Taxonomic imbalances in animal sleep studies

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Abstract:

Although sleep is essential for the survival of all animals, this behaviour is far from being studied in all species, especially in invertebrates. In this dissertation, we attempted to bring together current knowledge about sleep with a focus on arthropods, which have been much less studied in this regard than vertebrates. While some species appear to exhibit rest periods that combine all the characteristics of sleep, the existence of this state in most arthropods remains ambiguous, if not unknown. Even among insects, the arthropods most commonly seen in papers about sleep, the number of species studied is extremely low, compared to the sheer number of species that belong to the phylum of arthropods. This results in a very strong bias towards vertebrates, and especially mammals, whose sleep has been thoroughly studied in many different species, while this class includes very few species of the animal kingdom, in proportion. This taxonomic bias is explained by historical lack of interest in the sleep of arthropods, which however tends to be reduced, given that the current context of global changes encourages biologists to study the impact of anthropogenically-driven sleep disturbances in insects on the balance of ecosystems.

INTRODUCTION

Long before science began to focus on the mechanisms and evolutionary implications of this widespread behaviour, sleep was a source of inspiration for writers and artists (Klein, 2011). Through the character of Macbeth, Shakespeare described this state as "the death of each day's life, sore labour's bath, balm of hurt minds, great nature's second course, chief nourisher in life's feast" (Anafi *et al.*, 2019). When human sleep, they do cease all the activities of "each day's life" to recover from daily "sore labour" before resuming "life's feast" when they wake up. But is sleep really the "great nature's second course" for all animals? Indeed, Shakespeare only evoked it in humans without referring to other animal species. It is not until four centuries later that first studies addressing sleep in non-human mammals were carried out, completed by studies in other vertebrates (mainly birds) in the following years (Blumberg *et al.*, 2020; Campbell and Tobler, 1984; Lesku *et al.*, 2009; Siegel, 2009). Thereafter, some invertebrates, including arthropods, were subject to studies addressing sleep (Hendricks *et al.*, 2000; Tobler, 1983; Tobler and Stalder, 1988) although they were way less thorough. Yet some biologists claim that all animals sleep (Siegel, 2008), although the evidence is still slim. This lack of evidence is particularly blatant for insects, in which activity periods have been a lot more often studied than rest periods (Campbell and Tobler, 1984; Tougeron and Abram, 2017; Helfrich-Förster, 2018). However, insects represent the main species in the phylum Arthropoda, the latter accounting for nearly 80% of total animal biodiversity (Zhang, 2011). In the absence of studies about so many species, the hypothesis of a universal sleep among the animal kingdom cannot be confirmed.

Therefore, the objectives of this review are to summarize current knowledge about sleep in arthropods, particularly in insects, as well as estimating the extent of the taxonomic bias in studies addressing sleep. First we will define what is sleep by mentioning the different criteria that have been used in studies since the beginning of the 20th century, and we will check if these criteria apply to arthropods. Then we will address the issue of the taxonomic bias in studies by comparing the number of scientific articles about sleep in arthropods to the number of articles studying other animal models, and by evaluating more precisely current knowledge about sleep in the different insect orders.

BIBLIOGRAPHY REVIEW

I. Historical approach of studies addressing sleep

Before considering sleep in arthropods, it is necessary to establish a precise definition of this state, not only to differentiate it from other phenotypically similar states (hibernation, quiescence, torpor, tonic immobility, paralysis, coma ...), but especially to have a relevant point of comparison with mammals, birds, and other vertebrates. Indeed, it was by observing species of this taxon that the French psychologist Henri Piéron proposed a first definition of sleep in 1913 in terms of both behavioral and physiological characteristics (Piéron, 1913) defined sleep. Subsequently, many authors undertook similar studies in other taxa (notably in invertebrates) in order to test the universality of this definition and to refine it. Thus, sleep can be defined as a state of (i) temporary reduction in locomotor activity and (ii) change in brain activity (iii) associated with a specific posture, (iv) reduced responsiveness to external stimuli (but with a rapid reversibility of this state in response to a very intense stimulus), and (v) homeostatic and circadian regulation. (Anafi *et al.*, 2019; Campbell and Tobler, 1984; Cirelli and Tononi, 2008; Helfrich-Förster, 2018; Keene and Duboue, 2018; Siegel, 2008; Siegel, 2009).

However, this definition only addresses the behavioural aspect of sleep, which is insufficient to capture the complexity of this state. The first description of REM sleep in 1953, which revealed the presence of brain waves very similar to those of an awake brain in sleeping mammals (Aserinsky and Kleitman, 1953), justified the need to study the neurophysiological aspect of sleep. Therefore, the variations in the brain waves, the neural circuits and the hormonal secretions specific to sleep have been described (Helfrich-Förster, 2018; Hendricks *et al.*, 2000; Kaiser and Steiner-Kaiser, 1983; Siegel, 2008; Tobler and Stalder, 1988; Tononi and Cirelli, 2003). The following studies in phylogeny and genetics have shed light on the evolution of sleep across the animal kingdom and the expression of genes which are linked to this state. They also revealed many homologous genes in very distant taxa (Anafi *et al.*, 2019; Aulsebrook *et al.*, 2016; Helfrich-Förster, 2018; Keene and Duboue, 2018; Lesku *et al.*, 2009; Siegel, 2009; Tononi and Cirelli, 2003). Finally, an all too often forgotten aspect of sleep is its ecological aspect, which yet raises many questions: why this state which impedes the exploration of the environment and decreases vigilance (which should have a strong negative impact on fitness, especially by increasing the risk of predation) is still present in so many different species? Several studies have attempted to provide an answer by explaining how the benefits of sleep in an individual constitute an adaptation to their environment and are necessary to maintain their social interactions (Anafi *et al.*, 2019; Aulsebrook *et al.*, 2016; Blumberg *et al.*, 2020; Kayser *et al.*, 2015; Keene and Duboue, 2018; Lesku *et al.*, 2009; Siegel, 2009; Tougeron and Abram, 2017).

It would thus be interesting to check the validity of each of these characteristics in different species, especially in arthropods, to conclude whether sleep is present or absent in these animals.

II. Is sleep universal?

1. A valid definition for all species?

The difficulty of defining sleep is due to the fact that, despite many similarities in the exhibition of this state in different species, several specific cases have been noted.

Indeed, we cannot consider sleep as a period of total cessation of locomotor activity. Even if the vast majority of animals remain motionless while sleeping, it has been proven on several occasions that some marine mammals (dolphins, orcas, seals) keep swimming while exhibiting sleep-like behaviour (Blumberg *et al.*, 2020; Cirelli and Tononi, 2008; Siegel, 2008; Siegel, 2009). In arthropods however, all the studied species were immobile during rest periods.

With regard to brain activity, making comparisons between species is difficult because the recording material varies according to what animal is studied: electroencephalography (EEG) is widely used (Keene and Duboue, 2018; Lesku *et al.*, 2009; Siegel, 2009), but this method can generally not be applied to fishes and arthropods due to their small size or the inability to detect changes in neuroelectric activity (Hendricks *et al.*, 2000; Tougeron and Abram, 2017). The electrodes must then be replaced by probes measuring local electric potentials (Kaiser and Steiner-Kaiser, 1983; Keene and Duboue, 2018), which reduces the accuracy of the results. Nevertheless, it was possible to detect a common point in the brain activity of many studied species, which is the production of low-frequency high-voltage waves during sleep periods (Anafi *et al.*, 2019; Keene and Duboue, 2018; Lesku *et al.*, 2009; Siegel, 2008; Siegel, 2009; Tononi and Cirelli, 2003). In mammals and birds, this activity is associated with deep sleep (Siegel, 2008). During rest periods, this phase alternates with REM sleep, which is characterized by an electroencephalogram very similar to that of an awake individual, rapid eye movements, muscle twitches and an irregular respiratory and heart rate (Blumberg *et al.*, 2020; Cirelli and Tononi, 2008). While the presence of such properties is debated in many animals (reptiles, cetaceans, monotremes, fishes, amphibians) (Blumberg *et al.*, 2020; Lesku *et al.*, 2009; Siegel, 2008; Siegel, 2009), not many study so far have proven the presence of REM sleep in arthropods. Although some authors have observed movements of the antennae (Blumberg *et al.*, 2020, Tobler, 1983), the limbs (Tobler, 1983) or the mouth parts (Hendricks *et al.*, 2000) in a few insects during rest periods, nothing proves that these movements are comparable to the muscular contractions typical of this sleep phase in other animals. Rößler *et al.* (2022) however recently observed periodic bouts of retinal movements and limb twitching behaviors in a jumping spider, suggesting the existence of REM sleep in arthropods.

Regarding the posture exhibited during rest periods, lying position is observed in most species, with the exception of herbivorous mammals and birds (Blumberg *et al.*, 2020) which can go into deep sleep while standing. In arthropods, lowering of the thorax (or cephalothorax) to the ground has been associated with a sleep-like state in scorpions, bees, cockroaches and fruit flies. In addition, in the different bee species that have been observed, the orientation of the head and antennae downwards was also associated with rest periods (Tobler and Stalder, 1988; Helfrich-Förster, 2018).

Surprisingly, reduced responsiveness to environmental stimuli might not be a universal property of sleep. Indeed, a study found that bullfrogs always react to cutaneous shocks with a change in their respiratory rate, even during the periods when individuals are expected to exhibit the deepest sleep (Hobson, 1967). However, as this experiment has not been replicated, excluding this criterion from the definition of sleep would be a hasty decision. With regard to arthropods, an elevated arousal threshold during rest periods has been measured in scorpions (Siegel, 2008), crayfishes (Helfrich-Förster, 2018) and several families of insects (Keene and Duboue, 2018; Siegel, 2008). Furthermore, in some bees and butterflies, the decrease in neuronal sensitivity to visual stimuli is paradoxically associated with an increase in the sensitivity of retinal cells. It could be an adaptation allowing these insects to react quicker when attacked by a predator (Kaiser and Steiner-Kaiser, 1983). As for the rapid awakening in response to a sufficiently intense stimulus, it has been observed in all studied animals. In addition, a study conducted on fruit flies revealed that mechanical stimulation must be increasingly strong during rest periods in order to wake all individuals (Hendricks *et al.*, 2000), which can be linked to a progressive sleep deepening and a habituation to stimuli.

Finally, the study of the body systems controlling the duration and frequency of sleep periods has brought to light two types of major mechanisms: homeostatic regulation and circadian regulation. Homeostasis refers to the ability of an organism to maintain its vital parameters around an average (optimal) value despite various environmental disturbances. In the present case, the considered disturbances are those which lead to partial or total sleep deprivation, ranging from a shortening of rest periods to keeping individuals awake for several days, the latter being deadly for rats (Helfrich-Förster, 2018; Siegel, 2008; Siegel, 2009) but also for fruit flies and cockroaches (Cirelli and Tononi, 2008). If deprivation does not cause death, the individual will accumulate a sleep debt which will eventually lead, by homeostasis, to longer or deeper sleep at the next rest period (Aulsebrook *et al.*, 2016; Cirelli and Tononi, 2008; Helfrich-Förster, 2018; Keene and Duboue, 2018; Vázquez *et al.*, 2020) or even during a period when the animal is normally active (Hendricks *et al.*, 2000; Tobler, 1983). However, there are several exceptions to this phenomenon, such as migratory birds which do not sleep any longer after having flown continuously for several days (Siegel, 2008; Siegel, 2009), or young orcas and their mothers which swim actively during the first month of the postpartum period without negative health consequences (Anafi *et al.*, 2019; Siegel, 2008; Siegel, 2009). As for arthropods, an increase in sleep time following a long period of wakefulness has been measured in scorpions, fruit flies, bees and cockroaches (Anafi *et al.*, 2019; Keene and Duboue, 2018; Tobler, 1983). However, in the above-mentioned insects, homeostatic regulation has not always been observed (Cirelli and Tononi, 2008; Helfrich-Förster, 2018; Siegel, 2008). This could be explained by interindividual and interspecific differences linked to a variable need for sleep (Keene and Duboue, 2018).

A rhythm is said to be circadian if it is synchronized with the duration of a day and a night (nychthemeron), or about 24 hours. Sleep therefore corresponds to this type of rhythm (Aulsebrook *et al.*, 2016) since animals have a daily activity cycle that alternates with a rest cycle (Hendricks *et al.*, 2000), the latter taking place during subjective night in diurnal species (Hendricks *et al.*, 2000; Vázquez *et al.*, 2020) or subjective day in nocturnal species (Keene and Duboue, 2018; Tobler and Stalder, 1988). Various mechanisms detailed afterwards in this dissertation contribute to synchronize sleep-wake cycles with the duration of a day, hence the notion of circadian regulation. This cyclicality has been observed in arthropods, notably in scorpions (Figure 1) and cockroaches (Keene and Duboue, 2018; Tobler, 1983).

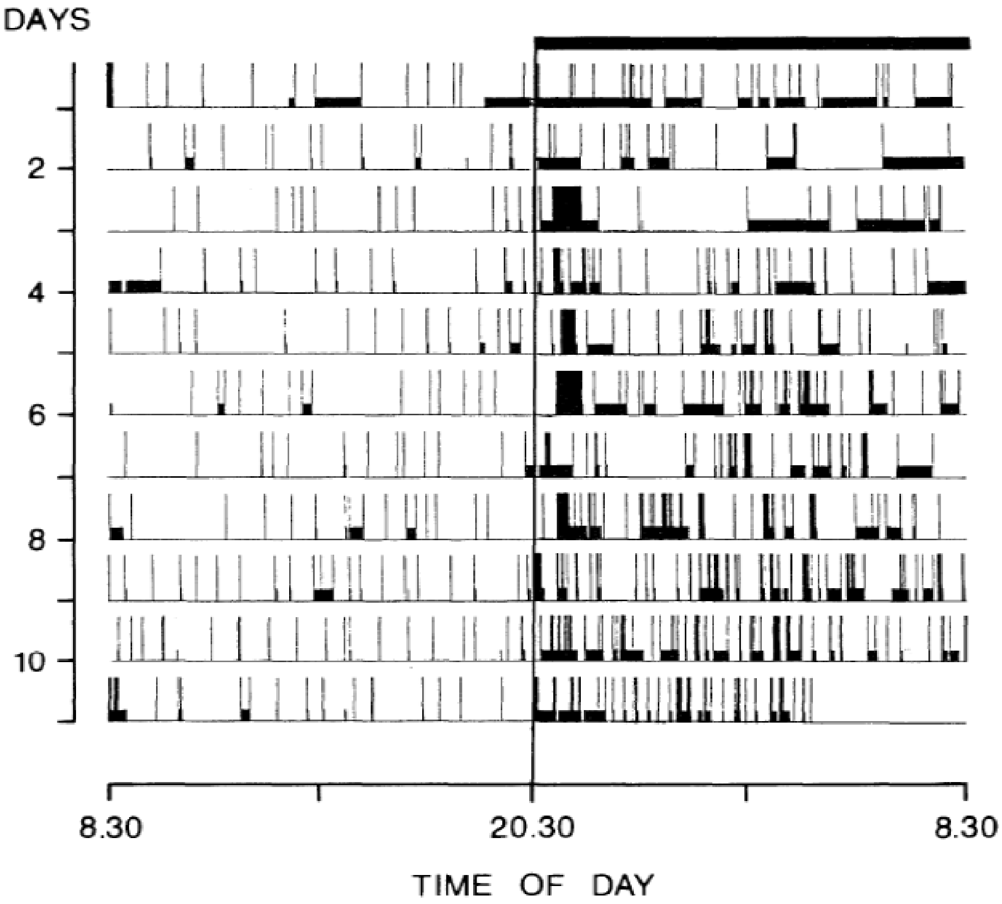

Figure 1: Activity plot of an individual scorpion (*Heterometrus spinnifer*) which was continuously recorded for 11 consecutive days. Three states were scored: high bars, locomotor activity and twitches; low bars, immobility with the cephalothorax off the ground (alert immobility); intervals between bars, immobility with the cephalothorax on the ground (relaxed immobility). The abscissa indicates the time of day. The black bar represents the 12 hour scotophase. The scorpion is a lot more active during the latter than during photophase, thus exhibiting a circadian activity-rest cycle typical of nocturnal species (modified from Tobler and Stalder, 1988).

2. Identical mechanisms and functions in all species?

As previously discussed, some species exhibit features that do not match with the common definition of sleep. We can therefore ask if this state fulfills the same vital functions in all animals.

At first glance, sleep represents energy benefits. In mammals, during rest, the organism saves the energy expended by its cells (Anafi *et al.*, 2019; Siegel, 2009), triggers synthesis pathways that cannot take place under the physicochemical conditions specific to wakefulness periods (Anafi *et al.*, 2019) and eliminates the metabolic waste accumulated during the activity period (Anafi *et al.*, 2019; Cirelli and Tononi, 2008). Even if these characteristics are not always measurable in arthropods, the existence of a homeostatic regulation within this taxon as indicated above seems to prove that sleep is necessary for the renewal of the energy expended by active individuals. Moreover, the numerous sleep deprivation experiments carried out on rats and bees showed that, in both mammals and insects, rest is essential for the proper functioning of the brain since all the tested individuals suffered from impaired cognitive performances (learning difficulties, inability to form new memories, space perception issues, etc.) (Helfrich-Förster, 2018; Kayser *et al.*, 2015; Keene and Duboue, 2018; Tackenberg *et al.*, 2020).

The link between sleep and the brain is all the more important considering that this organ set up the sleep-wake cycle. In insects, through compound eyes and extraretinal photoreceptors, sunlight stimulates the accessory medulla, a part of the brain that acts like a circadian clock. Depending on the amount of light it has detected during a given period, it will cause cascade reactions leading to the individual falling asleep or awakening (Dolezel, 2014), which synchronizes the activity of the latter with the period of a nychthemeron.

The above-mentioned cascade reactions involve numerous neurotransmitters, the actions of which have been thoroughly described in mammals (Ohno and Sakurai, 2008). Most of the known neurotransmitters in insects are similar to those in mammals (Helfrich-Förster, 2018; Vázquez *et al.*, 2020) or play at least an analogous role. For example, octopamine is unique to insects but it regulates sleep-wake transitions like norepinephrine in mammals (Kayser *et al.*, 2015). Moreover, male fruit flies subjected to sleep deprivation exhibit less competition for mating females, which can be compared to the decrease in aggressiveness observed in human subjects under the same conditions (Kayser et al., 2015). Thus, even in animals with no limbic system (cerebral center of emotions), sleep can directly influence social or mating behaviours. During sleep, the nervous system also triggers the secretion of hormones, notably growth hormone in mammals (Siegel, 2009). Regarding arthropods, the influence of hormonal secretions on the scorpion's sleep-wake cycle is still poorly understood (Tobler and Stalder, 1988). Yet, avenues for research suggest that there is a link between the cyclical secretion of a stimulating hormone and the maintenance of a circadian rhythm in cockroaches (Tobler, 1983).

Sleep is also associated with different gene expression compared to wakefulness. In mice, sparrows and fruit flies, sleeping individuals mainly express genes linked to protein synthesis, renewal of membrane lipids and synapses strengthening (Cirelli and Tononi, 2008; Helfrich-Förster, 2018), which confirms the hypothesis of the restorative aspect of sleep. In addition, the extensive work carried out on fruit flies since the 2000's has revealed a very close link between gene expression and the circadian rhythms of these insects: the existence of numerous SNPs (*Single Nucleotide Polypmorphism*) in the individuals' genome has been associated with a great variability in sleep time depending on the latitude where they live (Keene and Duboue, 2018), and the description of the genes "*per*" and "*tim*" proved that daily variations in the expression of these two genes, synchronized with the photoperiod, are necessary to maintain the flies' sleep-wake cycles (Giebultowicz and Hege, 1997; Hendricks *et al.*, 2000).

Lastly, in the current context of global changes, addressing the ecological aspect of sleep is a necessity, especially with regard to the impact of human activities on the sleep-wake cycle of animals. While some species of ants can, just like mice, become temporarily diurnal (an adaptation mostly observed in winter in order to conserve their energy during nights much colder than in summer), unusual nocturnal activity has been observed in fruit flies exposed to prolonged light or high temperatures (Helfrich-Förster, 2018), which is in accordance with the preponderant role of light in the maintenance of circadian rhythms as explained above, as well as the sensitivity of these insects to elevated temperatures (Kayser *et al.*, 2015). The artificial lighting of cities and the tendency of bitumen to retain heat are therefore likely to disrupt the sleep of insects in the long term. To boot, the noise and vibrations generated by human activities (Tougeron and Abram, 2017) and the use of pesticides such as neonicotinoids (Tackenberg *et al.*, 2020; Tasman *et al.*, 2020) or glyphosate (Vázquez *et al.*, 2020) in agrosystems can also cause a significant shift in their circadian rhythms. Consequently, urban sprawl and land artificialization could be at the origin of serious disturbances in the behaviour of insects, which would ultimately have a detrimental impact across ecosystems. For example, sleep-deprived parasitoids would be unable to effectively regulate pest populations (Tougeron and Abram, 2017), which would increase the risks of starvation by destruction of cultivated fields.

In conclusion, despite several exceptions within the animal kingdom, the definition of sleep as stated at the start of this dissertation seems satisfactory for describing the periods of rest observed in many species, including arthropods, even if exceptional behaviours are observed. The probable existence of sleep in insects and arthropods also reinforces the hypothesis that this metabolic and neuro-behavioural state is inherited from a common ancestor to all animals (Anafi *et al.*, 2019; Tobler and Stalder, 1988). However, although it appears to be a vital function, it is still too early to say that sleep is exhibited by all arthropods and that it is a universal property of the animal kingdom. Not only have its neurophysiological, genetic and ecological aspects been described in very few species, but the vast majority of species constituting this extremely dense taxon has never been studied in articles addressing sleep and therefore does not even admit a behavioural description.

Thus, the sequel of this dissertation will focus in more detail on the distribution of studies addressing sleep, in particular in insects, in order to better understand this taxonomic bias.

TAXONOMIC ISSUES AND IMBALANCE

I. A lack of representativity of arthropods in scientific studies

1. Material and methods

To assess the representativity of arthropods compared to other animals in studies addressing sleep, we started by looking for the number of known species in the different taxa that have been considered by the studies. For the sake of homogeneity, we used the numbers cited by a single reference: Zhang, 2011. Although new species have been discovered since the publication of this study, this has little impact on our results which only consider the percentage that the species of each taxon represent in the animal kingdom. Then, we reviewed the references of the main recent articles about sleep and we noted all the articles and reviews evoking sleep, or more generally sleep-wake cycle, whether explicitly (use of terms like "sleep", "sleep-like", "rest", "quiescence", "siesta", "wakefulness" and "arousal") or implicitly, through the mention of the role of circadian rhythms, the photoperiod, the nervous system or gene expression in the establishment of rest periods. We also noted which taxon or paraphyletic group(s) these studies dwelled on, retaining the groups most often cited in the articles: mammals, birds, fishes, reptiles, amphibians, arthropods, mollusks, nematodes, cnidarians and platyhelminths. Studies on very broad subjects and studies involving humans were also excluded. We thus obtained a graph similar to that of Campbell and Tobler, 1984 who dealt with the same issue, so we were able to make comparisons between their work and ours. Finally, we supplemented our search on Google Scholar, with the keyword "sleep" followed by the name of different vertebrates and arthropods belonging to the most studied species in order to compare the number of papers addressing sleep in these species, or at least referring to it.

2. Results and discussion

We noticed a strong increase in the representation of invertebrates (arthropods, molluscs, nematodes, cnidarians and platyhelminths) in studies addressing sleep over the past 40 years (Figure 2).

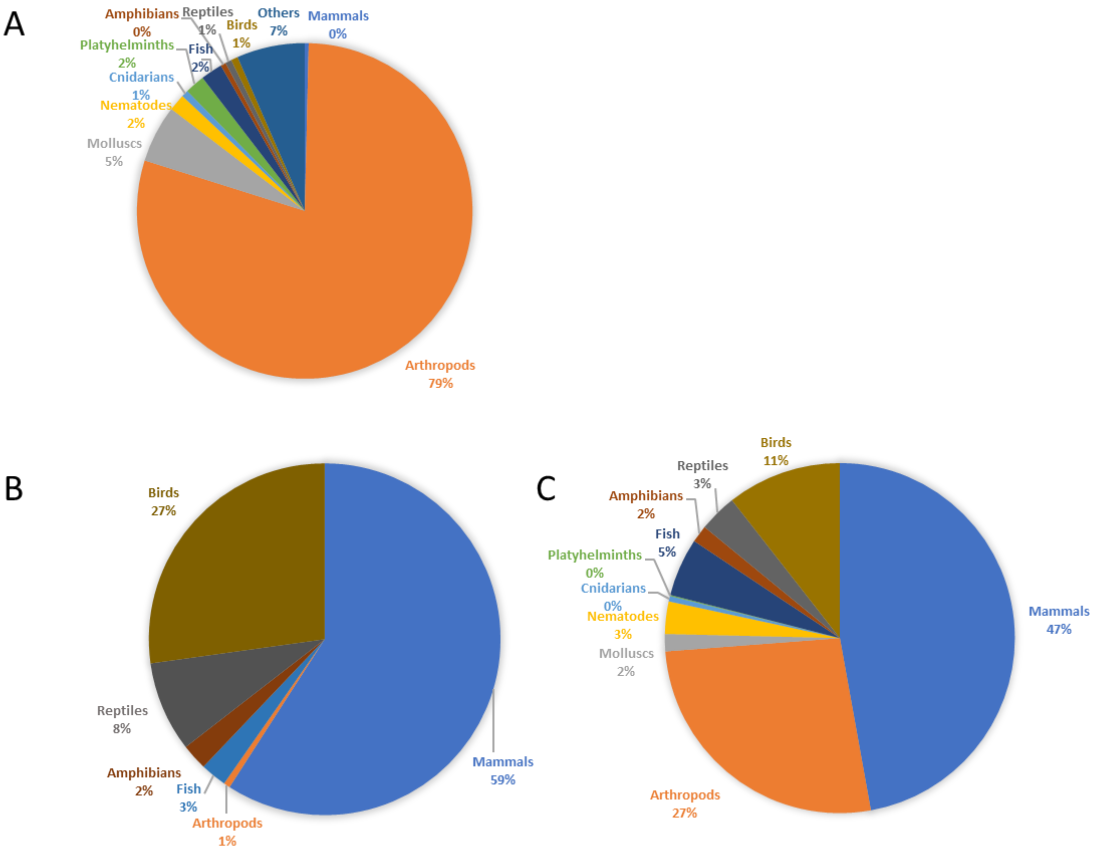

Figure 2: Species representation (A) in the animal kingdom (from Zhang, 2011) versus representation in studies addressing sleep, (B) according to Campbell and Tobler (1984) N = 169 studies and (C) according to our own research in 2020, N = 866 studies.

Invertebrates represent around 32% of our reference list, compared to only 0.6% of the articles reviewed by Campbell and Tobler (1984) with a comparable methodology. Arthropods alone count for more than 3/4 of studies in invertebrates, representing 27% of these references. These results can be explained by the discovery and description of sleep in an insect model, the fruit fly (*Drosophila melanogaster*), at the beginning of the 21st century (Hendricks *et al.*, 2000), which paved the way to numerous studies addressing sleep in this same insect, but also in the honey bee (*Apis mellifera*), another insect very often studied until recently (Tackenberg *et al.*, 2020; Vázquez *et al.*, 2020). This trend is confirmed our literature searches on Google Scholar: fruit flies and honey bees are by far the arthropods for which the study of sleep is the most often mentioned, with respectively 372,000 and 117,000 references (Arthropods: 549,900 references) found by the search engine.

However, mammals are still dominant even if their proportion in studies has fallen below 50%. On the 2,856,000 references found in Vertebrates, there is an overwhelming dominance by studies on the rat, which is associated with nearly 2,000,000 sleep studies according to Google Scholar. This is not surprising, given that sleep in rodents has been extensively studied since the 1970s (Campbell and Tobler, 1984) as part of medical and pharmaceutical studies. Moreover, following the great progress made in the field of neurobiology in recent years, the rat has found itself at the center of a large number of extremely detailed studies on neural pathways related to sleep (Ohno and Sakurai, 2008). Although the neurophysiological aspect of sleep has also been well studied in insects (Helfrich-Förster, 2018), arthropods therefore remain under-represented in studies for the benefit of mammals, which however do not even represent 1% of all animal species (Figure 2).

Furthermore, Figure 2 does not reflect the diversity of studies within each taxon, which reveals another significant bias: in addition to rodents, Campbell and Tobler (1984) found articles about various mammal groups (carnivores, insectivores, marsupials, primates, cetaceans, etc.), while for arthropods, the few insects and crustaceans cited before (flies, bees, scorpions, cockroaches and crayfish) constitute the majority of studies. Besides, it is possible that the proportion of arthropods in Figure 2C is exaggerated because we used fairly broad selection criteria, and therefore retained articles in which the authors were interested in characteristics related to sleep such as reduced responsiveness to external stimuli or circadian and / or photoperiodic regulation of activity, without however asserting that the studied animal was sleeping.

In any case, the conclusion of this first part remains the same as that of the bibliography review: despite a clear gain in interest over the past decades, sleep in arthropods is less studied and above all less detailed than that of vertebrates at the present time. In order to analyze this taxonomic bias more precisely, the next part of the manuscript will focus on the state of knowledge on sleep in the most widespread and diverse arthropod group: insects.

II. The question of the ubiquity of sleep in insects

1. Material and methods

We first noted the number of insect species currently identified in each order based on the data provided by Zhang (2013), which is an update of the 2011 paper by the same author. We then attempted to provide a comprehensive description of sleep in the most studied species in each order. Moreover, most of the complementary articles listed above have allowed us to analyse several other species in which sleep has been studied to a lesser extent.

2. Results and discussion

The full analysis is provided in Table 1.

Table 1: Description of sleep in the different insect orders that have been studied. Orders for which no study addressing sleep is available, and respective number of species: Archaeognatha, 500; Coleoptera, 389000; Dermaptera, 1900; Embioptera, 450; Ephemeroptera, 3100; Grylloblattodea, 32; Hemiptera, 102000; Mantophasmatodea, 17; Mantodea, 2400; Mecoptera, 400; Megaloptera, 350; Neuroptera, 5400; Odonata, 6000; Orthoptera, 23800; Phasmida, 3000; Phthiraptera, 5100; Plecoptera, 3700; Psocoptera, 5600; Raphidioptera, 180; Siphonaptera, 2000; Strepsiptera, 600; Thysanoptera, 5900; Trichoptera, 14500; Zoraptera, 36; Zygentoma, 550 (from Zhang, 2013). References cited: [1] Anafi *et al.*, 2019; [2] Andersen, 1968; [3] Aulsebrook *et al.*, 2016; [4] Campbell and Tobler, 1984; [5] Cassill *et al.*, 2009; [6] Cirelli and Tononi, 2008; [7] Dolezel, 2014; [8] Giebultowicz and Hege, 1997; [9] Haufe, 1962; [10] Hausl-Hofstätter, 2008; [11] Helfrich-Förster, 2018; [12] Hendricks *et al.*, 2000; [13] Kaiser, 1995; [14] Kaiser and Steiner-Kaiser, 1983; [15] Kayser *et al.*, 2015; [16] Keene and Duboue, 2018; [17] Klein *et al.*, 2003; [18] Siegel, 2008; [19] Swihart, 1963; [20] Tackenberg *et al.*, 2020; [21] Tobler, 1983; [22] Tobler and Stalder, 1988; [23] Tougeron and Abram, 2017; [24] Vázquez *et al.*, 2020; [25] Vega *et al.*, 2011.

Orders	**Number of known species**	**Number of species studied**	**Main species studied**	**Description of sleep**	**Other species studied**
Blattodea	7 500	3	Cockroach (*Leucophaea maderae; Blaberus giganteus; Diploptera punctata*)	- periods of immobility with slight movements of the limbs and the antennae ([21]), rapid awakening in response to strong stimuli ([23]) - specific posture (thorax laying on the ground) ([11]; [23]) - reduced responsiveness to external stimuli ([16]; [18]; [21]; [23]) - longer period of immobility after prolonged activity ([1]; [4]; [16]; [21]; [22]; [23]), but not systematically ([6]; [18]; [23]) - circadian activity-rest cycle (immobility mainly during subjective day) ([16]; [18]; [21]) - increased metabolic rate after sleep deprivation ([6]; [24]) until death ([6])	/
Diptera	156 000	2	Fruit fly (*Drosophila melanogaster*)	- periods of immobility ([1]; [11]; [12]) of 5 minutes or more ([20]) with slight movements of the limbs and the proboscis ([12]), rapid awakening in response to strong stimuli ([12]) - specific posture (thorax laying on the ground) ([11]) - reduced responsiveness to external stimuli ([1]; [6]; [11]; [12]; [16]),	Mosquito (*Aedes aegypti*) ([9])

				even more obvious after sleep deprivation (less frequent brief awakenings) ([24]) - longer period of immobility after prolonged activity ([1]; [11]; [12]; [23]), but not systematically ([11]) - circadian activity-rest cycle (immobility mainly during subjective night) ([1]; [7]; [8]; [11]; [12]; [20]) - rhythm synchronized with photoperiod ([7]; [8]; [20]) - modified brain activity ([3]; [6]; [11]; [16]) - modified gene expression ([6]; [11]; [12]) - increased metabolic rate after sleep deprivation ([6]; [24]) until death ([6]) - impaired cognitive performances (learning, memory) after sleep deprivation ([6]; [11]; [16]), but not systematically ([11]) - decreased lifespan and stress resistance after sleep deprivation ([16]) - suppression of aggressive behaviour after sleep deprivation ([15])	
Hymenoptera	153 000	26	Honey bee (*Apis mellifera*)	- periods of immobility of 5 to 15 minutes ([20]; [24]) about 50 times per nycthemeron ([24]), rapid awakening in response to strong stimuli ([23]) - specific posture (antennae downwards) ([11]; [22]; [24]) - reduced responsiveness to external stimuli ([18]; [22]; [23]) except for the eyes ([14]) - reduction in muscle tone ([24])	Ant (*Solenopsis invicta*) ([5]) Paper wasp (*Polistes flavus*) ([17]) Solitary bees and wasps (*Andrena ovatula; A. dalmatica; A. fulvitarsis; A. subterranea*; *Epeolus*

				- light sleep stage (very short, with reduced movements of the antennae and increased responsiveness to light stimuli) ([24]) and deep sleep stage (no movements of the antennae, slower respiratory rate, decrease in body temperature) ([16]; [24]) - longer period of immobility after prolonged activity ([16]; [23]), but not systematically ([6]; [18]) - circadian activity-rest cycle (immobility mainly during subjective night) ([20]) - circadian variations of neuronal sensitivity in the eye ([14]; [18]); minimal sensitivity during subjective night ([1]; [3]; [14]; [16]) - rhythm synchronized with photoperiod ([20]) - reduction of brain activity ([3]; [24]), except in mushroom bodies ([16]) - impaired cognitive performances (learning, memory, capacity to return to the hive, communication by waggle dances) after sleep deprivation ([11]; [20]; [24])	*variegatus; Epeolus sp.; Eupavlovskia obscura; Melecta albifrons; M. duodecimmaculata; M. leucorhyncha; M. tuberculata; Nomada femoralis; N. integra; Nomada sp.; Odynerus melanocephalus; Paranomada velutina; Protepeolus singularis; Scolia hirta; Syzeuctus fuscator; Triopasites penniger; Triepeolus sp.*) ([10]; [13]) Bumblebee (*Bombus atratus*) ([25])
Lepidoptera	158 000	2	/	not enough data for a behavioural description of sleep	Moth (*Anagasta kuehniella*) ([2]) Butterfly (*Heliconius erato*) ([19])
Other orders (25)	576 515	/	/	no description of a sleep-like state to date	/

Undoubtedly, Hymenoptera is the most studied order, with 26 species in which sleep has been confirmed and a very complete description of *Apis mellifera*'s sleep. There is also an exhaustive description for *Drosophila melanogaster*, but this fruit fly species represents the only dipteran that has been studied in detail. As for the order Blattodea, there is only a behavioural description for the three studied species. Finally, no lepidopteran has been the subject of sufficiently comprehensive papers to confirm the existence of sleep in this order. Andersen (1968) simply noted a link between a specific posture and reduced responsiveness to mechanical stimuli in the moth *Anagasta kuehniella* (like Haufe (1962) in the mosquito *Aedes aegypti*), and Swihart (1963) only observed circadian variation in eye sensitivity in the butterfly *Heliconius erato*.

Furthermore, it is interesting to underline that, even in species of hymenopterans much less studied than the honey bee, the behavioural aspect of sleep is rather well known. Cassill *et al.* (2009) revealed many details on the rest periods of the ant *Solenopsis invicta* such as the places in the nest where individuals fall asleep, the position and movements of the antennae during sleep, as well as the duration and frequency of rest periods in workers and queens. As for Klein *et al.* (2003), they demonstrated that, apart from homeostatic regulation, all aspects of the behavioural definition of sleep are present in the paper wasp *Polistes flavus*. Regarding the solitary hymenopterans, Hausl-Hofstätter (2008) pointed out in some species a preference for specific flowers on which the individuals rested, while Kaiser (1995) compared the sleep in other species to that in *Apis mellifera* and thus noted several similarities (deepening of sleep during the night, decrease in respiratory rate and muscle tone, specific position of the antennae), but also noteworthy differences. For example, solitary bees cling to the stems of plants with their mandibles before falling asleep and can remain motionless for several hours straight. Lastly, although sleep in bumblebees has been less thoroughly studied, Vega *et al.* (2011) emphasized on a relation between the role of individuals (warming the hive, feeding the larvae or foraging), the total duration of their sleep and the temperature at which they preferentially fall asleep.

Nonetheless, with only four out of 29 studied orders and a total of 33 species cited in the scientific literature out of 1,053,578 known species (Zhang, 2013), we notice once again how vast the taxonomic bias against arthropods is. On the one hand, the lack of data for some orders is easily understandable. For example, species of Grylloblattodea, Mantophasmatodea and Zoraptera are so rare (85 species in all three orders combined) that they are most certainly the subject of much more general studies than the characterization of rest periods, and mayflies (Ephemeroptera) are obviously not concerned by the study of a circadian rhythm such as sleep, given that their adult lifespan is often shorter than a day. This being said, it is also important to note that sleep is mainly studied in adults and the characteristic elements of this behavior in juvenile stages is extremely poorly known. On the other hand, it is surprising that no author has studied sleep in much more widespread orders such as Orthoptera, Hemiptera and especially Coleoptera, the order of insects that includes the most species by far. This observation can nevertheless be explained by the fact that, as indicated in the introduction, the study of the locomotor activity of insects is much more common than the study of their periods of immobility (Campbell and Tobler, 1984; Tougeron and Abram, 2017). Moreover, outside of activity periods, biologists are more interested in diapause (Dolezel, 2014) than in sleep in insects. Finally, it should be remembered that EEG cannot be used on these animals (Hendricks *et al.*, 2000; Tougeron and Abram, 2017), which may discourage researchers from carrying out studies as comprehensive as those on vertebrates. In addition, the study of parasomnias like narcolepsy with the aim of designing drugs for human patients always relies on mammal models such as, for example, dogs or mice (Ohno and Sakurai, 2008), because it is naturally much more practical to use animals with an anatomy very similar to ours in order to develop effective substances.

Thus, with the exception of *Apis mellifera* and *Drosophila melanogaster* which are considered excellent model species to analyse the genetic and evolutionary aspects of sleep (Helfrich-Förster, 2018; Hendricks *et al.*, 2000; Keene and Duboue, 2018), insects remain extremely little studied. Given the huge part that insects represent in the species of the phylum Arthropoda (nearly 87% of the 1,214,295 known species (Zhang, 2013)), this further amplifies the taxonomic bias that has been illustrated in the first part of this manuscript.

CONCLUSION

Sleep has been fairly well studied in several dozen species of arthropods, especially in insects of the order Hymenoptera and Diptera. In other species, the accuracy of the description of sleep is very variable, ranging from a simple behavioural characterization to studies of the mere variations of responsiveness to external stimuli. To boot, considering the total absence of data on the hundreds of thousands of other species constituting the most diverse phylum of the animal kingdom, current knowledge on sleep in arthropods can be described as extremely limited.

Despite a particular enthusiasm for the study of sleep in insects since the early 2000s, the taxonomic bias towards vertebrates remains significant, mainly because of mammals which are at the center of a huge number of studies addressing sleep since the last century. This lack of representativeness of arthropods seems to be linked to the technical difficulties of the analysis and the lack of interest toward a phylogenetically distant group. This is why several authors have proposed to better distribute the research effort in studies addressing sleep, since the 1980s:

> *"Traditionally, the examination of such variability in sleep length across species has been a principal feature of interest in the examination of sleep function. Yet, it is also clear that the data base upon which these comparisons are made remains sparse. This paucity of data continues to be the most important obstacle restricting the analysis of sleep duration measures in the effort to enunciate the functions of sleep. Sleep is ubiquitous across phylogeny and is manifested in many forms. Only by examining all forms of this behavior will it become possible to characterize sleep in terms of its evolutionary significance."* (modified from Campbell and Tobler, 1984)

Nowadays, beyond the contributions of the studies addressing sleep in the field of phylogeny, the ecological aspect of this state would benefit from being highlighted. Indeed, while human activities are proved to disturb animal sleep (Aulsebrook *et al.*, 2016), the consequences of these disturbances on insect communities are poorly understood (Tougeron and Abram, 2017). However, these consequences could have a large-scale impact if they involve insects providing essential ecosystem services such as pollination. Actually, in populations of *Apis mellifera*, the feeders synchronize their activity with the workers', so the disruption of the circadian rhythms of the latter could greatly affect the organization of the hive (Tackenberg *et al.*, 2020) and ultimately reduce the efficiency of pollinating bees. This hypothesis justifies the importance of studying sleep in species other than vertebrates and suggests that arthropods will be the subject of more studies on this topic in the following years, thus contributing to the reduction of the taxonomic bias in favor of other animals which was initiated at the beginning of the 21st century.

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