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Review Article

Does a flashing artificial light have more or conversely less impacts on animals than a continuous one? A systematic review

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Abstract

Background: Light pollution has been increasingly recognised as a threat to biodiversity, especially with the current expansion of public lighting. Although the impacts of light intensity, spectral composition and temporality are more often studied, another component of light, its flicker frequency, has been largely overlooked. However, flashing light could also have impacts on biodiversity, and especially on animal behaviour and physiology.

Objective: This systematic review aimed at identifying the reported physiological and behavioural impacts of flashing light on animals when compared to continuous light.

Methods: We followed the standards recommended by the Collaboration for Environmental Evidence (CEE) in order to achieve a comprehensive, transparent and replicable systematic review. Citations were primarily extracted from three literature databases and were then screened for relevance successively on their titles, abstracts and full-texts. Retained studies were finally critically appraised to assess their validity and all relevant data were extracted. Only studies which compared a flashing light to a continuous one were included.

Results: At first, we found 19,730 citations. Screening and critical appraisal resulted in 32 accepted articles corresponding to 54 accepted observations—one observation corresponding to one species and one outcome. We collated data on four main taxa: Aves (the most studied one), Actinopterygii, Insecta and Mammalia as well as on plankton.

Conclusions: The impacts of flashing light are currently critically understudied and varied between species and many light specificities (e.g. frequency, wavelength, intensity). Therefore, no definitive conclusions could be drawn for now. Thus, research on flashing light should be pressingly carried out in order to better mitigate the impacts of Artificial Light at Night (ALAN) on wildlife. In the meantime, we would recommend precautionary principles to be applied: flashing lighting should be limited when not deemed essential and flicker frequencies managed to prevent animals from experiencing any potential harm from flashing light.

Key words: Blinking light, critical flicker fusion frequencies, dark infrastructure, dynamic lighting, light emitting diodes, nature, sensory disturbance, vision

Introduction

Since the 1990s, species diversity has been decreasing at an accelerating pace (IPBES 2019; IUCN 2021). Among the main drivers affecting biodiversity, land degradation, overexploitation, climate change, chemical pollution and invasive species are now commonly acknowledged as the most impacting ones (IPBES 2019). However, during the last decades, other types of anthropogenic drivers have intensified as well, such as light pollution, which is now considered a serious cause of biodiversity erosion (Hölker et al. 2010, 2021). Indeed, satellite-detectable light has increased by at least 49% between 1992 and 2017, notably due to increased urbanisation and economic growth (Sánchez de Miguel et al. 2021). Simultaneously, Light Emitting Diode (LED) installations have increased, due to their reduced energetic consumption and cost compared to previous technologies such as gas discharge lamps (Zissis et al. 2021), and could lead to a potential 'rebound effect' where more anthropogenic light may end up being emitted (Kyba et al. 2017).

Artificial Light at Night (ALAN) have a wide range of impacts on biodiversity from alterations of an individual's physiology, behaviour and reproduction to ecosystem-wide consequences through impacts on species mobility, relationships and habitat use, threatening community persistence at the landscape level (Falcón et al. 2020; Pérez Vega et al. 2022). These effects of ALAN may depend on several key components of the light source (e.g. intensity, spectral composition, temporality, spatial distribution). For instance, Simons et al. (2021) showed the importance of light intensity on the distribution of runs of the California grunion *Leuresthes tenuis* and roosts of the western snowy plover *Charadrius nivosus* and identified a threshold of 50 mlx to 100 mlx at which the behaviours of both species started to be impacted by ALAN. Increasing intensity levels of ALAN have also been shown to alter cane toads *Rhinella marina* activity patterns and to strongly decrease their corticosterone levels (Secondi et al. 2021). As for ALAN spectral composition, Deichmann et al. (2021) observed an overall significant decrease of insect attraction to filtered-amber LED lamps (deprived in blue spectrum) in a tropical forest environment. Considering the temporality of ALAN, Davies et al. (2017) observed that switching off lighting during periods of low demand while also dimming, was the most promising alternative in order to mitigate the impacts of ALAN on the composition of grassland spider and beetle assemblages. However, on higher levels of the food chain, part-night lighting schemes have been shown to poorly reduce the ecological impacts of ALAN on bats (Azam et al. 2015; Hooker et al. 2022).

Another component of anthropogenic light sources has been largely overlooked despite its potential effects on species: its flicker frequency. Flicker results from the alternating nature of power supply (i.e. 50 Hz in Europe and 60 Hz in the United States) and may usually reach a frequency of 100 Hz (or 120 Hz). All light technologies may be affected by flicker, in particular vapour discharge—such as high-pressure sodium lamps—and LED which are more commonly used as outdoor lighting. Additionally, the expansion of the LED market has also enabled new advanced dynamic lighting to flourish, as exemplified by flashing shop fronts and ad panels or new traffic-regulated street lamps (Falcón et al. 2020; ICNIRP 2020). For the sake of conciseness and clarity and because the difference between flashing and flickering is purely based on how humans perceive flashing light, we will solely use 'flashing' in the rest of the article. Indeed, in the literature, a low flicker frequency (usually under 10 Hz) is more often called a flashing whereas a higher flicker frequency (usually superior to 100 Hz) is more often called a flicker.

The perception of a flashing light is variable according to the species and depends on a threshold frequency value, called the Critical Fusion Frequency (CFF) (Frank 1999; Boström et al. 2017). To this day, the knowledge of CFF distribution within the animal kingdom is still patchy (Inger et al. 2014). However, Lafitte et al. (2022) recently identified that some animal species, and more especially nocturnal and crepuscular ones, had exceptionally high CFF and could theoretically perceive ALAN as flashing. However, whether they are perceived or not, flashing lights have already been linked to alteration of behaviour and physiology in several species. For instance, Barroso et al. (2015) recorded fewer captured insects at traps lit with a flashing light compared to the ones lit with a continuous one. Greenwood et al. (2004) found that the starling *Sturnus vulgaris* was preferentially attracted to a continuous light source compared to a flashing one. Examining the ocular physiology of guinea pigs exposed to a 1 Hz flashing LED, Zhi et al. (2013) found that a significant myopia had been induced by flashing light after just three weeks of treatment. Flashing has also been linked to potential significant effects on human health such as headaches and eyestrains, as discovered by Wilkins et al. (1989).

Hence, we propose this systematic review which aimed at answering the following question: what are the known physiological and behavioural impacts of flashing artificial light on animals when compared to continuous light? We chose to only consider and report results comparing continuous and flashing lights because we felt they were the only ones to really evaluate the effect of the flashing characteristic of a light stimulus, as opposed to the effect of the light stimulus as a whole. We followed the method recommended by the Collaboration for Environmental Evidence (CEE) (CEE 2018). Adapted to the field of ecology, CEE systematic reviews are based on standardized protocols and provide a transparent, accurate and unbiased reporting of evidence to help practitioners make informed and efficient decisions (Haddaway et al. 2016; Berger-Tal et al. 2019; Pullin et al. 2022). We used a comprehensive search strategy based on several databases and performed a critical analysis of accepted observations in order to judge the level of confidence which could be granted to the reported impacts of flashing light.

Methods

This review followed the method for systemic reviews recommended by the Collaboration for Environmental Evidence (CEE) (CEE 2018) and conformed to ROSES RepOrting standards for Systematic Evidence Syntheses (Haddaway et al. 2017) (see Suppl. material 1). The procedure typically includes (i) a literature searching phase, (ii) a screening process related to several eligibility criteria, (iii) a critical appraisal phase during which the susceptibility to bias of each selected article is evaluated and (iv) the extraction of all relevant data in the form of a narrative synthesis. Deviations from CEE standards are listed in the section “Review limitations”.

Search for literature

We carried out a search for literature on three accessible databases from the Web of Science platform (Clarivate): Web of Science Core Collection, Biological

Abstracts, and Zoological Records. These databases were chosen for their functionalities, which enabled an advanced search strategy to be carried out, and because of their wide coverage on biological and ecological matters. For the Web of Science Core Collection search, SCI–EXPANDED, SSCI, A&HCI, CPCI–S, CPCI–SSH, BKCI–S, BKCI–SSH, ESCI and CCR–EXPANDED citation indexes were used. As for Biological Abstracts and Zoological Records, we had access to all indexed databases (respectively 1969–present and 1864–present). In order to achieve the best recovery of citations, several successive search strings were designed by both ecological scientists from the French National Museum of Natural History (MNHN) and physicists from the National Conservatoire of Arts and Crafts (CNAM). Each one was tested for comprehensiveness on a pre-established test list of articles—comprised of 35 articles identified as relevant while scoping the evidence on Web of Science Core Collection and Google scholar at the beginning of the project (see Suppl. material 2)—until the following search string was finally accepted:

(("light* flash*" OR "flicker* light*" OR "blink* light*" OR "light* strob*" OR "strob* light*" OR "light* wink*" OR "light* puls*" OR "puls* light*" OR "intermittent* light*" OR "dynamic* light*" OR "light*dimm*" OR "dimm* light*" OR "discontinuous light" OR "dynamic illumination" OR "flash rate" OR "change$ of light*") AND (ecolog* OR biodiversity OR ecosystem$ OR species OR vertebrate$ OR mammal$ OR reptile$ OR amphibian$ OR bird$ OR fish* OR invertebrate$ OR arthropod$ OR insect$ OR arachnid$ OR crustacean$ OR centipede$ OR animal$ OR plant$* OR bacteri* OR microorganism*)).

The search was then conducted on "Topic" (TS) on 1 February 2021 and reached a comprehensiveness of 86%, corresponding to the percentage of articles from the test list retrieved by the search string.

Screening process and eligibility criteria

Following CEE guidelines for systematic reviews (CEE 2018), a three-stage screening process was carried out on all citations to select only those relevant to our question, starting with titles, then abstracts and finally full-texts. Citation eligibility screening relied on Population–Exposure–Comparator–Outcome (PECO) criteria. At title and abstract screening stages, only restricted Population and Exposure criteria were considered due to the limited amount of available information (Table 1).

At the full-text screening stage, these Population and Exposure criteria were further refined (Table 2). Indeed, while our first aim was to assess the effects of flashing light on biodiversity as a whole, we had to limit the scope of this systematic review due to the high volume of literature retrieved by the search string

Table 1. List of eligibility criteria at title and abstract screening stages.

	Include	Exclude
Population	- All wild and domesticated species in all types of ecosystems (e.g. animals, fungi, plants, micro-organisms)	- Humans
		- Isolated organs (except those from the visual pathway, optical nerve and/or pineal gland)
Exposure	- Artificial flashing light sources at all wavelengths and correlated colour temperatures	- Natural (e.g. lightning) or unknown light sources

and thus, of accepted citations after title and abstract screening. As such, we decided to only keep alive and conscious wild animals while domesticated, dead (or animal parts) and anaesthetised animals were excluded—the generalisability of their results was considered too low for our review objectives. Plants, fungi and micro-organisms were discarded as well. In addition, Comparator–Outcome inclusion/exclusion criteria as well as language, document type and document content criteria were assessed as well. Only articles comparing a continuous light source to a flashing one were included as we considered that they were the only ones to really assess the sole effect of the flashing characteristic of a light stimulus as opposed to the effect of the light stimulus as a whole. Articles only comparing the obscurity (no light) to a flashing light source or comparing several flicker frequencies were thus excluded. Ideally, the flashing characteristic of light would be the only varying factor between the control and the exposed groups but the presence of confounding factors (e.g. type of light source, spectral composition, temporality) was not considered as an exclusion criteria and was further assessed during critical appraisal (see section 'Critical appraisal'). Only studies published in English and/or French were retained in this systematic review in respect to the competences of the review team. Articles without an appended abstract were not screened due to their high number and because of time limitations.

Screening was carried out by at least two reviewers: ML and RS for titles, ML, RS and YR for abstracts, ML, RS and AL for full-texts. For title and abstract screening, a Randolph's Kappa coefficient was computed on a random sample of 5% of all articles in order to assess the consistency of the inclusion/exclusion decisions between screeners. This process was repeated until reaching a Kappa coefficient value higher than 0.6, usually considered sufficient (Adams et al. 2019; Ghordouei Milan et al. 2022). All disagreements between reviewers were discussed before beginning the screening process to resolve any differences in the understanding of eligibility criteria. To prevent any conflicts of interest, special care was taken, at each stage of the screening process, to ensure that no reviewer would screen articles they co-authored.

Table 2. List of eligibility criteria at the full-text screening stage.

	Include	Exclude
Population	- All wild animal species in all types of ecosystems	- Domesticated animals
	- Alive specimens	- Humans, plants, fungi and micro-organisms
	- Conscious specimens	- Dead specimens and therefore isolated organs, tissues or cells
		- Anaesthetised specimens
Exposure	- Artificial flashing light sources at all wavelengths and correlated colour temperatures	- Natural or unknown light sources
	- Short-lived flashing patterns	- Very slow flashing light patterns spreading on possibly several hours (e.g. circadian patterns)
Comparator	- Studies comparing a continuous light source to a flashing one	- Studies only comparing the obscurity (no light) to a flashing light source
		- Studies comparing several flicker frequencies
Outcome	- Physiological and/or behavioural responses	
Language	- Articles written in English and/or French	
Document type	- Journal article, book chapter, technical report, Ph.D. or M.Sc. theses	
Document content	- Primary research articles	- Reviews and meta-analyses, modelling studies without experimental data

Other sources of literature

A call for literature—and in particular non peer-reviewed articles published in French and/or English—was also carried out by contacting a group of 40 experts on 12 February 2021. Indeed, as there exists a publication bias where only significant results may be accepted for publication, the CEE advocates for grey literature to be included in the literature search of systematic reviews to limit the risk of overestimating the effect of the exposure on the studied population (Haddaway and Bayliss 2015; CEE 2018).

Other sources of literature were added to improve the comprehensiveness of our search. First, we included references dealing with flashing light coming from Adams et al. (2019, 2021), who recently published a systematic map on the effects of artificial light on bird populations. Additionally, some other articles on the impacts of flashing light on animals identified by the review team but not directly extracted from the three considered databases were also included. All corresponding documents were screened on their full-texts according to the same inclusion/exclusion criteria as described above.

Critical appraisal

Critical appraisal is one of the defining stages of systematic reviews, albeit it remains rarely performed in environmental evidence syntheses (Stanhope and Weinstein 2022). Its aim is to assess the extent of systematic error that can be found in primary research articles included in the systematic review. Systematic error is usually estimated thanks to pre-built and objective risk of bias criteria (see below in the context of this review) and may lead to the exclusion of research considered as highly susceptible to bias.

Accepted articles after screening stages were split into observations, an observation corresponding to one species and one outcome, in order to carry out a critical appraisal and assess the validity of each single observation for a given article—e.g. an article analysing two responses of three different species would be split into six observations which would then be critically appraised individually. A test was conducted on a subsample of observations by two reviewers (RS and AL), then critical appraisal was performed by AL for all observations. To prevent any conflicts of interest, special care was taken to ensure that no reviewer would critically appraise articles they co-authored.

When hypothesizing a 'gold standard protocol', carried out in the context of an ideal and quasi-perfect study supposedly granted with unlimited financing, time and workforce (CEE 2018), we were able to identify six risks of bias criteria to evaluate the validity of each observation:

- the type of experimental design (Control criterion),
- the number of individuals (Replication criterion),
- the number of measures (Repetition criterion),
- the randomisation of individuals throughout experimental groups (Randomisation criterion),
- if individuals really perceived the exposure to flashing light (i.e. flicker frequency higher than their CFF) (Exposure criterion),

- if confounding factors have been accounted for (Confounding factors criterion),
- if any other risk of bias was detected (Other bias criterion).

Each of these criteria was assigned a 'high', 'medium' or 'low' risk of bias (see Suppl. material 7 for details). Finally, for each accepted observation, an overall risk of bias was attributed:

- 'high' for an observation which had a high risk of bias in the control or replication criteria or more than two high risks of bias criteria,
- 'medium' for an observation which had a medium risk of bias in the control or replication criteria or more than two medium risks of bias criteria,
- 'low' for remaining observations.

We considered an observation to be unreliable in the total absence of control or replication, therefore resulting in its exclusion. However, due to expected in-situ experimenting challenges and because we wanted to ensure the best comprehensiveness of study designs, in-situ observations with only one experimental site (but several replicates) were still kept but were given a high risk of bias in the Replication criterion.

Data extraction

Data on the influence of flashing light for a particular species or taxa were extracted by one reviewer (AL) although a test was first conducted on a subsample of observations by two reviewers (RS and AL) to assess agreement between reviewers. Metadata were also extracted for each observation, namely locations, specificities of population (age, sex) and light sources (type, wavelength, power, luminance, correlated colour temperatures and flicker frequency) as well as outcomes (e.g. behaviour, weight, mortality). Each species was associated with its taxonomic class and name updated with the latest taxonomy (GBIF 2021). Critical appraisal risks of bias were also appended to each observation included in the database.

Data synthesis and presentation

Accepted observations are described in an exhaustive narrative synthesis (see Suppl. material 9) and are arranged by subgroups based on taxa, outcomes and risks of bias. All statistical analyses were carried out on the R software (November 2021, version 4.1.2) and graphs were customized thanks to the 'ggplot2' package (Wickham 2016).

Results

Screening process and critical appraisal

A total number of 19,730 citations were extracted from the three databases from which 5,253 citations were kept after title screening. Among them, 2,145 citations had no indexed abstracts and were discarded. After abstract screening, 2,594 citations were kept. With the addition of 68 citations identified through the call for grey literature and 63 identified by the review team, 2,130 PDFs were successfully retrieved and screened on full-texts. The screening process resulted in 32 accepted articles (see Suppl. material 3 for inclusions/exclusions on titles, abstracts and full-texts, Suppl. material 4 for full-text reasons for exclusion and Suppl. material 6 for unobtainable full-texts).

All 32 articles accepted after the screening process were then split into 62 observations—an observation corresponding to one species and one outcome—and subjected to critical appraisal. Among them, 54 observations were accepted on which 22.2% (12 observations) were rated with a high, 70.4% (38 observations) with a medium and 7.4% (4 observations) with a low risk of bias (see Suppl. material 7). Complete screening and critical appraisal processes are presented on Fig. 1.

Bibliometric results

Year of publication

The earliest accepted observations were published in 1972. However, this research subject boomed at the start of the 2000s and the vast majority of observations (51 observations) were investigated between 2000 and 2020, with a slight increase over time (see Suppl. material 9).

Literature sources

The majority of accepted observations came from our search on Web of Science Core Collection database (32 observations) while 10 were provided thanks to the work carried out during Lafitte et al. (2022)'s systematic review on CFF, 8 were extracted thanks to Adams et al.'s systematic map on the effect of ALAN on birds (Adams et al. 2019, 2021), three were identified by the review team and finally one was provided thanks to the call for grey literature. No observations from Zoological Records or Biological Abstracts databases were accepted in the end.

Observation location

The United States (US) is the primary research location with 22 observations, followed by the United Kingdom (11 observations), Canada (6 observations) and Germany (4 observations). The 11 remaining observations were conducted either in Egypt, Switzerland, Israel, Japan, Taiwan and Brazil, as well as one joint experimental observation carried out between the US and Israel (Fig. 2 and Suppl. material 9).

Type of light source exposures

Most of the 54 observations used LED (17 observations), 11 used gas discharge lamps and three used incandescent bulbs. Experiments were also carried out thanks to lasers (3 observations), a video projector (1 observation) or a monitor screen (1 observation). Sometimes, several light sources were used at the same time: for instance, LED and gas discharge (4 observations), LED

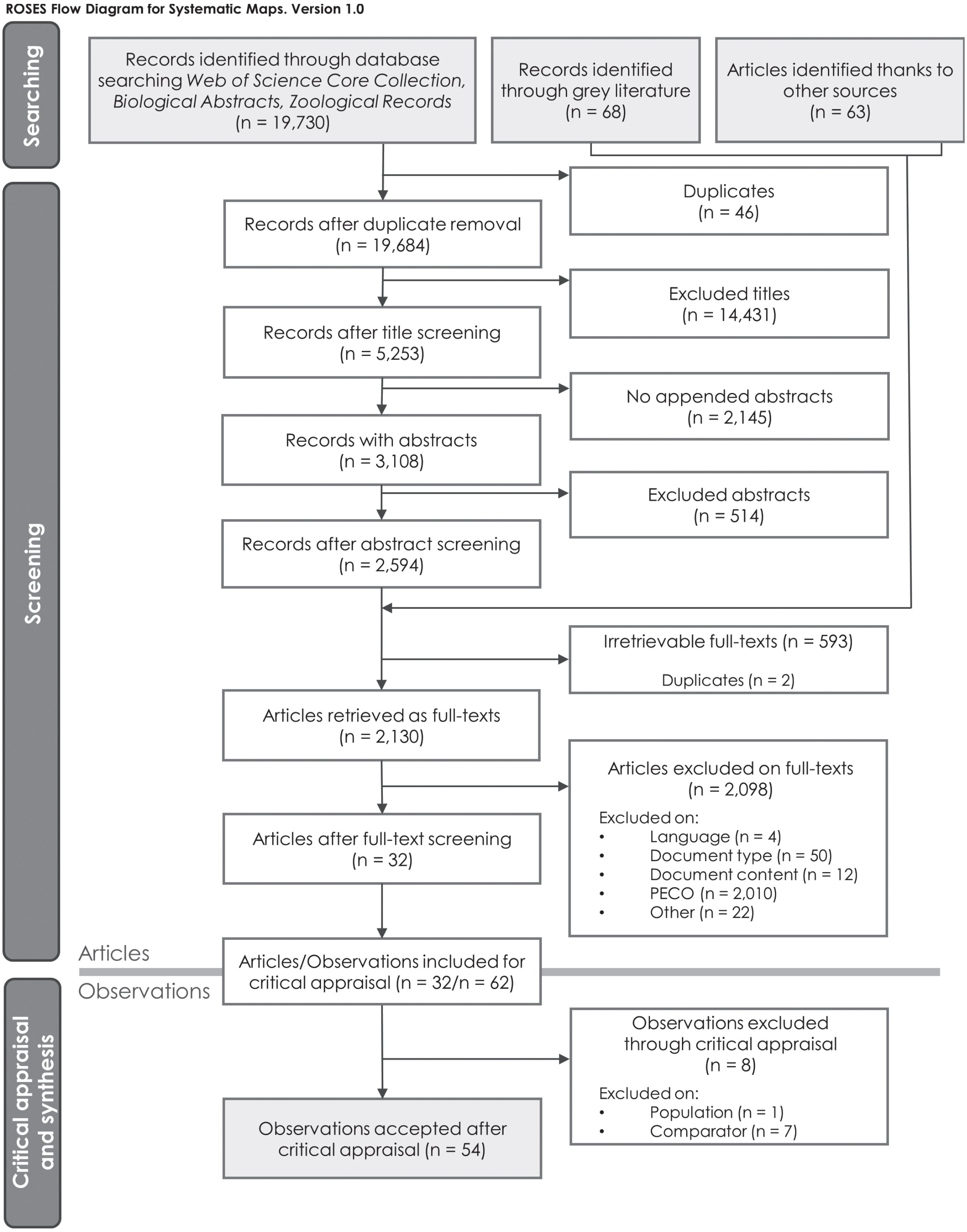

Figure 1. ROSES flow diagram reporting the screening process of articles and observations included in the review. (Haddaway et al. 2018). 'PECO' stands for Population–Exposure–Comparator–Outcome eligibility criteria.

and incandescent (3 observations). In some cases, the light source was not sufficiently reported which resulted in some observations having an unclear light source appended to them (see Suppl. material 9).

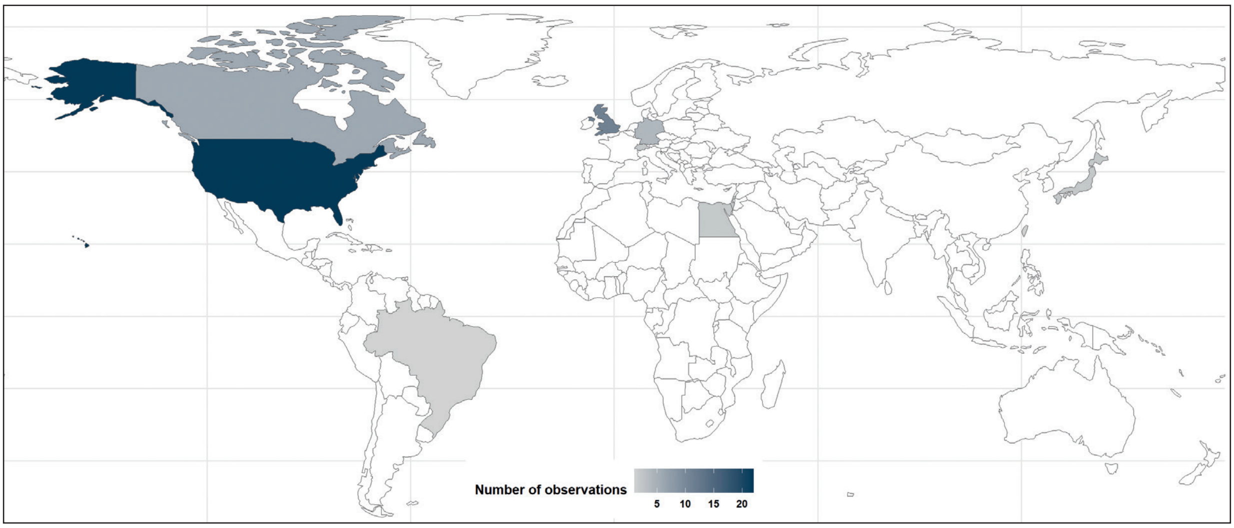

Figure 2. World map showing the number of included observations by country. The joint Israel/United States observation is not shown.

Studied taxa

Data on the four main taxonomic classes Aves (28 observations), Actinopterygii (10 observations), Insecta (8 observations) and Mammalia (6 observations) were collated (Fig. 3A). Additionally, two observations investigated the effects of flashing light on plankton (notably on Malacostraca and Polychaeta larvae). While a fraction of observations was conducted in-situ (18 observations), 70% of observations (36 observations) were carried out in laboratories. The starling *S. vulgaris* was the most investigated species with 13 observations (Fig. 3B), followed by the brown-headed cowbird *Molothrus ater* (4 observations) and the cat flea *Ctenocephalides felis* (3 observations). All other species or taxa were only studied once or twice.

Measured outcomes

In the vast majority of cases, observations measured the effects of flashing light on animals' behaviour (Fig. 4). Phototactic behaviour—i.e. the attraction of animals to flashing light when compared to a continuous one (or which should be perceived as continuous based on their CFF)—was mostly investigated (33 observations), but activity level (6 observations) and other types of behavioural responses such as disorientation, feeding, aggression (6 observations) were also assessed. Observations on the physiological responses of animals exposed to flashing light were also collected albeit more sparsely. Cortisol levels were studied four times while haematocrit, memory, neuronal activity, ocular physiology and weight were studied once each.

The impacts of artificial flashing light

Before reading the following results, the reader has to be reminded that only observations comparing a flashing light to a continuous one were included; all other comparisons were not reported in this review—e.g. obscurity compared to flashing light or comparing several flicker frequencies.

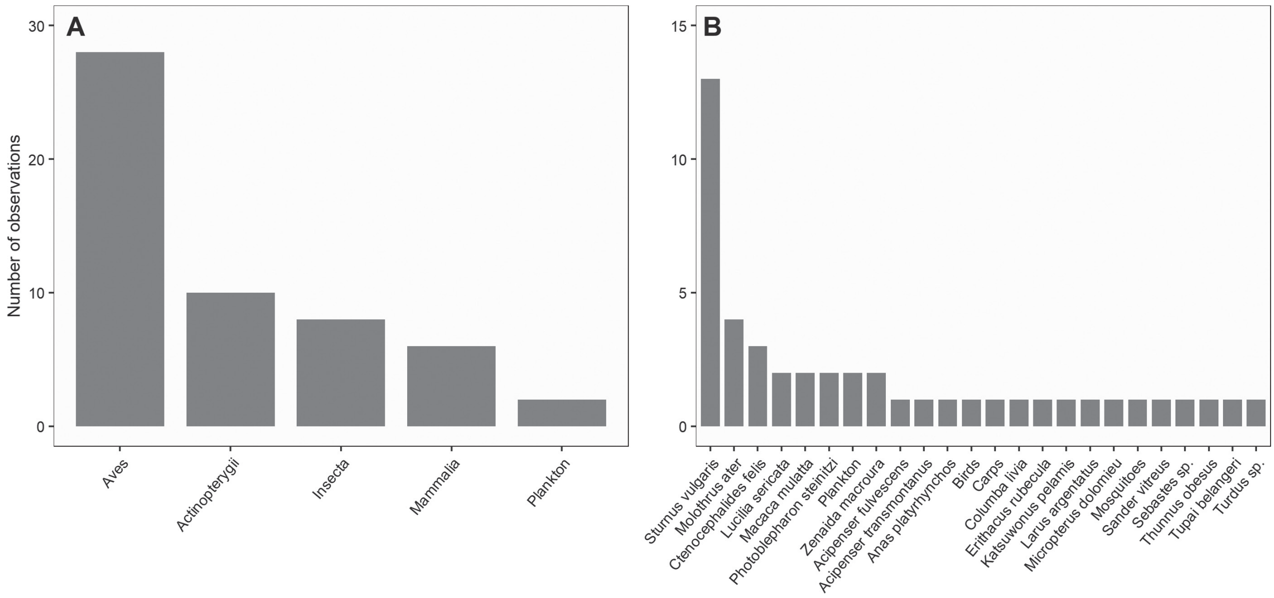

Figure 3. Proportion of included observations by taxa **A** total number of included observations by taxonomic classes and **B** number of included observations by detailed taxa.

	 Aves			 Actinopterygii			 Insecta		 Mammalia		 Plankton
Types of outcome	**L**	**M**	**H**	**L**	**M**	**H**	**M**	**H**	**M**	**H**	**M**
Phototactic behaviour	3	9	2	•	7	1	4	4	1	•	2
Activity level	•	•	3	1	•	•	•	•	2	•	•
Behaviour	•	4	•	•	1	•	•	•	•	1	•
Cortisol level	•	4	•	•	•	•	•	•	•	•	•
Haematocrit	•	1	•	•	•	•	•	•	•	•	•
Memory	•	1	•	•	•	•	•	•	•	•	•
Neuronal activity	•	•	•	•	•	•	•	•	•	1	•
Ocular physiology	•	•	•	•	•	•	•	•	1	•	•
Weight	•	1	•	•	•	•	•	•	•	•	•

Figure 4. Summary of the number of observations by outcomes and risks of bias for all taxa. 'L' low risk of bias, 'M' medium risk of bias, 'H' high risk of bias, '•' no data.

Taking the example of phototactic behaviour, the most studied outcome with 33 observations (60% of the corpus), a clear and definitive conclusion on the effects of flashing light remains hard to draw (Fig. 5)—even though one could argue that flashing light might be as attractive as continuous light, or even slightly less so. Overall, the impacts of flashing light are highly variable according to taxa (Fig. 6) as well as light parameters.

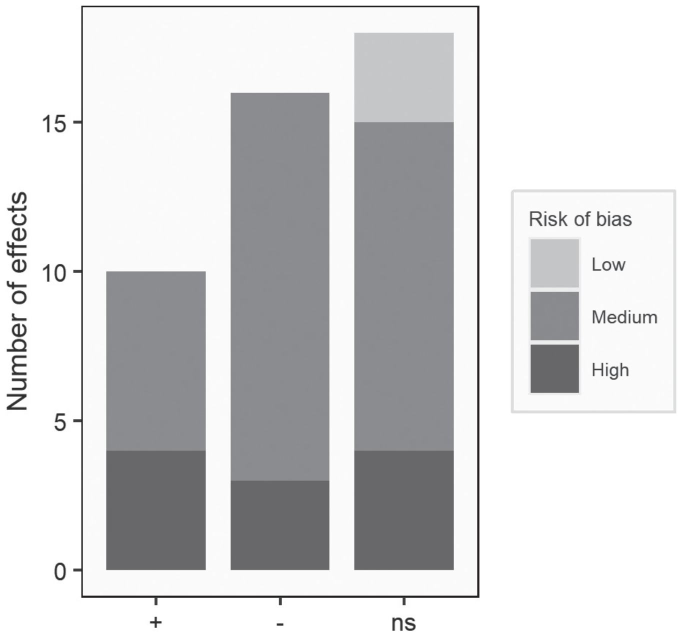

Figure 5. Number of reported effects for the outcome phototactic behaviour. '+' animals are more attracted to a flashing light than a continuous one, '-' animals are less attracted to a flashing light than a continuous one, 'ns' no significant effect. Sample size: Aves (n = 14 observations), Actinopterygii (n = 8), Insecta (n = 8), Mammalia (n = 1), Plankton (n = 2). As directions of effects are not homogeneous between the different types of reported outcomes, we decided to only show the number of effects for phototactic behaviour, the most studied outcome which accounts for 60% of the corpus with 33 observations.

	 Aves			 Actinopterygii			 Insecta		 Mammalia		 Plankton
Types of outcome	**L**	**M**	**H**	**L**	**M**	**H**	**M**	**H**	**M**	**H**	**M**
Phototactic behaviour	ns	+ | - | ns	- | ns	•	+ | - | ns	ns	+ | - | ns	+ | - | ns	ns	•	ns
Activity level	•	•	+ | ns	+ | ns	•	•	•	•	ns	•	•
Behaviour	•	+ | - | ns	•	•	+ | - | ns	•	•	•	•	-	•
Cortisol level	•	+ | - | ns	•	•	•	•	•	•	•	•	•
Haematocrit	•	ns	•	•	•	•	•	•	•	•	•
Memory	•	+	•	•	•	•	•	•	•	•	•
Neuronal activity	•	•	•	•	•	•	•	•	•	+ | -	•
Ocular physiology	•	•	•	•	•	•	•	•	ns	•	•
Weight	•	ns	•	•	•	•	•	•	•	•	•

Figure 6. Summary of flashing light effects by outcomes and risks of bias for all different taxa. 'L' low risk of bias, 'M' medium risk of bias, 'H' high risk of bias, '+' flashing light increases the outcome compared to continuous light, '-' flashing light decreases the outcome compared to continuous light, 'ns' no significant effect, '•' no data.

Due to this strong heterogeneity of results, we chose to provide, in the following section, a brief summary of our main findings. For a full and exhaustive narrative synthesis of all observations and results included in this systematic review, we refer the reader to Suppl. materials 8, 9.

On birds, we collated 28 observations. First, in 5 observations, flashing light appeared to be less attractive than continuous light to night-migrating birds and might thus help lower the number of avian fatalities with communication towers or wind turbines, even though such results could be wavelength-dependent (Evans et al. 2007; Gehring et al. 2009; Gehring 2010; d'Entremont 2015; Rebke et al. 2019). The impact of flashing light on bird vehicle deterrence was inconsistent and seemed to be species-, frequency- and speed-dependent (Blackwell and Bernhardt 2004; Blackwell et al. 2009; Doppler et al. 2015). Avian preference for high-frequency lighting (i.e. lighting frequency superior to 30,000 Hz) over low-frequency (i.e. lighting frequency of 100 Hz) followed a more complex pattern than predicted and may depend on the spatial frequency of the surrounding environment (Greenwood et al. 2004; Smith et al. 2005)—for example, a black and white grating. Bird behavioural responses to flashing light stimuli seemed very variable but were often altered after the exposure (Greenwood et al. 2004; Smith et al. 2005; Evans et al. 2012; Wiltschko et al. 2016). Flashing light was hypothesised to induce greater stress levels in birds kept under low-frequency lighting but results proved to be highly inconsistent (Maddocks et al. 2001; Greenwood et al. 2004; Smith et al. 2005; Evans et al. 2012). Bird activity levels have been shown to be affected by flashing light but such results were dependent on the species and type of light source (Lustick 1972). In addition, one observation on the common pigeon *Columbia livia* also indicated that flashing stimuli may be easier to remember for birds (Fetterman 2000). Haematocrit and weight were also investigated once and were not shown to be impacted by flashing light when compared with a continuous one (Smith et al. 2005).

On fishes, we reported the results of 10 observations. Fish phototactic behaviour was found to be highly variable and seemed to be, in part, species-, frequency- and wavelength-dependent (Ruebush et al. 2012; Rooper et al. 2015; Ford et al. 2018, 2019; Elvidge et al. 2019; Oshima et al. 2019), and even more so when flashing stimuli can be used by some fish species to communicate with conspecifics (Hellinger et al. 2020). In contrast to continuous light, flashing light was also found to significantly alter the behaviour of the flashlight fish *Photoblepharon steinitzi* (Hellinger et al. 2020) as well as to influence daily fluctuations in activity levels of the nesting smallmouth bass *Micropterus dolomieu* (Foster et al. 2016).

Regarding insects, 8 observations were collected. Overall, flashing light was shown to produce an effect on insect phototactic behaviour, but results were highly species- and frequency-dependent (Müller et al. 2011; Barroso et al. 2015; Eichorn et al. 2017; Liu et al. 2017; Bolliger et al. 2020). In addition, flashing light may be particularly important for insects as some species seem to use flashing signals to identify conspecifics and sexually-mature partners (Eichorn et al. 2017).

Mammals were investigated in 6 observations. Bat activity level was reported in two observations and phototactic behaviour once. Both outcomes were not found to be significantly influenced by flashing light (Jain et al. 2011; Bolliger et al. 2020). One observation on the tree shrew *Tupaia belangeri* showed that flashing blue light could cause myopia when the continuous blue one did not (Gawne et al. 2017)—the result, however, depended on the spectral composition of the light source. Two observations also found that the rhesus monkey *Macaca mulatta* could be less efficient at

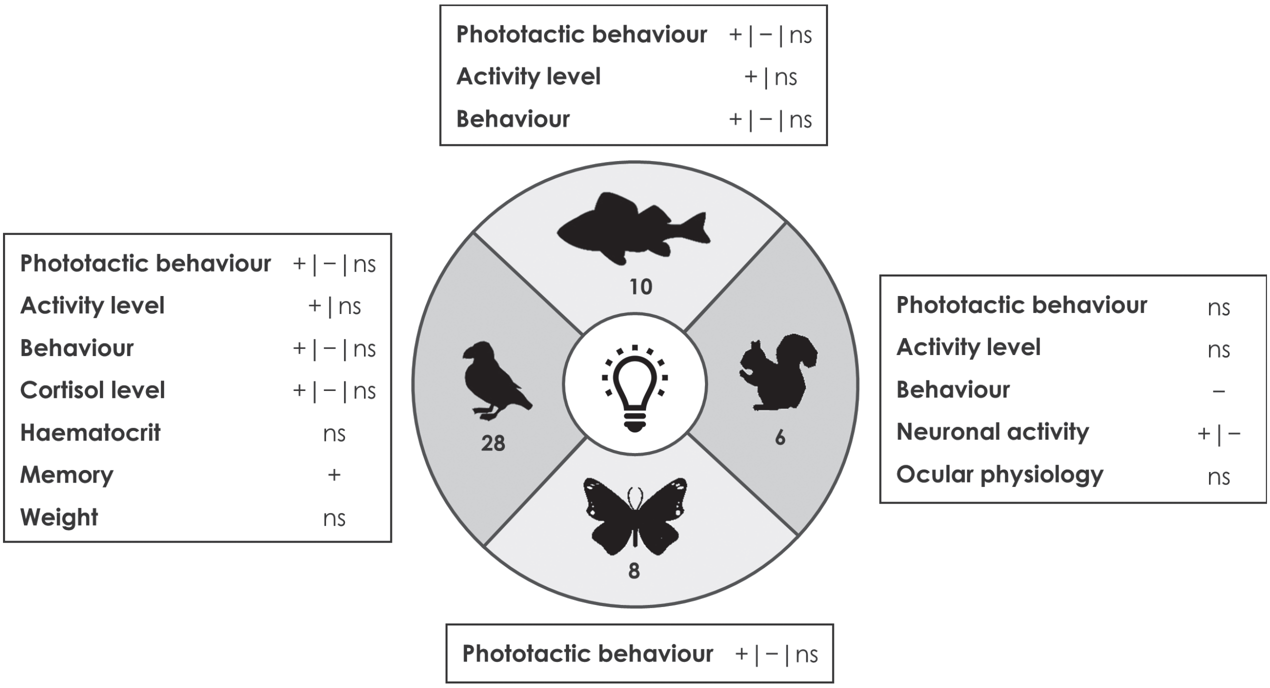

Figure 7. Summary of results for the four main studied taxonomic classes. '+' flashing light increases the outcome compared to continuous light, '-' flashing light decreases the outcome compared to continuous light, 'ns' no significant effect. For clarity, the two observations on plankton phototactic behaviour are not shown but were both found to be non-significant.

discriminating the direction of moving stimuli with a flashing background (Churan and Ilg 2002).

Finally, we also collated two studies on the phototactic behaviour of plankton, which did not find any significant impact of flashing light over continuous light (Dougherty et al. 2016).

Discussion

Within this systematic review, which aimed at summarising the physiological and behavioural impacts of flashing light on animals, 32 articles accounting for 54 observations were accepted. After carrying out screening and critical appraisal, 28 observations on birds, 10 on fishes, 8 on insects, 6 on mammals, as well as 2 on plankton were collected (Fig. 7). Overall, we found that: (i) the impacts of flashing light may vary according to the species and taxonomic classes; (ii) the various specificities of light sources (e.g. flicker frequency, light intensity, spectral composition, duration) may also influence the response of animals to flashing light; (iii) the available literature is scarce and more research should be carried out rapidly in order to give more definitive conclusions; (iv) therefore, in the meantime, precautionary principles should be applied to avoid adding potential negative impacts on sensitive animals.

The impacts of flashing light may vary between species and taxonomic classes

While the evidence still seems scarce, our results indicate that the effects of flashing light are highly variable between species and taxonomic classes. We found that, in some animal species, a flashing light could be less harmful than a continuous one. For example, the brown-headed cowbird *M. ater* showed a lower attraction to a 2 Hz flashing light (Blackwell et al. 2009; Doppler et al. 2015). Similarly, flashing lights on communication towers have been shown to reduce the number of avian collisions (Evans et al. 2007; Gehring et al. 2009; Gehring 2010; Rebke et al. 2019). Bolliger et al. (2020) showed that, in a street with intermittent lighting, fewer insects, and more especially fewer heteropterans, may be trapped compared to the one that would be lit all night. Alternatively, species exposed to flashing light may sometimes experience the same kind of effects as for a continuous light. For instance, bats were studied thrice and the impact of a flashing light was not shown to differ from that of a continuous one (Jain et al. 2011; Bolliger et al. 2020). No differences in plankton phototaxis to flashing or continuous light was observed either (Dougherty et al. 2016). Lastly, in some cases, flashing light have been shown to be more impactful than continuous light. For instance, one observation showed that flashing light could lead to greater daily fluctuations in fish activity levels (Foster et al. 2016). Some fish species, like the lake sturgeon *Acipenser fulvescens*, may also be more attracted to flashing light (Elvidge et al. 2019), which could then disturb their overall behaviour and hamper their ability to feed or reproduce. Such variability in the responses of different taxa to light pollution has already been highlighted in vertebrates, for which the impacts of ALAN on melatonin and circadian rhythms may be highly dependent on the species and taxonomic class considered (Grubisic et al. 2019). For bats too, the effects of ALAN can greatly vary between different species and foraging guilds (Voigt et al. 2021). These differences of responses to ALAN between and within taxa preclude us from drawing general conclusions on the impact of light pollution and, in our particular case, flashing light.

The impacts of flashing light may also vary according to several parameters of the light source

In addition to variations between species and taxonomic classes, the response to flashing light may also differ according to the type of exposure to the light source—i.e. flicker frequency, light intensity, wavelength and/or duration.

First and foremost, the response to flashing light depends on the frequency at which the source flashes. For instance, Eichorn et al. (2017) found that male green bottle flies *Lucilia sericata* were greatly attracted to flicker frequencies of 178 Hz, 190 Hz and 250 Hz, while no differences in phototaxis between flashing and continuous lights were found for flicker frequencies of 110 Hz and 290 Hz. In particular, as there exists for each species a threshold frequency at which a flashing light begins to be perceived as continuous, defined as the CFF, the importance of a light source flicker frequency seems paramount. Indeed, a species perception of a flashing light source could theoretically be inferred thanks to the knowledge of its CFF and the flicker frequency of a light source. To that end, Inger et al. (2014) first reviewed the actual perception of flashing light by animals by collating one of the first databases on animal CFF. Lafitte et al. (2022) then updated this work by following the method of systematic reviews recommended by the CEE (CEE 2018) and were able to collate a comprehensive database of 200 CFF values. As they identified that animal CFF ranged from 0.57 to a maximum of 500 Hz, they argued that outdoor lighting should exceed this upper threshold in order to limit the impacts of ALAN on wild animals. In addition, they reported that some nocturnal animals (e.g. moths and fishes) had CFF higher than the 100 Hz threshold sometimes found in some lighting technologies such as LED. Based on this analysis of both CFF and light source flicker frequencies, it can be assumed that some species could be subjected to the potential adverse effects of flashing light.

However, comparing a species CFF with the flicker frequency of a light source may prove insufficient in order to conclude on the existence or absence of impacts of flashing light on animals. Indeed, in real in-situ conditions, many factors can accentuate or limit the perception of a flashing light by an animal (Fig. 8). Indeed, the specificities of light sources, such as intensity, spectral composition, correlated colour temperatures, or timing and duration of exposure, have often been linked to the variability observed in the reported effects of ALAN on animals (Grubisic et al. 2019; Voigt et al. 2021). In the case of flashing light, we therefore advocate for a better regulation of outdoor lighting, as a precautionary measure. The light intensity and therefore the distance to the light source may influence the extent of potential impacts. Indeed, as a brighter continuous light source may be perceived from further away compared to a dimmer one, we therefore advocate for keeping light levels of flashing lights as low as possible. The orientation of the light source is also crucial as a horizontal, or worse, upward-oriented flashing light source may be detected from further away. In relation to the chromatic visual capabilities of each taxon, the spectral composition of the light source could also influence how flashing light is perceived and how it potentially impacts animals. Indeed, Evans et al. (2007) and

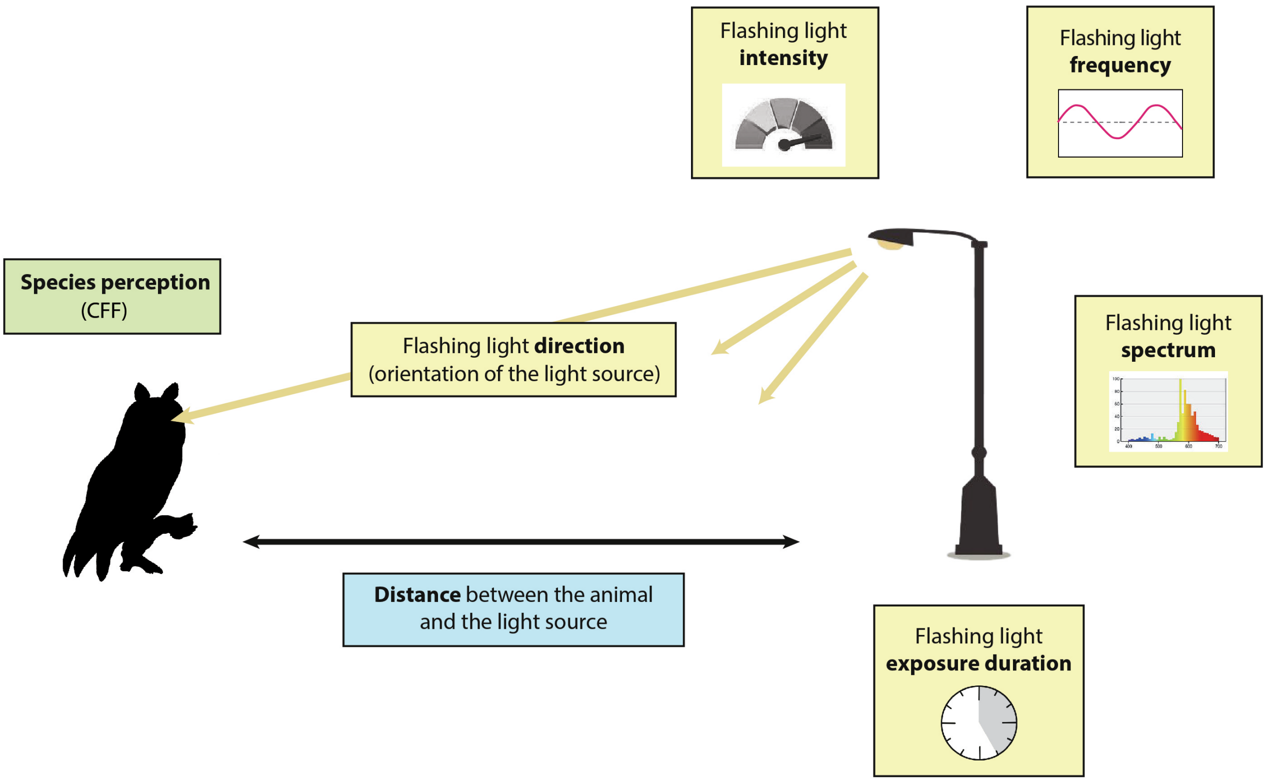

Figure 8. The in-situ perception of flashing light by animals depends on several parameters of the light source.

Rebke et al. (2019) showed that red-coloured lights, whether flashing or not, were less attractive for night-migrating birds, unlike other light colours such as green, blue or white which were less attractive only when flashing. Gawne et al. (2017) found that flashing light could induce myopia in the tree shrew *T. belangeri*, but the response seemed highly wavelength-dependent as well. Finally, the duration of the exposure to flashing light could also influence the extent of the recorded impacts. For instance, in several publications, we identified that similar exposures to flashing light, but with varying durations, produced very different behavioural responses in birds (Greenwood et al. 2004; Smith et al. 2005; Evans et al. 2012).

Thus, the impacts of flashing light on animals may be considered highly variable and may depend on the species, the taxonomic class, various parameters from the light source and on the surrounding environment (e.g. buildings, surfaces, vegetation).

A huge lack of knowledge for a timely subject

In the end, this systematic review highlights a dearth of knowledge on the effects of flashing light on animals. Although the research on this subject has gained momentum since the 2000s, the evidence remains scarce on this matter. While we were able to identify a relative knowledge cluster on birds' phototactic attraction to flashing light, many other taxa and outcomes were at least poorly studied or simply not investigated. These knowledge gaps on the effects of flashing light should be filled pressingly as lighting is expected to get more and more dynamic with on-demand or sensor lightings being currently rapidly scaled up. While these new technologies could help limit the duration of the exposure to ALAN, the new type of light pollution they may produce and its impacts on biodiversity are not fully understood for now. Likewise, LED, which may flash depending on their technology, are currently being deployed all over the world to reduce the energy consumption of lighting (Zissis et al. 2021) but without taking into account their potential adverse effects on animal populations.

Moreover, among the studies included in this systematic review, very few in-situ experiments were carried out. As such, the generalisability of these studies to real-world situations is low. Only one study dealt with sensor lighting (Bolliger et al. 2020) and some others investigated flashing lights on communication towers (Gehring et al. 2009, 2010) and wind turbines (d'Entremont 2015). We were not able to find any study on the effects of illuminated advertising, billboards or flashing signs which are very common sources of outdoor flashing light.

Another surprising point is that the majority of included studies involved diurnal species, with the starling *S. vulgaris* being the most investigated species. Indeed, diurnal species can be impacted by ALAN—for example, ALAN disturbs their sleep and can have repercussions on their immunology (Ouyang et al. 2017; Sun et al. 2017; Ulgezen et al. 2019). Nonetheless, nocturnal species are probably the most likely to discern whether night-time lighting is flashing or not.

Then, it appears from all previous points that more research on the subject of flashing light should be pressingly carried out in order to keep up with the fast-paced evolution of lighting practices.

Recommendations for further research

First, the studied species and taxonomic classes which were identified in this systematic review should be further investigated. Then, more research is pressingly needed on key taxa which have not yet been studied and could also be at risk of being impacted by flashing light—e.g. moths, amphibians, nocturnal raptors, glow worms. Further research on additional outcomes should also be contemplated such as fitness, foraging or reproductive behaviours as well as other key physiological or spatial outcomes—e.g. immunity, movement, spatial distribution. More in-situ studies should be carried out in order to take into account all light source parameters which may influence a species sensitivity to flashing light—i.e. distance from the light source, orientation, spectrum, intensity. In the case of these in-situ experiments, several locations should also be studied to account for local heterogeneity in species repartition. Based on our criteria for critical appraisal, we advocate for authors to use more robust experimental protocols (Fig. 9). For instance, few studies had protocols comparing two populations, one unexposed and one exposed, before and after the exposure to flashing light—i.e. BACE designs.

We also would like to stress the need for a better reporting of experimental designs specifications (Fig. 9). Light sources were rarely completely described and information on the flicker frequency of flashing or continuous light sources was rarely reported. This lack of reported data on the light sources used to expose specimens to light disturbances has already been noted in another review on the impacts of ALAN on melatonin and circadian rhythms on vertebrates (Grubisic et al. 2019). However, the actual perception of a light source as continuous by one species can only be proven by crossing the flicker frequency of the continuous light source with the CFF of this species. Therefore, if the flicker frequency of the continuous light source is not provided, it cannot be verified if the two light stimuli were perceived any differently by the specimens under scrutiny. In addition, other parameters of the light source like wavelength and light intensity could also influence the results of the experi-

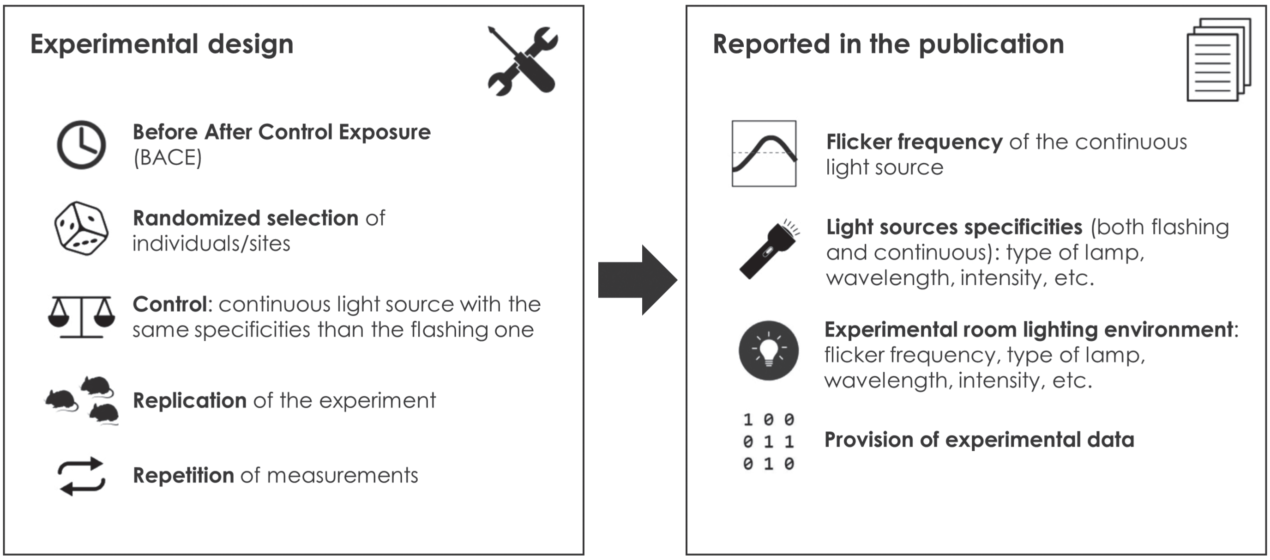

Figure 9. Selected recommendations for more robust and better reported experimental designs and results.

ment and should be reported thoroughly. As such, we recommend light sources to be strictly the same between the control and treatment groups in order to avoid adding any potential confounding factors. Finally, data on laboratories lighting conditions is rarely provided, which could also alter experimental results as some indoor light sources could flash and thus impact the specimens being investigated.

Review limitations

Our methodology comprised some biases which have to be pointed out. First, while the majority of articles found in this review came from our literature search, more than a third was provided by additional sources of literature, indicative that the scope of our search string might have been too limited.

In addition, we sometimes had to decide to reduce our requirements compared to CEE guidelines (CEE 2018) due to time limitations and financing constraints. First, we could not request supplementary databases (e.g. Scopus) or include search engines (e.g. Google Scholar) in our search strategy. However, doing so may have increased the number of test list articles indexed in the requested databases which would have probably increased the reliability of our search strategy. In addition, while consistency checks between reviewers were performed for the title and abstract screening stages, we could not do so for full-text screening. Likewise, CEE guidelines (CEE 2018) call for a double independent assessment by two reviewers during critical appraisal and data extraction. However, in this review, only one reviewer critically appraised and extracted data from all observations accepted after full-text screening. A test between two reviewers on a subsample of articles was still performed before starting critical appraisal and data extraction to check their agreement.

In addition, citations for which an appended abstract was not available were discarded during the screening process. Indeed, searching for these additional 2,145 full-texts was deemed to represent an unfeasible additional workload within the scope of our project. We nevertheless made sure to create an additional database which lists these citations without abstract (see Suppl. material 5). We hope that this database will prove useful for whomever would want to continue this work. Moreover, due to the high level of accepted citations after title and abstract screening and while the initial scope of this review included plants, microorganisms, domesticated animals as well as the impacts of ALAN timing on circadian rhythms, we had to downgrade our expectations and only carry out this systematic review on the sole behavioural and physiological impacts of flashing light on animals. However, if one wishes to disentangle the impacts of flashing on the other identified taxa, we made sure to create easily available categories in Suppl. material 3 to facilitate a potential future full-text screening on these citations. We chose to only consider and report results comparing continuous and flashing lights as we judged they were the only ones to really assess the effect of the flashing characteristic of a light stimulus alone, as opposed to the effect of the light stimulus as a whole. Any update of this systematic review could then also try to assess additional types of comparators which could be useful to draw a more complete picture. Indeed, some studies may also evaluate the effects of several different flicker frequencies or compare the obscurity (no light) to a flashing light source, such as in this recent study by Krivek et al. (2022).

We are aware that these limitations may reduce this review's scope but we believe that this work remains one essential first step in order to better identify and mitigate the impacts of artificial light on biodiversity.

Conclusion

Within this systematic review, more than fifty observations on the behavioural and physiological impacts of flashing light on animals were collected. Birds were the primarily studied taxon while fishes, insects and mammals were less investigated. Phototaxis to flashing light was the most studied outcome but, overall, very few outcomes were investigated. We found little available evidence on nocturnal species: bats were found to be alarmingly understudied while nocturnal raptors as well as glow worms have not been the subject of any research so far. The impacts of flashing light seemed to vary greatly between studied species. On the one hand, flashing light can be more impactful on animals than continuous light. On the other hand, more surprisingly, in the case of night-migrating birds, it might also reduce animals' phototaxis to ALAN and therefore limit some effects of light pollution. In some other cases, responses to flashing and continuous lights were not found to differ.

As LED and dynamic lighting are currently being rapidly scaled up, this systematic review represents a relevant first step in order to better grasp the actual state of the evidence base regarding the effects of flashing light on biodiversity. However, our results highlighted a crucial lack of knowledge and we therefore advocate for further research to be pressingly carried out. Many more species and outcomes should be investigated and more in-situ experiments conducted in order to better understand real-world lighting situations—e.g. illuminated signs and advertisements, sensor lighting, wind turbines. Then, an update of this review should be contemplated as it will surely allow for more complete and definitive conclusions on the impacts of flashing light to be drawn.

In the meantime, based on these first provisional results, we argue that some precautionary measures should be taken to reduce the potential adverse effects of flashing light on animals. First, from the point of view of lamp engineers and manufacturers, flicker frequencies should be kept way beyond the currently known highest critical frequencies of the animal kingdom—i.e. 500 Hz. Secondly, from a lighting management perspective, new regulations should be implemented in order to better consider this understated flashing parameter of light pollution—as it is the case for more acknowledged characteristics of light such as direction, spectral composition and intensity.

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Additional information

Conflict of interest

The authors declare the following competing interests: Gaël Obein is the president of the AFE (French Association on Lighting) and Virginie Nicolas is the president of the ACE (French Association of Lighting Designers and Lighting Engineers).

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: YR, RS, GO, VN. Data curation: ML, AL. Formal analysis: AL. Investigation: RS, YR, AL, ML. Project administration: RS, YR. Writing – original draft: RS, AL. Writing – review and editing: ML, RS, AL, VN, YR, GO.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

ROSES form

Authors: Alix Lafitte, Romain Sordello, Marc Legrand, Virginie Nicolas, Gaël Obein, Yorick Reyjol

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Supplementary material 2

Test list and comprehensiveness

Authors: Alix Lafitte, Romain Sordello, Marc Legrand, Virginie Nicolas, Gaël Obein, Yorick Reyjol

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Supplementary material 3

Citation screening

Authors: Alix Lafitte, Romain Sordello, Marc Legrand, Virginie Nicolas, Gaël Obein, Yorick Reyjol

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Supplementary material 4

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Supplementary material 5

Citations with irretrievable abstracts

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Supplementary material 6

Unobtainable articles at full-text screening

Authors: Alix Lafitte, Romain Sordello, Marc Legrand, Virginie Nicolas, Gaël Obein, Yorick Reyjol

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Supplementary material 7

Observation critical appraisal

Authors: Alix Lafitte, Romain Sordello, Marc Legrand, Virginie Nicolas, Gaël Obein, Yorick Reyjol

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Supplementary material 8

Systematic review observation database

Authors: Alix Lafitte, Romain Sordello, Marc Legrand, Virginie Nicolas, Gaël Obein, Yorick Reyjol

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Supplementary material 9

Additional bibliometric results and narrative synthesis

Authors: Alix Lafitte, Romain Sordello, Marc Legrand, Virginie Nicolas, Gaël Obein, Yorick Reyjol

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