THE ECOLOGY AND ECOSYSTEM SERVICES OF INSECTIVOROUS BATS IN RICE DOMINATED LANDSCAPES



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Abstract

Agriculture is a vital artery of the Indian economy, and supports more than half the population. Rice is a key crop of agriculture in the country, but sees consistent loss of yield to insect pests. Successive measures to stem this loss have not had a significant effect and with climate change threatening to further exacerbate the issue, developing biological methods to control pest insects is of prime importance.

This thesis proposes bats – top predators in the rice ecosystem – as a partial solution to the problem of insect pests. The studies detailed within describe bat behaviour in the context of the rice ecosystem from three angles. The first is how the changing conditions of a rice growing season affect the activity of bats. The second is identifying features in the landscape surrounding a rice field that influence bat activity, and the scales at which they are most influential. This would indicate the best design of an agricultural landscape to maximise pest control effect of insectivorous bats. The third is to experimentally test the value added to the rice crop by bats, and the effect that their removal or loss would have on the health and yield of the crop.

By considering one system from these three perspectives, this thesis not only assesses the value of insectivorous bats to rice, but also explores how this value may be bolstered for the benefit of bats and the agricultural industry together.

Set in rice-dominated landscapes of Assam, India, this thesis reports that bats are influenced by insect activity in rice fields, nightly temperature, and moonlight intensity. It also reports that landscape features related to tree cover, such as area of forest within 1km, distance to edge, and distance to forest, as well as urban landcover, all influence the activity levels of bats in rice fields. It also shows finally that when bats are prevented from hunting over crops, it results in a decrease in plant health.

Accompanying these results are more fundamental descriptions of bat morphology and acoustic characteristics from Assam, where such data are scarce, as well as data on the diet of bats active around rice fields. These data have not yet been analysed due to COVID complications, but in due course will add yet another dimension to the system under focus, and increase the resolution with which targeted interventions can be made.

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A doctorate has been likened to the tumultuous period between a wedding and the birth of one's first child. The relationship between a doctoral student and their supervisor is not too dissimilar to an arranged marriage. Spurred on by anxious parents, the student scours the appropriate websites for a suitable partner. Candidate chosen, the pair meet briefly to test the waters. Here they assess one another for shared passions, compatible personalities, and logistical feasibility. All going well, and with the dowry decided upon by a higher power, they embark on a journey of great uncertainty.

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Here it is, my wretched child, delivered with sweat, blood, toil and tears.

Look upon my work, and despair.

Scope

The focus of this thesis, and the studies detailed within, concern the relationship between insectivorous bats and insects in Indian rice fields. With an aim to lay the groundwork for agro-ecological interventions that increase the capacity for bats to suppress insect pests of rice, this thesis describes key patterns in bat behaviour over time and space in rice dominated landscapes and examines the effect of bat predation on the health of the rice crop.

The literature review that follows first reviews the current understanding of bat morphology and behaviour, in so far as it is relevant to this thesis. Given the scarcity of bat literature in India, the introduction necessarily draws from studies across the globe as a starting point. The review dips into bat evolution, and it shaped the morphology and feeding behaviour of insectivorous bats. It the describes the relationship of various habitat types on bat behaviour. The review then sets into context the history of agriculture in India, particularly that of rice, leading to the present day. Starting from the Green Revolution, I examine the factors that drive the growing economic insecurity faced by Indian farmers, and predictions for the future of Indian agriculture.

Chapters 3, 4 and 5 are the empirical chapters of this thesis. They detail three investigations of bat ecology. In order, the chapters examine bat activity patterns over time, over space, and the effect of bat exclusion on rice. Chapter 6 then sets the results of the empirical chapters in the context of the wider bat literature and describes their strengths and weaknesses. It narrates observations form field regarding the roosting ecology of bats. It then lays out direction for future chiropterologists working in India.

The path to this thesis was not straightforward. Not only was it riddled with the numerous potholes that plague all doctoral students, but COVID created an unprecedented

complication that upended many plans. While the three empirical chapters do justice to their objective, other directions of research were interrupted half-way through, and therefore can only be presented as preliminary data. These will be completed in due course, and the story will be richer for it.

CHAPTER 1: Literature review

To predict the behaviour of an animal, simple or complicated, one must first understand the physiological requirements of its body, and the tools it has gained through evolution to meet these requirements in a dynamic environment. From these constraints one may begin to appreciate the decisions – conscious or unconscious, instinctive or learned – that the animal makes, and then, with luck, predict how it will respond to an environment.

1.1 Bat classification

The task of predicting bat behaviour in a particular environment is complicated by a number of distinct morphological and physiological characteristics, and the behaviours that have evolved around them. There are roughly 1400 species of bats in the world, around two-thirds of which are insectivorous (Mammal Diversity Database 2021). Bats were previously classified based on whether their primary mode of orientation was laryngeal echolocation or not into the suborders Microchiroptera and Megachiroptera, respectively. By this classification, Microchiroptera contained all 17 microbat families, while Megachiroptera contained fruit bats of the family Pteropodidae. However, subsequent genetic analysis demonstrated that the microbat superfamily Rhinolophidae were phylogenetically closer to Megachiroptera than they were to other families of Microchiroptera (Teeling et al. 2000). This being the case, laryngeal echolocation must either have evolved twice, in the common ancestors of rhinolophoids, and the common ancestors of the remaining microbats, or it has evolved once in the common ancestor to all bats, but was subsequently lost in the family Pteropodidae (Eick et al. 2005, Jones and Teeling 2006). The latter theory currently holds more weight (Wang et al. 2017, Thiagavel et al. 2018). From an evolutionary perspective, it is more parsimonious to assume that a

system as complicated as ultrasonic echolocation evolved once and was subsequently lost, than that it evolved twice, independently. Accordingly, bats have been reclassified with all megabats and rhinolophoid microbats coming under the newly delimited suborders Yinpterochiroptera, and all microbats sans rhinolophoids under Yangochiroptera.

1.2. Bat morphology

Of the many distinctive features of this order, the capacity for active flight is unique within mammals to the chiropterans. The wing of a bat consists of a thin membrane of skin that stretches between the digits of the elongated forelimb and connects to the body at the ankle. Specialized muscles keep the wing membrane taut during flight (Hedenström and Johansson 2015) and light, flexible bones support the wing membrane under tension without being prohibitively heavy (Anderson and Ruxton 2020). Wing morphology and movement play a central role in determining how and where a bat flies, enabling bats to navigate different habitats, from dense forests to open fields, hunt and forage for a range of food (from agile flying prey to low hanging fruit), and migrate long distances (Denzinger et al. 2016).

Three key features of a bat wing determine the character of its flight: Aspect ratio, wing loading, and wing tip index (Norberg 1994). The aspect ratio of a wing is calculated as the ratio of the length to the mean chord (width of the wing – distance from the leading to trailing edge, which is represented by the red lines in Fig. 1.1). Wings with high aspect ratios are long and thin with greater aerodynamic efficiency (Norberg 1995). They provide lower drag, and allow faster flight but lower manoeuvrability. Due to this, bats with higher wing aspect ratios can travel longer distances and have a greater dispersal/migration ability. Higher aspect ratios are therefore seen in most migratory bats (Fleming 2010) and been found to correlate with greater geographic range (Luo et al. 2019). Wings with lower aspect ratios are short and broad, allowing for greater manoeuvrability, but slower flight.

This enables them to navigate cluttered environments that demand regular abrupt changes in direction. The same principle applies to all wings, which is why stunt planes tend to have short, broad wings, while gliders have long, thin ones. Wing loading is the ratio of the weight of a bat divided by the area of its wing, it speaks to the force that each downstroke must create to support the bat's weight. Higher wing loading forces bats to fly faster in order to stay airborne, reducing their manoeuvrability. These two ratios in conjunction with the shape of the wing tip (wing tip index) dictate the types of flight physically possible by different bats, and the energy spent in each (Norberg 1994).

As with any specialization, the evolution of powered flight was accompanied by, or resulted in, constraints that were accommodated by changes to bat physiology, life history, and behaviour. Powered flight in any form is metabolically costly. Bats have extremely efficient flight (Swartz et al. 2007). Nonetheless, the need to be fast and agile while chasing prey is not without its costs (Voigt et al. 2017). The metabolic costs of flight in bats is many times higher than their basal rate (Thomas and Suthers 1972, Duriez et al. 2014). This imposes an energetic demand that requires bats to eat enormous amounts. Flight also prevents bats from rearing multiple offspring concurrently, since each one needs to be carried and fed, imposing an additional cost. The cost is so high that only a few species from the Vespertilionidae family are known to rear more than one offspring per reproductive season (Barclay and Harder 2003). To make up for the slower rate of reproduction, bats live extraordinarily long lives compared to similarly sized mammals. Resting metabolic rate for a set of temperate insectivorous bats (Vespertilionidae family) was found to be many-fold lower than for a set of temperate insectivorous terrestrial shrews (from the genera *Sorex* and *Crocidura*) (Becker et al. 2013).



Fig. 1.1 Wings of *Megaderma lyra* (top), *Scotophilus kuhlii* (bottom) caught on 1 November and 28 October 2019, respectively, in Puthimari village of Assam's Sonitpur district. Red lines show the length of a 'chord'. Average chord length is a key measure in determining aspect ratio. *Megaderma lyra* has a low aspect ratio and wing loading while *Scotophilus kuhlii* has a relatively high aspect ratio and wing loading. Grid size is 1cm.

1.3 Echolocation

Coupled with flight is a second unusual feature, a sophisticated form of echolocation, which, while not being unique to mammals, is still exceedingly rare. Insectivorous bats have evolved the ability to echolocate by producing high frequency calls between 10kHz and 220kHz (Siemers 2006). These calls, which are usually between 1 and 20ms long (Siemers 2006), interact with the landscape ahead and return as information-laden echoes.

The first experiments that proposed echolocation as the means of orientation in bats were conducted in the late 1700s, and involved disabling the senses of sight, touch, hearing, and smell, to arrive at the conclusion that ears were the most important sense for spatial orientation (de Jurine 1798, Spallanzani 1826, Galambos 1942). This discovery was ignored for over a century before the technology to detect ultrasonic sounds was invented and with it the emission of ultrasonic calls by bats was discovered (Pierce and Griffin 1938).

Echolocation is used for spatial orientation, sociality, broadcasting distress, and foraging. In order to perform these functions nearly continuously, often at great speed, bats not only have specialized vocal systems, but also highly sophisticated auditory and nervous systems precisely tuned to receive and interpret returning echoes (Metzner and Müller 2016).

Most echolocation calls are ultrasonic and therefore attenuate quickly in air. The rate of attenuation varies greatly with call frequency (strong and positive correlation), temperature, relative humidity and atmospheric pressure (Goerlitz 2018). The high degrees of attenuation (over 6db/m in some species) requires that bats emit calls at extremely high amplitudes to receive useful echoes, which imposes an energetic cost (Currie et al. 2020). To minimize these costs, bats have evolved physical, physiological,

and behavioural traits that limit energy expenditure while maximizing resolution in time and space.

One of these adaptations is the synchronisation of wing beats and echolocation pulses (Koblitz et al. 2010). The coupling of the two processes reduces the energy spent per call. The rate of echolocation is high enough for most forms of orientation, and when a higher rate is required, such as when they are close to their prey, the echolocation rate increases, briefly decoupling from wingbeat rate, to provide greater resolution during the final stages of an attack (Stidsholt et al. 2021). This provides another hypothesis for why insectivorous bats are small. Wingbeat frequency is inversely proportional to body size. A larger bat has a slower wingbeat frequency. If coupled to their wingbeats, the rate of echolocation of a larger bat may not be sufficient to detect and track their prey, while at the same time decoupling may be too expensive to be practical (Heller 1995). Bats have also evolved features in their ears, nose, and face to best capture returning echolocation calls (Metzner and Müller 2016), and sophisticated neural pathways to interpret echoes returning from a complex and dynamic environment (Faure and Firzlaff 2016, Pollak 2016).

There are six distinct types of laryngeal echolocation calls produced by insectivorous bats, (and one type of non-laryngeal echolocation by the yinpterochiropteran genus *Rosettus)*. These are (Jones and Teeling 2006):

1. Narrowband fundamental harmonic
2. Narrowband multiple harmonic
3. Short, broadband calls with a fundamental harmonic
4. Short, broadband calls with multiple harmonics
5. Long, broadband, multiple harmonic calls
6. Constant frequency calls.

Within these classifications, different species can often be distinguished by the frequency of their echolocation calls. The type of echolocation call produced by a species is an adaptation to its habitat and foraging strategy. As a result, much can be gleaned about the ecology of a bat by the characteristics of its call (Denzinger et al. 2016).

1.4 Life history

Insectivorous bats are, in general, smaller than their frugivorous cousins. While the largest fruit bat, the giant golden crowned flying fox (*Acerodon jubatus)* weighs 1200g, insectivores typically range from 2g to 160g. This is partly because body size scales inversely with echolocation call frequency (Jones 1999, Thiagavel et al. 2017) and partly because weight and wing surface area do not increase proportionally, meaning that larger bats don't generate the same amount of lift per gram, making them slower and less agile (Brigham 1991, Hutcheon and Garland 2004). Fruits, unlike insects, don't try to run away when chased. Fruit bats can therefore afford to be slow fliers. Insectivorous bats can't.

Many small mammals survive and thrive with low body fat levels and high metabolisms, indeed metabolic rate scales inversely to body size. This relationship is not linear, however, and as a result the per-gram metabolic rate of larger animals is lower than that of smaller animals (Lomolino et al. 2017). In bats the limitations of low body fat and high metabolism are compounded by high average body temperatures and large surface area to mass ratios (Yalden and Morris 1975, O'Shea et al. 2014), which makes them particularly vulnerable to both daily and seasonal changes in climatic conditions (Geiser and Stawski 2011). This is especially true of females as their reproductive cycle plays a large role in dictating energy demands (Rydell 1993), and they must time parturition to favourable conditions to ensure their young have the highest chance of survival (Lewis 1993).

1.5 Abiotic factors

1.5.1 Temperature

In adapting to a variety of environments, and to cope with the demands of powered flight, bats have evolved a significantly larger thermal range than most homeotherms. These adaptations enable bats to survive extremes of high and low body temperatures. Many bat species, particularly insectivores, are heterothermic and have the ability to temporarily reduce their metabolic rate and body temperature in a process known as torpor (Lyman 1970, Stawski et al. 2014). Torpor, which is seen in most bat families (Yuan et al. 2011), allows bats to survive suboptimal temperatures. It also enables bats to reduce their energy expenditure, and as a consequence, reduce the time spent hunting. This allows them to survive low food availability and reduces the risk of predation (Geiser and Stawski 2011, Stawski et al. 2014).

The ability of bats to enter torpor varies, with some species only capable of short bouts within a day (Geiser et al. 2011) while others maintain torpor for multiple days at a time (Geiser and Ruf 1995, Stawski and Geiser 2010), or even hibernate (Jonasson and Willis 2012). This behaviour is not, as one might assume, limited to locations of extreme temperatures (Stawski et al. 2009). Bats all over the world, including those in the tropics and subtropics exhibit torpor, with the ability more prevalent in smaller species, and used more often in colder winter periods (Stawski et al. 2014).

High temperatures are also problematic. Less than 20% of the energy consumed during flight is used for mechanical action, the rest becomes heat (Speakman et al. 2003). In hot environments, or during prolonged flight, bats need to get rid of excess heat quickly. A lot of heat loss occurs through regional heterothermy. The large surface area of the wing makes it an ideal organ for heat loss. Hot spots on the wing, rich in arteries and veins, are flushed with blood when the body needs to be cooled, while blood flow is restricted when

heat needs to be conserved (Reichard et al. 2010). Maximum wing temperatures during flight can increase by 1.9-5.3°C, to over 40°C (Luo et al. 2021).

If ambient temperatures are above normothermic body temperatures, then passive methods of heat loss are not effective and active methods, such as evaporative cooling, need to be employed (Maloney et al. 1999, Cory Toussaint and McKechnie 2012). In arid environments, these methods might require an unsustainable loss of body water (Czenze et al. 2020). Species adapted to such environments have evolved methods to conserve water, such as concentrating urine. Another way that bats regulate hyperthermic condition is torpor. While torpor is primarily seen as a heat saving mechanism during hypothermic conditions, bats use it to reduce their metabolism below resting metabolic rate, and consequently reduce water loss, during hyperthermic conditions (Reher and Dausmann 2021).

1.5.2 Humidity and rain

Changes in atmospheric humidity can have a marked effect on energy expenditure during flight. In a low-humidity environment, bats can lose up to 30% of their body mass in a single day to evaporation (Webb et al. 1995). High humidity in the atmosphere and in roost sites results in lower water loss through the lungs during flight (Lacki 1984) and roosting (Webb et al. 1995). High humidity also increases the cost of echolocation by significantly increasing the rate of atmospheric attenuation, requiring bats to emit louder calls to have the same effect (Griffin 1971, Goerlitz 2018). Bats in humid environments have been found to have lower call frequencies, or modulate their call structure based on the season, in response to these costs (Snell-Rood 2012).

Rain is usually accompanied by an increase in humidity. Compounding increased call attenuation due to humidity, raindrops also directly interfere with echolocation calls by creating physical clutter in the air and increasing ultrasonic noise (Geipel et al. 2019).

Wet fur imposes an additional weight and changes the aerodynamic properties of wings, thereby increase the thermoregulatory costs of flight. Water being a good thermal conductor, wet fur could also result in more rapid heat loss (Voigt et al. 2011). This makes flight during rain considerably more taxing than normal. However, while heavy rainfall generally decreases bat activity, low-moderate rainfall typically does not (Bateman and Vaughan 1974, Appel et al. 2019, LaVal and Lawton 2021).

1.6 Biotic factors

1.6.1 Predation pressure

The nocturnal behaviour of bats is hypothesised to have originated during the 'nocturnal bottleneck', a period during mammal evolution when ectothermic predators were confined to the day, imposing a selection pressure on endotherms to be active at night (Gerkema et al. 2013). In the present day, what keeps bats nocturnal is the presence of diurnal predators, competition with insectivorous birds, and the risk of hyperthermia (Speakman 1995). However, while predation pressure might push bats to emerge from their roosts later, the presence of crepuscular prey entices them to emerge earlier. One would expect that for a given roost, all the individuals within would emerge more or less simultaneously, at a time where they incur the least risk while benefiting the most from prey availability. Yet this is not the case.

From the same roost, different individuals make different decisions on when to emerge, which is thought to reflect the perceived risk-reward trade-off for that individual. Pregnant and lactating bats, despite being slower, have significantly higher energetic demands, and so they risk higher levels of predation by emerging earlier. Sub-juveniles, yet to be weaned, needing fewer calories because they are still being fed by their mothers, and being at greater risk of predation because they are not yet adept fliers, emerge later (Duvergé et al. 2000). In species that do not hunt crepuscular insects, whose prey are

available through the night, emergence times are far later, minimising the risk of predation without compromising their nutritional intake (Jones and Rydell 1994).

While diurnal predation pressure keeps bats in their roost for longer, nocturnal predators also have their say in when and where a bat hunts. This is particularly true on moonlit nights, when nocturnal predators (such as owls) that rely on vision are at a distinct advantage. The same trade-off considered in the case of emergence times arises once more in the context of moonlight. Slow flying species and open spaces make for very risky flight when predators have greater ability to detect their prey visually. As in the case of emergence time (Rydell et al. 1996, Thomas and Jacobs 2013), some bats in some landscapes incur greater risk of predation than others and, having seemingly weighed this risk against nutritional requirements, adjust their behaviour accordingly (Meyer et al. 2004, Lima and O'Keefe 2013).

The term 'Lunar phobia', was coined in 1978 (Morrison 1978) to describe the reduced activity of some bat species on bright nights. The prevailing hypothesis to explain this behaviour is that predation pressure by nocturnal predators (primarily birds) increases on bright nights and this limits bat activity in both space and time (Meyer et al. 2004, Saldaña-Vázquez and Munguía-Rosas 2013, Lima and O'Keefe 2013, Appel et al. 2017).

This is supported by patterns of lunar phobia among bats under different degrees of predation pressure. Bats that can hunt in cluttered habitats (Meyer et al. 2004), those found on islands free of visually orienting predators (Gannon and Willig 1997, Rodriguez-Duran and Vázquez 2001), and those which are fast, agile flyers, show lower levels of lunar phobia, most likely due to the lower risk of being caught by visually orienting avian predators (Karlsson et al. 2002, Holland et al. 2011).

And, while causation remains unproven, severity of lunar phobia between tropical and temperate bats is believed to be different, reflecting with the fact that tropical bats,

which exhibit stronger lunar phobia, tend to coexist with larger communities of avian predators than temperate bats. The former are also, on average, larger and slower than their temperate cousins, making them easier to catch (Karlsson et al. 2002, Saldaña-Vázquez and Munguía-Rosas 2013, Roeleke et al. 2018a).

1.6.2 Prey availability

Just as bat behaviour is influenced by predator activity, so also insect prey of bats are influenced by their activity. For bats with lower levels of predation pressure, prey activity and distribution can have a dominating influence over their activity patterns. Insects are the primary food source of most bat species and their activity is influenced by a swathe of factors including predation pressure, moonlight, season, food availability, temperature, and humidity (Meyer et al. 2004, Lang et al. 2006, Khaliq et al. 2014, Zhu et al. 2017, Owens et al. 2020). In adapting to predation by bats, many flying arthropods concentrate their activity around sunset, at a time when diurnal predators may still be active (Rydell et al. 1996, Duvergé et al. 2000), with some insect species showing a second, smaller peak before dawn (Turner 2013). In order to maximise hunting success, bats which hunt these insects can also show a bimodal pattern in activity (Hayes 1997, Pavey et al. 2001, Esbérard and Bergallo 2010, Malmqvist et al. 2018). But despite an abundance of prey at dusk, bat activity is usually limited to darker hours to avoid predation by diurnal raptorial birds (Jones and Rydell 1994, Mikula et al. 2016, Malmqvist et al. 2018).

Bats which hunt aerial insects at dusk tend to be faster, more agile fliers, and so can afford to be out earlier as the risk of predation is lower than it is for slower bats. On the other hand, many moths are active more or less all night. Bats which hunt them, or those gleaning insectivores that hunt diurnal insects that are asleep at night, emerge later as early emergence would needlessly increase the risk of predation for little or no gain (Jones and Rydell 1994).

Although varying by species and location, patterns in insect activity have also been documented to track the lunar cycle (Brown and Taylor 1971). Insect species that are hunted by visually orienting predators benefit from darkness and tend to show lunar phobia, while those that are hunted by predators using acoustic or olfactory cues benefit from increased light, as they can see their predators coming and avoid them, and so are more active during bright periods (Lang et al. 2006). Bats which hunt lunar-phobic insects have a lower incentive to hunt during bright nights, when both predation pressure is higher and prey availability is lower (Meyer et al. 2004) On the other hand, bats which hunt lunar-philic insects have more to gain from hunting on bright nights but, depending on habitat and agility, might also incur a greater risk of predation. Lang et al. (2006) documented this for *Lophostoma silvicolum* within Barro Colorado Island, Panama. *L. silvicolum*, an understory perch-hunting insectivore, was active earlier (relative to dusk) around a full moon, despite the higher predation risk, coinciding with brief peaks in insect activity around these times. Similarly, Appel et al. (2017) documented two insectivorous species – *Pteronotus parnellii* and *Saccopteryx leptura* – in Brazil to increase their activity levels on bright nights. They postulated this to be due to the increased activity of those prey species that dominated their diet on moonlit nights. This would assume that the benefits of being more active on such nights outweighed the predation risk.

1.6.3 Eavesdropping

Due to the specialization of bat echolocation calls, unintended information regarding the species and sex of the sender and, importantly, the activity they are engaged in, are broadcast to anyone listening (Lewanzik et al. 2019). A search phase call (used for orientation) sounds different from a social call which, in turn, is very different from a feeding buzz. This makes it possible for other bats in the area to discern what activity their neighbours are engaged in (Jones and Siemers 2011) and to use this information to their

benefit. This is particularly valuable to bats hunting prey swarms that are unpredictable, patchy and transient (as insect swarms often are), which can neither be tracked at the start of each night, nor monopolized. Staying within earshot of their neighbours and eavesdropping has been shown to increase their prey detection range by over ten-fold, significantly improving their hunting success (Dechmann et al. 2009, Cvikel et al. 2015).

With conspecifics, eavesdropping bats can be sure that more feeding buzzes imply greater prey density and, consequently, most species are attracted to conspecific calls (Dorado-Correa et al. 2013, Übernickel et al. 2013). However, if too many conspecifics hunt the same insect swarm, their hunting success reduces dramatically because their attention is continuously diverted by the calls of other bats (Cvikel et al. 2015, Roeleke et al. 2018a, Lewanzik et al. 2019).

Heterospecifics with similar feeding ecologies broadcast more useful information to each other than those with dissimilar feeding ecologies. The former are likely to be hunting prey edible to the eavesdropper (Goodale et al. 2010, Hügel et al. 2017), while the latter are less likely to. As a result, similarity in diet affects the degree to which eavesdropping bats respond to calls of other species (Lewanzik et al. 2019).

Prey abundance is closely tied to competition. While two conspecifics impose roughly equal levels of competition on one another, with two heterospecifics this relationship can be quite skewed. The incentive for bats to respond to the feeding buzzes of heterospecifics is therefore affected by the inferred prey densities and the competitive advantage, or lack thereof, of the broadcasting species (Übernickel et al. 2013)

1.7 Feeding guilds

The ability of a bat to hunt an insect in a particular environment depends on it being able physically to navigate said environment and to accurately identify and capture its prey on the wing. These two aspects of hunting – orientation and tracking – rely on the wing

morphology and echolocation characteristics of the bat. Hence these two features are often used to categorise bats into feeding guilds (Denzinger et al. 2016). Fenton (1990) was the first to categorise the foraging habitats of insectivorous bats into three distinct habitats: open, cluttered/closed, and edge. These terms identify the acoustic characteristics of the habitat, which in turn determines the adaptations that bats need to navigate and forage in them.

1.7.1 Open-space foragers

Open-space foragers hunt in environments where the only loud echo that returns is what bounces off their prey. Background objects are scarce or far away, making the separation of prey from background easy. However, the same openness means that bats need to search a larger volume of space for prey and, having located them, need to catch them mid-air. As a result, open-space bats tend to have long, low frequency calls that are shallowly modulated. Duty cycle is proportion of time spent emitting calls in a unit time. Short calls with long gaps in between have low duty cycles, long calls with short gaps in between have high duty cycles. Open-space foragers tend to have high duty cycle calls, which increases their chance of detecting prey because movement by an insect is less likely to be missed. Lower frequencies attenuate less rapidly in air, allowing bats to detect prey further away. And, by keeping the signals relatively narrowband, open-space foragers can focus their auditory and neural sensitivity to a narrower range of frequencies, increasing the sensitivity to the returning echo, and therefore the detection ranges (Denzinger et al. 2016). To catch fast airborne prey, and sustain fast flight, open-space foragers usually have pointed wings with high aspect ratios and high wing loading (Norberg and Rayner 1987).

1.7.2 Clutter/Narrow-space foragers

Clutter space foragers hunt in dense vegetation, where the echoes bouncing off their prey and off the background overlap. Clutter space foragers issue very different calls depending on whether they are active or passive gleaners, which we shall investigate next. In order to navigate cluttered spaces, narrow-space foragers have short, broad wings with low aspect ratios and low wing loading (Norberg and Rayner 1987, Arita and Fenton 1997).

1.7.3 Edge-space foragers

Edge-space foragers hunt airborne prey against an acoustic background such as vegetation, buildings or water. While the echoes of the background do not overlap with that of the prey, they follow shortly after. The background echoes are used to judge distance as a bat hunts prey in the foreground. The wing morphology of edge-space bats depends on their mode of foraging.

Within these three broad categories, bats can also be subdivided into feeding guilds based on the manner in which they hunt prey (Denzinger et al. 2016).

1. Arial hawkers hunt on the wing, catching flying prey. These are normally open or edge-space foragers.

2. Trawlers catch prey from the surface of water bodies. These are edge-space foragers who use the surface of the water as an aid to detecting prey.

3. Gleaners catch prey sitting amid clutter. To distinguish prey from background clutter, they use one of three methods:

    a. Passive gleaners use other senses such as smell, sight, or listening for prey-generated sounds to identify their prey among the clutter (Bell 1985, Goerlitz et al. 2008).

    b. Flutter detectors listen for modulations in the returning echo, caused by the fluttering of wings, which indicate the presence and location of prey (active

gleaning). These bats emit long, constant frequency (CF) calls to detect their prey. Sound waves that have reflected off moving objects (such as insect wings) cause a deviation from the expected echo, which is detected by a highly attuned auditory and nervous system (Roverud et al. 1991, Denzinger et al. 2016).

c. Active gleaners detect motionless prey in cluttered environments using short, broadband, high frequency calls that explore the texture of a leaf, identifying insects from their characteristic shapes (Geipel et al. 2013).

1.8 Landscape requirements

Bats have physical and physiological requirements that they need to meet and limits that they must survive within. Their energetic demands are affected by a number of internal and external conditions detailed above, and their morphological characteristics describe the types of habitats that they may exploit. Given these constraints, bats can be highly selective when choosing the landscapes in which they roost and forage. Key features in the landscape influence key drivers of behaviour – such as prey availability, predation risk, and energetic costs – and are therefore strong determinants of the distribution and activity levels of bats.

1.8.1 Agricultural fields

Agricultural fields present interesting landscapes to insectivorous bats. Some types of agriculture, such as cacao, oil palm, vineyards or orchards, present perennial forest-like habitats (Charbonnier et al. 2021). Here the contrast to natural vegetation is relatively low and insect abundance remains relatively consistent over time, although seasonal changes are still felt, reflecting changing weather, the ripening of the crop, the application of pesticide, or the state of the surrounding vegetation.

Other types of agriculture are more complicated. Rice, the focus of this thesis, can be grown in one, two or three seasons per year. Rice fields can harbour rich biodiversity, which is strongly influenced by the management strategy and heterogeneity of the surrounding landscape (Way and Heong 1994, Lou et al. 2013, Dominik et al. 2018). Depending on the location of the farm and cultural practices of the farmers, water availability, the application of chemical pesticides and the application of fertilizers can vary significantly, all of which affect bat activity (Toffoli and Rughetti 2017, 2020, Sedlock et al. 2019).

Bats that can hunt in the open landscapes of rice fields are faced with seasonal fluctuations of prey. While these fields are extremely prey-rich during the growing season (Puig-Montserrat et al. 2015, Azofeifa et al. 2019), between seasons, when plots are left fallow, particularly in landscapes devoid of natural patches or bunds, the insect community is reduced (Way and Heong 1994), and bats must find alternative food sources. Herein lies the importance of the surrounding landscape, and the presence of alternative sources of prey.

1.8.2 Water

Water is a critical resource for bats. Bats in arid environments lose up to 30% of their body mass to evaporation every day (Webb et al. 1995). In arid environments, where water bodies are few and far between, and where high temperatures, low humidity, and erratic rainfall add to water stress, the distribution of water bodies in a landscape can have a large influence on bat behaviour (Korine and Pinshow 2004, Williams and Dickman 2004, Adams and Hayes 2008).

Bats drink on the wing, with the small agile species capable of drinking from narrow water troughs (Tuttle et al. 2009, Russo et al. 2012), while less agile species need larger bodies of water. This means that even small, temporary water bodies can meet the water

demands of many species, but that species richness and activity increase with size of the water body (Razgour et al. 2010).

Some species have evolved mechanisms to conserve water, including the production of highly concentrated urine and the use of torpor (Reher and Dausmann 2021), while other species interrupt hibernation to drink (Boyles et al. 2006). The importance of water bodies as a means to combat dehydration, leads bats to select roost and foraging sites based on their proximity to water sources (Adams and Thibault 2006, Adams and Hayes 2008, Campbell 2009, Rainho and Palmeirim 2011). Even in water-rich environments, water bodies can attract large populations of insects, which, in turn attract bats (Grindal et al. 1999, Rogers et al. 2006). Water can be especially important for females during pregnancy and lactation, influencing roost selection and driving them to visit water bodies far more often than non-breeding females (Adams and Hayes 2008).

1.8.3 Urban land

Urban areas present a complicated landscape to bats. On the one hand, urbanization is accompanied by increasing noise, air, and water pollution (Moretto and Francis 2017). On the other hand, roosting sites and foraging areas can be abundant, making them valuable to those species that can exploit them.

Urbanisation does not occur in a bubble. Changes to the chemical environment and landscape structure, levels of pollution, and anthropogenic activity in general do not stop at the gates of a city but typically gradually decease as one gets further away (Grimm et al. 2008). The effects of urbanization can be evident at great distances. Positively phototactic insects are attracted to cities by the diffuse sky glow and then to streetlights, where they find themselves trapped by instinctive behaviours driving them to the light (Owens et al. 2020). Street-lights act as deadly beacons to such insects and have a catastrophic effect on urban and semi-urban insect populations (van Langevelde et al. 2017, 2018) They also

inadvertently create prey-rich feeding areas for bats (Jung and Kalko 2010, Firebaugh and Haynes 2019). Just as moonlight increases the hunting success of predatory birds on bats, so do artificial street-lights. Unlike moonlight, however, street-lights also provide focussed prey-dense feeding grounds, prompting bats to aggregate near them, thereby exposing bats to increased levels of predation by nocturnal predatory birds (Hartley and Hustler 1993).

Overall, the capacity of urban spaces to host bats is strongly linked to the benefits they provide. As such, having green spaces within or near urban land can increase the use made of urban structures as roosting sites. Features that increase the canopy cover, including parks and patches of natural vegetation in cities have been shown to increase the activity of bats (Avila-Flores and Fenton 2005, Dixon 2012, Bailey et al. 2019).

Species specific responses of bats to landcover mean that each species or community of bats reacts differently to urbanization. While the general trend of urbanization is a decline in species richness and activity (Ancillotto 2015, Jung and Threlfall 2016), as with many mammal orders, generalists capable of doing so adapt and remain (Scanlon and Petit 2008, Schoeman 2016). In the right setting, activity levels might remain quite high, despite a decrease in species richness.

1.8.4 Forests

As natural land is converted for human purposes, areas of large, unbroken forests are diminishing across much of the world. Much of this conversion is for production of commodities (Curtis et al. 2018), leaving increasingly fragmented patches behind. As with most landscape changes, the responses of bats to fragmentation are species- and context-specific (Estrada-Villegas et al. 2010, Ethier and Fahrig 2011, Núñez et al. 2019). Wing morphology and foraging strategy are key determinants of a bat's response to habitat fragmentation (Norberg and Rayner 1987, Denzinger et al. 2016). The degree and manner

in which a bat interact with forests also dictates the impact that forest fragmentation will have on it.

While clutter space foragers rely on dense forests for roosting and foraging, many edge and open-space foragers also use forests to roost, or the edges of forests to hunt. Distance to the nearest forest is often a key predictor of bat activity in agricultural landscapes (Heim et al. 2015, Treitler et al. 2016, Rodríguez-San Pedro et al. 2019). The characteristics of a forest – such as whether it is a primary or secondary forest – can also impact the predation pressure and prey availability of a forest, thereby affecting bat activity (Gallagher et al. 2021, Appel et al. 2021).

Forest fragmentation almost always results in smaller patch areas, greater patch isolation, and a host of microclimatic changes. The responses of bats can be specific to one or more of these factors. In addition, the composition of the matrix plays a large role in determining the strength and direction of the response of bats to fragmentation (Estrada-Villegas et al. 2010).

Forest specialists, species that roost in trees, or forage in cluttered spaces, show a generally negative response to isolation and area effects (Struebig et al. 2008, Estrada-Villegas et al. 2010). On the other hand, edge and open-space foragers in forest-dominated landscapes often show insignificant or positive responses to fragmentation (Struebig et al. 2008). The edge effect often results in very high insect abundance at the borders of forests. While both area and isolation effects impact bat communities, small forest patches, even isolated ones, are still valuable habitats for bats (Meyer and Kalko 2008).

Many bats use different habitats for hunting and for roosting. This feature requires them to commute from their roosting sites to their foraging grounds. It also means that landscapes featuring both habitats in close proximity can be ideal for bats, because shortened commuting times result in more time spent resting or feeding. The presence of different habitats near each other, termed landscape complementation, can arise due to

fragmentation or forest management and can increase the activity of some bat species (Loeb and O'Keefe 2011, Ethier and Fahrig 2011).

1.9 Economic and environmental value of bats

1.9.1 Bioindicators

Starting in 2009, with a paper titled 'Carpe noctum: The value of bats as bioindicators', bats have been championed as indicator species for various measures of ecosystem health (Jones et al. 2009, Russo and Jones 2015) In part due to these arguments, policy at the international level has reflected the widely held view that bats make excellent bioindicators and the paper by Jones et al. (2009), which has been cited 950 times as of January 2022, was often at the heart of any suggestion that bats be conserved for their value as bioindicators.

Recent studies have tempered this enthusiasm (Russo et al. 2021). Bioindicators are used to detect environmental disturbance, detect the consequences of environmental change on biotic systems, or reflect a measure of biodiversity for a particular environment (McGeogh 1998). Good indicator species demonstrate characteristics such as being: (i) widespread in certain environments; (ii) representative of multiple other taxa; (iii) sensitive to key changes in their environment; and (iv) easy to sample and identify (McGeogh 1998, Parmar et al. 2016).

Some of these feature are seen in bats, others are not. While bats are sensitive to changes in their environment, determining which among the plethora of factors that have changed elicited a response in a bat population is difficult. This is further complicated by the fact that the response of bats to change is not only species-specific, but also context-specific, making extrapolation of results from one set of circumstances to another difficult. Monitoring and tracking bats is also complicated. While acoustic monitoring of bats is increasingly common, many species are acoustically indistinguishable from other species

due to high intra-specific variation in call structure (Russo et al. 2017). On the other hand, using genetic methods to identify bats requires capturing them, which remains logistically and legally cumbersome. Many other reasons also limit the use of bats as bioindicators (Russo et al. 2021).

1.9.2 Ecosystem services

In thinking of bats as ecosystem service providers, and with fruit bats being the most recognisable among the general public, the service of seed dispersal is usually the first and only service recognised. Fruit bats do indeed disperse the seeds and pollinate the flowers of hundreds of plants (Shilton et al. 1999). However, as the majority of bat species are insectivorous, and the focus of this thesis is the bat–insect relationship, we shall concentrate on the ecosystem service of pest control by bats. This is a service not quickly acknowledged by the wider public, but is one of the most important ecosystem service provided by bats (Boyles et al. 2011, Kunz et al. 2011).

Due to their high metabolism, bats consume a significant proportion of their bodyweight in insects every night (Kurta et al. 1989, Kunz et al. 2011, Moiseienko and Vlaschenko 2021). The reproductive cycle, in particular, dramatically changes the energetic requirements of bats. Females need to consume far more when pregnant and lactating (Kunz et al. 1995). To meet these requirements, pregnant and lactating bats become more generalist feeders (Anthony and Kunz 1977), preferring energy-rich prey when convenient (Kunz et al. 1995), and they also mobilize internal fat stores (Mclean and Speakman 1999). They also brave increased predation risk by emerging from their roosts earlier, thereby allowing them to spend more time foraging (Duvergé et al. 2000). During peak lactation, a single female Brazilian free-tailed bat will consume 10-20 cotton bollworm moths – a key pest of cotton – per night. Given that these bats roost in colonies of up to a million, the cumulative effect on insect pests can be substantial (Cleveland et al. 2006).

In agricultural landscapes, bats hunt and eat insect pests of various crops. Studies that have documented the diet of bats in agricultural landscapes have found that they consume a range of insect pests. These include pests of rice, such as the swarming armyworm (*Spodoptera mauritia*) (Kemp et al. 2019), the grass webworm (*Herpetogramma licarsisalis)* (Kemp et al. 2019), and the white-backed planthopper (*Sogatella furcifera*) (Leelapaibul et al. 2005); pests of corn such as the corn earworm (*Helicoverpa zea)* (Lee and McCracken 2002, McCracken et al. 2012) and the fall armyworm (*Spodoptera frugiperda*) (Lee and McCracken 2005); and pest of cotton such as the cotton webspinner (*Achyra affinitalis*) and Australian bollworm (*Helicoverpa punctige)* (Kolkert et al. 2020a). It is important, however, to note that bats also consume arthropods such as spiders (Pavey et al. 2001) and ants (Brigham 1990, Levin et al. 2009), which are themselves predators of insect pests, so the net effect on pest populations is not always a straightforward calculation.

The predation of agricultural pests by insectivorous bats is an interaction that has been acknowledged for many decades. The quantification of this value, however, only began in earnest in the last fifteen years. The methods used in these studies have varied greatly, as have the assumptions regarding the multitude of ecological interactions in play in agricultural ecosystems. Most methods used to evaluate the financial benefit of having bats preying upon agricultural pests centre around diet analyses (Cleveland et al. 2006, Wanger et al. 2014), mathematical models (Federico et al. 2008), exclusion experiments (Maine and Boyles 2015), and landscape scale manipulations of bat populations (Puig-Montserrat et al. 2015).

The highly species-specific responses of bats to their environment makes generalization a dangerous thing to do. Nonetheless, when it comes to the ability of bats to suppress insect pests of agricultural crops, the results tend to be positive or non-significant (Cassano et al. 2016, Ramirez Fráncel et al. 2021) and only very rarely negative (Karp and

Daily 2014). Among the studies reporting positive results, larger estimates tend to come from those that used diet analyses to calculate avoided costs to agricultural industries due to the presence of bats (Boyles et al. 2011, Wanger et al. 2014). Exclusion experiments also, by and large, report negative effects on crop yield and plant health when bats are excluded (Maas et al. 2013, 2016, Maine and Boyles 2015) as well as increases in insect abundance, although the latter is not measured as often, and is not as strong an effect.

One of the largest and most widely cited estimates of pest control by bats placed the value of bat pest control at $3.7-$53 billion per year for the United States of America (Boyles et al. 2011) based on data published between 2001 and 2005. This estimate was an extrapolation of a previous study (Cleveland et al. 2006), which estimated the value saved by Brazilian free-tailed bats (*Tadarida brasiliensis*) on the cotton industry of eight counties in Texas. Cleveland et al. (2006), in turn, based their estimate on two papers that described the diet of *T. brasiliensis* (Lee and McCracken 2002, 2005), and two that described the life histories of *Helicoverpa zea,* the cotton bollworm (Sansone and Smith 2001, Sansone 2002). Cleveland et al. (2006) made assumptions regarding the life history of the insect pest – here the cotton bollworm – and the effect that one species of bat consuming an estimated number of insects per night would have on the total yield of cotton. Boyles et al. (2011) further extrapolated from the 8 counties in Texas focused on by Cleveland et al. (2006), to every bat species and every crop in the United States of America. This study by Boyles et al. (2011) has since received criticism for the number of assumptions and degree of extrapolation (Fisher and Naidoo 2011). Nonetheless, the fact remains that the bat-pest interaction in an agricultural setting contains complexities that make sophisticated estimates difficult, and accurate extrapolations over time and space nearly impossible.

Given the complexities of an agricultural food web, the method that requires the fewest assumptions is exclusion experiments. These theoretically straightforward

experiments usually involve treatment and control plots where bats are excluded from the crop within the experimental plots and given full access to the control plots. Measures of plant health, crop yield, and insect population sizes are compared between the two plots to quantify the effect of bat exclusion. From this, inferences are made regarding the value added by bats to the crops.

Early exclusion experiments designed to investigate the ability of birds to control agricultural pests didn't consider the effect of bats. As a result, treatment plots were often covered around the clock, excluding bats as well. Despite confounding the effect of birds and bats, many studies attributed the entire result to birds (Van Bael et al. 2003, Koh 2008, Borkhataria et al. 2012).

While more recent studies have recognised the large role that bats can play in suppressing pests (Kunz et al. 2011, Maas et al. 2016), the practical nature of bat exclusion experiments – and the logistical challenges they present – have resulted in fewer such experiments being conducted, and there has been a bias toward Neotropical countries (Maas et al. 2019).

At the heart of the ideal bat exclusion experiment is the ability to observe and measure changes in a food web after the removal of a top predator. While exclusion experiments automatically account for changes in the food web several levels down from a top predator, something that diet analyses can't, they are not without their shortcomings. Accurate estimates of bat pest control require that birds have full access to both treatment and control plots, meaning that the nets used to exclude bats are not in place during the day. In a recent review of bat and bird exclusion experiments, only 7 out of 30 exclusion experiments included bat-only exclusion, all of which involved tree and/or bush crops, with coffee and cacao dominating the list (Maas et al. 2019). A notable exception to this trend is Maine and Boyles (2015), which excluded bats from corn fields in the USA.

The logistical constraints of building and manipulating bat exclosures also limit their size. This means that bats can fly and hunt above the enclosures, diluting the effect of the treatment enclosure. With small enclosures, bats hunting around the edges – which may be attractive acoustic edges – can produce echolocation calls that travel into the enclosure, influencing the behaviour and fitness of insects within (Surlykke and Kalko 2008, Kunz et al. 2011).

1.10 Indian agriculture

In the early 1960s, India was staring down the barrel of famine (Nelson et al. 2019). Until that point, agricultural production increased primarily through expansion of the area under cultivation (Estudillo and Otsuka 2013). By the 1960s, most arable land was already under cultivation and production of the primary food crops, including rice, could not keep up with the rapidly growing population.

Recognising the impending disaster, two research institutes, the International Rice Research Institute (IRRI), in the Philippines in 1960, and International Maize and Wheat Improvement Centre (CIMMYT), in Mexico in 1967, were established by the Rockefeller Institute and the Ford Foundation to tackle the problem of food security (Dalrymple 1985). These institutes, among others, studied native crops, such as rice, maize, and wheat, and developed the first genetically modified, high yielding varieties of these crops.

In 1966, the IRRI introduced IR5 and IR8, the first of many modern varieties (MV) of rice. These boasted short growth duration, high quality yield, and photoperiod insensitivity (Khush 2001). In the decades that followed, newer strains of MVs continued to be developed. These had even shorter growth durations, were productive in nutrient deficient soils, and were disease and insect resistant (Khush 1987, 1995).

The introduction of MVs in India was complemented by sustained private and governmental support in the form of subsidies for fertilizer, water and power, substantial

investments, and campaigns to educate farmers about farming techniques (Hazell 2009, Pingali 2012). Between 1965 and 1994, rice yield in India grew from 0.85 to 1.80 ton/ha, driven by a 68% adoption of modern varieties from 1963 to 1994 (Evenson and Gollin 2002).

Without a doubt, food security improved in the years following the Green Revolution, saving millions from starvation. However, while it alleviated hunger, it did not solve the root cause of the problem. The population of India continues to grow at an unsustainable rate and food security is an increasing problem. The various methods employed by the agricultural industry dramatically increased food production, but as time passed the environmental and social side-effects began to make themselves known (Nelson et al. 2019, John and Babu 2021).

To begin with, MVs were extremely responsive to fertilizers, and, encouraged by government subsidies on fertilisers, their use increased significantly (Hazell 2009). Pesticide use also became more widespread, but, with weak regulation, pesticide application is indiscriminate, both in quantity and in the type of chemical being used (Bowonder 1979, Abhilash and Singh 2009). Many of the most damaging pests in South-East Asia were of minor importance prior to the green revolution. These pests, particularly the brown planthopper (*Nilaparvata lugens*), have evolved resistance to high levels of chemical pesticides and to pest resistant varieties of crops, and now dominate the list of harmful pests (Stout 2014, Thorburn 2015).

Since modern varieties were photoperiod insensitive – meaning that they could be grown in any season – the number of crops grown per year increased, and with it grew the need for water and the depletion of nutrients from the soil (Estudillo and Otsuka 2013). Where previously farmers relied exclusively on rains or rivers, since the Green Revolution they have grown increasingly dependent on irrigation. Water use in many parts of the

country was and is unsustainable, and has led to a greater frequency and intensity of droughts (Singh 2000, Gupta and Deshpande 2004).

India has the second largest population in the world, predicted to surpass China by 2050. Food production has not kept pace. India currently ranks 101st out of 116 countries (with sufficient data) in the Global Hunger Index (IFPRI 2021). The conversion of natural land for agricultural purposes continues apace both globally (Malhi 2017) and, specifically, in India (Tian et al. 2014). This is neither sustainable for the country's shrinking biodiversity, nor an effective method to meet the growing demand for food, yet without both intensification and expansion of agricultural land, the disparity between food production and consumption is only going to increase (Hinz et al. 2020).

The agricultural industry around the world is predicted to come under increasing strain due to climate change at the same time as demand is going to skyrocket (FAO 2011). Predictions of the future foretell of increasingly erratic weather that will cause significant decreases in agricultural productivity (Lal 2011, Kutywayo et al. 2013, Hatfield et al. 2020). Pests are predicted to cause increasing damage as warming temperatures increase metabolic rates and changing distributions (Ladányi and Horváth 2010, Kutywayo et al. 2013). Changing distributions could result in a decrease in predation pressure as pests disperse to areas outside the range of their natural enemies (Thomson et al. 2010).

Indian farmers are already under immense strain due to insufficient state support, increasing frequency of erratic weather, and crop loss due to pests. In the 1960s, when availability of farmland became a factor limiting increased production, modern varieties allowed farmers to eke more yield out of their farms. In the 2020s, the improvement offered by new strains of rice is only incremental. Insect pests in India currently cause losses in yield of 18% every year (Deutsch et al. 2018). Hence, approaches to pest control that are resilient to changes in pest activity and distribution are essential to the health of the agricultural industry, and therefore the country.

1.11 Structure of the thesis

Chapter 1, which you have just read, describes the social and ecological context within which the empirical work of this thesis was carried out. Chapter 2, which follows, dives into the methods used in the subsequent chapters. It particularly focusses on early attempts, missteps and anecdotal information that is not contained in the empirical chapters, but is nonetheless valuable for future chiropterologists attempting similar work.

Chapters 3-5 are the empirical chapters of this thesis. They present results from three ecological studies of insectivorous bats in Indian rice fields.

Chapter 3 focusses on bat activity patterns over time. Set in a rice dominated landscape in Assam, India, this chapter tracks bat activity over a rice growing season at six sites, and models temporal patterns in bat activity as influenced by a number of key biotic and abiotic factors. I test the hypothesis that over a rice growing season, bat activity in a rice field is influenced by insect activity, temperature, moonlight, and interactions of the same.

Chapter 4 describes spatial patterns in bat activity. Here data were collected from different rice farms surrounded by a range of land cover types. The spatial variation in the dataset allowed me to describe how bat activity was influenced by the landscape surrounding rice fields. I assumed that differences in bat activity at different sites reflected the influence of different land cover types in the surrounding landscape on bat behaviour and test the hypothesis that land cover variables related to tree cover and water would have a positive effect on bat activity, while those variables related to urban land would have a negative effect on bat activity.

Chapter 5 demonstrates the effect that the exclusion of bats would have on the health and yield of rice crop. I hypothesise that the exclusion of bats, as a documented predator of a range of insect pests, from rice would cause an increase in pest abundance

and therefore a decrease in plant health and total yield. I test this using an exclusion experiment where bats were selectively excluded from five plots of rice. The health and yield of plants within these plots were compared to those in adjacent plots to which bats had free access.

Chapter 6 takes a broad view of the thesis as a whole, and its place and contribution to our understanding of the ecological and economic value of insectivorous bats. It describes a hidden process affecting bat populations in India, and highlights key directions of research to further our understanding of bat ecology in the country.

CHAPTER 2: Methods

2.1 Overview

Between April and December 2019 I collected data over two field seasons in the districts of Nagaon (Season 1) and Sonitpur (Season 2) in the state of Assam, India. These were timed to coincide with rice growing seasons as the methodology was designed to study the behaviour of bats in rice fields, and their effect on the rice crop.

Over the course of the two seasons, I collected the following types of data:

1. Passive acoustic recordings of bats active over rice fields.
2. Morphological data, scat samples, and acoustic recordings of bats caught in mist nets.
3. Data on plant health and yield from an exclusion experiment.

This chapter details the path to the collection and analysis of the above data, and, in particular, details and anecdotes that are relevant to ecologists of the future who attempt similar studies. Where the subsequent empirical chapters contain all the relevant details of a particular method, they are not repeated here.

2.2 Season one

The first season was conducted during the months of May and June of 2019 in the Nagaon district of Assam. Data from this season were in the form of passive acoustic recordings collected from multiple different sites over the season. The collection and analysis of these data are described in sufficient detail in Chapter 4 and so are not repeated here. The plan for this season also included an attempt to catch insectivorous bats for the collection of diet and other data. This attempt was ultimately unsuccessful, primarily due to the lack of a bat

lure, which are speakers that broadcast bat calls. These are set up near mist nets to increase the capture rate by enticing curious bats to the lures. I attempted to build such a device twice – once during and once immediately after the first season. Below is an account of my process and the resulting device.

2.2.1 The bat lure

The problem with getting speakers to emit bat calls is that said calls are ultrasonic. Since this is beyond the range of human hearing, most devices that output audio – mp3 players, phones, laptops, etc. – have built in filters that remove any ultrasonic signals. Likewise, most devices that amplify and emit audio – speakers with amplifiers – have high-pass filters built into the circuits that do the same. The logic for both being that there is no need to spend energy on frequencies that can't be heard by humans. What this means is that to built a bat lure, one needs to bypass the soft filters in the output device and hard filters in the speakers. To add to this, ultrasonic calls attenuate quickly in air (Griffin 1971, Goerlitz 2018), so bat lures need to be extremely loud to compensate for the high rate of attenuation. And, due to the length and frequency characteristics of a bat call, a lure needs to store and emit a signal with a high time and frequency resolution to convincingly mimic a real bat. The combination of these factors makes a bat lure a complicated device to construct.

My first attempt to build a lure, on field in Nagaon, involved an arduino, onto which was saved a call in the form of raw audio (saving it as a .wav or .mp3 on the computer automatically filters ultrasonic signal). The audio was sent to a cheap speaker, with a basic amplifier, via the raw output ports, because sending it through the audio jack would have filtered out ultrasonic signal. The best version of this 'lure' did, in fact emit a very soft, low time- and frequency- resolution bat call, which could be detected at a range of two meters (Fig. 2.1).

When this season ended, I attempted once again to build a lure, this time with access to better equipment, and advice from engineers. A raspberry pi replaced the arduino, and held multiple bat calls (extracted from the passive recording of the first season), which were sent as raw audio to through a digital-to-analog converter (DAC), then a home-made amplifier, and then to speakers. With the addition of the amplifier, the output from this lure was louder than the first lure, but still lacked the resolution needed to pass as a bat call. It was during the construction of this lure that I received the Rufford Grant and was able to purchase a Peersonic Bat Lure. In speaking to the manufacturer of the Peersonic lure, it emerged that my approach was the right one, but it was unlikely that I would have found a speaker that would have met my criteria.



Fig. 2.1 First attempt at building a bat lure, using an arduino and spare parts scavenged from old circuits.

2.3 Season two

My second field season lasted from August to December 2019 in the Puthimari village of the Sonitpur district of Assam.

2.3.1 Catching bats

During this season, armed with mist nets and two Peersonic bat lures, I captured insectivorous bats for the construction of an acoustic library of calls, and collection of data relating to the genetics, diet, and morphology.



Fig. 2.2 Unidentified bats roosting in a bamboo pole.

In total, I had four, six meter Avinet mist nets. These were erected using Decathlon telescopic fishing poles, which allow one to rapidly lower the nets when a bat is caught in a pocket too high to reach. A typical night of trapping involved leaving two to three hours before dusk with the nets, lures, labelled cloth bags, and other essentials to a preselected location, where an hour or so would be spent meeting the residents of the nearby houses and explaining our work. As dusk approached, we would set up our nets, usually along a treeline at the edge of a rice field. Our aim was to catch bats that were foraging in and around the fields, but nets set up in the open were far easier for bats to detect and avoid. Trees near field edges were an acceptable compromise.

Prior to the arrival of the lure, having had low capture success with the nets, our strategy involved searching for roosting bats to capture as they left the roost. We very quickly discovered that the bamboo frames of houses and sheds were ideal sites. The sloping roofs were built using bamboo poles, the ends of which formed narrow cavities perfect for bats. It was unusual not to find one or more bats in each house or shed (Fig. 2.2).

A net, or in some cases, a cloth bag, was set up at the mouth of this roost to catch bats as they left. It is worth noting that when multiple bats were present in one rod, they were often different species (although it must also be noted that this was determined

simply from visual observation, and we could not positively identify most of the captured bats). Each captured bat was placed into a different clean cloth bag so that scat samples left in the bag could be unambiguously attributed to one individual.

With the arrival of the lures, capture success in the mist nets increased dramatically. The lure came with a pen drive of social and search phase calls, including those of the following bat species:

1. Natterer's bat - *Myotis nattereri*
2. Nathusius' pipistrelle - *Pipistrellus nathusii*
3. Bechstein's bat - *Myotis bechsteinii*
4. Daubenton's bat - *Myotis daubentonii*
5. Greater horseshoe bat - *Rhinolophus ferrumequinum*
6. Common pipistrelle - *Pipistrellus pipistrellus*
7. Cayman velvety freetailed bat - *Molossus molossus*
8. Soprano pipistrelle - *Pipistrellus pygmaeus*

With two lures positioned at opposite ends of the row of nets, facing opposite directions, calls from the list above were played from each. Unsure of the best call to play, I often experimented with call species and repetition rates, but had too few nights to determine the success rate of one call over the other. On 2nd December 2019, captures were stopped. This was in part because the crop was beginning to be harvested, and in part because the nights were becoming colder and I did not want to subject the captured bats to undue stress.

2.3.2 Processing bats

Once caught, bats were stored in individually labelled cloth bags, for up to two hours, at which point the nets were taken down for the night. If the capture site was within 300

meters of the field station, then the bats were taken back to the field station to be processed and released. If not, they were processed and released on site.

The following data were collected from captured bats.

1. Morphological: Bats were measured for the following data:
    a. Photograph of:
        i. whole body;
        ii. dentition;
        iii. ear and tragus structure.
    b. Body mass: Measured with a digital weighing scale, accuracy of 0.01gm.
    c. Measurement: Forearm length measured with a digital vernier calliper, accuracy of 0.05mm.
2. Genetic data: A few individuals of each species, and all unidentifiable species, were sampled for DNA by collecting wing biopsies. These were collected using a sanitised metal punch against a flat metal plate.
3. Diet data: Scat samples from the bat bags were collected for diet analysis.
4. Acoustic data: Search phase calls were recorded using a handheld Pettersson D240X recorder on manually triggered time expansion mode. Bats were released toward a field assistant who was holding the recorder, which recorded the search phase call of the bat, and saved it in a time expanded format.

A total of 135 individual insectivorous bats were captured during the August-December field season 2019. The majority of these could not be identified to species, due to their cryptic features and the lack of a comprehensive library for bats in India. Three species were identified based on characteristic physical features, and are listed below. The remaining could not be identified with certainty.

1. *Megaderma lyra* – the Greater false vampire bat

2. *Scotophilus heathii* – the Greater Asiatic yellow bat

3. *Scotophilus kuhlii* – the Lesser Asiatic yellow bat

The acoustic characteristics of these three species, as well as all other unidentified species caught and recorded can be found in the supplementary material of Chapter 3 (Appendix A1.2). Spectrograms were created from the search-phase calls of bats recorded on release with a Pettersson D240X. It is possible that two or more of these entries are of the same species. Entries were added if individuals either had different physical or acoustic characteristics. As we know, however, the calls of stressed bats, when release from capture into cluttered environments, can be different from those recorded in different circumstances.

Recording search-phase calls on release is not a perfect method to create an acoustic library. Bats released from captivity are stressed, and usually facing an obstacle in the form of a person holding a recorder. The environment they must navigate is therefore cluttered, which may cause them to change the characteristics of their calls. These calls may not, therefore, accurately represent search-phase calls emitted in open spaces.

Points to note:

1. *Megaderma lyra* were never detected near the edge of fields, but were caught in abundance when we were directed to an abandoned house that was swarming with them. While we caught many individuals, scat samples were unusually difficult to collect as they didn't deposit any in the cloth bags. This was never an issue with other species.

2. On nights with multiple captures, not all captured bats were measured. This was primarily due to time constraints. However, I made it a point to get a full set of data for at least one individual of every species.

2.4 Exclusion experiment

Between 10 September and 28 November 2019, I conducted an exclusion experiment to investigate how the exclusion of bats would influence rice health and yield. Bat exclusion experiments need to be open during the day to allow birds free access to the crop. This ensures that the effect of bird insectivory isn't confounded with that of bat insectivory.

Our design for the exclusion experiment involved six pairs of experimental and control treatments. The two treatments of a pair were placed 8 meters from each other and no pair was within 90 meters of another. The control and experimental enclosures were identical except for the netting on the experimental plot, which was absent on the control plot. The frames were made of bamboo, harvested locally. Eight bamboo rods were sunk one meter into the ground and reached four meters into the air to form the 'legs'. Four bamboo rods were tied to the top of the eight legs to form a cube. The sides of each plot were nine meters in length, and enclosed a minimum of 900 individual rice plants of the same rice variety. Because the pairs were set in the land of different farmers, all of whom planted the rice by hand, it was not possible to standardize the number of plants within a 9m x 9m plot. Knowing that the edges of each plot were likely to be disturbed, a 0.5m track around each plot was cleared, and the plants within each plot were divided into a 'buffer' zone of the three outermost rows and 'core' zone of those within the buffer. Only plants from the 'core' zone were harvested and considered for analysis.

The experimental enclosure design went through a number of iterations before the final one was decided. Creating a cheap, easily constructed, and easily manipulated system proved quite challenging. The first challenge was sourcing the nets, the mesh size of which had to be large enough to allow free movement of insects, but small enough to stop even the smallest bats. Luckily, cricket nets proved to fit these criteria, and, being a common product in Indian markets, were easily sourced. I had previously considered fishing nets of

various sorts, but invariably the lighter ones had small mesh sizes, while the larger ones were too heavy to be practical.

Building the frame was the next challenge. In thinking about this at my desk, the most logical solution was to have three metal pipes welded together at right angles to create joints into which bamboo poles would be inserted. These would form the four top corners of the frame. In the middle of each edge, a 'T' shaped pipe would have a bamboo pole of the roof pass through it horizontally, and have one leg descend from it vertically into the ground (Fig. 2.3). This design made sense on paper, but when built in waterlogged fields, proved too top-heavy to be practical.

As is often the case, the best solution was discovered in the field, and consisted of bamboo poles tied together with rope (Fig. 2.4). The community in Puthimari (and much of Assam) have great skill in working with bamboo because it is locally grown and many people build their houses with it.



Fig. 2.3 First attempt at building the 'roof' of an enclosure. Eight bamboo 'legs' would fit into the eight empty sockets pointing downward. This design was too top heavy in waterlogged rice fields to be practical.

The final challenge in constructing the enclosures was designing and building a pulley system of nets that allowed one person to manually retract all four 'walls' and the 'roof' of six experimental enclosures reasonably quickly. The walls were relatively simple. The top of each 'wall' net was permanently attached to the bamboo frame above it (under construction in Fig. 2.5). The first design to retract them involved a long bamboo pole attached to the nets at the bottom.

Three ropes were looped over the top frame and threaded through the net all the way down to the free bamboo pole at the bottom, where they were attached. When the ropes were pulled, they raised the free bamboo pole and the net to the top frame. Since the rope was threaded through the net in a zigzag manner, the rope crimped as it went up, resulting in a relatively tight bundle on top. The ropes were then tied to the nearest 'leg' of the frame, keeping the nets in the retracted position.



Fig. 2.4 The final design of the enclosure frame involved only bamboo and rope. A pocket was cut into the end of each 'leg' onto which sat two bamboo poles of the 'roof', extending ninety degrees from each other.

After a few days of operation, it became clear that the free bamboo pole at the bottom was unwieldy, and so it was replaced by three stones that made the whole system more usable, because the ropes could be now operated individually, where with the bamboo pole all three ropes needed to be raised simultaneously, requiring three people. With the stone system, one person would raise each stone one at a time, and at the end the net would be crimped at the top (Fig. 2.6).



Fig. 2.5 Constructing an experimental enclosure. Nets were sown together (top) and attached to the frame to make a 'wall' or 'roof' of the enclosure (bottom).

This did result in some sagging between the stones, so an additional two thin ropes per 'wall' were threaded through the net halfway between the stones. These added to the overall crimping of the net, making the bundle tighter. The roof posed a more interesting challenge. Our final design of the roof was to have one side of the 'roof' net attached permanently to one bamboo pole of the roof frame. The opposite side of the roof net was attached to a free bamboo pole that rested on top of the roof. A total of six ropes were tied to this free bamboo pole. Three were threaded through the net and hung down on the side where the net was permanently attached to the frame. The other three hung down the



Fig. 2.6 One set of experimental and control enclosures. At night, the experimental enclosure was sealed using nets, while the control enclosure, 8 meters away, was not. The above pictures show the raising of the nets, which took place at dawn every day.

opposite side. By pulling the ropes that weren't threaded through the net, the pole slid across the top, bringing the net with it, until the net extended and became a roof. When the three ropes attached to the bamboo pole and threaded through the net were pulled, the bamboo pole slid back along the roof, bringing the net with it, and forming a tight roll at one end. Thus 'opening' the roof. There were still gaps where the net sagged on the side, and for this, two thin ropes were attached to the sides of the roof net. When these were pulled, the net slid sideways and over the bamboo frame of the roof, and any gap between the net and the frame was eliminated (Fig. 2.4). Every morning at dawn I, accompanied by a field assistant, would 'open' all six experimental enclosures. This took just under an hour to complete. In the evenings before dusk the six experimental enclosures were closed. With gravity on our side, this generally took around 40 minutes and was usually done by one field assistant and an energetic youngster from the village – the other field assistant and I having left to set up the mist nets to capture bats in.

Over the course of the field season, my enclosures were repeatedly damaged by thieves stealing the rope that was used to open and close the nets. These invariably occurred at night and were always fixed the following morning, but did involve a few hours where the nets did present an obstruction to flying birds. Near the end of the season it became clear that one pair of enclosures had been built on a different strain of rice than the remaining five. This pair was dropped from the analysis. Three types of data were collected from this experiment: two measures of plant health – leaf defoliation and leaf yellowing (Fig. 2.7) – collected in the middle of the growing season, and one measure of total rice yield, collected at the end of the growing season. These have been described in detail in Chapter 5.



Fig. 2.7 Examples of leaf defoliation (top) and leaf yellowing (bottom) in rice plants sampled in the middle of the rice growing season.

Below are a few noteworthy points about this experiment. These anecdotes detail important features of the landscape and the study that can interfere with the functioning of such an experiment.

1. Diurnal insectivorous birds – primarily swallows – were abundant in the landscape. I would see many hundreds sweeping through the fields in search of insects on my way back from raising the nets in the mornings. These birds used the frames of the enclosures (both experimental and control) to perch on, but none were ever found entangled in the rolled up nets. I suspect that the presence of the frames did allow the birds to go deeper into the field than they otherwise might have.

2. Owls were also abundant in the landscape, and made great use of the enclosures as perches. Being nocturnal, they were active while the nets were down, so if their predation of rodents was different between the experimental and control plots, then this effect would add to the effect of bat exclusion.

3. Although the management style of all my plots was standardized in that the same strain of rice was grown in all plots and no pesticide or fertilizer was added at any stage of growth, my plots were set in a mosaic of other plots and I know for a fact that some neighbouring plots were treated with chemical fertilizers and pesticides.

4. One thing that I could neither standardize nor account for was the treatment history of the soil upon which my enclosures were built. Neither short term nor long term records were kept, and the only source of such information was the farmers' memory. This proved relevant in one case, when the difference in yield between the experimental and control plots was found to be two fold, and in the opposite direction of what would be expected with bat exclusion. Subsequent conversation revealed that the farmer had not tilled his plot uniformly, and that one strip of land had received six more passes of the tractor than the rest of the plot. I believe that this was the primary factor influencing the difference in yield.

5. The village I worked in was located a few hundred meters from the Brahmaputra River, which floods regularly. This flooding is essential to the healthy growth of the crop, provided it doesn't last more than three weeks. The floods did recede after two weeks, but not completely. For an extra full week, the control enclosure of one pair was waterlogged while the experimental enclosure of the same pair was not. It so happened that this was the pair built over a different strain of rice, and so dropped from analysis, but it should be noted that the plants in the control enclosure were significantly taller than the plants in the experimental enclosure. Had I not been forced to exclude this pair from analysis, the difference in yield would no doubt have been significant, in the expected direction for such a study, but as a result of a totally different phenomenon.



Fig. 2.8 The view of the fields in which the exclusion experiment was conducted. One pair of experimental and control plots is visible to the right of the road, another hides behind it. A third pair is visible in the distance on the left side of the road.

2.5 Analysis

2.5.1 Acoustic classifier

Passive recordings from the two field seasons collected using Audiomoth 1.0.0 recorders (Hill et al. 2018) amounted to 3057.5 hours of raw audio, within which were millisecond long bat calls. Manually processing this quantity of data was out of the question, so I built a machine-learning acoustic classifier to isolate, parametrize, and classify the bat calls in my recordings.

Bat calls have extremely distinct acoustic characteristics. The trained human eye can distinguish them from natural and artificial sounds using these characteristics. It followed, therefore, that it should be possible to reduce individual bat calls to a few key numbers that best captured their 'shape', and that these numbers, when considered together, would allow a sufficiently sophisticated machine-learning algorithm to identify the species of bat that emitted it.

Of course, the human eye sees patterns that are not easy to quantify, and the recorded calls were far from perfect – differing from other individuals of the same species both because of varying distances from the recorder, and because bats change their calls according to the landscape they are in, and the activity they are engaged in. A range of non-bat sounds, particularly from insects, added noise to the acoustic environment and further complicated the task of accurately identifying bats.

The process of transforming the raw acoustic data into a dataset of classified bat passes was winding. For various reasons, the final classifier was broken into multiple scripts over the three languages – Python, Matlab, and R. I wouldn't recommend this for future coders, but learning on the job left me picking the easiest paths for each step of the process, which happened to involve multiple languages.

A total of four scripts converted the raw acoustic recordings into a dataset of time-and-location stamped bat calls. For clarity, a call is a single bat vocalization, while a pass was a series of calls in quick succession, made as the bat flew over the recorder.

- In 'Parameters 1' and 'Parameters 2', the bat calls were isolated and various measures were extracted from them. This produced one row of numeric data per call.
- In 'Classifier', the data from each entry were given a provisional identification based on a linear discriminant analysis that was trained on manually created acoustic templates for the different species/sonotypes.
- In 'Processor', the classified entries were filtered and hard limits imposed on a set of key data points to reclassify some incorrectly classified calls, and filter calls that were recorded before or after the relevant time points.

Parameters 1

The acoustic analysis itself – where the characteristics of calls were extracted – was conducted in Python. The classifier was built first with the acoustic data from Chapter 3, and later rebuilt for the data from Chapter 4. Over the course of the analysis for Chapters 3 and 4, this classifier went through innumerable iterations. Below is the path to what became the final set of classifiers.

The first step was to incorporate a high-pass filter. This was initially set at 19.5kHz, after manually checks of the recordings showed none of the recordings contained bats that called below this frequency.

Next, I defined the window length. None of the bat calls observed during the manual checks were longer than 25ms, so a moving window was defined with a length of 30ms and a 33.3% overlap. This mean that each window began at 20ms intervals, but was 30ms long, overlapping with the next block by 10ms. Each window was run through a Fast Fourier

Transformation. This breaks down an acoustic signal into its component waves, allowing one to collect information on, among other things, the energy contained in each frequency band.

After this, each window went through the first round of filtering, where only those with a maximum amplitude over 800 units, and an average amplitude between 85 and 100,000 units, and a Frequency of Maximum Amplitude (FMAXE) above 20kHz, were retained. These values aren't relevant outside this classifier as they are affected by the sensitivity of the microphone, the amplitude of the bat call, and the Python function itself. They were determined by trial and error. Calls with a maximum amplitude below 800 units tended to be non-representative of the species, and were usually found at the tail end of a bat pass, when the bat was quite far from the microphone. Windows with average amplitude values below 85 could not have viable calls. Those with an average amplitude above 100,000 units were invariably filled with static, rain, or some other constant ultrasonic noise, and were therefore useless. In addition, the frequency of maximum energy had to be over 20kHz, because I did not find any bat calling below this frequency.

A 600 second recording contained 30,000 windows. Those that passed the above filters were flagged, and buffered with 10 or 20ms on either side to accommodate calls that might have started or ended outside of the selected window. When a window was flagged, the window immediately after it was ignored, so as not to save two copies of the same call under different names.

Files were saved in such a way as to make them immediately identifiable. Each file was named by the millisecond at which it it began. It was saved in a folder named for the time when the recording was made. The recordings for each date were saved in folders named after the recorders - 'A' to 'F', which were saved in folders representing the date. Date → Recorder → Time → Millisecond.wav

Parameters 2

With the number of files to process now significantly reduced, the 50-60ms recordings saved during Parameters 1, were then accessed by a second Python script, 'Parameters 2'. This script was built not only to further filter out false positives, but to extract useful information from the remaining windows and output relevant numeric data for each suspected call.

Each recording was analysed on two primary axes – time and frequency. An easily quantifiable data point was the location in time that contained the most energy. This location was used as the anchor point for analysis, from which the start and end point of the call was identified (Fig. 2.9). (i) Call start point: Moving backward in time from this anchor point, the start of the call was defined as the first frame whose amplitude dropped to below 5% of that of the anchor point. (ii) Call end point: Moving forward from the anchor point, the end of the call was defined as the first frame whose amplitude dropped to below 30% of that of the anchor point.

A lot of trial and error went into finding the right thresholds, and different versions of 'Parameters 1' and 'Parameters 2' used different thresholds. Had I built a different classifier for each sonotype, I would have perhaps used different thresholds for each one, and indeed I did experiment with this for some sonotypes, but eventually I managed to get thresholds which worked for all sonotypes.

The recording was then clipped to include just the 'call' (though at this stage I still had many false positives), and run through a Fast Fourier Transformation in order to identify the characteristics of the call on the frequency axis. The frequency of maximum energy [FMAXE] was used as the anchor point on the frequency axis. As a consequence of bats' extreme acoustic sophistication, this parameter itself is a useful metric as it tends not to vary significantly within species. Moving away on the frequency axis from the FMAXE, the maximum and minimum frequency of the call were defined as the frequencies at which

the energy first dropped to below 5% of that of FMAXE. To the upper limit was added 2kHz, simply to help detect narrowband calls.

The calls were then filtered based on the following metrics:

- The Average FFT in window greater than 60000. This referred to the amount of energy in the call.
- FMAXE greater than 19kHz. Anything lower than this was assumed not to be a bat, because all the species I recorded called at frequencies higher than this value.
- Maximum amplitude of the call greater than 700 units.

Again, different parameters were used for different versions of the classifier, and final versions of 'Parameters 1' and 'Parameters 2' used on the datasets of Chapters 3 and 4 differed from each other.

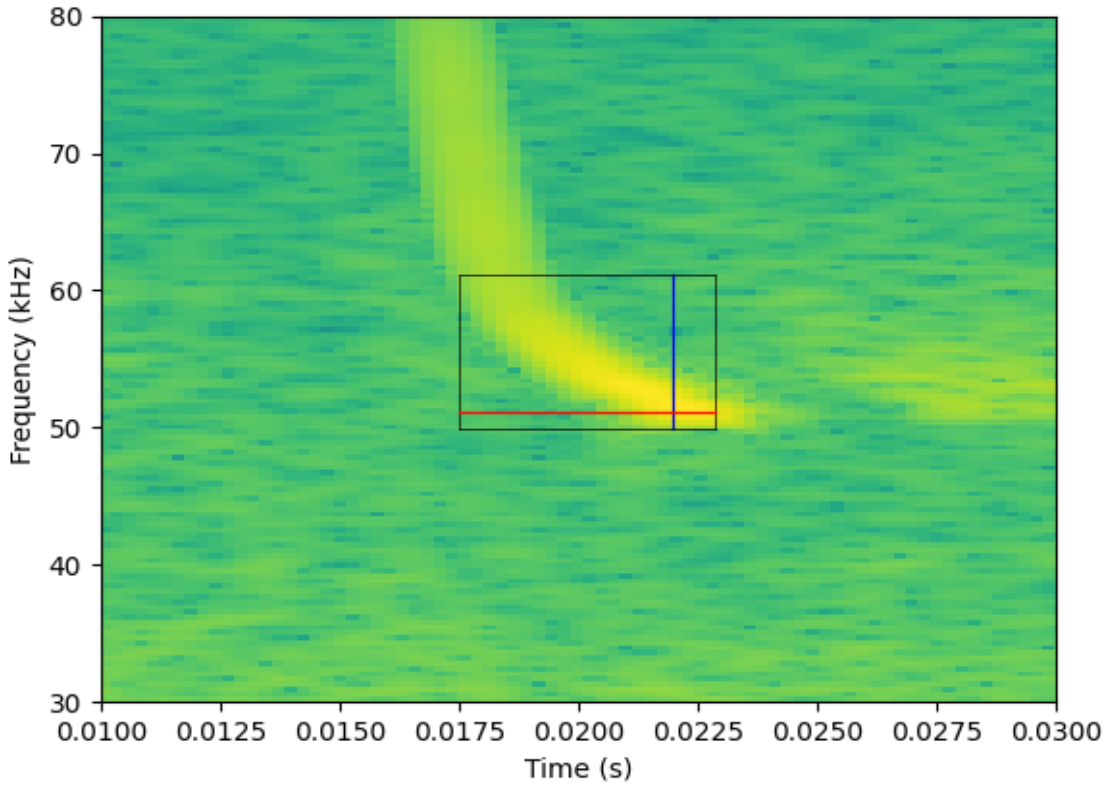


Fig. 2.9 Clipping a bat call to extract datapoints from it. The blue line represents the time point of maximum energy, which was used as a threshold for calculating the start and end points of the call. The red line was the frequency of maximum amplitude, which was used to calculate the minimum and maximum frequencies of the call.

Those windows that passed the above filters were exported not as audio files, but as a row of data containing the following measures:

1. Bandwidth
2. Start frequency
3. End frequency
4. FMAXE (Frequency of MAXimum Energy)
5. Call length (in milliseconds)
6. Average FFT in windows
7. Average amplitude
8. Average amplitude percent.

These include secondary variables that were not important in identifying species, but helped separate bat calls from non-bat noises.

While the entire process of parameter extraction could have been done in one script, using the more comprehensive filters from the very start, having two scripts allowed me to check the output in between and tweak parameters to better identify and measure calls.

Classifier

The process of classifying each potential call into bat species with an associated degree of confidence was done using MATLAB's classification learner app.

I first created an acoustic template for each species by manually identifying calls from passive recordings and running these calls through 'Parameters 1' and 'Parameters 2'. Every species went through this process to create a library. Some species, such as those above 40kHz were relatively easy to classify being distinct from other calls and at frequencies with little background noise. Others were more difficult. Pitfalls are detailed in the next section. Outliers for each species were often removed, because they would

increase the variability of each classification, making the classifier less strict and more likely to include false positives.

Early iterations of the classifier identified every pass to the species level using species names provided by experts in the field. However, the lack of an acoustic library reduced the confidence with which species level resolution could be used, and so the decision was made to use sonotypes instead. Sonotypes referred to the shape of call – Constant frequency (CF), Quasi-constant frequency (QCF), or Frequency modulated (FM) calls, and the associated FMAXE. For example, a call might be quasi-constant frequency at 35,000Hz, while another might be frequency modulated quasi-constant frequency calling at 47,000Hz. These would be referred to as QCF-35kHz and FM-QCF-47kHz respectively.
I began with a single script containing a single classifier trained on parameters of all the sonotypes. This was eventually split into two scripts. The first for all sonotypes above 25kHz, and the second for what came to be classified as FM-QCF-20k (S20). This was due to the frequent occurrence of non-bat noises around 19kHz, which made separating FM-QCF-20k far more difficult than the other sonotypes. The script for this sonotype also contained templates for multiple types of noise.

I used the library I created and a linear discriminant analysis with 5-fold cross verification (in the MATLAB classifier learner app) to create a trained classifier. Through this classifier were run the data obtained from 'Parameters 2'. To each row of data, which represented a single call, the trained classifier attached a sonotype that best fit the characteristics of the call and the confidence with which this classification was made.

The resulting dataset was then run through an R script 'Processor', which filtered out known false positives or time periods that weren't to be included in the analysis. For example, if placing the recorders in the field was delayed, then the bats recorded on the way to the site could not be considered for the analysis. Every night's recordings had a 'start time' dataset, which was used to filter out any calls identified prior to the recorders

being in place. Likewise, if light rain caused an abundance of false positives, then I would manually check the time period with rain and enter into a separate .csv file the time periods to ignore. This script also condensed the data into bat passes. With every recording broken into five second intervals, any such interval with three or more calls was considered a pass.

Notes on the acoustic analysis

The Audiomoth 1.0.0 uses a Knowles SPM0408LE5H-TB microphone. These show a decreasing sensitivity to ultrasonic frequencies, particularly around/above 40kHz (Lapp 2021). Additionally, our experimental setup involved putting the audiomoths into plastic zip-lock bags to protect them from the elements. This would have further exacerbated the bias against high frequencies as the plastic would cause comparatively more attenuation of higher frequencies than lower frequencies (Lapp 2021).

On multiple occasions, a single pass began first as a narrowband QCF call, which then turned into a broadband FM-QCF call, and then sometimes back into a QCF call. The same night would also have passes composed entirely of pure QCF calls, and those composed of FM-QCF calls. While initial versions of the classifier separated the two as being different species, on finding multiple passes where QCF turned to FM-QCF, the two sonotypes were merged into one. Future bat acoustic recorders might have microphones capable of capturing subtle differences in calls that would allow one to separate such overlapping species, but mine, being an early version of an Audiomoth, did not. Sonotypes were then referred to using 'S' followed by the frequency at which they called. For example, FM-QCF_38k became S38.

In addition to the changes in call structure was the routine variation in call frequency. This variation, which was most problematic in species calling between 30kHz and 40kHz, made distinguishing one species from another nearly impossible because of

the degree of overlap in call frequency. In the recordings of both field seasons combined, we recorded between three and six species calling within this range. The first to be dropped were the constant frequency calls around 32kHz. These were rare, and lacking many of the characteristics that helped in identification, were abandoned after several weeks of concentrated effort did not manage to distinguish them from noise and other species. The remaining three to five species were condensed into three sonotypes, S31k, S34k, and S38k (Fig. 2.10).

By far the most problematic species were those calling near 20kHz. These calls usually falling between 19.5kHz and 21kHz, were often very similar to insect calls, and even when distinct in shape, were still surrounded and overlapped by many non-bat noises, making it quite difficult to isolate them.

The striation of insect wings create sounds made up of multiple vibrations of the vibrating body. While an entire 'chirp' is far longer than a bat call, the individual units of noise are frustratingly similar in length and bandwidth. When taken against the backdrop of constant ambient noise, and overlapped with the calls of other insects, the combination far too often was enough to fool the classifier. Of course, it's worth mentioning that when an insect decides to sing, it doesn't stop, while a hunting bat will circle a location perhaps twice before moving on. Even when my classifier successfully filtered out 90% of the problematic insects, the remaining 10% often amounted to more calls than all the bats of that sonotype. Over the two seasons, we recorded between two and four species of bat calling at this range, all of which were condensed into one sonotype – S20k.

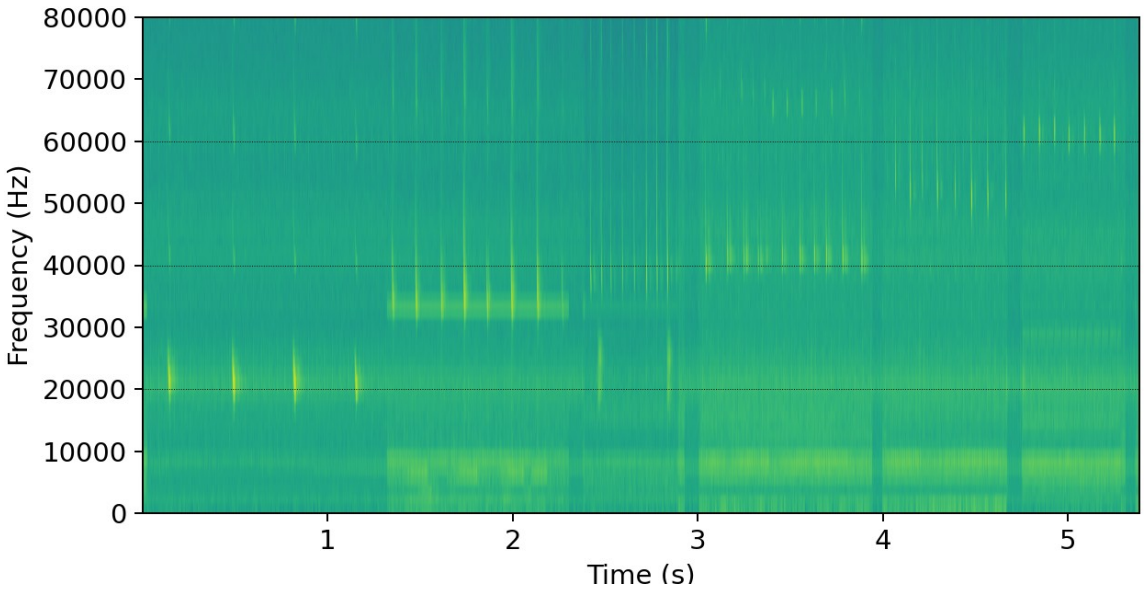


Fig. 2.10 Spectrogram of six sonotypes recorded during the second field season - S20, S31, S34, S38, S48, and S65. X-axis represents time (seconds), y-axis represents frequency (kHz). These were recorded at different times and locations and have been combined in one spectrogram for comparison.

2.6 Summary of aims

Bats in India have received very little attention thus far. A few studies have considered their distribution (Korad et al. 2007, Gaikwad et al. 2012, Aul et al. 2014), a few their ecology (Wordley et al. 2015, 2017, Ongole et al. 2018, Thapa et al. 2021), a few their virology (Mani et al. 2017, Dovih et al. 2021), and a few the attitudes of people towards bats (Deshpande and Kelkar 2015, Bhattacharjee et al. 2018). The only comprehensive library of bat morphology and distribution was published in 1997 (Bates and Harrison 1997), with a brief list of species in the country published in 2018 (Talmale and Saikia 2018).

Through the studies in this thesis, we endeavoured to fill a number of gaps in the literature of Indian bats. One of the more fundamental of these was to identify and document the acoustic and morphological characteristics of bats in Assam, particularly those that were active around rice fields. These data were important for a number of

reasons, not the least because a reliable acoustic library would make future studies using acoustic methods to monitor bats much easier.

The overarching theme of this thesis being to describe the behaviour of insectivorous bats in rice fields, capturing bats gave us the opportunity to collect a number of valuable types of data that furthered this goal. Wing biopsies were collected from captured bats to be used for genetic identification of the species. We also collected scat samples to identify the pest species in their diet, which will allow us to unequivocally link bat species to the pests they are hunting. When releasing that bats, we recorded their search phase calls. This will allow us to describe the acoustic characteristics of the search phase calls of each species. While the COVID-19 pandemic has delayed the genetic analysis of wing biopsies and scat samples, the data itself have been collected, bringing us one step closer to a library that connects bat species to their acoustic, morphological, and dietary characteristics.

Building on these endeavours were the investigations into bat activity and distribution patterns in rice-dominated landscapes. Here we tried to identify the primary drivers of bat activity in time and space in rice fields. With a long term view of increasing bat populations in such landscapes, these studies create a baseline of behavioural patterns that can be used to shape efforts to conserve and increase the ecosystem services of particular sonotypes.

The last element of the puzzle was to quantify the economic value provided by bats to rice farmers by virtue of their pest suppression service. This took the form of an exclusion experiment, which was the first such experiment that excluded bats from rice crop anywhere in the world.

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CHAPTER 3

Insectivorous bats in Indian rice fields respond to moonlight, temperature, and insect activity

3.1 Abstract

Rice is the most widely grown crop in India, but continues to suffer substantial yield loss at the hands of insect pests, a loss that is predicted to increase in the coming decades. Insectivorous bats are known to provide significant economic value to agricultural systems through the suppression of insect pests, yet their ecology in agricultural landscapes of India is poorly understood.

We assessed the influence of key biotic and abiotic factors on bat activity over a rice growing season in a site in the Sonitpur district of Assam, India. We used generalised linear mixed models to analyse the effect of insect activity, temperature, and moonlight intensity on the temporal activity patterns of six bat sonotypes. We also used a multimodal analysis to describe the nightly activity patterns of these six sonotype. These methods are not traditionally used on such data, but demonstrate great potential to describe patterns in bat activity.

Our results show that the activity of each of four bat sonotypes increases with insect activity. Minimum nightly temperature and moonlight intensity also had a positive and negative influence on the activity of all six bat sonotypes. Nightly activity of the bat sonotypes could be broadly divided into two patterns. Three sonotypes displayed a pronounced dusk peak in activity – similar to many insect pests of rice – while the remaining three sonotypes showed more consistent activity levels through the night. Our results broaden our understanding of the ecology of insectivorous bats and their relationship with insects in agricultural landscapes. These findings can be used to guide integrated pest management to increase bat activity in the rice agricultural landscape for economic and ecological benefit.

3.2. Introduction

Rice is consumed as a staple food by over half the world's population (IRRI 2019). Varying with geography, climate change is predicted to decrease global rice yields by 3.2±3.7% per degree Celsius increase in mean surface temperature (Zhao et al. 2017). In addition, the increased action of insect pests, which already have severe effects on yield (Pathak and Khan 1994), is predicted to decrease global rice yield by 19% for a 2° Celsius increase in mean temperatures (Deutsch et al. 2018).

Insect pests are hard to control. For many centuries, pest control relied heavily on chemical insecticides (Smith and Secoy 1976), a strategy long recognised as being unsustainable due to the build-up of resistance, biomagnification of chemicals, and a range of health impacts on humans and the ecosystem (Ripper 1956, Baker et al. 2020). One method to reduce our dependence on chemical pesticides is Integrated Pest Management, a cornerstone of which is the use of natural enemies to control pest numbers (Naranjo et al. 2015). Although not widely adopted for a number of reasons, including time and cost effectiveness (Savary et al. 2012, Lou et al. 2013), the control of agricultural pests by augmenting natural enemy populations of parasitoids (Sharma et al. 2019), birds (Long et al. 2013, Karp and Daily 2014, Maas et al. 2016), and fish (Halwart et al. 2012) has been used for many decades. Only in the last decade and a half, however, have insectivorous bats been widely recognised as a tool of insect control (Cleveland et al. 2006, Boyles et al. 2011, Maas et al. 2013).

Synchronous cropping, heavy insecticide use and homogenous landscapes that are characteristic of Asian rice fields disproportionately affect the arthropod natural enemies of rice pests (Settle et al. 1996, Bottrell and Schoenly 2012). Unlike most predatory arthropods, many insectivorous bats are opportunistic generalists that can change hunting grounds during the fallow period between seasons, and, during a season, commute long distances from their roost sites to rice fields every night (Marques et al. 2004, Popa-

Lisseanu et al. 2009, McCracken et al. 2012). Furthermore, insectivorous bats can consume anywhere from 25% to over 100% of their bodyweight in insects every night (Kunz et al. 2011), and roost in very high densities, some in colonies of over a million individuals (Ghanem and Voigt 2012). Their generalist diet also makes insectivorous bats potential buffers against non-native pest species, against which pre-existing pest control measures may be ineffective. These characteristics make insectivorous bats exceptionally suited for the control of rice pests. However, it is only by understanding the drivers of bat activity and distribution - spatial, biotic and abiotic - that one could, through targeted conservation, maximise the ecosystem services they perform.

Insectivorous bats have been shown to eat pests of cotton (Federico et al. 2008, Kolkert et al. 2020a), corn (Maine and Boyles 2015), rice (Puig-Montserrat et al. 2015, Kemp et al. 2019), cacao (Cassano et al. 2016), coffee (Classen et al. 2014), and a number of other crops (Whitaker et al. 1996). Economic valuations of this service have produced estimates from hundreds of thousands to billions of dollars per year (Cleveland et al. 2006, Boyles et al. 2011, Wanger et al. 2014), to say nothing of the secondary ecological and economic benefits that occur further down-stream (Kunz et al. 2011). Despite the increasing interest in the pest suppression service of bats, there remains a dearth of studies examining this service in the context of rice (but see Wanger et al. 2014, Puig-Montserrat et al. 2015, Kemp et al. 2019, Sedlock et al. 2019).

With a view to maximising the pest suppression ecosystem service, an economic estimate alone is insufficient unless complemented by a thorough understanding of the biology and ecology of insectivorous bats. This knowledge is sorely lacking in India (Wordley et al. 2015, 2017, Ongole et al. 2018), which boasts 127 species of bats, of which 113 are insectivores (Talmale and Saikia 2018).

Our study seeks to address that gap, by describing some of the main temporal drivers of insectivorous bat activity over a rice dominated landscape in Assam, India, a

state which, in 2018, grew rice on 2.43 million hectares of land (Directorate of Economics and Statistics 2019)

Optimal foraging theory postulates that animals employ foraging strategies that maximise net energy gain while minimising risk (Pyke et al. 1977, Lima and Dill 1990). These strategies – a combination of instinctive and learned behaviours - drive decisions behind what to eat, when, where, and for how long. Bats, with their unusual combination of powered flight, high metabolic rates and slow life histories, face a unique set of conditions that influence their foraging behaviour (Barclay and Harder 2003, Welbergen 2006, Prat and Yovel 2020).

Powered flight involves high energetic demands and rapid evaporative water loss, significantly so when temperatures are high (Studier 1970). While bats are heterothermic, and able to enter torpor to conserve energy, insects, their prey, are ectothermic. Low temperatures significantly decrease the availability of insects, forcing bats to either enter torpor (Yuan et al. 2011, Jonasson and Willis 2012, Stawski et al. 2014) or migrate to warmer climates (Fleming 2010) when their prey is scarce.

Many bats also display an aversion to moonlight, termed 'lunar phobia' (Morrison 1978). Lunar phobia is driven by the increased risk of predation from visually hunting nocturnal birds, a risk which increases on brighter nights and disproportionately affects those bats which can be caught by these predators (Saldaña-Vázquez and Munguía-Rosas 2013, Lima and O'Keefe 2013).

Other abiotic factors such as rain (Voigt et al. 2011) and wind speed (Smith and McWilliams 2016) also affect bat activity levels by increasing the energetic costs of flight, but the most important driver of insectivorous bat activity is prey abundance (Egert-Berg et al. 2018, Hałat et al. 2018). Bats go where there is food. For generalist species aiming to maximise energy intake, this means changing not just location but also target prey. To

what extent bats use rice fields to hunt is all but unknown, as is their relationship to most rice pests.

Rice in Asia goes through three broad stages of growth: vegetative, reproductive, and maturing or ripening stages (Moldenhauer and Slaton 2001). Arthropods found in rice fields, including pests, follow patterns of population growth tied to their mode of feeding. Detritivores arrive first and peak early (Way and Heong 1994, Sedlock et al. 2019). Herbivores arrive later, to feed on the root, stem, flower, and leaf of the plant, suck sap, or bore into the stem (Heinrichs and Aguda 1994). Different species peak at different points in the season, after which their population declines (Settle et al. 1996).

Of the herbivores, the brown planthopper (*Nilaparvata lugens*) and the white-backed planthopper (*Sogatella furcifera*) are worth mentioning for being major pests of rice (Catindig et al. 2009), and also prey of bats (Leelapaibul et al. 2005, Srilophan et al. 2018). Both species peak in population during the late vegetative or reproductive stages of rice growth (Zhong-xian et al. 2006, Sharma et al. 2018a).

Given the generalist diets of many insectivorous bats, we hypothesize that pest abundance will be the primary driver of bat activity over a rice field. We further hypothesise bat activity will increase with increasing temperature and decrease with greater moonlight intensity. Herein, we report the results of a season-long study of bat activity patterns over a rice field in Assam, India. We identify temporal drivers of bat activity, and infer from these drivers the nature of the relationship between insectivorous bats and insect pests of rice over a rice growing season. We also examine the patterns of bat activity through the night to further illustrate the influence of rice pests on bat behaviour. Studies such as this, in combination with habitat suitability models, exclusion experiments, and economic evaluations, can be used to shape policy to maximise the value of the pest suppression service provided by bats in the agricultural landscape.

3.3 Methods

3.3.1 Study area

This study was carried out in Puthimari, a village in the Sonitpur district of Assam 26° 38' 43.0" N, 92° 39' 55.7" E, and the rice fields adjacent to it. Rice is major crop in Assam, grown on 2.43 million hectares of land (Directorate of Economics and Statistics 2019). The rice in this village is grown as a mosaic of different strains, with different levels of pesticide and fertiliser use. No fertiliser or inorganic pesticide was added to the crop at the locations of this study. Data on chemical use on neighbouring patches were unavailable. Three rice crops, Ahu, Boro, and Sali, are planted in this village each year in the autumn, summer and winter respectively. Our field season was conducted over the Sali/winter rice season. While planting began at the end of July and continued till mid August, the rice at the six sites used in this study was planted by the 1st of August.

3.3.2 Data Collection

Acoustic data were collected from dusk until between 4:00am and 4:30am (beyond which we ran the risk of theft) at the same six locations (Fig. 3.1) simultaneously from 27th of August 2019 until 9th of December 2019. Recordings were made using Audiomoth 1.0.0 full spectrum recorders (Hill et al. 2018). Six recorders were put into plastic zip-locked bags and placed in shallow (4cm) baskets attached to bamboo poles, with their microphones pointing upward. The sampling rate was set to the detectors' maximum of 384 kHz, the gain at medium, and the recorders were programmed to record for ten minute intervals, separated by a one second break.

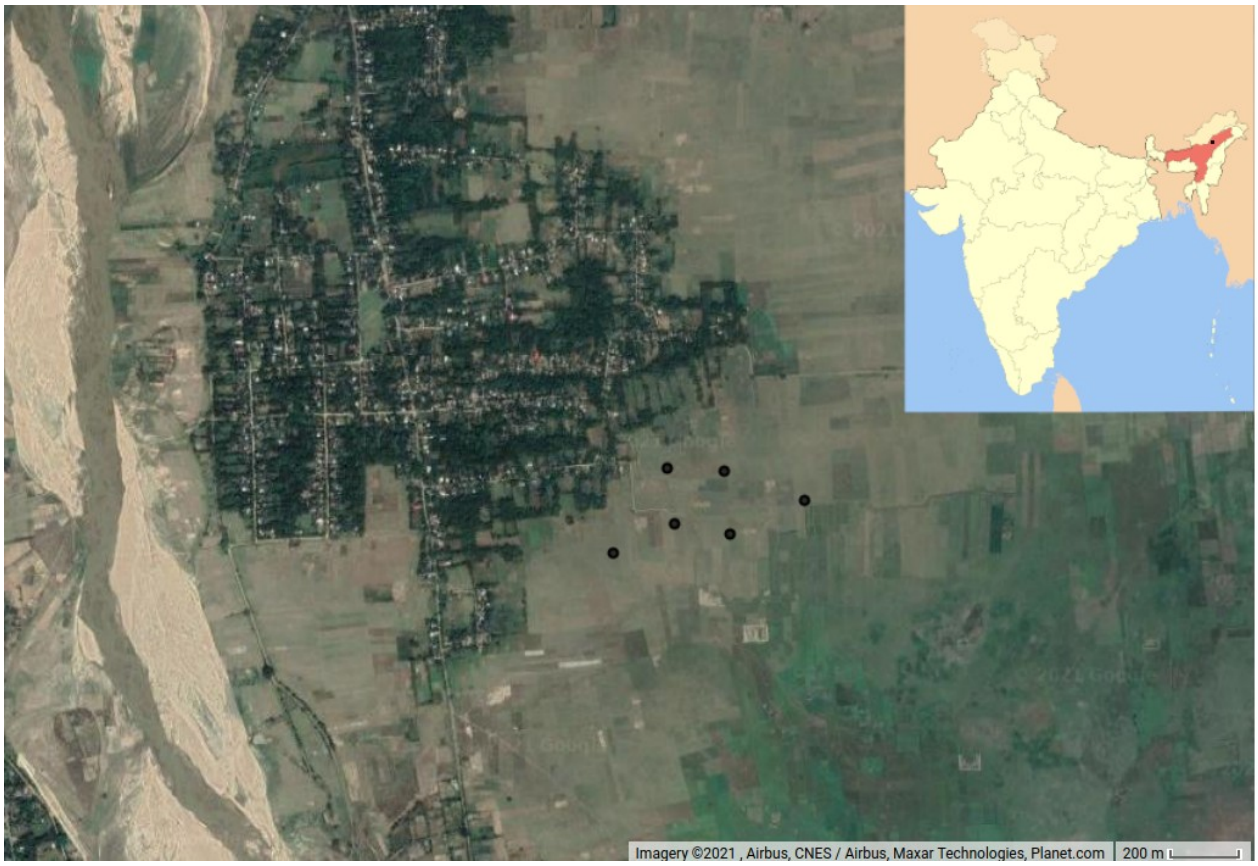


Fig. 3.1 Locations of six Audiomoth recorders in Puthimari village, Assam. Recorders were at least 100 meters away from each other, and the nearest forest. Red section in the map of India marks the state of Assam. Source: Map of India by Ganeshk (GFDL&cc-by-sa-2.5,2.0,1.0); Airbus, CNES/Airbus, Maxar Technologies, Planet.com

The six selected locations were east of the village. Each recorder was placed at a height of 1m, at least 100m from its closest neighbour, and also from the nearest forest line. Rice fields extended for over 1km to the north, south and east of the sites. Incidences of shorter recording periods due to logistical or technical issues were accounted for in the analysis. Between 30 September and 1 December 2019, bats were captured in four Avinet mist nets with the help of two Peersonic bat lures. These bats were weighed and photographed, and recorded with a Pettersson D240X recorder set to 'Time Expansion' mode upon release. Permission for this was granted by the Office of the Divisional Forest Officer, Sonitput West Division, Tezpur. Aniaml ethics approval was granted by

Institutional Animal Ethics Committee (IAEC) of the National Centre for Biological Sciences. The IAEC approval number is NCBS-IAE-2018/01(ME).

3.3.3 Acoustic data analysis

A total of 2576.5 hours of data were collected by six recorders over 48 nights of recording. The raw acoustic data were processed using custom written code in Python version 2.7 (Rossum et al. 1995) to isolate bat calls and extract key measurements of the call, as follows. (i) Frequency of maximum energy (FMAXE) - The frequency containing the most energy in the call (Wordley et al. 2014b). (ii) Minimum and maximum frequencies - Calculated as the lowest and highest frequencies that contained 5% of FMAXE. (iii) Bandwidth - The difference between the minimum and maximum frequency. (iv) Call length – The time between when the call first crosses 5% FMAXE, and when it last crosses 30% FMAXE. (v) Average amplitude – The average amplitude of the call. Once extracted, calls were classified into sonotypes using a MatLab Classification learner (The MathWorks Inc. 2019). Training data for each sonotype were created by extracting the parameters of manually identified calls. These training data were used by the classification learner in a linear discriminant analysis to classify all the extracted calls into sonotypes. Following this, the classified calls were run through a final round of processing in R version 3.63 (R Core Team 2020), where hard limits on FMAXE and bandwidth were used to reclassify calls that had been misclassified into a similar sonotype. The calls were then filtered to exclude undesirable sections of the audio, such as during heavy rain, instrumental failure resulting in static, or bats recorded prior to the recorders being in position.

Due to the absence of a complete acoustic library for Indian insectivorous bats, calls were classified to the sonotype level instead of species. Sonotypes were defined based on FMAXE and bandwidth into the following classes: (i) Constant Frequency calls (CF), and (ii) Frequency modulated-Quasi Constant frequency calls (FM-QCF). One pure QCF

sonotype was detected but could not be distinguished from a similar FM-QCF call. The two sonotypes were merged into one FM-QCF sonotype. Pure FM, and FM-CF-FM calls were not recorded. Constant frequency calls, though detected in the data, were not included in the analysis due to inability of the classifier to separate them from ultrasonic insect noises, which occurred at the same frequency. Taken forward for analysis were six FM-QCF sonotypes, which were identified by FMAXE values at 20kHz, 31kHz, 34kHz, 38kHz, 48kHz, and 65kHz, respectively.

The classification of calls was performed using the classification learner app in MATLAB (The MathWorks Inc. 2019), using a template created by manually identifying calls and extracting relevant parameters. Every recording was divided into five second intervals and a bat pass was defined as any interval with more than two calls of the same sonotype (Millon et al. 2015). We undertook a manual check of ten percent of the ~ 20000 extracted passes, selected by a random number generator, to verify the accuracy of the classification. The classifier accurately identified over 90% of all passes.

3.3.4 Statistical analysis

All statistical analysis was conducted in R. We used generalised linear mixed model (GLMM) to analyse the relationship between bat activity and its drivers (McCullagh 2019). Prior to building the model, outliers in the response variable 'bat activity' were identified and deleted using the 'check outliers' function from the 'Performance' R package (Lüdecke et al. 2020). All the variables were then standardised to zero mean and unit variance before analysis so that their effect sizes were comparable (Schielzeth 2010).

The following variables were considered relevant drivers of bat activity. (i) Temperature: Minimum nightly temperature was included to test for the effect of temperature on bat activity. For those sonotypes which showed a quadratic relationship between activity and minimum nightly temperature, minimum nightly temperature

squared was included as a variable in their supermodel. (ii) Moonlight: the percentage of the moon visible on each night, was included to test for the effect of moonlight intensity on bat activity. Temperature and moonlight data for Puthimari village were obtained, with permission, from the World Weather Online database (WorldWeatherOnline.com). (iii) Sampling effort: The recorders failed unexpectedly throughout the field season, leaving gaps in the dataset ranging from one to ten hours. To account for this, and for the logistical challenges that prevented the recording from starting on time on some nights, the total number of minutes sampled on any night was included as the factor 'sampling effort'. (iv) Ambient insect noise: Since the recorders were placed in the middle of rice fields, ambient noise above 5kHz was made up primarily of insects (frogs dominated frequencies below 5kHz). It was therefore included as a proxy for the activity of vocal insects. The ambient noise of each night was calculated by taking the mean amplitude between 5kHz and 24kHz, aggregated from all six recorders, and divided by the sampling effort of that particular night. (v) Day of the season: The number of days from 1st August 2019, which was the date by which rice at all six sites had been planted. This variable reflects the linear effect of rice maturity on bat activity, and seasonal changes in bat activity. Several major pests of rice – including leafhoppers and planthoppers – which are known prey of bats, are not vocal. Because these pests are known to peak in the middle growth stages of the rice (Heong et al. 1992, Zhong-xian et al. 2006), we also included in the model the quadratic transformation of the 'Day of the season' variable – 'Day of the season squared' – to capture a possible activity pattern that was high in the middle of the season and low at either end.

Two-way interactions between predictors were included in our analysis on an a priori basis when there was a biological reason to do so (Harrison et al. 2018). Also included in the global model was the random effect of 'site' – the six locations that the recorders were placed in – to account for non-independence of datapoints collected from the same location over multiple days.

Prior to running the model, all explanatory variables were tested for collinearity using Spearman's rank correlation, with a threshold of |0.7| to determine whether one factor had to be dropped (Dormann et al. 2013).

Day of the season was highly correlated with minimum nightly temperature (Spearman's rank correlation: r = -0.79), while day of the season squared was highly correlated with ambient insect noise (Spearman's rank correlation: r = -0.90). Therefore both day of the season and its quadratic – 'day of the season squared' – as well as all relevant interactions were removed from further analysis.

The remaining variables and interactions were included in a global model implemented with the 'glmmTMB' package (Brooks et al. 2017). The model was initially tested with a Poisson error distribution, since the response variable took the form of count data, but changed to a quasi-Poisson when the model tested positive for overdispersion (Bolker et al. 2009).

An information theoretic approach was then implemented to capture the best set of variables explaining bat activity by fitting all possible models and calculating Akaike's information criterion (AICc) corrected for sample size for each model; the best model being the one with the smallest AICc (Burnham and Anderson 2002). This was done using the 'dredge' function from the 'MuMIn' package (Bartoń 2020). Note that during the selection procedure, an interaction was included in a model only if its composite variables were also included, even if the variables independently were not statistically significant. All models with a ΔAICc value < 2 (the difference between each model's AICc and the lowest AICc) were considered as receiving equal statistical support (Burnham and Anderson 2002). When the 'dredge' function returned more than one model having an AICc within two units of the best model, the model with fewest variables was chosen (Symonds and Moussalli 2011).

One ‘best model’ was identified for each sonotype, as well as one model for all the sonotypes together. All best models were tested for overdispersion and zero inflation using the ‘testZeroInflation’ and ‘testDispersion’ functions from the DHARMa package (Hartig 2021). The residuals were analysed using the ‘simulateResiduals’ function, also from the DHARMa package. Residuals were checked for obvious patterns (heteroscedasticity, linear/quadratic trends), as well as deviance in the Kolgomorov-Smirnov test. A pseudo R-squared value based on the likelihood ratio test was calculated using the function ‘r.squaredLR’ from the ‘MuMIn’ package.

Finally, for a given model, the absolute values of the standardised regression coefficients were rescaled to sum to one to derive a measure of relative importance for each predictor.

3.3.5 Temporal distribution of nightly activity

Bat activity was also analysed for patterns over the night. Each sonotype was analysed separately, with calls being aggregated into ten-minute intervals starting from dusk.

First a clustering algorithm based on parameterised finite Gaussian mixture model was fitted to the data to identify clusters within the nightly activity data using the package and function ’Mclust’ in R (Scrucca et al. 2016). Second, the mean and sigma of each cluster recovered from the previous analyses were then used in a multimodal analyses to fit multiple normal distributions that best describe the nightly activity pattern of each sonotype. This was implemented with the ‘mix’ function from the ‘MixDist’ package (Macdonald and Pitcher 1979, Macdonald and Du 2018). In order to standardise for changing dusk times, data from each night were clipped to begin 20 minutes post-dusk and end 620 minutes post-dusk. This technique was developed originally to analyse the size frequency distribution of a population with overlapping age groups (Kell and Kell 2011).

This is the first time that this approach has been implemented to study temporal patterns in nightly bat activity.

3.4 Results

We identified a total of 18890 passes from six sonotypes over a period of 48 nights of recording. All six sonotypes were FM-QCF and featured FMAXE values around 20kHz, 31kHz, 34kHz, 38kHz, 48kHz, and 65kHz, respectively. Henceforth these sonotypes will be referred to using 'S' followed by their identifying frequency (e.g. S20). The most common sonotype was S38, accounting for 40.1% percent of all passes, followed by S48 (21.1%), S34 (15.3%), S65 (9.1%), S31 (8.9%), and S20 (5.3%). Nightly activity of all sonotypes peaked between 25 September and 28 October, with all but S34 peaking between the 15th and 28th of October.

3.4.1 Variables affecting bat activity

Overall, our models showed low to moderate R-squared values (0.166-0.389), which was to be expected given the many interacting factors that influence bat activity. Total bat activity over rice fields (best supported model R^2 = 0.262, Appendix Table A.1) increased with sampling effort (estimate = 0.291), ambient insect noise (0.237), minimum nightly temperature (0.164) and the interaction between ambient insect noise and moonlight intensity (0.100), but decreased with the interaction between ambient insect noise and minimum temperature (-0.213) and moonlight intensity (-0.126; Table A.1).

The activity of all six sonotypes increased with sampling effort, indicating that more bats were recorded when the number of hours sampled in a night was higher. The activity of three sonotypes (S31, S34, and S48) increased with ambient insect noise, a proxy for vocal insect activity (Fig. 3.2).

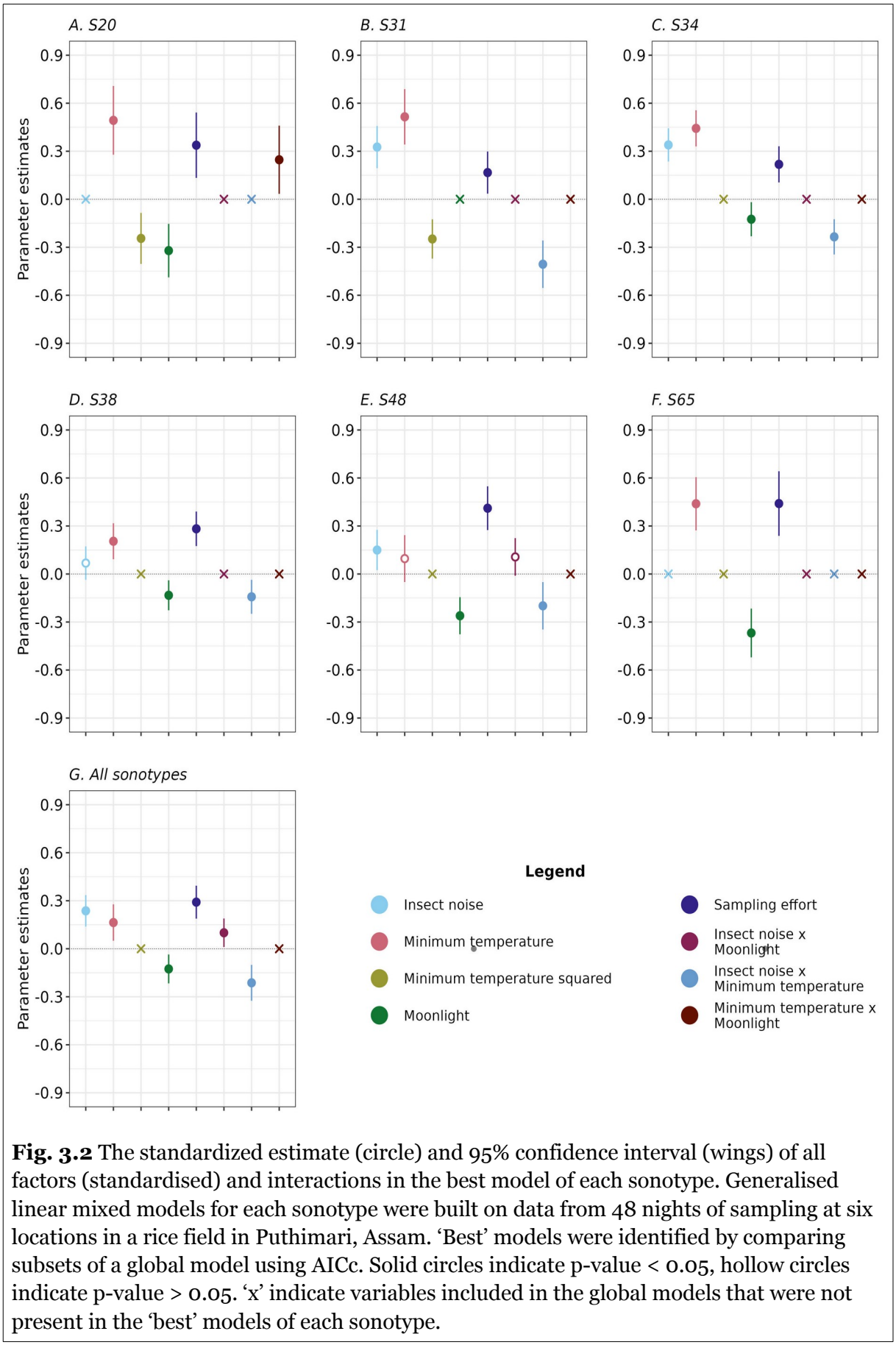


Fig. 3.2 The standardized estimate (circle) and 95% confidence interval (wings) of all factors (standardised) and interactions in the best model of each sonotype. Generalised linear mixed models for each sonotype were built on data from 48 nights of sampling at six locations in a rice field in Puthimari, Assam. 'Best' models were identified by comparing subsets of a global model using AICc. Solid circles indicate p-value < 0.05, hollow circles indicate p-value > 0.05. 'x' indicate variables included in the global models that were not present in the 'best' models of each sonotype.

For sonotype S38, ambient insect noise was significant only as part of an interaction with minimum nightly temperature. Minimum nightly temperature was a significant and positive driver of the activity of all sonotypes, apart from S48, for which minimum nightly temperature was only significant as part of the interaction with ambient insect noise (Fig. 3.2). The activity of S31 decreased with minimum nightly temperature squared, indicating that activity was lower during both very high and very low temperatures. Finally, the activity of every sonotype, apart from S31, decreased with moonlight intensity (Fig. 3.2).

Minimum nightly temperature squared was significant and negative in the best model of S31, indicating that activity was lower during both very high and very low temperatures. Moonlight intensity was a significant and a negative driver of the activity of five sonotypes (S20, S34, S38, S48, and S65).

The effect of the interaction between ambient insect noise and minimum nightly temperature was significant and negative in the models of four out of six sonotypes. On cold nights – the left end of Fig. 3.3B-E – bat activity was significantly higher when ambient insect noise was higher. On warm nights (the right end of Fig. 3.3B-E) when the energetic costs of flight are lower, activity increased when insects were scarce.

The interaction of ambient insect noise and moonlight intensity was significant and positive in the model of S48. High insect activity reduced the effect of bright nights on the activity of S48 (Fig. 3.3F). The interaction between moonlight and minimum nightly temperature was significant and positive for one sonotype. The activity of S20 was lower with the combination of low temperatures and high moonlight than it was with less extreme values of either variable (Fig. 3.3A).

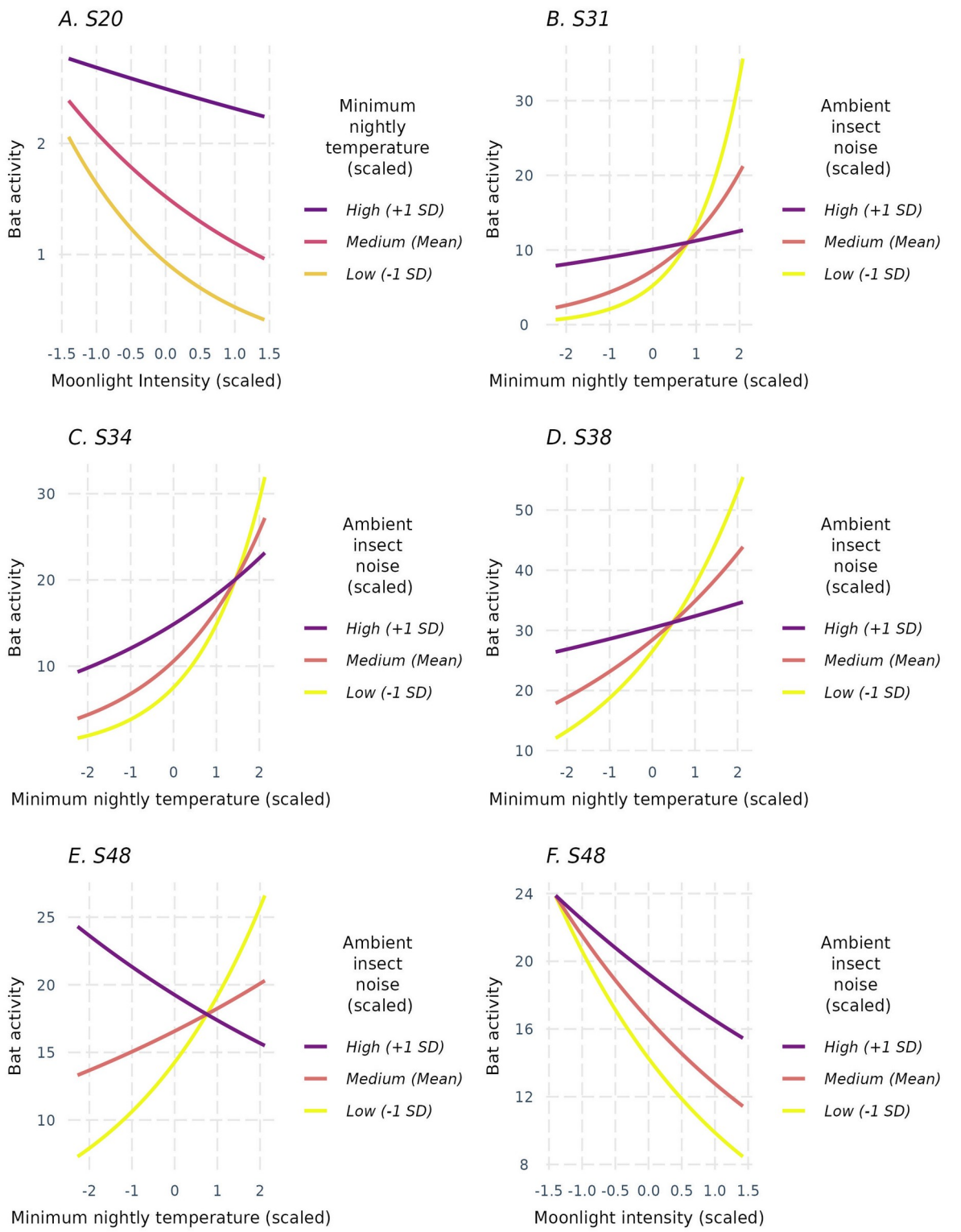


Fig. 3.3 The effect of two-way interactions on bat activity. Generalised linear mixed models for each sonotype were built on data from 48 nights of sampling at six locations in a rice field in Puthimari, Assam. Plots A to F show how the interactions between fixed effects in the model (minimum nightly temperature, moonlight intensity, and ambient insect noise) influence bat activity in those models where interactions are significant. All three variables are standardized, as they are in the model.

3.4.2 Temporal distribution of nightly activity

The multimodal analysis of nightly activity patterns of each sonotype produced two broad patterns. The first, exhibited by S31, S34 and S38 (Fig. 3.4B-D), show a primary peak early in the night, at 32, 38, and 88 minutes past dusk, respectively, followed by one to three smaller peaks through the night. The second pattern, seen in S20, S48 and S65 (Fig. 3.4A, E, and F), exhibited a more even distribution through the night, with the second or third peak being the highest. Details of the locations and standard error of each peak, as well as results of the chi-square goodness of fit test can be found in Appendix A (Table A1.2).

3.4.3 Bat captures

Of all the captured bats, only three species could be unambiguously identified by their physical and morphological characteristics. These were:

Scotophilus kuhlii – The Lesser Asiatic yellow bat,

Scotophilus heathii – The Greater Asiatic yellow bat,

Megaderma lyra – The Greater false vampire bat.

The photographs of one individual of every species (confirmed or unknown ID), along with a spectrogram of their calls on release can be found in Appendix 1 (Fig. A1.1 - A1.14). Spectrograms were created using the Matplotlib package (Hunter 2007) in Python 2.7. Their weights ranged from 3gm to 44gm, and the frequency of their calls ranged from 32kHz to 65kHz.

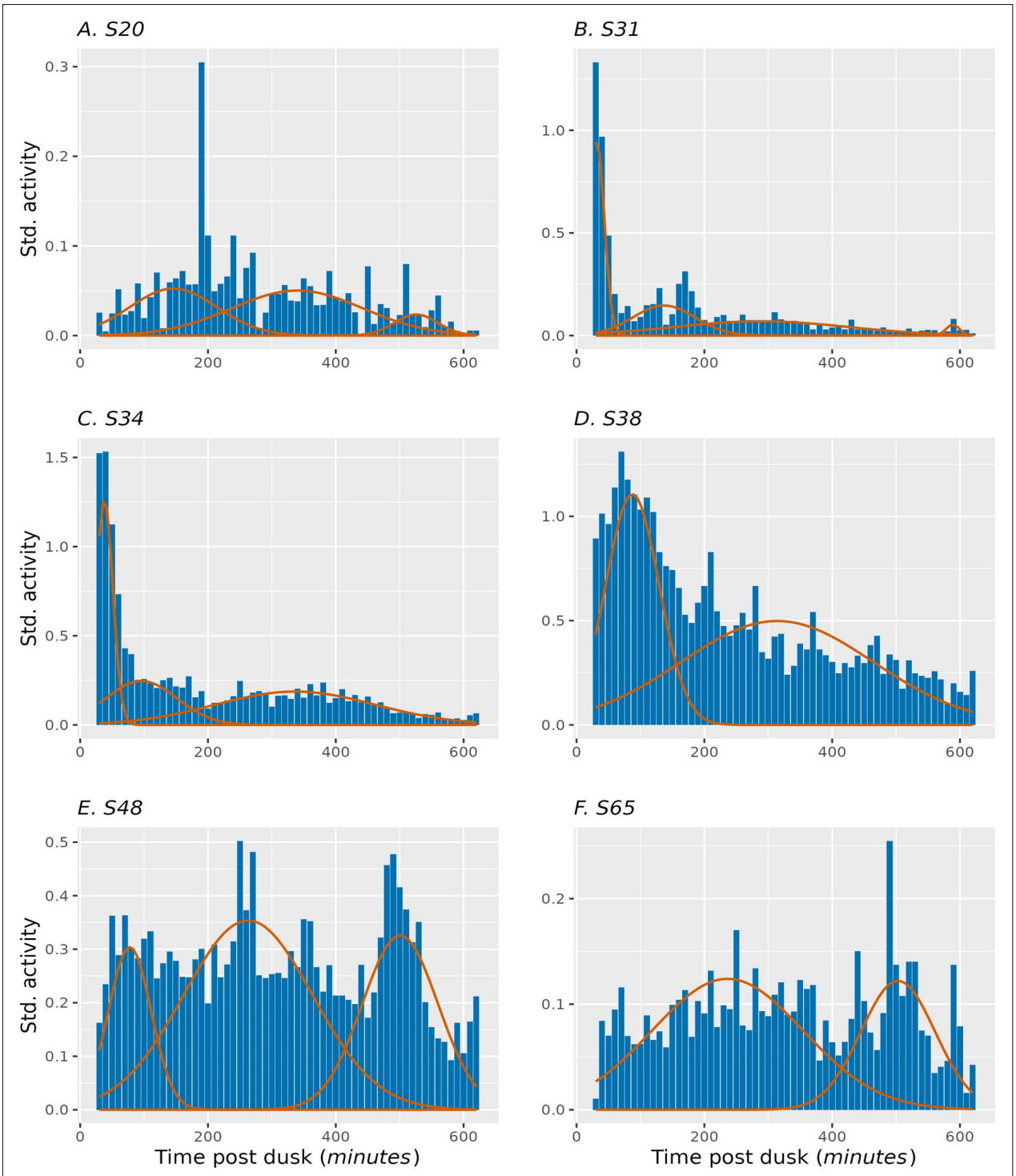


Fig. 3.4 The temporal distribution of nightly activity of six sonotypes. Data was collected at six locations over 48 nights of sampling in a rice field in Puthimari, Assam. Every night was divided into ten-minute intervals starting at dusk and ending ten hours post dusk. The number of passes of each sonotype in each ten-minute post-dusk interval was summed up over all 48 nights of sampling. Nightly activity was clipped from 20 minutes post dusk until 620 minutes post dusk. Composite normal distributions that best fit the overall pattern of nightly activity of each sonotype were fit using the 'mix' function, verified using a Chi-square goodness of fit test. S20 has an additional peak caused by the outlier at 190 minutes that is not visible due to a small standard deviation.

3.5 Discussion

We describe the activity of insectivorous bats foraging over rice fields, both over a rice season, and over the course of the night. In addition, we identify how biotic and abiotic drivers influence bat activity over the rice season.

3.5.1 Activity over the season

Although not always articulated as such, several studies have documented patterns in bat behaviour that fit predictions of optimal foraging theory (Geiser and Brigham 2012, Vesterinen et al. 2016, Prat and Yovel 2020). Bats in our study site also showed behavioural patterns consistent with foraging strategies that minimized risk and maximised net energy gain. These patterns differed between species, indicating a difference in the cost-risk-benefit trade-offs facing species with different physical characteristics – we assume that most of the species caught in our nets, which had a range of sizes, were also foraging over rice fields.

Our results indicate that three out of six sonotypes, which account for 67.4% of insectivorous bat activity in the study area, were positively influenced by our proxy of insect activity over the rice season. We started the analysis intending to use two proxies for insect activity - ambient insect noise and the quadratic function of day-of-the-season. The latter represented population growth patterns of important rice pests that were documented prey of bats (Zhong-xian et al. 2006, Sharma et al. 2018a). We were forced to drop this term due to the high covariation with ambient insect noise. The same covariation, however, implied one of two things. Either the two variables were acting as a proxy for the same insect community, or since many of the major rice pests are not vocal, alternatively the vocal insects, that may be pests themselves, have similar population growth patterns to non-vocal rice pests such as planthoppers and leafhoppers. It is ecologically parsimonious to assume that they grow more abundant as the rice matures, peaking in the middle stages

of rice growth, after which their population declines (Heong et al. 1992, Zhong-xian et al. 2006, Sharma et al. 2018a). The mid-season peak, documented in pests and now seen in vocal insects, was tracked by bats belonging to the sonotypes S31, S34, and S48. The strength of this effect suggests that the bats recorded at our sites were responding to changes in rice pest abundance by preferentially hunting over rice fields when insect activity was high.

Few studies have considered bats in rice-dominated landscapes. Most that do so focus on bat diet, and have established clear links between insectivorous bats and rice pests (Leelapaibul et al. 2005, Puig-Montserrat et al. 2020). Kemp et al. (2019) showed that insectivorous bats in Madagascar hunted over rice fields preferentially compared to nearby forested areas. Similarly, Puig-Montserrat et al. (2015), found that insectivorous bats in Iberian rice fields significantly increase their activity when moth activity increases. The moth in question was the rice stem borer (*Chilo supressalis*), one of the most significant rice pests in Asia (Yao et al. 2017). Puig-Montserrat et al. (2015) went further and installed bat boxes to increase the resident populations of insectivorous bats. After ten years, pest control by bats was so effective that the need for pesticides was eliminated. The direct financial value placed on this service was 21 Euro per hectare per annum. It is only the second valuation of the bat pest suppression service on rice, after Wanger et al. (2014) estimated this service to be worth 1.2 million USD per annum in Thailand. Our study presents the first quantitative indication that bats hunt and regulate pests in Indian rice fields.

While insect activity was a major driver of bat activity, it was not the only one. Although temporal heterothermy in Indian bats has not been studied, data from other tropical and subtropical bats suggests that insectivorous bats are likely to be heterothermic and capable of entering torpor to reduce energy expenditure on cold nights (Stawski et al. 2014).

Temperatures at our field site did not fall below 11°C, higher than the 6-10°C documented in other studies to constitute a physiological constraint to bat activity (Taylor 1963, Burles et al. 2009, Razgour et al. 2011). However, these temperatures were low enough to reduce insect activity (Stejskal et al. 2019), which in turn would influence bats. Whether the effect is direct or indirect, given that this pattern has been documented before (Barros et al. 2014, Wolbert et al. 2014, Appel et al. 2019), we predicted that bat activity would be positively correlated with temperature. This was true for five out of six sonotypes. The sixth sonotype, S31, was influenced by minimum nightly temperature squared, indicating that its activity is reduced at both low and high temperatures. What remains difficult to separate is whether lower bat activity on cold nights is an evolutionary adaptation based on the expectation of scarce prey and therefore incorporated into the foraging strategy, or whether bats leave the roost to hunt, only to return quickly when it is clear that their prey is scarce.

In the case of moonlight, we hypothesised that nocturnal avian predators – the field site hosted an abundance of owls (Iqbal Bhalla, personal observation) - would impose predation pressure on slower bat species that they could hunt, and that the risk of predation would be greater on brighter nights. Similar to previous studies (Morrison 1978, Meyer et al. 2004, Lima and O'Keefe 2013, Appel et al. 2017), we found that five out of six sonotypes decrease their activity on brighter nights.

While factors such as temperature, moonlight, and insect activity individually affect each of these considerations, our analysis suggests that combinations of them can shift the cost-risk-benefit balance. This has been suggested before (Appel et al. 2019), but rarely investigated. The interaction terms of our models explored these combinations.

To maximise fitness, a bat must employ a foraging strategy that efficiently weighs the cost-benefit trade-off between the risk of predation and the reward of successful hunting. Bright moonlight imposes a significant predation risk on bats, reducing their

activity. However, as seen in Fig. 3.3F, bright nights suppress the activity of S48 to a lower degree when insect activity is higher, implying that this sonotype is more likely to risk high levels of predation when the nutritional gains or prey detectability are higher. This, in part, concurs with recent studies which described bats increasing their activity, or moving to open spaces, on moonlit nights to maximise hunting success (Roeleke et al. 2018b, Kolkert et al. 2020a). A similar pattern is seen in Fig. 3.3A, where the activity of S20 is lower with increasing moonlight, but this effect is less pronounced when temperatures are high.

The activity of S31, S34, S38, and S48 was lower when temperatures and insect activity was low, pointing to an additive effect prompting reduced bat activity when insects are both less vocal and less active.

3.5.2 Nightly activity patterns

The activity patterns of the six sonotypes through the night are consistent with two primary foraging modes. The dusk peaks seen in three sonotypes (S31, S34, and S38) are characteristic of bats hunting crepuscular insects that also show dusk peaks in activity (Rydell et al. 1996, O'Donnell 2000). While these insects may peak earlier than bats, predation pressure from diurnal raptors delays the emergence of many bats, which then have a short window to maximise their feeding (Speakman 1991). Both planthoppers and leafhoppers, as well as other rice pests, which show a peak in population size during the middle of the rice growing season, exhibit daily peaks in activity around dusk (Macquillan 1975, Kersting and Başpmar 1995, Zhu et al. 2017, Mazza et al. 2020). Both patterns of activity - over a season and within a night - were also seen in two sonotypes, S31 and S34, lending support to the argument that they are tracking insect, and possible pest, populations.

The second broad pattern in nightly activity points to bats that hunt nocturnal prey that are active, or can be caught by gleaning, for a significant proportion of the night

(Jones and Rydell 1994). Without the incentive to emerge early and risk predation by diurnal predators, these bats emerge later and have a less skewed activity pattern over the night. Although nocturnal predators still impose predation pressure, this risk is more evenly distributed through the night. As a result, the three sonotypes which exhibited this pattern˜ S20, S48, and S65˜ had a more even nightly activity pattern, with only S20 exhibiting a clear peak around midnight. However, it is important to note that we did not have confirmed bat species identification on our sonotypes, or information on roost location, and therefore cannot be certain about the impact of distance from roosts on the observed patterns of activity.

The 'mixdist' package and methods contained within are not commonly used to analyse nightly patterns of activity in bats. It has previously been used to analyse the frequency of different age groups in a population (Macdonald and Pitcher 1979, Kell and Kell 2011, Wells et al. 2013), and its use in this study was exploratory. This method has its limitations, including, for example, the need for subjective decision-making in setting limits to the number of peaks permissible for each sonotype. Nonetheless, we believe that this method has potential to quantitatively analyse bat activity patterns that have up till now been primarily described qualitatively.

Bats in India are under-studied. Despite evidence from around the world of their importance as bioindicators (Jones et al. 2009) and providers of ecosystem services (Kunz et al. 2011), only a handful of studies have investigated the ecology of insectivorous bats in India (Wordley et al. 2015, 2017, Ongole et al. 2018). Any attempt to maximise the ecosystem services of insectivorous bats can only be made through an understanding of the requirements, limitations, and drivers of their distribution and activity. To that end, this study has demonstrated how insectivorous bats hunting in rice-dominated landscapes are influenced by insect activity, temperature and moonlight.

In the same fields as data collection for this study took place, Bhalla and Whittaker (2022, Chapter 5) conducted a bat exclusion experiment to measure the effect of bat exclusion on rice health and yield. They found that rice health but not total yield was negatively affected by the exclusion of bats. This would support the results of this study, which show that bats and insects in agricultural field have similar activity patterns, not only over a season but also over a night, strongly suggesting that they hunt and regulate insect (likely including insect pest-) populations.

A complete description of this pest suppression service, however, requires investigations into the landscape drivers of their distribution and analyses of their diet. Such studies will be relevant not only for describing bat ecology, but also for bat conservation, promoting environmentally-friendly agriculture, and sustainable development.

There are undoubtedly other natural enemies of insect pests active in rice fields. Personal observation of insectivorous birds on field suggested that they might play a large role in regulating insect pest populations, as would the numerous other communities that prey upon insect pests. Efforts aimed at reducing rice yield lost to insect pests must therefore include these natural enemy communities in order to have the greatest impact.

3.6 Acknowledgements

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CHAPTER 4

Landscape features drive insectivorous bat activity in Indian rice fields

4.1 Abstract

Context

Insectivorous bats have been shown to control a number of agricultural insect pests. Bats exhibit species-specific responses to the surrounding landscape, tied closely to their morphology and foraging mode. The activity and distribution patterns of bats are therefore influenced by the landscape characteristics.

Objectives

This study aimed to determine which features in the landscape surrounding rice fields influence the activity levels of insectivorous bats, and at what scales they were most influential.

Methods

We collected acoustic recordings to determine activity levels of seven bat sonotypes in rice fields surrounded by a variety of landcover types in the Nagaon district of Assam, India. Using this, we determined the most important set of features in the surrounding landscape, and the scales at which they were most predictive, for each sonotype.

Results

Our results suggest that variables related to tree cover are the most important predictors of bat activity in rice fields. Distance to nearest forest, area of forest within 1km, distance to nearest forest edge, and landscape heterogeneity influenced all five of the analysed bat sonotypes. Also important were the amount of urban land within 1km, which exerted a negative effect on the activity of one sonotype, and moonlight activity, which negatively influenced the activity levels of one sonotype.

Conclusion

Our results demonstrate that when in rice fields, bat activity is most influenced by presence and proximity of trees. Increasing tree cover in agricultural landscapes will increase bat activity and likely the level of pest suppression.

4.2 Introduction

Bats (order Chiroptera) are the second most diverse mammalian order on the planet, bringing with their diversity substantial ecological and financial value through their potential use as bioindicators (Jones et al. 2009, Russo et al. 2021), providers of fertilizer, and ecosystem services such as pest suppression, seed dispersal, and pollination (Kunz et al. 2011). Of the known >1400 species of bats (Simmons and Cirranello 2021), nearly two-thirds are insectivores, which thrive in a range of habitats – from deserts (Razgour et al. 2018) – to wetlands (Mas et al. 2021). In adapting to these environments, bats have evolved highly specialized acoustic and morphological characteristics that enable them to navigate different niches and hunt prey in a wide variety of conditions (Denzinger et al. 2016, Jones et al. 2016). These same specializations, however, also define the limits of their existence. As a result, bats specialised to a particular habitat cannot easily forage in another.

Interest in insectivorous bats in agricultural landscapes has risen dramatically in the last two decades, driven in part by the growing evidence of their value as pest suppression agents to crops such as rice (Puig-Montserrat et al. 2015), cotton (Cohen et al. 2020), cacao (Cassano et al. 2016), and corn (Maine and Boyles 2015). Their success as natural pest suppressors comes from a broad diet (Tournayre et al. 2021, Maslo et al. 2022), large energetic demands associated with flight, and, importantly, flexibility in foraging habitats. Insectivorous bats quickly switch to the most productive foraging habitat available. When an agricultural plot is fallow between seasons, bats can move to more productive regions elsewhere, to return when there are pest outbreaks (McCracken et al. 2012, Puig-Montserrat et al. 2015). This has led to the suggestion that bats might be uniquely suited to tackle the changing ranges of pests under climate change (Blažek et al. 2021).

A number of characteristics determine the suitability of a landscape to insectivorous bats. Chief among these is the composition of the wider landscape surrounding the crop fields. Studies of bats in agricultural landscapes consistently find that heterogeneous landscapes support a more species rich and diverse bat community than homogenous ones (Frey-Ehrenbold et al. 2013, Monck-Whipp et al. 2018, Rodríguez-San Pedro et al. 2019) and that higher levels of natural and semi-natural landcover within agricultural landscapes promotes bat activity (Kelly et al. 2016, Kahnonitch et al. 2018).

Linear elements such as hedgerows and lines of trees constitute a key type of natural landcover for echolocating bats. These are used both as landmarks for navigation, and for protection against avian predators and wind (Downs and Racey 2006). Even a single row of trees can be used for commuting and, if the trees are of the right structural form, for roosting (Fischer et al. 2010, Kalda et al. 2015). Increasing the width of the linear features is usually accompanied by larger insect communities, leading to higher bat activity (Russ et al. 2003). As a result, linear features around agricultural fields host bats in greater numbers and diversity than the field interiors do (Kelm et al. 2014, Finch et al. 2020). With many types of agriculture providing less-than-hospitable matrices between forest patches, the presence of suitable linear elements reaching into agricultural fields increases the permeability of such agricultural landscapes (Finch et al. 2020).

The edges between forest and non-forest habitats also provide productive feeding grounds for bats that offer (comparative) safety from predators. The relative safety and higher foraging success for the generally rich guild of edge-space foragers (Denzinger et al. 2016), results in significantly higher bat activity at edges or in close proximity to linear features compared to open and cluttered habitats (Jantzen and Fenton 2013, Finch et al. 2020).

Compounding the requirements for foraging habitats are the requirements for roosting and water. While many bats are capable of commuting long distances to forage,

such movements are often along edges. Many bats will avoid open spaces, which bring higher risks of predation, colder temperatures, and faster winds (Downs and Racey 2006). Landscape elements providing bats with access to water bodies support greater bat activity (Heim et al. 2018).

The carrying capacity of a landscape is therefore not solely determined by its composition, but also by the configuration of the elements within it, which shape a bat's access to food, roosts, and water (Heim et al. 2015). Landscape complementation – whereby close proximity of different landscape elements, and their resulting ease of access, increase the abundance of a species – is particularly evident in bats due to the often contrasting requirements of roosting (in mature trees) and foraging (in more open spaces). A study in Canada found that when the area of different landcover is kept constant, increased fragmentation led to increased bat activity (Ethier and Fahrig 2011).

Across the world, the intensification and homogenization of agricultural practices (Robinson and Sutherland 2002, Wang et al. 2015) are having severe impacts on bat populations (Park 2015). Given the strong preference of bats for specific landscape structures, changes which reduce treecover disproportionately affect those species that forage in dense natural vegetation. The general trend shows a greater decline of clutter foragers than open-space foragers with reduced treecover (Heim et al. 2016, Mtsetfwa et al. 2018).

As agricultural systems worldwide come under increased production pressure, the need for sustainable pest control has bolstered studies of natural pest control measures. Given that bats are valuable pest suppression agents, and that India is striving to increase agricultural production (Hinz et al. 2020), it is important to understand the relationship of bats and agricultural landscapes.

This study focussed on the insectivorous bats in rice-dominated landscapes of Assam, India. In India, rice makes up 22.01% of the gross cropped area (Directorate of

Economics and Statistics 2019). A small rice farm can offer an ideal habitat for a broad community of insectivorous bats, boasting an abundance of insects (Puig-Montserrat et al. 2015), edges (Harms et al. 2020), roosting sites (in trees and anthropogenic structures) (Kusuminda et al. 2021), and water bodies. As a matrix, rice is a harsh habitat, providing no landmarks, edges, tree cover, or resting sites. The larger the fields are, therefore, the less accessible we expect their interiors to be, as bats foraging in them are then further from water sources, shelter, edges, or roosting sites (Rainho and Palmeirim 2011, Frey-Ehrenbold et al. 2013).

This study used passive acoustic recordings from rice fields within the Nagaon district of Assam (26°21'0"N, 92°40'60"E) to investigate the importance and scales at which different landscape features drive the activity of insectivorous bats. By identifying how bats use the agricultural landscape, this study can contribute to designing agricultural landscapes for the protection of bats and the promotion of their ecosystem services.

4.3 Methods

4.3.1 Study site

The study was conducted in the Nagaon (26.3480° N, 92.6838° E), a district of Assam. Although the typical operational holding of agricultural land in Nagaon (of which rice is the primary crop) is 0.5-1.0 hectares (Saikiam et al. 2020), rice plots usually lie adjacent to one another, so the size of an uninterrupted stretch of rice varies considerably. A typical farming village in Assam has a central road with many branches, dotted on either side with buildings, both concrete and wood. Hubs in a village centre have the highest density of buildings and artificial light, which decrease as one moves further away. Forested or semi-forested vegetation is present in pockets and surrounding most structures. Data for this study came from rice fields surrounding such villages near the city of Nagaon. Nagaon tends to have hot and wet summers. During the months of May and June 2019, when

fieldwork took place, the average temperature was 28°C, with a minimum of 21°C and a maximum of 35°C (accessed on 15 Jan 2022 from timeanddate.com). The lack of irrigation leaves many farmers relying on the rains to water their crops. Historically, the months of May and June see among the highest rainfall of the year, averaging 219 and 311mm, respectively (accessed on 15 Jan 2022 from timeanddate.com).

4.3.2 Field data

We recorded acoustic data using six Audiomoth 1.0.0 full spectrum recorders (Hill et al. 2018) with a sampling rate of 384kHz and a medium gain. Data were collected over 18 nights between 9 May and 8 June 2019, with the six recorders placed as far away from each other as was feasible. Sites were chosen for a combination of logistical feasibility, diversity of the surrounding landscape, and contacts with local communities. Uniform data collection in this landscape proved difficult, and site locations and sampling effort were influenced significantly by logistical, cultural, and safety considerations. As a result, not every site was revisited, nor were recorders always in place by dusk. To account for difference in sampling effort between sites, any recorder that collected less than 90 minutes of audio in a night was excluded from the analysis, and sampling effort – the number of minutes sampled in a night – was included in the global model of each sonotype.

4.3.3 Acoustic data analysis

Acoustic recordings totalling 481 hours were processed using custom built code in Python version 2.7 (Rossum et al. 1995). From these recordings bat calls were isolated and extracted based on the following measurements:

(i) Frequency of maximum energy (FMAXE) – the frequency containing the most energy in the call (Wordley et al. 2014b); (ii) Minimum and maximum frequencies – the lowest and

highest frequencies that contained 5% of the energy of FMAXE; (iii) Bandwidth – difference in frequency between the minimum and maximum frequencies; (iv) Call length – the time interval between the point that the call first crosses 5% FMAXE, and when it last crosses FMAXE; and (v) Average amplitude – the average amplitude of the call. All code used during the analysis will be uploaded to a GitHub repository.

Using manually verified calls to form a template, a linear discriminant analysis in the MatLab Classification learner (The MathWorks Inc. 2019) was used to build a classifier that classified all the remaining calls into sonotypes. The classified calls were then processed in R version 3.63 (R Core Team 2020) to reclassify based on FMAXE and bandwidth those few calls that had been misclassified. The calls were also filtered to remove false positives arising from heavy rain, instrument failure, or bats that were recorded prior to the recorders being put in place.

There are limited acoustic libraries for Indian bats, none extending as far as Assam. Without such a library to use as reference, the isolated calls were classified to the sonotype level, rather than the species level. These were defined based on FMAXE and bandwidth into: (i) Constant Frequency calls (CF), (ii) Frequency modulated – Quasi Constant frequency calls (FM-QCF), (iii) Quasi-Constant frequency calls (QCF). Pure Frequency Modulated (FM) and FM-CF-FM calls were not recorded. A few CF calls were recorded, but could not be separated from insect noises, and so were excluded from the analysis. One QCF call was recorded in the same frequency range as another FM-QCF call, frequently changing from QCF to FM-QCF within a pass. These were therefore considered to be the same sonotype and were recorded as FM-QCF. Calls were classified into sonotype based on FMAXE values, resulting in one pure QCF call at 28kHz, and six FM-QCF calls at 20kHz, 31kHz, 34kHz, 38kHz, 48kHz, and 65kHz, respectively.

All recordings were divided into five-second intervals. One bat pass was defined as an interval containing more than two calls of the same sonotype (Millon et al. 2015). Using a random number generator, 10% of the extracted passes were selected for manual verification. The classifier accurately identified >90% of the passes.

4.3.4 Spatial data analysis

Landscape data used for the analysis came from Level-2A of Copernicus Sentinel data [2019], accessed on 13 January 2022. Different studies choose different radii around sites within which to calculate landscape statistics. These vary based on the objective of the study, bat species in question, and landscape. They range between 0.1km-1km (Kahnonitch et al. 2018) to 1km-5km around each site (Rodríguez-San Pedro et al. 2019). Due to lack of data on the home and foraging ranges of India bats, we chose intermediate scales of analysis for landscape variables, using scales of 500m, 1000m, 2000m, and 3000m, to account for difference in range sizes between different species. The landscape in a radius of 3km around every site was classified at a 10m resolution using a random forest supervised classifier in Google Earth Engine (Gorelick et al. 2017). Training data were collected using Google Earth Engine and classified landscapes were verified using Google Earth imagery from January 2019, and my knowledge of the fieldsites. The classification of rice fields was also ground-truthed.

Four bands were used for the classification, B3, B4, B8 and B11, which correspond to green, red, near infrared (NIR), and short-wave infra-red (SWIR), respectively. In addition to the above bands, the following three indices were calculated for use in the classifier. NDVI and NDWI (Xue and Su 2017) and one additional index (Mayer and Scribner 2002) were calculated using the formulae below.

1. NDVI: (NIR-Red)/(NIR + Red)
2. NDWI: (Green-NIR)/(Green+NIR)

3. (SWIR – Red)/(SWIR + RED).

To increase the accuracy of the classifier, the least cloudy image, selected using the 'CLOUDY_PIXEL_PERCENTAGE' band from data for each of January and May were considered. These two months represent the landscape before and during the rice season, respectively. The difference in the values of the above three metrics between the months of January and May exploited changes in the spectral characteristic of rice prior to and during the season, increasing the accuracy of the classifier.

Each 10m-10m pixel was classified into one of nine landscape types.

1. Dry Rice: Rice planted in dry fields.
2. Wet rice: Rice planted in waterlogged fields.
3. Water: Pixels covered completely with water that was not covered by any algae/plants.
4. Bank: Pixels filled partly with water and partly with another landcover type.
5. Edge: Land filled only partly with trees and partly with a different land cover type.
6. Field: Land with grass but no trees.
7. Forest: Pixels containing only trees.
8. Bare ground: Empty land without grass, trees, water, or rice, often roads.
9. Urban: Area with construction/houses, or roads. Although roads were often also classified as 'Bare ground'.

This list was later condensed by merging three pairs of classifications: dry rice and wet rice; and water and bank, and 'urban' and 'bare ground'. 'Dry rice' and 'wet rice', and 'water' and 'bank' were merged because these pairs were, from the perspective of a bat, nearly identical. 'Urban' and 'bare ground' were merged because roads were often

classified as 'bare ground', and represented many of the negative features of urban land – artificial light, noise, and pollution.

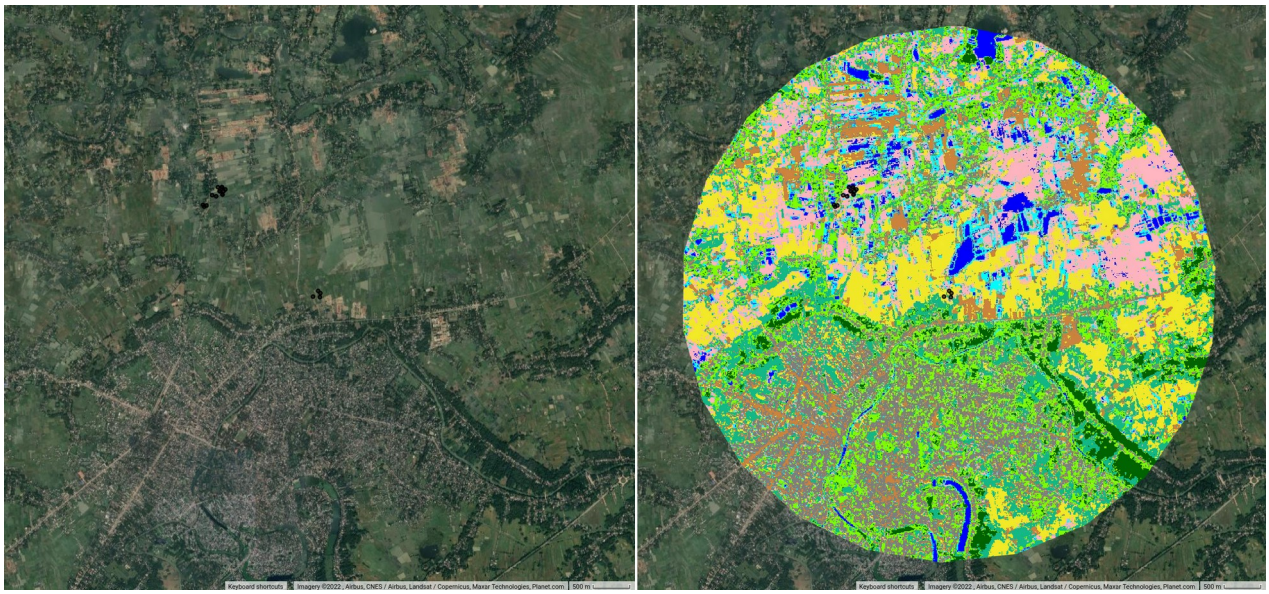


Fig. 4.1 An unclassified (left) and classified (right) map of the landscape around one set of sites in Nagaon, Assam. The landscape was classified within a radius of 4km around the centroid of one cluster of sites using a random forest supervised classifier in Google Earth Engine. The centroids are located at 92.61813539786188E, 26.353871760484573N. The landscape was classified into nine landcover types: Dry rice , wet rice , bare ground , water , bank , edge , field , forest (or algae) , and urban land . Black dots represent sampling sites. Maps for remaining sites can be found in online resource 1 (Fig. SI - SIII). Image source: Contains modified Copernicus Sentinel data (2022); Arbus, CNES/Airbus, Landsat/Copernicus, Maxar Technologies, Planet.com.

The following types of landscape metrics were calculated for the analysis:

1. Area of all landscape types except water within the four buffers. Size of water bodies was not considered because at the scale of analysis we used, without access to characteristics such as water depth, and in a landscape with an abundance of water bodies, distance to the nearest water body was considered to be the most important water variable.

2. Distance of each site to nearest patch of every landscape. Defining a 'patch' as 10 or more pixels of a water (equivalent to 50m * 20m) or 30 or more pixels of the other landscape types (equivalent to 50m * 60m), the distance to the nearest patch within

3000m from the recorder was measured. This metric was not calculated for rice because all the recorders were placed in rice fields.

3. Landscape structure metrics. Shannon's Diversity Index (SHDI) for landscapes, calculated as $-\sum_{i=1}^{m}(Pi * \ln(Pi))$ (Shannon 1948). Where 'i' is the selected landscape and Pi is the proportion of landscape 'i' in the selected buffer.

4.3.5 Statistical analysis

Part 1: Accounting for spatial autocorrelation

To maximise the use of the data, while acknowledging and accounting for non-independent datapoints, sites were grouped according to buffers that resulted in no significant spatial autocorrelation. All statistical analysis was performed in R version 3.63 (R Core Team 2020). A distance matrix of all the points was created and transformed into a hierarchical cluster tree. Points were then grouped based on a set of scales: 0.1km, 0.2km, 0.3km, 0.4km, 0.5km, 1km, 5km, 10km and 30km. At each scale, standardized bat activity was tested for spatial autocorrelation using the Moran's I test using the 'spdep' R package (Bivand and Wong 2018). The smallest scale at which sites could be grouped with no spatial autocorrelation was chosen for each sonotype. This grouping was used as the random effect in the subsequent models.

Part 2: Choosing one variable of each landcover

A total of five variables were derived for each land-cover type namely: area within buffers of 0.5km, 1km, 2km and 3km – and the distance of the site to the nearest patch of said landcover. In the case of rice and SDHI, distance to the nearest patch was not applicable.

For each landcover type, the most significant of the five (or four) variables was selected using a generalised linear mixed model (GLMM) implemented as below. Here, and for each sonotype, bat activity was the response variable, sampling effort and one variable of the focal landcover were explanatory variables, and the previously identified site grouping variable was included as the random effect to account for spatial autocorrelation. In addition, we defined an appropriate null model as GLMM model with intercept only to highlight a potential absence of relationship. The models of every variable of a landcover type and the null model were compared to each other using Akaike's Information Criteria corrected for sample size (AICc) to determine the most significant variable of a given landcover type (Bartoń 2020), the best model being the one with the lowest AICc. If the null model performed best, then the land-cover type in question was not taken forward, otherwise the variable included in the best model was incorporated into the global GLMM.

Part 3: Global model

The global GLMM was built for each sonotype separately with nightly bat activity as the response variable and the previously selected variable (if found significant in part 2) of each land-cover as the explanatory variables. Also included were the variables of 'moonlight intensity' (obtained from WorldWeatherOnline.com on 16 August 2021) and distance to water. The previously determined site grouping variables were used as the random effect. Prior to running the model, all of the variables were centered and rescaled to unit variance in order to derive comparable estimates (Schielzeth 2010). Multicollinearity was assessed among all the predictors using Pearson's correlation with a threshold of $r > |0.7|$ (Dormann et al. 2013). The global GLMM was fitted using the Template Model Builder method for the maximum likelihood estimation with R package

'glmmTMB' (Brooks et al. 2017), with a negative binomial distribution parameter to account for over-dispersion (Lindén and Mäntyniemi 2011).

Part 4: Best model

The resulting global model (above) was further reduced to a more parsimonious model including the best set of variables explaining bat activity. This was done by fitting all possible models and calculating AICc for each model; the best model being the one with the smallest AICc (Burnham and Anderson 2002) . However all models with a ΔAICc value < 2 (the difference between each model's AICc and the lowest AICc) were considered as receiving equal statistical support (Burnham and Anderson 2002). The model selection procedure was implemented with the function 'dredge' of the package MuMIn (Bartoń 2020). During the procedure, if any variable correlated with another by over a Pearson's correlation of |0.7|, then a condition was placed on the dredge function to test models with only one of the correlated variables. The residuals of the best models were tested again for spatial autocorrelation at the previously identified scales using moran.test() function. R^2 values – the coefficient of determination based on the likelihood ratio test – were calculated using the function r.squaredLR in the MuMIn R package (Bartoń 2020).

4.4 Results

A total of 13,263 calls belonging to seven sonotypes were isolated, identified, and analysed from 18 nights of recordings. These were divided into seven FM-QCF sonotypes, calling at 20kHz, 28kHz, 32kHz, 35kHz, 38kHz, 47kHz, and 65kHz, respectively (Table 4.1). Henceforth, these sonotypes will be referred to using 'S' followed by their identifying frequency (e.g. S20). An additional FM-QCF sonotype calling at 18kHz was identified, but separating calls from insect noise proved challenging and the large number of false positives led to it being dropped from further analysis. Sonotype S20 did not reach the

modelling stage because spatial autocorrelation was detected at a 10km scale during Part 1 of the statistical analysis. Grouping data points by a larger scale was deemed redundant and the sonotype was dropped. S65 was also dropped due to insufficient data for statistical analysis.

Table 4.1 Number and percentage of total passes recorded of each bat sonotype. Bat activity data were extracted from 481 hours of recordings collected using Audiomoth 1.0.0 full spectrum recorders over 18 nights between 9 May and 8 June, 2019, from rice fields in the Nagaon district of Assam. S.A. scale indicates the smallest scale tested at which spatial autocorrelation was not significant.

	Sonotype	Number of passes	Percentage of total (%)	S.A. scale
1	S38	4214	31.8	1km
2	S35	2709	20.4	5km
3	S32	1676	12.6	500m
4	S28	1630	12.3	1km
5	S20	1453	10.9	N.A
6	S47	1329	10	400m
7	S65	252	1.9	NA

Overall, variables indicative of the presence of trees were most prominent and significant in the final models (Fig. 4.2). Edge variables were present in the final models of S28 and S32. Forest variables were present in the final models of S28, S35, S38. SDHI was only found in the best model of one sonotype – S47. Urban landcover was present in the best model of two sonotypes, S28 and S38 (Fig. 4.2a, 4.2d). Sampling effort contributed to the best model of all sonotypes. Water, which had only been included in the global model as a distance variable, did not feature in the best model of any sonotype. Similarly rice, which had only been included in the global model as an area variable, also did not feature in the best model of any sonotype. There was also similarity in the type of variable of each

landcover type that made it into the best model. Edge was only present in the form of distance to edge. Forest was present in the form of distance to forest and forest area within 1km. Urban was only present as area of urban landcover within 1km (Fig. 4.2a). Full details of model results of individual sonotypes can be found in Appendix 2 (Table A2.1).

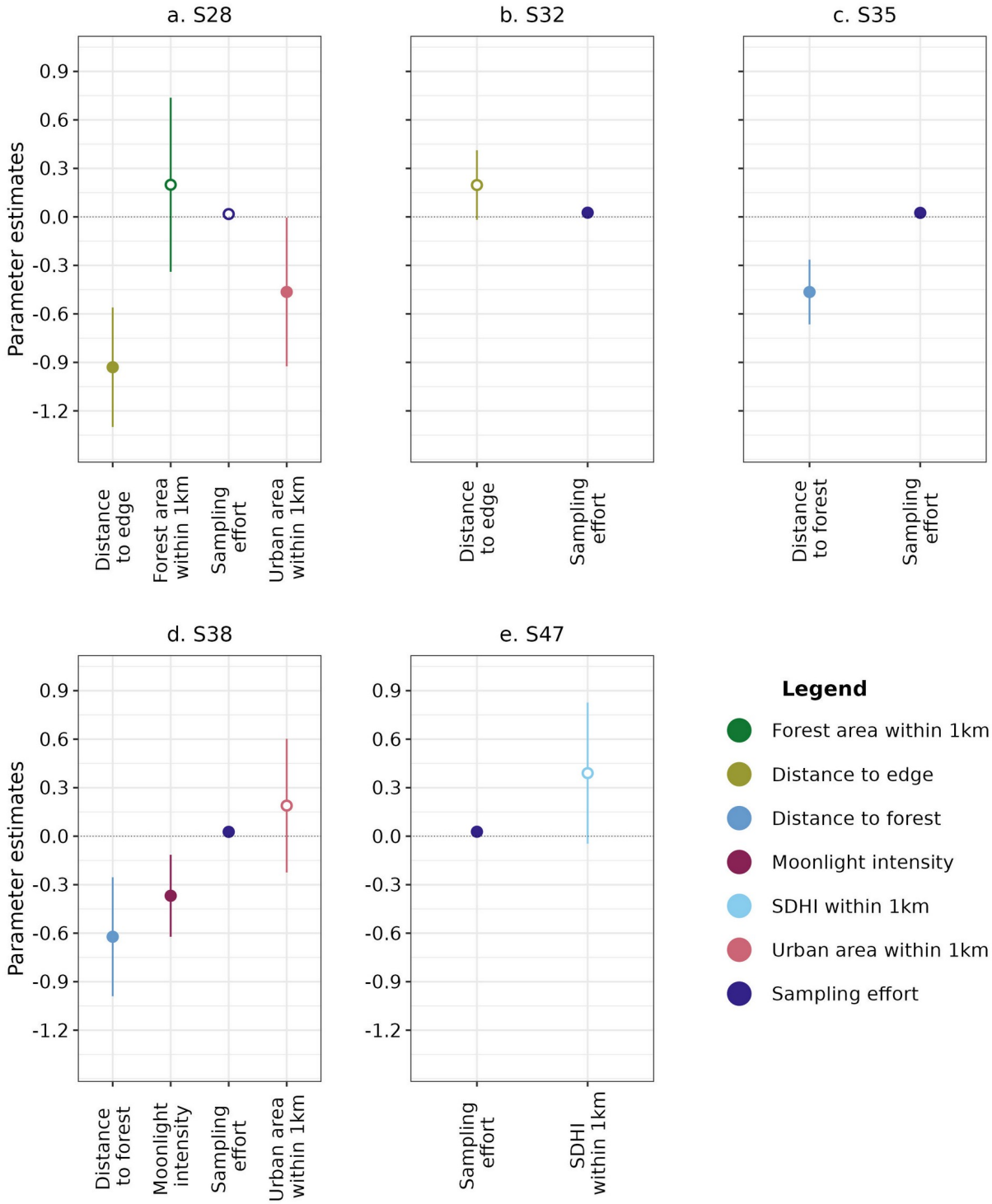


Fig. 4.2 Effect of landscape variables in the best Generalised linear mixed models of each sonotype. Data collected over 18 nights of recording between 9 May and 8 June 2019. Recordings were made using Audiomoth passive acoustic recorders in rice fields across the district of Nagaon, Assam. Variables were selected from a global model based on their contribution to significant decrease in AICc values. Dots represents the estimate, solid dots indicate a p-value < 0.05 and hollow dots indicate a p-value > 0.05. Error bars represent the 95% confidence interval. The confidence interval around 'Sampling effort' is not zero, but is too small for wings to extend beyond the perimeter of the solid dot.

In creating a model for overall bat activity, spatial autocorrelation was detected at all relevant scales. Despite this, an exploratory set of models were built by grouping points at the 400m, 1km and 5km scales. In addition to sampling effort, distance to forest and area of rice within 2km were the most important variables in the final models, with one model having area of edge within 1km as a predictor (Table A2.1). The similarity of the models, despite having points grouped at different spatial scales, would indicate a relatively low effect of spatial autocorrelation and suggest that these variables do influence bat activity in general.

In considering individual effects, Fig. 4.3 shows the relationship between bat activity and individual variables present in the final models of all sonotypes. Since the models we built were mixed models, they included random effects that cannot be represented in scatter plots. Nonetheless, these plots are useful for observing patterns in the raw data. Distance to edge and forest, area of urban land, and moonlight intensity, seen in Fig. 4.3a, 4.3c, 4.3e, 4.3f, and 4.3g, represent variables that were statistically significant in the best models of sonotypes S28, S35 and S38. Despite not accounting for the random effect, all of them show a clear negative correlation with bat activity, which is in line with the model estimates and with what other similar studies would predict. Fig. 4.3b and 4.3d represent forest area within 1km (S28) and distance to edge (S32). These are neither statistically significant in the final models (Fig. 4.2), nor do they show an obvious pattern in scatterplots (Fig. 4.3b and 4.3d). On the other hand Fig. 4.3h and 4.3i, which represent urban land and SDHI within 1km for sonotypes S38 and S47, respectively, show a clear pattern in the scatter plots, despite being not significant in the final models of these sonotypes. This pattern is also what one would expect based on other similar studies, showing bat activity decreases with an increase in urban land, but increases with an increase in landscape heterogeneity.

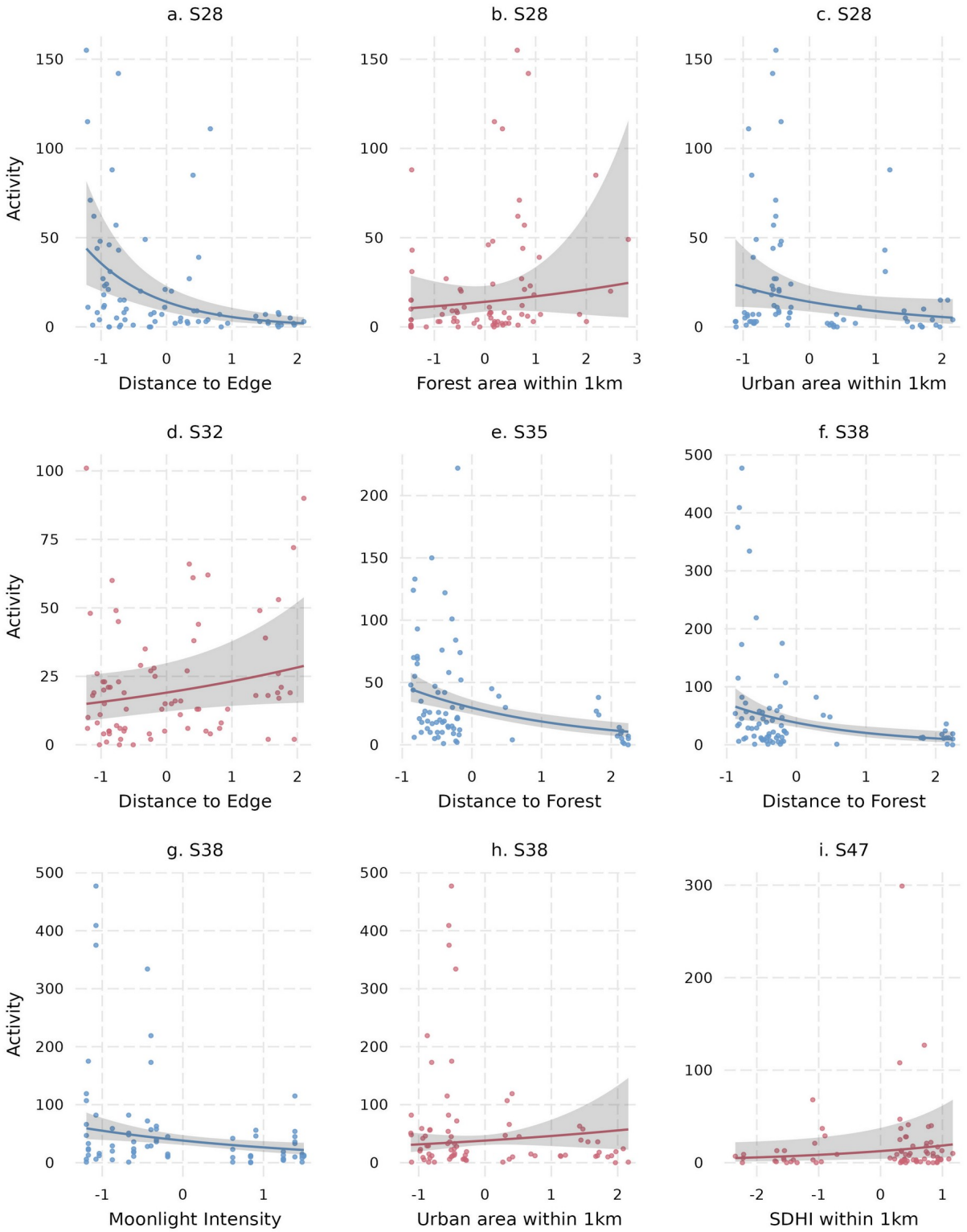


Fig. 4.3 Scatter plots of bat activity over all standardized variables present in the final models of each sonotype (except sampling effort). Blue dots indicate a p-value < 0.05, salmon dots indicate a p-value > 0.05. These points are raw data, and do not accurately represent the effect of variables in the final models. This is because mixed effect models used in this study included random effects that couldn't be accounted for in the above scatter plots. Lines and 95% confidence intervals represent the predicted values extracted from the relevant best models.

4.5 Discussion

This study examined bat activity levels in rice fields, with the aim of exploring why rice fields set in different landscapes see different levels of insectivorous bat activity. Our results showed that key landscape features, namely forest and edge cover, urban land, moonlight intensity and landscape heterogeneity influenced the activity of five sonotypes of insectivorous bats.

In warm and dry environments, bats lose water rapidly (Webb et al. 1995) and it must be replenished through their food and by drinking. While many species have evolved mechanisms to limit water loss (Reher and Dausmann 2021), the presence of water bodies still exert considerable influence on where bats choose to fly, particularly in arid environments (Razgour et al. 2010). Past studies have found distance to water to be a key factor in driving selection of roost sites and foraging grounds (Adams and Thibault 2006, Adams and Hayes 2008, Rainho and Palmeirim 2011). However, water bodies in these studies tend to be few and far apart, increasing their importance to foraging bats. Despite our study being conducted in the summer, when temperatures regularly exceeded 30°C, having been conducted in rice fields, our sites were all within 600m of a water body (defined here as areas of water of at least 1000sq meters, equivalent to a 50m by 20m plot), with an average distance of 204m. This distance being well within the foraging ranges of insectivorous bats, water was not found to be an influencing factor in the best model of any sonotype, suggesting that for the analysed species, the range at which water becomes a limiting factor is greater than bats in our landscapes were presented with.

Urban landscapes are not entirely uninhabitable, and many bat species have adapted to them. The use of urban land by bats is influenced by built infrastructure, light pollution, noise levels, tree cover, bat physiology, predation pressure, and prey availability (Moretto and Francis 2017, Moretto et al. 2019, Jung and Threlfall 2021). While light pollution in urban areas is harmful to insect populations on the large scale (Owens et al.

2020), the attraction provided by street lights can create local prey-dense zones (Firebaugh and Haynes 2019), which in turn can increase the activity of some bats (Rodríguez-Aguilar et al. 2017). Bat activity is higher when patches of forest, water, and/or agricultural landcover are nearby (Dixon 2012, Ancillotto et al. 2019), in part because of higher insect activity in such areas (Avila-Flores and Fenton 2005). Studies have found that the complementation of anthropogenic and natural landcover can result in high levels of bat activity, particularly of mobile generalist species (Johnson et al. 2008). More universally, canopy cover has been found to be a key determinant of bat activity in urban contexts (Bailey et al. 2019). Bats exhibit extremely species-specific responses to landscapes and while some studies have found increased activity of bats in urban landscapes (Rodríguez-Aguilar et al. 2017), many studies have found even moderate urbanization to have negative impacts on bat activity (Ancillotto 2015, Jung and Threlfall 2016). While our sites were set in rice fields, urban landcover was present around the sites in two forms: dense urban landscapes seen in Nagaon city and scattered nodes in villages. One or both of these negatively affected the activity of S28 and S38. For the other sonotypes, it is possible that the farmland and associated buildings, trees, and water bodies satisfied the requirements of most bats at the local scale, thereby overriding any negative (or positive) effects of the city.

Forests and forest boundaries, including linear features such as rows of trees, are important habitats for bats (Heim et al. 2015). However, separating the often concurrent incentives for the use of such habitats, including as roosting sites, for safety against predators (Heim et al. 2018) and the wind (Verboom and Huitema 1997), landmarks for navigation, and improved foraging (Jantzen and Fenton 2013), can be a challenge. Some of these benefits change with time. For example, brighter nights allow predators to see better (Prugh and Golden 2014), increasing the importance of shelter. Similarly, prey abundance relative to the surrounding landscape varies with season, particularly in agricultural

landscapes. Conversely, the provision of trees as roosting sites remains more consistent over time.

Prey availability is a strong driver of bat activity and while it is difficult to compare the activity of different bats in different settings, studies have found that insectivorous bats do, in general, consider in-season rice fields to be prey-rich habitat (Sedlock et al. 2019, Toffoli and Rughetti 2020). Activity is increased by the presence of forest patches nearby (Heim et al. 2015, Bailey et al. 2019). Some studies have shown insectivorous bats to preferentially hunt over rice fields compared to forested areas (Puig-Montserrat et al. 2015, Kemp et al. 2019, Katunzi et al. 2021). Other studies report that while rice fields were attractive foraging grounds, nearby natural wetlands saw higher levels of foraging activity (Toffoli and Rughetti 2017).

While the edge variables calculated and tested for in this study included area of forest edge (within various buffers from the focal site), only distance to the nearest edge was retained in the best models of S28 and S32. The activity of sonotypes S35 and S38 was influenced by the distance to the nearest forest patch while S28 was influenced by the area of forest within 1km. Given that our landscapes were surrounded by forested area, rather than natural wetlands, we hypothesize that our rice fields were more attractive foraging sites than the surrounding forests or forest edges and therefore that the primary attraction of forests and forest edges was not prey availability but safety or the presence of roost sites. This is augmented by the fact that the bamboo houses and sheds in villages were known to be used as roost sites (IB, rigorous personal observation). These structures, being smaller than concrete buildings, more enclosed by trees, and bearing thatched roofs, were usually classified as ‘edge’ rather than ‘urban’ landcover. This adds to the argument that ‘edges’, as classified in this study, also represented roost sites to bats in the study area.

Area of rice was not present in the best models of any sonotype. The most likely reason being that since our sites were all in rice fields, set in rice-dominated landscapes,

prey availability was high enough that larger areas did not improve foraging success through reduced competition or increased prey availability.

Rice-dominated landscapes present a harsh matrix interspersed with patches of forest-urban-edge combinations that provide foraging grounds, roost sites, and relative safety. Harsher (more contrasting) matrices evoke stronger reactions to fragmented landscapes (Rodríguez-San Pedro and Simonetti 2015, Farneda et al. 2020) and unbroken rice fields provide little by way of shelter or roost sites. Greater landscape heterogeneity increases the proximity of different landcover types. This can result in larger bat populations and higher bat activity because bats that roost and forage in different landscapes now have easy access to both, reducing potentially commuting costs (Ethier and Fahrig 2011). An increase in landscape heterogeneity also correlates with availability of edges between natural and agricultural landcover. These interfaces are important for edge-space foragers that avoid open spaces either because they are more vulnerable to predators in open spaces, or because they have a higher foraging success at edges (Lentini et al. 2012, Frey-Ehrenbold et al. 2013). Greater heterogeneity also increases insect populations by providing spaces for them to breed and survive fallow seasons (Sigsgaard 2000, Fahrig et al. 2015, Bertrand et al. 2016, Chaperon et al. 2022). Sonotype S47 was influenced by landscape heterogeneity, most strongly at the scale of 1km (Fig. 4.2e), supporting other studies that demonstrate the positive effect of landscape heterogeneity on bat activity (Frey-Ehrenbold et al. 2013, Monck-Whipp et al. 2018, Rodríguez-San Pedro et al. 2019).

Agricultural industries globally face an enormous challenge to reduce their reliance on environmentally unsustainable practices, such as the use of chemical pesticides, for both environmental and financial reasons. Pests are predicted to cause increasing losses to many major crops (Deutsch et al. 2018) and chemical methods of control, far from eliminating pests, have often prompted the emergence of more resistant strains (Normile 2013). The effective use of natural enemies as a sustainable alternative is only practised in

pockets around the world (Lou et al. 2013, Puig-Montserrat et al. 2015), but holds great potential to alleviate the dual burdens of declining agricultural and ecological health. Realizing this potential requires both an understanding of the ecological relationships that underpin these ecosystem services and the ecology of the service providers to make agricultural landscapes more habitable to them.

Studies of bats in agricultural landscapes have shown the need for connectivity, heterogeneity, and the presence of natural landcover (Downs and Racey 2006, Frey-Ehrenbold et al. 2013, Finch et al. 2020). Few have considered the rice landscape, and none in India. This study demonstrated that in rice landscapes of Assam, while proximity to urban land decreased bat activity, the presence of forest patches and edges, and higher levels of landscape heterogeneity promoted bat activity, and likely by extension also increased the control of insect pests.

4.6 Acknowledgements

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CHAPTER 5

Batting for rice: The effect of bat exclusion on rice

5.1 Abstract

Insectivorous bats are gaining increasing attention for their potential as biological agents of pest suppression. Studies around the world have demonstrated their tendency to track and hunt agricultural pest over time and space, and thus to have a positive impact on reducing plant damage and protecting yield of agricultural crops.

We documented the effect of insectivorous bats on the health and yield of a rice crop in Assam, India. Starting with six sets of paired experimental and control plots (of which five were analysed), where bats were selectively excluded from the experimental plots, we collected two measures of plant damage and one measure of total yield to assess the impact of bats on the crop. In parallel, bat activity at the six sites was recorded over the rice growing season using passive acoustic recorders.

Our results show that the exclusion of insectivorous bats causes an increase in the degree of defoliation suffered by rice plants. We also report non-significant differences in the degree of yellowing of rice and of the total yield between the experimental and control plots. Bat activity levels showed a mono- or bi-modal peak in activity over the growing season, which broadly tracked the maturity of rice, a pattern also seen in many insect pests.

Our results would strongly suggest that bats have suppressive impact on pest action in rice fields. The general trend in activity levels, as well as the significant difference in plant damage, would indicate that bats are hunting insect pests and that the non-significant difference in final yield was likely the result of methodological limitations. These findings would suggest that bats add significant ecological and economic value to Indian rice ecosystems and hold great potential to be used in IPM (integrated pest management) strategies aimed at controlling pests.

5.2 Introduction

Climate change, through increased temperatures, changing precipitation patterns and increasingly erratic weather (Shukla et al. 2019), has and will continue to decrease the reliability and profitability of agricultural industries (Lobell and Field 2007, Rosenzweig et al. 2014). Pests add to this burden. The range of many insect pests, particularly in the higher latitudes, is predicted to increase (Vanhanen et al. 2007, Stange and Ayres 2010), as is their metabolism and population growth rate (Deutsch et al. 2018). Rice (*Oryza sativa*) is consumed as a staple food by over half the world's population (Muthayya et al. 2014, IRRI 2019). Increased pest action, which already severely affects yield (Pathak and Khan 1994), is predicted to decrease global rice yield, for a two-degree Celsius increase in mean temperatures, by 19% (Deutsch et al. 2018).

The Green Revolution of the 1960s transformed Indian agriculture by means of the introduction of high yielding varieties of rice (Nelson et al. 2019). However, despite the disease- and pest-resistant nature of these varieties, pesticide use in India (Bowonder 1979, Parayil 1992) and indeed across much of Asia (Parveen and Nakagoshi 2001, Normile 2013, Huang et al. 2014, Wang et al. 2018), grew steadily, with conflicting evidence of its effect on pest populations. In the complex ecosystem of a rice field, indiscriminate pesticide use often does more harm than good, suppressing arthropod predator populations to a greater extent, and for longer, than the pest populations, leading to higher overall pest action and driving pests to evolve resistance (Way and Heong 1994). In India, erstwhile minor pests, such as the brown planthopper, became prominent post the Green Revolution, causing widespread damage that continues to the present day (Bottrell and Schoenly 2012). In response to this, Integrated Pest Management (IPM) strategies were developed as the sustainable alternative to chemical pesticides (Teng 1994). Foremost among them was the use of natural enemies of pests such as fish (Halwart et al. 2012), frogs, parasitoids (Babendreier et al. 2020), and ducks (Zhang et al. 2009, Teng et

al. 2016) to control pest populations. And, in the last decade, the potential of bats to be effective pest agents has emerged as a topic of attention.

Insectivorous bats have been shown to eat pests of cotton (Federico et al. 2008, Kolkert et al. 2020b), corn (Maine and Boyles 2015), rice (Puig-Montserrat et al. 2015, Kemp et al. 2019), cacao (Cassano et al. 2016), coffee (Classen et al. 2014), and other crops (Maas et al. 2019). They have been shown to reduce pest abundance (Kalka et al. 2008, Williams-Guillén et al. 2008), plant damage (Maine and Boyles 2015) and loss in yield (Librán-Embid et al. 2017). They have also been shown to limit disease spread by limiting disease spreading insects like mosquitoes and other flies (Kervyn et al. 2012, Siemers et al. 2012, Puig-Montserrat et al. 2020).

Many insectivorous bats are generalists, eating any insects that they can catch and handle (Kunz et al. 2011). In addition to controlling resident pest populations, this gives them the ability to buffer against sudden outbreaks, or the invasion of new pest species, against which existing pest control measures may be ineffective (Maas et al. 2016). The generalist diet of many bats is complemented by their high mobility, which allows them to change foraging grounds and survive on different prey when crop pests are not available (Lee and McCracken 2005).

Several methods have been used to estimate the value of the pest suppression service provided by bats. Among them, diet analyses (McCracken et al. 2012) and exclusion experiments (Maas et al. 2019) dominate, with mathematical models (Federico et al. 2008) and experimental manipulation of bat populations (Puig-Montserrat et al. 2015) also making an appearance.

The largest estimates of pest suppression by bats are rooted in diet analyses that used either microscopic (Leelapaibul et al. 2005, Lee and McCracken 2005, Wanger et al. 2014) or genetic (McCracken et al. 2012) tools to document the identity and proportion of agricultural pests in the diet of bats. These data can then be used to estimate the impact of

bat predation on pest populations, and therefore yield, per unit of farmland (Cleveland et al. 2006). Some studies have gone further, to extrapolate these estimates to entire countries. One study estimated the pest suppression service of the Brazilian free-tailed bat (*Tadarida brasiliensis*) to the cotton industry of the U.S.A to be worth $26.7 billion per annum (median) (Cleveland et al. 2006, Boyles et al. 2011), while another estimated that of the wrinkle-lipped bat (*Tadarida plicata)* to the rice industry of Thailand to be worth $1.2 million per annum (Wanger et al. 2014). While diet analyses establish crucial links between bats and their prey, economic valuations based on this method are limited by assumptions concerning how an agricultural ecosystem will respond to the removal of a top predator. These assumptions are further stretched when extrapolating over an entire country (Fisher and Naidoo 2011, Boyles et al. 2013, Maine and Boyles 2015).

Many insect pests of rice, including planthoppers, leafhoppers, leaf folders, and stem borers, show an *r*-selected reproductive strategy, with fast reproductive rates and short generation times (Heong et al. 1992, Gurr et al. 2011). The primary limits on the population growth of these insects are set at the egg to larval and larval to adult stages, imposed by natural enemies other than bats (Heong et al. 1992, de Kraker et al. 1999). Bats prey primarily on the flying adult stages of these pests, while most of the crop damage is done by the larvae (Maine and Boyles 2015). The impact of bat predation is therefore only felt in subsequent generations of pests.

Crops themselves have evolved alongside pests, and many are capable of compensating for pest damage, with some showing no decrease in yield for mild to moderate pest action (Hughes and McKinlay 1988, Way and Heong 1994, Lv et al. 2008). The impact of pest action on yield is further complicated when multiple pest species are acting on the same plant. While some studies have shown simultaneous attack by multiple pests on rice to have an additive or synergistic negative effect on plants (Litsinger et al. 2011a, 2011b), others have shown a less-than-additive effect (Pinnschmidt et al. 1995).

Even if the absence of bat predation was to increase the activity of some pests, it is by no means straightforward to determine the resulting contribution to plant damage or yield loss, particularly if the plants are under stress from other pests.

Rice fields, especially those managed in a non-intensive manner, are ecologically diverse and complex landscapes and host many non-pest arthropods (Drechsler and Settele 2001, Bambaradeniya and Edirisinghe 2009). Among these arthropods are predators like spiders and ants, which are also prey of insectivorous bats (Maas et al. 2013). The net effect of bat predation on pests therefore depends on their effect on mesopredators, as well as on their direct effect on the pests. Synergistic effects between bats and predatory arthropods may cause a net increase in pest suppression, leading to lower losses of yield (Mooney et al. 2010). On the other hand, bats may curtail the effect of mesopredators, leading to higher pest activity and plant damage than would be the case without bats (Karp and Daily 2014).

In theory, exclusion experiments can account for the above dynamics where methods rooted in diet analyses cannot. That is, a bat exclusion experiment can be designed to allow the biotic community within to reach a new equilibrium, which recreates the characteristics of the ecosystem minus bats (Boyles et al. 2013). The reality is more complicated.

Exclusion experiments involving bats are necessarily field based. This imposes practical restrictions on the size of the exclosures, and the control that one has over other variables such as weather, configuration of the exclosures, and management history of the chosen sites. Bats' nocturnality adds another complication: unless the barriers to access are removed during the day, the effect of bats will be confounded with those of birds. The logistical requirements of twice daily adjustment to the exclosure further limits the scale and extent of the exclosures. No doubt influenced by these considerations, the vast majority of bat exclusion experiments have focussed on tree/bush type crops, where

individual trees/bushes can be used as a unit of replication and covered by netting (Maas et al. 2019). Links between bat pest suppression and row crops have therefore primarily come from diet analyses and these estimates tend to be larger than those calculated from exclusion experiments. Previous exclusion experiments have been conducted on crops such as coffee (Karp and Daily 2014), cacao (Cassano et al. 2016) and corn (Maine and Boyles 2015) and have been set primarily in North and South America. Despite the acknowledged potential of bats to regulate rice pests and the glaring need for sustainable pest control of a crop which loses 30 % of its yield to pest and pathogen action (Savary et al. 2019), only two studies have attempted an economic evaluation of this dynamic (Wanger et al. 2014, Puig-Montserrat et al. 2015), neither of which were set in India or China, the two largest rice producing countries in the world.

This study reports the results of the first exclusion experiment of bats over rice fields. Set in Assam, India, five pairs of exclosures were used to compare the effect of excluding bats from rice. By pairing experimental plots with controls, this study documented the effect of removing these top predators from the rice food web on crop damage and total yield. To the best of the authors' knowledge, this is the first experiment for a rice field that excluded bats, while leaving birds undisturbed, in their access to a crop.

5.3 Methods

5.3.1 Study site

The study was conducted in the rice fields of Puthimari, a village in the Sonitpur district of Assam. Rice is a major crop in Assam, grown on 2.43 million hectares of land (Directorate of Economics and Statistics 2019). Of the three rice crops, Ahu (autumn), Boro (summer), and Sali (winter), planted in Puthimari each year, our field season was conducted over the Sali/winter rice season of 2019. This location was chosen because the fields to the east of

the village were large and uninterrupted, and offered sites that were identical in management strategy, set approximately 100 meters from each other (Fig. 5.1).

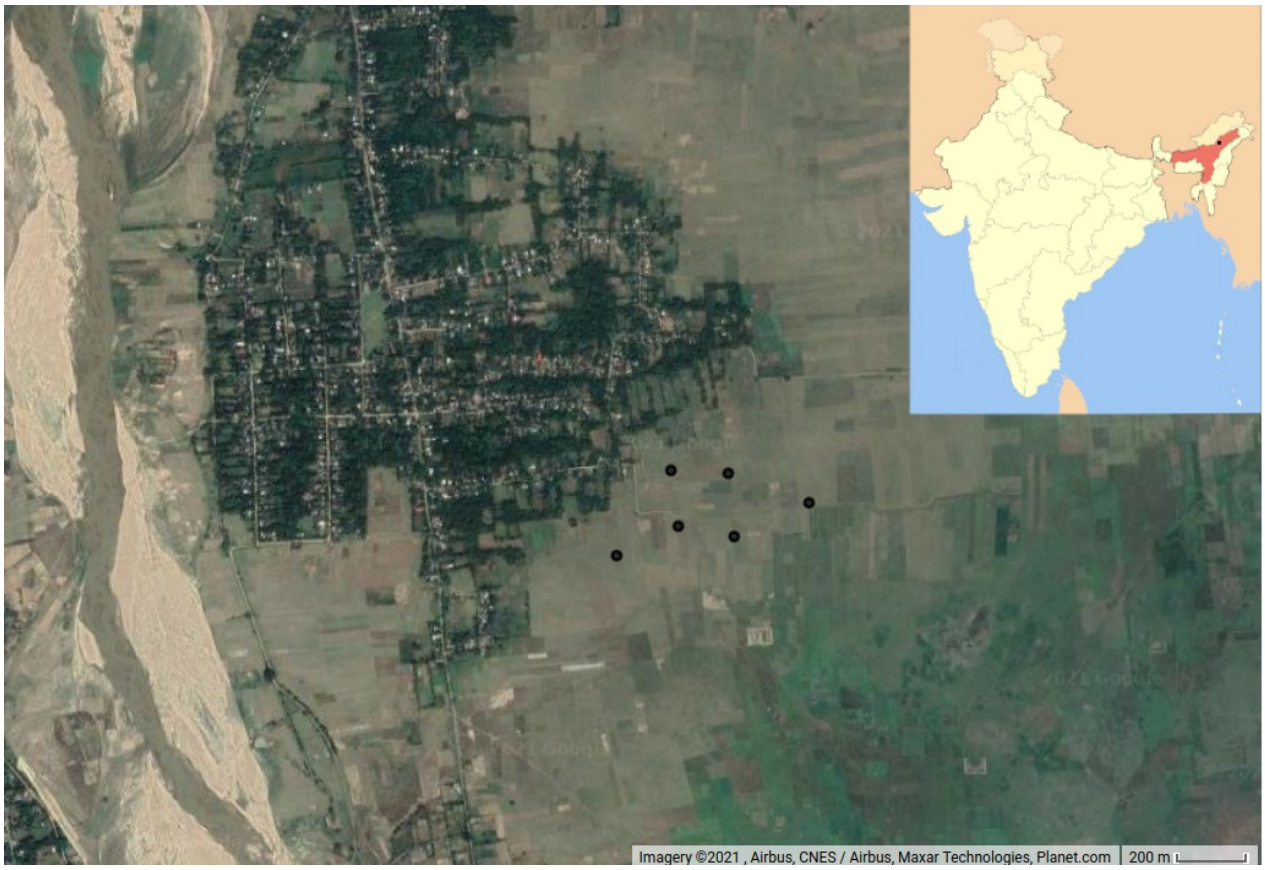


Fig. 5.1 Six sites chosen for the six experimental-control plots of the exclusion experiment. Located in Puthimari village, Assam, these sites were to the east of the village, and were part of a larger rice landscape in which rice were grown, within a mosaic of different varieties and management strategies. Source: Map of India by Ganeshk (GFDL&cc-by-sa-2.5,2.0,1.0); Airbus, CNES/Airbus, Maxar Technologies, Planet.com.

The six sites chosen for our study were set in the fields of five farmers. Each farmer was compensated for use of their land, amounting to the maximum possible value that the crop within the experiment could be sold for. After the final weighing had been conducted, they were also given the grain collected from the plots. Permission for this work was granted by the owners of each field, as well as the District Agricultural Officer of Sonitpur, Tezpur, and the Divisional Forest Officer, Sonitpur West Division, Tezpur.

5.3.2 Experimental setup

Six pairs of experimental-control exclosures were constructed (though data from only five were eventually used), each set at least 100 meters from its nearest neighbour and from the closest treeline. The fields were located west of the village, which features a mix of semi-forested areas and houses built of bamboo or concrete. Rice in Puthimari is grown in a mosaic of varieties and management strategies, depending in part on the religious and ethnic background of the landowner. While the fields selected for this study were not treated with pesticides or fertilizers, some of the surrounding fields were.

Each 'site' consisted of an experimental and control 'plot', set eight meters apart. The experimental exclosure was built using a bamboo frame 9m x 9m in area and 4 m tall (Fig. 5.2). Each frame consisted of eight vertical stilts and four horizontal beams on top. Nets used for cricket practice, with a 5cm mesh size, were used for the walls and roof of the exclosures. These nets were ideal for exclosures because the mesh size allowed for the free movement of insects while excluding all bats and the stiffness of the material ensured that birds would not get entangled in them. Although birds routinely perched on the exclosures, they were never caught in the nets. With the aim of excluding only bats, each 'wall' and the 'roof' of the experimental plots had a pulley system that allowed it to be retracted. The walls retracted upward and were pulled tight to the top frame. The net that comprised the roof was attached at one end to the exclosure frame, and at the other end to a sliding bamboo rod. Ropes attached to this sliding rod were used to pull the net across the top of the exclosure. Smaller ropes tied intermittently to the sides of the 'roof' net were used to ensure that, when extended, it was taut and left no space for bats to enter (Fig. 5.2).

Every experimental plot was paired to a control plot, which was an identical bamboo frame, sans nets. They accounted for the influence of birds using the frame as a perch, which may have biased their activity around the exclosures (Boyles et al. 2013).



Fig. 5.2 One of the six pairs of experimental (left) and control (right) plots built in the rice fields of Puthimari village, Assam. The experimental exclosure was a 9m by 9m by 4m bamboo frame with nets making up the walls and roof of the exclosure. The nets were retracted at dawn and extended again at dusk every day to exclude bats but not diurnal birds from the plants within. The control was an identical frame without any nets, set 8 meters away from the experimental plot. Both plots of each pair were constructed on the land of the same farmer. The frame in the control plot accounted for the effect of birds using it as a perch.

It was clear that the daily process of retracting and extending the nets would entail disturbing the rice immediately adjacent to the plot. To ensure that conditions at both plots were standardized, a 0.5 meter wide buffer around every exclosure, both experimental and control, was cleared of plants to permit access. In addition, within every exclosure, both experimental and control, the first three rows closest to the edge were treated as a 'buffer zone', and not considered. Only plants situated more than three rows from the edge - in the 'core zone' - were harvested.

The six pairs of experimental-control plots were constructed on the land of five farmers, with both experimental and control plots of each set being constructed on the

same farmers' land. This way, both plots of a site enclosed rice that was under the same management strategy – treated with neither pesticides nor fertilizers.

Rice in all six fields was planted in the last ten days of July, 2019. Construction of the exclosures began on the 17th of August and was completed on the 10th of September. Beginning on the 10th of September, the nets of all six experimental plots were retracted at dawn and extended at dusk every day. This continued every day until the rice within the exclosure was harvested and removed, which took place between the 11th and 28th of November.

5.3.3 Acoustic monitoring

In parallel to the exclusion experiment, the activity patterns of insectivorous bats were also monitored over the rice season using six AudioMoth passive acoustic recorders (Hill et al. 2018). On 48 nights between 27th August and 9th December 2019, these six recorders were placed adjacent to the control plot of the six exclusion experiments at a height of one meter, programmed to record from dusk till 4:30am with a sampling rate of 384 kHz and gain set to medium.

The raw acoustic data amounted to 2576.5 hours of recordings, with some nights seeing logistical or technical difficulties that prevented recording for the scheduled period of time. Using Python version 2.7 (Rossum et al. 1995), bat calls were isolated and extracted based on the following measurements. (i) Frequency of maximum energy (FMAXE) – the frequency containing the most energy in the call (Wordley et al. 2014b). (ii) Minimum and maximum frequencies – The lowest and highest frequencies that contained 5% of the energy of FMAXE. (iii) Bandwidth – Difference in frequency between the minimum and maximum frequencies. (iv) Call length – the time interval between the point that the call first crosses 5% FMAXE, and when it last crosses FMAXE. (v) Average amplitude – The average amplitude of the call.

Using manually verified calls to form a template, a linear discriminant analysis in the MatLab Classification learner (The MathWorks Inc. 2019) was used to build a classifier that classified all the remaining calls into sonotypes. The classified calls were then processed in R version 3.63 (R Core Team 2020) to reclassify based on FMAXE and bandwidth those calls which had been misclassified. The calls were also filtered to remove false positives arising from heavy rain, instrument failure, or bats that were recorded prior to the start time.

There are limited acoustic libraries for Indian bats, none extending as far as Assam. Without such a library to use as reference, the isolated calls were classified to the sonotype level, rather than the species level. These were defined based on FMAXE and bandwidth into: (i) Constant Frequency calls (CF), (ii) Frequency modulated – Quasi Constant frequency calls (FM-QCF), and (iii) Quasi-Constant frequency calls (QCF). Pure Frequency Modulated (FM) and FM-CF-FM calls were not recorded. A few CF calls were recorded, but could not be separated from insect noises and so were excluded from the analysis. QCF calls were recorded in the same frequency range as another FM-QCF call, frequently changing from QCF to FM-QCF within a pass. These were therefore considered to be the same sonotype and were recorded as FM-QCF. All the calls used for the analysis, therefore, had FM-QCF characteristics. Henceforth, sonotypes will be identified by 'S' followed by the frequency at which they called. For example, FM-QCF calling at 20kHz is S20.

All recordings were divided into five-second intervals. One bat pass was defined as an interval containing more than two calls of the same sonotype (Millon et al. 2015). Using a random number generator, ten percent of the extracted passes were selected for manual verification. The classifier accurately identified >90% of the passes. At a minimum of 100m apart, the six sites were not completely independent. A certain amount of pseudoreplication was therefore unavoidable when the same bat flew from one site to another.

5.3.4 Rice data

Rice was harvested twice during the season, once in the middle of the season, to assess pest damage, and once at the end, to assess yield. Site three was removed from consideration when it was discovered, late in the season, that it had been sowed with a different strain of rice. As a result, only data from five sites were used for the analysis.

Mid-season data

A unit of rice, transplanted to the field at the seedling stage, is composed of one to several plants, each bearing tillers, leaves and panicles. Such a unit is known as a hill.

Between the 9th and 22nd of October, roughly midway through the rice growing season, 30 hills were sampled from the 'core zone' of three pairs of experimental and control plots (plants from the remaining two pairs having accidentally dried out after collection). Hills were chosen by mapping each 'core zone' as a grid and using a random number generator in Python version 2.7 (Rossum et al. 1995) to identify the row and column number of the 30 plants. Since the hills were removed by hand and then washed to remove the mud, it was assumed that insect pests on the hill may have been jostled or washed off and that those that remained would be unrepresentative of the level of infestation and so they were not counted for analyses.

The 30 hills were analysed for the following measures of insect damage:

a. Yellowing of leaves, caused by green leafhoppers (IRRI 2014).

b. Defoliation of leaves, caused by caseworms (IRRI 2014), caterpillars (Tanwar et al. 2010) and grasshoppers (NICRA 2011).

Both measures were documented as proportion of affected leaves per hill.

End-season data

At the end of the season, up to 900 hills were harvested from the core zone of each plot, by hand, between 11th of November and 28th December. If the core zone had fewer than 900 hills in one of the treatments, then the same number of hills was harvested from the other treatment of that site. The hills at each site were harvested on the date that the farmer harvested the rest of his field.

The full 900 hills were collected from sites one, five, and six and 800 hills were collected from site two. It was only possible to harvest 400 hills from site four because while the experimental plot had 900 hills of the correct variety, the control plot had only 400 hills of the correct variety, so 400 hills were harvested from both.

Two types of data were collected from these hills.

a. Total yield: Grain from the harvested rice was removed from the hill by hand and placed into metal tins. The grain from every plot, both experimental and control, was dried for two days by spreading them on a plastic tarp, under a net to prevent birds from eating them, in the sun. After two days of drying, the grain was weighed.

b. 1000 grain weight: After the final weighing, a small box of grain from each plot was retained for the calculation of 1000 grain weight, which is another measure of yield (Huang et al. 2013). A handful of grain was dried at 80°C for 24 hours, and from this handful 1000 full grains were removed and weighed on a high precision balance.

5.3.5 Statistical analysis

Mid-season data

To test for the effect of treatment on plant damage caused by insects, a generalized linear mixed model (GLMM) was built using the 'glmmTMB' function (Brooks et al. 2017) in R version 3.63 (R Core Team 2020). Two types of damage – defoliation and yellowing – were

modelled separately as indicators of the action of two groups of pest. The data did not need to be transformed prior to being used in the model, but outliers were removed using the 'check_outliers' function from the 'performance' package (Lüdecke et al. 2020).

The response variable for both types of damage were in the form of proportion of leaves affected per hill, warranting the use of the binomial GLMM. The treatment – experimental and control – was taken as the explanatory variable and to account for non-independence of samples within each site, site number was taken as a random effect.

A generalized linear model was also built, without the random effect of site, and compared to the final mixed models of both types of damage. For both types of damage, the GLMMs had AICc scores more than two units lower than the corresponding GLMs, which justified the inclusion of site as a random effect. Model fit was gauged through visual assessment of the residuals.

End-season data

To test the effect of the treatment on total yield and 1000 grain weight, the two sets of data were checked for normality using a QQ plot and for comparable variances using an F test. Having ascertained that both sets of data are normally distributed and with comparable variances, a paired Student's t-test was used to compare the difference between the two treatments. All statistical analyses were performed in R version 3.63 (R Core Team 2020).

5.4 Results

5.4.1 Acoustic monitoring

In total, 18890 passes were identified across six locations over 48 nights of sampling – the same data as was collected for Chapter 3. As seen in Fig. 5.3, four out of six sonotypes peaked in activity (standardized to sampling effort) in the second half of October, corresponding to the mid-season peak characteristic of many herbivorous insect pests of

rice (Zhong-xian et al. 2006, Sharma et al. 2018a), and also to the activity of vocal insects in the study area (Bhalla et al. 2022 Chapter 3). In addition four sonotypes (S34, S38, S48, S65) showed a clear bimodal pattern in activity over the season, peaking once in early-mid September, and again in mid-October.

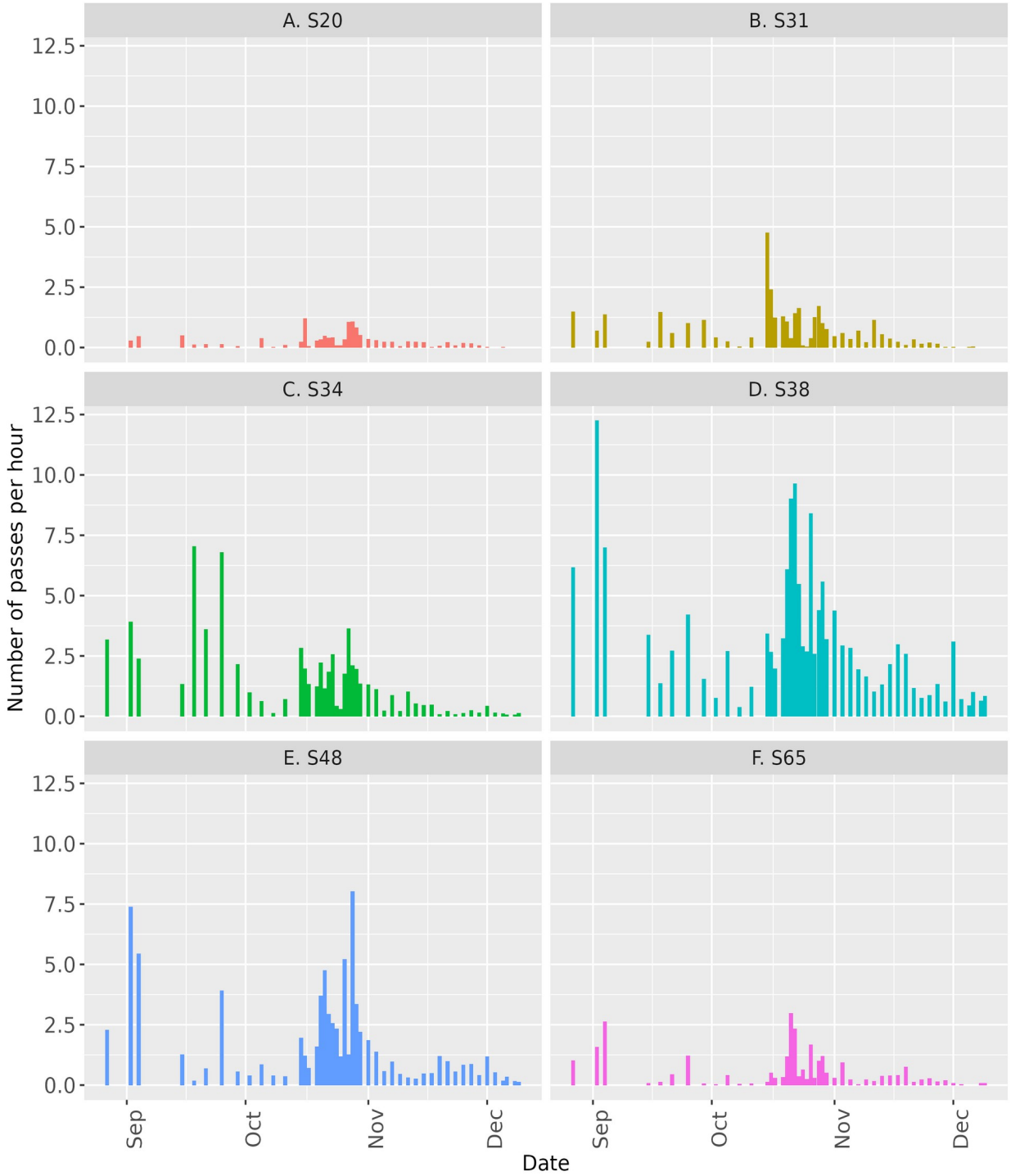


Fig. 5.3 The activity patterns of six sonotypes of insectivorous bats over a rice season. Data was collected at six locations between 27th August and 9th December 2019 in Puthimari, Assam. Recording began each night at dusk, and ended by 4:30am over 48 nights of recording. Activity at all six locations was summed and standardized to number of hours sampled.

5.4.2 Mid-season data

Model residuals were plotted and visually analysed for patterns. Neither of the two models showed any patterns in the residuals. The exclusion of bats in the experimental treatment contributed to significantly greater defoliation, indicative of damage by grasshoppers, caseworms, and caterpillars, in experimental plots (where bats were excluded) than in the control plots (Estimate = 0.168, P = 0.004; Table 5.1). Proportion of leaves yellowing, indicative of leafhopper damage, was not influenced by experimental treatment (Estimate = 0.101, P = 0.198; Table 5.1).

Table 5.1 Summary of two binomial generalized linear mixed models, one for each of the two types of damage – defoliation and yellowing – documented in the middle of the rice growing season. Data, in the form of proportion of leaves affected, was collected between 10th and 20th October 2019 from 176 hills harvested from three pairs of plots (three each of experimental and control). The experimental plot excluded bats from the rice within, while the control did not. The model contained one fixed factor - 'Treatment', and one random effect - 'Site'. The estimate indicates the direction and degree of influence that the experimental treatment had on plant damage.

	Fixed Effects	**Estimate**	**Standard Error**	**Z value**	**P value**	**AIC**
Model 1: Degree of defoliation	Experimental treatment	0.168	0.059	2.83	0.004	1115.13
Model 2: Degree of yellowing	Experimental treatment	0.101	0.078	1.288	0.198	762.26

5.4.3 End-Season Data

Total yield was not significantly different between the experimental and control plots (t = -1.4361, P = 0.1903; Fig. 5.4). There was also no significant difference in the 1000 grain weight between the experimental and control plots (t = -0.31746, P = 0.7586; Fig. 5.4).

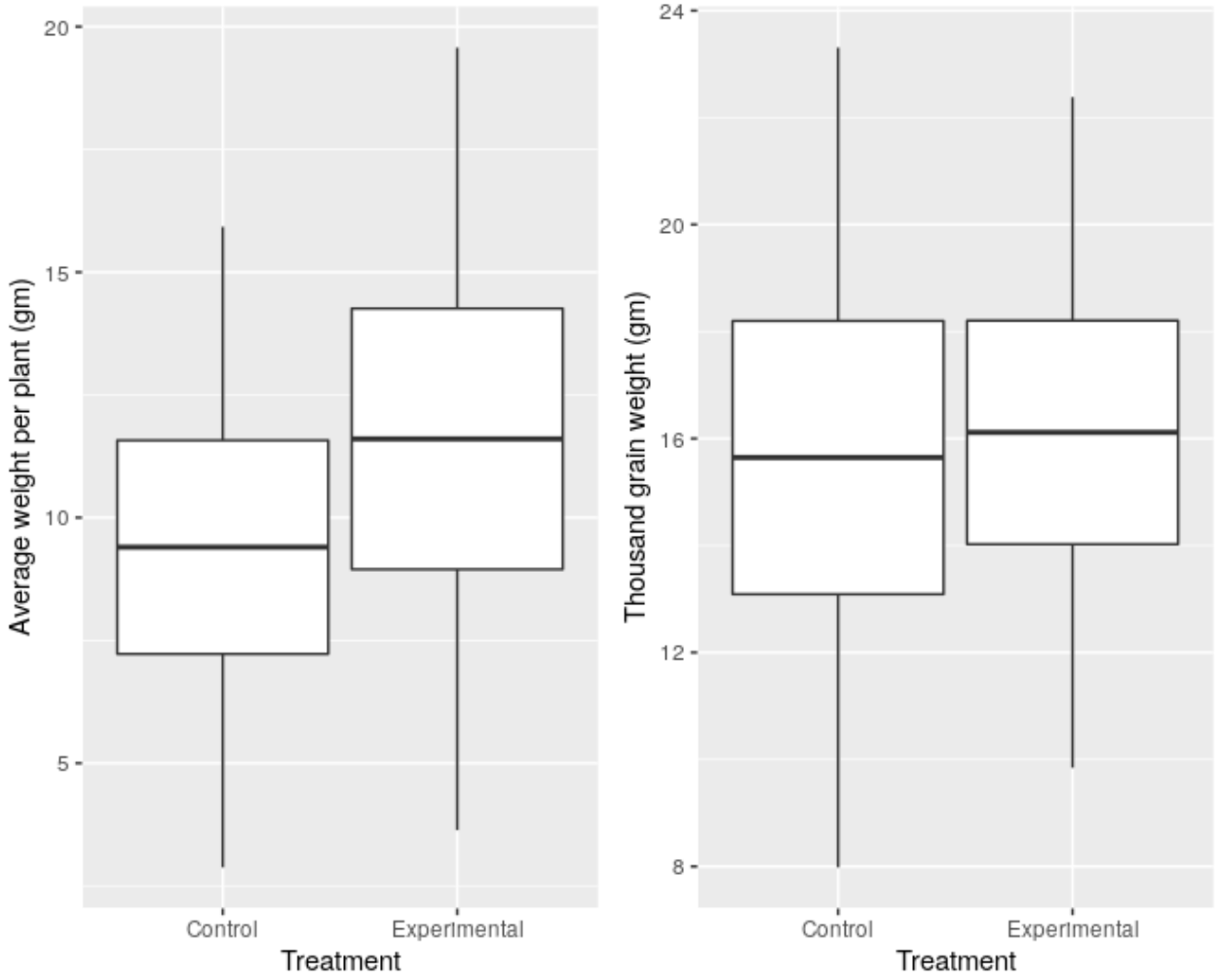


Fig. 5.4 The difference in average yield per pant and 1000 grain weight between the control and experimental plots of the exclusion experiment, showing average (black horizontal line), one standard deviation (white box), and three standard deviations (vertical line). Comparing the effect on yield of excluding bats from rice fields, the experiment selectively excluded bats from five experimental plots using retractable nets that were extended between dusk and dawn. Yield was calculated as the weight of grain per plant from all ten plots, and the weight of a 1000 full grains after they had been dried in an oven for 24 hours. The difference between control and experimental treatment was non-significant for both total yield (t = -1.4361, p = 0.1903) and 1000 grain weight (t = -0.31746, p = 0.7586).

5.5 Discussion

Our acoustic monitoring demonstrated that insectivorous bats were highly active in the landscape and that over the rice growing season their activity mirrored the known activity patterns of multiple rice pests (Zhong-xian et al. 2006, Sharma et al. 2018a). With over 18000 passes recorded at the six sites, even allowing for multiple records of the same individual, it is reasonable to assume that bats did consistently hunt insects over the rice crop, and that these insects must have included pests.

From an ecosystem services point of view, the most important metric is arguably final yield, as this speaks to a demonstrable value of the pest suppression service provided by bats to farmers. We found non-significant differences between the experimental and control plots of the exclusion experiment. A similar result was reported by the only other exclusion experiment involving bats and rice. Set in Florida, this study was focussed on blackbirds, but by keeping the nets in place throughout the experiment, they inadvertently also excluded bats (Borkhataria et al. 2012). They also reported a non-significant difference in final yield between the experimental and control plots. Similar non-significant differences in final yield have also been reported from other crops like cacao (Gras et al. 2016), and coffee (Karp and Daily 2014).

At face value, the results of our study would imply that the absence of bats from rice fields in Assam had no effect on rice yield, a conclusion that would be at odds with the observed patterns in bat activity. Assuming for the moment that the experiment functioned as expected, a number of biological mechanisms could still have resulted in a non-significant difference in yield between the two treatments. For instance (i) pest populations with and without bats might be comparable if bat predation is not a primary limitation on pest survival; (ii) mesopredators in the experimental plots, released from predation by bats, could have increased their activity resulting in similar overall levels of pest suppression; (iii) the rice plants themselves might compensate for damage by pests well

enough that lower pest action did not bring about an increase in yield; or (iv) the effect of bat activity may bring a general benefit to the level of infestation at the field level, bringing down crop damage *inside* the exclosures as well as in the rest of the field where the control sites were located.

In southern Illinois, Maine and Boyles (2015) also conducted an exclusion experiment on a row crop. Excluding bats from corn, they reported a non-significant difference in yield between their control and experimental plots. With six replicates, their final non-significant difference in yield weight was attributed to limited statistical power. However, their analysis of multiple measures of plant damage and pest abundance did show significant differences between the two treatments, based on which they concluded that bats were providing a pest suppression service.

Our study showed a similar pattern. We report a significant difference in one type of plant damage – degree of defoliation – between the two treatments, accompanied by a non-significant difference in total yield.

Assuming that limited replication contributed to the non-significant result in total yield, a significant difference in plant damage would strongly suggest that bats are reducing the effect of insect pest activity on the rice crop. This would support rice-based studies such as Wanger et al. (2014) and Puig-Montserrat et al. (2015) that indicate the same. It would also be in line with exclusion experiments involving bats and other crops (Maas et al. 2013, Rodríguez-San Pedro et al. 2020) that reported significant changes to yield and plant health as a result of bat- or bird- and bat- exclusion. However, while insufficient statistical power might have resulted in the non-significant difference in final yield, the same result might also have arisen from limitations in the methodology. Bat exclusion experiments function under the assumption that the ecosystem within the experimental exclosures are perfectly insulated against the influences of bats, but identical

in all other respects to the controls. This assumption is not watertight, and merits examination.

Bat exclusion experiments need to be manipulated twice daily, a logistic challenge that imposes limits on the number of replicates and, perhaps more importantly, the dimensions of the exclosures. Most exclosures aren't higher than seven meters, which makes it impossible to control for the hunting that is occurring above the exclosure, where insects fly and bats follow.

Many insect prey of bats have evolved behavioural and physical adaptations to reduce the risk of predation. Tympanate moths, many of which are agricultural pests, can detect the ultrasonic calls of bats through typanal organs evolved for this purpose (Zha et al. 2009, Miller 2009). These moths alter their foraging and reproductive behaviour when they hear bat calls, which increases their survival rate, but decreases fitness. For these insects, the mere presence of echolocating bats creates a 'landscape of fear' (Russo et al. 2018), and because the insects need only to hear the outgoing call of the bat, where a bat needs to hear the returning echo, the range at which tympanate insects hear bats is much greater than the range at which bats can detect them (Kunz et al. 2011). One study predicted that typmanate insects could detect the insectivorous bat *Cormura brevirostris* as far as 50 meters away (Surlykke and Kalko 2008). Were this range even 15 meters, tympanate insects at the very centre of most exclusion experiments would detect bats foraging around and above the exclosures and switch to less efficient foraging patterns. Adding to this, the nets used to exclude bats create acoustic edges. Edge-space bats that make use of edges to hunt might spend more time near these nets, creating a biased 'landscape of fear' near the experimental plots of the experiments.

Flying insects are, by their nature, mobile. Even if the absence of bat predation created a hotspot of pests within the exclosures, those with flying adult stages would almost certainly spread outside the exclosures, diluting the effect caused by a local absence

of bats. Taking such mobility into account, the effect of bats on yield may only be measurable at the field level, if average pest populations sizes are significantly reduced due to consistent predation by bats. All these factors may reduce the accuracy with which exclusion experiments can measure the impact of bats on pest communities. The final results, however, must also be taken in the context of the landscape they came from.

Rice in India is grown on more than 43 million hectares of land (Directorate of Economics and Statistics 2019). Rice farms, however, are still typically small in size (Wang et al. 2015) (the average operational farm size in India is 0.83 hectares) and they are farmed using labour-intensive methods (compared to China's more mechanized approach) (Wang et al. 2015). While the fields chosen for this study all grew the same strain of rice and were not treated with chemical pesticides or fertilizers, they were set in a mosaic of other fields, each with a different management strategy, from which the effect of pesticides may have carried over.

The small scale and often traditional farming practices are also often accompanied with poor documentation. The lack of historical records on yield, tilling and cropping patterns, and pesticide and fertilizer use detract from our ability to standardize all extraneous variables when conducting an exclusion experiment. A case in point, the experimental plot at site two produced nearly double the yield of the control. The most plausible explanation for this was that the land of the experimental plot received six more passes by the tractor during tilling than the land of the control plot, and that this resulted in plants in the experimental plot being grown on more nutritious soil. This information was provided post-facto, by the neighbour who had driven the tractor.

It is worth noting that bats are not the only agents preying upon insect pests. Birds, in particular, may play a very large role in these sites, as they could be seen at dawn flying over rice fields catching insects. Numbering well into the hundreds, they are likely to

complement the effect of bats on insect pests, as would the many natural enemies active in rice ecosystems (Wilby and Thomas 2002).

In considering the effectiveness of bat pest-suppression over rice, there also arises the question of seasonality. Rice is a highly seasonal crop, and rice fields are very different ecosystems at different times of the year (Toffoli and Rughetti 2017). The arthropod communities in rice fields show seasonal patterns of invasion, establishment, and decline in response to these changes (Settle et al. 1996). Insectivorous bats are strongly influenced by the availability of insect prey (Lang et al. 2006, Taylor et al. 2013) (Bhalla et al. 2022, Chapter 3), but also broader patterns in the weather and their reproductive cycle (Rydell 1993, Chaverri and Vonhof 2011, Barros et al. 2014). The energetic demands of a lactating bat have been reported to be double that during pregnancy (Kunz et al. 1995). This increased demand is managed through changes in their hunting behaviour (Duvergé et al. 2000). The food webs in rice ecosystems are likely, therefore, to have very different dynamics over different seasons. An ideal estimation of this service would require, at a minimum, a year-long study, to account for the different dynamics arising from changes in abiotic conditions and biotic communities over the different rice seasons.

The idiosyncrasies of rice stand in stark contrast to crops such as cacao and coffee, which show lower seasonal variation and pose fewer logistical challenges to the construction of exclosures. Since these challenges are not likely to change significantly, exclusion experiments may not be the most appropriate method to conduct an economic valuation of insectivorous bats in rice. Such an evaluation would need to be landscape-scale, where bat populations are bolstered at select sites to bring about differences in their numbers between sites. Given the comparatively slow life history of insectivorous bats, studies doing so with the intention of extrapolating in time and space must continue until the bat populations have stabilized, which would also allow seasonal differences to be discerned (Maas et al. 2013). Comparisons can then be made between sites and within a

site over time. Coupled with long term monitoring of arthropod communities, rice health and yield, and bat activity, such a study would provide a thorough exploration of the potential for bats to be effective pest suppressors in rice farms.

In 1999, one team in Northern Iberia deployed bat boxes to increase the resident population of the soprano pipistrelle bat. At the end of the ten years, the population of rice stem borers had dropped to below the threshold required to trigger aerial spraying of pesticides (Puig-Montserrat et al. 2015). Supporting the conclusions of Wanger et al. (2014), the multi-pronged approach of Puig-Montserrat et al. (2015), combining diet analyses and bat and pest monitoring, proved the potential of bats as pest suppression agents over rice.

A similar study is needed in Asia, which hosts diverse communities of bats and pests, and where most of the world's rice is grown and consumed (FAO 2019). An accurate assessment of this service, coupled with investigations of bat diet, distribution, and activity patterns would allow conservationists and agriculturalists to devise strategies to protect bat populations and maximise the value of their ecosystem services.

5.6 Acknowledgements

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CHAPTER 6: Discussion

6.1 Summary of results

6.1.1 Chapter 3: Patterns in time

The key result from Chapter 3 was that activity levels of three bat sonotypes over rice fields were directly influenced by the activity of insects. The pattern of insect activity, as measured by the ambient noise levels, showed a quadratic relationship with the growth of the rice crop. It increased steadily as the crop matured, peaked near the middle of the season and then decreased as the crop dried and was harvested. Pests undoubtedly contributed to this measure of insect activity because the quadratic pattern of activity over a growing season has been documented in several important rice pests (Zhong-xian et al. 2006, Sharma et al. 2018b). The identities of the insects that bats were hunting is impossible to discern with the acoustic tools on hand. However, it follows that since bats were tracking insect activity and this activity tracked the maturation of rice, pests were likely to be among the insects that bats hunted. The forthcoming diet analysis will inform us of what proportion of their diet comprised insect pests. Some of these pests are also known to exhibit that characteristic dusk peak in activity (Macquillan 1975, Kersting and Başpmar 1995, Zhu et al. 2017), which was likewise tracked by three bat sonotypes we recorded – S31, S34, and S38 – further strengthening the argument that pests are likely to be among the insects that bats are tracking and hunting in rice fields. Underlying the strong influence of insect activity on bats was the reactions of various sonotypes to moonlight (negative) and temperature (positive), both of which were supported by a wealth of studies from around the world.

6.1.2 Limitations of Chapter 3

The data from Chapter 3 was collected using Audiomoth passive recorders, which, while capable of recording up to 192kHz, are not equally sensitive to all frequencies. Bats calling at high frequencies, therefore, were less likely to be detected. The use of a plastic zip-lock bag as a case for the recorders further limited their sensitivity to higher frequencies. This biased the sampling, and the subsequent analysis. The analysis itself relied heavily on an acoustic classifier to extract bat calls from the acoustic recordings. This classifier was created for these datasets but, lacking an acoustic library of Indian bats, could not accurately identify bat calls to the species level, resulting in our use of sonotypes instead. While this level of classification is still extremely useful and it is hoped that forthcoming diet analyses will provide species names within most sonotypes, species level classification would have been more valuable for future studies.

6.1.3 Chapter 4: Patterns in space

Chapter 4 detailed the landscape features in and around rice fields that were most important in driving bat behaviour and the scales at which they were most influential. Consistent with existing literature from agricultural landscapes around the world, the most significant drivers of all sonotypes were related in some way to tree cover (Fuentes-Montemayor et al. 2013, Monck-Whipp et al. 2018, Bailey et al. 2019, Azofeifa et al. 2019). Edge and forest variables were present in the best models of most species, with SDHI (the Shannon's Landscape Diversity Index), a metric of landscape heterogeneity present in one. Also in line with other studies of bat ecology was the complicated effect of urban land cover on bat activity, which more often than not exerts a negative influence on bat activity (Rodríguez-Aguilar et al. 2017, Jung and Threlfall 2021, Chaperon et al. 2022). Two of the five sonotypes in our study were negatively affected by urban land, and the effect of both was strongest at a scale of 1km.

6.1.4 Limitations of Chapter 4

Cross sectional studies have limited power to comprehensively describe the behaviour of an animal because behaviour invariably changes with season. Yet to account for both seasonal and spatial patterns is logistically challenging as one has to collect behaviour simultaneously at many sites over a long period of time. Where Chapter 3 considered bat activity patterns in a single set of locations over time, Chapter 4 attempted to describe the activity patterns of bats in different locations as influenced by the composition of the surrounding landscape.

Data for Chapter 4 were collected from a narrow window of time – May to June 2019 – which corresponded more or less to the middle of the growing season at these sites. However as shown in chapter 3, and other studies (Bakar and Khan 2016, Sedlock et al. 2019, Azofeifa et al. 2019), the phase of the rice growing season strongly affects insect activity, and therefore bat activity. This difference could not be accounted for with the methodological design of the study.

To add to this, logistical difficulties made repeat measurements impossible at some sites, and limited the overall sampling methodology, leaving us with a less uniform spatial distribution of points that we would have liked. And, as was the case with Chapter 3, the recorders used were not equally sensitive to all bats and the lack of an acoustic library forced us to conduct our analysis at the sonotype level, rather than the species level.

6.1.5 Chapter 5: Effect of bat exclusion on crop health

Exclusion experiments have been touted as a method to account for these complexities, and examine the net effect of the bat-insect dynamic on crop yield. From an economic point of view, an impact on crop yield is the most relevant measure of an ecosystem service

such as pest suppression. Our exclusion experiment was meant to answer the question: 'Does the yield improve in the presence of bats?'

Exclusion experiments involving bats have reported both positive and non-significant effects of bat predation on crop health and yield. However, the logistical challenges of building and maintaining the experiment have often resulted in experiments yielding data insufficient for definitive statistical analysis (Maine and Boyles 2015).

Given the paucity of exclusion experiments on row crops, we were aware at the outset that an exclusion experiment on rice was not going to be straightforward. As has been explained, row crops and bats make for a difficult system to conduct such experiments on. The only study similar to ours, Maine and Boyles (2015), conducted an exclusion experiment on corn involving six pairs of experimental and treatment plots. They reported a non-significant difference on total yield weight accompanied by a significant difference in pest abundance and plant damage. They attributed the non-significant difference in total yield weight to a limited number of replicates.

6.1.6 Limitations of Chapter 5

This, we believe, was also the case in our exclusion experiment. What began as six sets of experimental and control plots, was reduced to five by the end of the experiment. And without a consistent and significant difference between the two treatments, we did not find a statistical difference between the total yield of the two treatments. The measures of plant health were not limited to five data points each, and one measure – degree of defoliation – did show a statistically significant difference between the two treatments. This is an encouraging result, as it indicates the presence and direction of an effect that, when supported by the results of Chapters 3 and 4, would suggest that bats are tracking insects, among which pests species likely feature.

The yet to be conducted diet analysis is expected to prove conclusively that bats are hunting insect pests, and even inform us of the proportion of their diet that insect pests contribute. However even if it is proven that bats are hunting insect pests, it does not necessarily imply that bats are having a significant effect on pests populations. What remains to be done is a more sophisticated valuation of bat pest suppression. While traditional exclusion experiments and diet analyses can prove ecological relationships and even produce approximate valuations, I believe that a truly accurate estimate cannot be produced by these methods. Such an estimate would require a landscape scale study, where pairs of large fields with standardized growing conditions have (naturally or artificially) different levels of bat predation. Comparisons of their yield and plant health between such fields would be the only way to accurately account for the complexities of the agricultural food web without imposing the limitations of physical enclosures.

6.1.7 All taken together

Taken together, the three empirical chapters detailed within and the evidence from the field experience point to a significant value provided by insectivorous bats in rice fields. The number of bats recorded, their patterns in time and space, the effect of their exclusion on rice health, and anecdotal observations by myself and my team indicate that rural agricultural landscapes in India host an abundance of insectivorous bats, which do hunt over rice fields, tracking insects in time, and reducing the damage done to rice plants. Further, we document the characteristics of the rice landscape that are important to different bat sonotypes, paving the way for more targeted studies to create designs for agricultural landscapes that maximize their habitability to bat populations.

This would be in line with a growing body of evidence that insectivorous bats do track agricultural pests over time and space (McCracken et al. 2012, Kolkert et al. 2020b). And, while different methods to evaluate the economic benefits of bat pest suppression are

limited by the assumptions and extrapolations underlying them, the consensus from the range of different studies focussing on bat pest suppression is that bats bestow enormous economic value to a plethora of crops around the world (Boyles et al. 2011, Kunz et al. 2011, Wanger et al. 2014, Karp and Daily 2014, Puig-Montserrat et al. 2015, Maine and Boyles 2015, Kahnonitch et al. 2018, Kolkert et al. 2020a, Maslo et al. 2022). The studies detailed in this thesis would suggest an ecological relationship between bats and insect pests of rice, and hint at potential economic value being derived from this relationship. The studies do not, however, prove these things.

From a conservation point of view, this work, particularly Chapter 4, provides the first exploration of the habitat requirements of Indian bats, and the features in the landscape that would be required to sustain their populations in rice landscapes.

From and agricultural and economic perspective, these hint at the potential value of insectivorous bats to rice farming, and should be should be used to spur further research into the effect of bats on pest of agriculture. In a country so reliant on agriculture, which is plagued by climate change, poor economic support, and pest outbreaks, finding sustainable methods to improve the condition of the agricultural system is essential, and these studies suggest that bats have a role to play, and should be investigated further.

6.2 Advantages and limitations of working with bats

Advances in the technology of automated recording have made collecting data about bat presence and activity increasingly easy. As passive recorders get cheaper and easier to use, the potential for citizen science based studies has increased, allowing easier data collection on a large scale and over a long period of time (Beeker et al. 2013, Barlow et al. 2015). The sheer volume of data that can be collected with moderate effort and cost makes it comparatively easy to reach the statistical power requirements of complicated models.

However, working with bats also poses its challenges. Bats are small, nocturnal, and airborne. Even up close, visual identification of species can be challenging. The high degree of inter- and intra species variation in call structure, influenced by habitat and activity the bat is engaged in, make acoustic identification of many species difficult, despite incredible advances in the field of automatic acoustic classification (Russo and Voigt 2016, Roemer et al. 2021). This limits the taxonomic resolution at which studies based on acoustic monitoring can be conducted. As was the case in Chapters 3 and 4, and other studies (Meyer et al. 2004, Frey-Ehrenbold et al. 2013), the inability to separate species with certainty can lead to the grouping of acoustically similar species, particularly in areas lacking comprehensive acoustic libraries.

GPS trackers continue to get smaller and more efficient and they can provide many days of high resolution data on the activity of a bat (O'Mara et al. 2014). However, with an ethical limit of 5% bodyweight for flying animals (Brigham 1988) these devices remain expensive for animals that can weigh less than 5g. If anything can be gleaned from the innumerable studies of bat behaviour, it is that no two species respond the same way to a set of conditions. For those of us interested in harnessing the benefits of bats for ecological and economic gain, our job is complicated by the species- and context- specific nature of the their responses.

6.3 Complexity of agricultural food webs

Agricultural settings bring their own complexities to the table. Rice hosts a diverse biological community, one that can vary from plot to plot depending on its management and can also change dramatically between and within growing seasons (Settle et al. 1996). The biological complexity of the rice food web is itself an asset to farmers. This rich biodiversity is a tool that can be harnessed for the control of insect pests, but too often we see agricultural landscapes homogenised and crop management intensified for the sake of

yield, which often decimates the resident biological communities, resulting in larger pest outbreaks (Way and Heong 1994, Drechsler and Settele 2001). Bats play an important role in the agricultural food web, but, like any other natural enemies of pests, they need to be protected if their populations are to be large enough to replace pesticides (Puig-Montserrat et al. 2015).

The use of natural enemies to control agricultural pests has been an integral part of Integrated Pest Management (IPM). Although not widely adopted, IPM techniques have had remarkable success at managing pests and growing healthier crops (Baker et al. 2020). Rice farmers in China, for example, herd hundreds if not thousands of ducks into their fields to eat pests and fertilize their crop (Zhang et al. 2009, Teng et al. 2016). The closest to such a system in bats is the long term study by Puig-Montserrat et al. (2015), who bolstered bat populations in rice landscapes of Iberia over a ten year period. Insect populations and insecticide use dropped precipitously as the bat population grew, to the point where further pesticide application would have a net negative economic impact.

6.4 Transmission of pathogens

While the academic interest in bats has grown in recent decades, their reputation among the general public has not. This is in large part because of their connection to a number of deadly disease outbreaks. In 2018, India saw the third outbreak of the deadly Nipah virus. Nipah was first reported in 1999 in a village in Malaysia and has an extremely high fatality rate (88.9% in the 2018 outbreak). In all three Indian outbreaks, fruit bats of the genus *Pteropus* were found to be the primary disease reservoir (Sadanadan et al. 2018). The Nipah virus joined a long list of deadly viruses known or suspected to have evolved in bats, which at some point have been transmitted, directly or indirectly, to humans. These include the Ebola virus (Leroy et al. 2009), MERS (Max et al. 2014, Mohd et al. 2016), rabies (Da Rosa et al. 2006), and SARS-like coronaviruses (Latinne et al. 2020).

6.5 Public perception

Myths around bats have existed for centuries, flowing into popular consciousness through books, movies, and comics (Wainer 2014). The classic myths – like Dracula – are negative, and play perhaps on the instinctive revulsion that many feel toward aesthetically displeasing animals like bats (Knight 2008). Even prior to the COVID pandemic, public perception toward bats was quite negative. Questions about whether or not to conduct mass culling of bats have been raised before (Olival 2016).

This negative opinion differs by age and profession and has been found to be inversely correlated with level of education (Musila et al. 2018, Castilla et al. 2020, Lu et al. 2021). In Kenya, 61% of a community surveyed reported the belief that bats were agents of the devil, while 58% of the community respectively believed that bats brought seeds of fruit trees to their land and 66% believed that bats destroyed farmers' fruits (Musila et al. 2018). A similar study in Pakistan reported a more uniformly negative attitude, with 100% of the respondents reporting that bats did not provide any positive value and 43.8% believing that bats inflicted heavy economic losses (Mahmood-ul-Hassan and Salim 2011).

In India, the perception of farmers and land owners, who are perhaps the most at risk of contracting pathogens from bats, was found to be quite different. One study, working in monoculture plantations of rubber, fruit orchards, and agroforestry plantations of the Western Ghats in Kerala, India, found that among plantation owners, farmers, and forest management staff, most could distinguish between fruit bats and insectivorous bats and most believed that fruit bats were either entirely beneficial (41%) or beneficial in some ways and harmful in other ways (25.5%). Only 17% of the respondents believed that fruit bats were exclusively harmful and 90% stated that flying foxes – *Pteropus spp.* – were valuable for their ecosystem service of seed dispersal (Deshpande and Kelkar 2015).

Where seed dispersal and pollination were the most widely acknowledged benefits of bats, damage to fruit crops was seen as the prime encumbrance. Investigations into the destruction of fruit crops by bats found the animosity felt by farmers in this regard to be well-founded. In the Indian states of Karnataka and Andhra Pradesh, bats were recorded to cause significant damage to grapes, areca nuts, sapota fruits, guava, and mango (Verghese 1998, Srinivasulu and Srinivasulu 2002, Chakravarthy and Girish 2003, Aziz et al. 2016).

Adding to the negative public perception is the continued resistance to providing with bats legal protection, which highlights a disconnect between policy-makers and scientists. This lack of protection, coupled with the intuitive belief that due to their ability to fly, bats are not impacted by habitat destruction and are not at risk of going extinct, has lead to severe population declines in many parts of the world. One study estimates that Southeast Asia will lose 20% of its bat species by the year 2100 (Lane et al. 2006). Against the backdrop of such attitudes, those invested in the protection and promotion of bats must venture forth and plead their case.

6.6 An invisible emergency

Fieldwork often presents situations, dynamics, or data that can't be quantified at the time, for lack of planning, resources, or equipment, but which is nonetheless significant and worth recording for future studies. Below is an account of such a situation.

When in the field, I constantly asked people about bats. A consistent response to my enquiries about bats in rural Assam was 'there used to be many bats flying here, but in the last few years there have been fewer'. When asked where specifically they knew bats were, a common answers was 'around my house'. After initial investigation revealed bats roosting in the bamboo frames of houses and sheds, I adopted the practice of inspecting such structures wherever I went. Bamboo being hollow, the bamboo frames of roofs

invariably ended with a downward pointing cavities. These could be 2cm-20cm deep, and a single house or shed might have anywhere from 40 to 150 of them. In four months of checking bamboo structures, I did not come across a single one that did not harbour at least one bat. On the occasions when I caught bats exiting these bamboo cavity, I would find anywhere from 1 to 17 individuals, sometimes representing more than one species, roosting in a single pocket. It became quite clear that these structures saw widespread use as roosting sites.

From August to December 2019, I stayed in the Puthimari village in rural Assam. During this time, I watched at least three houses in my street begin the conversion from bamboo to concrete. My hosts indicated that there had been a steady stream of conversion from 'kacha' bamboo houses to 'pukka' concrete houses in the last 5-10 years. This conversion of structures from bamboo to brick or concrete is, I believe, an invisible emergency for insectivorous bats. The kind of concrete houses I saw built did not have cavities for bats to roost in, not even in the form of roof tiles which are known havens for roosting bats. The conversion of bamboo houses to sheds, which would appear to be occurring at pace, will therefore drastically reduce the number of available roost sites for many species of insectivorous bats.

It is an emergency for two reasons. First, it exclusively affects bats. No other species or ecological process will be affected by it, save those that are influenced by changing bat numbers. Second, this transformation is all but invisible. One cannot yet automatically identify individual houses in rural landscapes using satellite data, and no map or census will show this change, because, fundamentally, no change is taking place. Where once stood a house, now still stands a house. The number of people in it stay the same. The only difference that may be detectable is the production of artificial light, but the scale of the conversion will make this feature difficult to detect.

Habitat loss is a well known driver of population declines, and in semi-rural agricultural landscapes, roosting sites are more likely to be the factor limiting bat population sizes than, say, prey abundance. If my anecdotal evidence represents the reality of rural landscapes across India, then the carrying capacity of these landscapes, which span the length of the country, will plummet for insectivorous bats. The resulting decline in bat populations is particularly damaging in rural landscapes because of the valuable pest suppression service I argue that they provide to the agricultural industry in such landscapes.

Unfortunately, this change is both inevitable and understandable. Bamboo houses are less comfortable that concrete ones, and need to be rebuilt regularly. As construction materials become cheaper, it is inevitable that most villages located reasonably close to cities will undergo this change.

Mitigating the effect of this conversion will be complicated. The COVID pandemic has undoubtedly led public opinion on bats to become more negative than it already was. Any proposal to increase bat numbers in close proximity with people will elicit a not-unreasonable reaction – given the history of zoonotic transmission of pathogens that evolved in bats. While rural communities rarely come into direct physical contact with bats, the fact remains that even indirect contact can have deadly results – the Nipah virus outbreak in Kerala being an apt example. The most straightforward solution of installing bat boxes is therefore likely to meet significant resistance from policy makers and the public.

That being said, farming communities do tend to have a far more accurate and balanced understanding of the forces that affect their crop and, even compared to biologists, have been documented having a more positive and balanced view of bats (although these studies were all conducted pre-COVID). Those I spoke to in the field did acknowledge the fact that insectivorous bats ate crop pests and that they were useful to

them as a result. Nonetheless, there is an urgent need to determine the degree to which the conversion of bamboo to concrete structures will affect bat populations in rural settings.

6.7 Conclusion

Around the world, the conversion of natural land to urban and agricultural land is occurring at an unprecedented rate (Winkler et al. 2021). This, in concert with climate change, increasing pollution, mining and a host of other factors is having a significant impact on bat populations (Frick et al. 2020). Bats are well known to exhibit species specific responses to landscapes, but as we have seen in Chapter 4 and as is documented in many studies, key features including canopy cover, connectivity, and landscape heterogeneity and can benefit a wide range of species. Bats' slow lift-history traits mean that their populations grow – and recover – slowly (Barclay and Harder 2003). To protect and increase bat populations will therefore take sustained effort driven by informed policy making. It will take investment in research and conservation efforts for decades to reverse the current trend. The benefits of this investment, ecological and economic, will far outweigh the costs.

When present in agricultural landscapes, results form around the world indicate that large insectivorous bat populations provide substantial economic and ecological value by suppressing the populations of important agricultural pests. India is primarily an agricultural nation and relies on crops such as rice, wheat, sugarcane, and cashew for both consumption and export (Directorate of Economics and Statistics 2019). India's landmass is dominated by agriculture, yet the studies detailed in this thesis are among the first to explore the behaviour of bats in agricultural landscapes (Wordley et al. 2014a, 2015, 2017, Ongole et al. 2018). Given the economic potential of bat pest suppression, a country as reliant on agriculture as India must develop a greater understanding of the ecology of bats in agricultural landscapes.

6.8 Future directions

Acoustic monitoring is one of the easiest and cheapest methods by which to study the activity and distribution patterns of insectivorous bats. The technology to collect immense volumes of acoustic data is getting cheaper and more accessible every year, as are the development of sophisticated acoustic classifiers capable of extracting these calls from raw audio (Roemer et al. 2021, Yoh et al. 2022). To be fully exploited in India, however, bats researchers must first create comprehensive acoustic libraries of the ~114 insectivorous bats in the country. Without these, the resolution at which bats can be identified will remain low, limiting our ability to understand and conserve bats at the species level.

Armed with these tools, ecologists can then look to make deep dives into the ecology of bats in India, to broaden our understanding of bat behaviour in the plethora of habitats found in the country. Of special importance are studies set in anthropogenic habitats. India is seeing rapid land use change across the country. While such changes undoubtedly have negative impacts on resident bat populations, it is also true that anthropogenic landscapes, including urban and agricultural landscapes, are capable of hosting large and diverse bat communities. The population of bats in these landscapes is largely determined by their structure, composition, and connectivity (Dixon 2012, Frey-Ehrenbold et al. 2013, Kalda et al. 2015, Heim et al. 2015). Understanding the ecology of bats in these landscapes will allow us to minimize the impact of land use change by making anthropogenic land as habitable as possible. Roosting ecology is of particular importance, because agricultural and associated rural landscapes in India may present unique habitats for bats. Their behaviour in such landscapes might therefore be harder to predict based on the results of studies conducted elsewhere in the world. Habitat destruction being the primary cause of population declines in bats, knowing the habitat requirements of bats in landscapes where they provide valuable ecosystem services is imperative to harnessing these services.

The conservation of bats in agricultural landscapes will no doubt increase the value derived from their ecosystem services. However they are not the only community providing such services. Insectivorous birds were abundant in my field sites, and were particularly active at dawn, when, by the hundreds, they would fly above the rice fields catching insects. Given their numbers, it is undeniable that insectivorous birds also contribute to insect pest suppression, and I submit that it is likely this value exceeds that provided by bats. There are undoubtedly other natural enemies at work in rice ecosystems, without which yield loss would likely be significantly greater. This value must be made clear to the public and policy makers. A greater understanding of ecosystem services (provided by bats and other communities) and the economic and ecological benefits they provide in different regions and agricultural industries, will improve public perception, making their conservation through targeted interventions easier.

Anthropogenic change is inevitable. In a country like India, where poverty and food insecurity is widespread, the challenge is to integrate the conservation of biological diversity and processes with human development. In many cases the two can go hand-in-hand, but we need a deep understanding of the natural world if we are to create policies, technologies, and ways of living that can protect our planet while also improving the baseline human condition.

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APPENDIX 1: Supporting information for Chapter 3

A1.1 Results of final models presented in Chapter 3

Table A1.1 Summary of best GLMM model of each sonotype - S20, S31, S34, S38, S48, S65 - and all sonotypes combined, describing the influence of biotic and abiotic variables on bat activity. 'Best' models were identified by comparing subsets of a global model using AICc. Where the best model was less than two AICc units from one or more others, the one with the fewest variables was chosen. Since the variables were all standardized, they could be compared. 'Imp' denotes the relative importance of each variable. P-value indicates the significance of each variable in the best model of a sonotype.

Variable by Sonotype	Estimate	Imp	p-value
S20 (R-squared: 0.169)			
Minimum Temperature	0.493	0.300	<0.001
Sampling Effort	0.338	0.205	1.19E-03
Moonlight Intensity	-0.320	0.195	<0.001
Minimum Temperature:Moonlight Intensity	0.247	0.150	2.32E-02
Minimum Temperature Squared	-0.244	0.149	2.63E-03
S31 (R-squared: 0.359)			
Minimum Temperature	0.515	0.31	<0.001
Ambient Insect Noise:Minimum Temperature	-0.406	0.244	<0.001
Ambient Insect Noise	0.326	0.196	<0.001
Minimum Temperature Squared	-0.248	0.149	<0.001
Sampling Effort	0.167	0.1	1.31E-02
S34 (R-squared: 0.389)			
Minimum Temperature	0.443	0.326	<0.001
Ambient Insect Noise	0.339	0.25	<0.001
Ambient Insect Noise:Minimum Temperature	-0.235	0.173	<0.001

Sampling Effort	0.218	0.16	<0.001
Moonlight Intensity	-0.125	0.092	2.15E-02

S38 (R-squared: 0.167)

Sampling Effort	0.282	0.34	<0.001
Minimum Temperature	0.205	0.246	<0.001
Ambient Insect Noise:Minimum Temperature	-0.143	0.172	8.53E-03
Moonlight Intensity	-0.133	0.16	5.39E-03
Ambient Insect Noise	0.068	0.082	2.00E-01

S48 (R-squared = 0.243)

Sampling Effort	0.411	0.336	<0.001
Moonlight Intensity	-0.261	0.213	<0.001
Ambient Insect Noise:Minimum Temperature	-0.199	0.162	8.50E-03
Ambient Insect Noise	0.15	0.122	1.97E-02
Ambient Insect Noise:Moonlight Intensity	0.107	0.087	7.55E-02
Minimum Temperature	0.096	0.079	1.98E-01

S65 (R-squared: 0.166)

Sampling Effort	0.44	0.353	<0.001
Minimum Temperature	0.439	0.352	<0.001
Moonlight Intensity	-0.368	0.295	<0.001

All sonotypes (R-squared: 0.262)

Sampling Effort	0.291	0.258	<0.001
Ambient Insect Noise	0.237	0.210	<0.001
Ambient Insect Noise:Minimum Temperature	-0.213	0.188	<0.001
Minimum Temperature	0.164	0.145	4.81E-03
Moonlight Intensity	-0.126	0.111	6.19E-03
Ambient Insect Noise:Moonlight Intensity	0.100	0.088	2.78E-02

Table A1.2 Nightly activity pattens of each sonotype. Every night was divided into ten-minute intervals starting at dusk and ending ten hours post dusk. The number of passes of each sonotype in each ten-minute post-dusk interval was summed up over all 48 nights of sampling. Composite normal distributions that best fit the overall pattern of nightly activity of each sonotype were fit using the 'mix' function. Mean and standard error of each normal distribution of each sonotypes' nightly activity pattern is given below. Mean refers to the time of the peak measured as number of minutes since the start of analysis (dusk + 20 minutes).

Sonotype	Peak number	Mean (minutes)	Standard Error	Chi-square	p-value
S20	1	145.72	68.03	0.61	1
	2	190	0.0018		
	3	339.8	102.43		
	4	525.75	34.12		
S31	1	31.57	11.75	0.70	1
	2	136.81	48.64		
	3	289.08	135.38		
	4	588.76	10.49		
S34	1	37.96	13.19	0.69	1
	2	95.88	55.57		
	3	336.46	125.17		
S38	1	87.4	41.90	3.83	1
	2	313.89	150.28		
S48	1	77.67	33.53	1.57	1
	2	262.73	100.79		

	3	500.71	59.42		
S65	1	236.35	117.83	1.22	1
	2	503.03	58.00		

A1.2 Photographs and calls of captured bats.

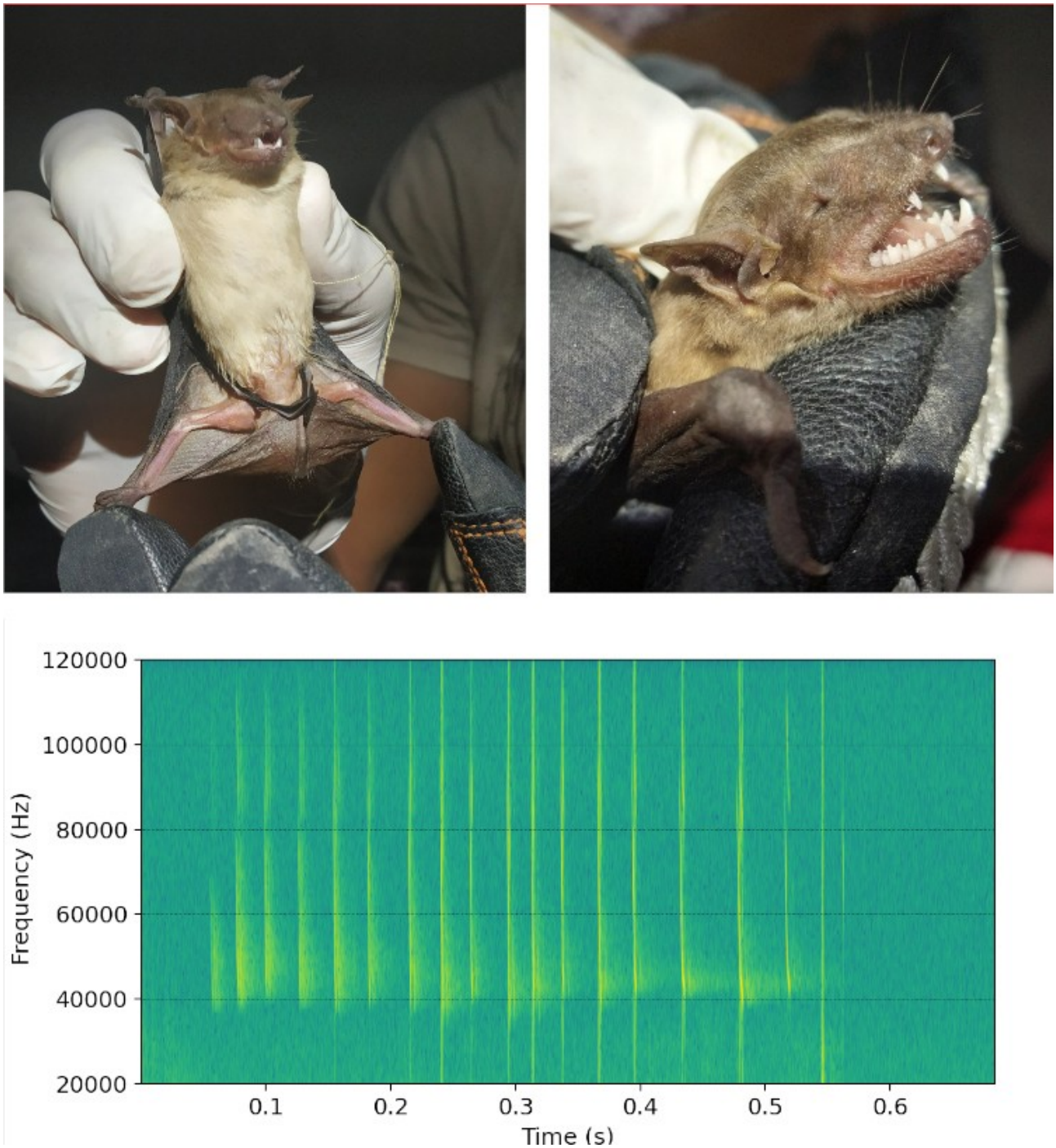


Fig. A1.1 Pictures and spectrogram of Scotophilus kuhlii. Individual was caught on 18 October and recorded on release with a Pettersson D240x recorder set to time expansion mode.

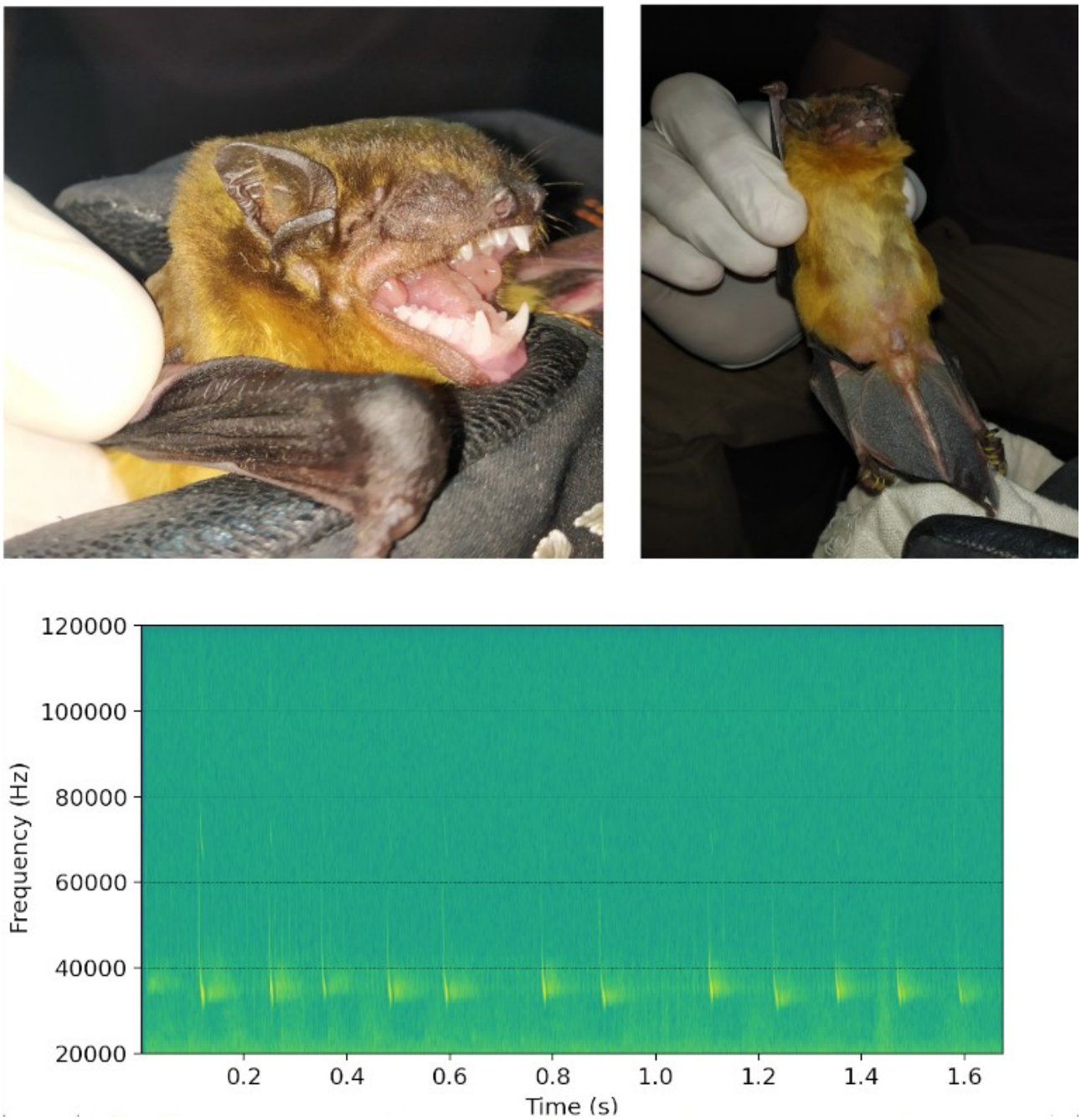


Fig. A1.2 Pictures and spectrogram of *Scotophilus heathii*. Individual was caught on 2 November and recorded on release with a Pettersson D240x recorder set to time expansion mode.

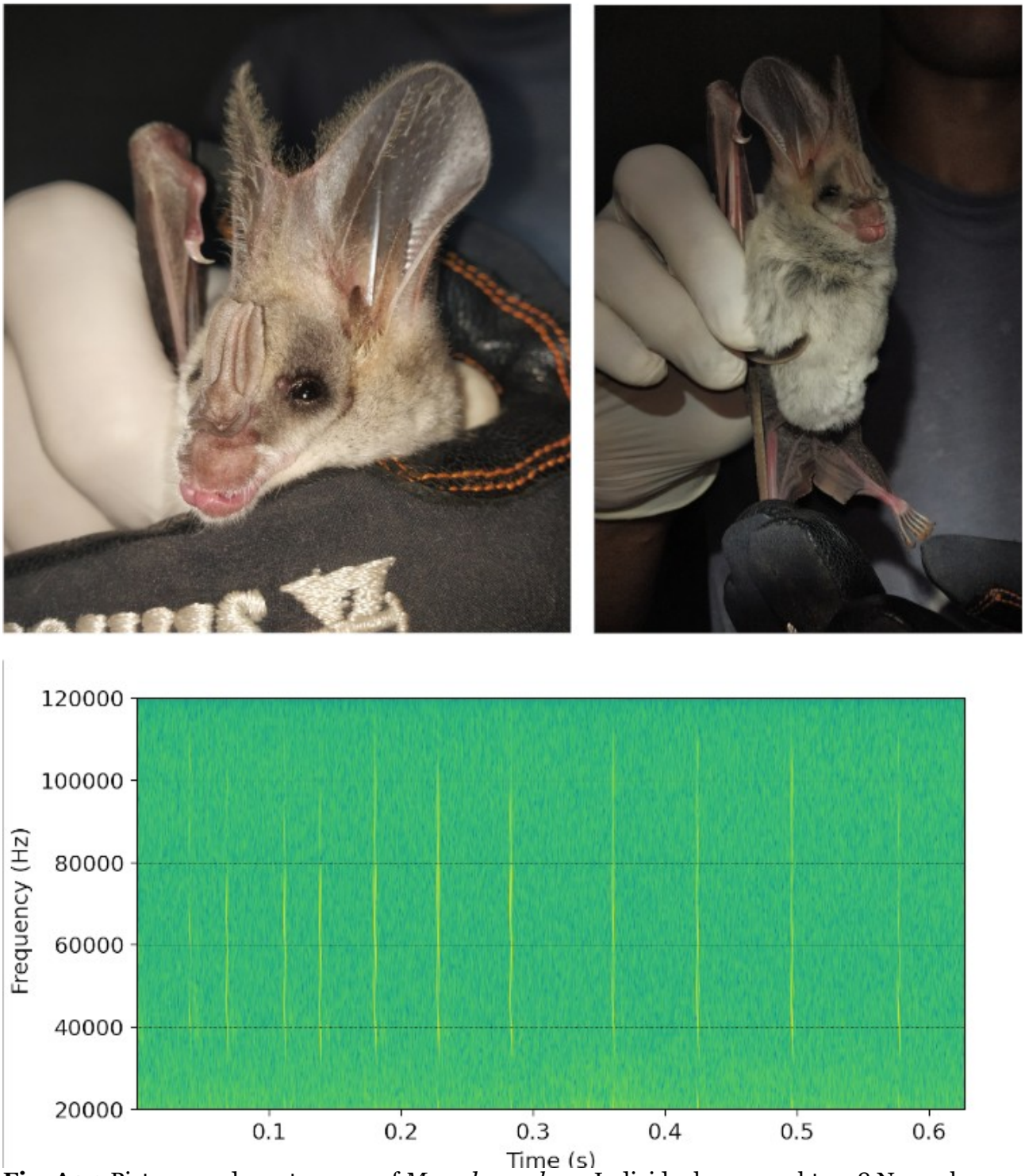


Fig. A1.3 Pictures and spectrogram of *Megaderma lyra*. Individual was caught on 8 November and recorded on release with a Pettersson D240x recorder set to time expansion mode.

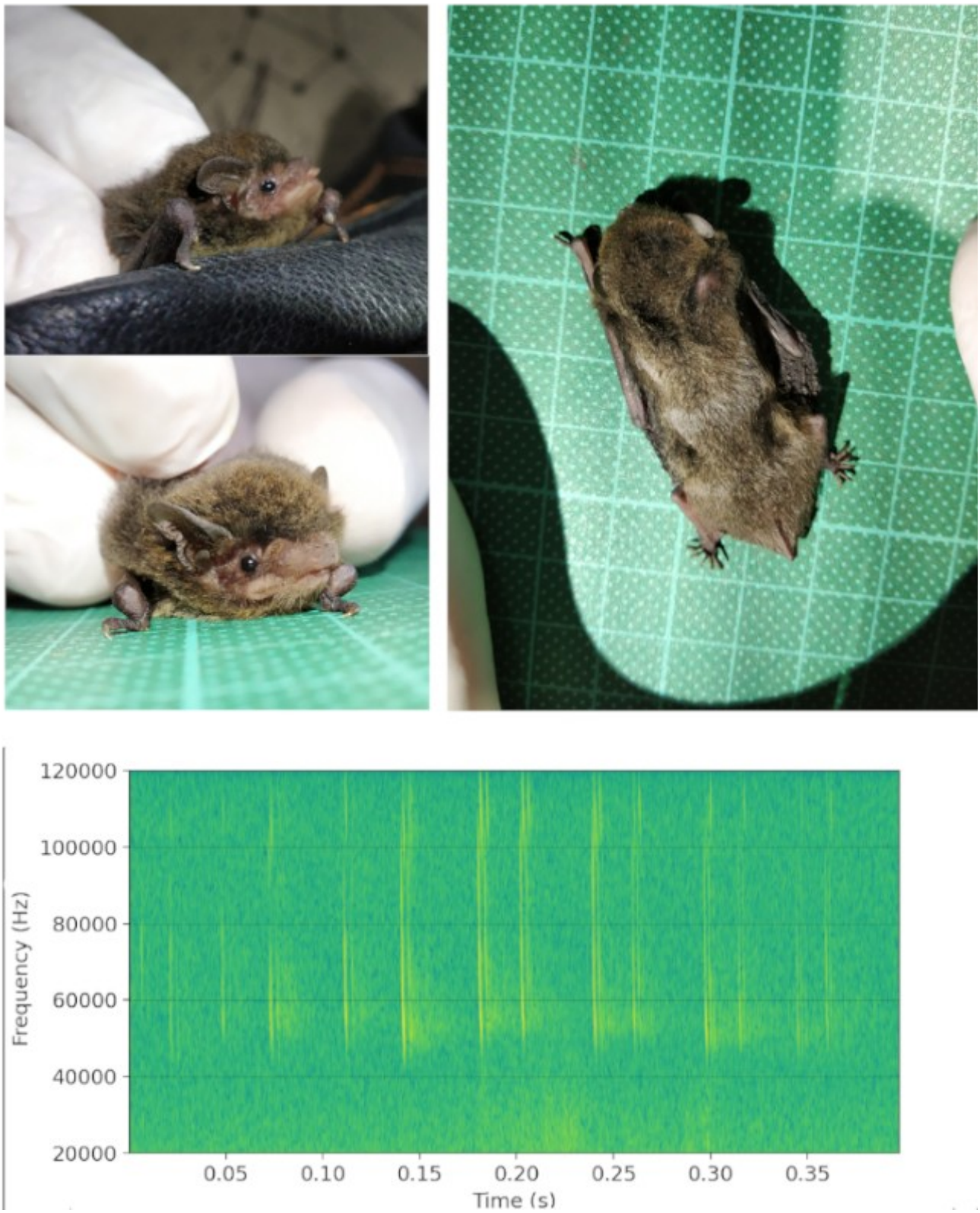


Fig. A1.4 Pictures and spectrogram of individual 4O2. Individual was caught on 4 October and recorded on release with a Pettersson D240x recorder set to time expansion mode.

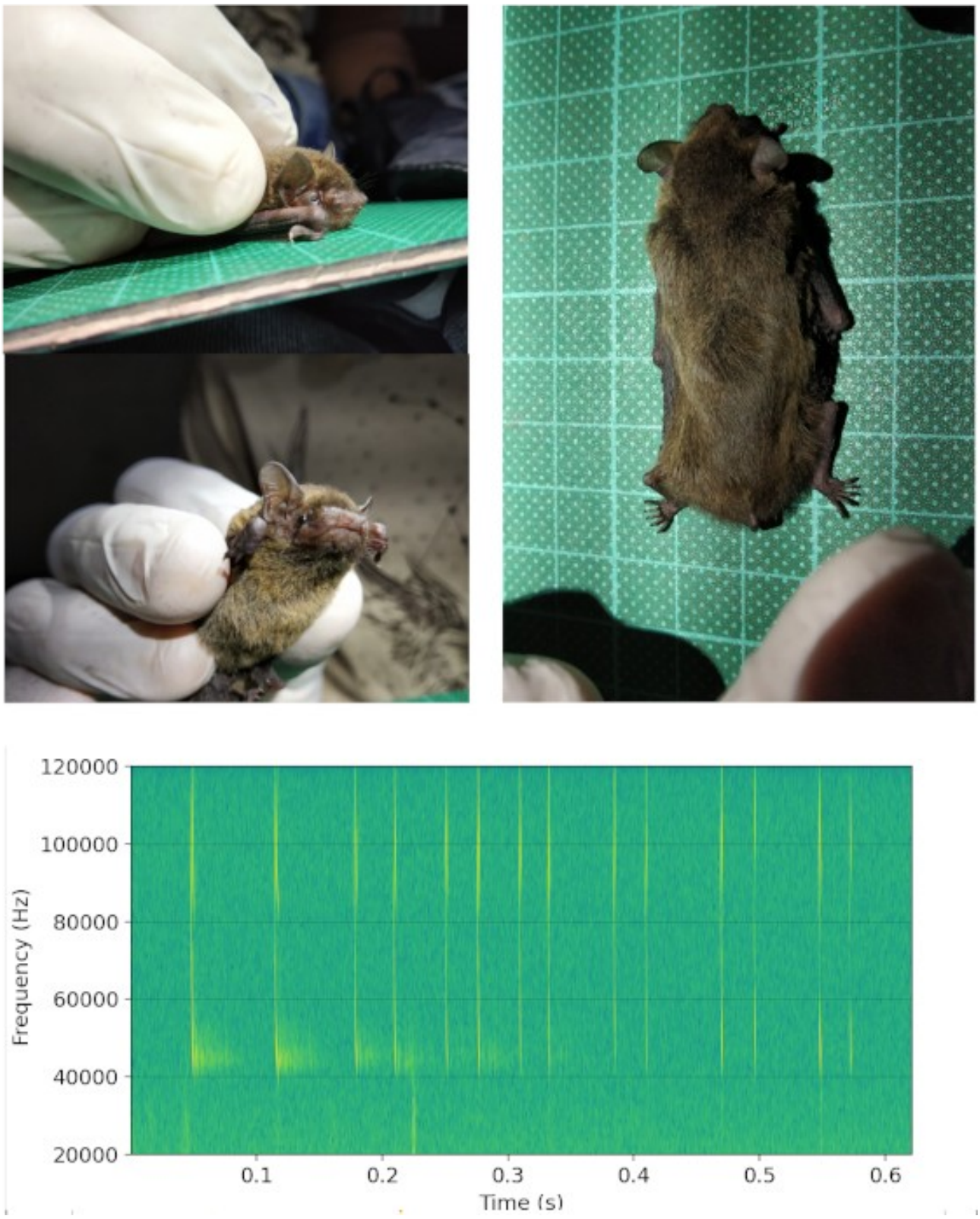


Fig. A1.5 Pictures and spectrogram of individual 405. Individual was caught on 4 October and recorded on release with a Pettersson D240x recorder set to time expansion mode.

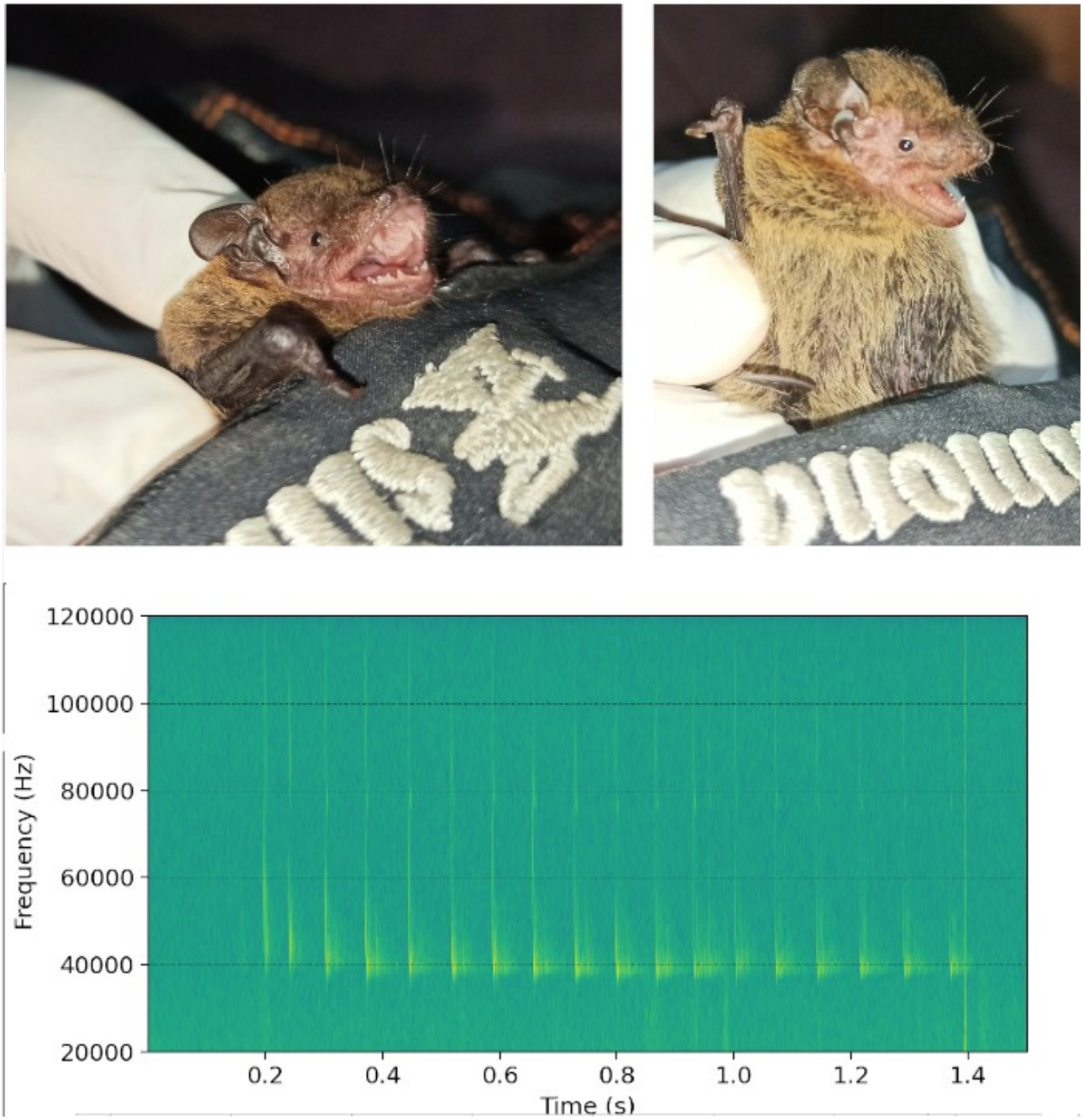


Fig. A1.6 Pictures and spectrogram of individual 17N4. Individual was caught on 17 November and recorded on release with a Pettersson D240x recorder set to time expansion mode.

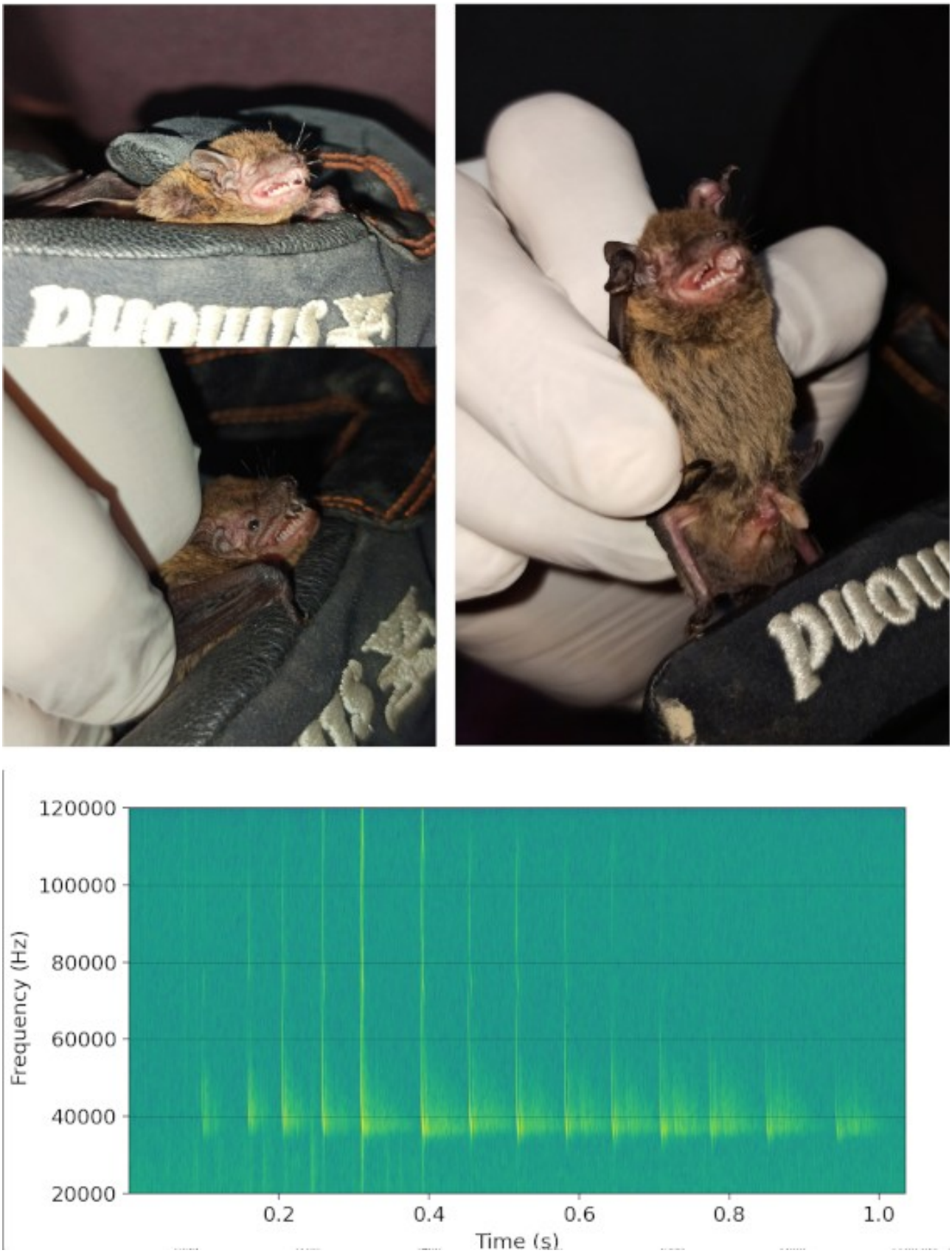


Fig. A1.7 Pictures and spectrogram of individual 17N5. Individual was caught on 17 November and recorded on release with a Pettersson D240x recorder set to time expansion mode.

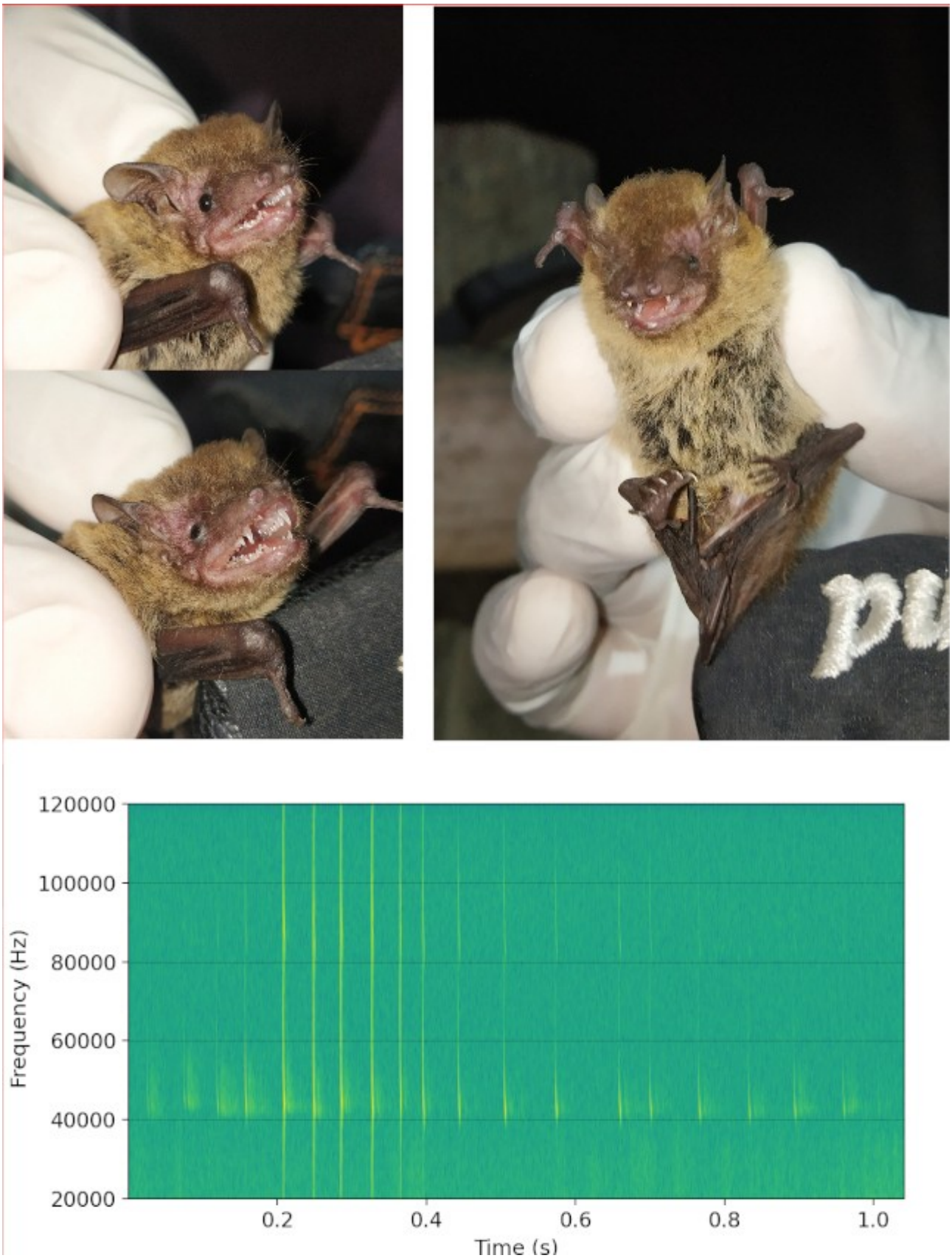


Fig. A1.8 Pictures and spectrogram of individual 9N1. Individual was caught on 9 November and recorded on release with a Pettersson D240x recorder set to time expansion mode.

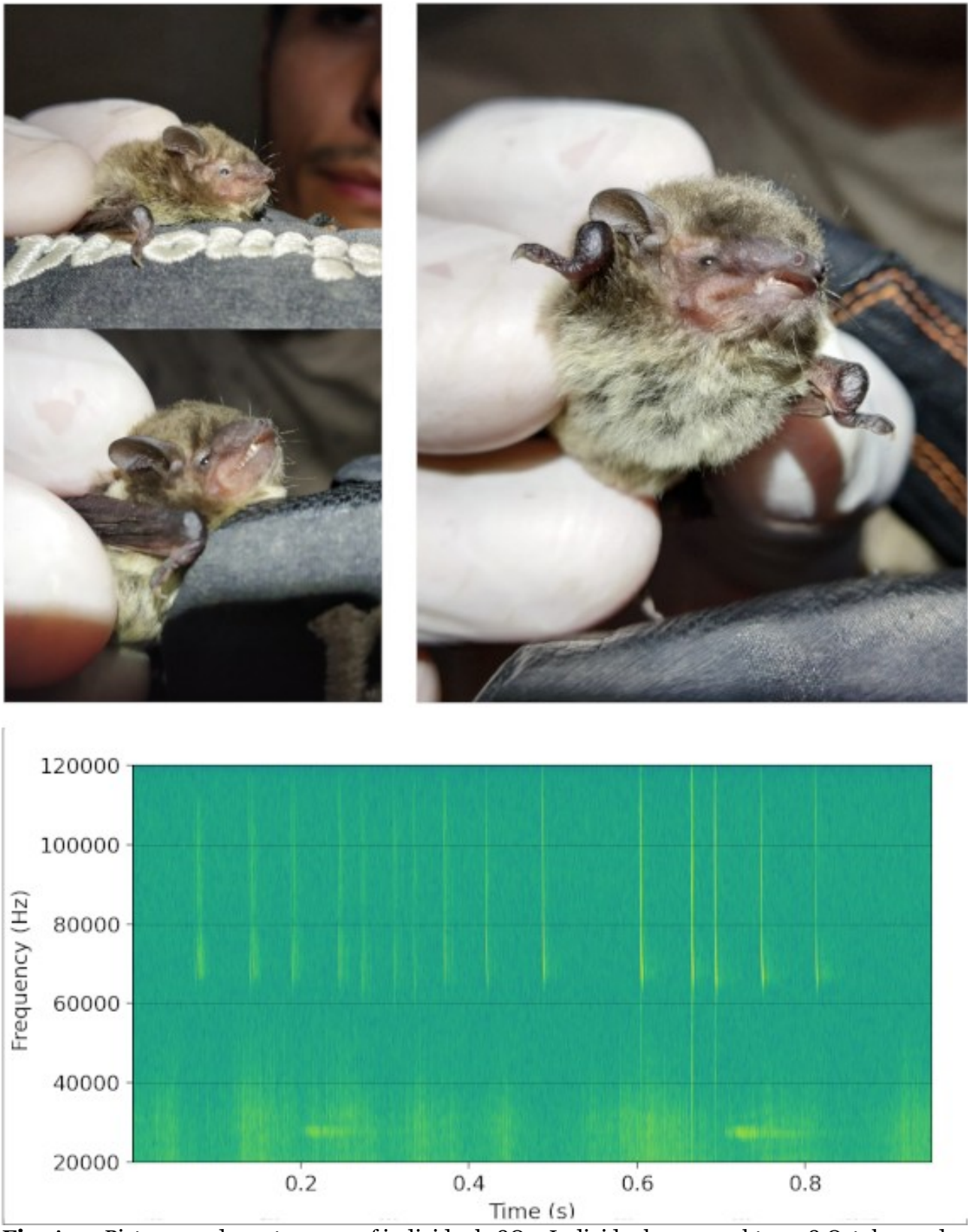


Fig. A1.9 Pictures and spectrogram of individual 18O3. Individual was caught on 18 October and recorded on release with a Pettersson D240x recorder set to time expansion mode.

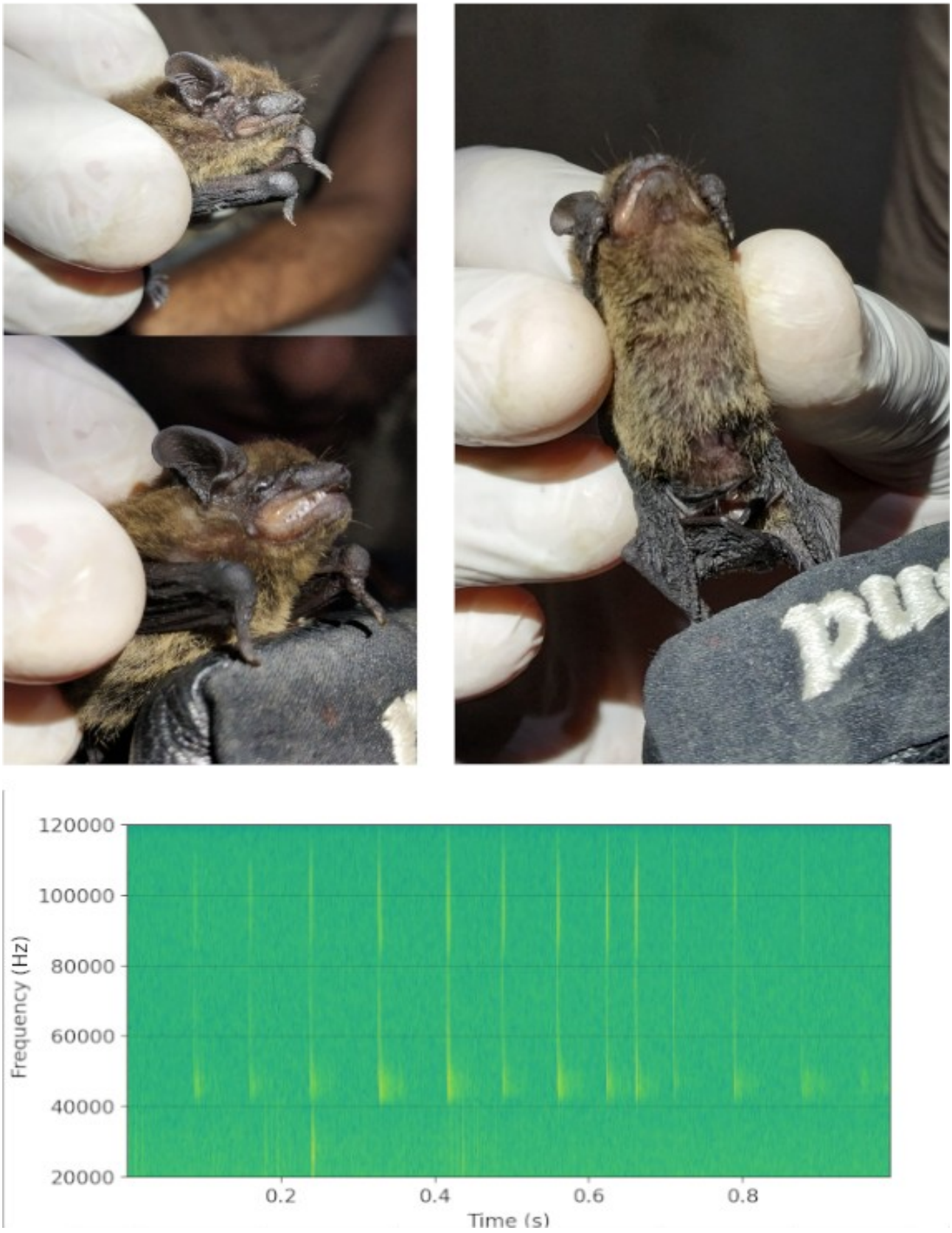


Fig. A1.10 Pictures and spectrogram of individual 18O5. Individual was caught on 18 October and recorded on release with a Pettersson D240x recorder set to time expansion mode.

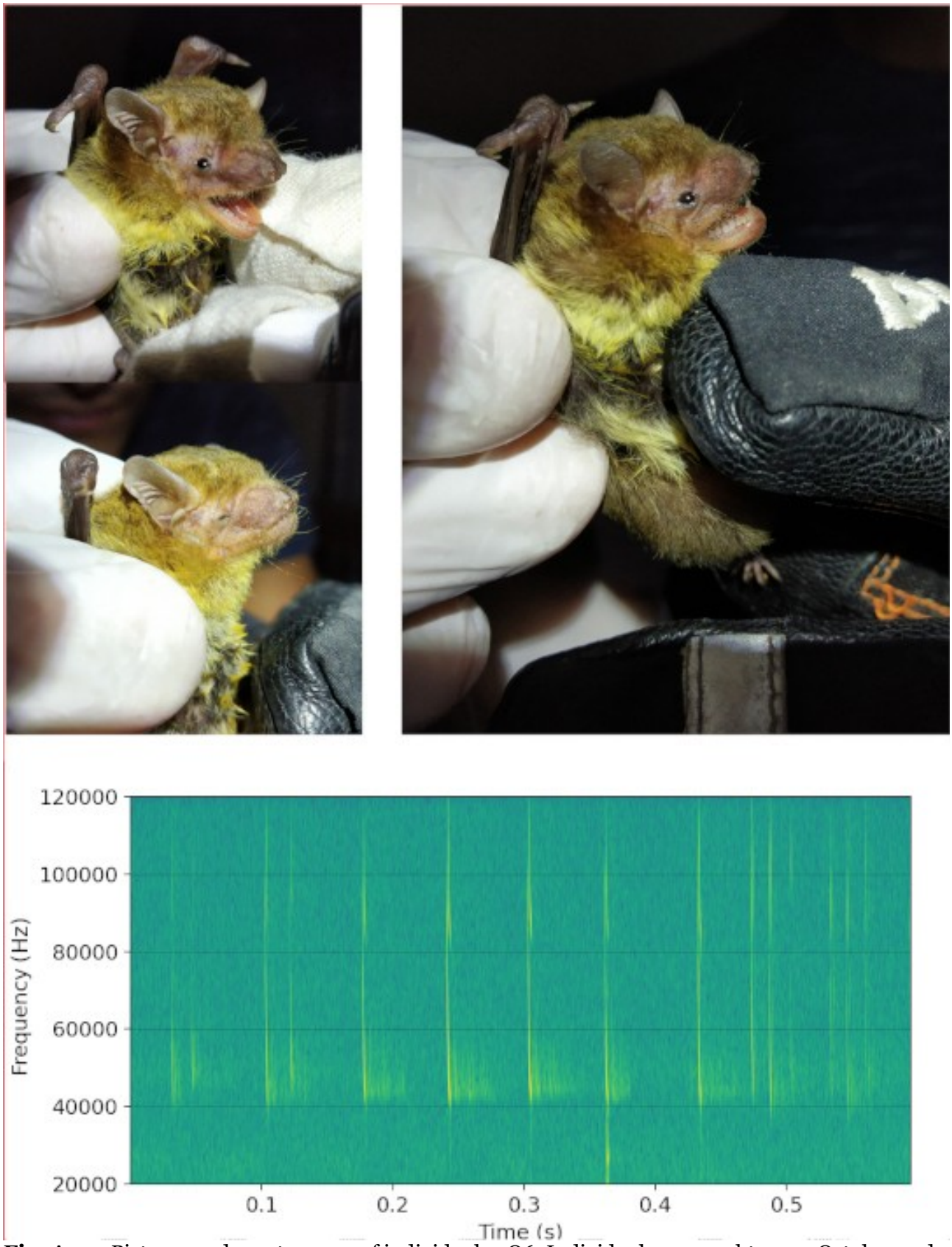


Fig. A1.11 Pictures and spectrogram of individual 1906. Individual was caught on 19 October and recorded on release with a Pettersson D240x recorder set to time expansion mode.

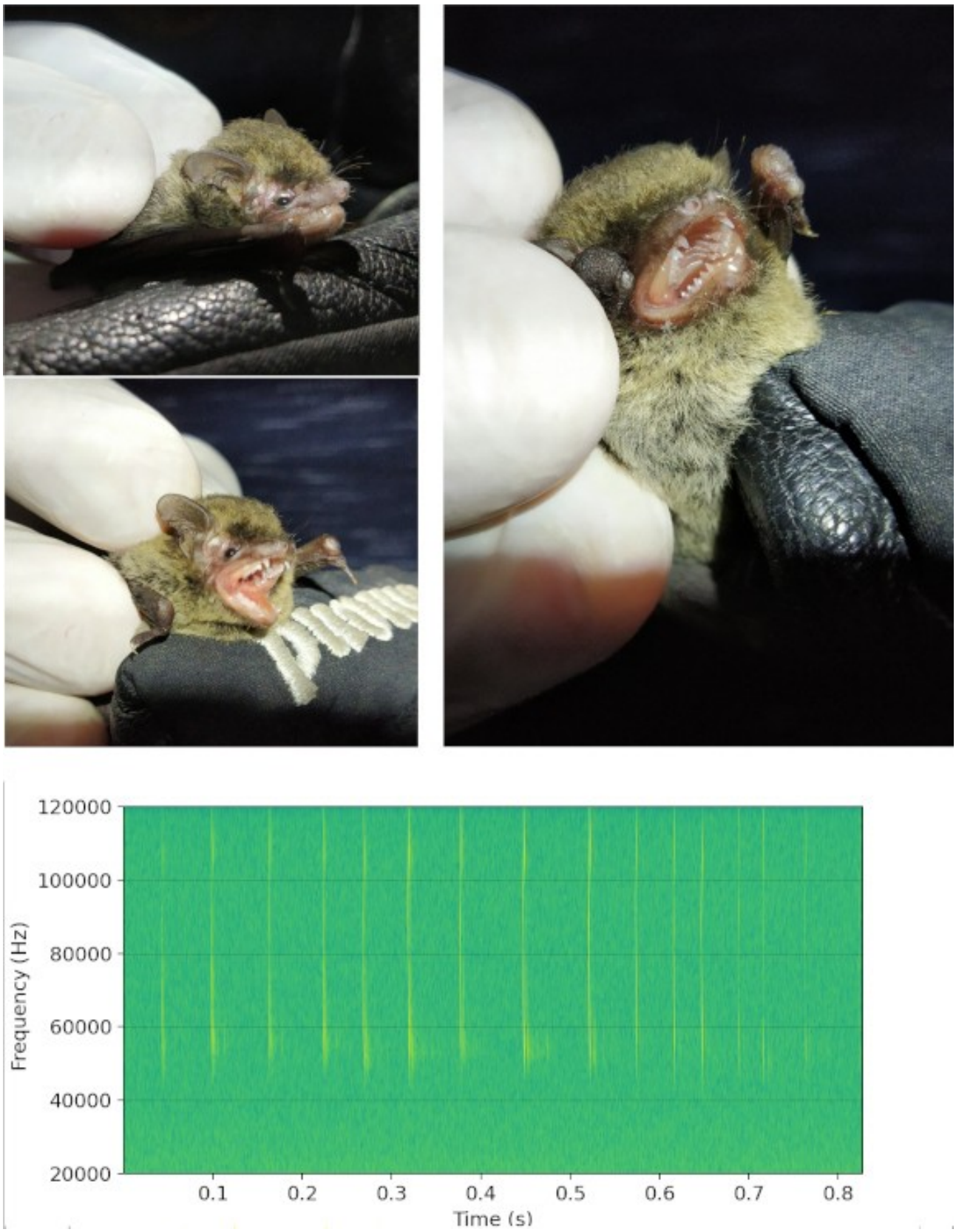


Fig. A1.12 Pictures and spectrogram of individual 1907. Individual was caught on 19 October and recorded on release with a Pettersson D240x recorder set to time expansion mode.

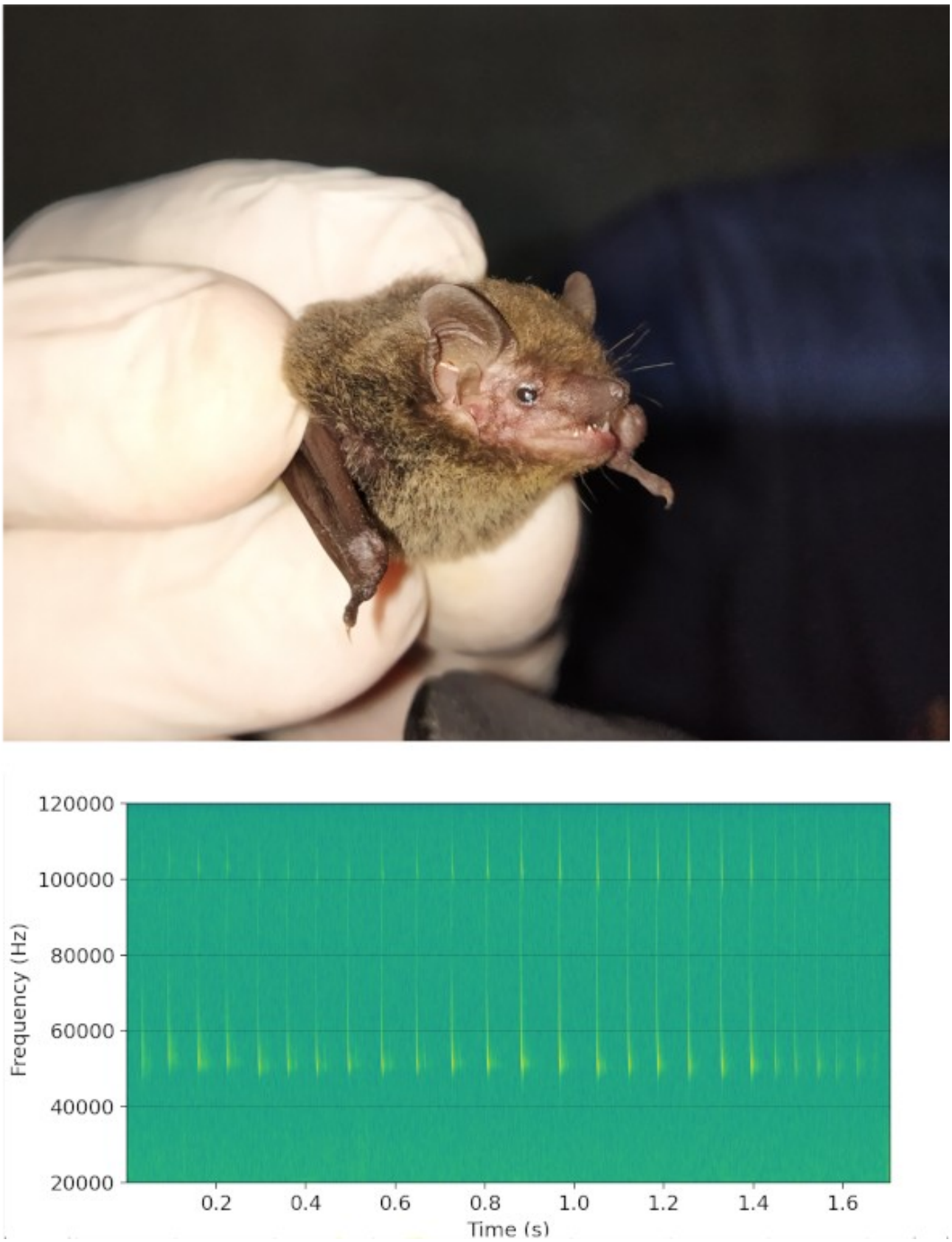


Fig. A1.13 Pictures and spectrogram of individual 30O3. Individual was caught on 30 October and recorded on release with a Pettersson D240x recorder set to time expansion mode.

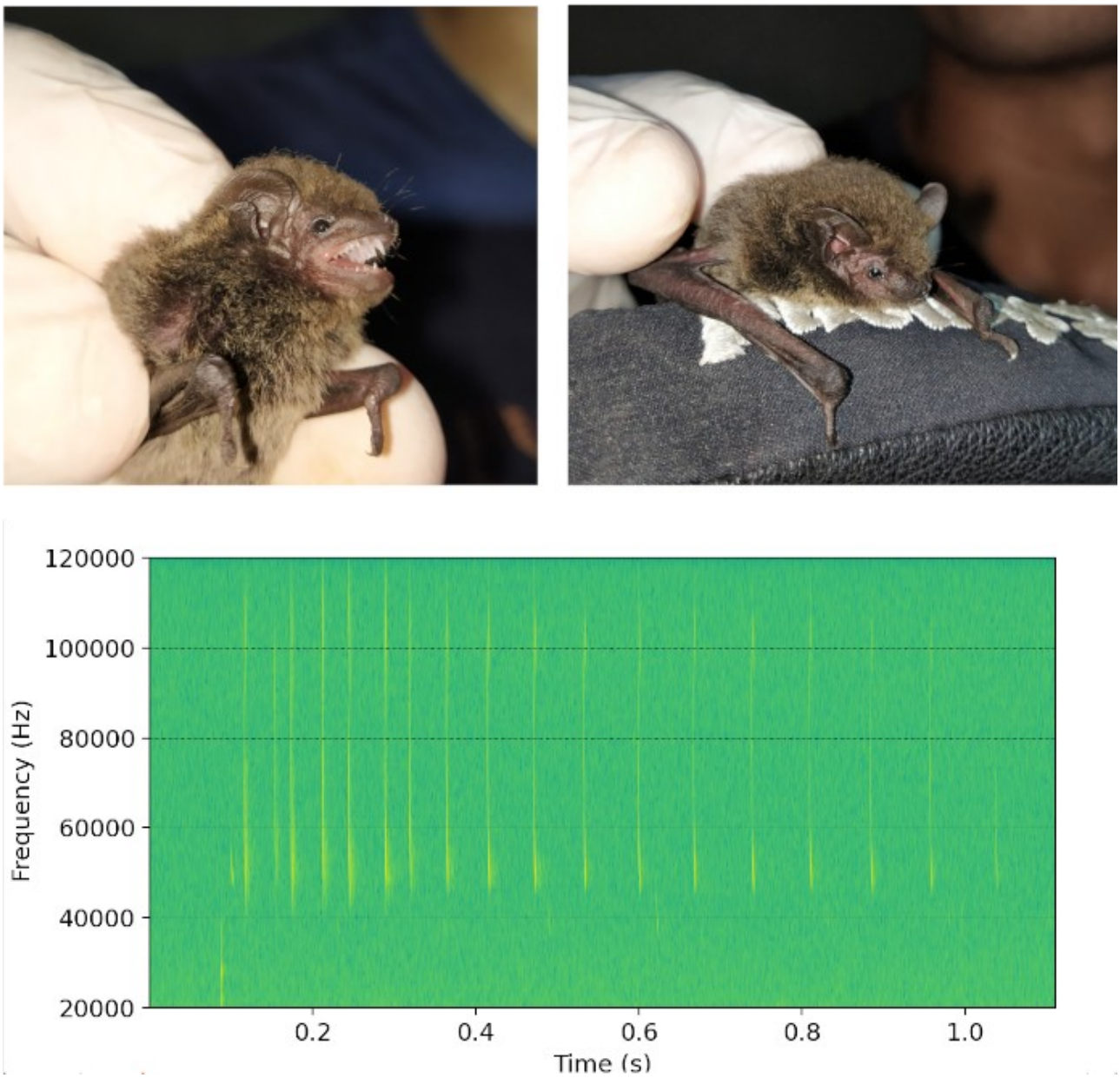


Fig. A1.14 Pictures and spectrogram of individual 31O5. Individual was caught on 31 October and recorded on release with a Pettersson D240x recorder set to time expansion mode.

APPENDIX 2: Supporting information for the results of Chapter 4

A2.1 Supporting information for the results of Chapter 4

Below are tables detailing the results of the Generalised Linear Mixed Models built to examine the response of five bat sonotypes to the landscape surrounding rice fields in the Nagaon district of Assam, India. Following them are three figures, each presenting two sets of maps. Each set contains an unclassified and a classified map of the same area, which contains set of sites from which data was collected.

Table A2.1 The best supported statistical models for each bat sonotype, including landscape variables included in the model, variable Estimate (effect on the standard deviation of sonotype activity for every standard deviation increase in the variable), importance (Imp) and p value, model AICc and R^2 values, and the smallest scale tested at which spatial autocorrelation was not significant (S.A. scale). Activity data of five sonotypes was extracted from 481 hours of recordings collected using Audiomoth 1.0.0 full spectrum recorders over 18 nights between 9 May and 8 June 2019 from rice fields in the Nagaon district of Assam.

Variable by sonotype	Estimate	Imp	p-value	AICc	R^2
S28					
Distance to edge	-0.93	0.58	<0.001	579.13	0.35
Urban area within 1km	-0.46	0.29	4.8E-2		
Forest area within 1km	0.2	0.12	4.7E-1		
Sampling effort	0.02	0.01	9.1E-2		
S32					
Distance to edge	0.2	0.88	7.3E-2	613.41	0.23
Sampling effort	0.03	0.12	<0.001		
S35					
Distance to forest	-0.46	0.95	<0.001	675.88	0.35
Sampling effort	0.02	0.05	<0.001		
S38					
Distance to forest	-0.62	0.52	<0.001	723.53	0.39
Moonlight intensity	-0.37	0.31	4.4E-3		
Urban area within 1km	0.19	0.16	3.7E-1		
Sampling effort	0.03	0.02	1.5E-3		
S47					
SDHI within 1km	0.39	0.93	8.0E-2	560.22	0.08
Sampling effort	0.03	0.07	1.4E-2		

Table A2.2 The best models created using data from all the sonotypes combined. Spatial autocorrelation was significant at all tested scales, so these models are here for descriptive purposes only. Models were built with points grouped at three scales – 400m, 1km and 5km. The best or, if two models were equivalent in AICc and parsimony then best two, models are presented below.

Variable by sonotype	Estimate	Imp	p-value	AICc	R^2
S_All					
Distance to forest	-0.36	0.94	2.7E-3	914.15	0.22
Sampling effort	0.02	0.06	<0.001		
S_All					
Distance to forest	-0.28	0.56	2.0E-3	913.05	0.26
Rice area within 2km	-0.21	0.4	4.8E-2		
Sampling effort	0.02	0.04	<0.001		
S_All					
Distance to forest	-0.35	0.6	<0.001	911.87	0.31
Edge area within 1km	0.21	0.36	2.5E-2		
Sampling effort	0.02	0.04	<0.001		
S_All					
Distance to forest	-0.28	0.56	2.0E-3	913.05	0.3
Rice area within 2km	-0.21	0.4	4.8E-2		
Sampling effort	0.02	0.04	<0.001		
S_All					
Forest area within 1km	0.28	0.49	1.7E-3	911.5	0.35
Rice area within 2km	-0.28	0.48	4.0E-3		
Sampling effort	0.02	0.03	0.001		

A2.2 Maps of field sites where data for Chapter 4 were collected

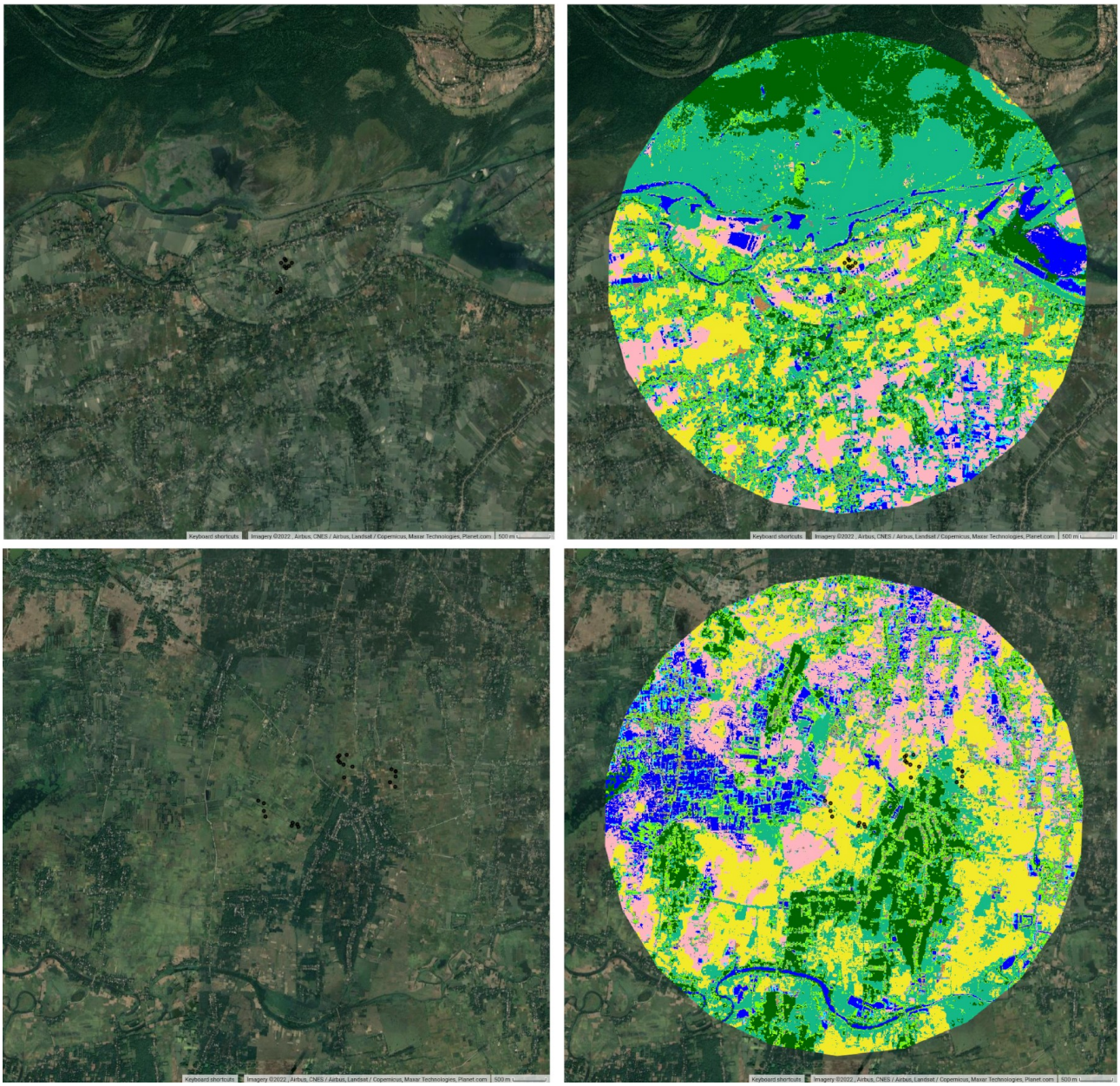


Fig. A2.1 Unclassified (left) and classified (right) maps of the landscape around two sets of sites in Nagaon, Assam. The landscape was classified within a radius of 4km around the centroid of one cluster of sites using a random forest supervised classifier in Google Earth Engine. The centroids are located at 92.69117387589556E, 26.483239162261455N (top) and 92.5608614883377E, 26.37818517339917N (bottom). The landscape was classified into nine landcover types: Forest (or algae), dry rice, wet rice, water, bank, edge, field, bare ground, and urban land. Black dots represent sampling sites. Image source: 2022, Arbus, CNES/Airbus, Landsat/Copernicus, Maxar Technologies, Planet.com.

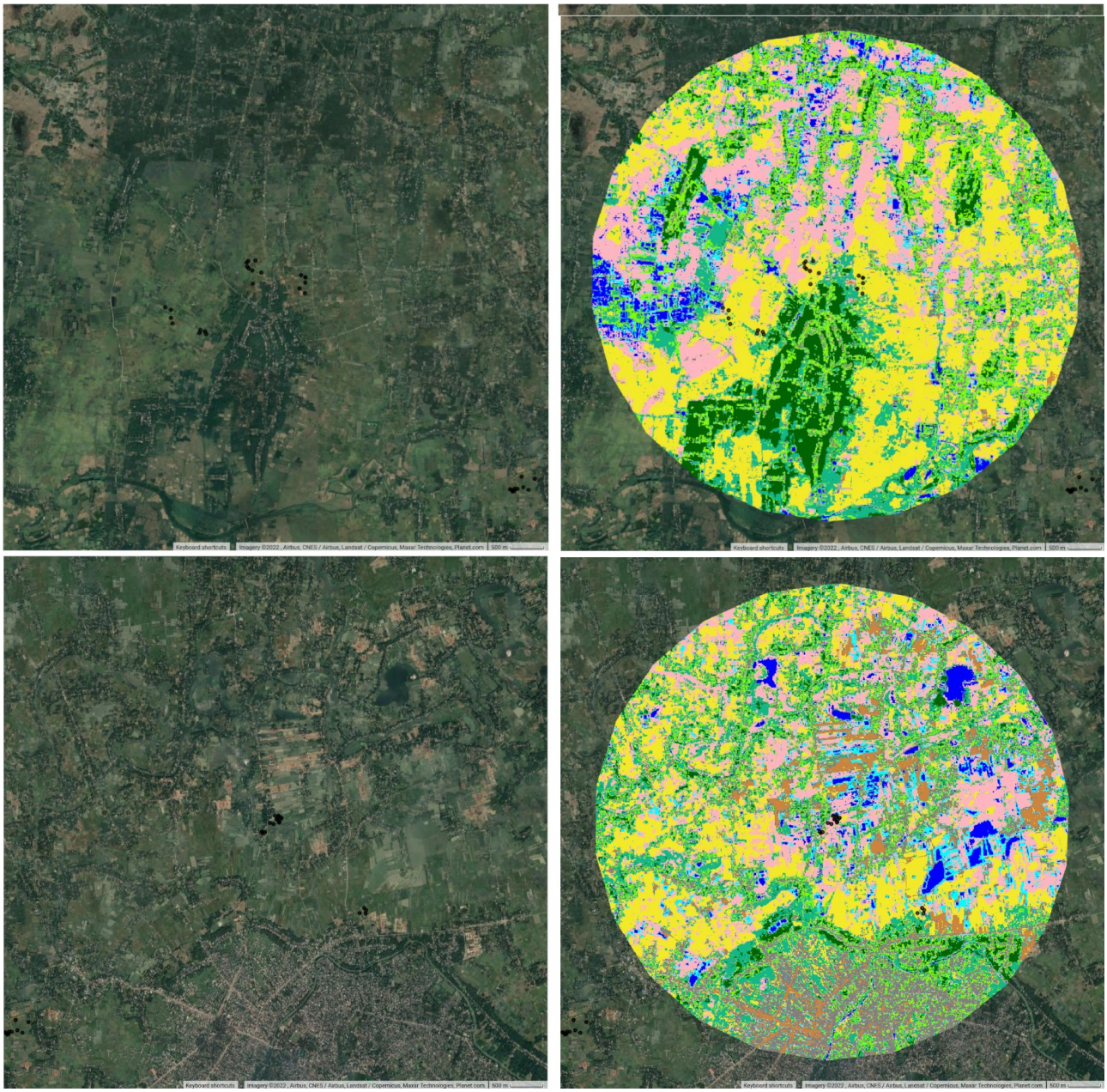


Fig. A2.2 Unclassified (left) and classified (right) maps of the landscape around two sets of sites in Nagaon, Assam. The landscape was classified within a radius of 4km around the centroid of one cluster of sites using a random forest supervised classifier in Google Earth Engine. The centroids are located at 92.57484408776948E, 26.384661404226662N (top) and 92.66009997072625E, 26.38503153230621N (bottom). The landscape was classified into nine landcover types: Forest (or algae), dry rice, wet rice, water, bank, edge, field, bare ground, and urban land. Black dots represent sampling sites. Image source: 2022, Arbus, CNES/Airbus, Landsat/Copernicus, Maxar Technologies, Planet.com.

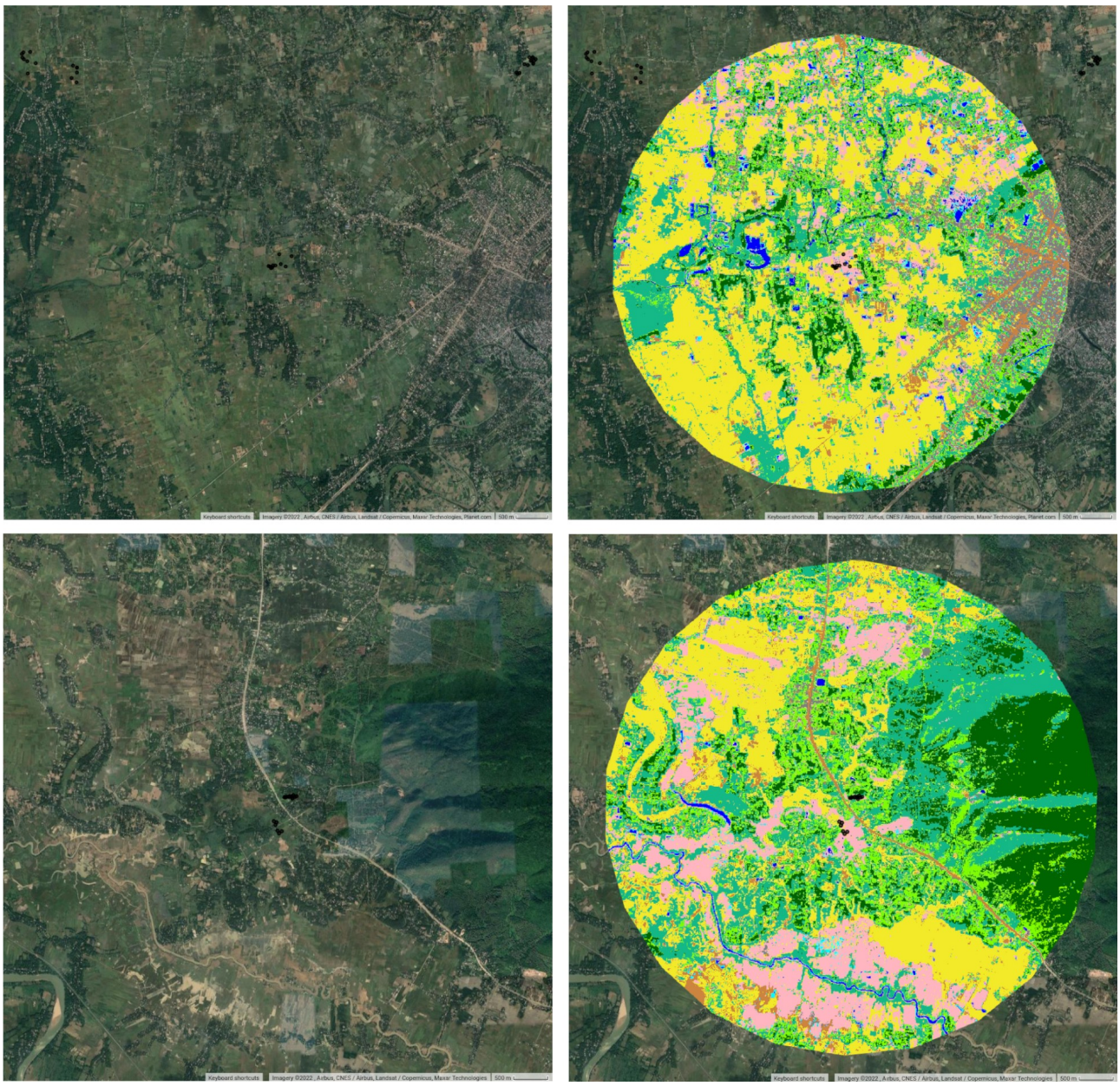
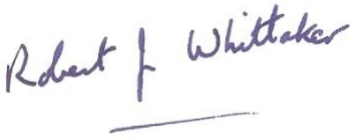


Fig. A2.3 Unclassified (left) and classified (right) maps of the landscape around two sets of sites in Nagaon, Assam. The landscape was classified within a radius of 4km around the centroid of one cluster of sites using a random forest supervised classifier in Google Earth Engine. The centroids are located at 92.61813539786188E, 26.353871760484573N (top) and 92.71898974609746E, 26.173619359566832N (bottom). The landscape was classified into nine landcover types: Forest (or algae), dry rice, wet rice, water, bank, edge, field, bare ground, and urban land. Black dots represent sampling sites. Image source: 2022, Arbus, CNES/Airbus, Landsat/Copernicus, Maxar Technologies, Planet.com.

APPENDIX 3: Authorship statements

Robert James Whittaker: I declare that the manuscripts presented as Chapters 3-5 within this thesis, for which I am a co-author are substantially the work of the first author, Iqbal Singh Bhalla. My role was limited to guidance on project structure, fieldwork practicalities, comments on the drafts of all chapters, and general scientific advice. I therefore consent to the inclusion of this material in Iqbal's thesis.



3 March 2022

Orly Razgour: I declare that the manuscripts presented as Chapters 3-4 within this thesis, for which I am a co-author are substantially the work of the first author, Iqbal Singh Bhalla. My role was limited to advice on bat ecology and behaviour, as well as comments on both drafts. I therefore consent to the inclusion of this material in Iqbal's thesis.

Signed:



Francois Regal: I declare that the manuscripts presented as Chapters 3-4 within this thesis, for which I am a co-author are substantially the work of the first author, Iqbal Singh Bhalla. My role was limited to statistical guidance, comments on the drafts of both

chapters, and small contributions to the code used for the statistical analysis. I therefore consent to the inclusion of this material in Iqbal's thesis.

Dr. François Rigal, the 11th of April, Pau, France

