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Musters, C.J.M.; Snelder, D.J.R.M.; Vos, P.

Universiteit Leiden

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C.J.M. Musters, D.J. Snelder & P. Vos

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A literature study of the effects of part of the spectrum of artificial light on species and communities

C.J.M. Musters, D.J. Snelder & P. Vos

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Department Conservation Biology

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Abstract

Present regulations to minimize the impact of light pollution focus on intensity of artificial light only. However, modern light equipments allow for the manipulation of other light characteristics as well, such as the spectral properties and polarisation of the emitted light. It might be possible to design lamps and lamp armatures in such a way that, within a certain setting, the emitted light has the sufficient quality to support human activities, but has at the same time no or minimal effects on biological processes of the organisms or communities nearby. This paper tries to assess the availability of knowledge of the effect of parts of the spectrum of artificial light on species and communities needed for that design.

Because we expected literature on the effects of light on ecological processes to be rare and because effects of light on, for example, physiological processes could possibly be used to hypothesise ecological effects, it was decided to collect information of effects on physiology, behaviour, populations, and interactions between species. To establish gaps in our knowledge of the effect of parts of the spectrum on ecological processes, we made tables that summarize the knowledge per main effect. To be able to appreciate the gaps in our knowledge we developed a simple system for weighting the relative importance of the potential ecological effect per species group. Combining the gaps in our knowledge with this weighting gives an indication of the priorities for future research.

Much is still to be learned about the effects of light on nature, and we found that this is especially true for the effect of coloured light (i.e., specific wavelength). As a matter of fact, studies on the effect of coloured light on populations, species interactions, or communities are almost completely missing. However, we also found that for some species groups detailed information is available of the effect of certain wave lengths on physiology and behaviour.

This knowledge seems to give enough clues to at least postulate a spectrum that might be of relatively low disturbance for a specific species group. Lamps can be designed based on these spectra and these lamps can be tested in the field. Any field study of the effects of coloured light on survival, dispersion or competition of species or species groups would be a considerable contribution to our knowledge.

1 Introduction

1.1 Artificial outdoor light as a problem

At the global level, 19% of the earth surface experiences night sky brightness from artificial sources (Rich & Longcore 2006) and 20% of the human world population has lost the ability to see the Milky Way with the naked eye (Smith, 2009). In developed countries this percentage is much larger. In the US, for example, 60% of the people no longer can see the Milky Way (Smith, 2009). This is only one form of what is sometimes called light pollution and is generally considered as a problem for both humans (the appreciation of the landscape) and nature conservation.

Studies showing the influence of artificial light on wildlife go back to the 19th century and light pollution seems to have been a focus of research since the second half of the 20th century, illustrated by overviews like those of Bainbridge et al. (1966; 1975), De Molenaar et al. (1997), and Rich & Longcore (2006). De Molenaar et al. (1997) speak about an “overwhelming” amount of literature on the effects of light on animals. Yet, Rich & Longcore (2006) end the introduction to their overview by stating that “much more remains to be learned”. As a matter of fact, the study of the ecological effects of artificial outdoor light is a huge research field.

Ever since its origin, light has been an important environmental factor for life. In one of the earliest serious theories of the origin of life – that of Oparin and Haldane from the 1920s -, UV-light plays a key role in the building of complex organic compounds (Dawkins, 2004). Because light contains energy and because its availability, primarily as sun light, is ever changing in daily, monthly (‘moonly’), and yearly cycles, almost all organisms have evolved adaptations to light and its cycles. Therefore, light is of the same order of importance for wildlife as water or nutrients. It has a number of characteristics, like intensity, wave length and polarisation, to each of which physiological, ethological and ecological processes have been adapted differently, though not necessarily independently. Besides, light sets time: it defines days, months, and years. Light pollution can therefore be supposed to disturb many long evolved adaptations and have all kinds of effects, on all kind of organisms and all kinds of processes. No wonder that even though a large body of literature exists on effects of light on certain biological processes, our knowledge of the ecological effects of artificial outdoor light is far from complete.

Although our knowledge is incomplete, the fear that light pollution may have an important impact on nature, has led the Dutch Directorate-General for Public Works and Water Management to adopt a ‘No, unless’ policy. This says that in or near nature conservation and recreational areas, streets will not be lightened unless there are important reasons, primarily from the point of view of road safety. Other Dutch regulations include the principle of ‘As Low As Reasonably Achievable’ (Anonymous 2007). Thus, these regulations focus on intensity of artificial light only. However, modern light equipments allow for the manipulation of other light characteristics as well, such as the spectral properties and polarisation of the emitted light. It might be possible to design lamps and lamp armatures in such a way that, within a certain setting, the emitted light has the sufficient quality to support human activities, but has at the same time no or minimal effects on biological processes of the organisms or communities nearby. This paper tries to assess the availability of the knowledge needed for that design.

1.2 *Spectral aspects*

From every introduction to biology for undergraduates it can be learned that plants have three types of chloroplast pigments, each absorbing a different part of the light spectrum for photosynthesis. The result is that plants use primarily the blue and red parts of the spectrum for photosynthesis, and not the green parts. That's why plants are green. From the same introductions it can also be learned that the vertebrate eye has rods and cones, that cones occur in different types and that each type is sensitive to a different colour, i.e., that these cones start firing signals to the brain only when light with a certain wave length and intensity falls upon them.

These are two well known examples of the fact that biological processes may be affected by only a limited part of the spectrum of natural light. Lamps that emit other parts of the spectrum would have limited effects on the processes. Green lamps will hardly make plants to photosynthesize during the night. However, photosynthesis is not the only process within plants that is affected by light. Direction of growth and timing of the start of leaf development in spring are also known to be affected by light, for example. Are these processes also not affected by green light? And how about the bees that are needed for the pollination of the plants? Are these also not affected by green light?

It is obvious that for the design of ecological friendly lamps based on spectral properties, one needs to know the effect of different parts of the spectrum on as many relevant processes as possible. This seems a rather vast task for the lamp designer. However, one should bear in mind that the list of relevant processes might not always be very long. The disturbance of bird migration routes by lighted oil platforms is a good example of a relative simple problem solved with a change in the spectral properties of the light (Poot et al, in press).

So, in situations where artificial light is essential for human activities but at the same location high valued wildlife might be disturbed by that light, using lamps that emit a limited part of the spectrum may be a solution. Problem is, of course, that in most cases the disturbance of wildlife by artificial light is poorly known, let alone which parts of the spectrum are relevant. Therefore, in many cases one would like to follow a prudent strategy: within or close to areas with high nature value, lamps are to be used that disturb wildlife as less as possible, according to present knowledge. Do we know enough of the effects of certain parts of the spectrum on biological processes to be able to design lamps for this purpose? In order to answer this question we performed a literature study of which this paper describes the results.

1.3 *Aim of this paper*

The aim of this paper is to summarize existing knowledge of the parts of the spectrum of natural light that affects biological processes most, in order to be able to either make recommendations for the spectral properties of ecological friendly outdoor lamps or to design an agenda for a research program needed for the development of ecological friendly outdoor lamps.

For outdoor lamps, we focus on lamps to be used in terrestrial environments under moderated climates. For aquatic systems this means that only relatively small fresh water bodies are to be taken into consideration.

2 Methods

2.1 Effects of spectral parts of artificial light

For the design of lamps with a nature friendly spectrum, one needs to know which parts of the spectrum have an effects on the populations of organisms and/or on communities, and which parts have no effect. The new lamps could be designed based on the idea that they should have a spectrum composed of parts that show no effect. Therefore, the information needed from literature is whether there is an effect or not of a certain part of the spectrum. The 'direction' of the effect is not really relevant: any effect can be regarded as a disturbance of the natural processes. For example, for this study it is irrelevant whether a bird is attracted or repulsed by red light. Attraction could result in a higher than natural chance of collision, and therefore to higher mortality rates, but repulsion could lead to lamps acting as barriers, and therefore to lower dispersion rates. Besides, what could be regarded as a positive effect for one species, i.e., an effect that enlarges the population of that species, will undoubtedly have to be regarded as a negative effect for its food source, prey or competitors, and again positive for its parasites or predators. So, because of this complexity of interpreting the meaning of the effect and because for the design of lamps it is not really necessary to know the exact meaning, we focussed our analysis of literature on assessing whether an effect was shown or not. This strongly simplified our literature analysis. Of course, once a certain lamp is tested in the field, for the interpretation of the results it becomes crucial to know the type and direction of the effects. But that asks for a different kind of literature analysis.

2.2 Scheme of analysing literature

In the end, our research question is an ecological one. However, because we expected literature on the effects of light on ecological processes to be rare and because effects of light on, for example, physiological processes could possibly be used to hypothesise ecological effects, we decided to collect information of effects on:

- Physiology
- Behaviour
- Populations
- Interactions between species.

Within these fields we identified the processes supposed to be keys to ecological functioning.

Next, for each process we tried to find out what is known of the effect of light and parts of the spectrum on:

- Plants
- Animals
    - Invertebrates
        - Insects

        - Non-insects
    - Vertebrates
        - Fish
        - Amphibians
        - Reptiles
        - Birds
        - Mammals

The description of our results follows this scheme of analyses.

2.3 Existing reviews

As stated before, a number of reviews are available on the ecological effects of artificial light. Of these, we used De Molenaar et al. (1997), De Molenaar (2003) and Rich & Longcore (2006) as starting point of our literature search. Summarises of the findings of these authors will be incorporated in our results.

2.4 New literature

Because the availability of recent reviews, we decided to restrict our literature search to articles in ISI journals published after 2000. The formal query applied is given in box 1. This resulted in 220 publications. However, much to our surprise we found that a number of relevant articles known to us, were not included in this list. For this reason, we supplemented the list with every relevant article we came across. This resulted in our final reference list.

2.5 Gaps in knowledge

To establish gaps in our knowledge of the effect of parts of the spectrum on organisms and ecological processes, we made tables that summarize the knowledge per main effect. To be able to appreciate the gaps in our knowledge we developed a simple system for weighting the relative importance of the potential ecological effect per species group. Combining the gaps in our knowledge with this weighting gives an indication of the priorities for future research.

Databases=SCI-EXPANDED, SSCI, A&HCI Timespan=Latest 5 years	Web of Science	all data bases 5 years	all data bases all years	
Topic= "artificial light*" OR "LED light*" OR "artificial night light*" OR "artificial outdoor light*" OR "road light*" OR "highway light*" OR "street light*" OR "streetlight*" OR "light pollution" OR photopollution AND:	**583**	642	3082	
Topic= "spectral composition" OR "light intensity" OR "spectral sensitivity" OR "wavelength discrimination" OR "wavelength sensitivity" OR "electromagnetic spectrum" AND :	**36**	44	251	**refined with 'bio': 220**
Topic= mammal* OR bird* OR reptile* OR amphibian* OR fish* OR insect* OR animal*	**15**	28	108	
Topic=(animal*)	**4**	28	106	
Topic=(mammal*)	**1**	8	34	
Topic=(bird*)	**2**	4	32	
Topic=(reptile*)	**0**	0	1	
Topic=(amphibian*)	**0**	0	1	
Topic=(fish*)	**7**	8	19	
Topic=(insect*)	**2**	2	14	
	16	**50**	**207**	

Box 1: Queries used for literature search.

3 Results

3.1 Physiology

Perception

Almost all organisms are known to perceive light in some way or another. However, information on the perception of light or spectral aspects of light is in itself not the goal of this study. Our aim is the disturbance of artificial light of organisms. Disturbance cannot be concluded from perception alone: it has to be demonstrated by a change in crucial physiological processes, in behaviour, in population processes or in interactions between organisms. For that reason we refrain from further discussion of perception as such.

Growth (table 1)

Light obviously affects growth of plants and other photosynthetic organisms. The use of artificial light in warehouses and laboratories proves that growth is also affected by artificial light on algae, corals and plants (Meseck et al. 2005; Sandnes et al. 2005; Demetropoulos & Langdon 2004; Ogbonda et al. 2007; Holcomb & Berghage 2001;Tazawa 1999; Fukuda et al. 2002; Schlager 2007). Plants show a two peak action spectrum of photosynthesis, with one peak in the short wave region and one in the long wave region. A low level is found in between, in the green and yellow region. Urbonaviciute et al. (2007a, b) confirm that a spectrum consisting of only two components may be enough: one in the red regions and one in the short-wave region either being cyan, blue or UV. However, they also found that adding light of the wave length in the blue-green region (505 nm) slightly improved growth and is favourable for biomass accumulation as compared to other wave lengths in the short wave length region. Under artificial light, plants seem to perform best when the red/infra-red ratio is close to the ratio of natural light (Ramalho et al. 2002). When infra-red dominates the spectrum, as in nature is the case in the shade of other plants, plants will elongate (Briggs 2006). Plants grow towards sources of light. This phototropism is known to be affected not only by infra-red light, but also by the blue parts of the spectrum (250-500 nm, with a peak around 450 nm, Briggs 2006).

Light may affect feeding efficiency and through this also indirectly growth in salmon (Taylor et al. 2006). Amphibian larvae grow fastest and larger in dark (Gutierrez et al., 1984) and poultry and steer raising show less problems under interrupted light regimes as compared to continuous lighting (Buyse et al. 1996; Kasuya et al. 2008). Growth of haddock larvae was not different under blue (470 nm) or green (530 nm) light as compared tot complete darkness, although survival was significantly higher under white light (Downing 2002). Green light stimulation of chicken and turkey eggs increased productivity (Rozenboim 2003; Shafey & Al-mohsen 2002), while hens produce less eggs under infra-red light (Rozenboim et al. 1998). Meat production of poultry was highest under blue light (Marosicevic et al. 1990).

So, based on experimental studies aim at productivity of plants, fish and poultry for commercial purposes, we can summaries that growth in plants and birds seems to be affected by both short wave lengths (violet, blue and green) and long wave lengths (red and infra-red), while in fish at least one study shows no effects of blue and green light.

Table 1

Growth		UltrViol -380	Violet 380-450	Blue 450-500	Green 500-550	Yellow 550-600	Orange 600-650	Red 650-750	Infra-red 750-	Light in general	Remarks
Phytoplancton & algae	+									x	Interaction with temperature, nutrients
	-										
Plants	+	x	x	x	x			x	x	x	Short wave & red in combination; blue: phototropism; red-infrared ratio
	-										
Corals	+									x	Interaction with temperature?
	-										
Fish	+									x	Interaction with photoperiod,light intensity and light distribution
	-			x	x					x	Any combinations in larvae; interaction with starvation?
Amphibians	+									x	Interaction with scotophase; speculative interaction with life stage
	-										
Birds	+			x	x				x	x	Interaction with lighting scedule, sex
	-									x	
Mammals	+									x	
	-										
All	**+**		**x**	**x**	**x**			**x**	**x**	**x**	
	-			**x**	**x**					**x**	

x: from laboratory data; X: from field data

Hormone regulation (table 2)

Virtually every aspect of multicellular organism growth, development and behaviour is regulated by hormones, of which a number are again regulated by light. Here we only discuss those that are not related to growth (see above). For plants, we only came across literature related to growth. Artificial light might suppress the release of pheromones in insects (Shorey & Gaston 1964, 1965; Sower et al. 1970; Fatzinger 1973). Several studies have shown that changes of length of day with artificial lights disrupt hormone regulation in amphibians and mammals (Bush 1963; Biswas et al. 1978; Green et al. 1999; Green & Besharse 1996; Lee et al. 1997; d'Istria et al. 1994; Nozake et al. 1990). This is at least partly due to the suppression of melatonin production, which takes place during the night in natural settings. Melatonin production is also suppressed by blue light in mammals (De Molenaar 2003) and by UV light in birds (Zawilska et al. 2000; Lewis et al. 2007), but stress hormone production is decreased in chicks when UV light is missing in the spectrum. Fish showed an increased production of stress hormones under high intensity blue light, but not under white light or low intense blue light (Migaud et al. 2007).

Table 2

Hormone regulation		UltrViol -380	Violet 380-450	Blue 450-500	Green 500-550	Yellow 550-600	Orange 600-650	Red 650-750	Infra-red 750-	Light in general	Remarks
Insects	+									x	
	-										
Fish	+			x							Interaction with intensity
	-			x						x	
Amphibians	+									x	Interaction with length of artificial lighting phase; with melatonin production
	-										
Birds	+	x									Interaction with age
	-										
Mammals	+			x						x	
	-										
All	**+**	**x**		**x**						**x**	

Circadian clock (table 3)

Both plants and animals show an internal, daily, i.e., circadian clock, which is not exactly 24 hours. Therefore, it must be synchronized to local time by a signal in the environment. The signal used to synchronize the internal clock is called a "Zeitgeber". In nature, the red/infra-red ratio in light seems to function as a Zeitgeber for plants (Briggs 2006). For vertebrates the primary Zeitgeber is change in quantity and spectral quality of light at dawn and dusk. The circadian rhythm can be disrupted by artificial light (Beier 2006).

Only two papers are available, that describe the effect of outdoor lamps on plants during a 16 hours night (Cathey & Campbell 1975a, 1975b). They show that plant species differ widely in their sensitivity to short day extended with this type of lamps: flowering was delayed in some short-day species, promoted in some long-day species, and vegetative growth was enhanced in several species, but some species showed no measurable response. Response depended of type of lamp used.

The circadian clock is supposed to get disturbed in moths that fly close to artificial light at night (Frank 2006), but this effect may be low for low pressure sodium lamps (589 nm) (Pittendrigh & Minis 1971). The two-spotted spider mite showed resetting of the circadian clock from blue (475 nm), yellow (572 nm) and orange (612 nm) light, but not from red light (658 nm) (Suzuki 2008). Intensity needed to result in resetting increased from blue to orange.

Larvae of salamanders show diurnal patterns in vertical migration within ponds that can be affected by artificial light (Anderson & Graham 1967). In *Xenopus*, the circadian cycle of melatonin synthesis was suppressed by monochromatic light with wave lengths equal and lower then 533 nm (Cahill et al. 1998). Several diurnal reptile species use artificial light for expanding there activities in the night (Perry & Fisher 2006). The sensitivity to light seems to have a diurnal pattern in alligator hatchlings, but depends on temperature (Kavaliers 2008). It is well known that artificial light affects the daily singing timing in songbirds (Outen 2002).

For mammals, many studies show that artificial light can disrupt the circadian clock

(Halle & Stenseth 2000; DeCoursey 1986; Sharma et al. 1997; Kayumov et al. 2005; Downs 2003). However, the effect of the different wave lengths seems to differ between species: in Golden Hamsters melatonin production is suppressed by light with wave lengths between 300-500 nm, but not by wave lengths smaller than 290 nm or larger then 640 nm (Brainard et al., 1994), while in laboratory rats melatonin production is suppressed uv (290 nm), red (670 nm) and yellow (570 nm), but not by blue light (450 nm) (Aral 2006). Bats showed shifts in circadian clocks after pulses of artificial light, but the effect depended on the moment the pulses were given: when given early during the rest period in their roots, blue (480 nm) and green light had a large effect (520 nm), but violet (430 nm) and yellow light (580 nm) had hardly any effect; when given late, violet (430 nm) and blue light (480 nm) had a high effect, but long wave lengths had not. When the pulses are given early, the optimum effect is reached by green light (520 nm), when given late the optimum is reached at violet light (430 nm). Yellow (580 nm) and red light (654 nm) never seem to have an effect (Joshi & Chandrashekaran 1982; 1985a; 1985b). The moment the bats leave their roost may be effected by artificial light, but also depends on light intensity. In relatively low intensities, red light does not seem to affect the bats (Down 2003).

Table 3

Circadian clock		UltrViol -380	Violet 380-450	Blue 450-500	Green 500-550	Yellow 550-600	Orange 600-650	Red 650-750	Infra-red 750-	Light in general	Remarks
Plants	+							x	x	x	Interaction with type of lamp; Red/infra-red ratio
	-										
Insects	+									x	
	-										
Spiders	+			x		x	x				
	-							x			No sensitivity in terms of induction of diapause
Amphibians	+		x	x	x					x	
	-										
Reptiles	+									xX	Interaction with temperature?
	-										
Birds	+									x	
	-										
Mammals	+	x	x	x		x		x		xX	
	-	x		x			x	x	x		
Bats	+		x	x	x					x	Interaction with circadian time; intensity
	-		x			x		x			
All	**+**	**x**	**x**	**x**	**x**	**x**	**x**	**x**		**xX**	
	-	**x**	**x**	**x**		**x**	**x**	**x**	**x**		

x: from laboratory data; X: from field data

Circannual clock (table 4)

Organisms have also an endogenous rhythm with a period of about one year. The circannual clock affects annual changes in body mass, hormones, reproductive status, hibernation, and the circadian activities over the year.

Plants are known to regulate their flowering time based on the length of the photoperiod, i.e., on the length of the night. Some species need a minimal night length (short-day plants), others a maximum night length (long-day plants), while others do not react to night length. Flowering timing can be disturbed by short flashes of red light (660 nm) during the night, but can be recovered by a infra-red flash (730 nm) after the red flash (Borthwick et al. 1952a). Also, seed germination, leaf expansion, development of photosynthetic machinery, and entry into dormancy are regulated by this red/infra-red reversible system (Borthwick et al. 1952b; Biggs 2006). Holcomb & Berghage (2001) showed that in lilies flowering was delayed and number of leaves produced increased as the photoperiod was increased, but it is unclear whether this is related to the circannual clock in the plants.

The importance of light as a circannual regulator in animals seems to relate to its crucial role in the production of melatonin and the importance of the latter in regulating the reproductive activity (Bartness & Goldman 1989).

Exposure of birds to artificial light during winter causes premature breeding conditions in the laboratory and a shift in migration timing in the field (Lofts & Merton 1968; Rees 1982). The development of gonads is induced by blue (450 nm), green (528 nm) and red light (654 nm) but depends on light intensity (Kumar & Rani 1996; Kumar et al. 2000). Remarkable is that a pair of African bat hawks had a less than 12 month year cycle in an urban area which was attributed to the year round availability of light attracted bats (Hartley & Hustler 1993). Wallabies showed no endogenous cycle with moonlight (Biebouw & Blumstein 2003).

Table 4

Circannual & lunar clock		UltrViol -380	Violet 380-450	Blue 450-500	Green 500-550	Yellow 550-600	Orange 600-650	Red 650-750	Infra-red 750-	Light in general	Remarks
Plants	+							x	x	x	
	-										
Birds	+			x	x			x		xX	Interaction with intensity
	-										
Mammals	+										
	-									X	
All	**+**			**x**	**x**			**x**		**xX**	
	-									**X**	

x: from laboratory data; X: from field data

3.2 Behaviour

General activities (table 5)

Under general activities we have tried to capture all animal activities that cannot be regarded as behaviour due to intern clocks or navigation. It includes foraging behaviour, anti-predator behaviour, schooling behaviour and sexual behaviour.

It has been shown that moths may not mate unless light intensity is below that of a quarter moon (Agee, 1969). Moths do not show their usual anti-predator behaviour when flying around lamps (Acharya & Fenton 1999; Svenson & Ryydell 1998). Lobsters did no show changes in anti-predator behaviour under red light as compared to darkness (Weiss et al.

2006).

Fish are known to change their activity under artificial light (Harden Jones 1956; Woodhead 1956; Nightingale et al. 2006), but also their foraging behaviour (Hobson 1965; Blaxter 1975, Reebs 2002; Mazur & Beauchamp 2006; Contor & Groffith 1995; Prinslow et al. 1980), schooling behaviour (Hobson 1965; Johansson et al. 2006; Woodhead 1966; Harden Jones 1956), anti-predator behaviour (Nightingale et al. 2006), and migration behaviour (Tabor et al. 2001). These effects have not only been shown in the lab, but also in the field (Johansson et al. 2006; Mazur & Beauchamp 2006; Nightingale et al. 2006; Contor & Groffith 1995; Prinslow et al. 1980; Tabor at al. 2001). In nature these effect can be observed as changes in fish behaviour following lunar cycles (Gibson 1978; Patter 1971). Reaction of fish on artificial light may depend on light intensity (Harden Jones 1956; Woodhead 1956), fish density (Johansson et al. 2006), predator density (Fraser & Metcalfe 1997) water temperature (Johansson et al. 2006), life stage (Hoar 1951; Folmar & Dickhoff 1981; Hoar 1976; McInerney 1964) and season (Fraser & Metcalfe 1997).

Surface activity of terrestrial salamanders is affected by artificial light (Adler 1969; Griffith 1985; Wise & Buchanan 2006).Toads and frogs are well known to select sources of artificial light for foraging (Baker 1990; Goin 1958; Goin & Goin 1957; Wright & Wright 1949; Henderson & Powell 2001), but it is unclear whether this behaviour is a reaction on higher prey density, better visibility of the prey, phototaxis, or a combination of these (Frank 1988; Buchanan 2006). Mating, nesting, and territorial behaviour might be affect by light (Rand et al. 1997; Tarano 1998; Buchanan 2006; Wise & Buchanan 2006; Nunes 1988), but some species were found not to change their calling behaviour under artificial lighting (Buchanan 2006). Foraging ability was affected by artificial light (Buchanan 1993; Placyk & Graves 2001), but may depend on the presence of chemical clues (Wise & Buchanan 2006). Foraging was not affected by uv light (Placyk & Graves 2001). Amphibians need time to adapt to changes in light, and can therefore temporarily be blinded by changes of light intensity (Buchanan 1993; Wise & Buchanan 2006).

Sea turtles avoid parts of the beach that are artificially illuminated for laying eggs (Witherington 1992; Salmon et al. 1995a; Salmon et al. 2000), but this effect is not present when the lamps used are low pressure sodium lamps (598 nm) (Witherington 1992). Foraging behaviour of reptiles may change under artificial light (Zhou et al. 1998; Clarke et al. 1996), also known from natural changes in light intensity from moon phases (Frankenberg & Werner 1979; Bouskila et al. 1992; Reichman 1998; Andreadis 1997; Clarke et al. 1996; Pacheco 1996; Bouskila 1995; Perry & Fisher 2006).

Poultry change their foraging and feather-pecking behaviour under different types of white artificial light, depending in light intensity (Boshouwer & Nicaise 1993; Kristensen et al. 2007). De Molenaar et al. (2000) found that Godwits changed their breeding behaviour near road lamps.

Rodents are shown to change their activity and foraging behaviour under artificial light, both in laboratories and field settings (Vasquez 1994; Kramer & Birney 2001; Brillhart & Kaufman 1991; Clarke 1983; Falkenberg & Clarke 1998; Kotler 1984; Bird et al. 2004), although there might be difference between species (Alkon & Saltz 1988; Vasquez 1994). This is in concordance with the observation that activities may be affected by moon light intensity (Rich & Loncore 2006). Bird et al. (2004) found that beach mouse were less affected by bug lights then by low pressure sodium lamps in their foraging behaviour (598 nm). De Molenaar et al. (2003) found that some species preferred to migrate under high pressure sodium lamps (550-650 nm), other avoided them - also found in juvenile pumas

(Beier 1995) – while other species were not affected. Wallabies showed changed foraging and anti-predator behaviour under both white light and red light (Biebouw & Blumstein 2003).

Some bats use lamp lit roads for foraging (Blake et al. 1994). Bats may prefer to use vision for foraging (Eklöf & Jones 2003), but it is unclear whether this explains the use of lamps for foraging, or that it is only a reaction on prey density. Anyhow, when orange road lamps are used that do not attract insects, bats no longer show an increased activity in these roads (Blake et al. 1994). Some species seem to avoid lamps (Rydell & Baagøe 1996; Alison Fure 2006). Artificial light might affect colony behaviour in that emergence can be delayed or prolonged in illuminated buildings (Sándor Boldogh et al. 2007). At light levels slightly above natural moonlight, migration behaviour along commuting routes might be disturbed (Kuijper et al. 2008).

Table 5

General activities		UltrViol -380	Violet 380-450	Blue 450-500	Green 500-550	Yellow 550-600	Orange 600-650	Red 650-750	Infra-red 750-	Light in general	Remarks
Insects	+									xX	
	-										
Crustacea	+										
	-							X			
Fish	+									xX	Interaction with intensity, density, temperature, life stage; season; predator density
	-										
Amphibians	+									xX	Interaction with chemical clues, period of lighting; intensity
	-	x								X	
Reptiles	+									xX	
	-					X					
Birds	+									xX	Interaction with age, time of day
	-										
Mammals	+					X	X	X		xX	Interaction with species
	-					X	X				
Bats	+									X	Interaction with weather
	-						X				Indirect effect through insect density
All	**+**					**X**	**X**	**X**		**xX**	
	-	**x**				**X**	**X**	**X**		**X**	

x: from laboratory data; X: from field data

Phototaxis (table 6)

Phototaxis is the movement of animals toward (attraction) or away (repulsion) from a source of light. Many animals show this behaviour and we have found relatively much information on it.

Flight to light behaviour is very well known for insects (Dufay 1964; Bowden & Morris 1975; Bowden 1982; Kolligs 2000; Frank 2006). The actual amount of insects found near a lamp depends on type of lamp, lamp density, and background illumination, such as moonlight (Bowden 1981, 1982; Kolligs 2000; Frank 2006; Robinson & Robinson 1950). Most moth species are attracted to all types of lamps (Frank 2006 gives an overview), except low pressure sodium lamps (589 nm) (Robinson 1952; Rydell 1992). Bishop et al. (2004;

2006) showed that midges are attracted to uv, blue (475 nm) and green light (520 nm), but not to yellow (595 nm) and red light (640 nm). Remarkable is that also incandescent white light did hardly attract midges. This seems to contradict the findings of Ali et al. (1994) who found that midges were attracted strongest to white light. In this research yellow light also attracted many midges, but red did least. A strong correlation between attraction and light intensity was shown. Male glow-worms are attracted to green light (555 nm), the wave length of the signalling females. But this attraction was reduced when blue (485 nm) was added to the light (Booth et al. 2004). Some shrimps, sensitive to green light (520 nm), avoid artificial light in

Table 6

Phototaxis		UltrViol -380	Violet 380-450	Blue 450-500	Green 500-550	Yellow 550-600	Orange 600-650	Red 650-750	Infra-red 750-	Light in general	Remarks
Insects	+	x		x	x	xX				X	Interaction with background illumination; intensity; density of lamps
	-			x		xX		xX		x	
Crustacea	+				x					xX	
	-							X			
Fish	+			x	x	x		xX		xX	Interaction with temperature, species; season
	-									x	
Amphibians	+		x	x	x	x	x	x		x	Interaction with intensity; species, light adaption
	-										
Reptiles	+		x	x	x						
	-										
Birds	+							X		xX	Interaction with age, weather
	-			X	X			X			
Mammals	+					X	X			X	
	-					X	X				
Bats	+									X	
	-										
All	**+**	**x**	**x**	**x**	**x**	**xX**	**xX**	**xX**		**xX**	
	-			**xX**	**X**	**xX**	**X**	**xX**		**x**	

x: from laboratory data; X: from field data

the field, while sandhoppers showed phototaxis in laboratory settings (Gal et al., 1999; Papi 2007). Lobsters showed no phototaxis toward red light (Weiss et al. 2006).

Fishermen use the attractiveness of light for fish while fishing at night, which is confirmed by research (Wickham 1973; Puckett & Anderson 1987; Oppedal et al. 2007; Nightingale et al. 2006; Haymes et al. 1984; Marchesan et al. 2005; Juell & Fosseidengen 2004). But some species avoid light (Contor & Grffith 1995; Van Aanholt et al. 1998).The actual phototaxis may depend on species, background illumination, water temperature, and season (Contor & Griffith 1995; Juell & Fosseidengen 2004; Marchesan et al. 2005; Oppedal et al. 2007). European seabass did not show phototaxis toward white light, but it showed repulsion for blue and green light, while the striped bream was attracted to white light at all illumination levels, but did not show any reaction to coloured light (Marchesan et al., 2005). Fish may show positive and negative phototaxis to red light (Patrick 1978; Weiss et al. 2006). Silver eels avoid sodium vapour lamps (Haymes et al. 1984).

Most amphibians show phototaxis, but whether it is positive or negative may depend on light intensity (Hartman & Hailman 1981), life stage (Wise & Buchanan 2006), time of the day (Sugalski & Claussen 1997), and wave length (Hailman & Jaeger 1974; Deutschlander et al. 1999). Amphibians are often been said to have a 'blue preference'. When studying anura species, Hailman & Jaeger (1974) and Hartman & Hailman (1981) found some kind of phototaxis for violet (440 nm), blue (480 nm), green (530 nm), yellow, orange and red light (650 nm), but most species preferred blue and green and were repulsed by violet and red. Turtle hatchlings are strongly attracted by violet to green wave lengths, but either indifferent or repulsed by longer wave lengths (Lohmann et al. 1997). Using filters that excluded wave lengths lower than 570 nm did seem to reduce the attractiveness of lamps, but the effect was strongly depended on light intensity and orientation clues, i.e., silhouettes (Salmon 2006; Nelson 2002).

Birds are attracted by artificial lights (Evans Ogden 1996; Kraft 1999; Gauthreaux & Belser 2006). This may lead to bird mortality, but this seems to depend strongly on the weather (Gauthreaux & Belser 2006). Literature on coloured light is not clear: red and blue light seem less attractive than white light (Wiese et al. 2001; Gauthreaux & Belser 2006), but Poot et al. (in press) found that birds were stronger attracted to white and red light than to green and blue light, although this study makes no clear distinction between phototaxis and disorientation.

Beier (1995) found that pumas showed a negative phototaxis toward urban lights, while Kuijper et al. (2008) found negative phototaxis in bats. De Molenaar et al. (2003) found no phototaxis toward high pressure sodium lamps for some mammal species and attraction for other (550-650 nm).

Orientation (table 7)

Some animals have an internal compass for orientation during migration. This compass may be disturbed by artificial light, resulting in disorientation of the animal.

The well known 'captivity effect' of insects that are unable to escape the near zone of lamps, may be a result of such disorientation (Baker & Sadovy 1978; Sotthidandhu & Baker 1979), although also other explanations for this phenomenon exist (Robinson & Robinson 1950; Hamdorf & Höglund 1981; McGeachie 1988; Hartstack et al. 1968). Drosophilas showed no disorientation in UV light (365 nm), but were disorientated in blue light (500 nm).

Disorientation through artificial light is also known from amphibians, i.e., newts. This was caused by wave lengths larger than 500 nm (Philips & Borland 1992), more specifically: homing orientation remained under full spectrum, violet (400 nm and 450 nm), but was lost under blue (475 nm), green (500 nm), yellow (550 nm) and orange light (600 nm) (Philips & Borland 1992, 1994). Artificial light is also known to disrupt seaward orientation of sea turtle hatchlings (Salmon et al. 1995b). This seems not the result of disruption of an intern compass, but from the absence of dark silhouettes on the landward part of the beach (Salmon & Wiltherington 1995). Adults are not disoriented by artificial light (Wiltherington 1997; Salmon 2006).

Disorientation was studied for several bird species. Undisturbed orientation was found under white, violet (424 and 443 nm), green (502 and 510 nm), and yellow light (565 nm), disorientation under uv (373 nm), yellow (590 nm), orange (630 nm), and red light (660 nm), but there seems to be an interaction with light intensity in that under high intensity, disorientation may also occur at short wave lengths (Munro et al. 1997; Wiltschko & Wiltschko 2001; Rappl et al. 2000; Wiltschko 2007). Disorientation may be age dependent (Gauthreaux 1982). Gautereaux & Belser (1999) and Poot et al. (in press) claim to find greater disorientation from red light (600-700, with a peak at 670nm) than from blue (450 nm) and green light (530 nm) in field settings, but the distinction between phototaxis and disorientation is not clear in these studies.

Table 7

Orietation		UltrViol -380	Violet 380-450	Blue 450-500	Green 500-550	Yellow 550-600	Orange 600-650	Red 650-750	Infra-red 750-	Light in general	Remarks
Insects	+			x						X	
	-	x									
Crustacea	+									X	
	-										
Amphibians	+			x	x	x	x				
	-		x							x	
Reptiles	+									X	Interaction with background illumination
	-									X	Interaction with age
Birds	+	x				x	x	xX			Interaction with intensity, age
	-		x	xX	xX	x				x	
All	**+**	**x**		**x**	**x**	**x**	**x**	**xX**		**X**	
	-	**x**	**x**	**xX**	**xX**	**x**				**xX**	

x: from laboratory data; X: from field data

3.3 Ecology

Populations (table 8)
Little is known about the effect of artificial light on populations. Egg-production is different under different light regimes in poultry (Davis et al. 1993; Siopes 1991; Siopes 2007) and fertility is affected by artificial light in rabbits under breeding conditions (Schudemage et al. 2000). Artificial light systems affect piglet mortality in pig breeding systems (O'Reilly et al. 2006). The decline in some Californian reptile species was correlated with a gradient in light pollution (Sullivan 2000) and De Molenaar (2000) found that Godwits avoided the vicinity of road lamps for nesting.

Table 8

Reproduction		UltrViol -380	Violet 380-450	Blue 450-500	Green 500-550	Yellow 550-600	Orange 600-650	Red 650-750	Infra-red 750-	Light in general	Remarks
Birds	+									x	
	-										
Mammals	+									x	
	-										
All	**+**									**x**	
	-										
Mortality		UltrViol -380	Violet 380-450	Blue 450-500	Green 500-550	Yellow 550-600	Orange 600-650	Red 650-750	Infra-red 750-	Light in general	Remarks
Mammals	+									x	
	-										
All	**+**									**x**	
	-										
Distribution		UltrViol -380	Violet 380-450	Blue 450-500	Green 500-550	Yellow 550-600	Orange 600-650	Red 650-750	Infra-red 750-	Light in general	Remarks
Reptiles	+									X	
	-										
Birds	+									X	
	-										
All	**+**									**X**	
	-										

x: from laboratory data; X: from field data

Interactions (table 9)

It has been suggested that artificial light might effect the competition between species, especially nocturnal specialists or species that avoid artificial light may suffer disproportional from it (Nightinggale et al. 2006; Arlettaz et al. 2000), but such an effect seems not yet proven.

Joseph & Hering (1997) found that germination of spores of rust – a fungus parasite of plants – was delayed by all artificial light sources containing infra-red (700-800 nm), while Vallavieille-Pope et al. (2002) showed that infection efficiency increased under artificial light. Farmed salmons had an overall increase of lice infestation under artificial light (Hevroy et al. 2003).

As fishermen use artificial light for fishing at night, predators of fish, including fish and mammals, are attracted to sources of artificial light, probably for the higher density of prey (Prinslow et al. 1980; Tabor et al. 1998; Tabor et al. 2001; Nightingale et al. 2006; Yurk & Trites 2000). The size of the fish eaten might change under artificial light (Elston &

Bachen 1976; Holzman & Genin 2003; Mills et al. 1986). Amphibians, reptiles and bats are know to occur at higher densities in the vicinity of lamps that attract insects (Baker 1990; Blake et al 1994; Rydell 1992; Rydell & Baagøe 1996). The change in the annual cycle of the pair of African bat hawks in an urban area suggest that these birds have changed their behaviour as a reaction on the higher density of bats near artificial light (Hartley & Hustler 1993).

Table 9

Predator-prey		UltrViol -380	Violet 380-450	Blue 450-500	Green 500-550	Yellow 550-600	Orange 600-650	Red 650-750	Infra-red 750-	Light in general	Remarks
Plants	+								x		Fungus infections
	-										
Fish	+									xX	Predation of fish by fish, by mammals, of zooplankton by fish and parastirsm of fish by lices; Interaction with prey size
	-										
Amphibians & reptiles	+									X	See ‘general activites’
	-										
Bats	+									X	
	-										
All	**+**									**xX**	
	-										

x: from laboratory data; X: from field data

4 Discussion

4.1 Introduction

As stated before, the above review of the effects of coloured light on nature is based on previous overviews, viz. De Molenaar et al. 1997, De Molenaar 2003 and Rich & Longcore 2006, supplemented with recent literature. Therefore it is not complete, especially as far as old literature is concerned. None the less, we think that table 10 gives a good overview of existing published knowledge. We deleted corals, not being terrestrial species, and added molluscs, being an important above ground terrestrial group.

Table 10

– = no information
L = at least one source on light
S = at least one source on spectral aspect

			Physiology				Behaviour			Populations			Interaction	
			growth	hormone regulation	circadian rhythm	circannual & lunar clock	general activities	phototaxis	orientation	reproduction	mortality	distribution	predator-prey	competition
plants	phytoplancton		L	–	–	–	–	–	–	–	–	–	–	–
	terrestrial plants		S	–	S	S	–	–	–	–	–	–	S	–
animals	invertebrates	spiders	–	–	S	–	–	–	–	–	–	–	–	–
		insects	–	L	L	–	L	S	S	–	–	–	–	–
		crustacea	–	–	–	–	S	S	L	–	–	–	–	–
		mollusca	–	–	–	–	–	–	–	–	–	–	–	–
	vertebrates	fish	S	S	–	–	L	S	–	–	–	–	L	–
		amphibians	L	L	S	–	S	S	S	–	–	–	L	–
		reptiles	–	–	L	–	S	S	L	–	–	L	L	–
		birds	S	S	L	S	L	S	S	L	–	L	–	–
		mammals	L	S	S	L	S	S	–	L	L	–	–	–
		bats	–	–	S	–	S	L	–	–	–	–	L	–

In interpreting our results, one should take into consideration that not all knowledge is published, though. The motivation to publish negative results is probably much lower than that to publish positive results, both of authors and of journal redactions. So the fact that we did not come across literature on the effects of light of wave lengths larger then 500 nm on hormone regulation may not only indicate that no research is done, but also that no effects were found.

In many cases, results of research show interactions between the effect of the studied spectral part of light on the species with other factors. One obvious factor is the intensity of light, others are life stage of the species, season, density of the species, density of other species, etc. This makes straightforward interpretation of effects complicated. Whenever possible we have tried to indicate these interactions in the tables 1-9.

Another complicating factor for interpreting our results is that much research we found was performed under laboratory conditions (table 11), while we are especially interested in effects in the field. In the field, many animals may be able to regulate their exposure to artificial light. That is why we regard phototaxis as being of special importance for our end goal: designing nature friendly outdoor lamps (see below).

Table 11

Legend: (empty) = no information on spectral aspects; lab = laboratory studies; field = at least one source from field studies

			Physiology				Behaviour			Populations			Interaction	
			growth	hormone regulation	circadian rhythm	circannual & lunar clock	general activities	phototaxis	orientation	reproduction	mortality	distribution	predator-prey	competition
plants	phytoplancton													
	terrestrial plants		lab		lab	lab							lab	
animals	invertebrates	spiders			lab									
		insects						field	lab					
		crustacea					field	field						
		mollusca												
	vertebrates	fish	lab	lab				field						
		amphibians			lab		lab	lab	lab					
		reptiles					field	lab						
		birds	lab	lab		lab		field	field					
		mammals		lab	lab		field	field						
		bats			lab		field							

We did hardly come across studies of aspects of artificial light like polarisation, ultra sonar emissions of lamps, or armature. We think that these aspects need more attention. At least one study suggests the importance of polarisation in attracting aquatic insects (Krista et al. 2006) and we have noticed ourselves that some lamps emit ultra sonic sounds in the wave length region that is also used by bats.

4.2 Knowledge needed

We started our review stating that according to some authors (viz. Rich & Longcore 2006) much is still to be learned about the effects of light on nature, and we found that this is especially true for the effect of coloured light (i.e., specific wavelength) on nature. As a matter of fact, studies on the effect of coloured light on populations, species interactions, or communities are almost completely missing. However, we also found that for some species groups detailed information is available of the effect of certain wave lengths on physiology and behaviour. Might this information be enough to design nature friendly outdoor lamps, or at least formulate hypotheses on what wave lengths these lamps should not emit?

In theory this seems possible. If we need a lamp to be used in an area where only one species groups is of high conservation value and it happens that for this group the physiological or behavioural effects of coloured light is known, we could design such a lamp and study the ecological consequences when used in the field. Amphibians and birds seem species groups for which this could be true.

However, in most cases areas will have conservation value for a combination of species, and information should be available on the effect on all of these groups. Of course, we do not plead here for the design of lamps for every possible combination of species groups. A practical way of working could be that, based on the potential effects of coloured light on species, a limited number of typical landscapes are chosen and for each a lamp is designed. Such a typology of landscapes could start with the distinction between open en closed areas, because the scale of the effect of light will be different in these two types. A second distinction could be the presence of open water within the landscape. When not present, species groups like crustaceans and fish can be ignored. A further distinction could be the presence of a certain relatively rare group of animals, like reptiles.

Such a typology would not be able to prevent that certain species groups will turn out to be of conservational relevance in almost every type of landscape, such as insects, spiders, molluscs, amphibians, birds, mammals, and bats. This means that even for designing lamps for specific areas, knowledge for all these groups is crucial. Much of this knowledge is still missing.

So we need more research before we can actually design ecological friendly lamps. But which issues are the most urgent to be studied? In order to have some indication for this we tried to assess

- Relative importance of the effects: in the end we are concerned with the ecological consequences of using the lamps. But the information to be used for the design of the lamps or for the formulation of hypotheses on the effects of the lamps is to be based on known effects on physiology and behaviour. So the question is how these effects are related to potential ecological effect.
- Relative importance of the species group concerned: not all species groups may have the same ecological vulnerability for a physiological or behavioural effect. Besides, different species groups may play different roles within a community.

Importance of effects

The following discussion of the relative importance of the effects focuses on both individual species and total communities of conservational importance.

For the conservation of vulnerable species, such as red list species, or species otherwise designated as of conservational importance, the survival of local populations is the main issue. This survival is directly correlated with the size of the population. Population size in an area is dependent on birth rate, immigration, death rate and emigration (sometimes referred to as the BIDE-model). Any potential effect of light on any of these parameters may also have effects on the population size of the species considered important for conservation, and should therefore be taken into consideration.

For the assessment of the potential effects on communities, we base our self on the recent discussion of the relative importance of niche partitioning and ecological drift for community composition (Hubbell, 2001; McGill et al. 2007). The ecological process determining niche partitioning is competition and depends on the ecological differences between species. Ecological drift is a so called neutral process, not depending on differences between species, but on chances of colonisation and extinction of all the species in the species pool. Most authors seem to agree now that both mechanisms are relevant, but that the actual importance of each is still not known and may be different in different ecosystems (McGill et al. 2007; Adler et al. 2007). At least some of the authors participating in this discussion argue that niche partitioning may regulate the relative frequency of the species that are abundant in the system, while ecological drift is determining the presence of rare species (Ulrich & Ollik 2004). This would mean that the relative abundance of the common species is mainly dictated by competition, while the species richness - that depends on the presence of rare species - is mainly dictated by colonisation and extinction. Species interactions other than competition, such as predator-prey or parasite-prey relationships, are here regarded as affecting mainly birth and death rates, although the relative vulnerability of prey species for predators/parasites/pathogens can also be regarded as an aspect of competition. Anyhow, *competition*, *dispersion* (i.e. colonisation rate and for the individual species the net immigration-emigration), and *survival* (i.e. reciprocal extinction rate and for the individual species the net birth-death rate) are regarded here as the three key processes dictating species population size and community composition.

Is it possible to translate the physiological or behavioural effects of light into effects on these ecological processes? We will try to do that in the next section, but we should keep in mind that the more reasoning steps we need for connecting the effects to the ecological processes, the more speculative they are. As a consequence, the ecological consequences of physiological effects are more uncertain than those of behavioural effects. This is strengthened by the fact that almost all known physiological effects are from laboratorial experiments, and not from field studies. For this reason we will give less weight to physiological than to behavioural effects.

The ecological impact of effects of light on *growth* works typically through competition: species will change in their ability to transform resources into biomass. This ability will be different between species and therefore their relative competitive strength will change. Changes in *hormone regulation* will probably also change competition, but it may also directly effect reproduction if sex hormones, such as pheromones, are involved. We did not come across examples of changes in mortality due to changed hormonal anti-herbivore of anti-predator mechanisms, nor changed dispersal due to hormonal changes although these also may occur. Changes in *circadian clocks* alter the time available for daily activities of a species and seem again to work through competition when species have different shifts in time available. Changes in *circannual clocks* will result in changes in the timing of seasonal activities such as reproduction, migration and hibernation. Here a more direct relation with dispersion and survival can be expected.

Under the heading *general activitie*s we have included all kind of behaviour, some directly related to competition, such as feeding behaviour, some to reproduction, such as mating behaviour, or mortality, such as anti-predator behaviour, and other to dispersal. For all these types of behaviour we found examples of changes due to the effect of light. Differences in *phototaxis* may result in changes in competition between species if some species avoid light while others are attracted to it. It may also result in direct mortality due to collisions. And for some species, it may result in barriers, so affecting dispersion. Phototaxis plays a special role in the effects of light on species, because it may function as a kind of a multiplier:

when attracted from relative large distances to a light source, animals may expose themselves to light intensities that will also have other effects, such as hormonal changes or disorientation. This is especially true for flying animals that can come very close to a light source. By this mechanism, positive phototaxis may enlarge the area on which other effects of light work, while negative phototaxis may decrease it. *Disorientation* obviously affects migration, and thereby survival through exhaustion. But it can also result in direct mortality through collisions. Since migration is directed toward a specific location, such as winter habitat or breeding place, it is not the same as dispersion which can be regarded as the undirected change of living area. For such undirected movements, disorientation may not be relevant.

Importance of species groups

The relative importance of a species group can be assessed taking the conservation value of the species group into consideration. For example, the relative number of Red List species within the species group could be used, but also the public appeal of a species group. We do not apply this way of weighting here, because we think that the conservation value should be assessed at the level of species, not of species group.

A good way of assessing the relative importance of a species group could be by comparing the groups according to their vulnerability for the effects discussed above. Another way of looking at the importance of species groups is by looking at the relative dominance of the group within the community. We will work out both approach a little further.

As we stated before: all organisms are completely adapted to the natural light and it changes in their living environment. As a consequence, it is difficult to find differences between species groups in the importance of disturbing effects of artificial light on their *physiology*. One might think of a distinction between diurnal versus nocturnal species, a subdivision that in some cases follows group division, amphibians and mammals being mainly nocturnal, while reptiles and birds are in general diurnal, at least in our regions. But the suggestion that nocturnal species may suffer greater physiological disturbance from artificial light may not be true, since for example hormone production during the night might strongly be disturbed in diurnal species. Concerning *behaviour*, we stated that we regard flying animals as especially vulnerable for the multiplying effects of positive phototaxis. These are in our typology of species groups the insects, birds, and bats, and we will give extra weight to light impacts concerning these groups. Another distinction that can be made based on a high vulnerability to a certain light effect is the distinction between non-migrating and migrating species, the latter being special vulnerable to disorientation. The insects, fish, amphibians, birds and bats of the Netherlands include migrating species. These species groups will also be weighted extra. On the larger scale, some mammal species, like large herbivores, also migrate.

Another way of weighting species groups is by looking at the relative dominance of the groups within the community. By dominance we mean that a relative large part of the biomass within a trophic level might be produced by a certain group. Changes in such a group will probably affect the entire community, although it might not be clear how these changes affect biodiversity. This weighting is therefore speculative, and we regard it as of relatively small importance. The dominant species group of the primary producers are vascular plants in terrestrial systems and phytoplankton in aquatic systems. At the secondary level, we regard insects and mammals (mice) as dominant in terrestrial systems and zooplankton, especially small crustaceans, and fish as dominant in aquatic systems. All other groups we regard as non dominant.

Weights in summary (table 12)
The above discussed weighting results in table 12. Since reproduction, survival and dispersion also affect competition, competition is always a potential effect.

Table 12 **weights**

			Physiology				Behaviour			Populations			Interaction	
			growth	hormone regulation	circadian rhythm	circannual & lunar clock	general activities	phototaxis	orientation	reproduction	mortality	distribution	predator-prey	competition
plants	phytoplancton		●	●●●	●	●●●				■	■	■	■	■
	terrestrial plants		●	●●●	●	●●●				■	■	■	■	■
animals	invertebrates	spiders	●	●●●	●	●●●	●●●	●●●	●●	■	■	■	■	■
		insects	●	●●●	●	●●●	●●●	●●●	●●	■	■	■	■	■
		crustacea	●	●●●	●	●●●	●●●	●●●	●●	■	■	■	■	■
		mollusca	●	●●●	●	●●●	●●●	●●●	●●	■	■	■	■	■
	vertebrates	fish	●	●●●	●	●●●	●●●	●●●	●●	■	■	■	■	■
		amphibians	●	●●●	●	●●●	●●●	●●●	●●	■	■	■	■	■
		reptiles	●	●●●	●	●●●	●●●	●●●	●●	■	■	■	■	■
		birds	●	●●●	●	●●●	●●●	●●●	●●	■	■	■	■	■
		mammals	●	●●●	●	●●●	●●●	●●●	●●	■	■	■	■	■
		bats	●	●●●	●	●●●	●●●	●●●	●●	■	■	■	■	■

The darker the blue, the more direct the effect is supposed to be related to an ecological effect; red: species groups of the first trophic level; orange: species groups of the second trophic level; yellow: species groups of the third trophic level; ● = related to competition ; ●● = related to competition & survival; ●●● = related to competition, survival & dispersion; ■ = direct ecological relevance

4.3 Gaps in knowledge

The available information we came across during our study is represented in table 10. One should keep in mind that the indication that information is available might be based on only one single source. For example, we know of only one study of the phototaxis of crustaceans, i.e., lobsters, toward red light. We did not come across any (research on the) effects of coloured light on important crustacean groups of zooplankton, like the copepoda or the cladocera.

By subtracting the available information, now restricted to the available information on the effect of parts of the spectrum (table 11), from our weight-table, we can see were the important gaps in information lie in the effects on physiology and behaviour that could be used to design nature friendly lamps or formulate hypotheses on the potential effects of such lamps on populations or communities (table 13). Again, it should be kept in mind that in the cells coloured green, the available information might be far from complete.

Table 13 **weights minus available**

			Physiology				Behaviour			Populations			Interaction	
			growth	hormone regulation	circadian rhythm	circannual & lunar clock	general activities	phototaxis	orientation	reproduction	mortality	distribution	predator-prey	competition
plants	phytoplancton		●	●●●	●	●●●				■	■	■	■	■
	terrestrial plants			●●●						■	■	■		■
animals	invertebrates	spiders	●	●●●		●●●	●●●	●●●	●●	■	■	■	■	■
		insects	●	●●●	●	●●●	●●●			■	■	■	■	■
		crustacea	●	●●●	●	●●●			●●	■	■	■	■	■
		mollusca	●	●●●	●	●●●	●●●	●●●	●●	■	■	■	■	■
	vertebrates	fish			●	●●●	●●●		●●	■	■	■	■	■
		amphibians	●	●●●		●●●				■	■	■	■	■
		reptiles	●	●●●	●	●●●			●●	■	■	■	■	■
		birds			●		●●●			■	■	■	■	■
		mammals	●			●●●			●●	■	■	■	■	■
		bats	●	●●●		●●●		●●●	●●	■	■	■	■	■

The darker the blue, the more direct the effect is supposed to be related to an ecological effect; red: species groups of the first trophic level; orange: species groups of the second trophic level; yellow: species groups of the third trophic level; ● = related to competition ; ●● = related to competition & survival; ●●● = related to competition, survival & dispersion; ■ = direct ecological relevance; green cells: at least one literature source is available on the effect of a part of the spectrum; dark green cells: at least one source is available based on field studies.

It should be no surprise that the effects of coloured light on ecological processes is almost completely unknown. Also effects on invertebrates are still largely unknown. Especially the spiders and molluscs are mostly ignored, but as said before, also the crustaceans in plankton deserve much more attention. For vertebrates, it is remarkable that disorientation in fishes, reptiles and mammals is not well studied. Also phototaxis of bats towards coloured light is not yet studied, but it should be noticed that even for birds, phototaxis is not yet very well studied, and a clear distinction between phototaxis and disorientation is usually not made in field studies.

4.4 A strategy for further study

From the above, it can be concluded that there is a need for research of the effects of coloured light on the ecological processes of all organisms. Preferably such research should be performed in field studies. What parts of the spectrum should be studied? The tables presented in our results give clues to hypothesize which colours might have relative low effects on which species groups.

As we have stressed, phototaxis might be regarded as a multiplier and therefore as of special importance to ecological effects in nature. As it happens, phototaxis is also the effect on which most literature is available. So, we think that phototaxis might be a good starting point to design the first generation of testing lamps. For example, based on phototaxis literature it should be possible to design outdoor lamps with an amphibian friendly spectrum.

These first generation lamps should then be tested in the field using a 'Before-After-Control-Impact-approach' (BACI). For that, locations where these lamps are applied should be compared before and after the application of the lamps with locations with common used standard lamps and locations with non-working lamps. Preferably locations are chosen of which the community is already well known. In these locations, not only the target species group - the amphibians of the above example - but also other relevant groups should be studied. A multi-trophic approach is recommended, so that all important groups of the community are taken into consideration. In all cases, the research should be focussed on trying to assess effects on survival, dispersion and competition.

Although field studies might show the effects on a variety of species groups of applying lamps with a certain spectrum, they will not do to explain the effects found. For that, additional laboratorial studies remain necessary, for example, in order to the disentangle phototaxis and disorientation. Such research might also be fruitful for studying groups that are largely ignored up until now and are hard to study in the field, such as spiders, molluscs and small crustaceans.

4.5 Conclusions

Our knowledge of the effects of coloured light on the physiology, behaviour and ecology of plants, animals and communities is still far from complete. On the other hand, however, knowledge in some fields, such as phototaxis, seems to give enough clues to at least postulate a spectrum that might be of relatively low disturbance for a specific species group. Lamps can be designed based on these spectra and these lamps can be tested in the field. Any field study of the effects of coloured light on survival, dispersion or competition of species or species groups would be a considerable contribution to our knowledge.

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