JOURNAL OF FOREST SCIENCE, *60*, 2014 (4): 154–165

Spring phenology of cockchafers, *Melolontha* spp. (Coleoptera: Scarabaeidae), in forests of south-western Germany: results of a 3-year survey on adult emergence, swarming flights, and oogenesis from 2009 to 2011

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ABSTRACT: Cockchafers are among the most dreaded insect pests in many European countries, causing economic losses in agriculture, horticulture and forestry. In forests of south-western Germany, populations of the forest cockchafer (*Melolontha hippocastani*) and also the field cockchafer (*M. melolontha*) have been increasing during the past three decades and, therefore, monitoring of these populations has been intensified. In the present field study, data on adult emergence from the soil, male swarming flights and female oogenesis, collected at three infestation sites by visual inspection, with soil eclectors and with light traps in early spring 2009–2011, are presented and discussed in the context of the current knowledge of cockchafer biology. Furthermore, three air temperature sum models for the prediction of the onset of the swarming flight period in spring, published in the early/mid 20th century, were validated in view of their applicability in forestry practice.

Keywords: light trap; soil eclector; maturation feeding; temperature sum

The forest cockchafer (*Melolontha hippocastani* Fabr.) and the field cockchafer (*Melolontha melolontha* L.) are among the most dreaded insect pests in many European countries, causing serious damage and economic losses in agriculture, horticulture, viticulture as well as in forestry (Niklas 1974; Keller 1982; Švestka 2007). In Germany, above all the intensive use of broad-spectrum insecticides in the mid-20th century led to a collapse of cockchafer populations (Zimmermann 2010). Since the 1980s, however, population densities have been increasing anew along with damage to a variety of grasses, herbaceous and especially woody plants (Dubbel 1991; Schmid-Vielgut et al. 1992; Delb 2000; Delb, Mattes 2001; Meinert et al. 2001; Delb 2004; Zimmermann, Jung 2004). Damage is mainly due to the feeding activity of cockchafer larvae – the so called white grubs – on the roots of plants. Resulting fine root losses negatively affect the uptake of water and nutrients, leading to the dieback of young forest plants and at higher grub densities possibly to a chronic weakening of the older ones. The main cockchafer infestation areas in Germany currently comprise the federal states of Baden-Wuerttemberg and Hesse (Zimmermann, Jung 2004). In Baden-Wuerttemberg, there are four populations of *M. hippocastani*, inhabiting about 25,000 ha of forests that grow on comparatively sandy and dry soils alongside the northern part of the Upper Rhine Valley (Delb 2004). The beetles of each population are highly synchronised, leading to years of mass flights followed by years when hardly any beetle can be observed. Hotspot agricultural areas infested by *M. melolontha* in Baden-Wuerttemberg are the ‘Kaiserstuhl’ and ‘Kraichgau’ regions where damage has been reported especially from tree nurseries, orchards and vineyards (Schnetter et al. 1996; Meinert et al. 2001). Nearby the airport Baden Airpark an example of atypical grub development of *M. melolontha* inside forest stands took place on an area of 565 ha, which is a rather uncommon habitat for this species because its grubs usually develop in open landscapes and forest edges only serve as spots for mating and maturation feeding at the adult stage (Schneider 1952a). However, the respective forests were heavily thinned out by the storm 'Lothar' in winter 1999, apparently providing a suitable habitat for egg-laying and larval development. In South-West Germany, *M. melolontha* is commonly known for a 3-year developmental cycle whereas development in *M. hippocastani* usually takes 4 years. However, it appears that the developmental cycle of parts of both species has shortened during the last decades. With increasing frequency this is leading to hitherto hardly known adult flight activity between years of mass occurrence.

Increasing infestation levels and especially damage to forest regeneration during the past three decades made it necessary to intensify the monitoring of cockchafer populations. In order to support and optimise control measures, an important element of the monitoring programme was the survey of adult emergence from the soil, male swarming flights, female maturation and egg-laying. The aim of the present work was to summarise the results of this monitoring programme and to discuss them in the context of the current knowledge of cockchafer biology. Existing predictive models of cockchafer emergence and oviposition should be evaluated under the currently existing conditions in the forest sites of the northern part of the Upper Rhine Valley.

MATERIAL AND METHODS

In spring 2009–2011, cockchafer mass flights were surveyed at three study sites in Baden-Wuerttemberg (South-West Germany). For each observation period, a data-logger was installed in the study areas recording air temperature (at 2 m height), soil temperature (at 10 cm depth) and precipitation half-hourly. Data on sunset and the dusk period were obtained from www.calsky.com.

In 2009, there was a massive occurrence of *M. melolontha* in the forest area adjacent to the airport Baden Airpark (study site 1; 48°46'N, 8°06'E). A mean of 3.4 cockchafers per m^2 was detected in sample soil excavations performed in the infestation area in winter 2008/09. Adult emergence (hereinafter the term "emergence" refers to the appearance of adult beetles from their hibernaculae in early spring rather than the eclosion from the pupae which takes place about six months earlier) was surveyed with eight soil eclectors which had been installed on the ground of mixed beech/Scots pine stands at the beginning of April. Each eclector consisted of a gauze net (20–22.5 m^2) whose edges were entrenched into the soil. The net was tent-like erected at two spots, allowing the emerging beetles to crawl upwards and being trapped in two plastic boxes at the top. The boxes were surveyed daily for freshly emerged beetles. Additionally, a light trap (black light; 12 V; 15 W) was run on 25 April, 2 May, and 20 May. It was installed at the height of 1.5 m in the vicinity of the soil eclectors and consisted of four Plexiglas plates which were placed at a right angle to each other. The attracted beetles were collected in a bag which was fixed below the Plexiglas plates. Attracted beetles were counted at intervals of 30 min between 20:30 and 22:30.

In 2010, massive occurrence of *M. hippocastani* was predicted for 470 ha of forests north-east of the town of Iffezheim (study site 2; 48°49'N, 8°10'E). Prior to emergence, a mean of 2.4 cockchafers per m^2 was detected in excavations. Two eclectors were installed along with 2 light traps in a mixed beech/Scots pine stand and a red oak stand. The light traps were run daily from 23 April to 16 May (except 2 May) and the beetles were counted at intervals of 15 min between 20:00 and 22:30. At the same time intervals, the intensity of male swarming flight activity in the canopy as well as female oviposition flight activity near the ground (for details see Burchard 1988) was estimated by visual inspection on a 5-step scale (0 – none; 1 – weak; 2 – medium; 3 – heavy; 4 – massive).

In 2011, a mass flight of *M. hippocastani* was predicted for 10,560 ha of forests north of the city of Karlsruhe. One eclector and a light trap were placed inside a red oak stand nearby the village of Staffort (study site 3; 49°04'N, 8°30'E). Prior to emergence, a mean of 12.7 cockchafers per m^2 was detected in excavations in the vicinity of the study site. The light trap was run daily from 9 April to 11 May (except 12 April and 9 May). The beetles were counted at intervals of 15 min between 20:00 and 22:00. At the same time intervals, the intensity of male swarming flight activity as well as female oviposition flight activity was estimated by visual inspection on a 5-step scale (classification see above).

Using our observations on cockchafer emergence, we were able to verify the predictive models previously published by Decoppet (1920), Horber (1955), and Richter (1969). Decoppet (1920) predicted cockchafer emergence from the soil as soon as the temperature sum exceeds 355 degree-days when adding up the mean daily air temperatures from 1 March onwards and supposing a lower thermal threshold of 0°C. According to Horber (1955), cockchafer emergence is initiated at 256.3 ± 16.3 degree-days added up from 1 March onwards and assuming a lower threshold of 8°C. Finally, Richter (1969) hypothesised a negative linear relationship between the time duration spent in the soil and the required temperature sum necessary for adult emergence, assuming a lower threshold of 7.7°C. This model suggests adult emergence on 15 April, provided that a thermal sum of 273.5 degree-days (dd) is reached. With every day that passes, the required temperature sum is reduced by 5.39°C. As the onset of adult emergence was earlier than 15 April in 2011, 5.39°C were added for each day prior to 15 April.

In order to trace the state of maturation feeding and oogenesis, each female that had been attracted to the light trap(s) in 2009 and 2010 was dissected in the laboratory. In 2011, approximately half (n = 233) of the total number of females attracted to the light trap was dissected as well. Dissection was carried out in water under a stereomicroscope. Cockchafer ovaries are of the panoistic type (Vogel 1950). Generally, a female has 2 ovaries with 6 ovarioles each (ovariole status: 6/6). It appeared that *M. melolontha* ovaries vary from this rule (6/6) more often compared to *M. hippocastani*: 89.4% of *M. melolontha* ovaries were of 6/6 status in 2009, compared to 96.5% (2010) and 96.1% (2011) in *M. hippocastani*, respectively. In each of the ovarioles, up to 4 (mainly 1–3) eggs develop simultaneously, depending on the number of previous batches already deposited (Vogel 1950, 1955; Richter 1962). As only part of the population produces a second or third egg batch and the number of eggs per batch decreases continuously, mainly the first batch could be regarded as of practical importance (Schuch 1938; Vogel 1955; Burchard 1988). This was the reason why our observations were ceased after the first oviposition period in 2011.

To resolve the question if the number of eggs a female develops is dependent on body size, 30 females were randomly collected in a red oak stand during their oviposition flights prior to the first deposition of eggs in 2011 and subsequently dissected in the laboratory. The number of eggs per female (fertility) was determined and plotted against the width of the pronotum, i.e. body size. For each female that had been dissected, one of its largest oocytes was measured as a measure for the state of oogenesis. Schwerdtfeger (1928) suggested a spheroid to be the best approximation of the shape of a cockchafer oocyte, whose volume (V) can be calculated using the formula:

$$V = 4/3 \times \pi \times a \times b^2 \qquad (1)$$

a, b – semi-major and semi-minor axis, respectively.

According to Schwerdtfeger (1928), the variable term ($a \times b^2$) – named “egg factor” (German: “Eifaktor”) – was used as a measure for the volume of the oocytes. ‘Constrictions’ at the proximal end of the ovarioles or *corpora lutea* were clear indications that females already deposited the first batch of eggs (Fig. 1a–c).

By comparing the courses of adult emergence and oogenesis, the temperature sum (in degree-days = dd) necessary for egg maturation was calculated assuming a base temperature of 6.5°C (Richter 1964a) and 7.0°C (Vogel 1955). Both base

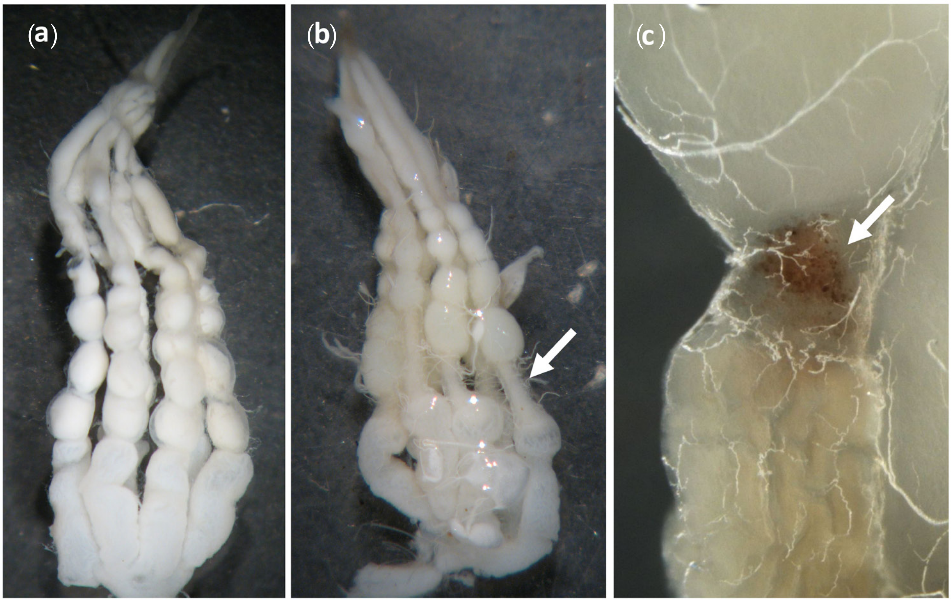

Fig. 1. Immature ovaries of *Melolontha hippocastani* when leaving the soil after hibernation (a) or after oviposition (b, c). ‘Constrictions’ (b: arrow) or brownish *corpora lutea* (c: arrow) at proximal ends of the ovarioles indicate that females already deposited eggs. *Corpora lutea* were stained with dioxan und xylol according to Vogel (1950) (photos: E. Wagenhoff)

temperatures seemed reasonable as cockchafers were observed to feed at temperatures down to 7°C (Schneider 1981). Besides, Richter (1962) proposed a hyperbolic relationship between the number of days necessary for egg maturation and the ambient temperatures using the equation:

$$D = (25 / (T - 8.2)) + 6.6 \qquad (2)$$

D – number of days between the onset of adult emergence from the soil and oviposition,

T – mean air temperature within that period (°C).

With our observations on adult emergence and oogenesis, we intended to verify the predictive temperature sum models by Richter (1964a) and Vogel (1955) as well as the above-mentioned model by Richter (1962) for 2010 and 2011.

In order to monitor body weight development throughout the swarming period, 50 females and 50 males were collected every day from the canopy of a heavily infested red oak stand in 2011. The beetles were weighed and the daily mean weights were plotted in a graph.

Finally, throughout the period of maximum flight activity (2010: 23 April–16 May; 2011: 14 April–3 May) Pearson's correlation coefficient was calculated for the relationship between the daily number of males/females attracted to the light trap(s) and mean air temperatures during light trap exposure.

RESULTS

In spring 2009, 2010 and 2011 total numbers of 1,078 (58.8% ♂♂ and 41.2% ♀♀), 952 (53.3% ♂♂ and 46.7% ♀♀), and 282 (46.1% ♂♂ and 53.9% ♀♀) cockchafers were collected from soil eclectors, respectively (Table 1).

The first swarming flight activity was detected in mid-April (2009, 2010) or even at the beginning of April (2011) when the mean soil temperature at a depth of 10 cm was approximately 10°C and mean air temperatures were between 12°C and 15°C (Table 2). One to two days after the first detection of adult flight activity in the forest area, single cockchafers were recognised in the eclectors. Following the temperature sum models of Decoppet (1920), Horber (1955), and Richter (1969), the onset of swarming could be predicted with a maximum deviation of 7 days (Table 2). Mean discrepancies between predicted and observed swarming flights were 3 days (Decoppet 1920; range +2 to +4 days), 3 days (Horber 1955; range 0 to +7 days) and 2 days (Richter 1969; range –2 to +3 days), respectively.

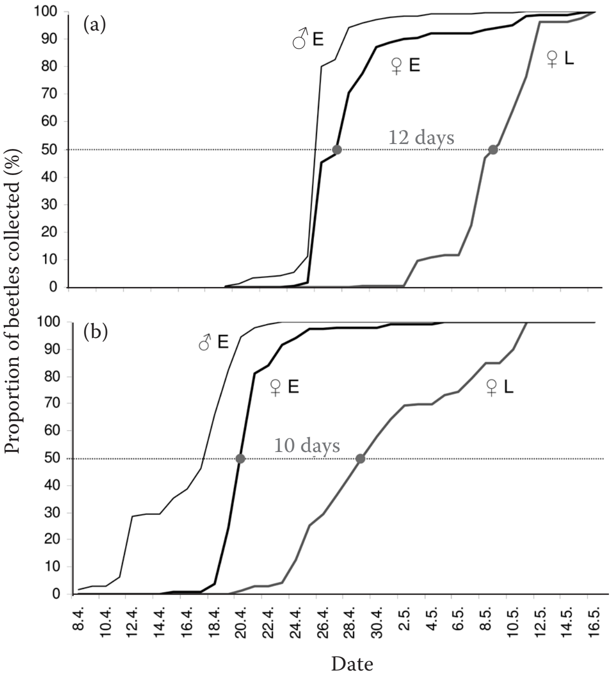

Fig. 2. Daily cumulative emergence of male and female beetles of *Melolontha hippocastani* in soil eclectors (E) in 2010 (a) and 2011 (b) along with the daily cumulative percentage of females trapped with light trap(s) (L)

Generally, the male cockchafers started emerging a few days earlier than the females (Fig. 2). Within 10 days after the first swarming flight activity, peak emergence from the soil was recognised. Adult emergence was observed to occur in good synchrony with the foliation of the main host trees. The main host species for maturation feeding in the study area are *Quercus rubra, Q. robur*, and *Q. petraea* where severe defoliation was

Table 1. Number of cockchafers collected from soil eclector(s) and attracted to light trap(s) in spring 2009, 2010 and 2011

Year	Species	Eclector(s)				Light trap(s)					
		n	♂♂	♀♀	♂/♀	*n*	nights	time period	♂♂	♀♀	♂/♀
2009	*M. melolontha*	8	634	444	1.43	1	3	20:30–22:30	154	75	2.05
2010	*M. hippocastani*	2	507	445	1.14	2	23	20:00–22:30	1767	510	3.46
2011	*M. hippocastani*	1	130	152	0.86	1	31	20:00–22:00	738	450	1.64

n – number of eclectors/light traps used; ♂/♀ – sex ratio

Table 2. Phenology of cockchafer emergence [observed and predicted according to Decoppet (1920), Horber (1955), and Richter (1969)], maturation feeding (see also Fig. 2) and oviposition in the study area

Year	Onset of swarming (observed) (date in April)	Onset of swarming (predicted) (date in April)			Mean temperature (°C)		Earliest detection of beetles in the eclectors (date in April)		Peak emergence from the soil (date in April)		Duration of maturation feeding (days)	Temperature sum for completion of oogenesis (dd)		Date of egg-laying (1st batch)	
		Decoppet	Horber	Richter	air	soil	♂♂	♀♀	♂♂	♀♀		T0 (°C)		earliest	peak
												6.5	7.0		
2009	12	14	19	15	13.7	9.9	12	12	18	20	n.d.	n.d.	n.d.	n.d.	n.d.
2010	16	18	16	14	12.2	9.7	18	23	25	25	~ 12	65	59	29.4.	7.–12.5.
2011	6	10	7	5	15.3	10.3	7	14	11/17/18	18–20	~ 10	85	80	18.4.	23.–30.4.

n.d. – no data available

observed regularly. *Fagus sylvatica*, *Acer pseudoplatanus*, *Juglans regia* and *J. nigra* were readily accepted as well, whereas *Carpinus betulus* and *Betula pendula* were of minor importance. *Fraxinus excelsior*, *Alnus glutinosa* and *Tilia spec.* were nearly or completely avoided. Ordinarily, cockchafers were observed feeding on preferred deciduous trees as long as their leaves were not too much hardened.

In 2010, the earliest oviposition flights were observed on 29 April, while egg-laying peaked between 7 and 12 May. In 2011, the earliest oviposition flights were recognised on 18 April, while egg-laying peaked between 23 and 30 April (Table 2).

As almost the same percentage, 65.4 and 66.8%, of the females attracted to the light trap(s) carried ripe eggs – i.e. egg factor > 1.75 according to Schwerdtfeger (1928) – in 2010 and 2011, respectively, the discrepancy between the dates when 50% of the females appeared in the soil eclectors and when 50% of the females were attracted to the light trap(s) served as an estimation of the duration of maturation feeding, i.e. oogenesis (Fig. 2). Hence, maturation of the first batch of eggs was estimated to take about 1.5 weeks (also shown in Table 2). The temperature sum required for egg maturation was 65 dd and 85 dd assuming a base temperature of 6.5°C according to Richter (1964a), and 59 dd and 80 dd assuming a base temperature of 7.0°C according to Vogel (1955), respectively (Table 2). By using equation (2) published by Richter (1962), egg-laying was predicted to start 12 and 14 days after the onset of adult emergence in 2010 and 2011, respectively. Comparing those two values with our observations, the beginning of egg-laying started 13 days (1 day later than predicted) and 12 days (2 days earlier than predicted) after the first swarming flights were recognised in 2010 and 2011, respectively. After the earliest detection of female beetles in the eclectors it took 6 and 4 days until the beginning of the first oviposition period in 2010 and 2011, respectively.

Generally, body weight is higher in female cockchafers compared to the males. Concerning the entire observation period, mean body weight of male cockchafers fluctuated on a low level (Fig. 3). In contrast, mean female body weight was observed to increase from the onset of emergence from the soil until the day when peak egg-laying starts (Fig. 3). As soon as egg-laying was initiated, female body weight fluctuated roughly on the same level (Fig. 3).

Male swarming flights in the canopy and female oviposition flights near the ground started 45 to 60 min before sunset, peaked around sunset and declined as darkness increased – namely, female oviposition flight intensity declined more rapidly than male swarming flight activity (Fig. 4a). At the beginning of dusk, female attraction to the light trap(s) was at its height (Fig. 4b; see also Fig. 7).

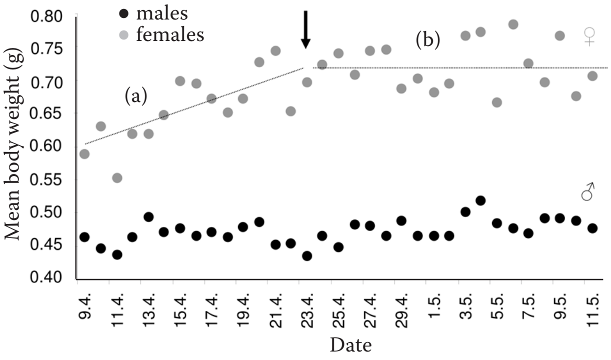

Fig. 3. Daily mean body weight in *Melolontha hippocastani* in 2011. The black arrow depicts the onset of the first peak egg-laying period (Pearson's correlation coefficient: (a) period prior to peak egg-laying: $n = 14$; $r^2 = 0.564$; $P = 0.002$; (b) period after the start of peak egg-laying: $n = 19$; $r^2 = 0.023$; $P = 0.895$)

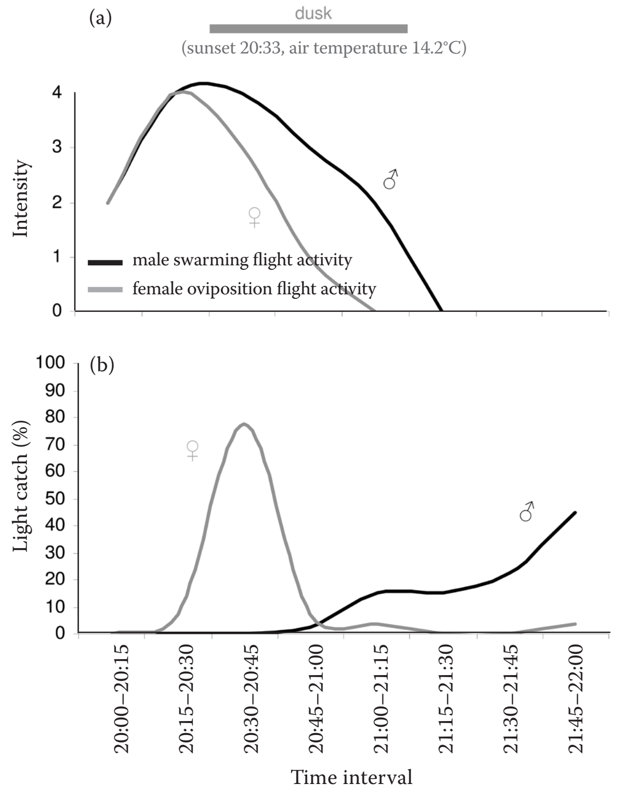

Fig. 4. The course of visually inspected male *Melolontha hippocastani* on 25 April, 2011 (a); proportion of male and female beetles trapped at the light trap within the same time intervals (males: $n = 40$; females: $n = 27$) (b); grey bar above the graphs depicts the dusk period

Most of the females (2010: 65.4%; 2011: 66.8%) attracted to the light trap(s) carried mature eggs (mean egg factor 1.92), indicating that they were searching for oviposition sites to lay their first batch of eggs. By contrast, male attraction to the light trap(s) continuously increased with falling night (Fig. 4b, Fig. 7). As dusk is postponed continuously throughout the swarming season, there was a similar temporal shift of the swarming activity (Fig. 5a) and light trap attraction (Fig. 5b) of male beetles.

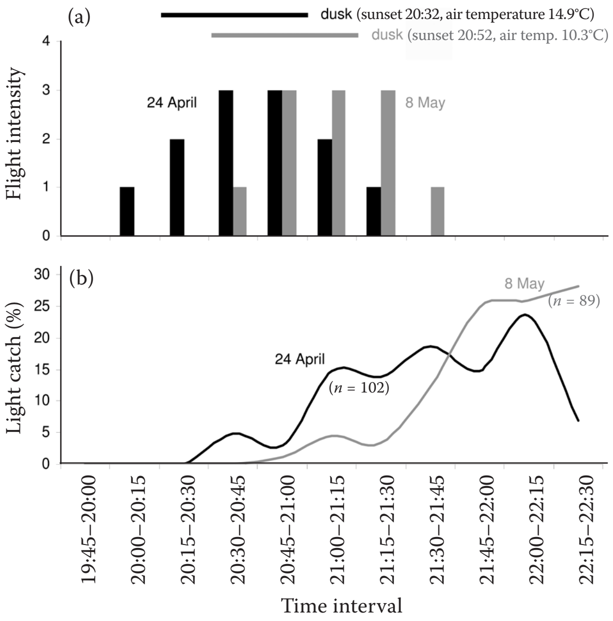

Fig. 5. The course of visually inspected swarming flight activity of *Melolontha hippocastani* males on 24 April and 8 May, 2010 (a); proportion of males trapped with light traps within the same time intervals (b); bars above the graphs depict the corresponding dusk periods

For 30 mature females collected shortly before egg-laying in 2011, the mean egg-factor was determined as 1.80 ± 0.18 (min 1.49, max 2.33). The pronotum width (i.e. body size) was a good predictor for the number of eggs carried (Pearson's correlation coefficient $n = 30$; $r^2 = 0.438$; $P < 0.0001$; Fig. 6a). On the other hand, there was no correlation between the pronotum width and the egg factor, i.e. egg size (Pearson's correlation coefficient $n = 30$; $r^2 = 0.0002$; $P = 0.941$; Fig. 6b). In May 2011, several soil samples were surveyed for egg batches and it appeared that the eggs were deposited 15–20 cm under the soil surface.

In 2009, 2010 and 2011, a total of 229 (67.2% male, 32.8% female), 2,277 (77.6% male, 22.4% female) and

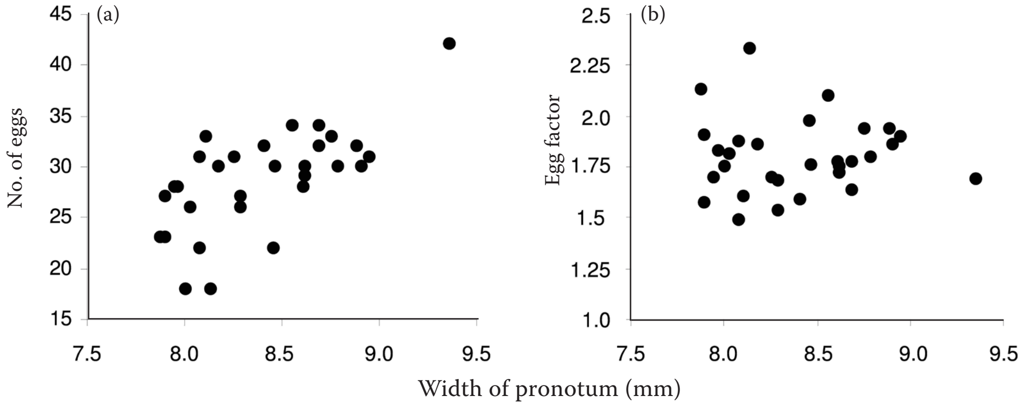

Fig. 6. Correlation between the pronotum width (body size) and (a) the number of eggs carried (fertility) or (b) the egg factor (egg size) of 30 females of *Melolontha hippocastani* collected shortly before oviposition in 2011

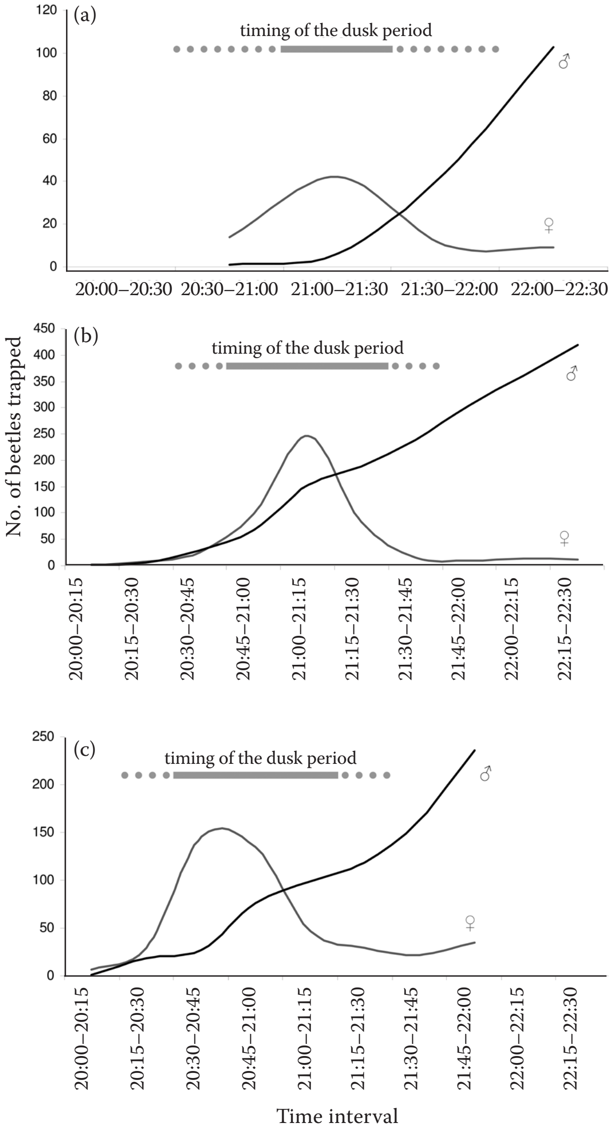

Fig. 7. The course of male and female cockchafers attracted to light trap(s): (a) *Melolontha melolontha* in 2009, (b) *M. hippocastani in* 2010, and (c) *M. hippocastani* in 2011

1,188 cockchafers (62.1% male, 37.9% female) were attracted to the light trap(s) during the dusk/early night period (Table 1). Looking at the sex ratio, male beetles significantly prevailed (χ^2-test: all $P < 0.001$; Table 1). Female attraction to the light trap(s) started with the beginning of sunset, peaked during dusk and decreased rapidly close to nightfall, whereas male catches increased continuously when darkness fell (Fig. 7a–c). There was a good correlation between daily maximum swarming flight intensity and the number of males attracted to the light trap(s) (Spearman's correlation coefficient – 2010: $n = 23$; $\rho = 0.557$; $P = 0.006$; 2011: $n = 31$; $\rho = 0.764$; $P < 0.0001$). There was also a correlation between the number of males attracted to the light trap(s) and the air temperature during exposure of the light trap(s) (Pearson's correlation coefficient – 2010: $n = 23$; $r = 0.779$; $P < 0.0001$; 2011: $n = 20$; $r = 0.748$; $P < 0.0001$; Fig. 8).

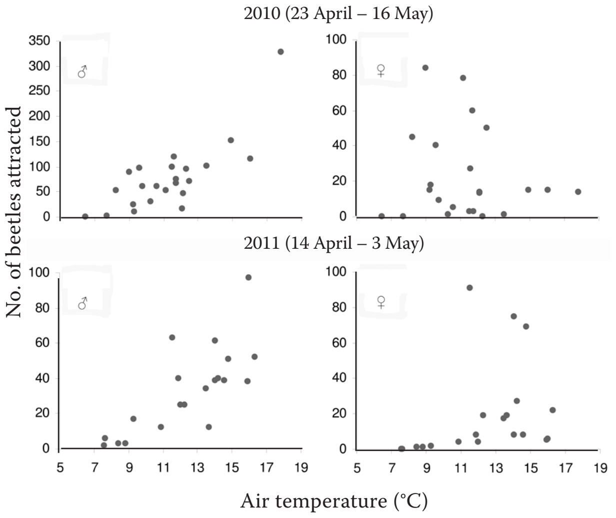

Fig. 8. Correlation between mean air temperatures during the light trap exposure (2010: 20:00–22:30; 2011: 20:00–22:00) and the respective number of cockchafers attracted on a daily base

Moreover, a strong correlation was observed between the daily maximum intensity of females' oviposition flights and the number of females attracted to the light trap(s) (Spearman's correlation coefficient – 2010: $n = 23$; $\rho = 0.847$; $P < 0.0001$; 2011: $n = 31$; $\rho = 0.802$; $P < 0.0001$). The number of females attracted to the light trap(s) did not depend on air temperature during light trap exposure (Pearson's correlation coefficient – 2010: $n = 23$; $r = -0.103$; $P = 0.639$; 2011: $n = 20$; $r = 0.307$; $P = 0.188$; Fig. 8). By far the largest proportion of females attracted to the light trap(s) was either immature or mature (Fig. 9). On the contrary, hardly any female carried oocytes of medium size, i.e. them being in the state of vitellogenesis (Fig. 9).

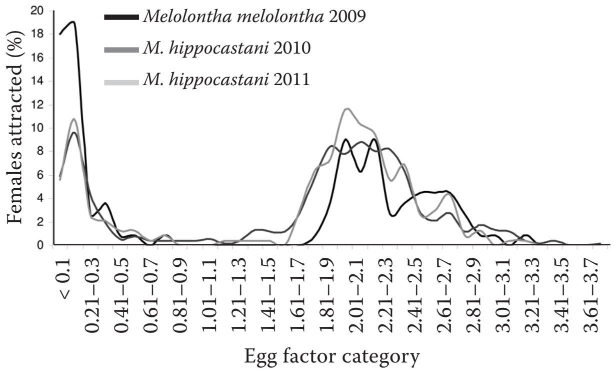

Fig. 9. Percentage distribution of the state of egg maturity in female cockchafers attracted to light trap(s). According to Schwerdtfeger (1928), egg factors < 0.25 can be regarded as immature whereas egg factors > 1.75 can be regarded as mature

A proportion of 61.9%, 36.3% and 68.2% of immature females attracted to the light trap(s) already deposited their first batch of eggs in 2009, 2010 and 2011, respectively. In 2009, all mature females (egg factor > 1.75) attracted to the light trap on 2 May carried their first batch which consisted of 24 eggs on average (interquartile range 22–25 eggs). On the other hand, all mature females attracted to the light trap 18 days later (20 May) carried their second batch which consisted of 15 eggs on average (interquartile range 14–16 eggs). In 2010, 99.4% of all mature females attracted to the light traps during the entire observation period were trapped shortly before deposition of their first egg batch (median 25 eggs; interquartile range 20–29 eggs), whereas 0.6% of the mature females carried their second batch (median 14 eggs; interquartile range 8–21 eggs). The onset of the second egg deposition period was determined for 11 May. In 2011, all mature females attracted to the light trap during the entire observation period were trapped prior to deposition of their first batch, carrying 24 eggs on average (interquartile range 22–28 eggs). The 2011 survey was ceased before the second maturation period had been completed.

DISCUSSION

The use of soil eclectors and light traps enabled us to trace adult emergence from the soil as well as female oogenesis and egg deposition in areas of cockchafer mass propagations. It is well known that the developmental stages of cockchafers within a certain area are highly synchronised and indeed, in the respective study areas massive swarming flights occur every 3rd (*M. melolontha*) or 4th year (*M. hippocastani*).

Synchronous swarming is hypothesised as an adaptation to guarantee good synchrony with the host tree budburst and to reduce the efficiency of enemies (Reichholf 1979). Indeed, cockchafer emergence from the soil was observed to occur when the main host trees came into leaf which may provide feeding on soft leaves containing lower levels of phytochemicals. This becomes particularly obvious in the case of *Q. rubra*, *Q. robur*, and *Q. petraea*, which are the preferred host species when the foliage is fresh. As soon as the leaves hardened, cockchafers were observed to avoid these trees. Similar results were obtained in the laboratory by Schneider (1978). The same author hypothesised that mechanical properties of the leaves are of vital importance whereas chemical quality is of secondary importance. However, the fact that even fresh and soft foliage of lime, ash, and alder is ignored implies that chemical properties may also play a major role in the selection of host trees for maturation feeding in cockchafers. To our knowledge it is not known how synchronisation with budburst is mediated. It might be indirectly by using the same environmental cues as their hosts – namely temperature and photoperiod – or rather directly by detecting the physiological state of their host trees through changes in the activity of the roots (Reichholf 1979).

In early spring and after approximately six months of diapause, cockchafers are known to leave their hibernation cells, entering the upper soil layer and waiting for favourable weather conditions to leave the soil for swarming, mating, and maturation feeding (Schwerdtfeger 1938; Richter 1962). In the present study, cockchafers were observed leaving the soil in early/mid April when mean temperatures in the upper soil layer reached 10°C, which is in close accordance with Zivanovic (1972) and Niklas (1974). On the contrary, Richter (1962) and Trotuş et al. (2013) reported adult emergence at higher (12.8–17.4°C) or even lower (6.1–14.2°C) mean soil temperatures for East Germany and Romania, respectively. Differences might be due to regional adaptations of the cockchafer populations to local conditions (e.g. temperature regime in spring, soil characteristics, or host tree phenology). Even though cockchafers are exposed to soil conditions before they leave for swarming, air temperatures are usually used to predict adult emergence. To our knowledge there are three models for the prediction of the onset of the cockchafer swarming flight period on the basis of air temperature sums by Decoppet (1920), Horber (1955), and Richter (1969). In this regard it is worth noting that *M. hippocastani* and *M. melolontha* do not differ in the onset of the swarming flight period when they live in the same habitat (Richter 1964b; Švestka 2006), which was also the case in the present study. By comparing two of the models for *M. melolontha* in South-West Germany, Horber's method appeared to predict the onset of the swarming period more precisely than Decoppet's model (Lüders 1962). Brenner (2004), who tested Horber's rule with a series of field data in Switzerland, came to the conclusion that in general this method is highly accurate. Burchard (1988) got good results when applying both Horber's and Decoppet's method. However, both models did not prove satisfactory for the prediction of cockchafer swarming in East Germany, and therefore a third predictive model was developed by Richter (1964b). In the present study, each of the three models proved satisfactory as the differences between predicted and observed swarming did not exceed 7 days. Even though the temperature sum models gave a fairly good prediction of the onset of cockchafer swarming for practical purposes, the underlying physiological processes are not known. Besides temperature, Reichholf (1979) hypothesised also the photoperiod to be a releaser of the swarming flight. However, laboratory experiments where hibernating cockchafers are exposed to different temperature/photoperiod regimes are still missing, which may uncover the possible interaction of temperature and photoperiod in the determination of adult emergence. Nevertheless, male cockchafers are known to start leaving the soil first under lower temperatures (Horber 1955; Vogel 1955), which is in line with the present findings. The course as well as the duration of adult emergence from the soil depends on ambient weather conditions (mainly temperature), and in the present study it took 4–5 weeks in total. However, adult emergence peaked 1–1.5 (♂♂) and 1–2 (♀♀) weeks after first detection of swarming flight activity while the onset of the oviposition period was detected after 12–13 days, which is in close accordance with the laboratory findings by Schuch (1938). About 2.5–3.5 weeks after the first detection of swarming flight activity, mass oviposition flights of mature female beetles took place. The duration of egg maturation in cockchafers is known to depend on ambient weather conditions, mainly air temperature (Vogel 1955). Thus, Vogel (1955) and Richter (1964a) suggested temperature sum models to predict egg-laying in *Melolontha*. By applying both models, our results are in accordance with Richter (1964a), who stated that the beginning of egg-laying could be expected as soon as a threshold of 73 dd (base temperature 6.5°C) and 71 dd (base temperature 7°C) is reached, respectively. Thus, in the context of the present study both models are deemed suitable for the prediction of egg-laying and are regarded as a useful tool for the precise timing of control measures in order to prevent cockchafer females from oviposition.

Oviposition in cockchafers is known to take at least 2–4 days whereas the depth the egg are laid depends on soil texture and humidity. In our study area, where dry and sandy soils prevail, the egg batches were found at a depth of 15–20 cm which is in line with the findings of Švestka (2009). After oviposition, females may leave the soil again for a second or even third maturation feeding (Vogel 1955). Our findings suggest that female fecundity depends on the body size, i.e. on the body size and certainly on nutritional condition of the grubs prior to pupation. The mean number of eggs ripened during the first and second maturation feeding was observed to be 24–25 eggs (ø 2–2.1 eggs/ovariole) and 14–15 eggs (ø 1.2–1.3 eggs/ovariole), respectively, which is less compared to previously published research (e.g. Schneider 1952b: 1st batch 3–4 eggs/ovariole; 2nd batch 2–3 eggs/ovariole; Vogel 1955: 1st batch 2.3–3.0 eggs/ovariole; 2nd batch 2 eggs/ovariole; Schuch 1938 [laboratory]: 1st batch ø 28.8 eggs; 2nd batch ø 21.8 eggs). The reasons for this have not been known until now. Population density (competition), weather conditions during egg maturation, composition of the food of the grubs (possibly expressed as body size), and nourishment of the female beetles might be factors determining female fertility. Reduced fecundity might be an indicator of reduced fitness and possibly population decline. In the present case, however, this is very unlikely to be the case, as the respective populations are quite 'young' and still in the phase of population growth. Moreover, food shortage is currently very unlikely to occur.

Light traps have been successfully used in the monitoring of cockchafer swarming flights (Reichholf 1979, 1985, 1993; Švestka 2006, 2007, 2010; Trotuş et al. 2013). It became apparent that male cockchafers outnumber the females at the light trap (Reichholf 1979, 1985; Švestka 2006, 2007, 2010), a phenomenon which was also observed in the present study. Swarming flights at dusk are performed by unpaired males in search of females (Ruther et al. 2001; Reinecke et al. 2006). Male cockchafers are guided by volatile leaf alcohols and sex pheromones released by the females (Ruther et al. 2001; Reinecke et al. 2002) which remain on the leaves for maturation feeding. Thus, the flight activity is very high in male cockchafers but not in females, except for pre-feeding flights, oviposition flights, and post-oviposition flights. These are the periods when most of the females were caught in the light trap(s) – independently of ambient temperatures and mainly during the dusk period when the attractiveness of light traps is not at its maximum. This indicates that the females were trapped rather randomly when they got in close vicinity of the light trap(s) – namely during (1) their pre-feeding flights or their post-oviposition flights from the soil to the canopy after hibernation or egg-laying and (2) during their oviposition flights in the opposite direction – rather than being attracted from their feeding sites at greater distances. Indeed, dissection of female beetles revealed that most of the females collected at the light trap(s) carried ripe eggs. The remaining proportion of the females

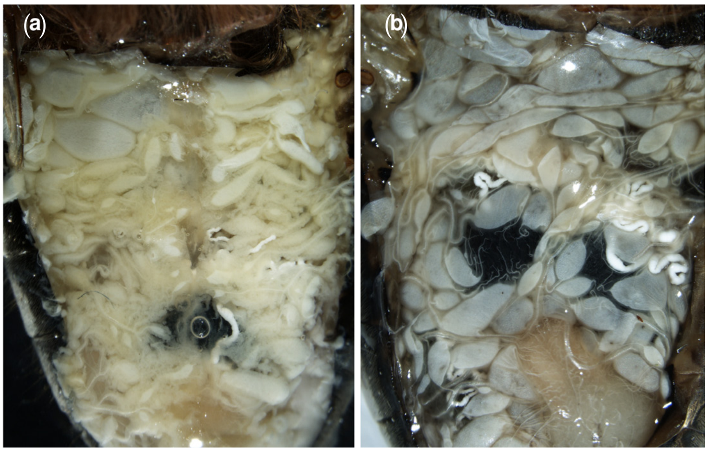

Fig. 10. The abdominal fat body of *Melolontha* prior to hibernation in the soil in autumn (30 October) (a) and after emergence from the soil in spring (16 April) (b). The fat body is located around the spiracles. It is apparent that the abdominal fat storage is nearly depleted at the end of the hibernation period (photos: E. Wagenhoff)

trapped was immature, many of them shortly after deposition of their first egg batch. On the contrary, hardly any female was attracted during the process of egg maturation (i.e. carrying oocytes of medium size) even though ambient weather conditions were warm and dry, usually facilitating flight activity in insects. This indicates that the female flight activity in cockchafers is very low during the physiological state of oogenesis. According to Wheeler (1996), activity and oogenesis may compete for nutrients and energy, which might be an explanation for the observation that the flight activity during egg maturation is quite low. As abdominal fat storage in cockchafers is conspicuously reduced after the hibernation period (Fig. 10), females need to feed on leaves to mature their eggs (Scheidter 1926; Schwerdtfeger 1928; Schuch 1938; Fels 1975).

As long as immature females are prevented from feeding, they do not produce any (own unpublished observations) or hardly any eggs (Keller et al. 1995), clearly indicating that oogenesis in adult cockchafers is a nutrient-limited process which is triggered only if sufficient food is consumed. In this regard, the mean female body weight was observed to continuously increase at the same time as egg maturation proceeds, which is in consistence with the observations made by Vogel (1955). The first oviposition flights were observed as soon as a plateau in the female body weight had been reached. Provided that females appear from the soil quite synchronously, the course of oogenesis could be roughly estimated by continuously weighing a representative sample of female cockchafers collected from the canopy. On the other hand, the mean body weight in male cockchafers stayed on a similar level throughout the entire observation period, indicating that nourishment primarily ensures the replenishment of energy demands needed for swarming and mating. Contrary to the females, the number of males trapped depended on ambient air temperatures and increased with decreasing light intensity, i.e. increasing attractiveness of the light trap(s), illustrating their higher mobility in the adult stage. Minimum temperatures for swarming flight activity are 8–9°C (Schwerdtfeger 1981; Burchard 1988) while swarming culminates at 15–23°C (Švestka 2010). Male swarming flights as well as female pre-feeding flights, oviposition flights and post-oviposition flights are performed around sunset and at dusk which might be an adaptation to reduce the pressure from diurnal avian predators. According to the findings of Labhart et al. (1992), orientation during cockchafer migratory flights is mediated by skylight polarisation which is particularly conspicuous at twilight (Able 1989) and persists until one hour after sunset. The onset of swarming is triggered by decreasing light intensity (Niklas 1974) and thus, male swarming is postponed continuously as days get longer from early April to the end of May. The same was reported by Richter (1962) and Niklas (1974).

CONCLUSIONS

In conclusion, the main issues of the present study can be briefly summarised as follows:

– The combined usage of soil eclectors and light traps proved to be appropriate to trace adult emergence from the soil and female oogenesis in cockchafers.

– Male cockchafers started leaving the soil first when temperatures in the upper soil layer were approximately 10°C.

– Peak emergence from the soil took place quite synchronously 1–2 weeks after the first swarming flights had been detected. It occurred in good temporal coincidence with the foliation of cockchafers' main host trees, namely oak and beech.

– The air temperature sum models of Decoppet (1920), Horber (1955), and Richter (1969) proved fairly satisfactory for the prediction of the onset of the swarming period. Swarming could be predicted with a maximum discrepancy of one week compared to our observations in the field.

– The models by Richter (1962, 1964a) proved satisfactory for the prediction of the duration of maturation feeding and the onset of the egg-laying period.

– The onset of the first oviposition period was observed 12 and 13 days after the first detection of swarming flight activity or 4 and 6 days after the earliest detection of female beetles in eclectors at mean air temperatures of 11.5°C and 13.3°C during that period.

– Female fecundity depends on the body size, i.e. certainly on the nutritional condition of the grubs prior to pupation.

– The mean number of eggs ripened during the first and second maturation feeding was 24–25 eggs (ø 2–2.1 eggs/ovariole) and 14–15 eggs (ø 1.2–1.3 eggs/ovariole), respectively.

– The number of female cockchafers attracted to the light trap(s) peaked at dusk and at the time when oviposition flights culminated, independently of ambient air temperatures. Hardly any female could be attracted during the process of oogenesis, i.e. maturation feeding.

– By contrast, the number of male cockchafers attracted to the light trap(s) continuously increased after the termination of swarming flight activity when darkness fell. There was a strong correlation between the number of males trapped and ambient air temperatures during the light trap exposure.

Acknowledgements

The authors would like to thank Manfred Dick and Edeltrud Bruckert for practical support, Lars Henke (GeoOmnia) for technical support, and Hansjochen Schröter for his expert contribution.

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Received for publication January 10, 2014
Accepted after corrections April 3, 2014

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