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Night, light and flight - Light attraction in Trichoptera

Malin Larsson

Examiner, Lars Westerberg, Linköping University
Supervisor, Per Milberg, Linköping University

LINKÖPINGS UNIVERSITET

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Division, Department

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Författare
Author

Malin Larsson

Sammanfattning
Abstract

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Nyckelord
Keyword

Trichoptera, light attraction, artificial light, biodiversity, insects

Content

1 Abstract

Artificial light is an important and necessary part of our urban environment, but has become a threat to biodiversity. It can have substantial direct and indirect effects on populations of all kinds of organisms. While light attraction in bats and moths has been well studied other organisms such as Trichoptera have been largely neglected, despite Trichoptera being one of the most abundant insect orders in freshwater systems. The light attraction of Trichoptera was studied through seasonal data from three different locations in Sweden. The data was examined through meta- and regression analyses to compare catches in light traps and passive traps. The use of relative abundances excluded bias from the species with large populations, and the difference in individuals caught between passive traps and light traps. The results indicated that artificial light could affect Trichoptera populations. Unlike moths, female Trichoptera were more attracted to light than males and attraction to light varied between species. In both cases, size dimorphism could explain the variation. Day-, evening- and night-active species were all attracted to light, but the latter more so. Research has shown that a false flight activity can occur in day-active Trichoptera when a lamp is lit during night, which could explain the capture of day- and evening-active species in a light trap. In all, artificial light could alter Trichoptera populations, changing sex ratios and species composition. This impact should be considered when erecting light sources near waterways.

2 Introduction

Light plays a vital part of life on earth; it affects feeding behaviour and functions as a cue for predator avoidance (Perkin et al. 2011) and oviposition (Nowinszky et al. 2012). Light is also used for navigation and it is a well-known fact that some insects fly to light. Navigation by light is also common in other animals (Rowse et al. 2016). Two main hypotheses have been proposed to explain this behaviour: the open space theory and the compass theory (Altermatt et al. 2009). The open space theory states that insects aim for clearings and boarders of forests which are perceived as brighter at night (Altermatt et al. 2009). The compass theory states that nocturnal insects use celestial light sources, like the moon, to navigate (Altermatt et al. 2009). Using distant light such as starlight or moonlight for finding one’s way is possible because light rays travel in parallel lines. Keeping a constant angle to a distant light allows an organism to travel in a straight path (Frank 2006). When light instead come from a local source which has diverging rays, any organism keeping a constant angle to it will spiral around the light source eventually ending up at the lamp (Lloyd 2006). So, what happens when the world no longer becomes fully dark at night?

Artificial light has become an integral part of urban environments (Degen et al. 2016) and there have been rising concerns about its effect on nature. Attraction to light is a problem as insect species seem to lack the ability to resist the stimulus of light (Eisenbeis 2006). It has been shown that artificial light can decrease biodiversity as it changes insects' behaviour at night, such as reproduction and migration, but it can also have a direct lethal effect (Altermatt et al. 2009, Hölker et al. 2010, Perkin et al. 2011). The direct effect consists of burning, increased predation (Frank 2006, Altermatt et al. 2009), overheating, and dehydration (Frank 2006). It has been estimated that the death rate of insects at artificial light sources is approximately 33% (Eisenbeis 2006). Apart from the direct mortality, artificial light can potentially reduce populations indirectly by disturbing normal activity and dispersal (Eisenbeis 2006). Disturbance of normal activity could keep the organism from mating, reproduce and oviposit. More than 50% of moths approaching a light source stops on the ground and cannot escape the near zone of lighting (Eisenbeis 2006). A population can be demographically affected as young specimens are more likely to fly to light than older ones (Frank 2006). In all, artificial light pose a considerably threat for any organism it affects.

Studies of moths have revealed that there is a difference in light attraction between species and between sexes (Altermatt et al. 2009, Merckx et al. 2014). Light can for example affect sexes differently if one sex has a higher flight activity and thus a larger risk of passing an artificial light source (Altermatt et al. 2009). Sexual dimorphism is another factor which causes one sex to be more prone to fly to light, either by having eyes more sensitive to light or eyes larger than the other sex (Altermatt et al. 2009). Increased mortality for one sex could lower the effective population size by reducing the number of mating pairs or egg-laying females. The variation in light attraction can affect research and biomonitoring performed only with light traps as non-attracted species could be overlooked in such studies. Introducing artificial light to a new area could change species composition by increased mortality for some species but not others.

Light mainly attracts insects during darkness, so theoretically there should be larger impact during longer periods of darkness (Svensson 1972). This would implicate that catches in light traps should be smaller during brighter (shorter) nights. No studies on this have been identified. In northern Europe, nights can vary from being completely dark to completely light (due to midnight sun), depending on season and latitude. This makes the region ideal for surveying the effect of the nights' length on the phenomenon of light attraction.

The effect of artificial light can be particularly harsh on freshwater systems as people tend to live around fresh water (Perkin et al. 2014). Trichoptera (caddisflies) is one of the most abundant groups of freshwater insects (Roy & Harper 1981, Hirabayashi et al. 2011). Like 60% of all invertebrates, many of them are nocturnal (Hölker et al. 2010, Barnard & Ross 2012, Nowinszky et al. 2012, Gullefors 2016). This makes them a suitable taxon for studying light attraction. However, not all Trichoptera are night active and Svensson (1972) proposed that day-active species should not be attracted to light and thus would not be disturbed by artificial light. Until recently (Gullefors 2016), the diurnal patterns of Trichoptera species had not been classified and no previous tests of Svensson's hypothesis have been identified.

The aim of this study was to investigate how artificial light can influence Trichoptera species and their sex ratio. Are Trichoptera species attracted to light? As suggested by Svensson's (1972) hypothesis, are day-active species less attracted to light? Is one sex more attracted to light than the other? Furthermore, the study investigated if longer nights lead to a larger light trap catch.

3 Materials & methods

3.1 Study organism

The adults of Trichoptera resemble small moths, with wings held roof-like over the body. This stage is often short-lived and the main function is mating, dispersal and oviposition (Barnard & Ross 2012). The adults are terrestrial but they lay their eggs in or near water and the offspring proceeds through several water-bound larvae instars before they pupate and emerge (Barnard & Ross 2012). As larvae Trichoptera hold different niches; some species decompose larger plant material, while others can only handle microscopic particles (Williams & Feltmate 1992). Studies on periodicity have shown that Trichoptera are generally night-active and most active between about ten and midnight (Andersen 1979, Wright et al. 2013, Brakel et al. 2015).

Female Trichoptera are often larger than males (Jannot & Kerans 2003, Salavert et al. 2011), but in some cases males have longer wings (Gullefors & Petersson 1993). Wing length is also suitable as a measure of body size in Trichoptera (Gullefors & Petersson 1993). The sex ratio of Trichoptera is poorly known. Two studies on Trichoptera found male dominance in the light trap (Svensson 1972, Crichton & Fischer 1982) while two studies trapped more females than males (Harris 1971, Smith et al. 2002). Two of these studies compared attracting traps and passive traps with diverging results (Svensson 1972, Smith et al. 2002).

Many Trichoptera species are attracted to light (Barnard & Ross 2012) and this is a common method of collecting adult Trichoptera for entomological studies (Walker & Galbreath 1979). Collecting adult Trichoptera through light trapping is considered to be an efficient method for biomonitoring of water quality (Houghton 2006, Blinn & Ruiter 2013, Wright et al. 2013). Artificial light should have most impact during times when it is most efficient, which is when it is dark (Rich & Longcore 2006). Would this mean it only has effect on species active during night? Smith et al. (2002) found that some Trichoptera species were found in Malaise traps but not in the light traps and presented two alternatives; either that these species were diurnal or that they were not attracted to light. The research on the periodicity of Trichoptera has led to some species having a known circadian rhythm which allows for testing according to the classifications of day-active, evening-active and night-active species. To analyse if day-active species were less attracted to light, the diurnal activity pattern per species was taken from Gullefors (2016). Not all species found in the surveys had been analysed by Gullefors; these species were labelled unclassified.

3.2 Survey sites

Material was collected during 2016 at Pjältån, Norrköping municipality, Östergötland, Sweden, just downstream of Lake Näknen (Figure 1, Table 1). Pjältån has a small catchment area of 64 km^2 and with a modelled average flow of 0.5 $m^3\ s^{-1}$. The survey site encompassed a stretch of approximately 100 m with both traps set up at slight riffles. The waterway ran in a crevice and was heavily shadowed by deciduous trees and shrubs. A light trap (cf Olsson 1971), with a 15 W incandescent light tube, was set up on 3rd of April. A Malaise trap (cf Malaise 1937; modernized with plastic containers for capture in liquid) was set up upstream one week later. The traps were emptied weekly on Sunday afternoons until 30th October 2016, and then emptied a last time at December 18th. Data between 3-10 April and 19-26 June were excluded as the Malaise trap was not set up until April 11th and during June the jar accidentally fell out during collection. The light trap catches at 11-18 September might be underestimated as the timer on the light trap malfunctioned and the light tube might not have turned on properly every night.

Figure 1. Map over Sweden with sampling locations. (Modified by adding sampling locations, source: Lokal_Profil 2007)

A second set of data (Figure 1, Table 1) was collected during summer of 1972 and 1973 by Anders Göthberg at Rickleå, Robertsfors municipality, Västerbotten, Sweden. The river has a catchment area of 1 600 km^2 and a modelled average flow of 16.4 $m^3 s^{-1}$. Rickleå is a large waterway in an area forested with coniferous trees and is bordered by alder trees. The sampling point was approximately 1 km upstream the outlet to Bottenviken (the Baltic) and consisted of one light trap and one suction trap (cf Müller & Ulfstrand 1970). The light trap was set up on an open rock surface, with the suction trap set up some 15 m upstream in an area with shrubs. The traps were emptied every second hour and the data compiled to a weekly sum.

A third set of data (Figure 1, Table 1) was collected June - October 1974 by Anders Göthberg at Kaltisjokk, Jokkmokk municipality, Norrbotten, Sweden. Kaltisjokk was a tributary to the river Stora Lule älv but has since been completely drained. The watercourse had a catchment area of 90 km^2 and a modelled average flow of 1.2 $m^3\ s^{-1}$. The survey site encompassed a few hundred metres of fast flowing water not far below some waterfalls. The stream ran through a landscape with pines, spruce and birches. The sampling used light traps (cf Olsson 1971) and window traps. The traps were partly flooded 16-24 July and 6-21 August and these catches were excluded from analyses. The traps were emptied once a day until July 10th and later once every few days. Two pairs of traps were used from this location; the first pair (Kaltisjokk 1) was situated approximately 190 m and 240 m downstream of a bridge serving road 811, not far from the intersection with road 818. The second trap pair (Kaltisjokk 2) was situated 160 m and 190 m upstream of the bridge. In both instances, the light trap was situated upstream of the passive trap.

Table 1. Descriptive information of the survey sites.

	Pjältån	*Rickleå 1972*	*Rickleå 1973*	*Kaltisjokk 1*	*Kaltisjokk 2*
No of traps	Two	Two	Two	Two	Two
Period	259 days	152 days*	-	122 days*	121 days*
Type of traps	Light/Malaise	Light/Suction	Light/Suction	Light/Window	Light/Window
Year	2016	1972	1973	1974	1974
Coordinates**	6506552, 566763	7120240, 789249	7120240, 789249	7406670, 736631	7406670, 736631
Latitude	58	64	64	68	68

*during which Trichoptera were found (data not available for more details)
**Coordinates given according to SWEREF99 TM (N, E).

3.3 Sampling

Specimens were collected with light traps and passive traps in all five surveys. Few studies have compared the results from an attracting (light or pheromone) and a non-attracting (passive) trap (Scanlon & Petit 2008).

The passive traps were of different types at each location. The Malaise trap at Pjältån was similar to a tent with a central wall and a roof which is inclined both to the sides and longitudinally. Insects were trapped under the roof and ended up in a container at the highest corner of the trap. Samples at Pjältån were collected in propylene glycol and then preserved in 70% ethanol. All specimens of Trichoptera were identified to species and sex by the author and Anders Göthberg according to Malicky (2010), Macan and Worthington (1973), and Tobias (1972).

At Kaltisjokk, large window traps (approximately 200*40 cm) were set up across the waterway. These window traps were made of transparent glass and insects flying against the glass would fall into a tray below. During times of low water levels, a net was hung underneath the trap so to lead insects up and into the tray. At Rickleå, a suction trap (cf Müller & Ulfstrand 1970) was used for passive sampling. It was similar to the light trap, but used a stream of air trapping the insects as they passed. The samples from Kaltisjokk and Rickleå were identified and sexed by Anders Göthberg. All insects were preserved in 70% ethanol.

Using meta-analysis will minimize the influence of any differing efficiency between the passive traps.

3.4 Statistical analysis

Differences in light attraction per species and sex were analysed through proportion or odds ratio with 95% confidence interval (CI). Odds for light attraction per species were calculated by dividing the number of individuals for each species and survey with the total number of individuals in that trap (1). The odds for the light trap were then divided with the odds for the passive trap to calculate the odds ratio. If the odds were higher in the light trap, the natural logarithm of the odds ratio was above 0 and the species was considered to show an attraction to light. If it was below 0, the species was considered to avoid light. Species which represented 20% or more of the catch in each survey were excluded when calculating odds ratio for light attraction per species so not to skew the result for the less abundant species.

$$\ln\left(\frac{Light_{odds}}{Passive_{odds}}\right) \pm\ 1.96 \times \mathrm{SE} \qquad (1)$$

$$Odds_{Light} = \frac{Light_i}{\sum Light} \text{ for species} \leq 20\% \text{ of the total}$$

$$Odds_{passive} = \frac{Passive_i}{\sum Passive} \text{ for species} \leq 20\% \text{ of the total}$$

$$SE = \sqrt{\frac{1}{Light_i} + \frac{1}{\sum Light} + \frac{1}{Passive_i} + \frac{1}{\sum Passive}}$$

$Light_i = number\ of\ species\ i\ in\ light\ trap,\ \ Passive_i = number\ of species\ i\ in\ passive\ trap$

For the abundant species (≥ 20%), the attraction to light per species were analysed through proportion instead of odds ratio. Proportion was calculated as the number of individuals in the light trap divided with the total for both traps, using Wald’s formula. If the proportion was 0 or 1, the 95% CI was calculated as if it was one-sided (MeasuringU 2017).

The odds ratio analysed sex ratio in a similar manner by dividing the odds for female specimens being caught in the light trap with the corresponding odds for male specimens. If the ratio between light and passive traps was higher for females than males (the natural logarithm of the odds ratio larger than 0), the species was considered to have females more attracted to light than males. If the ratio was lower for females, males were assumed to be more attracted to light. The confidence interval for odds ratio for sex ratio was calculated per species and survey following the example below (2).

$$\ln\left(\frac{F_{odds}}{M_{odds}}\right) \pm\ 1.96 \times \mathrm{SE} \qquad (2)$$

$$F_{odds} = \frac{F_{light}}{F_{passive}} for\ F = females$$

$$M_{odds} = \frac{M_{light}}{M_{passive}} for\ M = males$$

$$SE = \sqrt{\frac{1}{F_{light}} + \frac{1}{F_{passive}} + \frac{1}{M_{light}} + \frac{1}{M_{passive}}}$$

$F_{light} = number\ of\ females\ in\ light\ trap,$ $F_{passive} = number\ of\ females\ in\ passive\ trap$

$M_{light} = number\ of\ males\ in\ light\ trap,$ $M_{passive} = number\ of\ males\ in\ passive\ trap$

Meta-analysis on light attraction was performed based on species and survey (the values were calculated for Species 1 Survey 1, then Species 1 Survey 2, Species 1 Survey 3, etc.). The results per species and survey were then compiled with subgrouping for the final results. Subgrouping was done on four levels: in total, per activity class, per family, and per species.

To analyse the effect of the night's length on the light catch, simple linear regressions were used. The natural logarithm of light/passive ratio (number of individuals in the light trap divided with number of individuals in the passive trap) was correlated to number of hours of darkness per night. The length of darkness was calculated for each location as an average per each week of sampling, from sunset to sunrise. For each of the five surveys, the four species with the longest flight periods were chosen for analysis. This did not necessarily coincide with the most abundant species. The effect was also calculated in total and per activity class.

Meta-analysis and regression were calculated in the software R version 3.3.1 (R Core Team 2016). The results from the five sets of data (surveys) were compiled by meta-analysis with the package “metafor” (Viechtbauer 2010). For all meta-analyses, the method of residual maximum likelihood (REML) was used to fit the model. Worth noting is that previous studies on Trichoptera looked at the absolute abundance. However, there can be great differences in trap efficiency between light traps and passive traps. At Pjältån, only 3% of the individuals were caught in the passive trap. Species found in both traps will thus seem more attracted to light. To compensate for any difference in trap efficiency, I used relative abundance. This approach has not been used in any other studies. The results are thus not directly comparable but conclusions drawn in my study suffer less from bias in trap efficiency.

4 Results

In total, 131 species were identified and 13 of those occurred in all surveys. Approximately 90 000 individuals were analysed (Table 2).

Table 2. Descriptive information from the five surveys. Some individuals were not possible to sex which leads to the male and female abundance not adding up to the same as the total.

	Pjältån	***Rickleå 1972***	***Rickleå 1973***	***Kaltisjokk 1***	***Kaltisjokk 2***
No of species total	60	86	86	56	47
Light trap	57	81	81	50	41
Passive trap	28	46	42	35	32
Abundance in total	30 550	20 671	15 372	18 306	7 527
Light trap	29 673	16 728	11 719	7 316	3 270
Passive trap	877	3 943	3 653	10 990	4 257
Females	19 251	11 531	8 106	7 999	4 307
Males	11 212	9 124	7 256	10 307	3 220

Five species were only caught in passive traps, but only one species (*Adicella reducta*) were represented by more than two individuals. There were 38 species caught only in light traps.

4.1 Species’ attraction to light

It was generally more common for species to be attracted to light in all surveys (Table 3).

Table 3. Numbers of species with a significant preference for either trap type according to odds ratio, per survey.

	Pjältån	***Rickleå 1972***	***Rickleå 1973***	***Kaltisjokk 1***	***Kaltisjokk 2***
Preference for light trap	9	20	17	15	18
Preference for passive trap	9	11	10	5	4
No of species ≥ 20% (excluded)	2	1	0	2	1

Thirteen species occurred in all five surveys. Two of these species dominated in the samples, i.e. compromised 20% or more of the individuals caught, and therefore was not examined through meta-analysis (see methods). These two species were analysed separately (Table 4). Of the remaining eleven species, three were day-active, four were evening-active, three night-active and one was not classified.

Table 4. Proportion and 95% confidence intervals for the two species which occurred in all surveys and dominated in one or several of them.

	Pjältån	***Rickleå 72***	***Rickleå 73***	***Kaltisjokk 1***	***Kaltisjokk 2***
Hydropsyche siltalai					
Proportion in light trap	0.99*	0.99*	1.00*	0.31*	0.55
Confidence interval	0.989 - 0.992	0.985 - 0.1	0.996 - 1.00	0.262 - 0.357	0.481 - 0.629
Rhyacophila nubila					
Proportion in light trap	0.91*	0.90*	0.88*	0.57*	0.26*
Confidence interval	0.891 - 0.927	0.894 - 0.909	0.867 - 0.896	0.554 - 0.5577	0.245 - 0.269

* Significantly over or under proportion 0.5

Both *Rhyacophila nubila* and *Hydropsyche siltalai* showed attraction to light in the majority of the five surveys (Table 4).

The meta-analysis (Figure 2) showed that Trichoptera in general preferred light traps compared to passive traps. The analysis was separated into activity classes as well as for each of the eleven species found in all surveys. Night-active species showed an attraction to light which was further shown as all of the three night-active species occurring in all surveys had significant preferences for the light trap. Evening-active and day-active Trichoptera had a tendency to be attracted to light.

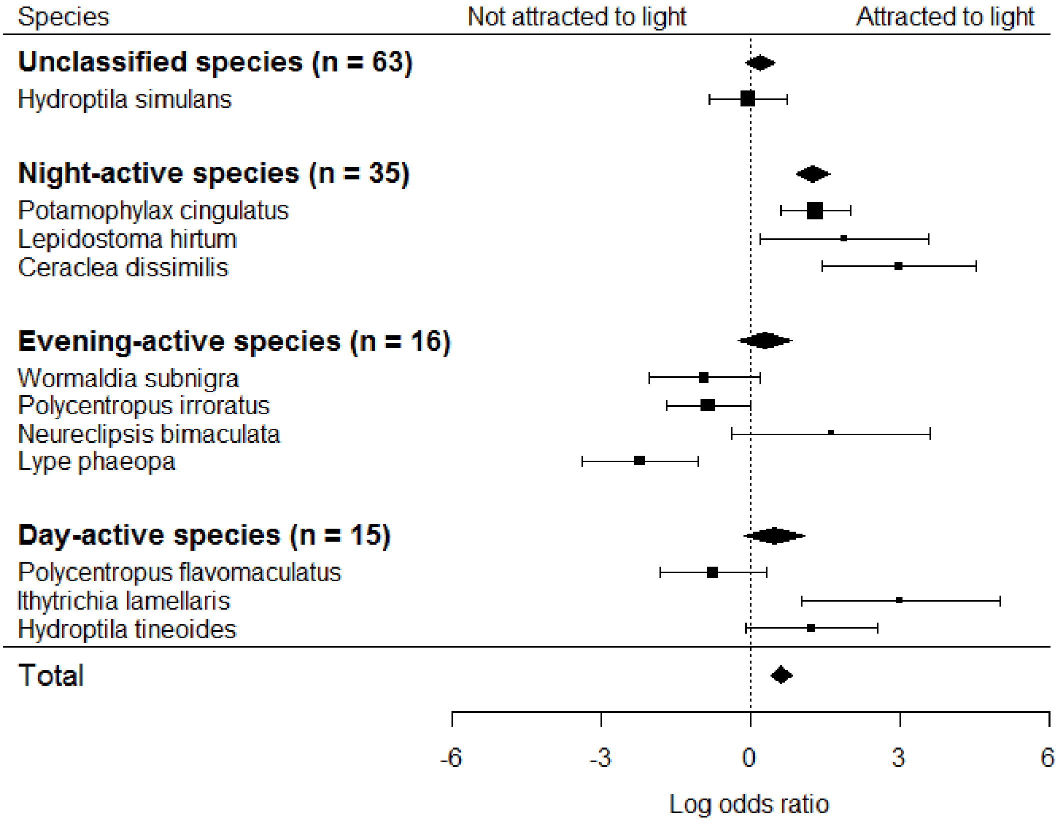

Figure 2. Meta-analysis of trap preference based on all surveys and excluding dominant species. Diamond shapes represents summaries. For activity classes the summary was made on all species. Only those species which occurred in all surveys are shown with separate estimates. If the species preferred light to the passive trap, the values were positive. A negative value showed the species avoiding or not being attracted to light.

4.2 Sexes' attraction to light

The meta-analysis showed that over-all, there was a tendency for females to be more attracted to light than males (Table 5, Figure 3). Night-active species stood out as having no difference between sexes when it came to light attraction.

Table 5. Number of species with significant sex differences to light attraction, according to odds ratio.

	Pjältån	*Rickleå 1972*	*Rickleå 1973*	*Kaltisjokk 1*	*Kaltisjokk 2*
With females sign. to light	6	10	8	1	1
With males sign. to light	4	0	1	5	4

Females of evening-active and day-active species were significantly more attracted to light than males.

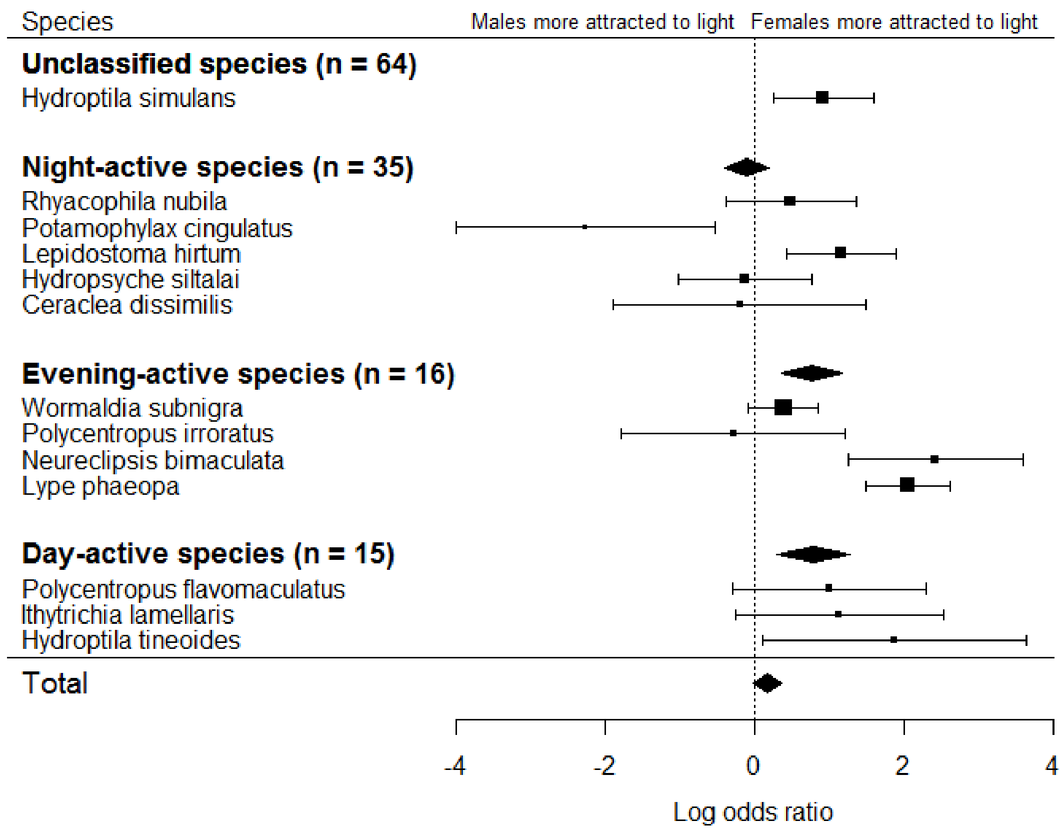

Figure 3. Meta-analysis of light attraction of Trichoptera according to sex ratio. Summaries per activity class were based on all species. Diamond shapes represent summaries. Only those species which occurred in all surveys are shown with separate estimates. When females were more attracted to light than males, the values were positive. A negative value showed males being more attracted to light than females.

Of the sixteen families found in the five surveys, four showed a general pattern of females having stronger attraction to light than males: Glossosomatidae, Hydroptilidae, Lepidostomatidae, and Psychomyiidae. Two families, Limnephilidae and Molannidae, showed males having stronger attraction to light (Figure 4).

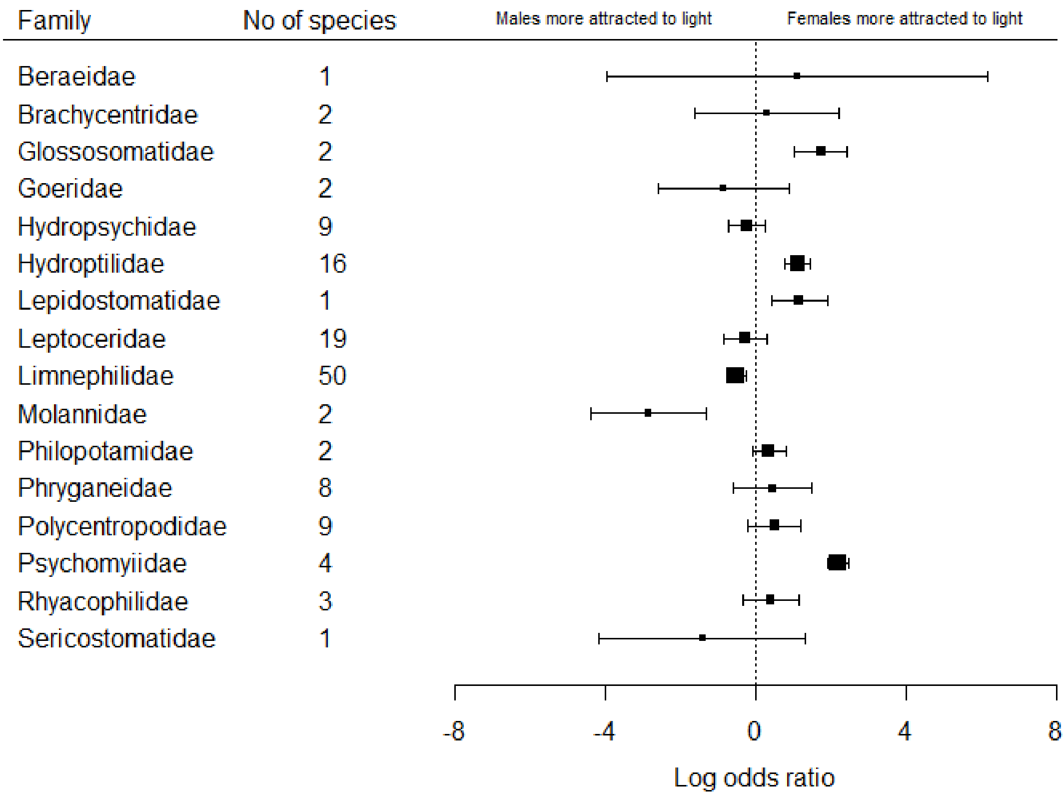

Figure 4. Meta-analysis of sex differences in light attraction according to taxonomic Family. When females were more attracted to light than males, the values were positive. A negative value showed males being more attracted to light than females.

4.3 Night, light and flight – longer nights and changes in light trap catches

Three surveys (Pjältån at latitude 58 and Kaltisjokk 1 and 2 at latitude 68) indicated that light trap catch increased with longer night for species in at least one of the activity classes (Figure 5).

The linear regression of the total was only significant at Kaltisjokk 1, where more individuals were caught in the light trap during longer nights (Figure 5, Appendix 6). Night-active species at Kaltisjokk 1 had an increase in light catches during longer nights. At Kaltisjokk 2, day-active species increased in light catches during longer nights. For evening-active species, the same trend was significant at Pjältån.

Especially at Pjältån, it rather appeared that there was a non-linear correlation between longer nights and light ratio. The non-linear pattern could be discerned in the other surveys as well (Appendix 6).

When it came to analysing the species with the longest flight periods, species in three surveys (Pjältån at latitude 58 and Kaltisjokk 1 and 2 at latitude 68) indicated that light trap catch increased with longer nights (Figure 5, Appendix 7). However, none of the species showed significant correlation in all surveys.

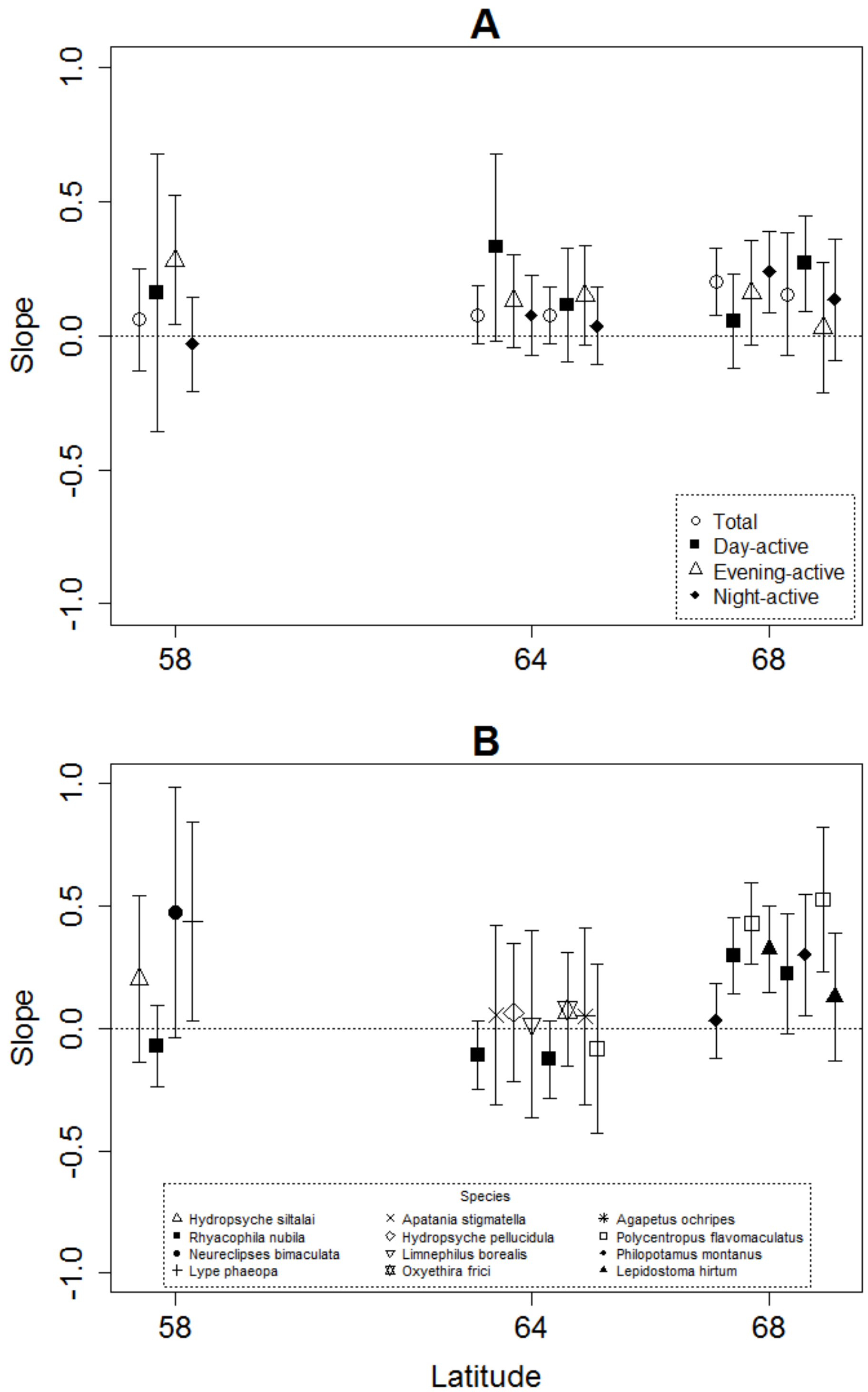

Figure 5. Comparison of slope from linear regression and latitude per survey for a) the total and the three activity classes, and b) the four species with longest flight periods. Any value with error bars completely above or below the horizontal line shows a significant correlation between the light trap catch and longer nights. A negative slope shows a decrease in light catches with longer nights. Error bars represent the confidence intervals for the slope estimate.

5 Discussion

As an order, Trichoptera was attracted to light but the species varied in their attraction to light. Night-active species were more attracted to light than day- and evening-active ones, but all activity classes were generally attracted to light. When analysing differences in light attraction per sex, females were often more attracted to light than males and analyses per taxonomic Family indicated that five families had females more attracted to light and two families with males being more attracted to light. There was no clear trend of longer nights leading to an increase in light catches.

5.1 Light attraction in general and per species

The results showed that Trichoptera are strongly attracted to light, and populations could therefore be seriously reduced when artificial light is used close to freshwater. Even though the overall pattern was of light attraction, not all species were equally attracted. Four of the eleven species present in all surveys were attracted to light while two were more common in the passive traps. Studies on other insect orders have noted the same variable pattern, and one species can be 5000 times more probable to fly to light than another (Taylor 1961). Both surveys at Rickleå used the same type of traps as Taylor (1961) and the difference in attraction was at the same magnitude, with *Apatania stigmatella* about 5500 times more likely to fly to light than *Lype phaeopa* in Rickleå 1972. It is well known that light affect species differently –and this behaviour can be seen in many organisms, from moths and beetles (Rich & Longcore 2006) to mammals (Rowse et al. 2016). For example, species of forest-dwelling bats avoid lit areas while other bat species use artificial light for foraging (Rowse et al. 2016). When light affects species differently, any installation of artificial light could cause a skewed mortality with one species becoming less abundant than before. As species hold different niches, any change in the abundance of a species could affect the efficiency of their particular ecosystem service. The variation in species' attraction to light is thus important to consider for preservation of biodiversity.

Light is known not only to attract insects but also repel them. This has been used to protect crops from pest species and to keep copulating species from being hit by cars on highways (Frank 2006, Lloyd 2006). Research on light avoidance of insects is, for natural reasons, difficult to estimate. My analysis used comparisons between passive traps and light traps to estimate a degree of avoidance. 18% of the species in the analysis had a larger relative presence in the passive traps than the light traps, showing an avoidance of light. A handful of species were only caught in the passive traps which even stronger suggest that some, for example *Adicella reducta*, avoid light. It is not unusual that light causes a dazzling effect, with insects landing on the ground immobilised by the light source (Frank 2006, Rowse et al. 2016). The effect could last for hours, sometimes the remainder of the night (Frank 2006). For insects which only fly for a part of night and do not live for long periods, such as Trichoptera, this could be costly through delay of mating and oviposition (Frank 2006). Artificial light can thus be detrimental for species even if they are not attracted to light.

A few previous studies have looked on the light attraction of Trichoptera with different results. Svensson (1972) found that passive traps caught many specimens but only of a few species and that some species were caught in higher numbers in the passive trap than in the light trap. Smith et al. (2002) presented opposite results and found more species in the passive trap than the light trap and seven species were caught only in passive traps. In my analysis, all passive-trap-only species apart from *Adicella reducta* were caught in one or two specimens so chance could play a large part. In Smith et al. (2002) the catch differences varied during the season and with location - light traps were more efficient in open pastures. This is likely because light traps only catch insects within their attraction zone and light traps on open areas are visible at greater distances. Some studies show that the attraction zone for light traps vary between 50-700 m (Eisenbeis 2006) but the zones can be as small as 3 m in radii (Degen et al. 2016). The attraction zone was not determined for lights traps in my analysis.

Day-active species were less attracted to light than night-active species, but they did not differ from evening-active species. The fact that several day-active species were caught in light traps partly negates the hypothesis provided by Smith et al. (2002). They suggested that the reason some species were only caught in passive traps was because they were diurnal and thus not attracted to light. Smith did not test the hypothesis. My analysis showed that being day-active did not necessarily mean the species was not attracted to light.

Laboratory experiments have shown that Trichoptera have species-specific reactions to any change from light to dark and dark to light (Jackson & Resh 1991). Some had a photonegative response, where light inhibited their flight activity. Other species (both diurnal and nocturnal) reacted on lights being turned on by increasing their flight activity. This means that the method of light trapping could create an artificial product of higher flight activity at night even for day-active species. The reaction to lights being turned on was different between sexes for one of the species they tested, which could indicate a similar artificial product when analysing differences between sexes. Andersen (1979) noted that *Philopotamus montanus* appeared night-active when collected in light traps and day-active when collected in suction traps. This further indicates that light traps can give a false flight activity pattern.

Why are some species more attracted to light than others? For one thing, there are several ways for organisms to navigate: aerodynamic, gravitational, chemical, geomagnetic, acoustic and imaging cues are all ways of guidance that compete with light (Frank 2006). More active species are more likely to pass a light source and larger species usually have larger eyes which perceive light sources better (Altermatt et al. 2009). My results suggested that night-active species could be particularly at risk from artificial light sources and that using light as navigational cue is what makes some species more attracted than others. However, there could be many ecological explanations and more studies are needed to further investigate what causes different responses to light in the order Trichoptera.

5.2 Light attraction in males and females

Females were generally more attracted to light than males, which is the opposite pattern from moths (Altermatt et al. 2009). Of the thirteen species which occurred in all surveys, five species showed that females were significantly more attracted to light and one species had males more attracted to light. When one sex experiences a higher mortality than the other, an unequal sex ratio is created and the effective size of the population is reduced (Frankham 1995). Males can usually fertilize many females, but when females are at risk of a higher mortality – from artificial light in this case – the population can be reduced as there are fewer clutches produced (Grübler et al. 2008). A smaller effective size can decrease the genetic variation in a population and risk inbreeding and genetic drift (Frankham 1995), which can make the population less able to adapt to changes in the environment in the long term (Harris et al. 2017). The stronger attraction to light in females could therefore have larger impact on population structure and conservation than what would be assumed when looking at the overall effect.

It is known that sex ratio in Trichoptera is not equal and that the ratio varies with species (Harris 1971, Crichton et al. 1978, Smith et al. 2002, Nowinszky et al. 2014). My analysis found more females than males in absolute numbers, especially in light traps. The meta-analysis of odds ratios showed a tendency for females to be more attracted to light. Day- and evening-active species had females significantly more attracted to light while neither sex in night-active species were more attracted than the other. In other studies, the sex ratio is rarely compared between light and passive traps, and never based on relative abundance. Svensson (1972) found a higher proportion of males than females in light traps and the opposite in passive traps. Crichton et al. (1978) found a higher proportion of male Trichoptera in light traps but noted that some species differed from this pattern. In contrast, Harris (1971) found 65% females in his light trap catches, and fourteen of the sixteen most common species had a higher proportion of females. Smith et al. (2002) found more females than males in both light and passive traps. Hence, my results were both confirmed and refuted by other studies but comparisons between studies are complicated by differing methodologies and analyses. The studies with opposite results from mine used sampling methods which were likely biased towards sampling of males. The bias is less in Harris (1971), Smith et al. (2002) and this study, which suggests that females are more attracted to light than males.

There are biological reasons for the differences between studies. That Svensson (1972) found more males than females in his study can be due to two reasons, 1) his catches were dominated by limnephilids, and 2) the majority of his traps were set far from water. Firstly, the only species in my meta-analysis that showed a higher male ratio in light traps was a limnephilid. In my analysis, it was a general trait of this family that males were more attracted to light than females. Limnephilidae is a family of medium to large species with strong flight ability, often found far from their larval habitats (Crichton & Fischer 1978) and even far from water (Crichton & Fischer 1982). Secondly, Svensson (1972) only had five light traps close to the stream. The twelve other light traps were located in vegetation 50 to 1000 m away from the stream. Malaise traps (four) were only placed along the stream. All five surveys in my analysis included traps situated in or at a close proximity to the water. Placing traps far from the larval habitat (far from water in the case of Trichoptera) could cause a biased catch of males. In a study on moths, traps closer to the trees (and thus the host plants for the moth larvae) only caught females while males dominated in traps far from the host plants (Frank 2006). Svensson (1972) noted that the location of the traps strongly influenced the sex ratio, with fewer females found in traps far from water. So in his study, the domination of females in passive traps could be due to the proximity of those traps to the stream. The higher male catch in Crichton et al. (1978, also Crichton & Fischer 1982) could suffer from the same bias as they also used traps far from water. Both studies which were dominated by females had light traps situated close to water (Harris 1971, Smith et al. 2002). Placement of traps far from water can thus cause a domination of males in light traps. The female domination in my study should thus be more representative of Trichoptera composition than results from samples taken far from a water source.

For moths, males have been found to be more attracted to light than females in both an enclosed environment (Altermatt et al. 2009) and in nature (Degen et al. 2016). My results showed that in nature, females of most Trichoptera species were more attracted to light.

5.2.1 Reasons for stronger attraction to light in one sex

As been mentioned, females - at least for some species - have been found in greater absolute numbers than males and three reasons have been suggested for this: they are more attracted to light, have a higher flight activity or that the natural female-to-male ratio of adults is higher (Crichton et al. 1978, Waringer 1989, Nowinszky et al. 2014). Below, these three reasons will be further discussed.

The first reason for one sex being more attracted to light than the other is due to physical differences, so called sexual dimorphism. In general, larger insects have larger eyes, so any size dimorphism would lead to the larger sex in general having larger eyes (Degen et al. 2016). Having larger eyes could make a specimen more attracted to light (Altermatt et al. 2009). In my meta-analysis, only one species had a significantly higher male ratio in the light traps while five species showed significantly higher female ratio in light traps. Among insects it is common that females are the larger sex as there is an intense selection on fecundity and the abdominal space seems to limit the number of eggs produced (Jannot & Kerans 2003, Salavert et al. 2011). Larger size can be selected for in males (Jannot & Kerans 2003, Salavert et al. 2011) but for the 29 hydropsychid species Jannot and Kerans (2003) tested, males were never larger. Size differences ranged from no difference to 39% larger females. These 29 measured hydropsychid species did not occur in the analysed datasets, but another species in the family, *Hydropsyche siltalai*, showed no sex difference in attraction to light. The size difference in this species is uncertain but it seems to be insignificant. The lack of size difference could explain the fact that none of the sexes in this species was more attracted to light than the other. *Neureclipsis bimaculata* (family

Polycentropodidae), had 48% larger females (Jannot & Kerans 2003) and showed a strong female attraction to light in my study. Sexual size dimorphism could thus explain the difference in light attraction between sexes.

A higher flight activity is a second reason for one sex being more attracted to light than the other. The results showed that Leptoceridae as a family had a tendency for males being more attracted to light, which matched studies on the swarming behaviour which showed that males usually have a higher flight activity (Gullefors & Petersson 1993). However, this was not apparent on species-level. *Ceraclea dissimilis*, a species with females more active, showed no difference in light attraction between males and females. Thus differences in flight activity between sexes do not conclusively affect attraction to light, at least not on species-level.

The third reason for differences between sexes is that the ratio is naturally different, for example through a higher mortality for one sex. A female domination has been especially noted for species within the genus Hydropsyche (Crichton et al. 1978, Crichton & Fischer 1982, Waringer 1989, Diken & Boyaci 2008, Nowinszky et al. 2014) even if one study showed males to be more abundant (Harris 1971). My analysis showed that 77% of *Hydropsyche siltalai* individuals were female and thus that there was a larger absolute number of females. However, no sex of this species was more attracted to light than the other. Thus it seems that this species has a naturally skewed sex ratio. A skewed sex ratio could be due to a higher mortality for males in larval or pupal stages (Crichton et al. 1978, Nowinszky et al. 2014). Looking at the whole family Hydropsychidae it seemed that males were more attracted to light than females. To avoid the problem of naturally skewed sex ratios confusing results, my study used relative abundances instead of absolute ones.

The ecological reasons for differences between sexes are several and needs to be further examined. No single reason seemed to explain the variation between species although size dimorphism is a likely candidate. Population ecology underlines the importance of knowing the sex ratio as it affects the long term viability of a population. As the sexes in Trichoptera were unequally attracted to light, the negative impact of artificial light can be larger than appears in a simple census of population size.

5.3 Night, light and flight – longer nights did not conclusively lead to larger light trap catches

Artificial light is used during the darkest hours and less during the summer, which is a season with bright nights in the northern hemisphere. This study evaluated whether shorter nights lead to less severe negative effects of artificial light. My analysis showed some evidence that light traps would be more efficient during longer nights. Svensson (1972) showed that flight periods were different when comparing catches in light traps with those in Malaise traps, especially for summer species. He suggested that this was due to the inefficiency of light during the short and bright nights of summer. At Kaltisjokk there is one month of midnight sun, with no darkness at night whatsoever, which could explain the significant results at this location. Pjältån, which is further south and has longer nights, also showed some increase in light catches during longer nights. Rickleå, which is on a latitude between Kaltisjokk and Pjältån, showed no significant increase with longer nights. As Trichoptera often have their most active period for only a few hours per night (Jackson & Resh 1991), this could explain why there is not a stronger relationship between longer nights and the efficiency of artificial light. Even as nights become longer, most Trichoptera likely stay active for short periods of one or two hours and are thus attracted only for that time period regardless the length of night.

A visual analysis of the linear regression graphs (Appendix 6 and 7) showed a pattern that appears not to be linear in its structure. This indicates that regardless of correlations, there does not seem to be a simple linear correlation. More detailed studies of interactions and parameters are needed to analyse this complex relationship. The lack of a consistent pattern for species in all surveys indicate that the effect of longer nights do not strongly influence the efficiency of artificial light. There could be confounding factors but the use of passive traps as controls should have excluded most of them, such as weather patterns. The linear regression was performed on a mix of significantly light-attracted and significantly non-attracted species. To conclude, there is no consistent pattern in the analysis of light catches and longer nights. Further studies are needed to answer the question whether longer nights increase the attracting effect of artificial light.

5.4 Societal and ethical considerations

The trapping of insects in propylene glycol or ethanol cause an increased mortality. Unfortunately this is required in order to properly identify

Trichoptera specimens, as close inspection of their genitals are in many cases the only way to identify the species. However, the mortality caused by this research should be negligible compared to for example the mortality of insects against moving cars (Baxter-Gilbert et al. 2015). A worrying fact from the most recent sampling in Pjältån is the recurring pollution from a factory downstream of the sampling location. Two times during the sampling period this factory accidentally released masses of cooking oil (aimed for recycling) into the stream. There were then several leaks after the sampling period. This most likely had a much larger impact on insect (and other) life in the area than the sampling, but together it could cause a decrease in insect numbers. The sampling at Kaltisjokk had little long term consequence as the water was later redirected into the Messaure hydropower dam, which means that Kaltisjokk no longer exists. Rickleå is a very larger river and the sampling at a small segment would not cause major impacts on the populations. The number of insects sampled should thus not have a large impact on the species in any of the areas. Care has to be taken when sampling large number of insects, but the current study should not have depleted the population in any of the streams.

At Pjältån, the landowner was contacted and permission to set up the traps acquired. The closest neighbors were informed of the traps and were positive toward and curious about the research. Information was set up on both traps and on the wall of the nearby building from where electricity was taken. Overall, the traps had no negative societal consequences.

5.5 Conclusions

As a group, Trichoptera were strongly attracted to light but not all species were equally attracted. Night-active species were especially prone to being attracted to light compared to day- and evening-active species. Females had a tendency to be more attracted to light than males. The ecological reasons for differences between sexes and between species are several and needs to be further examined. No single reason seemed to explain the variation between species although size dimorphism was a likely candidate. A naturally skewed sex ratio was apparent in one species of Hydropsyche.

There was some evidence that light traps would be more efficient during longer nights, however the results were not conclusive.

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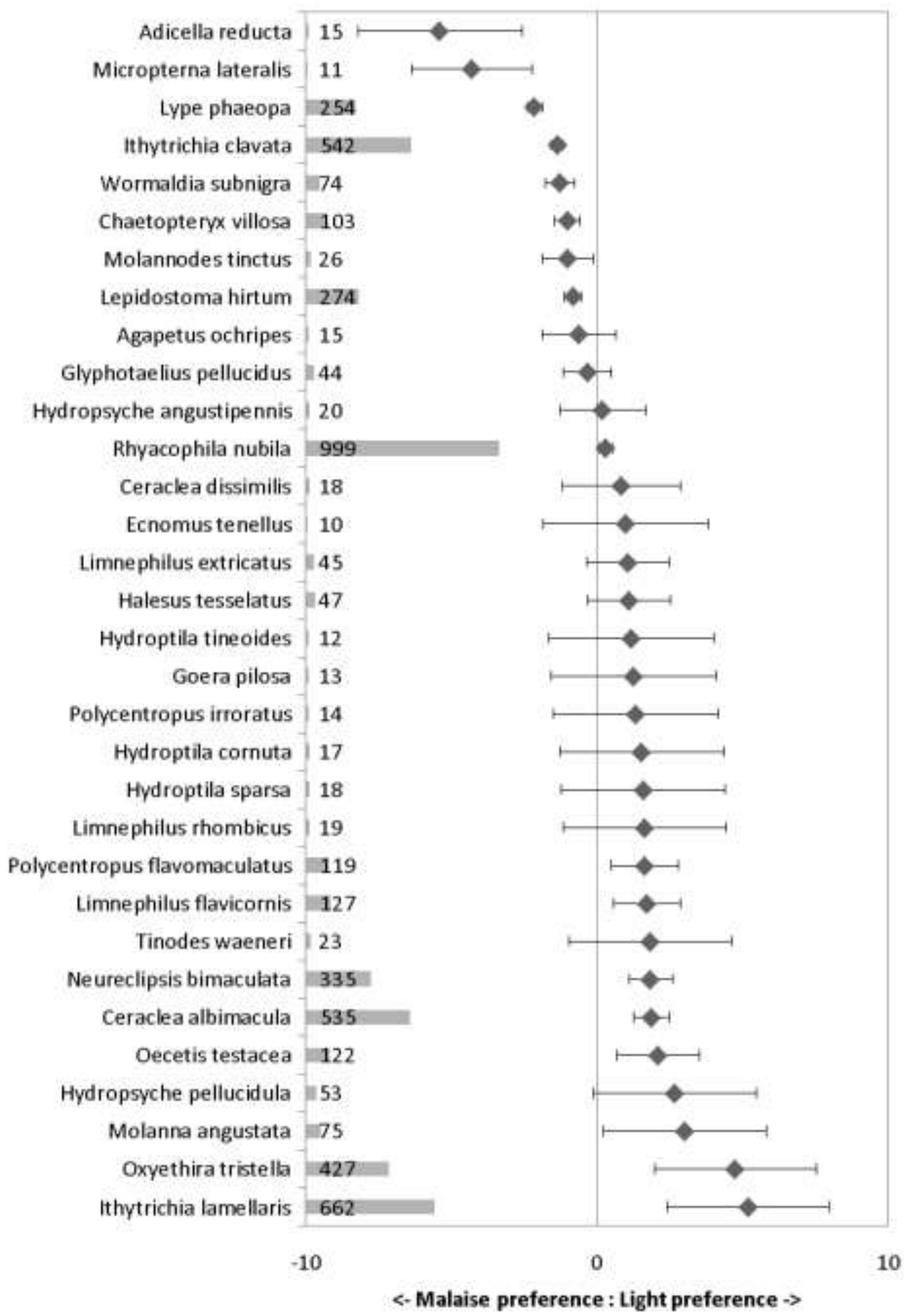
8 Appendix

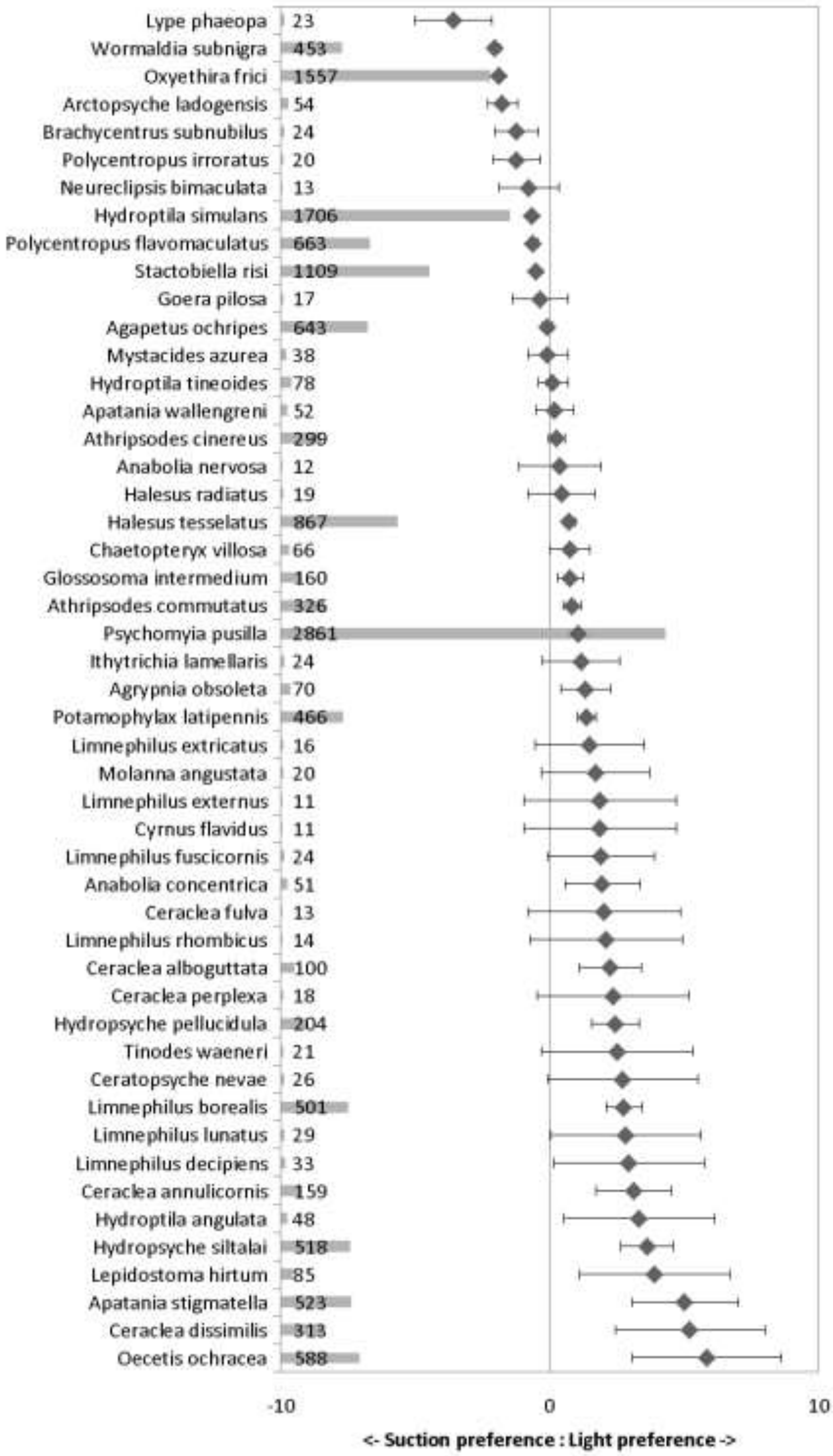
8.1 Appendix 1. Pjältån - Odds ratio and abundance

Natural logarithm of odds ratio with 95% CI (points and error bars) and abundance (sideways bar plot) for species with more than 10 individuals. Species which composed more than 20% of the total number of individuals were excluded. Pjältån, Norrköping, Sweden in 2016.



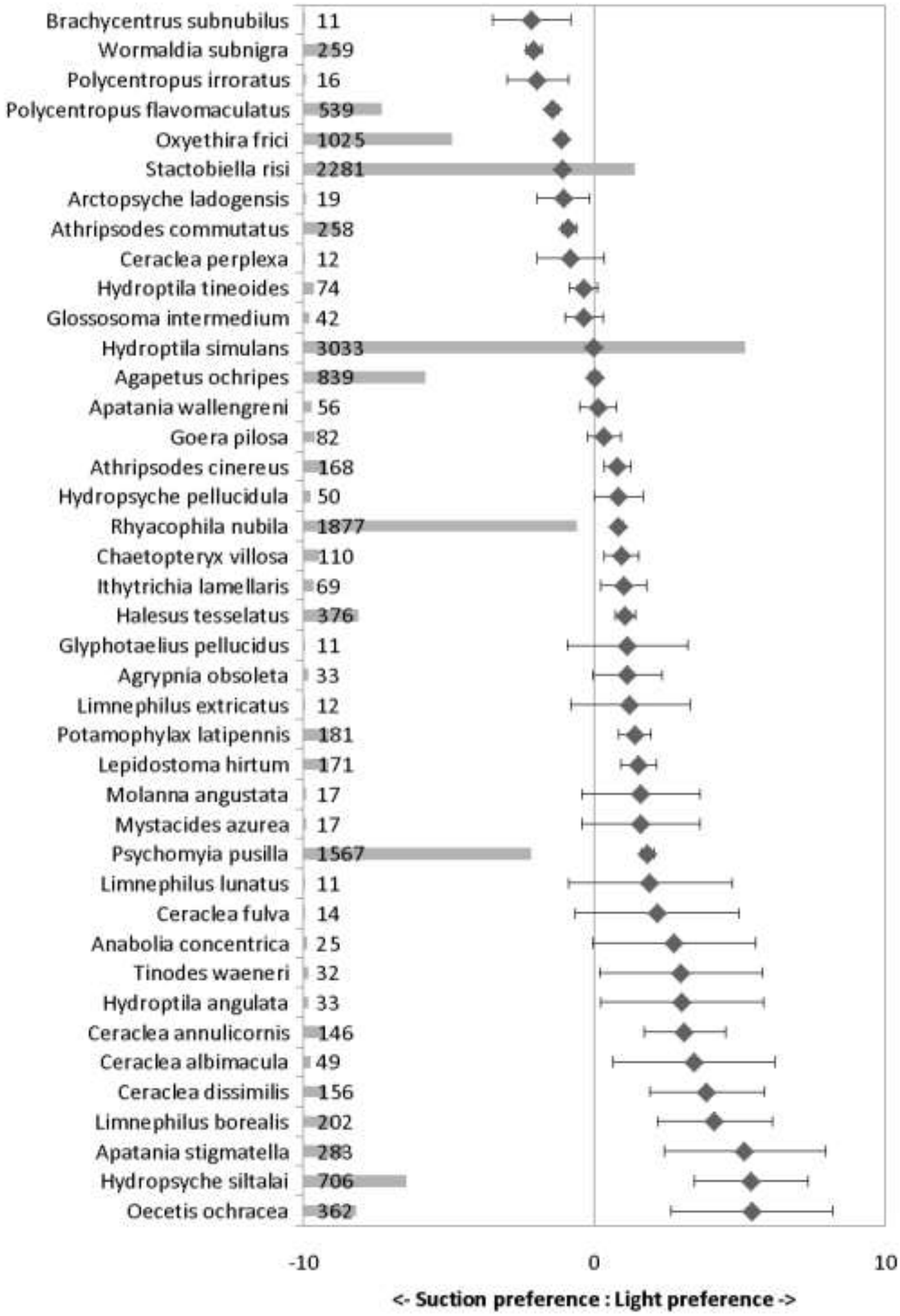
8.2 Appendix 2. Rickleå 1972 - Odds ratio and abundance

Natural logarithm of odds ratio with 95% CI (points and error bars) and abundance (sideways bar plot) for species with more than 10 individuals. Species which composed more than 20% of the total number of individuals were excluded. Rickleå, Robertsfors, Sweden in 1972.



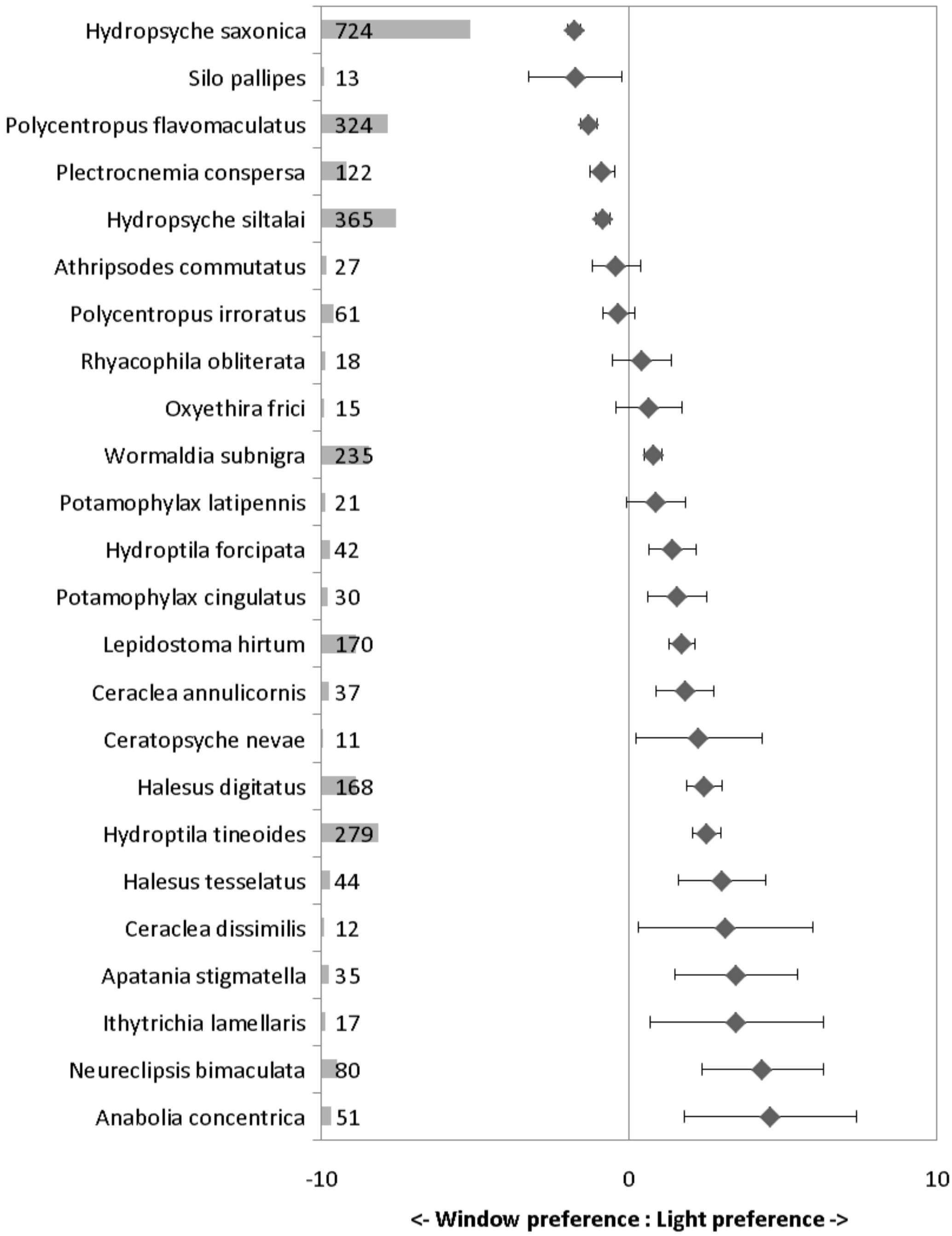
8.3 Appendix 3. Rickleå 1973 - Odds ratio and abundance

Natural logarithm of odds ratio with 95% CI (points and error bars) and abundance (sideways bar plot) for species with more than 10 individuals. Species which composed more than 20% of the total number of individuals were excluded. Rickleå, Robertsfors, Sweden in 1973.



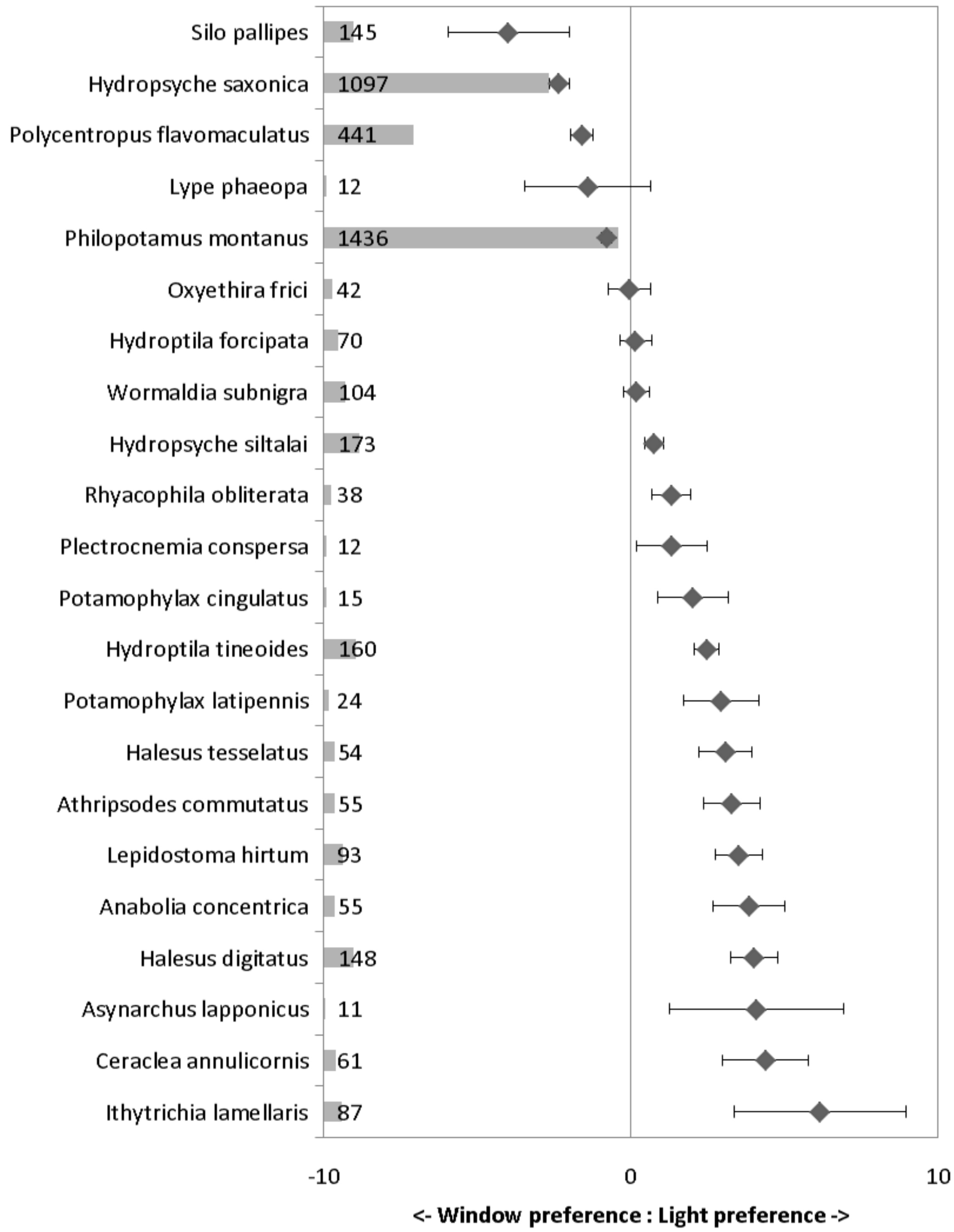
8.4 Appendix 4. Kaltisjokk 1 - Odds ratio and abundance

Natural logarithm of odds ratio with 95% CI (points and error bars) and abundance (sideways bar plot) for species with more than 10 individuals. Species which composed more than 20% of the total number of individuals were excluded. Kaltisjokk, Jokkmokk, Sweden in 1974.



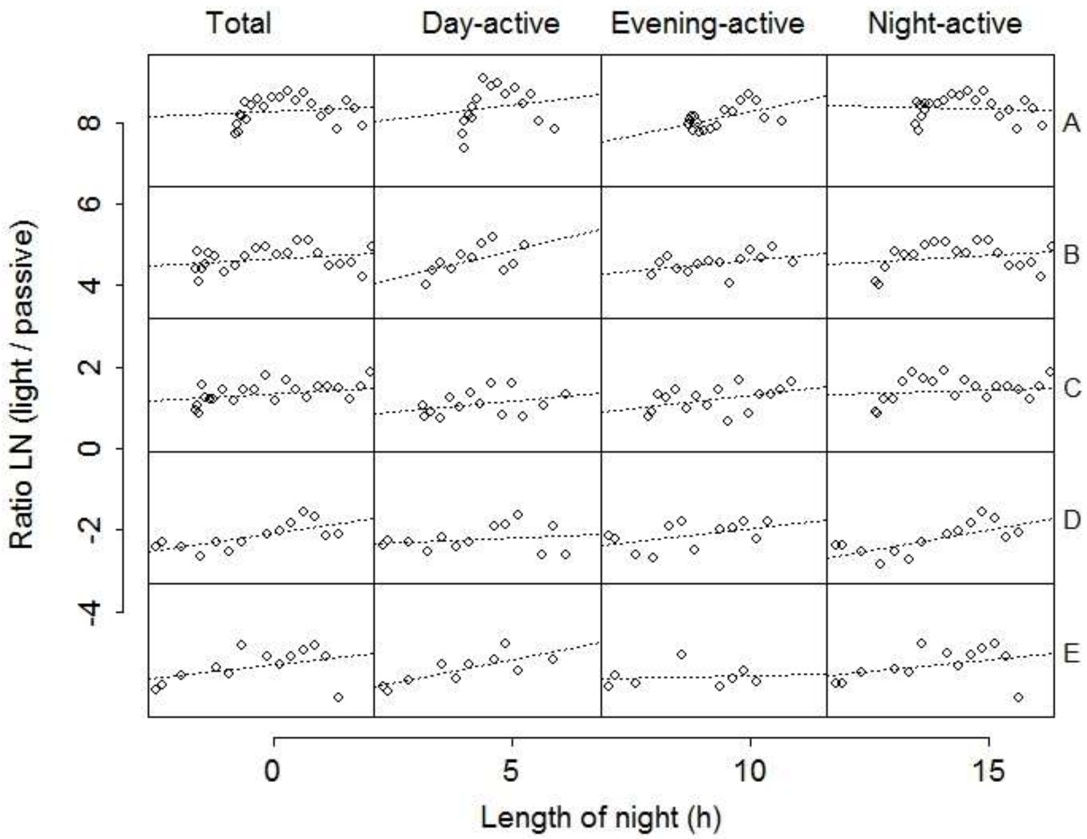
8.5 Appendix 5. Kaltisjokk 2 - Odds ratio and abundance

Natural logarithm of odds ratio with 95% CI (points and error bars) and abundance (sideways bar plot) for species with more than 10 individuals. Species which composed more than 20% of the total number of individuals were excluded. Kaltisjokk, Jokkmokk, Sweden in 1974.



8.6 Appendix 6. Simple linear regression analysis per survey for all species and per activity class.

Y-axis is the natural logarithm of the ratio between catch in light trap and passive trap. X-axis is the length of night in hours, ranging from 0 to 15h. A) Pjältån, B) Rickleå 1972, C) Rickleå 1973, D) Kaltisjokk 1, and E) Kaltisjokk 2.



8.7 Appendix 7. Simple linear regression analysis per survey of the four species with the longest flight periods.

Y-axis is the natural logarithm of the ratio between catch in light trap and passive trap. X-axis is the length of night in hours, ranging from 0 to 15h. A) Pjältån, B) Rickleå 1972, C) Rickleå 1973, D) Kaltisjokk 1, and E) Kaltisjokk 2.