora arctica*, *Coenagrion hastulatum*: see Ott, 2001, 2006, 2007). So the presence of *C. erythraea* indicates changes on the biotope-level (e.g. after heat waves: Mouthon & Daufresne, 2006), and without doubt it indicates also changes in the structure of the food-web, the whole landscape or ecological system (e.g. Emmerson et al., 2005, Schröter et al., 2006). As all recent scenaria (e.g. IPCC) expect an increase of greenhouse gas emissions and an ongoing global warming, we have to expect effects on the waters and a continuing range expansion of southern species (Ott, 2007).

CONSEQUENCES FOR THE RED LISTS

When *Crocothemis erythraea* was seen more often in Germany and had established its first populations, all odonatologists were happy and proud to have this “new member”. Consequently the species was included in the red lists, as in the early years it did of course not appear in big numbers. E.g. in the federal state of Rhineland-Palatinate it was classified at first in 1983 as a “vulnerable guest” (Itzerott et al., 1988) and then in 1993 – now having autochthonous populations – as “vulnerable” (Eislöffel et al., 1993), in Northrhine-Westfalia (Schmidt & Woike, 1986) as a “Vermehrungsgast” (a guest sometimes reproducing), and in Baden Württemberg still in 1994 even as “endangered” (SGL, 1994).

In the first national list of 1984 (Clausnitzer et al., 1984) it was also classified as a “Vermehrungsgast” (a guest sometimes reproducing).

The problems of including this continuously spreading species in the red list were pointed out by Ott (1996) for the first time, and consequently it was excluded from the following national red list of 1998 (Ott & Piper, 1998). Why some authors – e.g. Jurzitza (2000) – still today classify the species as “vulnerable” for the south western parts of Germany remains unclear; for Baden-Württemberg Hunger & Schiel (2006) classify *C. erythraea* as “not endangered”, a seemingly correct classification, as the species is still extending its range, in particular in the south, and so it has to be excluded from the red list according to the IUCN-criteria (IUCN 2006).

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