Studies on sleep patterns and sleep homeostasis in birds

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APPENDIX I

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APPENDIX II

Nederlandse Samenvatting

Slaap is een staat van rust en herstel en alle dieren die zijn bestudeerd laten een vorm van rust-activiteit patronen zien. Echter, het gros van wat bekend is over slaap en slaap-regulatie komt voort uit onderzoek dat is gedaan in nacht-actieve knaagdieren zoals ratten en muizen. Studies in deze zoogdieren hebben aangetoond dat een minimale hoeveelheid slaap per nacht nodig is om goed te functioneren. Zodra deze hoeveelheid niet is gehaald wordt dit verlies gecompenseerd door meer en dieper te slapen in de daaropvolgende nacht. Recent onderzoek naar slaap in vogels laat zien dat deze regel voor de regulatie van slaap niet altijd van toepassing is. Met name als vogels lange vluchten moeten maken van meerde dagen of tijdens drukke periodes in het broedseizoen. Tijdens deze periodes waarbij het noodzakelijk is om dagen achter elkaar wakker en actief te zijn is er geen duidelijke herstelfase. Om de fundamenten van slaapregulatie in vogels beter te begrijpen hebben we in dit proefschrift drie vogelsoorten onderworpen aan verschillende slaap experimenten in het lab, maar ook daarbuiten.

In hoofdstuk 2 en 3 hebben we slaap onthouden in kauwen en spreeuwen om de regulatie van slaap te bepalen. Hierbij hebben we de hersenactiviteit gemeten. Kauwen en spreeuwen behoren tot dezelfde orde van zangvogels maar laten een groot verschil in samenstelling van slaap zien. Slaap bestaat uit twee componenten die beiden een eigen functie wordt toegedicht: REM slaap en NREM slaap. De NREM slaap wordt gekarakteriseerd door een afwisselend verminderde en sterk gesynchroniseerde activiteit van de zenuwcellen in het brein. Tijdens de REM slaap daarentegen zijn de zenuwcellen in de hersenen juist erg actief, ook al is het organisme in rust en zich vrijwel onbewust van zijn omgeving. Van de totale hoeveelheid slaap die de vogels tijdens de nacht hebben, laten kauwen een behoorlijk aandeel van REM slaap zien terwijl bij de spreeuwen dit nagenoeg nihil is. Na slaapdeprivaties van 4 en 8 uur laten beide diersoorten een toename zien in de hoeveelheid NREM slaap. Kauwen hebben ook duidelijk een toename in REM slaap na slaapdeprivatie, dit in tegenstelling tot de spreeuwen. Deze experimenten zijn gedaan onder gestandaardiseerde laboratorium condities, wat betekent dat naast een licht-donker cyclus alle andere omgevingsfactoren zoals temperatuur niet veranderen.

Om een beter beeld te krijgen hoe vogels slapen onder meer natuurlijke omstandigheden hebben we de spreeuwen en brandganzen tijdens verschillende seizoenen in buitenverblijven gehuisvest. Uit deze metingen blijken brandganzen in de zomer 1.5 uur minder te slapen dan in de winter. Spreeuwen slapen zelfs 5 uur minder (hoofdstuk 4). Dit komt omdat de zomernachten een stuk korter zijn dan in de winter. De reden waarom bij brandganzen dit verschil tussen de seizoenen kleiner is komt hoogstwaarschijnlijk doordat de ganzen in de zomer geen 24-uurs ritmiek meer hebben en daardoor overdag net zoveel kunnen slapen als tijdens de nacht. De spreeuwen behouden hun 24-uurs ritmiek wel en ervaren daardoor tijdens die korte zomernachten dan ook een hogere slaapdruk. Deze data duidt erop dat onder natuurlijke omstandigheden de regulatie van slaap niet op elk moment van het jaar hetzelfde is.

In hoofdstuk 5 hebben we de brandgans onderworpen aan slaapdeprivaties in de winter en de zomer om te testen of de regulatie van slaap verschilt tussen de seizoenen. Deze metingen laten zien dat brandganzen in de zomer het slaapverlies volledig compenseren door meer te gaan slapen. In de winter daarentegen is er geen enkele compensatie waargenomen. Dit betekent dat de regulatie van slaap in brandganzen inderdaad seizoensafhankelijk is.

Naast seizoenseffecten op slaap in spreeuwen en brandganzen heeft de maan ook invloed op de hoeveelheid NREM slaap. Beide diersoorten slapen 1.5 – 2 uur minder tijdens nachten met een volle maan vergeleken met nachten zonder maan (hoofdstuk 4 en 5). Het is aannemelijk dat het maanlicht ervoor zorgt dat de dieren wakkerder zijn. Dit kan als voordeel hebben om ’s nachts te kunnen foerageren en tegelijkertijd potentiele predatoren zien. Vogels blijken dit niet alleen te doen tijdens nachten met een volle maan, maar ook tijdens bewolkte nachten (hoofdstuk 6). Dit komt doordat in stedelijke gebieden het kunstlicht wordt weerkaatst door het wolkendek en zo weer terug op de aarde komt. De hoeveelheid kunstlicht rondom onze onderzoeksfaciliteit bleek even sterk te zijn als tijdens wolkeloze nachten met een volle maan.

Slaapstudies onder natuurlijke omstandigheden blijkt waardevol te zijn in het verkrijgen van nieuwe inzichten over de regulatie van slaap. Het is niet altijd even makkelijk om slaap in het wild te meten. Dit hangt af van de grootte van het diersoort en zijn habitat. Een alternatief hiervoor zou het meten van activiteit zijn. Om dit te testen, hebben we gekeken hoe betrouwbaar activiteit metingen zijn voor het bepalen van slaap in brandganzen (hoofdstuk 7). De activiteit metingen kan in hoge mate slaap en waken voorspellen. Om de gedetailleerde aspecten van slaap te kunnen bepalen, zoals het onderscheid tussen NREM en REM slaap neemt de onzekerheid sterk toe. Naast activiteit metingen kan het ook handig zijn om interval metingen te doen in plaats van continue slaap metingen. Dit kan de batterijduur behoorlijk verlengen en tegelijkertijd loopt de geheugenopslag ook minder snel vol. Om dit te testen hebben we de brandgans dataset gemanipuleerd en verschillende opname schema’s gemaakt dat oploopt van 1 minuut per 5 minuten tot 1 minuut per 60 minuten (hoofdstuk 8).

Met het toenemen van het opname interval neemt de betrouwbaarheid af vergeleken met de continue dataset. Tot en met een interval van 1 minuut per 40 minuten kan een hoge nauwkeurigheid behaald worden als naar uurgemiddelden gekeken wordt. Dit kan een uitkomst bieden om in de toekomst lange metingen in het veld te kunnen uitvoeren.

De bovenstaande analyses kunnen met name gebruikt worden om te bestuderen hoe brandganzen slapen tijdens de tweejaarlijkse migraties tussen Nederland en Rusland. Met behulp van deze data kunnen we erachter komen of brandganzen tijdens de vluchten met één hersenhelft kan slapen terwijl de andere wakker is, of in het geval dat ze helemaal niet slapen of dit slaapverlies ingheaald moet worden. Om deze vragen te kunnen beantwoorden moeten brandganzen gevangen worden in het Arctische broedgebied en uitgerust worden met EEG loggers en GPS zenders. In 2018 zijn we naar een veldstation in Tobseda in Rusland geweest om te verkennen of dit een goede studielocatie is voor toekomstige slaapstudies in brandganzen (hoofdstuk 9). Op deze locatie zijn de aantallen ganzen flink afgenomen maar dat weerhoudt ons niet om te zoeken naar alternatieve plekken om deze studie voort te zetten. Wordt vervolgd...

Conclusie

De studies beschreven in deze thesis waarbij slaap is gemeten in vogels en rekening werd gehouden met de ecologie van slaap leverden belangrijke nieuwe inzichten op over de regulatie van slaap. Vogels laten een (seizoensafhankelijke) homeostatische regulatie van NREM slaap zien. De bevindingen over de regulatie van REM slaap is in tegenstelling tot NREM slaap niet eenduidig en voedt hierdoor de discussie over de functie van REM slaap. Met behulp van kleine dataloggers kunnen we de ecologie van slaap bestuderen. Slaap onder seminatuurlijke omstandigheden laat een enorme hoeveelheid aan flexibiliteit in slaap zien dat onopgemerkt zou zijn gebleven bij studies onder traditionele lab condities.

APPENDIX III

English summary

Sleep is a state of rest and recovery and all animals that have been studied show some form of rest-activity patterns. However, most of what is known about sleep and sleep regulation are derived from research done in nocturnal rodents such as rats and mice. Studies in these mammals have shown that a minimum amount of sleep is needed for optimal function. When this minimum amount of sleep is not reached, sleep is recovered by sleeping more and/or deeper. Recent research on sleep in birds shows that this rule of sleep regulation does not always apply. These birds disregard this rule when they need to be active for several days in a row, for instance during migration or busy breeding seasons. When these busy periods of activity end, there is not a clear recovery phase. To better understand the fundamentals of sleep regulation in birds, we present a series of unique studies in this thesis where we have subjected three bird species to different sleep experiments in the lab, but also beyond.

In Chapters 2 and 3, we deprived sleep in jackdaws and starlings to determine the homeostatic regulation of sleep by measuring brain activity. Jackdaws and starlings belong to the same order of songbirds but show large variations in the composition of sleep. Sleep consists of two components, each of which has its own function: REM sleep and NREM sleep. NREM sleep is characterized by an alternation between reduced and highly synchronized activity of the nerve cells in the brain. During REM sleep, on the other hand, the nerve cells in the brain are very active, even though the organism is at rest and almost unconscious of its environment. Of the total amount of sleep that the birds have during the night, jackdaws show a considerable portion of REM sleep. Starlings, on the other hand, show almost no REM sleep at all. After 4 and 8 hours of sleep deprivation, both birds showed an increase in the amount of NREM sleep. Jackdaws also clearly showed a response in REM sleep after sleep deprivation compared to no REM sleep response in the starlings. These experiments were done under standardized laboratory conditions, which means that besides a light-dark cycle, all other environmental factors such as temperature are kept constant.

To better understand the regulation of sleep under natural conditions, we housed starlings and barnacle geese in outdoor enclosures across different seasons. These measurements show that barnacle geese sleep 1.5 hours less in the summer than in the winter. Also, starlings show a difference in the amount of sleep across the seasons with 5 hours less sleep in summer compared to winter (chapter 4). This difference in the amount of sleep across the seasons can be explained by the differences in daylength between winter and summer. Barnacle geese show less variation across the seasons and this is probably because barnacle geese lost their daily rhythm in sleep and therefore they can sleep as much during the day as they do during the night. The starlings, on the other hand, retain their 24-hour rhythm and sleep much less during the day. During the summer nights, starlings experience more sleep pressure compared to the winter nights. These data indicate that the regulation of sleep changes across the year under natural conditions

In chapter 5, subjected the barnacle geese to sleep deprivations in the winter and the summer to test seasonal changes in sleep regulation. The outcome of this experiment is that barnacle geese show a clear regulation of sleep in summer. In winter, on the other hand, no sign of a sleep compensatory response has been observed. This means that the regulation of sleep in barnacle geese is season-dependent.

Other environmental factors, such as the moon, have a clear effect on sleep in starlings and barnacle geese. Both species sleep 1.5 – 2 hours less during nights with full moon compared to no moon nights (chapter 4 and 5). It is most likely that the light reflected from the moon's surface cause the suppressing of sleep. This extra light at night might be useful for the birds to safely forage during the night where they can see potential threats and predators. Birds also do this during cloudy nights, independent of full moon (chapter 6). This is because cloud cover reflects artificial light at night back to the surface of the earth. The intensity of artificial light at night around our research facility reaches similar levels as the full moon.

Sleep studies under natural conditions prove to be valuable in gaining new insights into the regulation of sleep. It is not always easy to measure sleep in the wild. This depends on the size of the species of interest and its habitat. An alternative to measuring sleep based on electrophysiology is to measure activity only. To test how reliable activity is in determining sleep, we correlated sleep to activity in our barnacle geese dataset (chapter 7). Activity measurements alone can largely predict sleep and wakefulness. However, to determine the detailed components of sleep, such as NREM and REM sleep, the reliability of using activity as a proxy for sleep rapidly decreases. Besides measuring activity, it might be also beneficial to measure sleep based on electrophysiology intermittently. Measuring sleep intermittently significantly saves battery life and memory capacity. To test how reliable intermittent sleep recordings are, we manipulated the goose dataset and converted it into 12 datasets where we simulated a recording scheme of measuring sleep 1 minute every 5 minutes up to 1 minute every 60 minutes in steps of 5 minutes (chapter 8). The reliability of intermittent recordings rapidly decreases when the recording interval increases. However, high hourly accuracy can be achieved up to a recording scheme of 1 minute per 40 minutes. These intermittent sampling techniques can be very valuable for future sleep studies, particularly for sleep studies in the wild.

The outcomes of the analyses in the previous paragraph can be used to study how barnacle geese sleep during the biennial migrations between the Netherlands and Russia. Recording sleep during the migration can provide insights into whether geese are capable of sleeping during flight by sleeping with one hemisphere at the time, or in case they forgo sleep whether they need to recover from it. To answer these questions, barnacle geese have to be captured in the Arctic breeding area and equipped with EEG loggers and GPS transmitters. In 2018 we went to a field station in Tobseda, Russia to explore whether this is a good study location for future sleep studies with barnacle geese (chapter 9). The numbers of geese have decreased considerably at this location, but that does not prevent us from looking for alternatives to pursue this study. To be continued…

Conclusion

The studies presented in this thesis revealed important new insights in the flexibility and regulation of sleep. Birds show (season-dependent) homeostatic regulation of NREM sleep. The findings on the regulation of REM sleep are inconclusive and fuel the discussion on the function and necessity of REM sleep in birds. By using small dataloggers, we have shown that it is possible and important to include the ecology in sleep studies. Sleep under semi-natural conditions shows a tremendous amount of flexibility that would have gone unnoticed in traditional laboratory conditions. Taken together, our research can be used as building blocks to further unravel the mysteries that lie behind the evolution of sleep.

APPENDIX IV

Chinese summary

睡眠是一种休息和恢复的状态，所有被研究过的动物都表现出某种形式的休息模式。然而，目前为止我们对睡眠和睡眠调节的绝大多数认知都来自于对大鼠和小鼠等夜间啮齿动物的研究。对这些哺乳动物的研究表明，这些哺乳动物都需要至少达到一定的睡眠时间才能维持最佳身体功能。当这个最低睡眠量没有达到的时候，这些哺乳动物通过更多和或更深的睡眠来恢复身体功能状态。然而，近期关于鸟类睡眠的研究显示，鸟类睡眠调节机制并不总和哺乳动物中的睡眠弥补机制一致。当鸟类需要维持连续几天活跃状态时，例如在迁徙过程中或者在繁忙的繁殖季节中，这些鸟类会无视睡眠弥补机制。当这些繁忙的活动期结束后，这些鸟类并没有明确的睡眠恢复阶段。为了更好地了解鸟类睡眠调节的基本原理，我们在本论文中进行了一系列独特的研究，我们使用了三种不同鸟类在实验室内以及实验室外进行了几种不同的睡眠实验。

在第2和第3章中，我们分别在寒鸦和椋鸟中进行了睡眠剥夺实验并且测量了它们的脑部活动以此来研究它们的睡眠平衡调节机制。寒鸦和椋鸟是同属于一个鸣禽目的鸟，但它们的睡眠组成却有很大的差异。睡眠由两部分组成，每部分都有自己的功能：快速眼动睡眠（REM）和非快速眼动睡眠（NREM）。非快速眼动睡眠的特点是大脑中神经细胞在低频和高度同步活动的不断交替。另一方面，在快速眼动睡眠期间，即使机体处于休息状态并且几乎对外界环境毫无意识，大脑中的神经细胞却非常活跃。相比于鸟类夜间的总睡眠量，寒鸦显示了相当一部分的快速眼动睡眠。另一方面，椋鸟几乎完全没有快速眼动睡眠。在对它们进行4和8小时的睡眠剥夺实验后，这两种鸟类的非快速眼动睡眠量都有所增加。在睡眠剥夺实验后，寒鸦的快速眼动睡眠量也清楚地显示出了变化，然而椋鸟的快速眼动睡眠量并没有任何变化。这些实验是在标准化的实验室条件下进行的，这意味着除了昼夜循环外，所有其他环境因素（如温度）都保持恒定。

为了更好地了解睡眠在自然条件下的调节机制，我们将椋鸟和藤壶鹅安置在户外的鸟圈中并且跨越不同的季节。这些实验测量结果显示，藤壶鹅在夏天的睡眠时间比冬天的少1.5小时。此外，椋鸟在不同季节的睡眠量也有所不同，与冬季相比，它们夏季睡眠时间要少 5 小时（第 4章）。这种不同季节睡眠量的差异可以用冬季和夏季之间的昼长差异来解释。藤壶鹅的睡眠量在不同季节的变化较小，这可能是因为藤壶鹅失去了睡眠的昼夜规律，所以它们白天的睡眠量可以和夜间的一样多。另一方面，椋鸟依然保持着 24 小时的节奏，所以它们白天的睡眠时间要少得多。与冬夜相比，椋鸟在夏夜的睡眠压力更大。这些数据表明，在自然条件下，睡眠调节机制全年都在发生变化。

在第5章中，我们对藤壶鹅在冬季和夏季分别进行了睡眠剥夺实验以此来测试睡眠调节机制的季节性变化。这个实验的结果是，藤壶鹅在夏季中表现出明显的睡眠稳态调节。在另一方面，在冬季，藤壶鹅的睡眠中没有显示任何睡眠补偿机制的存在。这意味着藤壶鹅的睡眠调节显然是受季节影响的。

其他环境因素，例如月亮，对椋鸟和藤壶鹅的睡眠有明显影响。与没有月亮的夜晚相比，这两个物种在有满月的夜晚睡眠时间要少 1.5 到 2 小时（第 4 章和第 5 章）。从月球表面反射的光很可能会抑制睡眠。这种夜间额外的光线可能有助于鸟类在夜间安全觅食，帮助它们看到潜在的威胁和捕食者。和满月无关的是，这些鸟类的睡眠时间在多云的夜晚也同样有所降低（第 6 章）。这是因为云层在夜间将人造光反射回地球表面。我们研究所设施周围夜间人造光的亮度与满月的光强相似。

自然条件下的睡眠研究被证明了它们对于获得有关睡眠调节机制的新见解很有价值。然而在野外测量睡眠并不总是那么容易。这取

决于研究物种的大小及其栖息地。除了电生理学测量睡眠的方式以为，测量睡眠的另一种方式是仅测量活动。为了测试活动在研究睡眠方面的可靠性，我们用藤壶鹅的数据测试了睡眠和活动之间的关联（第 7 章）。单独活动测量可以在很大程度上预测睡眠和觉醒状态。然而，为了确定睡眠的详细组成部分，例如非快速眼动睡眠和快速眼动睡眠，这种使用活动来测量睡眠的方式的可靠性迅速降低。除了测量活动外，使用间歇性地电生理学测试方式来测量睡眠也可能是有益的。间歇性地测量睡眠可显着节省电池寿命和内存容量。为了测试间歇性睡眠记录的可靠性，我们操作了藤壶鹅的数据集并将其转换为 12 个子数据集，我们根据模拟了一个记录方案，从每 5 分钟测量睡眠 1 分钟到每 60 分钟 1 分钟的记录方案（每次五分钟不同）（第 8 章）。当记录间隔增加时，间歇性睡眠记录的可靠性迅速降低。然而，一直到每 40 分钟 1 分钟的记录方案依然可以达到很高的每小时精准度。这些间歇采样技术对于未来的睡眠研究非常有价值，特别是对于野外的睡眠研究。

之前段落中的分析成果可以被用于研究藤壶鹅在荷兰和俄罗斯的年度迁移过程中的睡眠。记录迁徙过程中的睡眠可以用来了解藤壶鹅是否能够在飞行过程中通过一个脑半球来睡觉。要回答这些问题，我们在北极繁殖区捕获藤壶鹅，并配备EEG 记录器和 GPS 发射器。2018年，我们前往了位于Tobseda（俄罗斯）的一个野外站，探讨这里是否是一个好的研究基地进行未来的藤壶鹅睡眠研究（第9章）。在这个地点的藤壶鹅的数量已经大大减少，但这并不影响我们寻找其它地点来进行进一步的研究。未完待续…

结论

本论文中展示的研究揭示了关于睡眠灵活性和调节的重要新见解。鸟类表现出（取决于季节）非快速眼动睡眠的稳态调节机制。关

于快速眼动睡眠调节的研究结果尚无定论有待进一步研究，但推动了对于鸟类 快速眼动睡眠功能和必要性的讨论。通过使用小型数据记录器，我们已经证明将生态学纳入睡眠研究是可能且重要的。半自然条件下的睡眠显示出极大的灵活性，这在传统的实验室条件下是不会被注意到的。我们在本论文中提及的研究成果为接下来进一步解密不同物种睡眠进化背后的奥秘进行了奠基。

APPENDIX V

Acknowledgements

Na iets meer dan 4 jaar en 172 uur aan slaapdeprivaties later, sta ik hier nu met mijn dokters titel! Dit avontuur begon al tijdens mijn master waar ik als studentje slaap ging meten in spreeuwen. Ik ben trots dat mijn masteronderzoek ook onderdeel is van mijn proefschrift. Tijdens mijn promotietraject heb ik de meest fantastische vaardigheden geleerd en heb ik ervaren hoe veelzijdig de wetenschap is. Bijvoorbeeld, het bedenken, ontwerpen en het uitvoeren van een experiment, de data plotten in figuren en het schrijven en presenteren ervan vergt dan ook veel energie, creativiteit en aandacht. Daarnaast heb ik drie bijzondere expedities mogen maken naar het Arctisch gebied in Alaska en Rusland. Ik ben dan ook ontzettend trots op het eindresultaat. Het traject van beginnend PhD'er tot een zelfstandige wetenschapper gaat niet vanzelf, en hiervoor wil ik een aantal mensen bedanken die me hierbij geholpen hebben.

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