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Kevin Brewer

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orsettpsychologicalservices@phonecoop.coop

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Kevin Brewer BSocSc, MSc

An independent academic psychologist, based in England, who has written extensively on different areas of psychology with an emphasis on the critical stance towards traditional ideas.

A complete listing of his writings at <http://psychologywritings.synthasite.com/>. See also material at <https://archive.org/details/orsett-psych>.

CONTENTS

| | Page Number |
|--|-------------|
| 1. Insect Monitoring | 4 |
| 2. Nature-Positive Economics | 15 |
| 3. Managing Ecological Novelty | 21 |
| 4. Diversity-Dependent Dispersal | 30 |
| 5. Long Term Potentiation Fifty Years Later | 33 |
| 6. Acoustic Communication and Group Dynamics | 38 |
| 7. Light Pollution in Complex Ecosystems | 52 |

1. INSECT MONITORING

- 1.1. Overview
- 1.2. Molecular methods
- 1.3. Computer vision
- 1.4. Autonomous acoustic monitoring
- 1.5. Radar-based monitoring of insect movements
- 1.6. References

1.1. OVERVIEW

"Insects are the most species-rich group of animals on Earth, and, together with other arthropods, make up most of the terrestrial animal biomass. They provide a myriad of ecosystem functions and interact with species across the tree of life. They also provide services and disservices that make insects inextricably intertwined with human lives: for instance, many plants, including important agricultural crops, depend on insect pollinators; other insect species are among our worst crop pests or are disease vectors for plants, animals and humans" (van Klink et al 2024 pp1-2). Accurate monitoring of insect biodiversity is thus important. The traditional method is identification and counting of collected individuals by human researchers, which is time-consuming to say the least.

van Klink et al (2024) outlined four methods involving technological developments (table 1.1):

i) Molecular methods - Identifying species from molecular traces left in the environment (ie: DNA or RNA).

DNA extracted from the environment (eDNA) can involve water samples. "Importantly, the use of eDNA for assessing biodiversity of macro-invertebrates largely relies on fragments of DNA shed by organisms into an ecosystem, thus requiring no specimens to be collected or killed in its application. This consideration renders the use of eDNA distinctly favourable for conservation of threatened freshwater biodiversity" (Blackman et al 2024 pp2-3).

ii) Computer vision - Using computer vision rather than human eyes to observe insects.

iii) Autonomous acoustic monitoring - Continuous recording of sounds of soniferous insects, which are automatically identified by trained AI.

iv) Radar-based remote sensing - Identifying insects by body shape and size, for example, using radars that omit electromagnetic beams that are reflected by objects in the air.

| METHOD | INFORMATION OBTAINED | MAIN PROBLEM |
|--------------------------------|---|--|
| Molecular methods | Species identify | Depends on information already known as comparison |
| Computer visions | Identity of species, and relative abundance | Accuracy of system |
| Autonomous acoustic monitoring | Identity of species, and relative abundance | Only insects that make sounds that can be identified |
| Radar-based remote sensing | Biomass, and movement information | Expensive equipment required |

(Based on van Klink et al 2024 figure 1)

Table 1.1 - Four methods for assessing insect biodiversity.

All the methods depend on equipment that is expensive, but that varies by degree, and the information already known (ie: the "library" or database ¹). The latter is equally true for human observers.

The cost is a specific problem in poorer countries. This is important as "the lack of data for most of the tropics is deeply worrying, because 14 of the 17 mega-diverse countries are located in what is sometimes called the 'Global South'. Many of these countries lack biodiversity baseline data, let alone biomonitoring capacity" (Brydegaard et al 2024 p2).

Brydegaard et al (2024) proposed the solution of "frugal science", where scientific tools are developed that "emphasise affordability, accessibility and sustainability" (p2), and that "techniques popular in high-income countries should undergo a phase of 'innovation through simplification' before they are implemented more broadly" (p1).

Low-cost solutions include the use of digital colour cameras in smartphones (instead of specialist equipment), the repurposing of household goods, and the building of equipment as done over the years by enthusiastic

¹ Databases can be "noisy" (ie: include mislabelled entries or missing information) (Li, R et al 2024). Psychology Miscellany No. 206; September 2024; ISSN: 1754-2200; Kevin Brewer

hobbyists. The Internet provides much "DIY" (do-it-yourself) information along with open and shared information sites. "Whereas research groups in countries with high salary costs hesitate to spend on reverse engineering, researchers in other countries and enthusiasts in entomological societies are often ready to spend time instead of money" (Brydegaard et al 2024 p2).

This is particularly relevant to the "Global South"², where data are lacking. Sanchez Herrera et al (2024) argued for prioritising insect monitoring in this part of the world. However, this is not without challenges. "Among these, a primary obstacle is the extraordinary diversity of insect species in tropical ecosystems, presenting a formidable challenge for their comprehensive identification and monitoring. Compounding this, the scarcity of taxonomic expertise and resources in many tropical countries further impedes the identification and monitoring of insect species. The logistical complexities associated with working in remote and challenging-to-reach tropical ecosystems, such as forests in outlying mostly inaccessible areas, add a layer of difficulty to insect monitoring initiatives. Additionally, establishing and maintaining long-term, continuous monitoring programmes can be resource-intensive, demanding sustained funding commitments that are often unable to be met by local budgetary allocations. Lastly, the active involvement of local communities and stakeholders becomes paramount for garnering support for conservation endeavours and ensuring the enduring sustainability of monitoring programmes through conservation policy" (Sanchez Herrera et al 2024 p2).

Sheard et al (2024) considered the different technologies in relation to "citizen science" (defined by them as "community science or public participation in scientific research"; p2). They explained: "The number and diversity of citizen science projects and their significance have grown in the twenty-first century, thanks in large part to advancements in technology, including the widespread availability of the Internet and the proliferation of digital platforms. Today, technological equipment, such as mobile phones and digital cameras, along with their applications (eg:

² "The 'Global North' and 'Global South' are often compared, with distinctions typically revolving around differences in wealth, economic development, income distribution, and the level of democracy, as well as political and economic freedom, as measured by various indices. These terms do not refer to geographical position alone. The Global South broadly comprises Africa, Latin America and the Caribbean, Asia (excluding Israel, Japan and South Korea), and Oceania (excluding Australia and New Zealand). The Global North broadly comprises North America and Europe, Israel, Japan, South Korea, Australia and New Zealand" (Sanchez Herrera et al 2024 p10).

smartphone apps), are commonly used in citizen science projects, potentially shifting project design towards simpler, mass-participation approaches" (Sheard et al 2024 p2). On the negative side, the cost of technology, and the technical knowledge required for use may discourage participation by ordinary people.

Sheard et al (2024) outlined four impacts of technology on citizen science:

a) "A facilitator of current citizen science" - eg: a comparison of two projects on mosquitoes, sending physical samples by post versus submitting photographs via an app, found that the latter involved more younger, female, non-scientists.

b) "An enabler of new research opportunities" - eg: AI algorithms to check citizen science data quality.

c) "A transformer of science, policy, and public participation" - eg: encouraging everybody to monitor the natural world, not just "professionals".

d) "An inhibitor of participation, equity and scientific rigour" - Sheard et al (2024) commented that "many technologies are in a developmental stage and ceding authority to them prematurely may lead to an increase in inaccurate or biased data. It is easy to get excited by new technologies, but just because we can implement them in citizen science activities does not mean that we should. Traditional citizen science monitoring projects, especially for insects, are generally biased towards older generations and men, which may affect rates of uptake of new technologies. Current participants may disengage if the deployment of technology restricts the range of potential contributions that they can make, resulting in tasks that are either overly simplistic or excessively complex. Technology can create a barrier between people and nature, increasing people's distance from nature or the sense of commodification of nature, thus reducing nature connectedness" (p8).

The sharing of data via platforms on the Internet is a development primarily of the 21st century. The "Global Biodiversity Information Facility" (GBIF) is one such platform³. Researchers can contribute data through GBIF-endorsed publishing organisations. For example, "Xenocanto Foundation for Nature Sounds" publishes insect

³ <https://www.gbif.org/>.

acoustic occurrence records. Lack of standardisation of methods, and incomplete data are two key concerns (Svenningsen and Schigel 2024).

1.2. MOLECULAR METHODS

Meier et al (2024) outlined the data collection process: "The workflow starts with individually barcoding all specimens in a mass sample ('megabarcoding' [Chua et al 2023]), grouping them into molecular operational taxonomic units (MOTUs), revising the MOTU boundaries to obtain species limits, training artificial intelligence (AI) identification algorithms for common species, and using vouchers to collect trait and natural history data at scale. Once this pipeline has been applied to a few samples at each monitoring site, all subsequent monitoring becomes easier, because AI tools can be used to identify at least some of the common species. In addition, species lists and abundances become more meaningful, because the samples can be analysed at species-level and use trait data for functional analysis" (pp1-2).

But there are "dark taxa" (Hartop et al 2022) (ie: "high-diversity clades (greater than 1000 species) that are poorly known (fewer than 10% of species described)"; Meier et al 2024 p2). This is the risk of "taxon bias" (Meier et al 2024).

DNA-based molecular methods include "DNA barcoding" and "DNA metabarcoding". The former is best for individual species identification, while the latter is used for "community-level characterisation" (Iwaszkiewicz-Eggebrecht et al 2024) ⁴.

Iwaszkiewicz-Eggebrecht et al (2024) explained: "In metabarcoding, DNA is isolated directly from mixtures of different specimens and species (bulk samples) or the samples' fixative. DNA traces shed in the environment by organisms can also be extracted from environmental substrates (eg: soil, water, air), yielding so-called environmental (e)DNA metabarcoding. Subsequently, taxonomically informative DNA regions – barcodes – are mass-amplified and sequenced in parallel using high-

⁴ "Taxonomy, the science of classifying living organisms, has significantly evolved in recent years, influenced by major advancements in molecular biology and DNA sequencing technologies. This shift has led to a new era in which organisms are classified more on their genetic makeup than just on their physical traits. In this era, the merging of genomics with taxonomy has created the field of molecular taxonomy. This field aims to clarify the complex relationships among species, uncover unknown biodiversity, and improve our understanding of evolution" (Li, R et al 2024 p1).

throughput technologies (HTS). By bioinformatical analysis of sequences and by comparisons to reference databases, we may thus identify a broad spectrum of species present in those complex samples" (p2).

Iwaszkiewicz-Eggebrecht et al (2024) made three technical recommendations for standardising DNA barcoding:

i) The use of synthetic "spike-ins" - In the process of DNA sequencing a sample, spike-ins are deliberate additions of a known DNA sequence, which provide "a consistent reference point against which the abundance of a sample's DNA sequences can be gauged" (Iwaszkiewicz-Eggebrecht et al 2024 p2).

ii) The use of polymerase chain reaction (PCR) on multiple regions in the sample.

iii) Publication and transparency of data and methodology in a standardised fashion.

Li, Y et al (2024) produced distribution maps for 76 arthropod species in a forested landscape in the USA based on DNA coding of individuals caught in traps combined with remote imaging and identification by a deep neural net system.

Taking a slightly different approach, Lukasik and Kolasa (2024) focused on microbial symbionts of insects (ie: microbes that live in or on insects without causing harm to the host). Surveying these microbes (via their DNA) could help in understanding insect populations and responses to change as the host (insect)-microbe relationship is important.

1.3. COMPUTER VISION

The monitoring of nocturnal insects, for example, requires a light to attract insects, a digital camera for collecting images, and a computer system to store and process these images (and a power source for the equipment). These light-trapping camera systems have been particularly effective for detection of moths (Roy et al 2024).

Such systems allow insect detection, classification at different levels (eg: moth vs non-moth; species), and tracking (within the visual range of the camera(s)).

1.4. AUTONOMOUS ACOUSTIC MONITORING

Madhusudhana et al (2024) reported an example of passive acoustic monitoring (PAM) combined with machine-learning technology to recognise the calls of katydid species (over eighty different species) in a Panamanian rainforest. "Neotropical katydids produce complex species-specific calls, spanning mere milliseconds to seconds and spread across broad audible and ultrasonic frequencies. However, subtle differences in inter-pulse intervals or central frequencies are often the only discriminatory traits. These extremities, coupled with low source levels and susceptibility to masking by ambient noise, challenge species identification in PAM recordings" (Madhusudhana et al 2024 p1). The success of the machine-learning programme depended on the training data (ie: previous recordings of the insects).

The same researchers (Symes et al 2024) used the recordings to study calling by katydids and moonlight illumination level. Half of eight species increased their calling with greater moonlight and half reduced their calls. The researchers stated: "Response to moonlight varied by species, but the response was not easily predicted from existing natural history information. Sub-family, body size and colouration did not predict whether relationships were positive or negative" (Symes et al 2024 p6).

The recordings occurred between 6 pm and 6 am over three years (January 2019 to January 2022). The recording equipment was placed in the trees 24 m above the ground. This height was chosen, Symes et al (2024) explained, "because it is where moonlight levels would vary the most compared to the shaded understorey, making it more likely that we would detect changes in behaviour with light levels" (p2).

Symes et al commented on the PAM methodology: "Like other sampling approaches, acoustic sampling comes with a set of advantages, constraints and considerations for interpretation. The data collected in this study were collected in situ, providing a large sample size and capturing behaviour in the full complexity of the tropical forest. However, the species that we focused on for this study produced signals that occurred relatively frequently (appearing often in human-annotated test datasets), and for which precision was high with substantial recall. It is possible that species that call more rarely or are less well-recognised by automated approaches may show greater sensitivity to moonlight" (p6).

1.5. RADAR-BASED MONITORING OF INSECT MOVEMENTS

"Trillions of insects use the airspace for key activities of their life cycle, such as daily foraging movements and seasonal migrations. Their movements link otherwise separated habitats, communities and ecosystems, and have implications for various ecological processes such as nutrient transfer, pollen dispersal and gene flow, foodweb interactions and pathogen dynamics. Insect movements also provide services, eg: pollination, seed-dispersal, and pest control; and disservices, eg: pathogen dispersal and agricultural damage that are relevant to human agriculture, economy and health" (Bauer et al 2024 p1).

Bauer et al (2024) outlined four aspects of radar-based insect monitoring:

i) Quantification of abundance and biomass - eg: migration over southern UK estimated at 3.37 trillion insects, and a biomass of 3200 tons (Hu et al 2016).

ii) Show aerial movements that take place above eye level - eg: migration of noctuid moths between the UK and North Africa at 200 - 1000 m altitude (Chapman et al 2012).

iii) Show interaction of species of different sizes - eg: two hoverfly species in UK based on differences in body mass (Wotton et al 2019).

iv) Show movement in ecosystems - eg: mayflies in a single emergence event transport 3078 tons of biomass from aquatic systems to the air (Stepanian et al 2020).

Drake et al (2024) explained: "Radar designs are very diverse, each optimised for its specific application: the type of target, the information about it that is required, the volume of space to be covered, the rapidity with which the information is to be obtained, whether the radar is at a fixed location or on a moving platform, the budget available, etc" (p2). The first purpose-built "entomological radar" was created in 1968, and it was able to pick out larger insects, like grasshoppers and locusts (Drake et al 2024).

Drake et al (2024) presented a case study of an automatic and continuous vertical-beam entomological radar located at Hay, New South Wales, Australia. Overall insect numbers and biomass are key metrics collected, but individual species cannot be distinguished by the radar.

Gao et al (2024) reported data from the southern UK using vertical-looking insect radars (VLRs) to monitor high-altitude nocturnal insect migration. The variables influencing movement were surface-level temperature at time of take-off, air temperature, and moonlight illumination (particularly in relation to navigation and orientation).

Haest et al (2024) compared migratory insect movements between 50 and 500 metres above ground level across Europe in mid-2021 during four periods of the 24-hour day - daylight, crepuscular evening (evening twilight), night, and crepuscular morning (morning twilight). Most activity was recorded during crepuscular evening on average.

A network of seventeen VLRs between the Pyrenees (southwestern France) (in the south) and Helsinki (Finland) (in the north), and between Amsterdam (the Netherlands) (in the west) and Gotthard (Switzerland) (in the east) were used in the study.

1.6. REFERENCES

Bauer, S et al (2024) Monitoring aerial insect biodiversity: A radar perspective Philosophical Transactions of the Royal Society B 379, 20230113

Blackman, R.C et al (2024) Measuring the state of aquatic environments using eDNA - upscaling spatial resolution of biotic indices Philosophical Transactions of the Royal Society B 379, 20230121

Brydegaard, M et al (2024) Towards global insect biomonitoring with frugal methods Philosophical Transactions of the Royal Society B 379, 20230103

Chapman, J.W et al (2012) Seasonal migration to high latitudes results in major reproductive benefits in an insect Proceedings of the National Academy of Sciences, USA 109, 14924-14929

Chua, P.Y.S et al (2023) Future of DNA-based insect monitoring Trends in Genetics 39, 7, 531-544

Drake, V.A et al (2024) Monitoring insect numbers and biodiversity with a vertical-beam ontological radar Philosophical Transactions of the Royal Society B 379, 20230117

Gao, B et al (2024) Effects of nocturnal celestial illumination on high-flying migrant insects Philosophical Transactions of the Royal Society B 379, 20230115

Haest, B et al (2024) Continental-scale patterns in diel flight timing of high-altitude migratory insects Philosophical Transactions of the Royal Society B 379, 20230116

Hartop, E et al (2022) Towards large-scale integrative taxonomy (LIT): Resolving the data conundrum for dark taxa Systematic Biology 71, 6, 1404-1422

Hu, G et al (2016) Mass seasonal bioflows of high-flying insect migrants Science 354, 1584-1587

Iwaszkiewicz-Eggebrecht, E et al (2024) Three steps towards comparability and standardisation among molecular methods of characterising insect communities Philosophical Transactions of the Royal Society B 379, 20230118

Li, R et al (2024) PROTAX_GPU: A scalable probabilistic taxonomic classification system for DNA barcodes Philosophical Transactions of the Royal Society B 379, 20230124

Li, Y et al (2024) Combining environmental DNA and remote sensing for efficient, fine scale mapping of arthropod biodiversity Philosophical Transactions of the Royal Society B 379, 20230123

Lukasik, P & Kolasa, M.R (2024) With a little help from friends: The roles of microbial symbionts in insect populations and communities Philosophical Transactions of the Royal Society B 379, 20230122

Madhusudhana, S et al (2024) Extensive data engineering to the rescue: Building a multi-species katydid detector from unbalanced, atypical training datasets Philosophical Transactions of the Royal Society B 379, 20230444

Meier, R et al (2024) Towards holistic insect monitoring: Species discovery, description, identification and traits for all insects Philosophical Transactions of the Royal Society B 379, 20230120

Roy, D.B et al (2024) Towards a standardised framework for AI-assisted, image-based monitoring of nocturnal insects Philosophical Transactions of the Royal Society B 379, 20230108

Sanchez Herrera, M et al (2024) Systematic challenges and opportunities in insect monitoring: A Global South perspective Philosophical Transactions of the Royal Society B 379, 20230102

Sheard, J.K et al (2024) Emerging technologies in citizen science and potential for insect monitoring Philosophical Transactions of the Royal Society B 379, 20230106

Stepanian, P.M et al (2020) Deadlines in abundant aquatic insect, the burrowing mayfly, across major North American waterways Proceedings of the National Academy of Sciences, USA 117, 2987-2992

Svenningsen, C.S & Schigel, D (2024) Sharing insect data through GBIF: Novel monitoring methods, opportunities and standards Philosophical Transactions of the Royal Society B 379, 20230104

Symes, L.B et al (2024) Multi-year soundscape recordings and automated call detection reveals varied impact of moonlight on calling activity of neotropical forest katydids Philosophical Transactions of the Royal Society B 379, 20230110

van Klink, R et al (2024) Towards a toolkit for global insect biodiversity monitoring Philosophical Transactions of the Royal Society B 379, 20230101

Wotton, K.R et al (2019) Mass seasonal migrations of hoverflies provide extensive pollination and crop protection services Current Biology 29, 2167-2173.e5

2. NATURE-POSITIVE ECONOMICS

- 2.1. Introduction
- 2.2. Companies
- 2.3. Nature capital accounting
- 2.4. Natural capital approach
- 2.5. Ecosystem resilience
- 2.6. Children
- 2.7. References

2.1. INTRODUCTION

Economic development and decisions impact nature, usually negatively, and in recent years “nature-positive economies and businesses” have emerged as a response. It is described as “bringing nature into decision-making” (Malhi and Daily 2024).

“How exactly bringing nature into decision-making can be achieved across sectors and at scale remains a major challenge. However, there has been substantial progress in developing successful demonstrations of integrating nature into decision-making in a variety of sectors and regions, and an increasing number of approaches to the challenge of scale” (Malhi and Daily 2024 p1). Malhi and Daily (2024) edited a series of papers on this subject.

2.2. COMPANIES

Concentrating on transnational companies, Bebbington et al (2024) outlined three issues for incorporating nature into their decision-making processes:

i) The ability to trace the linking of company actions to outcomes in particular settings – This is the transparency of company decision-making, which thus “underpins the possibility of accountability” (Bebbington et al 2024 p3).

Example: “Nippon Sulsan Kaisha Ltd” (fisheries) provides traceability data on volume and species harvested from the ocean.

ii) The development of organisational processes that translate strategic intent into on-the-ground behaviour.

Example: “LaFargeHolcim Spain” (aggregates and
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cement) “developed a monitoring system to evaluate restoration processes by studying nature assets/resources based on field samples by cataloguing flora, identifying vegetation, establishing the distribution of birds and insects, assessing the status of biodiversity in the quarry and developing strategies and action plans” (Bebbington et al 2024 p6).

iii) Financial stakeholders and organisations that incentivise bringing nature into company decision-making.

Example: “ASN Bank” specialises in sustainability banking products.

2.3. NATURE CAPITAL ACCOUNTING

Many industries are dependent on nature (an estimated US\$44 trillion globally of economic value; Ingram et al 2024), and those “that are vulnerable to nature loss may need to proactively manage these nature-related risks to avoid negative business implications and may decide to positively impact nature in ways that generate new business opportunities. However, the majority of businesses, investors and lenders are not yet aware of, nor measuring or monitoring, their nature-related dependencies and impacts, and how these may lead to financial risks and opportunities across supply chains, operations, loan books or investment portfolios” (Ingram et al 2024 pp1-2). For example, only 1% of 400 large companies studied knew their dependency on nature, and 5% had measured their impact on nature (Ingram et al 2024).

Ingram et al (2024) suggested that business leaders lacked relevant information and this explained their behaviour. “Nature capital accounting” (NCA) is an approach to collect and organise relevant data. NCA refers specifically to “the use of a structured, rules-based framework to systematically measure and report on stocks of natural capital and flows of ecosystem services” (Ingram et al 2024 p3).

A company example is “Forico”, a forestry-based firm in Tasmania, Australia (Ingram et al 2024). “Forico focused on measuring and valuing provisioning services (wood fibre from sustainable plantations to be converted to sawlogs and wood fibre products) and regulating services (carbon sequestration from plantation and natural forests, water usage and impact on both high and low downstream flows, control of erosion and sediment

retention by riparian areas and habitat areas for supporting biodiversity) and impacts from carbon emissions from supply chains..." (Ingram et al 2024 p5).

2.4. NATURAL CAPITAL APPROACH

"Nature recovery" (eg: tree-planting; "rewilding") is crucial to reverse biodiversity loss. The "natural capital approach" is a possible way to address this. "The natural capital approach is a way of thinking about the natural environment in economic terms. In essence, nature is regarded as a source of myriad ecosystem services (for example, carbon sequestration, flood mitigation and pollination) that deliver benefits to humans in society and, in that regard, are no different from the services provided by private companies and public agencies. Moreover, the natural capital approach advocates the use of non-market valuation to allow the benefits delivered by ecosystem services to be quantified in monetary terms" (Day et al 2024 p2).

The natural capital approach, however, faces a number of challenges, including that it is not easy to quantify the costs and benefits of the environmental projects (Day et al 2024).

Day et al (2024) used the example of a UK policy to incentivise landowners to establish natural habitats on farmland as a means of nature recovery. Their modelling found that offering landowners flat-rate payments per hectare was inefficient, while payment based on the value of the ecosystem services delivered was better. Inefficient means a poor return for public money.

2.5. ECOSYSTEM RESILIENCE

The resilience of social-ecological systems (SESs) (Holling et al 1973) is a concept of growing importance. This involves strategies to ensure sustainability.

"Berkes and Jolly [2001] associate 'coping' with short-term, often reactive, strategies and activities, while 'adaptation' entails strategies over the longer term. These authors stress that using coping strategies over the long-term can actually be maladaptive in the context of climate change. Many short-term adaptation strategies, which are in fact coping strategies, do not consider the SES but rather the social components, neglecting to assess the adaptive capacity of the ecological system to sustain changes, thus leading to its

possible collapse" (Vasseur and Andrade 2024 p2). "Transformative adaptation", defined as "changes that fundamentally alter the entire system's ecological and/or social properties and functions" (Fedele 2019 quoted in Vasseur and Andrade 2024), is the ideal.

The "International Union for Conservation of Nature" (IUCN) collects data on biodiversity loss, environmental degradation, and SES collapse. Their "Red List of Ecosystems" (RLE) has five criteria to assess ecosystem collapse: "(A) reductions in geographical distribution; (B) restricted ecosystem distribution; (C) rates of environmental degradation (of natural and anthropogenic nature); (D) rates of decline in biotic processes and species interactions; and (E) quantitative estimates of ecosystem collapse risk" (Vasseur and Andrade 2024 p2). Around 4000 ecosystem types have been assessed, according to Vasseur and Andrade (2024), and in terms of collapse in the next fifty years, half were labelled "critical", 20% "endangered" and 10% as "vulnerable".

For example, the core inland temperate rainforest of British Columbia, Canada, may collapse within twenty years due to intensive logging since the 1970s (Vasseur and Andrade 2024).

Vasseur and Andrade (2024) concentrated on Colombia, where there are 81 terrestrial ecosystem types, of which fourteen were classified as "endangered", while Andean paramos were categorised as "critically endangered". The transformation of the latter into agricultural land, and water consumption in cities are key factors here. "Increasing average annual temperatures and less predictable rainfall patterns, along with land-use transformations, are affecting the integrity of those ecosystems and increasing the risk of collapse. The decline in the capacity of ecosystems to provide services, as well as habitat for key species, in high mountain ecosystems and moorlands (paramos) further threatens their resilience. The high vulnerability of high mountain ecosystems to climate change impacts has led the Colombian government to develop policies and plans to not only reduce the impacts from climate change but also adapt and restore these ecosystems to improve resilience..." (Vasseur and Andrade 2024 p4).

2.6. CHILDREN

Hazell and Clarke (2024) began with this observation: "As many societies become more urbanised and digitised, with a higher proportion of people living in

towns and cities than in rural environments and spending more time on electronic devices, interactions with the natural world have declined. This has raised concern about possible feedback loops whereby less time spent in nature leads to lower concern for its protection and so higher nature loss, which in turn reduces opportunities for connecting with nature" (p1).

Thus, the importance of children spending time in nature, which studies confirmed as positively associated with future pro-environmental attitudes (eg: Gill 2014). Note that the studies are correlational, while how the time is spent in nature is important (eg: "playful engagement"; Gill 2014).

Hazell and Clarke (2024) outlined four categories of benefits of children's engagement with nature from the literature:

i) Physical health - eg: exercise and fitness; diverse gut microbiome.

ii) Mental health - eg: reduced stress and depression; "constructive hope" (Chawla 2020) in relation to future climate change (ie: "a sense of agency in what can otherwise feel like an overwhelmingly bleak environmental crisis"; Hazell and Clarke 2024 p2).

iii) Psychological development - eg: social and emotional development; skills learning.

iv) Educational outcomes - eg: improvements (though the studies here are not high methodological quality; Hazell and Clarke 2024).

Despite these benefits, surveys in England by "Nature England", for example, found that engagement with nature among children is actually falling in recent years, especially among lower socio-economic groups (Hazell and Clarke 2024).

2.7. REFERENCES

Bebbington, I et al (2024) Shaping nature outcomes in corporate settings Philosophical Transactions of the Royal Society B 379, 20220325

Berkes, F & Jolly, D (2001) Adapting to climate change: Social-ecological resilience in a Canadian western Arctic community Conservation Ecology 5, 2, article 18

Chawla, L (2020) Childhood nature connection and constructive Psychology Miscellany No. 206; September 2024; ISSN: 1754-2200; Kevin Brewer

hope: A review of research on connecting with nature and coping with environmental loss People and Nature 2, 3, 619-642

Day, B et al (2024) Natural capital approaches for the optimal design of policies for nature recovery Philosophical Transactions of the Royal Society B 379, 20220327

Fedele, G et al (2019) Nature-Based Transformative Adaptation: A Practical Handbook Arlington, VA: Conservation International

Gill, T (2014) The benefits of children's engagement with nature: A systematic literature review Children, Youth and Environments 24, 2, 10-34

Hazell, J & Clarke, E (2024) Nurturing future leaders for nature: The example of the UK's National Education Nature Park Philosophical Transactions of the Royal Society B 379, 20220330

Holling, C.S (1973) Resilience and stability of ecological systems Annual Review of Ecology, Evolution and Systematics 4, 1-23

Ingram, J.C et al (2024) Leveraging natural capital accounting to support businesses with nature-related risk assessments and disclosures Philosophical Transactions of the Royal Society B 379, 20220328

Malhi, Y & Daily, G.C (2024) Bringing nature into decision-making Philosophical Transactions of the Royal Society B 379, 20220313

Vasseur, L & Andrade, A (2024) Using the Red List of Ecosystems and the Nature-based Solutions Global Standard as an integrated process for climate change adaptation in the Andean high mountains Philosophical Transactions of the Royal Society B 379, 20220326

3. MANAGING ECOLOGICAL NOVELTY

- 3.1. Introduction
- 3.2. Functioning stewardship of emerging novel ecosystems
- 3.3. Enlisting new technologies to study ecosystem dynamics
- 3.4. Biodiversity projections under global change
- 3.5. Understanding novel ecosystems
- 3.6. Appendix 3A - Phenological mismatch
- 3.7. Appendix 3B - Invasive alien species
- 3.8. References

3.1. INTRODUCTION

Svenning et al (2024) outlined four issues where science could help in future management of biodiversity and sustainable stewardship of national resources:

i) "Functioning and stewardship of emerging novel ecosystems" - "Rising environmental and ecological novelty poses strong challenges for responding to current dynamics in ecosystems and biodiversity as well as for forecasting their future dynamics" (Svenning et al 2024 p2) (appendix 3A). This includes modelling climate change, and understanding the changes as well as using information from past climate events.

ii) "Biodiversity projections under global change" - "Given the ongoing and uncertain nature of expected changes in the Anthropocene era, managing ecological systems requires us to project changes in biodiversity under alternative scenarios, consider the rates of ecological change, and take a long-term perspective" (Svenning et al 2024 p4).

iii) "Enlisting new technologies to study ecosystem dynamics under rising biosphere novelty".

iv) "Integrating people into understanding, forecasting, and management of the dynamics of novel ecosystems".

In advocating for "effective ecosystem stewardship at local to planetary scales in the Anthropocene", Svenning et al (2024) admitted that "it is improbable that the pathway towards such stewardship will be free of conflict as finding the optimal solutions for all

stakeholders probably involves friction, compromise and costs. A biodiverse future is unlikely to be free of such complexities" (p7).

3.2. FUNCTIONING STEWARDSHIP OF EMERGING NOVEL ECOSYSTEMS

Enquist et al (2024) gave the example of the loss of American chestnut trees in the USA in the 20th century due to a fungal pathogen mainly. This tree was the dominant species in deciduous forests, and so its loss impacted whole ecosystems (eg: nuts as food for wildlife; use of its wood in human building). Enquist et al (2024) outlined the "pressing system" of whether such disturbances lead to ecological reorganisations that align with general patterns of recovery and function or diverge into idiosyncratic and diverse pathways that substantially shift ecosystem functioning. If the former holds, it suggests the potential for a predictive theory of resilience. The latter would indicate that our future is much more idiosyncratic and uncertain in the face of increasing global change though we still might be able to identify tipping points, points of no return, and management strategies as we approach such an idiosyncratic set of dynamics" (p2).

"Compensatory dynamics" are important for resilience (ie: changes in the population of one species is offset by changes in the population of another species). Also known as colonisation-extinction dynamics, if as one species declines, the another increases to take its place. "The ability of ecosystems to exhibit compensatory biodiversity responses is likely to depend on the overall number and magnitude of perturbations and the environmental setting relative to the traits and life-history strategies present. Environmental perturbations can be either buffered or amplified by biodiversity depending on characteristics of local ecosystems, such as the magnitude of the changes and their effects on dominant species. Perturbations are likely to have greater impacts when the dominant species are near the limits of their distributions and already under stress" (Enquist et al 2024 p14).

One response to climate change by animals is a shift in geographical range ⁵. "Range shifting can lead to massive redistributions of entire species communities with profound effects on ecosystem functioning and human

⁵ Plant species also move in response to climate change to higher elevations or latitudes, depending on their seed distribution, and soil factors in the new area (Ni and Vellend 2024).

well-being, and even feedback loops to the climate system itself. Such range shifts have been observed for different taxa and along latitude, altitude and ocean depth. Empirical results suggest that terrestrial species are lagging behind the shifting climate more than marine species. The pace and magnitude of species range shifts is determined by extrinsic factors such as velocity of climate change, and by a number of ecological processes such as dispersal, demography, species interactions and evolution that mediate the species ability to track shifts in climatically suitable areas" (Zurrell et al 2024 pp1-2).

Concentrating on birds in Europe and North America, Zurrell et al (2024) analysed bird survey data from the 1980s to the 2010s. European birds had shifted their ranges north and north-eastwards (on average by 70 km) during that period, while US birds had shifted westwards (on average by 125 km).

3.3. ENLISTING NEW TECHNOLOGIES TO STUDY ECOSYSTEM DYNAMICS

Predicting the future requires data (from the past and the present). Alsos et al (2024) observed: "Ecosystem response to climate change is complex. In order to forecast ecosystem dynamics, we need high-quality data on changes in past species abundance that can inform process-based models. Sedimentary ancient DNA (sedaDNA) has revolutionised our ability to document past ecosystems' dynamics. It provides time series of increased taxonomic resolution compared to micro-fossils (pollen, spores), and can often give species-level information, especially for past vascular plant and mammal abundances" (p1).

Ancient DNA can be found in different substrates, including ice cores, permafrosts, soils, and archaeological artefacts. SedaDNA in lake sediments can be particularly useful (Alsos et al 2024).

"Invasive alien species (IAS) (appendix 3B) are a major driver of global biodiversity loss. The pressing need to understand and manage this ubiquitous and ongoing environmental threat has long been recognised by the international community and is reflected in a number of policy targets for IAS" (Henriksen et al 2024 p2). Data, however, are needed to work towards such targets. But there are gaps in the knowledge about, for example, "those species causing the impact, the variety of ways in

which they bring about an impact (their impact mechanisms, eg: predation or herbivory), or on the types of impact they inflict (eg: ecosystem effects or habitat degradation). Individual IAS commonly have multiple mechanisms and types of impact, and particular areas are increasingly exposed to impacts from multiple species. It is also crucial that the location and timing of impact events are comprehensively recorded" (Henriksen et al 2024 p2).

Henriksen et al (2024) argued for the importance of open data in distinguishing between "realised impact" and "potential impact". Impact is defined as "the presence of one or more IAS known to negatively affect the environment (biodiversity and ecosystems) in any location globally" (Henriksen et al 2024 p2). IAS become realised when their impact has been assessed in a particular ecosystem, while potential impact is based on the "assumption that alien species with a history of impact elsewhere are likely to become impactful if introduced in other regions" (Henriksen et al 2024 p2).

3.4. BIODIVERSITY PROJECTIONS UNDER GLOBAL CHANGE

Allen et al (2024) noted that most projections of the impacts of climate change tend towards the year 2100, while longer term projections may be better. These researchers modelled three different CO₂ emission scenarios up to the year 2500. In summary, under a "business-as-usual" scenario (ie: the current levels of CO₂ emissions) "up to 40% of terrestrial area is expected to be suited to a different biome ["plant communities"] by 2500. Cold-adapted biomes, particularly boreal forest and dry tundra, are predicted to experience the greatest losses of suitable area" (Allen et al 2024 p1). The other two scenarios were an unmitigated increase in emissions ("worst scenario"), and medium mitigation (reduction) ("best scenario").

Allen et al (2024) commented: "As biomes change, the stocks and flows of ecosystem services they provide will come into question. These include services fundamental to human survival and habitability, such as food and water. They also include protecting human populations against the increasing frequency and severity of various weather events; for example, tropical mangrove forests reduce the severity of storm surges. Such events might otherwise require adaptations that may face significant social, technological, and physiological challenges or limits, or could even force human relocations. However, as some

regions become less habitable, others may open, and society must develop plausible, desirable and equitable strategies to share landscapes, access ecosystem services, and avoid conflict while learning to live with these changes" (p8).

Systematic conservation planning (SCP) is a means to "help bridge the gap between politically driven area targets and the stated ambition of conserving biodiversity by identifying a set of areas requiring conservation management that satisfy a series of conservation objectives (eg: for species, ecosystems or ecological processes). It leverages tools from decision theory to identify optimal management strategies in the face of uncertainty and multiple, often competing, objectives" (Jung et al 2024 p2).

Jung et al (2024) reviewed the studies (n = 266) of applied SCP in Europe. "Most studies aimed to either identify priority areas (40.3%) or investigate representation gaps and sufficiency (30%) of existing protection measures" (Jung et al 2024 p3).

3.5. UNDERSTANDING NOVEL ECOSYSTEMS

Hussain and Baumann (2024) highlighted how "the biodiversity crisis has deep-historical roots" (p2). Put simply, humans have always had an impact on ecosystems. This fits with the idea of "niche construction", which suggests that the active involvement in ecosystems rather than simply adapting to them. "Humans have been described as the 'ultimate niche constructors' [Smith 2007], continuous 'niche modifiers' [Low et al 2019], planetary 'geoengineers' [Bohle 2017] and, coupled with the distinct human capacity for cumulative culture, these proclivities likely contribute to a uniquely potent feedback dynamic between human adaptations and the outlines of the human niche" (Hussain and Baumann 2024 p2).

An early example in human evolutionary history is the use of fire to clear areas. "Although human landscape burning, introducing novel disturbance regimes, seems to have reduced plant diversity and promoted fire-resistant species in the system, it also activated alluvial erosion and created open spaces of grassland, in turn framing new niches for other animals and the attendant distinct foraging opportunities for humans" (Hussain and Baumann 2024 p3).

The concept of the “palaeo-synanthropic niche”⁶ has been used to describe the impact of humans around 30 000 years ago (Hussain and Baumann 2024). “Synanthropy refers to behavioural innovations and adaptations in non-human animals as a result of human neighbourhoods and is attributed to animals who take advantage of such human presence and thrive in human-influenced environments. Palaeo-synanthropy has been invoked to trace these human impacts on animal ecologies in the context of mobile hunter-gatherers of the Pleistocene without the kinds of infrastructure projects characteristic of settled human societies in the Holocene, which provide the overriding adaptive context for many animal synanthropes in the present” (Hussain and Baumann 2024 p4). For example, common ravens appear to have changed their diet in this period, “consuming primarily large herbivores such as bison and horse (but not reindeer) and especially mammoths, animals also preferentially targeted by their human neighbours” (Hussain and Baumann 2024 p4).

Hussain and Baumann (2024) did not want to give the impression of humans as negative only in their impact on ecosystems. They stated that “it is important to pay more attention to the nuances and complexities of past human involvements in the biosphere. This entails working towards a more balanced view of past human-biodiversity relations, not only focusing on allegedly negative biodiversity impacts but also making space, both empirically and conceptually, for the possible positive biodiversity effects of human behaviour. At the same time, however, we should be wary not to frame this problem as an either-or question as past ecologies can be recognised as complex systems with specific trade-offs and non-linear dynamics. Biodiversity-promoting effects in one part of the system may so incur negative biodiversity consequences in another part of the system. It is therefore imperative to examine the overall patterns and configurations of biodiversity as they emerge within specific human-environment systems” (p2).

3.6. APPENDIX 3A – PHENOLOGICAL MISMATCH

The timing of different events is key in ecosystems as in the case of the pied flycatcher, caterpillars and oak trees. Caterpillars hatch in spring to coincide with

⁶ Hussain and Baumann (2024) defined “palaeo-synanthropy” thus: “Novel animal behaviour taking advantage of human ecosystem services and the specific affordances (behavioural possibilities) created by human neighbourhoods before the dawn of agricultural life (eg: high-caloric, dense and/or easy-to-forage food sources, anthropogenic predator exclusion, nest-building options)” (p11).

the appearance of oak foliage (their food). Meanwhile, flycatchers produce large broods that can be fed on the time-limited caterpillar abundance. Temperature triggers the oak, caterpillars, and birds. "In some parts of Europe, birds are hatching too late to catch peak caterpillar, reducing the chicks' chances of survival" (Lawton 2022 p44). This is known as "phenological mismatch"⁷.

Changes in temperature through climate warming will influence such a balance. For example, using 19th century records, it was estimated that plants were flowering eight days earlier on average in the spring in Boston, USA, today than 120 years ago (Primack et al 2004).

Other triggers to animal behaviours are also changing, like rainfall patterns, and this and temperature interact with the trigger of day length (Lawton 2022).

There are cases (eg: Bauer et al 2010), however, of birds responding to the mismatch over a few generations, probably through adaptation (Lawton 2022).

3.7. APPENDIX 3B - INVASIVE ALIEN SPECIES

McGeoch et al (2024) offered a pragmatic approach: "A 'nature-positive future' (NPF) is an aspirational vision of nature in the future, painted for the purpose of setting trajectories for how we might achieve outcomes that are positive for nature and society. In practical terms, the NPF vision accepts that biodiversity losses are inevitable. However, they should be more than fully compensated so that nature is retained or restored in net terms. The key phrase is 'net terms', which implies a balance between achieving human development and preventing biodiversity losses that are not ecologically replaceable or socially acceptable. The shift in thinking and emphasis that NPF with biological invasions (NPF-BI) brings is an acceptance that the living world is already irreversibly changed, in most cases owing to long trajectories of human land use and the movement of plants and animals across biogeographical barriers" (p1).

Put simply, rather than trying to stop IAS, because all ecosystems are already impacted, the task is to learn to live with IAS. The "resist-accept-direct" (RAD) framework is a way to manage this situation (McGeoch et al 2024):

⁷ "Phenology" is a term for the study of recurring life phases, coined in the 19th century by Charles Morren (Lawton 2022).

R = "the conventional approach to prevent, eradicate and control negative changes following biological invasions for the purpose of maximising biodiversity value" (McGeoch et al 2024 p7).

D = "accommodating persistent alien species that have a neutral or desirable effect on the ecosystem or its value, including interventions to 'direct' mixed species communities towards more desirable, resilient and biodiverse states" (McGeoch et al 2024 p7).

A = "interventions that 'accept' the ecosystem transformation brought about by multispecies invasion, while simultaneously adapting to reduce the negative impacts of the transformed community on biodiversity and people" (McGeoch et al 2024 p7).

McGeoch et al (2024) concluded: "Achieving a nature-positive future given the realities of biological invasions rests on the key message from invasion biology that (i) landscapes and local communities will be host to multiple, persistent introduced species, (ii) that populations of these species will vary from place to place and over time, in the degree to which they impact natural and societal values, and (iii) that effective environmental stewardship necessarily involves integrated management of invasions by manipulating ecological processes alongside multiple, interacting drivers of change" (p8).

3.8. REFERENCES

Allen, B.J et al (2024) Projected future climatic forcing on the global distribution of vegetation types Philosophical Transactions of the Royal Society B 379, 20230008

Alsos, I.G et al (2024) Using ancient sedimentary DNA to forecast ecosystem trajectories under climate change Philosophical Transactions of the Royal Society B 379, 20230017

Bauer, Z et al (2010) Changing climate and the phenological response to great tit and collared pied flycatcher populations in floodplain forest ecosystems in Central Europe International Journal of Biometeorology 54, 99-111

Bohle, M (2017) Ideal-type narratives for engineering a human niche Geosciences 7, 1, article 18

Enquist, B.J et al (2024) Scaling approaches and macro-ecology provide a foundation for assessing ecological resilience in the Anthropocene Philosophical Transactions of the Royal Society B 379,

Psychology Miscellany No. 206; September 2024; ISSN: 1754-2200; Kevin Brewer

20230010

Hussain, S.T & Baumann, C (2024) The human side of biodiversity: Co-evolution of the human niche, palaeo-synanthropy and ecosystem complexity in the deep human past Philosophical Transactions of the Royal Society B 379, 20230021

Henriksen, M.V et al (2024) Global indicators of the environmental impacts of invasive alien species and their information adequacy Philosophical Transactions of the Royal Society B 379, 20230323

Jung, M et al (2024) An assessment of the state of conservation planning in Europe Philosophical Transactions of the Royal Society B 379, 20230015

Lawton, G (2022) Missing the beat New Scientist 25th June, 42-45

Low, F.M et al (2019) Niche modification, human cultural evolution and the anthropocene Trends in Ecology and Evolution 34, 883-885

McGeoch, M.A et al (2024) A nature-positive future with biological invasions: Theory, decision support and research needs Philosophical Transactions of the Royal Society B 379, 20230014

Ni, M & Vellend, M (2024) Soil properties constrain forest understory plant distributions along an elevation gradient Philosophical Transactions of the Royal Society B 379, 20230373

Primack, D et al (2004) Herbarium specimens demonstrate earlier flowering times in response to warming in Boston American Journal of Botany 91, 8, 1260-1264

Smith, B.D (2007) Niche construction and behavioural context of plant and animal domestication Evolutionary Anthropology: Issues, News and Reviews 16, 5, 188-199

Svenning, J-C et al (2024) Navigating ecological novelty towards planetary stewardship: Challenges and opportunities in biodiversity dynamics a transforming biosphere Philosophical Transactions of the Royal Society B 379, 20230008

Zurrell, D et al (2024) Range and climate niche shifts in European and North American breeding birds Philosophical Transactions of the Royal Society B 379, 20230013

4. DIVERSITY-DEPENDENT DISPERSAL

- 4.1. Overview
- 4.2. Factors
- 4.3. References

4.1. OVERVIEW

The population of a species is influenced by the birth and death rates, and dispersal (ie: emigration and immigration). Dispersal is defined as "the process by which an organism reproduces away from where it is born" (Fronhofer et al 2024 p2). It is "therefore different from seasonal migration or foraging, which do not lead to gene flow. Dispersal can be quantified in multiple ways, such as through dispersal distance, dispersal frequency in long-lived mobile organisms, the proportion of dispersed offspring, or even the proportion of immigrants among a population's reproductive cohort" (Fronhofer et al 2024 p2).

Dispersal is mainly studied at the individual or population level, but also there is the ecosystem (or meta-community) level, which takes account of the interaction between species. This can be called "diversity-dependent dispersal", and Bonte et al (2024) introduced three key issues:

i) The mechanisms underlying diversity-dependent dispersal.

ii) The impact of dispersal on the ecosystem (or meta-community or meta-food web).

iii) The application of insights from diversity-dependent dispersal.

Studying dispersal at a single-species level is not the same as the "complex" world of ecosystem-level. In the latter case, there will be horizontal and vertical interactions. The former refers to competitive interactions between species that are not prey or predator, while vertical interactions include prey-predator, and host-parasite (Fronhofer et al 2024). In ecosystems there may be "co-dispersal", where "two interacting partners disperse together" (eg: rats (host) and fleas (parasite) (Fronhofer et al 2024).

Dispersal can evolve in environments that vary

greatly across time (eg: seasonal gluts and famines), with high competition and population density, or inbreeding risk, for instance. However: "Dispersal need not be a fixed trait, but can respond plastically to internal and external cues" (Fronhofer et al 2024 p3).

Intermediate dispersal over evolutionary time leads to more new species (speciation rate) and greater biodiversity, while very low and very high dispersal can produce low biodiversity, according to a hump-shaped relationship between species diversity and dispersal. "Specifically, low dispersal can lead to low colonisation and geographically restricted species, while high dispersal can lead to high species-wide genetic homogenisation via gene flow" (Hagen et al 2024 p2).

In the case of seed dispersal, this can occur via animals eating the fruit of a plant. In a study of birds at six sites in North and South America, and the Caribbean, Carlo et al (2024) found that "birds tended to select fruits of plant species that were proportionally rare in their communities, or that became rare following phenological fluctuations, while they mostly under-utilised abundant fruit resources" (p1). This showed how plant diversity was maintained in an ecosystem.

4.2. FACTORS

The theoretical position is that "individuals should leave habitats with adverse conditions and search for better ones, as long as the energy, time, and risk barriers to dispersal (ie: dispersal costs) do not offset the benefit" (Bestion et al 2024).

So, "detrimental interactors" (consumers/predators, parasites or competitors) increase the propensity to disperse, while this is lessened by "beneficial interactors" like resources, hosts and mutualists. This is "context-dependent dispersal" (Bestion et al 2024).

Bestion et al's (2024) meta-analysis of 118 studies, however, found only partial support for these predictions. There were several variables which influenced dispersal (eg: dispersal phase ⁸; species'

⁸ Bestion et al (2024) stated: "We expected predators, parasites, and competitors to increase the dispersal of the focal species to avoid the potential negative consequences on fitness, and this was the case for emigration and full dispersal. However, transience is a particularly vulnerable stage where the risk of predation may be heightened; thus, a decrease in dispersal distance for instance may be expected. Similarly, hosts may increase their dispersal behaviour to escape an infested habitat, and parasites themselves can manipulate their hosts' dispersal to increase contact rate and the transmission of parasites. However, by diverting their hosts' resources, parasites can constrain their ability to move". Psychology Miscellany No. 206; September 2024; ISSN: 1754-2200; Kevin Brewer

interaction strength; ecosystem composition and complexity). Methodological issues of the studies also influenced the findings (eg: duration of the study; experiment versus observation).

Bestion et al (2024) summed up thus: "Dispersal is indeed a multi-causal process, responding to multiple internal and external cues that are themselves intertwined".

Competition over resources from other species can influence dispersal (Hagen et al 2024). The decision to disperse from a habitat may also be linked to prey tracking and/or predator avoidance. The densities of both of these are important. Congregation behaviours are further relevant, particularly for animals that migrate in groups, and "the cues used to synchronise group movements may include those from other species" (Lawton et al 2024 p7).

Factors in dispersal at a single-species level include kin competition, risk of inbreeding, costs of dispersal, life-cycle stage, and variations in the environment over time (Fronhofer et al 2024).

4.3. REFERENCES

Bestion, E et al (2024) Species interactions affect dispersal behaviour: A meta-analysis Philosophical Transactions of the Royal Society B 379, 20230127

Bonte, D et al (2024) Species interactions and eco-evolutionary dynamics of dispersal: The diversity dependence of dispersal Philosophical Transactions of the Royal Society B 379, 20230125

Carlo, T.A et al (2024) Negative density dependence characterises mutualistic interactions between birds and fruiting plants across latitudes Philosophical Transactions of the Royal Society B 379, 20230128

Fronhofer, E.A et al (2024) Evolutionary ecology of dispersal in biodiverse spatially structured systems: What is old and what is new? Philosophical Transactions of the Royal Society B 379, 20230142

Hagen, O et al (2024) The macro-eco-evolutionary interplay between dispersal, competition and landscape structure in generating biodiversity Philosophical Transactions of the Royal Society B 379, 20230140

Lawton, P et al (2024) Interspecific dispersal constraints suppress pattern formation in metacommunities Philosophical Transactions of the Royal Society B 379, 20230136

5. LONG-TERM POTENTIATION FIFTY YEARS LATER

- 5.1. Introduction
- 5.2. Hippocampus and learning and memory
- 5.3. Schema
- 5.4. References

5.1. INTRODUCTION

Long-term potentiation (LTP) is the enhancement of synaptic efficacy between cells due to activity, and Bliss and Lemo (1973) and Bliss and Gardner-Medwin (1973) published the key studies (Abraham et al 2024).

Put simply, LTP is involved in learning and memory. The opposite is long-term depression (LTD) (Abraham et al 2024).

The concept that cells change in response to use had been suggested previously - eg: Hebb (1949) stated: "When an axon of cell A is near enough to excite a cell B, and repeatedly and persistently takes part in firing it, some growth process or metabolic changes takes place in one or both cells such that A's efficiency in firing B is increased" (quoted in Abraham et al 2024). There is also a similarity to "engram" (physical and/or chemical changes with a specific memory), a term coined by Richard Semon in 1904 (Fayed et al 2024).

Both LTP and LTD show the plasticity of the brain, for instance, at a cellular level, and Abraham et al (2024) observed that "the study of LTP and associated plasticity phenomena remains a cornerstone of contemporary neuroscience research" (p3) today ⁹.

5.2. HIPPOCAMPUS AND LEARNING AND MEMORY

Hagena and Manahan-Vaughan (2024) began: "There is broad consensus that persistent, use-driven and experience-dependent modifications of synaptic strength form the cellular basis of long-term information storage and memory updating by the hippocampus" (p1). Synaptic plasticity as seen in LTP (and LTD) is well-studied in relation to learning and memory.

In vitro studies of cells are common, and LTP is

⁹ Sleep and quiet wakefulness are "periods of offline reactivation", which are seen as important in consolidation of stored information. "Brain activity during sleep and quiet wakefulness is referred to as the 'idling brain'. Idling brain activity is believed to play a pivotal role in abstracting essential information, comprehending underlying rules, generating creative ideas, and fostering insightful thoughts" (Fayed et al 2024 p1).

defined here as an increase in synaptic strength lasting for one hour at least. This is sometimes called "short-term potentiation" to distinguish it from synaptic changes lasting hours, days and months in in vivo studies (often with rodents) (Hagena and Manahan-Vaughan 2024).

Rodent studies of LTP associative memory include teaching an association and then inhibiting LTP in the hippocampus (which leads to forgetting), recording of electrical activity of cells before and after learning an association, or the creation of transgenic animals that cannot produce LTP. A common association learning is a mild electric shock at a certain place in the cage ("fear memory") (Hagena and Manahan-Vaughan 2024).

Animal studies of the hippocampus have distinguished "multiple forms" of persistent LTP and LTD, varying in the sub-regions of the hippocampus, and the molecules involved, for instance (Hagena and Manahan-Vaughan 2024).

Hagena and Manahan-Vaughan (2024) commented: "It would be remiss to fail to mention that synaptic plasticity is not the only physiological process that modulates synaptic strength in the hippocampus. In addition to LTP and LTD, two other cellular phenomena have been described in the dorsal hippocampus that either indirectly or directly instigate changes in synaptic efficacy, namely meta-plasticity [Abrahams 2008] and slow-onset potentiation [Bashir et al 1993]" (p6).

Hippocampal activity is also state-dependent. For example, novelty or saliency change the activity of the cells and their synapses (Hagena and Manahan-Vaughan 2024).

In summary, based on rodent studies, Hagena and Manahan-Vaughan (2024) noted that "both LTP and LTD fulfil specific and complementary roles in the acquisition and retention of spatial memory. LTP is likely to be responsible for the generation of a record of spatial experience, which may serve as an associative schema that can be re-used to expedite or facilitate subsequent learning. In contrast, LTD may enable modification and dynamic updating of this representation, such that detailed spatial content information is included and the schema is rendered unique and distinguishable from other similar representations. Together, LTP and LTD engage in a dynamic interplay that supports the generation of complex associative memories that are resistant to generalisation" (p1).

Song et al (2024) noted that "most recent studies of Psychology Miscellany No. 206; September 2024; ISSN: 1754-2200; Kevin Brewer

long-term potentiation have been carried out on rodents, while the information on LTP in primates is still scarce" (p1). This led these researchers to study the tree shrew, which is "considered to have a close affinity to primates" (Song et al 2024 p1). In vitro experiments showed differences in the LTP of adult tree shrews as compared to adult mice.

5.3. SCHEMA

Knowledge is stored in the brain in the form of "schema" (a concept first introduced by Bartlett 1932). This is a conceptual scaffolding system that allows for the storing of information, and the integrating, understanding and remembering of new related information. It is an psychological explanation, but what about the neurobiology of schema?

"Recent neuroscience research posits that schemas consist of three fundamental components: first, they form an adaptable framework that incorporates associative knowledge from repeated past experiences; second, this framework facilitates and accelerates the processing of new information, encompassing encoding, consolidation and retrieval, thereby shaping future behaviour; and third, they are underpinned by a complex network of interconnected neocortical representations, with the hippocampus/medial temporal lobe (MTL) and medial prefrontal cortex (mPFC) playing pivotal roles in their formation and function" (Sekeres et al 2024 p2).

The formation of a new episodic/event memory occurs at the cellular/synaptic level involving the plasticity of the brain as shown in LTP. "Shortly after novel events are first experienced and encoded, the hippocampus plays a critical role in the retrieval of the episodically detailed elements of the experience. Over time and with repeated reactivations of the memory, distributed representations form within the hippocampus and mPFC" (Sekeres et al 2024 p2).

If an appropriate schema already exists, the new information is rapidly incorporated. In rodent studies (eg: Tse et al 2007), damage to the hippocampus three hours after learning impairs recall, but not if the damage occurs at 48 hours after learning. "Once the consistent schema was established, relevant new information became assimilated into cortical areas and rapidly became hippocampal-independent" (Sekeres et al 2024 p2).

But what about an experience that does not fit

existing schema? Sekeres et al (2024) proposed "a gradient theory of schema and novelty to elucidate the neural processes by which schema updating or novel memory traces are formed. It is likely that experiences vary along a familiarity-novelty continuum, and the degree to which new experiences are increasingly novel will guide whether memory for a new experience either integrates into an existing schema or prompts the creation of a new cognitive framework" (p1). The more unfamiliar the experience, the more the hippocampus is involved in the formation of new schema.

The hippocampus identified novelty (or the type of novelty) of the new experience (Sekeres et al 2024). For example, Duszkiewicz et al (2019) distinguished between "common novelty" and "distinct novelty". The former includes "novel events that have overlap with previous experiences" while distinct novelty covers "novel events that share minimal overlap with previous experiences" (Sekeres et al 2024 p3).

5.4. REFERENCES

Abraham, W.C (2008) Meta-plasticity: Tuning synapses and networks for plasticity Nature Reviews Neuroscience 9, p387

Abraham, W.C et al (2024) Long-term potentiation: 50 years on: Past, present and future Philosophical Transactions of the Royal Society B 379, 20230218

Bartlett, F.C (1932) Remembering: A Study in Experimental and Social Psychology Cambridge: Cambridge University Press

Bashir, Z.I et al (1993) Induction of LTP in the hippocampus needs synaptic activation of glutamate metabotropic receptors Nature 363, 347-350

Bliss, T.V.P & Lemo (1973) Long-term potentiation of synaptic transmission in the dentate area of the anaesthetised rabbit following stimulation of the perforant path Journal of Physiology 232, 331-356

Bliss, T.V.P & Gardner-Medwin, A.R (1973) Long-lasting potentiation of synaptic transmission in the dentate area of the unanaesthetised rabbit following stimulation of the perforant path Journal of Physiology 232, 357-374

Duszkiewicz, A.J et al (2019) Novelty and dopaminergic modulation of memory persistence: A tale of two systems Trends in Neuroscience 42, 102-114

Fayed, M.R et al (2024) Sleep and quiet wakefulness signify an idling brain hub for creative insights Philosophical Transactions of the Royal Society B 379, 20230226

Hagena, H & Manahan-Vaughan, D (2024) Interplay of hippocampal long-term potentiation and long-term depression in enabling memory representations Philosophical Transactions of the Royal Society B 379, 20230229

Hebb, D.O (1949) The Organisation of Behaviour New York: Wiley & Sons

Sekeres, M.J et al (2024) To update or to create? The influence of novelty and prior knowledge on memory networks Philosophical Transactions of the Royal Society B 379, 20230238

Song, Q et al (2024) Enhanced long-term potentiation in the anterior cingulate cortex of tree shrew Philosophical Transactions of the Royal Society B 379, 20230240

Tse, D et al (2007) Schemas and memory consolidation Science 316, 76-82

6. ACOUSTIC COMMUNICATION AND GROUP DYNAMICS

- 6.1. Overview
- 6.2. Acoustic communication and collective behaviour
 - 6.2.1. Different types of calls
 - 6.2.2. Group decision-making
 - 6.2.3. Acoustic communication vs movement cues
 - 6.2.4. Zebra finch
 - 6.2.5. Communication complexity
- 6.3. Acoustic communication and social interactions in the group
 - 6.3.1. Bonding
 - 6.3.2. Vocal accommodation
 - 6.3.3. Vocal complexity
 - 6.3.4. Null findings
- 6.4. References

6.1. OVERVIEW

Acoustic communication is important in the co-ordination of social activities in many species. "Acoustic signals can encode many pieces of information about the emitter, including both static (eg: species, sex, individuality) and dynamic (eg: motivation, emotion) information, and can in some species also carry information about external events (eg: presence and type of predator, food). This information is often perceived and used by receivers, hence influencing their behaviour and subsequent social interactions" (Briefer et al 2024 p1).

For example, group-foraging species, like meerkats, produce contact calls to co-ordinate the movement of the group (Briefer et al 2024) (table 6.1). This is the first of two overarching themes for acoustic communication and group behaviour, highlighted by Briefer et al (2024).

Vocalisations also encode information about social relationships within the group. Coppinger et al (2018), for example, found that individual Carolina chickadees placed in flocks with individuals unfamiliar to each other called differently to when in flocks of familiar individuals (Briefer et al 2024). This is an example of Briefer et al's (2024) second overarching theme.

Communication in a social group (as opposed to one-to-one) includes "audience effects" ("where signallers behave differently depending on the presence of listening conspecifics"; p1), and "social eavesdropping" ("where a

receiver gathers relative information about other interacting individuals by listening to their signal exchange"; p1) (Xie et al 2024).

| BEHAVIOUR | EXAMPLE * |
|--|--|
| Maintaining and co-ordinating current behaviour | "Chuck" calls by southern pied babblers when foraging to maintain space between individuals, but keep group members together |
| Timing of departure | African wild dogs and "sneeze" sounds |
| Food-associated calls to attract group members to food patches | "Purr" calls of southern pied babblers |
| Mobbing calls to approach predators | Great tits respond to the number of individuals making such calls |
| Alarm signals to avoid predators | "Whistle" alarm signals by crested pigeons |

(* from Liao et al 2024)

Table 6.1 - Acoustic Communication in Co-ordinating Behaviours.

Reviewing ninety-nine published studies on acoustic communication in groups, Xie et al (2024) distinguished four themes:

i) Vocalisations and collective movement - Collective movement is defined as "a group of individuals departing synchronously, moving in the same direction and maintaining cohesion during movement, until they stop... A collective movement consists of several steps, including a pre-departure period (a period to reach some kind of consensus on timing and direction for movements), the initiation of movement, joining and movement of all individuals, staying together during movement and termination of movement. Group-living animals heavily rely on signals to transfer information among group members, and vocalisations, with their potential multi-receiver benefits, have been shown to be exchanged frequently during collective movement" (Xie et al 2024 p2).

Vocalisations have different functions during movement (eg: chimpanzees use "travel hoos" to initiate movement, "pant-hoos" during movement and "rest-hoos" to stop) (Xie et al 2024).

Features of the vocalisations (eg: rate of

utterance; intensity) are also important. For example, longer calls signify longer distance to be travelled in greater spot-nosed monkeys (Xie et al 2024).

ii) Vocalisations and separation risk - "Staying together as a group can be challenging. Activities such as foraging entail separation risk and make cohesion maintenance more challenging, resulting in an effort for groups to synchronise and co-ordinate in order to mitigate the risk and maintain cohesion" (Xie et al 2024 p3).

"Contact calls" are the best example here. Vocalisations by certain macaques and lemurs, for example, have been found to vary in duration and frequency depending on the distance between group members (Xie et al 2024).

iii) Vocalisations and fission-fusion dynamics - "The term 'fission-fusion dynamics' describes processes where sub-groups split and merge over time, leading to temporal changes in group composition and size" (Xie et al 2024 p4).

Particular calls on reunion have been studied here (eg: elephants; chimpanzees), as well as "foraging calls" to attract group members to feeding spots.

iv) Vocalisations and social networks - "Social network" refers to "the pattern of social connections between individuals" (Xie et al 2024 p5). Vocalisations strengthen social bonds between individuals, for example.

Themes (i) to (iii) above fit with Briefer et al's (2024) first overarching theme, and theme (iv) above with their second.

6.2. ACOUSTIC COMMUNICATION AND COLLECTIVE BEHAVIOUR

6.2.1. Different Types of Calls

Calls (or signalling events) can vary between a single-caller to multi-participant vocal interactions including call-and-response exchanges, duets, and highly synchronous vocal choruses (Demartsev et al 2024).

"Signal exchanges" are calls made by one individual that expect a response from another individual, while "signal broadcasts" are "signalling events that are mainly driven by an environmental stimulus or internal state and are not directly contingent on the perception

of conspecifics' presence or calls. While such events can be intensified by social facilitation, there is no response per se to preceding signals nor are there necessarily expectations for receivers to reply" (Demartsev et al 2024 p2) (eg: solo songs).

Studying meerkats, Demartsev et al (2024) distinguished between "close calls" emitted mainly during foraging (an example of signal exchanges), and "short note calls", which "appear mainly in sequences produced by single individuals and show little dependence on social surroundings, suggesting a broadcast signalling mode" (Demartsev et al 2024 p1).

Close calls have the function of maintaining group cohesion, "with higher individual call rates when meerkats are foraging closer together, and these 'vocal hotspots' have been shown to guide distant individuals towards them. Additionally, spatially isolated individuals (>10 m to nearest neighbour) showed a tendency to increase their close call rates, perhaps to attract group members and prevent further separation" (Demartsev et al 2024 p2). On the other hand, short note calls are produced "in a sentinel (guarding) context and, dependent on the call sub-type, function as 'all-clear' calming or low-level warning signals. Outside of the sentinel context, short notes are emitted during meerkats' morning sunning behaviour and are hypothesised to have a bonding and appeasing function. Additionally, short notes have been observed to be emitted during fast, directed travel bouts, which often involve multiple individuals or the entire group" (Demartsev et al 2024 p2).

Data were collected over 26 days in 2017 and 2019 in South Africa from well-studied groups of 7-18 individuals (with over 70 000 calls in total). Around 60 000 calls were close or short note calls. Individual callers could be identified as many of the meerkats were GPS and audio collared (a 5 mm wide leather strap containing a GPS unit and a miniature audio recorder).

6.2.2. Group Decision-Making

Broad et al (2024) pointed out: "To reap the benefits of group living, such as predator avoidance, increased foraging efficiency and access to mates, social groups require decision-making processes to maintain cohesive movements. There is increasing evidence that consensus decisions and group movements are mediated by acoustic communication across taxa, including mammals,

birds and insects. For instance, groups of meerkats... and African wild dogs... reach consensus to move between foraging patches or hunting grounds when a certain 'quorum threshold' of individuals are calling, while in birds, decisions to leave roosting sites en masse are triggered by a growing crescendo of callers" (p1).

Anthropogenic (human) noise impacts acoustic communication and so collective behaviour. The impact may be direct in that human noise is louder than the calls of the animals, or indirectly via the affect of noise on cognitive performance (eg: through sleep disturbance).

Broad et al (2024) reported a study of the impact of noise on wild jackdaws, who use acoustic communication to co-ordinate behaviours like collective movement, and anti-predator mobbing. "Jackdaws form winter roosts that can comprise up to several thousand birds. Upon arrival at dusk, they make loud, distinctive calls that gradually decrease as they settle down to sleep for the night. In the early mornings, jackdaws become increasingly vocal again prior to a sudden mass departure. Observational and experimental evidence indicates that jackdaws vocalise to signal their readiness to depart from roost sites. Steep increases in calling up to a high level of intensity trigger a group-level consensus, leading to mass collective departures" (Broad et al 2024 p2).

The researchers studied five jackdaw roost sites in rural and urban locations in Cornwall, south-west England, during the winter of 2021-2022. Audio recordings were made (n = 329 nights), and roost behaviour was observed (n = 29 videos of morning departures). One site was urban, three rural, and one classed as inbetween. Background noise levels were measured at the time of the jackdaws' evening arrival to the roost, midway during the night, and one hour before morning departure calling began.

Five hypotheses were tested:

1. Jackdaws would take longer to settle down and stop calling in the evening in areas of more human noise. This was supported by the data.

Broad et al (2024) explained: "If signals are masked by high noise pollution upon arrival at roost sites, the exchange of information regarding predators and food availability could be detrimentally impacted. Therefore, if anthropogenic noise reduces the fidelity of these signals, limiting the capacity of calls to be heard and information to be extracted by receivers, jackdaws may

have to call for longer after arriving at the roost in order to share information effectively" (p8).

2. More night-time noise would lead to more birds calling during this period. This was supported by the data, and it suggested disrupted sleep.

3. More disturbance during the night would lead to less calling in the morning (ie: a lack of consensus). Not supported by the data.

4. More night-time noise would lead to less co-ordinated departure in the morning. Not supported.

5. More night-time noise would lead to longer time to empty the roosts. No significant difference found.

The predictions in hypotheses 3-5 had some support indirectly through night-time disturbance. Broad et al (2024) explained that "rather than noise disrupting the establishment of a vocal consensus by masking calls, the disruption may be linked to the energetic expenditure of night-time calling and/or noise-induced sleep deprivation negatively impacting cognition and signal processing. For instance, a reduction in sleep overnight could reduce the jackdaws' capacity to process and relay acoustic signals, thereby also reducing the efficiency of their voting-like vocal consensus decision-making. It is also possible that disruption to sleep could increase the discrepancy between individual interests, which may reduce the efficacy of consensus decisions. Overall, our results are consistent with growing evidence that sleep plays an important role in maintaining cognitive processes that facilitate acoustic communication and group dynamics" (p9).

6.2.3. Acoustic Communication vs Movement Cues

Acoustic communication is important in collective decisions to move, but so are movement cues (ie: visual communication) - for example, "the direction of departures is often determined by individuals 'voting with their feet', with individuals co-ordinating movements following in the footsteps of others. In starling murmurations, individuals co-ordinate their flying direction and speed by copying the behaviour of nearby individuals, rather than relying on acoustic communication" (Liao et al 2024 p2).

Liao et al (2024) asked the question: "What dictates the use of acoustic signals versus movement cues?" (p2). They offered the reply, context - "A group of mammals resting on a hot day would avoid unnecessary activity if they could communicate their preference to leave using acoustic signals rather than movements. By contrast, in highly dynamic flocking birds, using vocalisations to communicate intentions like 'I want to turn right' or 'I want to turn left' is likely to be unsuitable, being prone to errors owing to signal interference (if many individuals communicate simultaneously), low efficacy (if the sound of flight adds noise) and difficulties in locating the source individual (as the flock is moving fast). Thus, while in some contexts, animals can use acoustic signals to communicate contextual information, in other contexts, movement cues may be more efficient for co-ordinating actions" (Liao et al 2024 p2).

Liao et al (2024) presented a framework for acoustic communication or movement cues in collective decision-making:

i) Sensory limitations - Acoustic calls are ineffective in noisy environments (known as "information masking"), while movement as a signal requires a line of sight of the mover.

ii) Assessment of number and intensity - Collective decisions to move are often based on the number of "voters", particularly when there is no group leader(s). This requires the cognitive ability to discriminate some form of number or quantity.

iii) Encoding limitations - Individual calls may be used in different contexts (ie: have more than one meaning) which could be confusing, whereas movement in one direction is specific communication.

iv) Salience (conspicuousness) vs complexity - Liao et al (2024) used this example: "Consider the difference between shouting 'stop' versus 'please finish eating'. The latter contains more information but is less salient, and would be more difficult to discern in a busier acoustic environment owing to the increased potential for information masking. By contrast, 'stop' is easy to receive and interpret but conveys no specific information. Thus, the salience of acoustic signals will decrease if they are used to convey more information, and at some point, will become lower than movement cues or signals" (pp7-8).

v) Speed vs accuracy - "Faster decisions are often made using information acquired only from one or a few individuals, meaning that they are more prone to errors because they do not benefit from information pooling. By contrast, decisions involving information from more individuals can take much longer to resolve" (Liao et al 2024 p8). Quick escape from a predator, for example, requires speedy communication (a call), whereas with selecting a migration route, accuracy is better and movement cues may be more appropriate.

vi) Quorum thresholds - A certain number of individuals "voting" in the same way is required for a collective decision.

Putting all the information together, Liao et al (2024) drew the conclusion that "behaviours involving the timing of events or expression of specific actions should rely more on acoustic signals, whereas decisions involving complex choices with multiple options (eg: direction and destination) should generally use movement cues..." (p1).

Finally, the researchers recommended two areas for further research - multi-modal communication (ie: acoustic communication and movement cues together), and collective decision-making in mixed-species groups (eg: birds).

6.2.4. Zebra Finch

The zebra finch song has been well studied in captivity, particularly with reference to song learning, and mate choice, but there is less research on wild populations and the role of singing in relation to social behaviour (Loning et al 2024).

The Australian zebra finch forms life-long pair bonds that live in groups with other pairs and single individuals, and they breed in synchrony. Both sexes call "almost constantly", and males also sing (Loning et al 2024).

The first observation from studies in the wild is that singing is a close range social phenomena. Loning et al (2022), for example, observed only 13% (of 94 observations) of males singing when alone compared to singing in proximity (within 20 m) of a female or larger group. Playback experiments show that songs attract other individuals towards them (Loning et al 2023). This is "a clear departure from the traditionally assumed primary

function of birdsong as a long-range advertisement signal used in territory defence and mate attraction" (Loning et al 2024 p5).

Also there is evidence of "social hotspots" (trees and bushes where the birds gather during the day). "During these social gatherings, males may use song to establish and maintain individual social relations with others, and repeated singing may facilitate individual recognition in a dynamic social environment with many singers. Specifically, the prominent individual distinctiveness of the zebra finch song is likely to be a key component to maintain social connectivity because individuals will be able to readily identify familiar individuals near their nests or in social hotspots" (Loning et al 2024 p5).

6.2.5. Communication Complexity

Bousquet et al (2024) argued for high ecological heterogeneity and complex communication in group decision-making ¹⁰. "Physical environments with high levels of heterogeneity can constrain information transfer and increase ecological uncertainty. According to the 'habitat constraints hypothesis', effective group decision-making should be more difficult to achieve in environments with high ecological heterogeneity. Indeed, whilst simple copying of motion among group members can enable groups to navigate and make decisions in environments that are homogeneous and predictable, this becomes more difficult in heterogeneous environments where visual information can be reduced and acoustic information can be attenuated or distorted" (Bousquet et al 2024 p1).

The researchers compared meerkats and Cape ground squirrels. The former live and forage in environments that vary (eg: open land; grassland; dunes) (ie: high ecological heterogeneity) and so have more complex communication than the squirrels which forage near their burrows (low ecological heterogeneity) (Bousquet et al 2024).

6.3. ACOUSTIC COMMUNICATION AND SOCIAL INTERACTIONS IN THE GROUP

Social interactions are often studied as dyads (one-

¹⁰ Ecological heterogeneity is defined as variation in land cover and vegetation, change in resources over time, and species diversity (Bousquet et al 2024).

to-one interactions), but interactions of three or more individuals at a time happen in the real world. Higher-order network approaches were developed for this reason. They are statistical models used to predict behaviour (Iacopini et al 2024).

6.3.1. Bonding

More contact calls and matched specific call types are exchanged by group members with stronger bonds (eg: spider monkeys; Briseno-Jaramillo et al 2018).

The role of vocalisations in relation to bonding has been studied in Indo-Pacific bottlenose dolphins in Shark Bay, Western Australia. Unrelated adult males form alliances, particularly for "consortships". Pairs or trios of males work together to keep fertile females with them (for hours or weeks) and away from rival alliances (ie: it is a form of co-operative mate-guarding). Chereskin et al (2024) explained: "During consortships, males can display aggression towards the female, both physically and through vocalisations termed 'pops', which compel the female to remain close to the males. Pops are produced only by males, with adult females having never been observed or recorded producing pops in over four decades of research. Pops are narrow-band, low frequency, pulsed calls that are produced in repetitive sequences (called 'trains'), and are almost exclusively used by males during consortships. Pop trains can vary in both the number of individual pops they contain and in the pop rate (pops per second), ranging from 3 to 30 pops per train and 6-12 pops per second. Allied males will also co-ordinate pop production by actively matching each other's tempo and synchronising their pop trains" (p2).

Chereskin et al (2024) reported data that showed that greater vocal synchrony of pops was linked to the strength of the social bond between the males. Acoustic data had been collected on dolphins in Shark Bay over a number of years, and those from 2016 to 2022 were analysed in this study. Five different alliances of males were observed based on photo-identification of individuals. The strength of a bond between individuals was scored based on the number of times the individuals were observed together. Specifically, Chereskin et al (2024) analysed 30 hours of acoustic data from fourteen consortship events.

In summary, it was found that "social bond strength influenced pop use in a co-operative context, suggesting dual functions of pop use: to induce the female to remain

close, and to promote social bond maintenance and co-operation among males" (Chereskin et al 2024 p1).

The sample size of the study was relatively small (Chereskin et al 2024).

6.3.2. Vocal Accommodation

"Social accommodation" is where animals modify their calls to become more similar (convergence) or dissimilar (divergence) to group members. The other type of vocal accommodation is the modification of calls to changes in the environment (Ruch et al 2018). Social convergence of calls is a way to facilitate group cohesion, while social divergence is a means to highlight differences between groups or individuals of the same species (Langehennig and Scheumann 2024).

Langehennig and Scheumann (2024) described social accommodation in adult grey mouse lemurs in captivity. Females tend to form long-term stable sleeping groups in the wild, while males sleep alone. Nearly trill calls from thirty-six individuals were analysed from recordings made between 2003 and 2012 at a Germany zoo. "A trill call consists of up to 30 syllables, which are distinguished into three structural parts: (i) the first part, a variable initial modulation; (ii) the middle part comprising down- and/or up-modulated syllables; and (iii) the end part consisting of syllables of almost constant frequency" (Langehennig and Scheumann 2024 p3). An acoustic dissimilarity score was calculated based on the similarity of individual's calls using twenty-nine acoustic parameters.

The researchers summed up: "Our results showed that female trills become more similar the more time females spend with each other, independent of genetic relationship, suggesting vocal convergence. In contrast, male trills were affected more by genetic than social factors. However, focusing only on socialised males, increasing time as cage partners caused greater divergence in males' trills. Thus, grey mouse lemurs show the capacity for social accommodation, with females converging their trills to signal social closeness to sleeping group partners, whereas males do not adapt or diverge their trills to signal individual distinctiveness" (Langehennig and Scheumann 2024 p1).

Put simply, females' calls became more similar to enhance group cohesion, whereas male calls remained different between individuals in order to advertise their genetic/individual differences to potential mates.

6.3.3. Vocal Complexity

The "social complexity hypothesis for communicative complexity" (SCHCC) (eg: Freeberg 2006) proposes that vocal complexity will be higher in more complex social environments. Vocal complexity is the combination of individual calls to produce longer, meaningful vocalisations.

Walsh et al (2024) provided support for the SCHCC in Western Australian magpies, who live in stable groups ranging from two to eleven individuals. Simply, it was found that "callers in larger groups give call combinations: (i) in greater diversity and (ii) more frequently than callers in smaller groups" (Walsh et al 2024 p1).

Audio recordings and observations were made in the suburbs of Perth, Western Australia, in 2019-20 and 2020-21. In total 196 observation sessions of twelve different groups. Call combinations and types were scored.

6.3.4. Null Findings

Chaverri et al (2024) studied the Spix's disk-winged bat to understand individual differences in contact calls. The researchers explained that these bats form "small groups of about five bats... that roost inside the young, developing tubular leaves of plants in the order Zingiberales, such as heliconias and bananas. The tubular structure of these leaves unfurls after approximately one day. Given the ephemeral nature of their roosts, the bats must rapidly find new roost sites. To do this while maintaining group cohesion, they rely on a call-and-response contact calling system. When a single individual, or a group, is searching for a new tubular leaf, they produce 'inquiry' calls, which help maintain contact with group members. When one or several individuals find and enter a roost, they often produce a distinctive 'response' call in reply to inquiry calls" (Chaverri et al 2024 p2).

An experiment was performed to test the prediction that inquiry and response calls would vary with the genetic relationship and/or familiarity of individuals. Pairs of bats were tested in 139 trials. The inquiry and response calls were measured.

Overall, in each trial, the average was 71 inquiry calls and ninety-nine response calls. The calling did not vary based on the relationship of the pair, as expected, which suggested that "inquiry and response calls appear

to serve the purpose of maintaining group cohesion rather than being specifically targeted at particular individuals to maintain or strengthen within-group affiliations" (Chaverri et al 2024 p8).

The same research group (Sagot et al 2024) reported an association between higher calling rate and low group fragmentation during movement to a new roost.

6.4. REFERENCES

Bousquet, C et al (2024) Individual and ecological heterogeneity promote complex communication in social vertebrate group decisions Philosophical Transactions of the Royal Society B 379, 20230204

Briefer, E.F et al (2024) The power of sound: Unravelling how acoustic communication shapes group dynamics Philosophical Transactions of the Royal Society B 379, 20230182

Briseno-Jaramillo, M et al (2018) Age and social affinity effects on contact calls interactions in free-ranging spider monkeys Behavioural Ecology and Sociobiology 72, article 192

Broad, H.R et al (2024) Anthropogenic disturbance affects calling and collective behaviour in corvid roosts Philosophical Transactions of the Royal Society B 379, 20230185

Chaverri, G et al (2024) Calling to the collective: Contact calling rates within groups of disc-winged bats do not vary by kinship or association Philosophical Transactions of the Royal Society B 379, 20230195

Chereskin, E et al (2024) In pop pursuit: Social bond strength predicts vocal synchrony during co-operative mate guarding in bottlenose dolphins Philosophical Transactions of the Royal Society B 379, 20230194

Coppinger, B.A et al (2018) Carolina chickadee (*Poecile carolinensis*) calling behaviour in response to threats and flight: Flockmate familiarity matters Journal of Comparative Psychology 132, 16-23

Demartsev, V et al (2024) Mapping vocal interactions in space and time differentiates signal broadcast versus signal exchange in meerkat groups Philosophical Transactions of the Royal Society B 379, 20230188

Freeberg, T.M (2006) Social complexity can drive vocal complexity Psychological Science 17, 7, 557-561

Iacopini, I et al (2024) Not your private tete-a-tete: Leveraging the power of higher-order networks to study animal communication Philosophical Transactions of the Royal Society B 379, 20230190

Langehennig, A & Scheumann, M (2024) Sex differences in the Psychology Miscellany No. 206; September 2024; ISSN: 1754-2200; Kevin Brewer

impact of social relationships on individual vocal signatures in grey mouse lemurs (*Microcebus murinus*) Philosophical Transactions of the Royal Society B 379, 20230193

Liao, C-C et al (2024) The relative contribution of acoustic signals versus movement cues in group co-ordination and collective decision-making Philosophical Transactions of the Royal Society B 379, 20230184

Loning, H et al (2022) Zebra finch song is a very short-range signal in the wild: Evidence from an integrated approach Behavioural Ecology 33, 37-46

Loning, H et al (2023) The social role of song in wild zebra finches Current Biology 33, 372-380

Loning, H et al (2024) The evolution of zebra finch song and its implications for vocal communication in multi-level societies Philosophical Transactions of the Royal Society B 379, 20230191

Ruch, H et al (2018) The function and mechanism of vocal accommodation in humans and other primates Biological Reviews 93, 2, 996-1013

Sagot, M et al (2024) Group vocal composition and decision-making during roost findings in Spix's disk-winged bats Philosophical Transactions of the Royal Society B 379, 20230187

Walsh, S.L et al (2024) Call combination production is linked to the social environment in Western Australian magpies (*Gymnorhina tibicen dorsalis*) Philosophical Transactions of the Royal Society B 379, 20230198

Xie, B et al (2024) Exploring the role of vocalisations in regulating group dynamics Philosophical Transactions of the Royal Society B 379, 20230183

7. LIGHT POLLUTION IN COMPLEX ECOSYSTEMS

- 7.1. Introduction
- 7.2. Ecosystem-level impacts
- 7.3. Predators
- 7.4. Street lighting
- 7.5. Marine environments
- 7.6. Skyglow
- 7.7. Mosquitoes
- 7.8. Invertebrates
- 7.9. References

7.1. INTRODUCTION

Light is a source of information in the animal kingdom, such that “variability in the light regime works like a metronome for many organisms by determining the timing and duration of days, months (or moon cycles) and seasons. For example, some plants use this information to time the onset of developing leaves or flowers, while corals have been shown to align the time point of spawning with the moon and nocturnal animals usually start their daily activity after solar irradiance drops below a certain level. Furthermore, some animals use light for orientation. For example, sea turtle hatchlings find their way to the ocean by moving towards the brighter horizon, which under natural conditions is over the ocean and some birds and other animals can even navigate by starlight” (Hirt et al 2023 p1). Human artificial light at night (ALAN) disrupts the natural light regime ¹¹.

This is caused by the different properties of artificial light - spectral composition, duration and timing, intensity, and scattering (ie: “the artificial light that is scattered (ie: diverted) back to Earth by molecules, aerosols and clouds within the atmosphere”; Hirt et al 2023 p3).

Research has tended to focus on the impact of ALAN on individual behaviour (eg: movement patterns; activity; hormone levels; reproductive behaviour), but Hirt et al (2023) considered the impact on complex ecological systems: “Because virtually all organisms are embedded in communities within ecosystems, therefore directly and indirectly influenced by species interactions, the responses of ecosystems are more than the sum of

¹¹ One estimate from 2016 stated that more than 80% of the world’s population “live under light-polluted skies”, though this figure may have increased since then (Bara and Falchi 2023). Psychology Miscellany No. 206; September 2024; ISSN: 1754-2200; Kevin Brewer

individual organism's responses. In consequence, an understanding of the effects of ALAN at higher organisational levels is essential for predicting how biodiversity and ecosystem services ultimately respond" (p3) ¹².

ALAN impacts plants (eg: changes in plant traits like leaf hairiness; Bucher et al 2023), which in turn affects soil (eg: changes in abundance of plant-feeding nematodes; Cesarz et al 2023).

7.2. ECOSYSTEM-LEVEL IMPACTS

Sanders et al (2023) outlined four major pathways by which ALAN impacts an ecosystem:

i) Impacting primary production - The impact of light pollution on species at the base of the food chain, in particular, plants.

ii) Acting as an environmental filter affecting species survival - This refers to the fitness impact and the evolutionary consequences.

For example, strictly nocturnal species will be impacted most negatively by ALAN, while diurnal species may see positive consequences (Sanders et al 2021), but distinguishing direct and indirect effects of ALAN is difficult (Sanders et al 2023).

iii) Influencing the movement and distribution of species through phototaxis (ie: "the attraction and avoidance of species to light sources"; Sanders et al 2023 p4).

For example, bat species have been found to amass around light sources that attract flying insects. "Communities [of animals] that are exposed to ALAN may therefore experience an increased influx of some prey and predators, while other species will be driven away, eg: nocturnal pollinators. This can lead to the long-term redistribution of species, especially if it happens at larger spatial scales. These dynamics can increase predation/consumption and energy flux, which may then result in larger body sizes. Overall, these alterations may also affect the roles of species within their community" (Sanders et al 2023 p4).

¹² Of 79 studies found by Seymoure et al (2023), seventy-five showed that ALAN altered species interactions. Most studies focused on predator-prey relations. "Enhancements and reductions of species interactions were equally documented" (Seymoure et al 2023 p1).

iv) Changing activity patterns - "For example, diurnal or crepuscular (dawn- and dusk-active) species can extend their activity into the night when ALAN exposure changes the night-time light levels and unlocks the nocturnal niche for them" (Sanders et al 2023 p4).

This could mean that predators and prey meet when previously that had not happened. So, "a diurnal predator may over-exploit resources through higher levels of activity or shift to novel prey species, or a nocturnal prey species may reduce its activity and become unavailable to a predator" (Sanders et al 2023 p4).

Overall, Sander et al's (2023) interest was the overlaps between diurnal, crepuscular, and nocturnal species caused by ALAN. The potential changes can be summarised as:

a) Crepuscular species expand their activity into the night with increased encounters with nocturnal species and reduced encounters with diurnal species.

b) Nocturnal species reduce their period of activity due to ALAN.

c) Diurnal species expand their temporal niche, and so encounter crepuscular and nocturnal species more (or for the first time).

This has been called the "night light niche" (Fobert et al 2023). With reference to shallow marine environments, Fobert et al (2023) outlined three consequences of this change: (i) increased time for visual-based predators and foragers; (ii) novel interactions between diurnal and nocturnal species; and (iii) "altering the landscape of fear for nocturnal foragers" (p6).

The exact changes will depend upon the species, the ecosystem, and the nature of the light pollution.

Outdoor light sources of any type, as well as indoor sources whose light spills outdoors, increase the concentration of light particles (photons) in the environment, giving rise to light pollution" (Bara and Falchi 2023 p1). The term "light pollution" has been used in different ways, sometimes in distinction to "useful light", and not necessarily viewed as pollution in a "real sense", but Bara and Falchi (2023) emphasised that:

- All ALAN is an "actual pollutant" (ie: it has measurable environmental effects).

- The expression of light pollution in terms of lux (where one lux is "equivalent to 1.36×10^7 photons per cubic metre propagating towards the measurement surface, within the human visual band"; Bara and Falchi 2023) is different to other pollutants which are presented as concentrations (eg: number of molecules per unit volume).
- There is no distinction between "good" and "bad" ALAN, it is all a pollutant.

Bara and Falchi (2023) asserted: "Chemical or biological contaminants, particulate matter, sound and light, among others, are pollutants that affect the quality of the atmospheric and underwater environments. Within this framework, artificial light at night should legitimately be considered an air and water pollutant".

Like any other pollutant, light varies in intensity between the area around the source and the distant dark areas with "the deterioration of former pristine sites" (Bara and Falchi 2023).

Light pollution also changes in terms of higher luminous lamps, and the shifting colours (on the optical spectrum).

7.3. PREDATORS

Large predators move over large ranges and encounter areas of ALAN. Barrientos et al (2023) studied mountain lions (also known as pumas, cougars, or panthers) in Southern California.

"Mountain lions are likely to respond differently to light of different characteristics. The moon produces elevated illumination of a night-time scene when skies are clear, with a single dominant point source of light in the sky. Skyglow – the reflected light in the atmosphere from anthropogenic sources on the ground (intensified by light reflecting off clouds when present) – similarly increases scene brightness with diffuse illumination from the atmosphere... Light at night may also appear as direct glare sources, which even when not substantially increasing scene brightness can be visible as high-contrast point sources on the visible horizon or closer to mountain lions, dependent on their elevation and distance at the time" (Barrientos et al 2023 p2). So, ALAN will be skyglow (zenith glow) and nearby lights (upward radiance).

Data from 102 radio-collared lions for 2001 to 2022 were analysed. Nearby lights, skyglow, and natural illumination from moonlight were the variables compared, and the outcome measure was habitat selection. Nearby lights was found to be key (ie: lions avoided such areas), which suggested that lions used artificial illumination to signal human activity, and their preference was not to interact with humans.

Other studies of mountain lions have shown a preference to avoid humans, as have studies with other large felids (eg: jaguars in Mexico; leopards in Kenya; lynx in Europe) (Barrientos et al 2023).

The avoidance of lit areas by lions "can have cascading effects on both the redistribution of species in the region and the ecosystem functions provided by wildlife. However, these interactions are certainly complex. In the case of the mountain lions themselves, they are top predators that act as providers of resources like carrion for other species as scavengers, while limiting the number of meso-predators through direct predation" (Barrientos et al 2023 p8).

7.4. STREET LIGHTING

Understanding the impacts of street lighting (and type of lighting - eg: high-pressure sodium (HPS) or light-emitting diode (LED) lamps) will help in finding ways to mitigate the impacts (Evans 2023).

For example, Longcore et al (2015) used the idea of species response curves to predict which configuration of LED lights would attract fewer insects. "While this approach shows promise for mitigating the impacts of street lights on whole communities of species, predicting biological responses to different lamp technology and lighting strategies is still hampered by the current lack of readily available response curves across taxonomic groups. Gaining more complete data on species response curves is thus a research priority" (Evans 2023 p2).

Looking more widely at the ecosystem level, MacGregor et al (2014) studied pollination by moths around street lights in the UK, finding reduced pollen transport (ie: carried on the moth's body) at lit areas. While Knop et al (2017) used mobile street lamps in an experiment in a dark meadow in Switzerland. "They found a significantly lower number of flower visits (62%) and flower-visiting species (29%) at illuminated sites" (Evans 2023 p3). These two studies showed the negative consequences of ALAN for plant reproductive success.

Evans (2023) reported an experiment in a field in northern England with nine lit and unlit areas. There were around one-third fewer arthropods found in lit compared to unlit areas.

Boyes et al (2021) found differences between LED and HPS lamps and nocturnal-feeding caterpillar abundance in an experiment in south-east England. There were significantly fewer caterpillars found in LED-lit areas compared to unlit areas of a field, but no statistically significant difference between HPS-lit and unlit areas.

Evans (2023) stated: "Protecting (and expanding) natural unlit areas is likely to be the most effective option for reducing the ecological effects of lighting. However, this could conflict with other social and economic objectives. According to Gaston and de Miguel [2022], the conventional sequence of mitigation hierarchy elements, in order of progressively reducing desirability, is: avoid, minimise, restore or rehabilitate, then offset. In the case of ALAN, however, they argue that the hierarchy should probably be: avoid, restore or rehabilitate, minimize and then offset" (p4).

Practical ideas include part-night lighting (ie: switched off during periods of low need; table 7.1), shielding (ie: prevent light overspill beyond intended area), minimise the number of street lights in an area, and dimming (Evans 2023).

- Unexpectedly part-night lighting was found to have a stronger negative impact on aphid colony growth than full ALAN in an experiment (Heinen et al 2023) (20% lower aphid numbers).
- The colony growth of the English grain aphid on barley was studied in full ALAN (20 lux), half nights of ALAN, and no ALAN in climate controlled chambers for 20 nights (of eight hours).

Table 7.1 - Part-night lighting.

7.5. MARINE ENVIRONMENTS

Light pollution also impacts marine environments. "Both direct sources of light (eg: from marine infrastructure, coastal lighting) and skyglow... from urban centres contribute to the artificial light that can disrupt marine life in coastal habitats. In fact, ALAN from coastal developments reaches more than 22% of the world's near-shore environments" (Fobert et al 2023 p1).

Concentrating on tropical and temperate reefs,

Fobert et al (2023) outlined four natural processes driven by light that ALAN directly and/or indirectly impacts ¹³:

i) Primary production - For example, natural light is used in photosynthesis by algae, and so extra light could influence growth.

ii) Physiology, reproduction, and survival - eg: increased stress caused by artificial light. With prey that forage in the dark, for instance, "enhanced vigilance (ie: refuge-seeking) under ALAN reduces time allocated to foraging, and this may have long-term impacts on fitness and productivity" (Fobert et al 2023 p6).

iii) Interfering with biological timings - "Many critical biological events in the ocean are highly attuned to daily, lunar, and seasonal changes in light produced by the reliable movements of the Earth and Moon around the Sun. Therefore, the addition of ALAN to an environment can mask or imitate natural light cues, resulting in an ALAN driven mismatch in life cycle timing" (Fobert et al 2023 p4). For example, spawning synchrony (ie: the broadcasting of sperm and eggs into the water at the same time); hatching; daily activity patterns (eg: sea urchins increase foraging at night).

iv) Movement - Many mobile marine organism show phototactic behaviour, with some attracted to light, while others are repulsed.

Fobert et al (2023) summed up: "ALAN can further shift the balance of 'winners' and 'losers' in coral communities through its direct influence on settlement patterns and impact on physiological stress and symbiotic relationships of some species, and indirectly through changes to competitive pressure for space (increased growth of turfing and macro-algae) and altered grazing pressure from primary consumers. This shift in coral community composition is likely to result in a loss of coral diversity and an overall reduction in coral cover" (p6).

Holker et al (2023) focused on freshwater

¹³ The impact of the natural light of the moon, for instance, can be direct in terms of its illumination, but also indirect in extra-large spring tides twice each month when Earth, moon and sun align to create extra gravitational pull. Furthermore, lunar cycles have been found to influence the activity of genes in coral species (Marchant 2020).

ecosystems, which include freshwater shoreline, rivers and lakes, and they detailed the key issues as including:

a) The interference with biological processes including the alteration of the physiology of aquatic organisms.

b) Light as a barrier to movement - "Critical structures include illuminated overpasses and other crossing structures such as bridges and weirs. Some salmonids and eels occasionally interrupt their migration at such lit structures, suggesting that ALAN can increase landscape resistance in river networks. Such effects are not limited to fish. The lighting of crossing structures and waterways also has adverse consequences for bats that use the linear water courses as flyways and feeding habitats, and female mayflies are attracted by bridge lights during upstream compensatory flights" (Holker et al 2023 p8).

c) Altered predator-prey relationships - "Predators have evolved sophisticated techniques over millions of years to detect and capture prey, while prey species constantly improve defence strategies. Artificial light at night can shift the balance in the arms race" (Holker et al 2023 p8).

For example, prey that forage in the darkness are vulnerable to visual predators even with low light at night, while aquatic insects attracted by illuminated bridges, say, will benefit terrestrial predators like spiders and bats.

d) Novel communities - Holker et al (2023) felt that an important point was "the substantial variation to be expected in responses to ALAN both among and within taxonomic groups, which could change species distribution patterns and create novel communities with no historical analogue, resulting from the loss of previously established and arrival of new species. An example are cane toads introduced to and highly invasive in various islands throughout Oceania and the Caribbean, as well as Australia, which benefit from insects attracted by street lights, especially in areas with low ambient light pollution. The 'vacuum cleaner effect' [Eisenbeis 2006] referring to such aggregation of individuals in artificially illuminated areas reduces abundances of the attracted species in the darker surroundings" (p8).

e) Indirect light pollution from skyglow could

impact zooplankton, for example, and consequently the whole food web.

f) Evolutionary consequences - For example, bright-light areas would favour insensitive over photosensitive genotypes (ie: selection pressure), or lead to differences in mate choices (eg: female tungara frogs less choosy in brighter light levels; Holker et al 2023).

7.6. SKYGLOW

In an experiment with various insects, Dyer et al (2023) found that even low-intensity skyglow (below average full moon illuminance - 0.3 lux) led to a shift in movement activity from day to night, and a shift from vegetated areas to open habitats at night.

Seven ground beetle species from the local area in Germany (totalling 792 individuals) were studied in experimental (indoor) grassland-patch landscapes with simulated light and moon cycles, and skyglow (varying from 0.0014 lux (slightly brighter than starlight) to 30 lux (brighter than current skyglow)). Four meadow patches were created.

7.7. MOSQUITOES

The impact of ALAN in terms of wider consequences beyond an individual species can be seen in the case of disease vectors, like mosquitoes. "ALAN can alter mosquito behaviour and biting propensity, and so must alter disease transfer rates" (Coetzee et al 2023 p1). Put simply, ALAN will suppress the biting propensity of nocturnal groups and increase it for diurnal feeders.

So, Coetzee et al (2023) argued, it is important to understand the role of light (and artificial light) for mosquitoes. Natural light synchronises circadian activities including when to feed. Disruption of this process by ALAN will change the timing of biting, for example. "Although mosquitoes can feed on humans at any time, the peak biting frequency of the main African malaria vector species, belonging to the Anopheles genus, is the period from midnight to 4.00 in the morning, although there is geographical variation. This coincides with the time that most people are asleep. Biting can start as early as 19.00 and continue until the morning... The majority of these vectors, however, prefer to be active at night. Like malaria vectors, some vectors of

arboviruses (*Culex pipiens*) also readily feed on humans between dusk and dawn, while others, like *Ae. aegypti*, are diurnal. *Aedes* have a bimodal biting behaviour: biting increases early in the morning then subsides and resurges again during the afternoon, with little activity at night. This natural biting pattern of arbovirus vectors can be interrupted by a marked increase in biting rate when mosquitoes receive stimulation with artificial light during the night" (Coetzee et al 2023 p2).

ALAN is so often considered in isolation, but Coetzee et al (2023) emphasised the interaction with other "global change drivers" (eg: climate change; land use change and urbanisation). ALAN also alters human behaviour with implications for exposure to mosquitoes. Another interacting factor is vector control strategies (eg: insecticide-treated based nets). For example, an individual sleeping under such a net may be safe during darkness, but when active in ALAN is more vulnerable to biting.

7.8. INVERTEBRATES

"ALAN has a particularly strong impact on invertebrates. The effects are variable, ranging from the disturbance of daily and seasonal rhythms, shifts in foraging behaviour, physiology and immune responses, and disruption to reproductive behaviours and physiology. One of the most conspicuous and widely known effects is the attraction of flying insects to light at night. This effect can have severe consequences for local insect densities and may be an important driver behind global insect declines" (Spoelstra et al 2023 p1).

Spoelstra et al (2023) experimentally compared the impact of three spectra of ALAN - white-, green-, and red-dominated light - on ground-dwelling invertebrates in a forest area in the Netherlands over four nights. There was little difference in the invertebrates caught between the three light conditions. "The invertebrate community composition, however, was significantly affected by the presence of light. Keeping lights off during single nights did show an immediate effect on the composition of trapped invertebrates compared to illuminated nights. These effects of light on species composition may impact ecosystems by cascading effects across the food web" (Spoelstra et al 2023 p1). In summary, no light is better than changing the colour of the light for ground-dwelling forest invertebrates.

Freshwaters and the adjacent land areas (river banks & wetlands) (known as riparian zones) are linked in particular by insects that move between them, and are resources for fishes, bats, birds, and spiders (termed "resource subsidies") (Parkinson and Tiegs 2023).

ALAN impacts these ecosystems, and specifically LED lighting. Parkinson and Tiegs (2023) showed this in a field experiment on one night in June 2022 of a pond and riparian zone in Michigan, USA. Four light conditions were used that varied the light wavelengths - violet, green, red, and white - as well as a dark control condition. The lights were turned on at sunset and off at sunrise. Invertebrate numbers were sampled on land, and on and over the water.

It was found that different wavelength of light attracted different communities of insects (eg: leafhoppers (Cicadellidae) and red light (longer wavelength)), while violet light (shorter wavelength) attracted the most insects overall. For flying insects, both a "barrier effect" (ie: light stopping flight into an area) and a "vacuum effect" (ie: illumination attracting insects) were found.

Tidau et al (2023) studied the impact of ALAN on two marine invertebrates vital to their ecosystem - a mussel species and a barnacle species. ALAN was found to "adversely affect larval survival". Barnacle larvae survival declined by over 10% with increasing light while for mussel larvae it was over 50% over 60 days.

The experiment involved incubators for rearing larvae, which are light sensitive, with LEDs in six light conditions (varying from 0 to 50 lux).

7.9. REFERENCES

Bara, S & Falchi, F (2023) Artificial light at night: A global disruptor of the nighttime environment Philosophical Transactions of the Royal Society B 378, 20220352

Barrientos, R et al (2023) Nearby night lighting, rather than skyglow, is associated with habitat selection by a top predator in human-dominated landscapes Philosophical Transactions of the Royal Society B 378, 20220370

Boyes, D.H et al (2021) Street lighting has detrimental impacts on local insect populations Science Advances 7, eabi8322

Bucher, S.F et al (2023) Artificial light at night decreases plant diversity and performance in experimental grassland communities Philosophical Transactions of the Royal Society B 378, 20220358

Coetzee, B.W.T et al (2023) Scaling artificial light at night and disease vector interactions into socio-ecological systems: A conceptual approach Philosophical Transactions of the Royal Society B 378, 20220371

Cesarz, S et al (2023) Artificial light at night (ALAN) causes shifts in soil communities and functions Philosophical Transactions of the Royal Society B 378, 20220366

Dyer, A et al (2023) Insect communities under skyglow: Diffuse night-time illuminance induces spatio-temporal shifts in movement and predation Philosophical Transactions of the Royal Society B 378, 20220359

Eisenbeis, G (2006) Artificial night lighting and insects: Attraction of insects to streetlamps in a rural setting in Germany. In Rich, C & Longcone, T (eds) Ecological Consequences of Artificial Night Lighting Washington DC: Island Press

Evans, D.M (2023) Mitigating the impacts of street lighting on biodiversity and ecosystem functioning Philosophical Transactions of the Royal Society B 378, 20220355

Fobert, E.K et al (2023) The impacts of artificial light at night on the ecology of temperate and tropical reefs Philosophical Transactions of the Royal Society B 378, 20220362

Gaston, K.J & de Miguel, A.S (2022) Environmental impacts of artificial light at night Annual Review of Environment and Resources 47, 373-398

Heinen, R et al (2023) Part-night exposure to artificial light at night has more detrimental effects on aphid colonies than fully lit nights Philosophical Transactions of the Royal Society B 378, 20220357

Hirt, M.R et al (2023) Light pollution in complex ecological systems Philosophical Transactions of the Royal Society B 378, 20220351

Holker, F et al (2023) Light pollution of freshwater ecosystems: Principles, ecological impacts and remedies Philosophical Transactions of the Royal Society B 378, 20220360

Knop, E et al (2017) Artificial light at night as a new threat to pollination Nature 548, 206-209

Longcore, T et al (2015) Tuning the white light spectrum of light emitting diode lamps to reduce attraction of nocturnal arthropods Philosophical Transactions of the Royal Society B 370, 20140125

MacGregor, C.J et al (2014) Pollination by nocturnal Lepidoptera, and the effects of light pollution, a review Ecological Entomology 40, 3, 187-198

Marchant, J (2020) Moonstruck New Scientist 5th September, 41-45

Parkinson, E & Tiegs, S.D (2023) Spectral composition of light-emitting diodes impacts aquatic and terrestrial invertebrate communities with potential implications for cross-ecosystem subsidies Philosophical Transactions of the Royal Society B 378, 20220361

Sanders, D et al (2023) How artificial light at night may rewire ecological networks: Concepts and models Philosophical Transactions of the Royal Society B 378, 20220368

Seymoure, B et al (2023) A framework for untangling the consequences of artificial light at night on species interactions Philosophical Transactions of the Royal Society B 378, 20220356

Spoelstra, K et al (2023) Long-term exposure to experimental light affects the ground-dwelling invertebrate community, independent of light spectra Philosophical Transactions of the Royal Society B 378, 20220364

Tidau, S et al (2023) Impacts of artificial light at night on the early life history of two ecosystem engineers Philosophical Transactions of the Royal Society B 378, 20220363