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Influence of Illumination and Polarized Moonlight on Light-Trap Catch of Caddisflies (Trichoptera)

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Abstract

The study analysed the potential effects of moon phases on the light-trap catches of eight species from seven Trichoptera families. The light-traps operated between 1981 and 2005 at ten Hungarian sampling sites. Relative catches calculated from daily collected data were arranged by the moon phase angle groups within lunar cycle. Linear and non-linear regression analyses were carried out to test the influences of two moonlight variables (illumination of the moon and rate of polarized moonlight) and the collecting distance changing with moon phase angle groups on the averaged relative catch. The relative catch level of caddisflies significantly varied in a species-specific way to changing moonlight characteristics through the lunar month. Two species showed a rising trend of catch levels with increasing moonlight illumination around the full moon period. Only one species expressed significantly increasing relative catches by the increasing theoretical collecting distance caused by the decreasing moonlight illumination between full and new moon. The study demonstrated for the first time the effect of increasing polarized moonlight in the first and last quarter on the flying activity of five caddisfly species. Supposedly, caddisflies use these moonlight characteristics as orientation cues increasing the number of flying and, consequently, captured adults.

Keywords*: Caddisflies, Light-Trapping, Polarized Moonlight, Illumination, Moon Phase, Orientation*

1. Introduction

Caddisflies are frequently represented by more abundant assemblages among aquatic insect groups; consequently, their larval and adult populations contribute to several important ecosystem functions. Caddisfly larvae serve as food base for fishes and other aquatic predators (Giller & Malmqvist, 1998 and Shubina, 2006), they intensively take part in the decomposition of organic matter (Giller & Malmqvist, 1998 and Graca, 2001), and they are widely used as bioindicators in water quality assessments (Chantaramongkol, 1983; Usseglio-Polatera & Bournaud, 1989 and Stuijfzand et al, 1999). During their flight to inland, the emerging caddisfly adults may serve as preys for many invertebrate (insects, spiders etc.) and vertebrate (e.g. frogs, lizards, bats, birds etc.) predators living in the surrounding vegetation (Chan et al, 2007). This dispersal process contributes to a considerable nutrient, matter and energy flux from the lotic and lentic aquatic ecosystems to the terrestrial ecosystems (Gratton & Zanden, 2009).

Several collecting methods were developed to obtain large quantitative samples in order to study these functional roles of adult caddisflies. One of the best of these methods is light trapping e.g. thousands of adults were collected in the study of Svensson, 1974 and Almeida & Marinoni, 2000. This trapping method has been extensively used by trichopterologists from temperate areas (e.g. Crichton, 1960; Svensson, 1974; Malicky, 1981; 1991; Usseglio-Polatera & Bournaud 1989; Waringer, 1989 and Kovats et al, 1996), Mediterranean aquatic habitats (e.g. Bonada et al, 2004 and Diken & Boyaci, 2008) and from subtropical/tropical regions (e.g. Corbet, 1958; Almeida & Marinoni, 2000 and Chan et al, 2007).

The light-trap is the most commonly used sampling device to study the flight characteristics, swarming period, population dynamics, or daily activity of nocturnal insects at different (from daily to yearly) time scales (Nowinszky, 2003). The Hungarian light-trap network supplied a huge scientific material over the past five decades for entomological basic research, plant protection prognostics and environmental protecting research (Szentkirályi, 2002 and Nowinszky, 2003). However, the effectiveness of light-trapping as an insect sampling method was influenced by many environmental variables from meteorological to cosmic factors.

Meteorological elements are the most known environmental factors influencing the light trap collection of caddisflies. Several investigations were carried out to measure the effects of various weather variables, like precipitation, wind speed, cloud cover, relative humidity, and night air temperature (Mackay, 1972; Usseglio-Polatera & Auda, 1987; Waringer, 1991; 2003 and Smith et al, 2002). While these abiotic factors influenced more or less the frequency of take-off and the timing and duration of flight (Waringer, 1991), most studies indicated that only air temperature had a highly significant effect on the catching success. Among the abiotic variables one of the most interesting environmental effects is caused by the periodic change in moonlight during lunar cycles. The influence of the moonlight on the catches of light-traps has been examined for decades (Nowinszky, 2008). In one of the earliest light-trapping studies, Williams (1936) found that much fewer insects were collected at full moon compared to new moon. Williams (1936) established two reasons, which may be responsible for lower catch levels at full moon periods: (1) increased moonlight reduces the flying activity of insects, consequently, a smaller rate of active population will be accessible for the light-trap, or (2) the artificial light of the trap collects moths from a smaller area in the concurrent moonlit environment. Based on latter concept, several researchers calculated collection distances for different light-trap types under the variation of lunar cycle (Dufay, 1964; Bowden & Morris, 1975 and Nowinszky, 2008). Bowden & Morris (1975) made some corrections for daily catches by an index calculated from the changes of collecting distance during lunation.

However, other studies reported increasing captures of light-traps during full moon, a phenomenon that should reflect an increased insect activity in some cases. The possible moonlight effects on insects sampled by light-trapping were published by Nowinszky (2008) in a detailed review.

Horváth & Varjú (2004) and Warrant et al (2006) documented in detail that many insects are able to use the polarization pattern of the sky in daytime and at dusk – formed by the setting sun and moon – for spatial orientation. Nowinszky et al (1979) and Danthanarayana & Dashper (1986) recorded maximal light-trap catches of some moth species in the first- and last-quarter of moon, when the polarization proportion of moonlight is the highest. Based on this catch pattern Nowinszky et al (1979) suggested that the increasing rate of moonlight polarization is used as an orientation cue by night-flying insects, consequently, in the first- and last-quarter more individuals will be active elevating the catching probability.

Gál et al, (2001) investigated the polarization pattern of the nocturnal sky at full moon, which was practically identical to that of the diurnal sky, when the zenith distance of the sun and the moon was the same. Important experiments by Dacke et al (2003) proved that the African scarabid beetle (*Scarabeus zambesianus* Péringuey) is able to navigate with the use of polarization sky pattern of moonlight. They later concluded that night-active insects may be extremely sensitive to detect the sky polarization pattern of moonlight, since they navigated with the same precision under the pale moonlight intensity (Dacke et al, 2011 and Warrant & Dacke, 2011).

Besides polarized moonlight and perhaps polarization pattern of the night sky, many aquatic insects are also able to detect their habitats by the perception of linearly horizontally polarized light reflected from the water surfaces. Detailed studies discussed that apart from various taxonomic groups of aquatic insects, Trichoptera use horizontally polarized light reflected from natural aquatic (Schwind & Horváth, 1993; Horváth 1995a; b; Horváth & Gál, 1997 and Horváth & Varjú, 1997) or artificial surfaces (Horváth & Zeil, 1996; Kriska et al, 1998 and Bernáth et al, 2001) for navigation. For example, Kriska et al, (2008) documented that the caddisfly *Hydropsyche pellucidula* (Curtis) can be attracted *en masse* to the vertical glass surfaces of buildings near the river. Their experiments showed that glass surfaces can reflect horizontally polarized light so strongly that they were detected by caddisflies as water bodies (Kriska et al, 2008 and Horváth et al, 2010).

The daily distribution of flight activity is an important aspect in the study of potential moonlight effects on caddisflies because the nightly duration of the moon disc staying above the horizon use to change during the various quarters (Nowinszky et al, 1979 and Nowinszky, 2008). Caddisflies may have very different type of daily activity patterns. Many trichopteran species fly exclusively in daylight (Flannagan, 1978 and Cobb et al, 1981). Most of the caddisflies are active during evening or night, but some species have a daily bimodal activity pattern (Lewis &

Taylor, 1964). Other studies reported that the swarming of caddisfly adults starts mainly after dusk and peaks before midnight during early or late evening hours but the flying of many species continues till dawn (Tshernyshev, 1961 and Jackson & Resh, 1991). Jackson & Resh (1991) monitored the daily flight pattern of three caddisfly species using female sex pheromones to attract males: *Dicosmoecus gilvipes* (Hagen) (Limnephilidae), *Gumaga nigricula* (McL.) (Sericostomatidae) and *Gumaga griseola* (McL.). They found that the light intensity influenced the flight activity of these species but not their flight periodicity.

According to Nowinszky (2008), if the insects are able to navigate by the polarized moonlight, it can not limit the collection of light-trap. The collection radius may influence the catch level only if the environment is free of light pollution and when the collected species are able to fly larger distances. Mackay (1972) reported that the number of caddisflies (*Pycnopsyche* spp, Limnephilidae) caught by BL (Black Light) trap was low on nights of full moon, especially, when the moon disc was above the horizon. Corbet (1958 and 1964) collected African Plecoptera, Ephemeroptera, and Trichoptera over a hundred consecutive nights using Robinson-Type light-traps (125W mercury vapour bulbs) on the shore of Lake Victoria. Only four of the 37 species showed a periodical fluctuation in the number of individuals corresponding well to the changes of the lunar phases. In his study, the timing of mass emergence of adult caddisfly *Athripsodes ugandus* Kimmins (Leptoceridae) followed the periodic changes in lunar cycle, specifically, an activity peak was found in the first and last quarter. He proposed that these catching peaks reflect the emergence pattern of adults influenced by moonlight rather than changes in the catching ability of light-traps (Corbet, 1958 and 1964). Bowden (1973) also suggested that peak periods of oviposition and emergence of some insects could be influenced by photoperiodism determined by the amount, duration and distribution of moonlight. According to Harris (1971), crepuscular Trichoptera could not be caught by the light-trap when the reflected solar light was greater than sixteen cd. The swarming of caddisflies started when the light intensity dropped below four cd, a threshold serving as a cue for beginning of flying (Harris, 1971).

Within the Hungarian light-trap network, some traps operating near different aquatic habitats collected rich caddisfly materials in the last decades. From these trapping materials we selected the most abundant Trichoptera species to evaluate how flight patterns are modified by periodic changes of moonlight factors. Light-trapping investigations (Nowinszky et al, 1979 and Nowinszky, 2008) suggested that the most effective moon variables were the reflected moonlight illumination and the polarized rate of moonlight. The illumination by the moonlight can influence the capture level in two ways during the lunar cycle (Williams, 1936): (1) the rising moonlight intensity directly increases/decreases the number of flying insects primarily during the maximal illumination in the full moon phase, (2) the rising moonlight intensity decreases the effective trapping distance competing with the artificial light source and thus the number of captured insects is the lowest around full moon and highest in the new moon phase. The rate of direct polarized moonlight has two increasing periods with peaks of 6.6% in the first and 8.8% in the last quarter. Catch peaks in the number of flying moths and beetles corresponding to the periods with higher proportion of polarized moonlight were first documented by Nowinszky et al (1979). The reaction of insects to these moonlight changes may be species-specific as it was found in numerous cases (Nowinszky, 2008). The aim of present study was to analyse and describe the possible influences of the moonlight illumination, the polarization rate of moonlight and the change of collecting distance during the lunar cycle on the light-trap catches of several caddisfly species.

2. Material and Methods

2.1. Collecting Sites and Characteristics of Light-Trappings

Light-traps collected the investigated caddisflies at the following sites (near Hungarian villages or towns) and time periods:

Szilvásvárad (48.64N; 20.23E): 1980, Vöröskő-völgy (48.34N; 20.27E): 1981-1982, Dédestapolcsány (48.11N; 20.28E): 1988, Maroslele (46.27N; 19.35E): 2001, Fülöpháza (46.89N; 19.44E): 2001-2002, Csongrád (46.71N; 20.14E): 2003-2005, Tiszakóród (48.10N; 22.71E): 2003-2005, Tiszaroff (47.39N; 20.44E): 2003-2005, Tiszaszőlős (47.55N; 20.71E): 2003-2005 (Kiss, 2003).

The light source of the applied Jermy-type light-traps was a 100W normal white light electric bulb hanged under a metal cover (Ø: 1m) at 200 cm height above the ground. Collections were conducted by modified Jermy-traps near Fülöpháza and Maroslele using a compact fluorescence light source (Philips PL-T 42W/830/4p). In each case chloroform was used as a killing agent. The traps were operated through every night during the season from April until October.

2.2. Species Investigated and Their Catching Data

For our analyses the light-traps produced suitable data sets only from 8 species of the sampled caddisflies as it follows. Some characteristics of these caddisflies are based on works of Kiss (2003), Malicky (2004) and Graf et al (2008).

2.3. Data of the Moon-Phases, Polarization of Moonlight and Collecting Distances

The mean revolution time of the moon on its orbit around the Earth is 29.53 days. This time period is not divisible by entire days, therefore, we rather used phase angle data. For every midnight of the flight periods (UT = 0 h), we have calculated phase angle data of the moon. The 360° phase angle of the complete lunation was divided into 30 phase angle groups. The phase angle group including the full moon (0º or 360º) and ± 6º values around it was called 0. Beginning from this group through the first quarter until a new moon, groups were marked as -1, -2, -3, -4, -5, -6, -7, -8, -9, -10, -11, -12, -13 and -14. The next division was ±15, including the new moon. From the full moon through the last quarter to the new moon the phase angle groups were marked as 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13 and 14. Each phase group consists of 12° (Nowinszky, 2003). These phase angle groups are related to the four quarters of lunar cycle as it follows: full moon (-2 to +2), last quarter (3 to 9), new moon (10 to -10) and first quarter (-9 to -3).

Because the increasing moonlight intensity can decrease the catching radius of a light-trap (Nowinszky, 2008), the required illumination of the moon corresponding to each night of moon phase angle divisions was calculated by our custom-made computer program (Nowinszky & Tóth, 1987). This software calculates the illumination (lx) originating from the sun at dusk, the light of the moon and the nocturnal sky for any given geographical locality, day and time, including some corrections for cloudiness. The collecting distance (actual effective catching radius of a trap) was calculated from the environmental illumination components by the following formula:

$$r_0 = \sqrt{\frac{I}{E_S + E_M + E_{SS}}}$$

Where: r_0 = collecting distance, I = illumination from the bulb of trap, E = the illumination coming from the environment consisting of the light of the setting or rising sun (E_S), the moon (E_M), and the starry sky (E_{SS}).

The collecting distances for Jermy-type light-trap were calculated for each phase angle groups and given in Table 1.

2.4. Data Processing and Statistical Analysis

Basic data was the number of individuals caught by one trap in one night. The number of basic data exceeded the number of sampling nights because in most collecting years more light-traps operated synchronously. In order to compare the differing sampling data of a species, relative catching values were calculated from the number of individuals. For each examined species the Relative Catch (RC) data were calculated for each sampling days per site per year. The RC was defined as the quotient of the number of individuals caught during a sampling time unit (1 night) per the average catch (number of individuals) within the same generation relating to the same time unit. For example, when the actual catch was equal to the average individual number captured in the same generation/swarming, the RC value was 1. Since, most caddisfly species showed more or less continuous swarming over the seasons with overlapping generations, we use the daily average of total catches in a year in RC calculations.

The RC values of a species from all sites and years were arranged into the proper phase angle groups. Then 3-point moving averages were calculated from the RC values and arranged by the consecutive phase groups for each species. In the first step, the greater catch peaks were detected in temporal patterns of RC ranging through the phase angle groups of lunation. The mean of the peak RC and RCs of the next 3-3 phase groups on both sides of the peak was compared with t-test to the mean of the remaining phase groups' RC values. If the t-test produced a significant difference between the two RC means then we considered the possibility that the higher catching level within the peak was promoted by one of the moonlight variables investigated. In order to identify the potential influencing factor, the allocation of each significant catching peak in the lunar cycle was compared with the pattern of moonlight characteristics (illumination level, percent of polarized moonlight) and effective trapping distance variation by phase angle groups.

The moonlight variables were not available in all phase angle groups (e.g. illumination or polarized moonlight in new moon phase, therefore the regression analyses were carried out for those phase angle groups where the moonlight variables could be calculated.

Between moonlight variables (x-axis) and mean RC values (y-axis) regression analyses were made using linear and non-linear fitting. The regression equations yielding the best fits were given in the figures with the R^2 values and probability levels.

3. Results

3.1. Changes in Moonlight Variables and Effective Trapping Distance in the Lunar Month

The degree of illumination varied periodically between the new and full moon phase during the synodic month (29.53 d). The illumination had a maximal value at full moon (0 phase group: 0.179 lx) and a minimal value at new moon (15. phase group: 0.0012 lx). The multiplication factor between the minimal and maximal illumination was 15. The calculated effective radius of trapping corresponding to the changing moonlight illumination varied between 23.2 and 365.1 metres equivalent to a 15.7 times increase (Table 2).

The ratios of mean peak RC and mean of other phase groups were 2.2 and 2.0 in case of *H. instabilis* and *O. albicorne*, respectively.

The fourth type was found in the catching patterns of *L. lunatus* and *H. digitatus* characterised by a definite RC peak in the first quarter between -11 and -7 phase groups.

Table 1. Trichoptera Species Investigated and Their Catching Data

Trichoptera Species	Collecting Sites	Years	Individuals	Observing Data
Rhyacophila fasciata (Hagen, 1859)	1	2	132	64
Psychomyia pusilla (Fabricius (1781)	1	2	718	91
Ecnomus tenellus (Rambur, 1842)	7	8	24763	1105
Hydropsyche instabilis (Curtis, 1834)	4	3	5539	205
Odontocerum albicorne (Scopoli, 1763)	2	2	369	89
Limnephilus lunatus (Curtis, 1834)	1	2	309	58
Halesus digitatus (Schrank, 1781)	2	3	978	105
Agraylea sexmaculata (Curtis, 1834)	4	4	887	81

The proportion of linearly polarized moonlight (Table 2) has a bimodal temporal pattern with two peaks during the lunar cycles. One of the maximal polarization rates is reached in the first quarter between -10 and -7 phase groups (6.57%), and the second peak can be recorded in the last quarter between 7 and 10 phase groups (8.76%).

3.2. Types of Catching Pattern in the Lunar Cycle

After the detection of significant catching peaks, we grouped the caddisfly species on the basis of their similar type of flying patterns expressed through lunar cycle. Next types of catching patterns were identified. Two species, *R. fasciata* and *P. pusilla* showed a clear catching peak at full moon (0±3 phase groups) compared to the mean RC of other phase groups.

E. tenellus demonstrated another catching pattern with a characteristic bimodal RC distribution over the lunar cycle. The light-trap catches of this caddisfly peaked in the first quarter (range: -10 and -7 phase groups) and the last quarter (range: 6 and 8 phase groups). Significant difference was detected between mean RC values of peaks and other phase groups ($t = 3.792$, $P < 0.001$). The ratio of peak to mean of other RCs was 1.8 in the first and 1.6 in the last quarter.

The third type of RC pattern in lunar cycle was shown by *H. instabilis* and *O. albicorne* with a significant RC peak allocated in the last moon quarter between 7 and 11 phase groups. The RC peaks were significantly higher than the mean RCs of other phase groups for both *H. instabilis* ($t = 4.554$ $P < 0.001$) and *O. albicorne* ($t = 3.43$, $P < 0.001$).

These catching peaks differ significantly in *L. lunatus* ($t = 4.183$, $P < 0.01$) and *H. digitatus* ($t = 4.236$ $P < 0.001$) from the mean RC of other phase groups. The ratios of peak RC relative to the mean of other phase groups were 2.3 and 2.7 in *L. lunatus* and *H. digitatus*, respectively.

The last type of catching patterns was shown by *A. sexmaculata* with the highest trapping level in the moonless period of new moon (between 13-15 phase groups) and the lowest level during full moon (0±2 phase groups). The difference between the mean RCs of the new moon and other moon phase groups was significant ($t = 2.11$, $P < 0.05$). The ratio for mean RC of new moon compared to the mean of other moon phases was 2.9.

3.3. Results of Regressions between Moonlight Variables, Trapping Distance and RC

The results of regression analyses are illustrated in Figures 1-8. Only those regressions are presented in the figures, which produced significant effects on the light-trap catches by the above-mentioned pattern type of moonlight and trapping distance as independent variables.

The RC values of caddisflies *R. fasciata*, and *P. pusilla* were regressed against the illumination level around full moon because of the significant corresponded trapping peak (Figures 1-2). The significant positive slopes of regression lines reflect the increasing catches with the rising moonlight illumination around full moon between 0.1 and 0.18 lx. Illumination explained a greater part from the total variance of RC, as suggested by the high values of R^2 (> 0.6).

Table 2. Calculated Illumination, Polarization Rate of the Reflected Moonlight, and Collecting Distance Arranged by the Consecutive Moon Phase Angle Groups

Phase Angle Group	Illumination (lx)	Polarized Moonlight (%)	Collecting Distance (m)
15	0.0012	0.000	338.1
-14	0.0034	0.000	282.8
-13	0.0097	3.563	223.6
-12	0.0199	4.422	200.0
-11	0.0332	5.365	178.9
-10	0.0492	6.000	139.7
-9	0.0665	6.324	105.4
-8	0.0854	6.576	88.1
-7	0.1041	6.285	58.6
-6	0.1221	5.788	49.1
-5	0.1389	4.950	45.0
-4	0.1533	3.697	41.8
-3	0.1654	2.412	31.0
-2	0.1736	0.412	26.6
-1	0.178	0.115	23.2
0	0.1791	0.000	26.5
1	0.1772	0.115	31.9
2	0.1713	0.041	33.9
3	0.1618	2.511	36.5
4	0.1497	3.927	42.7
5	0.1345	5.412	49.9
6	0.1181	6.869	72.8
7	0.1001	7.941	90.1
8	0.0825	8.714	107.7
9	0.0646	8.765	126.5
10	0.0475	7.212	141.4
11	0.0321	6.083	163.3
12	0.0193	4.939	239.0
13	0.0097	0.000	282.8
14	0.0033	0.000	365.1

Note: *Phase angle groups of moon quarters: full moon = (-2 to 2), last quarter = (3 to 9), new moon = (10 to -10), first quarter = (-9 to -3); the illumination caused by the Moon; the collecting distance was calculated for Jermy-type light-traps used in this study*

The pattern of light-trap catches (RC) of five caddisfly species showed positive correlation with the rate of polarized moonlight either in the first, last or both quarters.

For the last case, an example was provided by *E. tenellus* with maximum catches both during the first and last moon quarters. The regression line on Figure 3 expressed increasing RC in response to the increasing rate of polarized moonlight from 0 to near 9%. Polarized moonlight above 6% seemed to cause greater RCs in particular (Figure 3). The significant effect of this moonlight component was underlined by R^2 values explaining more than 60% of total variance.

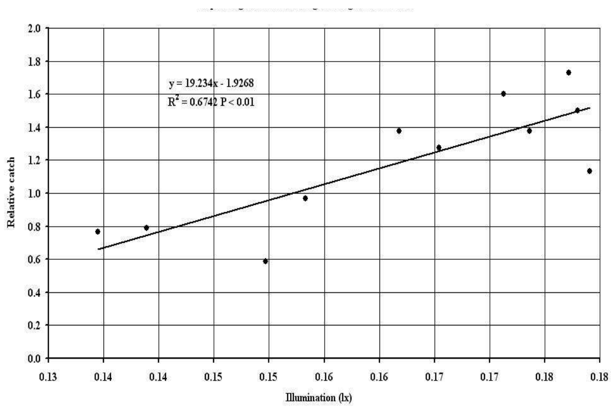

Figure 1. Changes in the Mean Relative Light-Trap Catch (RC) of *Rhyacophila fasciata* (Hagen) around Full Moon Depending on the Increasing Moonlight Illumination

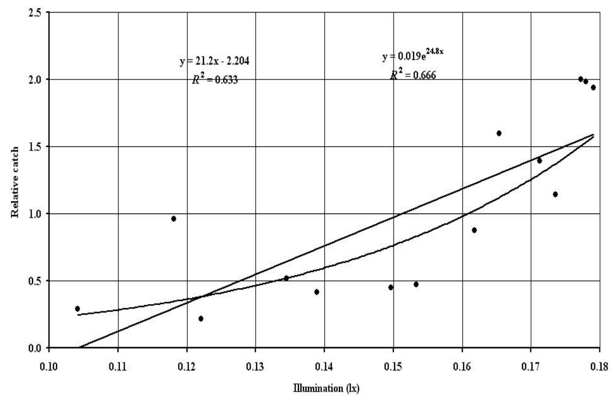

Figure 2. Changes in the Mean Relative Light-Trap Catch (RC) of *Psychomyia pusilla* (Fabricius) around Full Moon Depending on the Increasing Moonlight Illumination

The peak of relative catch level of *H. instabilis* and *O. albicorne* was associated with the maximum of polarized moonlight only in the last quarter. Based on this correspondence the regression showed a near linear significant fit of increasing catch depending on polarized moonlight for both *H. instabilis* (Figure 4.) with a high explanation of variance (R^2= 0.9) and for *O. albicorne* (Figure 5) with less explanation of variance (R^2= 0.45). For these two species the increasing trapping level was recorded between 2 and 9% rate of polarized moonlight.

Based on their RC pattern *L. lunatus* and *H. digitatus* seemed to be under influence of polarized moonlight peak only in the first quarter. Regression of RCs for both species (Figures 6-7) yielded significant linear dependence on the rate of polarized moonlight in the range between 2 and 7%. The ratio of variance explained by R^2 was 77% in *L. lunatus* and 52% in *H. digitatus*.

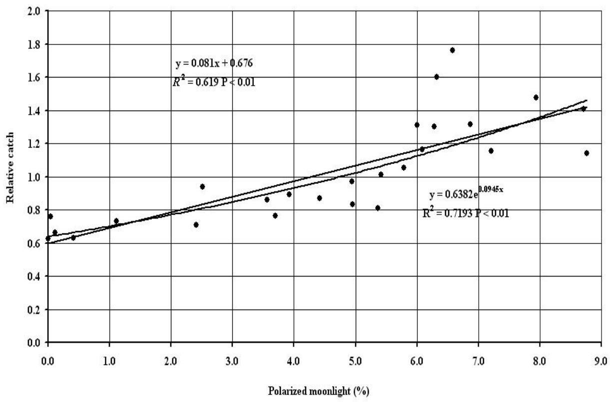

Figure 3. Changes in the Mean Relative Light-Trap Catch (RC) of *Ecnomus tenellus* (Rambur) Depending on the Increasing Rate of Polarized Moonlight in the First and Last Quarter within a Lunar Cycle

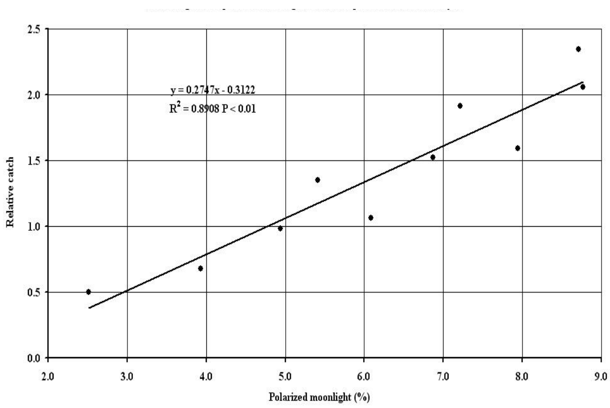

Figure 4. Changes in the Mean Relative Light-Trap Catch (RC) of *Hydropsyche* instabilis (Curtis) Depending on the Increasing Rate of Polarized Moonlight in the First and Last Quarter within a Lunar Cycle

Only one caddisfly species showed clear response to the changes of collecting distance during the lunar cycle. The regression of rising RC values of *A. sexmaculata* (Figure 8.) against the calculated increasing collection radius showed a significant linear relationship with R^2= 0.5. In Figure 8, the gradually decreasing level of illumination is also represented in parallel with the increasing trapping radius.

4. Discussion

For astronavigation nocturnal insects can potentially use several celestial cues such as the direct light of the bright moon disc, the circular sky pattern of polarized moonlight around the moon (atmospheric scattered light), or the constellation of stars (Wehner, 1984; Horváth & Varjú, 2004 and Warrant & Dacke, 2011). Insect species may be able to use more than one of these nocturnal orientation cues for navigation. Of these orientation cues insects can easily see the large and bright moon disc because its perception does not require a specialised visual system (Dacke et al, 2004 and 2011).

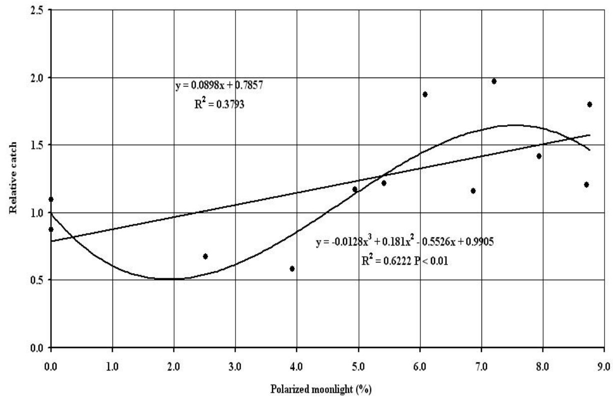

Figure 5. Changes in the Mean Relative Light-Trap Catch (RC) of *Odontocerum albicorne* (Scopoli) Depending on the Increasing Rate of Polarized Moonlight in the First and Last Quarter within a Lunar Cycle

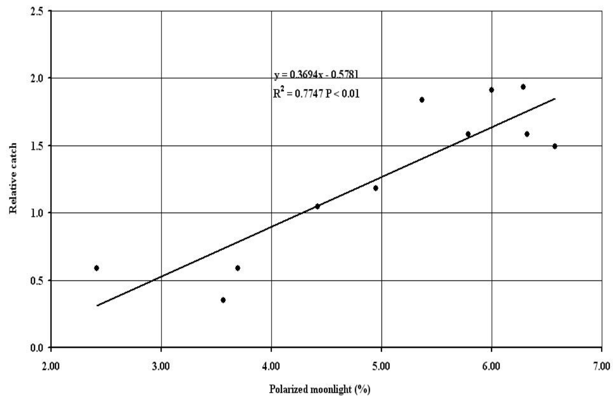

Figure 6. Changes in the Mean Relative Light-Trap Catch (RC) of *Limnephilus lunatas* (Curtis) depending on the increasing Rate of Polarized Moonlight in the First and Last Quarter within a Lunar Cycle

In order to explain our results on catch level variation during the lunar month, we assumed that (1) caddisfly adults use at least one moonlight characteristics as an orientation cue in certain periods of lunation and (2) if this way the navigation of caddisflies becomes safer and more precise, then a higher number of individuals can swarm during nights of a favourable lunar phase. Consequently, the probability level of captures by light-traps will also increase (catching peaks).

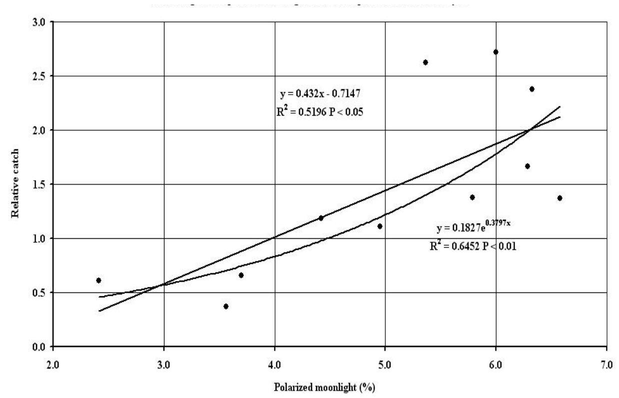

Figure 7. Changes in the Mean Relative Light-Trap Catch (RC) of *Halesus digitatus* (Schranck) depending on the increasing Rate of Polarized Moonlight in the First and Last Quarter within a Lunar Cycle

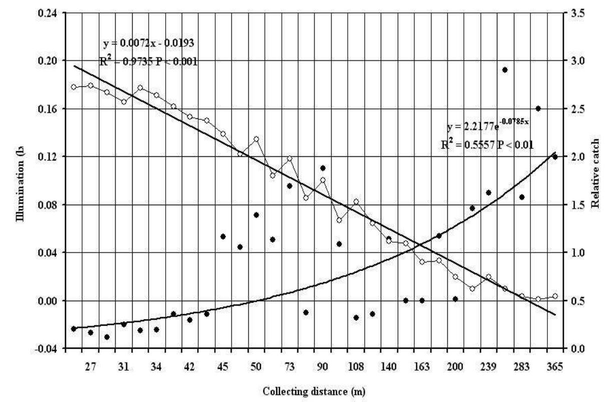

Figure 8. Changes in the Mean Relative Light-Trap Catch (RC) of *Agraylea sexmaculata* (Curtis) Depending on the Collecting Distance

4.1. Influence of Moonlight Illumination on the Catch Level of Caddisflies

The light-trap catches of two caddisfly species, *R. fasciata* and *P. pusilla* were positively correlated with the level of moonlight illumination, especially during the full moon period. The explanation for these significant catching peaks may be that the brightest full moon disc staying above the horizon throughout the whole night could be used as a compass for flying caddisfly adults (moon compass hypothesis). The full moon disc is bright and effective enough at infinity to be perceived as a point-like light source serving for the navigation (keep a flying direction) of nocturnal insects like these caddisfly species (Wehner, 1984). Although the theoretical effective light-trapping area is expected to be the smallest during the full moon period, the significant catch peak of these caddisfly species recorded at full moon reflects the increasing effect of illumination on the flight activity level (higher number of flying individuals, longer flight period during nights).

4.2. Influence of Effective Trapping Distance on the Catch Level of Caddisflies

Among caddisfly species investigated only *A. sexmaculata* had maximum catch level near new moon and minimal catch around the full moon period. This catch pattern supports the idea about the effective collecting distance, which depends on the competition between the fixed brightness of the trap's light-source and the changing moon light illumination during the lunar month (Williams, 1936 and Bowden & Morris, 1975). The caddisfly *A. sexmaculata* inhabits standing waters (Graf et al, 2008), thus during its dispersion the adults tends to navigate in longer distances when they search for aquatic habitats. This species was characterised as a strong flier caddisfly by Svensson (1974). Therefore, a less direct dependence of spatial navigation on periodic moonlight changes may be an important adaptive trait of *A. sexmaculata*. Thus, the moonlight illumination can only indirectly influence the catch probability of this caddisfly via changes of effective trapping radius.

The small difference between the two peaks of polarization percent is caused by the dissimilarity of reflected light characteristics from the two moon hemispheres (Nowinszky et al, 1979). At full moon (phase group: 0) the moonlight is not polarized (0%) but in a narrow interval (± 2.5 d) the polarization plane of moonlight turns over (Pellicori, 1971 and Nowinszky et al, 1979).

4.3. Influence of Polarized Moonlight as a Possible Navigation Cue to Catching Level

Analyses of the collecting patterns of caddisflies revealed clear peaks of the light-trap catches of five species in relation with the increasing percent of polarized moonlight at the first and last quarter of lunar month. These peaks of light-trap catches corresponded to a significant two-fold increase (range: 1.6-2.7) in the number of swarming caddisfly individuals. Among the studied species *E. tenellus* responded to both peaks of polarized moonlight in the lunar cycle. The other caddisflies reacted only to the polarization maximum in the first (*H. digitatus* and *L. lunatus*) or last quarter (*H. instabilis* and *O. albicorne*). Since the captures of caddisflies by light-trapping decreased but never ceased at minimal or no rate of moonlight polarization, we propose that this moonlight variable only periodically contributes to the accuracy of orientation and the number of active adults increases via this mechanism.

Species-specific circadian rhythm of nocturnal swarming activity of caddisflies may serve as an explanation for these different responses given to polarized moonlight. The more or less synchronized flight of adults in the same period of nights can guarantee a successful reproduction (mating, oviposition) and mass dispersal for most nocturnal caddisfly species, when visual observation is difficult. Some caddisfly species are characterised with a flying peak allocated before or after midnight hours, while others continuously swarm through the night (Tshernyshev, 1961; Lewis & Taylor, 1964; and Jackson & Resh, 1991).

Within the lunar month the moon disc is visible in different parts of the night depending on the actual moon phase. During the first quarter the moon is above the horizon mainly in the hours before, while in the last quarter mainly after the midnight period. From this fact we conclude that some caddisflies like *E. tenellus*, probably fly throughout the night, so it can see the moon disc both in the first and the last quarter and is able to use the polarized moonlight as navigation cue. Because this caddisfly species is a standing water inhabitant, its adults must fly longer distances to find a required pond, lake etc. Similar catching pattern was recorded for another caddisfly i.e. *A. ugandus* with peaks in first and last quarter (Corbet, 1964). Caddisfly species with a catch peak only in the first quarter (*H. digitatus* and *L. lunatus*) may have a swarming period allocated predominantly to the first half of night, while species with catch peaks in the last quarter (*H. instabilis* and *O. albicorne*) may have a flying period in the second half of nights.

More studies have documented that the aquatic insects, involving caddisflies use the horizontally, linearly polarized light reflected from water and other flat surfaces to detect their habitat (Horváth & Varjú, 2004; Kriska et al, 2008 and Horváth et al, 2010).

Although the upstream and downstream movements of caddisflies are well-known, relatively few field experiments were conducted to document the lateral dispersal flight of adults. Using various trapping systems the samplings of adults were carried out at different distances in the surrounding vegetation: <100 m to 1500 m (Crichton, 1965; Svensson, 1974; Jackson & Resh, 1989; Kovats, et al, 1996; Collier & Smith, 1998; Griffith et al, 1998; Lynch et al, 2002; Petersen et al, 2004; Chan et al, 2007 and Winterbourn et al, 2007). These assessments of inland dispersal of adult caddisflies showed rapid declines in abundance levels as the distances increased from the waterside. However, the trappings extended between 150-5000 m showed that caddisflies may disperse to terrestrial habitats of larger distances (Svensson, 1974 and Kovats et al, 1996). Similar results were found at our sampling sites, as thousands of caddisfly adults were captured at several hundred meters (100-580 m) or even 3.8 km away from the waterside. The dispersal flights of adults showed interspecific variation and were significantly influenced by the structural patterns of the surrounding vegetation as well as by the reproductive behaviour (Svensson, 1974 and Kovats et al, 1996). We think, the use of moonlight during these movements should be another orientation mode, especially for vagrant caddisfly species associated with standing waters. While the polarized light reflected by the water may be used by caddisfly adults for their compensation flight to keep their route above the stream surface or for detecting aquatic habitats, the changing moonlight characteristics should promote the orientation during travels of larger distances over the terrestrial landscape.

5. Conclusion

The results of these experiments support the concept that our studied caddisfly species were able to perceive the very low intensity of direct polarized moonlight and use it for navigation. The increased number of flying individuals with the improved orientation at polarization peaks produced higher catching levels in the first and last quarter. We presented here for the first time a possible navigation role of the direct polarized moonlight during the flight of caddisflies. We think that this moonlight variable is only one of further environmental cues contributing to the efficiency of nocturnal navigation and it has an evolutionarily advantage for caddisfly species with the synchronization of mating, egg-laying, or dispersion flights of adults.

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