The Role of Natural Image Statistics in the Evolution of Courtship Signals

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Contribution Statement

Chapter 1 | General Introduction

Marie-Christin Hardenbicker: writing–original draft. **Jutta M Schneider:** writing–review and editing (equal). **Morgan Oberweiser:** writing–review and editing (equal). **Alfonso Esteban Aceves Aparicio:** writing–review and editing (equal).

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Chapter 4 | Signal–Background Contrast in Spectral Slope Modulates Female Attention

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Abstract

Elaborate courtship displays, often characterized by vivid coloration, complex movements, acoustic signals, and/or substrate-borne vibrations, are prevalent across the animal kingdom. Establishing a unifying framework to understand the mechanisms that facilitate the evolution of such exaggerated and seemingly arbitrary traits has challenged evolutionary biologists for decades. While sexual selection pressure on the competing sex is typically strong, selection also acts on the choosy sex to detect, process, and respond to signals efficiently. Outside the framework of *adaptive mate choice*, it has been suggested that mating preferences are based on neurological constraints, and that courtship signals evolve to exploit these pre-existing biases. The so-called “processing bias hypothesis” assumes that sensory systems are tuned to the statistical properties of the natural environment to maximize processing efficiency. Signals that match these properties may be less costly to process and therefore elicit a positive response. Conversely, drawing on signal detection theory, it is just as likely that courtship signals contrasting with background statistics are advantageous, as they can be easily detected, thereby reducing the cognitive costs of mating decisions.

Vividly ornamented Australian peacock jumping spiders (*Maratus* spp.) present an excellent study system to investigate the relevance of these two theories, particularly with regard to the visual modality, as they have excellent vision, setting the stage for the extravagant and extremely diverse visual sexual signals that we find in this genus. In my thesis, I explore how natural image statistics, specifically spectral slope as a measure of spatial frequency distribution, may influence the evolution of visual courtship signals in these spiders with regard to female preference. I use an integrative approach including behavioural experiments, computational techniques, and multispectral imaging to gain insight into how natural image statistics may shape female preferences and signal evolution.

I found that spiders of the species *M. spicatus* show a preference for random noise images that posess the spectral slope of natural scenes, which is in line with psychophysical and computational aesthetics research in humans. However, the colour patterns of *M. spicatus* males exhibit diverging spectral slopes, for which the spiders show no preference. These results suggest that what is determining the spectral slope of *Maratus* patterns is not so much a processing bias towards image statistics of the natural environment, but rather, the need to be conspicuous. This notion is further supported by my second study, in which I compare the spectral slopes of 21 *Maratus* species between the sexes and the natural spectral slope. Male slopes differed significantly from female slopes and the slopes of natural scenes, whereas female slopes matched closely with the natural slope. Not only does this confirm that male slopes contrast with the natural slope, it also suggests that females evolve colour patterns with matching slopes in order to blend in. Conspicuousness as a driver for the evolution of courtship signals is therefore likely causing the divergence from the natural slope in male colour patterns. To learn more about the evolutionary relevance of spectral slope in signal design, I tested whether signal-background contrast in spectral slopes modulates female attention (as a proxy for female preference). The results of this study suggest that courting in front of a background with a spectral slope that differs from the slope of their colour pattern may indeed increase male mating success, as females tracked males longer when they displayed against contrasting compared to matching backgrounds.

Together, these findings indicate that while Maratus spiders exhibit a processing bias for natural image statistics, male visual signals appear to have evolved not to exploit this preference, but to stand out against the visual background. This thesis highlights the nuanced interplay between perceptual adaptation, signal design, and sexual selection, and contributes to a broader understanding of how cognitive and ecological factors shape the evolution of mating signals.

Contents

1

General Introduction

The Evolution of Courtship Signals

In nature, we observe a remarkable diversity of courtship displays featuring vibrant colours, intricate movements, and acoustic or substrate-borne signals, perhaps exemplified best by the astonishing courtship dances of birds of paradise (Scholes, 2008). Beyond birds, extravagant courtship displays have been documented in a variety of taxa. In many frog species, males perform conspicuous vocal and visual signals during courtship (e.g., Ryan & Guerra, 2014; Starnberger et al., 2014; Sullivan & Kwiatkowski, 2007); many spiders exhibit elaborate visual and vibratory displays (e.g., Clark et al., 2002; Elias et al., 2006; Girard et al., 2018; Hebets et al., 2006); and whales produce complex songs to attract mates (Garland & McGregor, 2020; Janik, 2009), to name just a few examples. Understanding how such striking and seemingly arbitrary sexual signals originate and persist has long been a fundamental question in evolutionary biology, yet despite decades of research, the underlying mechanisms driving their evolution remain elusive.

The Origin of Mating Preferences

Through mate choice, sexual selection acts on traits that influence mating success rather than directly enhancing viability, which are instead targeted by natural selection (Andersson, 1994; Darwin, 1871). Within the framework of *adaptive mate choice*, courtship signals function as indicators of signaller quality that may benefit the chooser, either directly, via access to resources or parental care, or indirectly, via heritable advantages contributing to the success of offspring, i.e., *good genes*.

Indicator models suggest that mating preferences for traits correlated with high quality are favoured by selection (Andersson, 1986; Hamilton & Zuk, 1982; Kodric-Brown & Brown, 1984; Milinski & Bakker, 1990; Zahavi, 1977); however, the adaptive nature of preferences has been and continues to be hotly debated (Achorn & Rosenthal, 2020; Patricelli et al., 2019; Prum, 2012).

Echoing Darwin's original concept of females having a "taste for the beautiful,“ a rich body of theory has emerged suggesting that preferences may coevolve through aesthetic selection alone, independently of survival or reproductive fitness outcomes (Mendelson et al., 2025; Renoult & Mendelson, 2019). This idea traces back to Fisher's runaway model, further developed by Lande and Kirkpatrick, who formalised how genetic covariance between female preference and male ornamentation can lead to the exaggeration of secondary sexual traits without requiring a direct link to fitness advantages (Fisher, 1930; Kirkpatrick, 1982; Lande, 1981). The debate about the adaptive nature of mating preferences has been invigorated in recent years by a series of papers on aesthetic evolution (Prum, 2010, 2012) and the widely discussed book "The Evolution of Beauty: How Darwin's Forgotten Theory of Mate Choice Shapes the Animal World - and Us" (Prum, 2017). In his book, Prum lays out his concept of the "Beauty Happens" hypothesis, drawing on the Fisher-Lande-Kirkpatrick model to argue that mating preferences evolve arbitrarily and sexual traits evolve and persist simply because they are attractive.

However, if a preference, random or otherwise, reduces cognitive or energetic costs associated with mate choice, it would still be considered adaptive. Having a preference per se could make an individual more efficient at choosing mates quickly, thereby reducing predation risk, energy expenditure, or lost opportunities to mate. For example, a female with a pre-existing preference for a red spot may more rapidly select mates that match this criterion, reducing cognitive effort, or minimizing time spent exposed during mate choice. Thus, even preferences originally unrelated to survival or reproductive fitness can become adaptive by enhancing processing efficiency.

Detectability as Evolutionary Driver

The idea that mating preferences can be favored when they reduce cognitive or energetic costs fits with another well-established theoretical framework that explains the evolution of conspicuous courtship signals in terms of signal detectability itself. Signal detection theory evaluates decision-making under uncertainty, balancing the costs and benefits associated with correct detections, missed mating opportunities, false alarms (responding to non-signal cues), and correct rejections. When receivers face this trade-off between detecting true signals and avoiding false alarms during mate choice, traits that enhance detectability, regardless of their specific form, are more likely to be selected. A preference for easily detectable signals becomes adaptive because it allows individuals to make faster and more accurate decisions, reducing the costs and risks associated with prolonged mate assessment. Consequently, conspicuous signals may evolve not because they are inherently attractive, but because they facilitate quicker and more accurate recognition of suitable mates in noisy environments, thereby helping receivers make efficient decisions under uncertainty (Wiley, 2006; Wiley, 2013). The evolution of elaborate courtship signals under sexual selection for detectability can therfore be understood as an adaptation to the challenges of reliable signal detection in complex natural environments.

While conspicuousness is mostly discussed in terms of the level of contrast between a signal and its background (e.g., Endler, 1992; Sibeaux et al., 2019) it is also determined by how well a signal transmits through the environment. For instance, in the tropical wandering spider *Cupiennius salei*, male vibratory courtship signals match the resonance properties of plant substrates used by the species, minimizing attenuation and ensuring effective signal transmission in a nocturnal, low-visibility environment (Barth et al., 2002). Similarly, in the jumping spider *Habronattus dossenus*, males signal on substrates that enhance the propagation of their seismic courtship signals, and female receptivity increases with transmission efficacy, indicating that substrate-dependent signal propagation directly affects mating success (Elias et al., 2004). These examples show that conspicuous courtship signals evolve not only through visual or acoustic contrast but also via effective environmental transmission, ensuring reliable mate detection.

Sensory and Processing Bias Hypothesis

For a signal to be effective, it must be adapted not only to environmental conditions but also to how receivers perceive and filter sensory information, therby aligning with the structure and organization of the receiver's sensory system. Consequently, the evolution of sexual signals is constrained or *biased* by sensory system properties (Endler, 1992; Ryan & Cummings, 2013). In T‘ungara frogs, males enhance the attractiveness of their calls by adding a secondary call component that simultaneously stimulates both inner-ear sensory organs in females. Female preference for these complex calls is independent of overall call intensity, suggesting that stimulation of the auditory system can outweigh increased signal efficacy through amplitude alone (Ryan & Rand, 1990).

Responding to the tuning of a receiver's sensory system can enhance signal efficacy, but it can also serve to exploit pre-existing preferences that evolved in non-sexual contexts. Sensory systems are typically shaped by ecological pressures and are often biased toward stimuli that are relevant in contexts such as foraging, potentially resulting in preferences for properties that match food items or prey. Such sensory biases can be co-opted in a sexual context to elicit a positive response or to attract and retain the attention of the choosy sex. In Goodeinae fish, males of several species possess a terminal yellow band (TYB) on their tail fin that resembles the size, colour, and motion of damselfly larvae, eliciting feeding responses in females. In a mating context, females show a preference for males that have conspicuous bands, even in species where males do not express this trait. Interestingly, while TYBs elicit strong feeding responses in females from species lacking the trait, females from species with highly conspicuous TYBs show reduced responses (Garcia & Ramirez, 2005). The results of this study strongly suggest that the preference for the yellow band predates the evolution of the sexual signal, and therefore facilitated its emergence. Moreover, it appears that females may have evolved mechanisms to disentangle feeding and mating responses, as they seem to no longer identify tails with yellow bands as prey items when they are familiar from a sexual context; yet the sexual attractiveness of the TYB persists. Females may adapt by evolving an increased response threshold that reduces maladaptive foraging responses, which in turn would favour more elaborate signals in males that overcome that threshold.

This means that even seemingly arbitrary preferences may reflect adaptive tuning of the perceptual system. Crucially, perceptual biases are not restricted to particular modalities or ecological functions; they can emerge wherever certain patterns are more readily detected, processed, or remembered. As such, perceptual biases can form the initial conditions for the evolution of mating preferences, providing a foundation upon which signal evolution builds. This theoretical perspective provides a compelling explanation for the repeated evolution of certain visual traits such as symmetry, high contrast, or certain textures, which are disproportionately represented in courtship signals across diverse taxa, even when their connection to fitness remains ambiguous (Dawkins & Guilford, 1996; Endler, 1992; Endler & Basolo, 1998).

Processing bias extends the concept of sensory bias by focusing on the energetic and computational efficiency of signal processing. According to efficient coding theory, perceptual systems have evolved to encode environmental information in ways that reduce redundancy and maximize information transfer while minimizing metabolic cost (Barlow, 1961; Field, 1987; Laughlin, 1983; Olshausen & Field, 1996; Simoncelli, 2003). Neural processing is metabolically costly; for example, the human brain alone accounts for about 20% of total energy expenditure. Costs are directly proportional to neural firing rates (Attwell et al., 2001; Laughlin, 1983), so there is strong selective pressure for neural systems to minimize the number of active neurons. The use of *sparse coding* allows encoding information to be represented with minimal redundancy, so that it can be transmitted using only a small number of cells, thereby conserving capacity in subsequent stages of processing (Olshausen & Field, 2004; Simoncelli & Olshausen, 2001). Tuning neurons to relevant features that the sensory system is constantly exposed to can therefore save metabolic energy (Simoncelli & Olshausen, 2001). Since these features are likely those found in natural environments, assuming that efficient coding elicits a positive neural response, a preference for features of the natural environment may arise (Reber et al., 2004; Warrant, 2016; Wehner, 1987; Winkielman et al., 2003). Such preferences evolve as byproducts of neural architecture, however, once established, they may exert directional selection on courtship signals that mirror these efficient-to-process patterns. Processing bias offers a mechanistic explanation for aesthetic preferences: visual features that reduce cognitive or metabolic load may be perceived as more pleasing, and thus become favored in mate choice contexts, even in the absence of an explicit link to genetic or ecological quality (Dibot et al., 2023; Héjja-Brichard et al., 2024; Renoult & Mendelson, 2019). As a result, traits that exploit the efficient coding strategies of the sensory system may be sexually selected for, setting the stage for more elaborate courtship signals shaped by the visual ecology of the perceiver.

Natural Image Statistics

The natural world is characterised by spatial regularities that are remarkably consistent across habitats. These regularities reflect a high degree of redundancy. According to information theory (Shannon & Weaver, 1962), this means that visual input from the natural world can be compressed by summarising redundancies, thus requiring less bandwidth for transmission without loss of information.

Spatial regularities can be described using second—order image statistics, which involve quantifying the correlations between neighbouring pixels. For digital images this is achieved by transforming the image from the spatial domain to the frequency domain using a discrete two-dimensional Fourier transform (2D DFT). Applying this transformation decomposes the image into its individual two-dimensional sinudoisal components, each defined by a particular spatial frequency, phase, and orientation. The 2D DFT is defined as:

$$F(u,v) = \sum_{x=0}^{M-1}\sum_{y=0}^{N-1} f(x,y), e^{-2\pi i\left(\frac{ux}{M}+\frac{vy}{N}\right)} \tag{1.1}$$

where $f(x, y)$ is the intensity at pixel location (x, y), and $F(u, v)$ is the complex coefficient representing the amplitude and phase of the spatial frequency indexed by (u, v). The summation is taken over a discrete grid of size $M \times N$.

The resulting amplitude spectrum $|F(u, v)|$ displays the relative strength of each sinusoidal component in the image. When averaged over orientation, the amplitude at each spatial frequency quantifies how much contrast energy is present at that scale, revealing underlying structure that is not apparent in the spatial domain. The relationship of spatial frequencies and their corresponding amplitudes tends to follow a power-law distribution with low frequencies having high amplitudes and low frequencise having relatively low amplitudes. Hence, when plotted in a log-log plane this relationship is linear. In images of natural terrestrial scenes, amplitude typically falls with spatial frequency at a slope around -1, which I will hereafter refer to as *natural spectral slope* (Field, 1987; Pamplona et al., 2013; Ruderman, 1997; Tolhurst et al., 1992). Notably, this distribution shifts in underwater habitats, where natural images tend to show a steeper average spectral slope of approximately -1.5, probably reflecting differences in the transmission of frequencies through different media (Balboa & Grzywacz, 2003).

In the field of empirical aesthetics, which uses principles from efficient coding and neurobiology to investigate the basis of human aesthetic perception, the natural spectral slope has been proposed to be a general factor determining attractiveness. Although a single mathematical rule for attractiveness remains elusive, empirical work has shown that humans indeed exhibit a preference for a slope of -1 (Spehar et al., 2015). Across history and culture it appears that artists seem to even recreate the natural spectral slope in their paintings independant of content or medium (Graham & Redies, 2010; Redies, Hänisch, et al., 2007; Redies, Hasenstein, & Denzler, 2007). Since the natural slope seems to be prevalent across habitats, the question arises whether other animals exhibit a similar preference, reflecting a universal neurological bias shaped by the spectral slope of the natural world. It is unlikely that real visual systems' spatial filtering works in the same way as a Fourier transform; still, in early stages, visual processing does evaluate the information of different spatial frequencies via receptive fields presumably tuned to the spatial characteristics of the environment (Campbell & Robson, 1968; Godfrey et al., 1987). Such a processing bias/aesthetic sense could be driving the evolution of sexual signals in that they evolve to reflect the natural spectral slope.

It has, however, been well demonstrated that the spectral slope plays a role in the context of camouflage, in that pattern statistics that match those of the background can reduce visibility, and patterns with contrasting spectral slopes are more conspicuous. For instance, cuckoo eggs closely mimic the spectral slope of host eggs, thereby decreasing the likelihood of being detected by the host (Stoddard & Stevens, 2010). Likewise, cuttlefish dynamically adjust their appearance to align with the spectral slope of their substrates when attempting to remain hidden, but shift toward more contrasting slopes when they engage in intraspecific signalling (Barbosa et al., 2008; Zylinski et al., 2011). This is also reflected in sexual signalling in darters. Although male spectral slopes are correlated with those of their natural habitat backgrounds, they are consistently steeper, emphasizing lower spatial frequencies to enhance visibility and salience against a finer-grained background (Hulse et al., 2020). In contrast, female patterns do not show this systematic offset and tend to more closely match background statistics.

Australian Peacock Jumping Spiders

Spiders of the *Maratus* genus are renowned for their vividly ornamented abdominal fans and elaborate courtship dances, rivaling those of birds of paradise in both extravance and diversity (Girard et al., 2021; Otto & Hill, 2021). With over one hundred species currently described, and likely many more awaiting discovery, aptly named peacock spiders present a compelling system to study the evolution of exaggerated sexual signalling. Like all jumping spiders, *Maratus* have acute vision, featuring high spatial resolution and colour sensitivity (Land, 1969), presumably setting the stage for the evolution of males' intricate colour patterns and complex motion displays. During courtship, males raise their brightly coloured abdomens to a 90° angle to present them towards females, typically accompanied by lifting and waving their third pair of legs (see for example *M. vespa* in Figure 1.1). Besides visual signals males also employ vibrational cues while courting the females, making the dispaly even more complex. Previous research on visual courtship in *M. volans* has provided a detailed account of how specific components of the male display influence female choice. Girard et al. (2015, 2018) found that the contrast within colour patterns and the duration of visual displays play a significant role in mating success. To a lesser extent, vibratory effort and display vigour contribute to female choice and associated mating parameters as well. Given that mating rates are only at 25% (in *M.volans*, Girard et al., 2015), it is apparent that extreme selection pressure driven by female choice is responsible for the evolution of these exaggerated displays, making this group particulary interesting for studying the evolutionary interplay between perceptual capacity, preference, and sexual signaling.

Among them, the small *M. spicatus* (body length ~3 mm, Figure 1.2), which belongs to an early diverging clade of small peacock spiders (Girard et al., 2021), stands out for its relatively stationary courtship behaviour. Males raise their

Figure 1.1: A Female *Maratus vespa* abdominal pattern from above and **B** a male of the same species mid-courtship with ophistosoma and third leg pair raised as seen from the female point of view (see **C**). Photos by Jürgen Otto peacockspider.org

colourful abdomen toward the female but do not engage in the dynamic leg-waving or lateral movements typical of many other *Maratus* species, aside from sporadic wiggling of the abdomen and occasional rapid position changes during the display. Compared to other peacock spiders, this display appears less complex and focuses primarily on presenting colourful patterns, making this species particularly suitable for investigating potential drivers of pattern evolution while isolating the visual effects of static pattern properties from those induced by movement or synchronised multimodal cues.

Thesis Aims

Objectives

Given that peacock spiders have a sophisticated visual system (Land, 1969) and consequently rely heavily on visual cues in the context of mate choice (Girard et al., 2015, 2018), it follows that studying how female preferences drive the evolution

Figure 1.2: **A** A Male and female *Maratus spicatus* during courtship. **B** Male raising his abdomen to a vertical position to present his intricate colour pattern towards the female. **C** Close up of male colour pattern. Photo **A** by Jean and Fred Hort, previously released under a Creative Commons Attribution 2.0 Generic license; Photos **B,C** by Jürgen Otto, peacockspider.org

of males' colourful ornaments, requires understanding how the design of these signals is related to visual information processing mechanisms. Second—order image statistics provide an opportunity to study a potential link between neural architecture and visual preference in that visual input resembling the spectral slope of the natural world might elicit a positive reaction, due to an efficient processing experience (i.e., processing bias, Graham & Redies, 2010; Redies, Hänisch, et al., 2007; Spehar et al., 2015). However, second—order image statistics of visual signals have also been identified as a means to enhance detectability, favouring signals that possess spectral slopes contrasting with the slope of the background (Barbosa et al., 2008; Stoddard & Stevens, 2010; Zylinski et al., 2011). The central aim of this thesis is to investigate whether male colour patterns have evolved to exploit a potential processing bias by mirroring the spectral slope of the natural world, or if female preference may be based on increased detectability, achieved by signals reflecting spectral slopes that contrast with the slope of the background.

By applying tools from computational image analysis and visual perception research to a highly visual invertebrate model, this thesis aims to bridge disciplinary boundaries and contribute a novel perspective to the study of animal signalling. Such an approach is particularly timely given growing interest in how the ecological tuning of sensory systems may be linked to preference and aesthetic experience as a framework for understanding the evolution of seemingly arbitrary courtship signals (Mendelson et al., 2025; Renoult & Mendelson, 2019).

Outline

The spectral slope of peacock spider colour patterns. Using multispectral images of male colour patterns mimicking the spectral sensitivities of salticids, I measure the spectral slope of *M. spicatus* (Chapter 2), as well as the colour patterns of other *Maratus* species, in both males and females (Chapter 3). Additionally, I validate the natural spectral slope using images of natural scenes taken with the same multispectral camera, using the same computational methods to ensure comparability (Chapter 3).

Preference for the natural spectral slope. In the first empirical chapter (Chapter 2) I explore whether there is a basis for a potential processing bias for image statistics, by behaviourally testing the general preference of *M. spicatus* for images with particular spectral slopes. Given that male *M. spicatus* spectral slopes diverge from the natural spectral slope , I specifically assess whether individuals of this species prefer visual stimuli that match the spatial statistics of natural scenes or those characteristic of male ornamentation.

Comparison of males, females, and the slope of natural scenes. Chapter 3 provides a comprehensive overview of the spectral slopes measured for 21 different species of *Maratus*. In this chapter, I address the relevance of spectral slope in the context of both mate choice and camouflage by systematically comparing the spectral slopes of male and female colour patterns with those obtained from natural scenes.

Female preference for detectability due to background contrast in spectral slope. For the last empirical chapter of this thesis (Chapter 4), I examine the relevance of the spectral slope of male colour patterns in a mating context with regard to detectability in *M. spicatus*. In a second behavioural experiment, I explore a potential effect of the spectral slope of the background (matching or contrasting the slope of the male colour pattern) on mating preference, using female attention as a proxy.

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2

Peacock Spiders prefer Image Statistics of Average Natural Scenes over those of Male Ornamentation

The origins of preferences that drive the evolution of arbitrary sexual signals have been hotly debated for more 150 years. An emerging but little-tested theory, efficient coding theory, proposes that male visual courtship displays are adapted to pre-existing processing biases shaped by the statistical properties of the natural environment. Natural scenes show strong spatial correlations with average amplitudes of spatial frequencies falling with an average spectral slope of -1, and humans have been shown to prefer random amplitude spectrum images that possess similar slopes. It has been proposed that other animals may also prefer the statistics of their natural environment and that this preference drives the evolution of sexual signalling displays. Here, we measure the spectral slope of the male display pattern of the Australian peacock jumping spider *Maratus spicatus* and test for a general preference towards that slope. We present spiders (male, female and juvenile) with random images of the male slope of -1.7 compared with a) a shallower slope of -1.0 and b) a steeper slope of -2.3. Spiders spent more time oriented towards the shallower slope than towards the male slope, and spent the same amount of time oriented towards the male slope and the steeper slope. Our results indicate that spiders, like humans, prefer the average natural slope of -1, suggesting that this is likely the slope typically found in their natural habitat. Rather than exploiting a potential processing bias it seems that males have evolved slopes that contrast with the visual background to enhance conspicuousness.

2.1 Introduction

Intricate visual courtship displays that are extremely diverse across closely related species can be found in many animal systems. It is a phenomenon that usually occurs when sexual selection pressure is high and male mating success depends to a large extent on being attractive to females (Andersson, 1994; Darwin, 1871). How female preferences originate is still unclear and has been vigorously debated among evolutionary biologists over the years (Endler & Basolo, 1998; Enquist & Arak, 1993; Marler & Ryan, 1997; Payne & Pagel, 2001). In some cases, sexual signals are linked to fitness for survival and tell females about the quality of a potential mate (Griggio et al., 2010; Mcglothlin et al., 2008; Stuart-Fox & Ord, 2004), but in other cases, sexual signals appear arbitrary as they do not convey any direct information about male quality (Fisher, 1930).

One major hypothesis is that such intricate visual signals evolve to maximize detectability, defined by the level of contrast to the background and/or within a colour pattern (Endler, 1992; Endler & Mappes, 2017; Endler et al., 2005; Sibeaux et al., 2019; Wiley, 2013). Signals that stand out in the natural environment should be favoured by evolution because they can be more easily detected by a receiver and therefore should have a greater chance of being chosen in a mating context. This may be the reason why, for example, plumage colouration of lekking birds differs most with the visual background at locations where courtship displays take place (Endler & Thery, 1996). Anolis lizards also seem to make use of contrast in order to get female attention, in that they use sinusoidal frequency components in their head-bobbing display that are not present in the movement of vegetation blowing in the background (Fleishman, 1992). Males of the muscid fly *Lispe cana* increase signal contrast by displaying their bright iridescent faces against dark backgrounds, which positively influences female attention, leading to higher mating success (White et al., 2020). In guppies, however, females do not show any preference for males based on how strongly their sexual signals contrast to the background (Lynn & Cole, 2019). The importance of signal-background contrast also extends to non-visual modalities; for example, birds adapt the amplitude and frequencies of their songs to differ from background noise (Brumm & Todt, 2002; Kirschel et al., 2009).

Another hypothesis that could potentially explain the evolution of arbitrary sexual signals was proposed by Darwin in 1871, although since then it has received very limited consideration. Darwin suggested that arbitrary secondary sexual traits evolve because females choose males based on an aesthetic sense or a "taste for the beautiful." This rather controversial idea has recently been revived by linking it to sensory bias theory, which predicts that female mating preferences are by-products of selection acting on their sensory system outside the context of mate choice, and that males evolve traits that match those sensory system characteristics to either enhance efficacy or to trigger an innate attraction (Basolo & Endler, 1995; Ryan & Guerra, 2014). Guppies, for example, show a context-independent attraction to the colour orange, probably originating in the context of food detection, which is potentially the reason for females preferring males with larger and more chromatic orange spots (Rodd et al., 2002). Efficient coding theory assumes that the visual system is not only adapted to properties like colour and luminance, but is also shaped by characteristics of the environment that are analysed at an earlier stage of visual processing. Visual input is noisy and visual systems can save metabolic energy by encoding it to be represented with minimal redundancy so that information can be transmitted with only a small number of cells using up less capacity in subsequent stages (Barlow, 1961; Field, 1987; Simoncelli, 2003). By matching filters, i.e., arrangements of neurons, circuits and sensory structures, to the characteristics of the environment, visual systems can increase the efficiency of coding sensory input (Warrant, 2016; Wehner, 1987). It has been proposed that signals that match the characteristics of the environment that the visual system is tuned to elicit some kind of positive neuronal response because they are less costly to process, which one could describe as an aesthetic experience (Prum, 2017; Renoult & Mendelson, 2019).

Natural scenes are not random and show great similarities in their spatial characteristics. Fourier amplitude spectra reveal statistical dependencies, with low spatial frequencies having high amplitudes and high frequencies having relatively low amplitudes. Plotted in a log-log plane, amplitudes averaged across each spatial frequency f fall linearly with $1/f$, typically with a slope around -1 in terrestrial habitats, with normally distributed slopes ranging from -1.6 to -0.7 (Balboa & Grzywacz, 2003; Burton & Moorhead, 1987; Field, 1987; Párraga & Tolhurst, 2000; Tolhurst et al., 1992; van der Schaaf & van Hateren, 1996; Pamplona et al., 2013, hereafter called the *spectral slope*). It is unlikely that real visual systems' spatial filtering works in the same way as a Fourier transform; still, in early stages, visual processing does evaluate the information of different spatial frequencies via receptive fields presumably tuned to the spatial characteristics of the environment (Campbell & Robson, 1968; Godfrey et al., 1987). Male sexual traits could exploit a potential processing bias/aesthetic sense to be more appealing to females by evolving similar image statistics to the environment.

The influence of image statistics on visual preferences has yet only been assessed in humans. Studies found spectral slopes of natural scenes to be similar to those of paintings both realistic and abstract (including non-natural scenes) from different artists, countries, and centuries, and across different media like drawings, paintings and engravings (Graham & Redies, 2010; Redies, Hänisch, et al., 2007; Redies, Hasenstein, & Denzler, 2007). It was suggested that artists have implicit knowledge of image statistics and prefer those of natural scenes, and hence unconsciously attempt to copy them in their artwork. Consistent with these findings, it has been shown that humans prefer random images with a $1/f$ amplitude spectrum that reflect the average spectral slope of natural scenes and that this preference is correlated with the ability to detect changes in spectral slopes in an "odd-one-out" task (Spehar et al., 2015).

In an attempt to find evidence for a possible effect of an aesthetic sense on the evolution of courtship signals, Hulse et al. (2020) analysed different darter species for the spectral slopes of their displays and compared them with the slopes of their respective underwater habitats. Spectral slopes from underwater images are steeper than those from atmospheric images and also seem to show more variation (Balboa & Grzywacz, 2003). Hulse et al. (2020) found a correlation between the spectral slopes of male pattern and underwater habitat, which was absent for females, and concluded that male spectral slopes evolved in response to female preference for the spatial statistics of their natural habitats. However, male darter slopes did not actually match the slopes of their respective habitats but were always steeper (with an average difference of 0.4), which in fact appears to contradict the theory of males copying the spectral slope of the environment to be more attractive. One could argue, however, that the correlation found is suggestive that pattern biases in darters may play a role in driving the evolution of sexual signals, but that this is counterbalanced by selection for detectability. In other words, male slopes might evolve to be just distant enough from the habitat slope to stand out from the background, but not so distant that they are completely dissimilar.

In this study, we use the Australian peacock jumping spider *Maratus spicatus* to test for a general preference for the spectral slope of the male display as a result of a potential underlying processing bias. This is the first study to experimentally test for a general preference for image statistics in another animal than humans. Peacock jumping spiders of the *Maratus* genus present an ideal study system to address such a question. Males have distinctively patterned abdomens, which they lift up and display towards the female during courtship (Girard et al., 2021), and previous work on courtship success in *M. volans* has shown that mating rates are very low (25%), suggesting that those patterns are highly shaped by sexual selection (Girard et al., 2015). Like most salticids, peacock spiders are cursorial hunters and have an acute visual system which likely evolved as an adaptation to stalking prey and presumably set the stage for the evolution of complex visual displays. To date, there are over 90 described *Maratus* species with males varying greatly in their ornamentation and courtship dances (Girard et al., 2021; Otto & Hill, 2021). Such great diversity in seemingly arbitrary sexual signals makes it interesting to study the origins of the female preferences that facilitated the evolution of these signals. In *M. volans*, it has already been shown that display effort, vibratory songs (Girard et al., 2015) and within-pattern contrast (Girard et al., 2018) predict mating success, but what the underlying mechanisms are that led to female preferences have not been investigated yet. *M. spicatus* belongs to an early diverging clade of small peacock spiders and, unlike most species of the *Maratus* genus, when *M. spicatus* raises its abdomen, it does not lift up the third pair of legs, showing an untypically stationary courtship routine, apart from sporadic wiggling of the abdomen (Girard et al., 2021). This makes *M. spicatus* an ideal species to study visual signals independently from motion-induced attention of the female. In our experiment, we present spiders with random $1/f$ amplitude spectrum image stimuli that possess the spectral slope of the male courtship display next to a) a random image with a shallower slope or b) a random image with a steeper slope, and quantify the time they spend oriented towards the image stimuli as a measure of preference.

2.2 Methods

2.2.1 Study Subjects

All *M. spicatus* used in this study were hatched and raised in the laboratory. Spiders were housed individually in plastic containers (juveniles: 10 cm × 6 cm × 3.5 cm, adults: 14.5 cm × 11 cm × 7 cm) with plastic mesh-covered cut-outs to allow airflow. Each box contained a folded paper towel on the ground, some accordion-shaped black paper, and wood wool to provide structure. Boxes of adult spiders were separated by opaque barriers to prevent them from seeing each other. Room conditions were kept at 25°C and 55% humidity on a natural 14:10 light:dark cycle. Spiders were fed a diet of *Drosophila melanogaster* twice a week, and the containers were sprayed with water six days a week.

We tested 56 individuals, aged between 84 and 197 days, in each of the two paired treatments (1st trial: 40 juveniles, 2 males, and 14 females; 2nd trial: 31 juveniles, 6 males, and 19 females; some individuals matured between trials). Juveniles had molted at least three times to ensure that the visual system was fully developed (age was also included in the statistical model as a covariate). In other jumping spider species, the visual system develops at an early stage, and juveniles have high visual acuity even at a young age (Blest et al., 1988; Goté et al., 2019). Since in *M. spicatus* the number of molts until maturity varies and some individuals mature after only four molts (MCH, personal observation), we can safely assume that the visual system is well developed after the third molt.

2.2.2 Spectral Slope of the Male Courtship Display

Prior to the experiment, we analysed the male courtship display of *M. spicatus* for its spectral slope. We photographed abdomens of six freshly killed males (by overanesthesia with CO_2) with a multispectral camera containing three bird-based optical filters (U, M and L) previously described in (Tedore & Nilsson, 2019) and two additional filters previously described in (Glenszczyk et al., 2021). By taking a weighted sum of these pre-existing camera filters, we calculated computational filters to generate new spectral sensitivities matching the spectral sensitivity of the salticid green receptor, which typically peaks around 530 nm (Blest et al., 1981; De Voe, 1975; Glenszczyk et al., 2021; Yamashita & Tateda, 1976; Zurek et al., 2015). We assume this photoreceptor class to be responsible for achromatic vision since it is the most densely-packed photoreceptor class in the salticid retina (For fits of computational sensitivity curves, see Supplementary Data Figure S1; the computational filter technique is further described in Tedore and Nilsson (2021) and Glenszczyk Glenszczyk et al. (2021)).

For photography, the abdomen was detached from the prosoma of the spider and mounted vertically (as it would be positioned during the male courtship display) using insect pins in front of a 20% reflective 2-inch fluorilon grey standard (Avian Technologies, New London, NH, USA), which reflects light evenly across the UV-VIS spectrum. Surrounding horizontal surfaces were covered with an undyed brown paper whose reflectance spectrum is similar to that of leaf litter. Five specimens were illuminated by natural skylight with varying levels of cloud cover and one specimen was photographed under a xenon light source filtered to simulate the natural outdoor spectrum (XE-140BF, Seric Ltd., Tokyo, Japan; for absolute irradiance spectrum see Supplementary Data Figure S2). Since *M. spicatus* males are very small (~3 mm), extension tubes needed to be added between the 60 mm lens and the filter wheel of the camera such that the abdomen filled a large part of the frame (Kenko Extension Tube Set DG, Kenko Tokina Co., Ltd., Tokyo, Japan).

Photos were edited by subtracting dark noise from all pixels; this was calculated from several columns of pixels on the camera sensor that receive no light. Exposures were set to minimise the number of over- and under-exposed pixels; however, a few isolated pixels in the black portions of the colour pattern were generally underexposed. In the computational filter images, these pixels had had their values recalculated as the mean of surrounding adjacent pixels. To simulate adaptation of the eye to the intensity of the illuminant, we normalised each pixel value of the computational images by the mean pixel value of the grey standard in each image. Pixel values P were then converted to non-linear receptor excitation values E following (Naka & Rushton, 1966):

$$E = \frac{P}{P+1} \tag{2.1}$$

For the calculation of the spectral slope, we cropped out the largest square that would fit inside the male abdomen in every image using a custom MATLAB script (mean crop size: 398 px ± SD: 80.07 px) and transformed the images from the space domain to the frequency domain using a two-dimensional fast Fourier transform. To avoid artificial edge effects in the process of the analysis, each cropped image was windowed by a cosine taper with a spatial frequency of four, tapered out to the mean pixel value of the image. We obtained the spectral slope for each individual by estimating the slope of a best fitted line (by least squares method) to the rotationally averaged amplitudes across spatial frequency plotted in a log-log plane. To calculate the slope, we only included frequencies 5 to the dimension of each cropped image divided by 10 to avoid aliasing. Since higher frequencies are given more weight due to a log-scaled x-axis, we averaged frequencies used for calculating the slope in nine evenly spaced bins. The general slope for the *M. spicatus* male colour pattern was then calculated by taking the mean of all six individuals' spectral slopes, resulting in a mean slope of -1.7 (± SD: 0.1; different illumination methods did not affect the mean spectral slope).

2.2.3 Display Distance

The optimal focus distance of *M. spicatus* is not known. To estimate at which distance to place image stimuli so that the spiders see them in focus, we measured the average distance at which males start displaying towards females during courtship (since peacock spiders start courtship at a further distance and then gradually move closer to the female, this usually equals maximum display distance (MCH, personal observation, Girard & Endler, 2014; Girard et al., 2011). We assume objects at this distance to be in good focus, since it is unlikely that males would recognise the female and invest energy in a visual display when they cannot see each other clearly. In *M. spicatus*, males increase non-stationary elements of the display, i.e., wiggling of the abdomen, the closer they move towards the female (MCH, personal observation). At further distances, the visual display mostly consists of presenting the ornamented abdomen to the female in a stationary manner, which means at that stage the spectral slope probably has the highest impact on female preference.

We analysed videos of mating experiments for the distance at which males first lifted their abdomen towards the female. In these experiments, a virgin *M. spicatus* male and female were transferred from their home boxes to a circular arena consisting of a 10 cm high transparent plastic tube with a 15 cm diameter. For the ground of the arena, polyamide stockings with a thread density of 20 denier were drawn and fixed taut over a circular wood frame at a tension of approximately 0.5 N at 1 cm distance to allow vibratory signalling. To simulate the natural outdoor spectrum, the experimental setup was illuminated by the xenon light source described in the Spectral slope of the male courtship display section, and the temperature was kept at 30°C by placing a heating plate under the experimental arena. After each trial, we cleaned the polyamide surface with 70% ethanol to remove possible chemical cues. The spider's behaviour was filmed with an iPhone SE 2nd generation (4K resolution, 60 frames per second). When the male lifted his abdomen for the first time, we took a screenshot and measured the distance between the vertical abdomen and the principal eyes of the female using ImageJ.

2.2.4 Experimental Design

In each trial, a spider was presented with a pair of random images, one of them always representing the spectral slope of the courtship display of *M. spicatus* males (-1.7) and the other representing either a shallower slope of -1.0 or a steeper slope of -2.3. Every spider was tested with both combinations at intervals of 7 days (± 1 day), and the amount of time the spiders looked at each image was recorded.

Each trial was conducted in one of two identical arenas, consisting of a tube made from 3 mm quartz glass (transparent to UV) with an inner diameter of 60 mm and height of 50 mm. The two image stimuli were attached to the outside of this tube, each covering one half of the circular walls. For the test, a spider was placed into a smaller 1 mm quartz glass tube with an 8 mm inner diameter and 50 mm height in the centre of the arena (Figure 2.1A). This way the spider was able to see the images but could not move towards them, so the viewing distance between the spider and the stimuli was always 2.7 cm. We based this decision on the distance at which males usually start displaying towards the female during courtship (see Display Distance Section; Mean: 26.69 mm ± SD: 3.73 mm, $N = 15$). To prevent spiders from climbing the walls, the inner surface of the glass tube that kept the spider in place was coated with nano coating (CleanglaS, Unterschleissheim, Germany). The setup was lit by two UV and one visible LED light strips (realUV 365 nm and 395 nm and ABSOLUTE SERIES 6500K, Waveform Lighting, Vancouver, WA, USA) simulating the natural outdoor spectrum (for irradiance spectrum see Supplementary Data Figure S3). LED strips were attached to a removable 3D-printed framework placed on top of the outer glass tube with the lights tilted towards the inside so the image stimuli were illuminated evenly. During the experiments, all other light sources were switched off and the windows were covered with blackout shades so that illumination of the arenas was consistent for all trials. To minimise vibrations, the floor of the arena consisted of grey-painted granite which was kept at a temperature of 29°C with a heating plate. Together with the heat coming from the LED lights, this resulted in a constant temperature of 30°C inside the arena. The spider's behaviour was filmed from above with an iPhone SE 2nd generation (HD resolution, 30 frames per second) for 30 min (for a photo of the complete setup, see Figure 2.1C). After each trial, the floor and the inside of the inner tube were cleaned with 70% ethanol to remove possible chemical cues.

Video analysis was performed with BORIS software (Friard & Gamba, 2016). We scored the viewing direction (left image, right image) by following the direction of a bright stripe naturally occurring on top of the prosoma: a) when the spider was on the ground (at least six legs touching the ground) and b) when the spider was scrambling (at least three legs touching the walls of the tube). If it was not clear which direction the spider was looking, the time was categorised as "undecided" and excluded from the analysis. In order to standardise the way this was scored, a line was drawn on each side of the spider starting at the back end of the bright stripe on the prosoma, along the lateral edges of the secondary eyes, by holding a straight edge up to the computer screen. This gave a viewing angle of roughly 30° (dotted lines, Figure 2.1B), which is similar to the field of view of the principal eyes when typical retinal movements are considered (Land, 1969). If both images were in this arbitrarily defined field of view, we could not be sure which image the spider was looking at, so it was excluded from the analysis (the actual field of view of *M. spicatus* is not known).To further reduce any potential biases by the individual scoring the videos, 29 out of 112 videos were analysed blindly by a second observer. In order to synchronise the scoring, 5 videos were analysed by both observers to match the way each behaviour was scored prior to further analyses.

Several experimental parameters were randomised to avoid spurious effects. These included the order in which the two different combinations of spectral slopes were presented to a spider in the two trials, the side the different spectral slopes were attached to (left or right), and the arena the trial was conducted in. We generated two different random images of each spectral slope, which were also randomised for all trials.

2.2.5 Image Stimuli

Image stimuli with specific spectral slopes were generated in Matlab (2020) first performing a Fourier transform (using the `fft2` function) on a random noise pattern (matrix of uniformly distributed floating point random numbers between 0 and 1

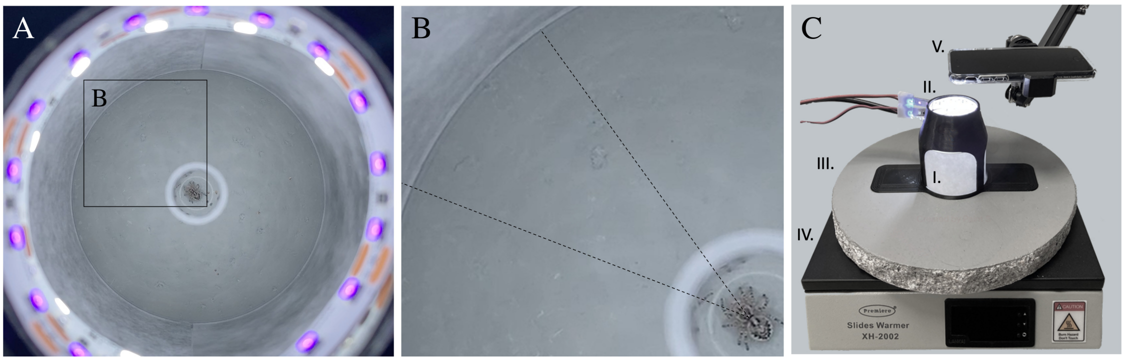

Figure 2.1: Experimental setup. **A** Experimental arena viewed from above: Two image stimuli are attached to the left and right outside walls of a quartz glass tube, respectively. Another smaller quartz glass tube in the center of the outside tube keeps the spider that is to be tested in place. On top on the arena, three LED strips (365 nm, 395 nm and visible light) are fixed to a removable framework (see **CII.**). **C** Dotted lines indicate the arbitrarily-defined viewing angle starting at the back on the spiders prosoma along the lateral edges of the secondary eyes. **C** Complete setup: **I.** Experimental arena, **II.** removable framework holding LED strips, **III.** piece of granite painted with gray paint, **IV.** heating plate, **V.** iPhone SE 2nd generation.

using the `rand` function). The resulting coefficient matrix was then adjusted by multiplying the amplitude of each frequency f by $g(f)$, which is defined as:

$$g(f) = e^{\alpha \log(f+1)} \tag{2.2}$$

Where α denotes the desired spectral slope. By doing an inverse Fourier transform on manipulated coefficient matrices, we created three random greyscale images with spectral slopes of $\alpha = -1.0$, $\alpha = -1.7$ and $\alpha = -2.4$ (Figure 2.1 B-D).

From these images, we produced digitally-made chromogenic prints (LightJet print on Ilford Baryta paper; WhiteWall Media GmbH, Frechen, Germany). Prior to printing, we generated a linearisation curve to accommodate the non-linearity of the printing process. To accomplish this, we measured the reflectance of printed greys having RGB values of 0 to 255 in increments of 5. For measurement, printed greys were illuminated by a xenon light source (PX-2) channelled through a solarisation-resistant fibre optic cable oriented at $45\circ$ relative to the surface normal. Reflectance was measured relative to a PTFE diffuse white standard (WS-1) using a solarisation-resistant fibre optic cable oriented normal to the surface being measured. This fibre channelled reflected light into a spectrometer (QE Pro; all sourced from Ocean Optics, Ostfildern, Germany). Total reflectance integrated from 300–700 nm was calculated. After normalising each integrated reflectance measurement by that of the brightest grey (RGB = 255), we fitted a two-term exponential model to integrated reflectance values and extracted the coefficients a, b, c and d. New RGB values P for each pixel value p (0–255) were then calculated by:

$$P(p) = a^b p + c^d p \tag{2.3}$$

where p is the original pixel value. To maintain the full range of greys, the new pixel values in the images were then rescaled from 0 to 255.

To avoid any modifications of greys due to recalculation of pixel values during the printing process, we fitted the size of the images exactly to the specifications of the photo development company, which worked with a resolution of 300 pixels per inch, resulting in 127 mm × 127 mm images with 1500 px × 1500 px. From each image, we cut two 50 mm × 103 mm pieces to fit exactly half of the circular walls of the arena. Beforehand, we measured the mean RGB value of each piece prior to linearisation to make sure all images had the same brightness (Mean: 136.13 ± SD: 5.97).

As a final control, we photographed a vertically oriented 36 mm × 36 mm part of each image stimulus with the multispectral camera. To include a potential effect of bending the image stimuli when attaching them to the circular arena, we bent the images to the same degree as they would be bent during the experiment. The images were illuminated by the same xenon light source described under Methods:Spectral slope of the male courtship display, with the light directed towards the image at 30○ relative to the surface normal of the image (for absolute irradiance spectrum see Supplementary Data Figure S3). We developed the images using a computational filter mimicking the salticid green photoreceptor, following the same methodology we used for developing multispectral images of the males' abdomens. We then analysed those photos for their spectral slopes (following the same methods described above for male colour pattern) to confirm that they corresponded to the slopes of the original generated images prior to printing (for results see Figure 2.1 F-G). The images mimicking the male slope and the shallower slope conformed to the target slopes of -1.7 and -1.0, whereas the steeper slope deviated slightly from the target slope of -2.4 (actual value of -2.3).

2.2.6 Statistical Analysis

We only analysed the time spiders were on the ground looking at one of the images, i.e., when at least six legs were touching the ground and only one of the images was in the estimated field of view. The time they spent scrambling or crawling up the walls was excluded from the analysis, since it was not clear whether the spider was looking at the image stimuli, and we assumed that scrambling and climbing

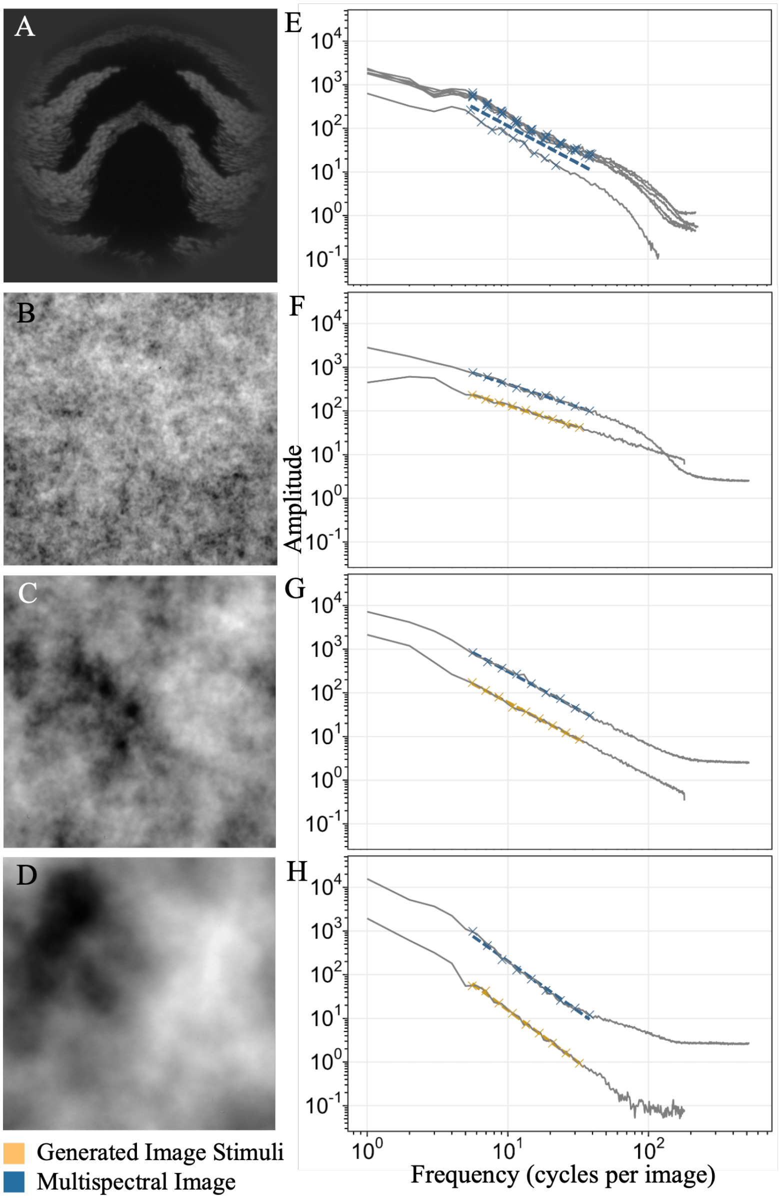

Figure 2.2: Spectral slopes of male display and random image stimuli. Green photoreceptor receptor excitation image of a male *M. spicatus* abdomen with a cosine tapered window **A** and generated random noise image stimuli (before linearisation and printing) with expected spectral slopes of **B** −1.0, **C** −1.7 and **D** −2.4. **E** Rotationally averaged amplitude spectra of six different abdomens (grey lines). Frequencies five to the highest frequency divided by ten were averaged in nine evenly spaced bins (blue crosses) and the spectral slope of each individual was calculated by linear regression. The blue dashed line represents the mean spectral slope of −1.7 (y-intercept was shifted down slightly for viewing purposes). **F**, **G**, **H** Comparison of rotationally averaged amplitude spectra of generated random image stimuli before printing and green photoreceptor receptor excitation images after printing photographed while bent into the cylindrical shape of the experimental arena (grey lines) with binned frequencies between 5 and dimensions of the image divided by 10 represented by yellow crosses and blue crosses, respectively. Spectral slopes were calculated by linear regression (shown in corresponding colours). Slopes: **F** −1.0 (yellow), −1.0 (blue); **G** −1.7 (yellow), −1.7 (blue); **H** −2.4 (yellow), −2.3 (blue).

behaviour was rather motivated by an urge to escape the arena than a particular interest in the image on the side the spider was oriented towards.

First, we tested for an influence of the spectral slope on the time the spiders were looking at the left or right image stimuli in each of the two treatments separately. In a GLMM model with binomial error structure, we combined the observed time spiders spent oriented towards the left vs the right image stimulus as a binomial proportion for the response variable, using the `cbind` function: `glmer(formula = cbind(left, right) ~ other variables, family = binomial)` As a fixed effect, we fitted the spectral slope of the image stimulus on the left side of the arena (same results would be obtained by fitting the image stimulus on the right side). Other fixed effects included maturity/sex (juvenile (sex unknown)/female/male), and, since we tested all individuals in both treatments, we included order of testing (first/second). Spider age was included as a continuous covariate. To correct for overdispersion, we fitted trial ID as an observation-level random effect. All other random factors, including the arena the experiment was conducted in (two levels), the version of the image stimuli representing the male spectral slope (two levels), and the version of the image stimuli representing a higher/lower slope (two levels), were dropped because the random effect variance was estimated as zero or very near zero, causing a singular fit of the model.

To account for possible effects of repeated measures, we fitted an additional GLMM with the same error structure and dependent variable for all data, including spider ID (56 levels) as a random effect. We fitted treatment (1st treatment: male slope (-1.7) vs shallower slope (-1.0); 2nd treatment: male slope (-1.7) vs steeper slope (-2.4)) and spectral slope of the image stimulus on the left side of the arena as the interacting fixed effects to test for a difference in the effect of spectral slope in the two treatments. Sex/maturity, age, and trial order were included as additional fixed effects. Besides spider ID, random effects included arena, the version of the image stimuli representing the male spectral slope, and trial ID as an observation-level random effect. The version of the image stimuli representing a higher/lower slope as a random effect was dropped due to variance estimated very near zero.

All statistical analyses were conducted in R version 3.6.2 (R Core Team, 2019).

2.3 Results

Printed image stimuli slopes matched their target slopes quite well, with only the -2.4 target slope being slightly off with an actual value of -2.3. Henceforth, the -2.4 target slope will be referred to as -2.3, since that is the slope that was in fact tested.

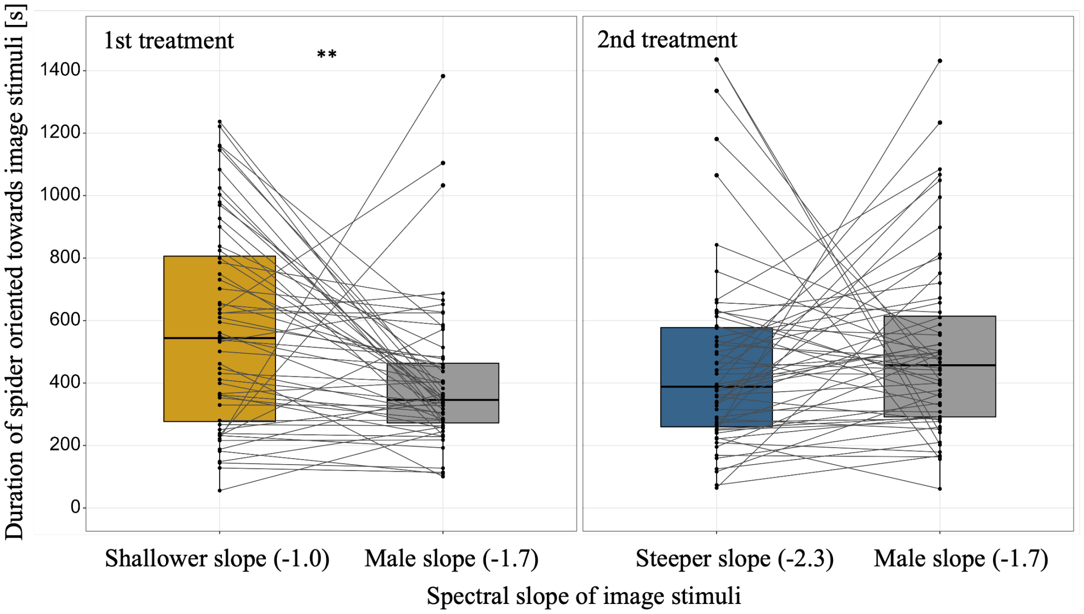

Figure 2.3: Observed duration spiders looked at the two image stimuli that were presented to them in two different treatments. Datapoints from the same trial are connected by grey lines.

We found no evidence that the spiders preferred the male spectral slope of -1.7 over a shallower slope of -1.0 or a steeper slope of -2.3, but we found strong evidence that they exhibited a preference for the average natural slope of -1.0 when compared to the male slope.

In the first treatment, when presented with one random image having the male slope next to another one with the average natural slope, the spiders spent more time oriented towards the natural slope (Chi-square: $\chi^2 = 8.664$, $df = 1$, $P = 0.003$; see Figure 2.3, left panel). In the second treatment, in which spiders were presented with a random image with the male slope next to a random image representing a steeper slope of -2.3, there was no difference in the time spiders spent oriented towards the two image stimuli (Chi-square: $\chi^2 = 1.236$, $df = 1$, $P = 0.266$; see Figure 2.3, right panel). Maturity/sex, age, and the order in which the spiders were tested in the two treatments did not have an effect in either of the treatments (Table 2.1). When analysing all data from both treatments, accounting for repeated measures, we found a significant interaction between treatment and spectral slope (Chi-square: $\chi^2 = 6.185$, df $= 1$, $P = 0.013$), which confirms that there is a difference in the amount of time the spiders looked at the two image stimuli between the two treatments.

Table 2.1: GLMM results for the amount of time spiders spent oriented towards the image stimuli on the left and right side of the arena.

Source	*df*	χ^2	*P* value
1st treatment			
male vs. shallower spectral slope			
sex/maturity	2	3.417	0.181
trial order	1	0.567	0.452
age	1	3.291	0.697
spectral slope	1	8.664	**0.003**
2nd treatment			
male vs. steeper spectral slope			
trial order	1	0.001	0.975
sex/maturity	2	0.332	0.847
age	1	0.149	0.7
spectral slope	1	1.236	0.266
both treatments			
treatment × spectral slope	1	6.185	**0.013**
sex/maturity	2	1.697	0.428
trial order	1	0.594	0.441
age	1	1.319	0.251

2.4 Discussion

We did not find evidence that spiders prefer the spectral slope of male displays, suggesting that *M. spicatus* males do not evolve visual sexual signals adapted to a general female preference for particular spectral slopes. However, spiders did spend significantly more time oriented toward the shallower slope of -1.0, which is the slope that is typical for natural scenes and that humans prefer as well. Spiders did not show a preference when presented with the male slope (-1.7) and a steeper slope (-2.3), suggesting that their peak preference is or is at least very close to the average natural slope of -1. This is the first study that provides evidence that there is a general preference for the image statistics of natural scenes in a different species other than humans. That such distantly related species show the same preference suggests that such a preference could potentially be prevalent across the animal kingdom. However, our results do not confirm that such preferences drive the evolution of visual sexual traits (as suggested by Hulse et al., 2020; Renoult, 2016; Renoult & Mendelson, 2019), but rather contribute to the large body of literature on sexual selection favouring signals that contrast with the environment (Brumm & Todt, 2002; Clark et al., 2011; Endler & Thery, 1996; Fleishman, 1992; Kirschel et al., 2009).

All spiders used in this experiment were lab-reared and had never experienced the image statistics of their natural environment. Man-made objects/indoor environments, which is what the spiders were exposed to, strongly deviate from the average natural slope of -1 (Redies, Hänisch, et al., 2007). The preference for the spectral slope of -1.0 that we observed in our experiment must therefore be an innate one, which we cannot safely assume for humans, since all humans that have been tested must have experienced time outside in nature and could have learned to prefer the natural slope due to its association with other rewarding aspects of spending time in nature (e.g., Spehar et al., 2015; Viengkham & Spehar, 2018).

Aside from having an innate preference for the image statistics of the natural habitat that is based on a positive response due to efficient coding, spiders may have spent more time oriented towards the image stimuli with the slope of -1.0 because it reflects or is closer to the slope of the natural surroundings that they are adapted to and are therefore beneficial for them to be in. We do not know what the spatial statistics are that describe the natural environment of *M. spicatus*. Yet, if we assume that animals prefer the spatial statistics of their respective habitat, our results suggest that the spectral slope of *M. spicatus*' natural environment is close to the preferred slope of -1.0 from our experiment. This would be consistent with the findings of other studies analysing images of natural terrestrial environments (e.g., Balboa & Grzywacz, 2003; Field, 1987; van der Schaaf & van Hateren, 1996). The only study so far that has tested for differences in slopes across different habitats is (Hulse et al., 2020). They found differences in five underwater darter habitats with averaged slopes ranging from -1.5 to -0.9, with an average slope across all darter habitats of -1.2, which was very close to the average natural slope typical for underwater images of -1.3 found by (Balboa & Grzywacz, 2003). Differences among terrestrial habitats have not been tested, so we do not know if there is variation in the slopes of different *Maratus* habitats and if habitat slopes are potentially different to the typical slope of -1. However, slopes of terrestrial images have previously been found to be normally distributed between -1.6 and

−0.7 (Field, 1987; Párraga & Tolhurst, 2000; Tolhurst et al., 1992). At −1.7, the slope of the male *M. spicatus* courtship display is outside of that range, making it rather unlikely that this is the slope found in the spiders' habitat.

With hindsight, it is perhaps not surprising that visibility should play a greater role than processing biases in driving jumping spider colour pattern evolution. Peacock jumping spiders in particular are tiny animals (~2–6 mm) living in a cluttered environment (mostly leaf litter and grass plants) where visibility is limited and a major part of courtship success depends on being detected by females, especially when females are camouflaged and hard to find. When a female sees a male, it usually triggers a reaction or movement, which makes it easier for the male to detect the female. Also, during courtship, females appear easily distracted, and males constantly need to recapture their attention, which they usually do by vibrating (Girard et al., 2015; Girard et al., 2011). In *M. spicatus*, vibrating is not as prominent as in other species; instead, they seem to rely more on a stationary display and fast movements like wiggling the abdomen in later stages of the courtship dance (personal observation). For this reason, having a colour pattern that stands out in front of the background may be particularly important for males of this species. In other jumping spiders, it has already been shown that males are more likely to succeed when they attract female attention first (Clark & Uetz, 1992), and detectability due to background contrast has been shown to be selected for in other traits that describe visual sexual signals such as colour or luminance (Brumm & Todt, 2002; Clark et al., 2011; Endler & Thery, 1996; Fleishman, 1992; Kirschel et al., 2009; White et al., 2020). Spectral slope is likely yet another, less commonly studied factor contributing to selection pressure for conspicuousness in visual sexual signals.

Previous studies have shown that adapting the amplitudes of different spatial frequencies to the background can help animals avoid being detected, suggesting that the contrast in spectral slope to the slope of the natural background can be used as a measure of camouflage (Barbosa et al., 2008; Stoddard & Stevens, 2010). Matching the slope of the background can be expected to reduce detectability, whereas differing slopes would enhance it. This seems to be true, for example, in cuttlefish. Spectral slopes of camouflaged individuals closely resemble those of their background, whereas signalling individuals have slopes that differ from the background, presumably contributing to the desired conspicuousness during this state (Zylinski et al., 2011). Comparing stripes of zebras and tigers, Godfrey et al. (1987) found that in higher frequency bands, tiger stripes cannot be detected in front of their natural background, whereas zebra stripes are quite conspicuous. In tigers, spatial frequencies in all bands are present to the same extent as in the background, whereas amplitudes of spatial frequencies of zebra stripes diverge from the background in higher frequency bands, rendering zebras more conspicuous. These results are consistent with the literature showing that tiger stripes evolved for camouflage (Ortolani, 1999), whereas zebras evolved stripes to confuse and disorientate biting flies, which means they need to be visible (Caro et al., 2014, 2019). How being conspicuous relates to aposematism has been extensively studied in arthropods with regards to colour and luminance (e.g., Arenas et al., 2014; Briolat et al., 2018; Prudic et al., 2007), but a potential relationship with the spectral slope of a pattern has yet to be investigated. If we apply what is known about spectral slopes adding to the conspicuousness or camouflage of a signal to *M. spicatus*, we would expect males' sexual traits, in addition to being extremely colourful, to have evolved patterns with contrasting slopes to enhance conspicuousness, whereas female and juvenile patterns should have evolved patterns with slopes similar to their environment. To test this, we photographed and analysed female abdomens and found that they were closer to the average natural slope than males' abdomens were (Mean: $-1.4 \pm \mathrm{SD} : 0.1$, $N = 5$), and that they differed significantly from the male slope (Wilcoxon rank sum test: P value $= 0.009$, effect size $r = 0.771$, $N = 11$). We also tested if female and male slopes differed from the average natural slope of -1 and found that this was true for males (Wilcoxon signed rank test: P value $= 0.031$, effect size $r = 0.899$, $N = 6$) but not for females (Wilcoxon signed rank test: P value $= 0.063$, effect size $r = 0.905$, $N = 5$).

Our results are consistent with the findings of Hulse et al. (2020), who found that male darter slopes were steeper than the slopes of their environments. Interestingly, they observed a positive correlation between habitat and male darter slope, which could be due to male colour patterns evolving to balance opposing sexually selective pressures: (a) to respond to a processing bias by matching the slope of their respective habitat, and (b) to stand out from the background. Such a trade-off might explain why the slope of male courtship displays in *M. spicatus* is just outside the range of slopes found in terrestrial habitats. That said, if the male slope were close enough to the spiders' habitat slope to be processed efficiently, then we would expect spiders to prefer the male slope over a slope even further from the ideally processed slope. Since spiders showed no discrimination between these two slopes, we think it is likely that any selective pressure for efficiently processed ornamentation has been overshadowed by selective pressure to be conspicuous. It is also worth mentioning that conspicuity increases the risk of predation, which might be another contributing selective force toward a less contrasting spectral slope. If the need to be conspicuous to females were the only selection pressure operating on male colour patterns, we would expect the male slope to diverge even further from the average natural slope.

To confirm that -1.0 is the spiders' peak preference, and that this matches the slope of their natural habitat, further studies using a continuous array of spectral slopes are needed, as well as an analysis of the spectral slopes of the natural habitat where the spiders are found. To gain more insight into how image statistics of the natural environment affect the evolution of male and female colour patterns in Australian peacock spiders, future studies could analyse a wide range of species for their spectral slopes to see if what we found for *M. spicatus* holds true in general for the *Maratus* genus. It would also be interesting to test whether species with more attention-getting mechanisms, such as vibratory displays, leg waving, or abdomens with expandable flaps (the latter two of which *M. spicatus* lacks), have less contrasting spectral slopes than species that rely more on relatively smaller, more static visual signals, as in *M. spicatus*.

2.5 Conclusion

The results of this study demonstrate that *M. spicatus* males have not evolved courtship displays that match the spatial statistics of the environment. Still, this is the first study to experimentally show that animals other than humans exhibit a preference for a visual stimulus based solely on its spectral slope. Consistent with human studies, spiders seem to prefer random image stimuli with a spectral slope typical of natural scenes. Since male courtship displays of *M. spicatus* have a differing spectral slope, whereas female slopes are closer to the average natural slope, it seems that what determines the spectral slope of *Maratus* patterns is not so much a processing bias towards image statistics of the natural environment, but rather, differing needs to be conspicuous, with males evolving contrasting slopes to stand out and females evolving matching slopes to blend in. Our study reveals that natural image statistics play a role in the evolution of colour patterns in *Maratus*, contributing to the existing body of literature that has found contrast in spectral slopes to increase the conspicuousness of visual signals. Whether this is typical for sexual signals across the animal kingdom, or peculiar to specific evolutionary contexts, like being tiny in a cluttered environment, we do not know. To resolve this question, more research is needed on a wider range of taxa in diverse ecological and evolutionary contexts.

Supplementary Data

Supplementary material can be found at beheco.oxfordjournals.org. Analyses reported in this article can be reproduced using the data and codes provided at doi.org/10.5061/dryad.2jm63xsv2.

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3

A Comparison of Image Statistics of Peacock Jumping Spider Colour Patterns and Natural Scenes

The form of arbitrary sexual signals may be driven by the need to be detectable against the background or, alternatively, by selection for efficient processing by the nervous system. This latter alternative is a prediction of the sensory drive hypothesis extended to include efficient coding as a driver of the form of sexual signals. This hypothesis posits that animal visual systems are adapted to process the visual statistics of natural scenes, and that easily-processed stimuli induce a sensation of pleasure in the viewer. In support of this, natural scene statistics have been found to be preferred not only by humans, but by the peacock spider *Maratus spicatus*. Here we test if male peacock spiders of the highly sexually dimorphic *Maratus* genus generally (a) evolve colour patterns with image statistics that contrast with the natural background or (b) exploit a potential processing bias by evolving colour patterns with visual statistics similar to those of natural scenes. We analyse and compare multispectral images of male and female spiders of 21 *Maratus* species and of natural scenes similar to the spiders' habitat. We find that the image statistics of male patterns diverge from those of natural scenes, whereas the statistics of female patterns do not. Our results support the idea that colour patterns evolve contrasting image statistics to increase conspicuousness and matching image statistics to be camouflaged. Any processing bias for natural scene image statistics in *Maratus* thus appears to play little role in the evolution of their sexual signals.

3.1 Introduction

Sexual selection pressure often leads to complex and elaborate courtship displays in the competing sex (Andersson, 1994; Darwin, 1871; Fisher, 1930). Whereas some courtship signals are directly linked to information about the quality of a potential mate, others seem arbitrary, with their only benefit being the capacity to attract mating partners (Fisher, 1930). How preferences that drive the evolution of arbitrary sexual signals evolve has long been subject to behavioural ecology research (e.g., Endler & Basolo, 1998; Enquist & Arak, 1993; Marler & Ryan, 1997; Payne & Pagel, 2001). Signal detection theory predicts that courtship signals should evolve to be conspicuous in front of a natural environment to increase efficacy (Endler, 1992; Endler & Mappes, 2017; Endler et al., 2005; Sibeaux et al., 2019; Wiley, 2013). Conversely, the more recently introduced processing bias hypothesis, which couches efficient coding within a model of sensory drive, predicts that signals with statistics matching those of the natural environment are preferred because the receiver's sensory and nervous systems are tuned to process them more efficiently (Renoult & Mendelson, 2019). It is likely that different mechanisms take effect for different traits and taxa, as well as at different stages of evolution; however, the relative frequency of different mechanisms is not well established.

For a signal to be effective in a mating context, it is crucial that it can be easily detected and discriminated by the receiver, that is, the choosy sex. This is particularly relevant when a signal is transmitted in a modality cluttered with extraneous stimuli. In the visual modality, extraneous stimuli could, for example, take the form of tangles of vegetation or variegated leaf litter. Animals can increase the probability of being detected either by exploiting pre-existing biases, for example by imitating properties of prey (e.g., Proctor, 1991) or other food items like fruit (Rodd et al., 2002), or by expressing traits that contrast with the background and are hence more conspicuous. There are many examples where the need to be conspicuous, achieved by the level of contrast of a signal to the background, provides a good explanation for the form of sexual signals; that is., is a good predictor for preference in a mating context. Males of the muscid fly *Lispe cana*, for example, display their bright iridescent faces against dark backgrounds to enhance signal contrast, which increases the attention they get from females, and with that, mating success (White et al., 2020). In the wolf spider *Schizocosa ocreata*, male forward-facing secondary sexual traits used in visual signalling have colour values highly contrasting with the natural environment, whereas when viewed from above by a potential predator, the spiders' colours overlap with the background (Clark et al., 2011). The same is true for Aegean wall lizards (*Podarcis erhardii*), whose colourful visual signals are tuned to be conspicuous to conspecific vision while being less conspicuously perceived by avian predators in front of the same visual background (Marshall & Stevens, 2014).

Conversely, framed within the context of sensory drive, the processing bias hypothesis predicts that signals that match the properties of the environment should be sexually selected for. The hypothesis assumes that perceptual systems are tuned to the statistical properties of their respective environment to reduce redundancy and process information with minimal cost. Visual systems can save metabolic energy by matching the arrangement of neurons and circuits to the statistical characteristics of the environment so that otherwise noisy visual input can be encoded to only use a small number of cells for transmission and processing in subsequent stages (Barlow, 1961; Field, 1987; Olshausen & Field, 1996; Simoncelli, 2003; Warrant, 2016; Wehner, 1987). It seems likely that animals have an innate preference or a pre-existing bias for certain signal properties based on how efficiently they can be processed. A signal that matches the statistical properties that the system is tuned to should be processed using less energy, which potentially leads to a positive response and consequently elicits a preference (Dibot et al., 2023; Reber et al., 2004; Renoult & Mendelson, 2019; Winkielman et al., 2003).

In addition to the more commonly-studied properties of colour and brightness, visual signal properties are defined by spatial content; however, studies investigating the role of spatial content in visual courtship signals are scarce. Whereas colour and brightness in an image can be described by first-order statistics using individual pixel values, summarising spatial information requires calculating the interaction of neighbouring pixels, that is, second-order image statistics. Any given 2D-signal can be approximated by the sum of 2D-sinusoidal waves of particular amplitudes, spatial frequencies, and phases. Second order image statistics describe how pronounced brightness contrast is in a colour pattern at different spatial scales and orientations. A tool to measure relative brightness contrast across different spatial scales of an image is the Fourier transform. With it, we can decompose any image into the individual 2D-sine waves that it is made of and measure their relative strength (= amplitude/brightness contrast) by transforming the image from the spatial domain into the frequency domain. Averaged over orientation, spatial frequency and amplitude typically have a linear relationship in a log-log plane, with low spatial frequencies usually having relatively high amplitudes and high frequencies having relatively low amplitudes. The slope of this linear relationship will hereafter be referred to as the spectral slope and is commonly used to describe the spatial frequency content of images (Cheney et al., 2014; Graham & Redies, 2010; Hardenbicker & Tedore, 2023; Hulse et al., 2020; Redies, Hänisch, et al., 2007; Renoult & Mendelson, 2019; Spehar et al., 2015).

Interestingly, Fourier analyses of images of natural scenes produce surprisingly uniform results when it comes to the spectral slope. In terrestrial habitats, amplitudes typically fall with increasing spatial frequency with a spectral slope of -1 (normally distributed, ranging from -1.6 to -0.7, Burton & Moorhead, 1987; Field, 1987; Pamplona et al., 2013; Párraga & Tolhurst, 2000; Tolhurst et al., 1992; van der Schaaf & van Hateren, 1996), which is typically attributed to scale-invariance (Field, 1987; Mandelbrot, 1977; Ruderman, 1997). This "natural spectral slope" has been associated with visual aesthetics in that humans seem to prefer images that possess this slope (Brichard et al., 2023; Isherwood et al., 2021; Spehar et al., 2015) and unconsciously recreate it in their artwork (Graham & Redies, 2010; Redies, Hänisch, et al., 2007; Redies, Hasenstein, & Denzler, 2007).

Comparatively little has been done to study a potential preference for the natural spectral slope in other animals. In a recent analysis of colour patterns in different species of darters and their respective habitats, it was proposed that male colour patterns are adapted to be efficiently processed by matching the slope of their natural backgrounds (Hulse et al., 2020). The study found male slopes to be correlated but offset from habitat slopes such that their colour patterns were more dominated by lower spatial frequencies, whereas spectral slopes of female patterns showed no relation to habitat slopes. The correlation in males is suggestive that efficient coding could play a role in the spatial design of courtship patterns. However, the offset between male slopes and those of the background suggests a counteracting selective pressure for males to stand out from the background. A later study corroborated the idea that male darters are adapted to contrast with the background by comparing distances between darters and darter habitats in the feature space of individual layers of a convolutional artificial neural network (Hulse et al., 2022). Gram matrices (representative of image texture) of male darters plotted further away from darter habitats than those of females did, again suggesting that male colour patterns are adapted to stand out from the background. A recent study found evidence that a species of Australian peacock spider (*Maratus spicatus*) exhibits a preference for the natural spectral slope of -1, which humans seem to prefer as well. However, females of this species have a pattern with a spectral slope closer to the natural slope than the slope of the male colour pattern, suggesting that this preference does not seem to be driving the evolution of male visual courtship display (Hardenbicker & Tedore, 2023), although this might not be true for other species of this genus. The results given above are in line with results from earlier studies that investigated spectral slopes in the context of camouflage rather than in the context of sexual signalling. Cuckoo eggs, for instance, mimic the spectral slope of host eggs to avoid being identified as parasites (Stoddard & Stevens, 2010). Cuttlefish alter their appearance so they match the slopes of the background (Barbosa et al., 2008), but when signalling, that is, when they intend to be seen, they change their pattern to contrast with the spectral slope of the background (Zylinski et al., 2011). Taken together, these findings suggest that colour pattern image statistics serve primarily as a means to decrease or increase colour pattern to background contrast. That said, studies of the image statistics of animal signals remain scarce, and more studies of a broader range of taxa are needed.

Australian peacock jumping spiders present an intriguing system to study the role of image statistics in the evolution of visual courtship displays. With currently about 100 described species, exhibiting a variety of elaborate courtship displays and intricate colour patterns, the *Maratus* genus is one of the most diverse groups in the animal kingdom when it comes to sexual signalling (Girard et al., 2021; Otto & Hill, 2021). Peacock jumping spiders, like other salticids, have a highly developed visual system and many of their behaviours are visually guided (Land, 1969). Accordingly, courtship displays, to a large extent, target the visual modality. A major part of the display is colourful ornaments on the abdomen, which males lift up during courtship and present towards females. In a detailed description and analysis of the complex courtship behaviour of *M. volans*, Girard et al. (2015, 2018) found that pattern contrast, the duration of visual display, but also to a lesser extent vibratory effort and vigour, influence mating success and other parameters that are linked to female choice. So far, Hardenbicker and Tedore's (Hardenbicker & Tedore, 2023) aforementioned study of *Maratus spicatus* is the only one that has looked at the spatial characteristics of *Maratus* colour patterns and what role they may play in the context of sexual selection. To determine whether the relationship between *M. spicatus* male and female slopes and those of natural scenes are representative of other *Maratus* species, in the present study, we expand our sampling to include 21 peacock spider species. We also analyse the slopes of ground microhabitats, since this is where *Maratus* are found. We aim to find out if what is true for *M. spicatus* is also true for other species of peacock jumping spiders; namely, whether (a) colour patterns of male peacock jumping spiders differ in their second-order image statistics to the environment, whereas females have patterns with similar statistics, or (b) male slopes of other *Maratus* species are similar to the slope of natural scenes, which would suggest that a processing bias does, in fact, play a role in the evolution of colour patterns in the *Maratus* genus.

3.2 Methods

3.2.1 Multispectral Imaging

We photographed adult spiders of 21 different species of *Maratus* (for 18 species we photographed both sexes and for three species we only photographed males) with median sample sizes per species and sex of 5 (IQR: 1–5), depending on how many specimens could be found. Spiders were collected as adults between September and October 2019 in Western Australia, Australia (except *M. tasmanicus*, which was collected in Melbourne, Victoria, Australia). All individuals of *M. chrysomelas* and *M. spicatus*, as well as some individuals of *M. pavonis*, *M. mungaich* and *M. gemmifer*, were raised in the lab and photographed after they matured (for sample sizes and collection sites, see Supplementary Data Table S1).

Before being photographed, each spider was killed overnight, while chilled in a refrigerator, by overanesthesia with CO_2. The abdomen was then detached from the prosoma and positioned using insect pins such that it was oriented vertically as it would be during a male courtship display. For males with extendable flaps on the sides of the fan, these were held open in an extended position by additional insect pins. Spider abdomens were photographed in front of a 20% reflective 2-in. fluorilon grey standard (Avian Technologies, New London, NH, USA), which reflects light evenly across the UV-VIS spectrum. We covered all surrounding surfaces with undyed brown paper with a reflectance spectrum similar to leaf litter. Adding to a naturalistic setup, specimens were illuminated by natural skylight with varying levels of cloud cover. To ensure there was no temporal variation in lighting across photos taken through different filters, we acquired multiple sets of the five images taken through each filter in sequence (i.e., images 1, 2, 3, 4, 5; 1, 2, 3, 4, 5; 1, 2, 3, 4, 5; etc.). Image sets with greater than 0.5% variation across three consecutive images taken through the same filter were discarded.

We used a multispectral camera with a customised set of filters. With this camera, we are able to mimic the salticid green channel, which peaks around 530 nm and is likely responsible for achromatic vision since it is the most densely-packed photoreceptor class in the salticid retina (Blest & Price, 1984; Blest et al., 1981, 1997; De Voe, 1975; Land, 1969; Nagata et al., 2012; Yamashita & Tateda, 1976; Zurek et al., 2015). Spiders were photographed using three bird-based filters (U, M and L) and two additional filters, previously described in Glenszczyk et al. (2021). From these filters, we calculated computational filters by taking the weighted sum of the existing set of five filters to generate new spectral sensitivities that matched the spectral sensitivity of the salticid green receptor (Blest et al., 1981; De Voe, 1975; Glenszczyk et al., 2021; Yamashita & Tateda, 1976; Zurek et al., 2015). The computational filter technique is further described in Tedore and Nilsson (2021), Glenszczyk et al. (2021), and Tedore (2024) (For fits of computational sensitivity curves, see Supplementary Data Figure S1a). Since peacock spiders are very small, we added varying numbers and lengths of extension tubes (Kenko Extension Tube Set DG, Kenko Tokina Co., Ltd., Tokyo, Japan) between the 60 mm lens and the filter wheel of the camera according to the size of the respective species, such that the abdomen filled a large portion of the frame. Each extension tube allows focus at only a single distance from the camera lens. This setup enabled us to later measure the camera's field of view in millimetres for each extension, which was important for standardising the range of frequencies analysed in each image and for determining whether the analysed frequencies likely corresponded to those the spiders are capable of resolving (see Calculation of Spectral Slope).

Natural scenes photos were taken from the existing publicly-available project dataset entitled "Natural Scenes through UVS and VS bird eyes: 6-filter set" available on multispectral.tedore.net (Tedore & Nilsson, 2019, 2021; Tedore et al., 2022). Since peacock jumping spiders live on the ground, we decided to limit our analysis to 41 ground shots. Images in which the entire depth of field was not in focus were excluded from analysis. The scenes we chose are dominated by leaf litter and little sticks, which is what the typical habitat of the spiders consists of. Photos were taken at different locations in either Skåne, Sweden or Queensland, Australia and categortised into five different habitat types (for detailed information on each image, see Supplementary Data Table S2). As described above, we converted the photos to images representative of the salticid green receptor by creating computational filters from the existing real filters in the camera (for fits of computational sensitivity curves, see Supplementary Data Figure S1b).

Before converting the original, real filter images to computational filter images, we subtracted dark noise from all pixels, which we calculated from columns of the camera sensor that do not receive any light. Although we adjusted exposures to minimise the occurrence of over- and underexposed pixels, there were often a few isolated pixels, and in 5 of 145 images, 1-2 small clusters of pixels that were either over- or underexposed. After converting them to computational filters, we recalculated the values of these pixels using the mean of the surrounding adjacent pixels (excluding adjacent over- and underexposed pixels). After cropping images to a square for analysis (see below), only one image contained clusters of >1 such pixel: one cluster of two and one cluster of eight overexposed pixels in a male specimen of *M. icarus.*

To simulate the adaptation of the eye and brain to the spectral distribution of light in a scene, we normalised each pixel value by the mean pixel value of the grey standard (for images of spider abdomens) or the mean pixel value of the image (for images of natural scenes). Following Naka and Rushton (1966), pixel values P were then converted to non-linear receptor excitation values E,

$$E = \frac{P}{P+1} \tag{3.1}$$

3.2.2 Calculation of Spectral Slope

To calculate the spectral slope, we transformed the images from the space domain to the frequency domain using a two-dimensional fast Fourier transform. This analysis can only be applied to square images, so we cropped images of natural scenes from their original size of 1036 px × 1392 px to a square of 1036 px × 1036 px from the centre of the image. For images of spider abdomens, we extracted the largest square that could fit within the respective spider abdomen using a custom MATLAB script, resulting in images with an average size of 391 px × 391 px ($\pm$ SD : 10 px; Figure 3.1). A cosine taper with a spatial frequency of four, tapered out to the mean pixel value of the respective image, was applied to the cropped images to avoid artificial edge effects.

From the frequency domain, we calculated the spectral slope for each cropped image by fitting a line (using the least squares method) to the rotationally averaged amplitudes across spatial frequency in a log-log plane (Supplementary Data Figures S2-S4). Regression models explained a substantial amount of variance, with R^2-values for natural scene data ranging from 0.91 to 0.95 (mean: $0.93 \pm$ SD : 0.01) and for spider data from 0.60 to 0.90 (mean: $0.81 \pm$ SD : 0.06).

To prevent aliasing and to exclude the cosine taper, we only considered frequencies ranging from a minimum of 5 cycles per cropped image to the dimension of each cropped image in pixels divided by 10. For the spider abdomen images, it was important to maintain consistency in the range of spatial scales considered between males and females of the same species because it is unknown whether their spectral slopes are scale-invariant. Therefore, we further restricted the range of frequencies analysed in the spider images to be consistent across all individuals of the same species.

To achieve this, we converted the minimum frequency analysed in each image to units of cycles per millimetre. We then identified the lowest such value across all individuals of a given species and excluded frequencies that fell below this range. We did this on a species-by-species basis rather than across the entire dataset because substantial size variation across species would have caused visually prominent low frequencies to be excluded from larger species.

Since the maximum spatial frequency analysed was calculated relative to the size of the crop (dimension in pixels divided by 10), the resulting maximum spatial frequency in units of cycles per mm was consistent for images photographed with the same extension tube. Two males of *M. chrysomelas* and five males of *M. spicatus* were photographed using 124 mm and 136 mm extension tubes, respectively, while all remaining images were taken through a 68 mm extension tube. We calculated the maximum frequency in units of cycles per millimetre for images taken with the shortest extension and adjusted the maximum spatial frequency in cycles per image of spiders photographed with larger extension tubes accordingly. This frequency $f_{\max}$ in units of cycles per millimetre was calculated as:

$$f_{\max} = \frac{1392\,\mathrm{px}}{\mathrm{FOV} \times 10} \tag{3.2}$$

where FOV is the horizontal field of view of the camera with the 68 mm extension (5.7 mm) and 1392 is the original width of the image in pixels. This gave a value of 24.4 cycles/mm. To assess whether the spiders were likely able to resolve this spatial frequency, we estimated the spiders' highest possible spatial resolution in cycles/mm f_s by:

$$f_s = \frac{1\,\mathrm{mm}}{4d\,\tan\left(\frac{0.04^\circ}{2}\right)} \tag{3.3}$$

where d denotes the distance during courtship in mm, and 0.04° is the interreceptor angle of the salticid *Portia fimbriata* (Williams & MeIntyre, 1980). *Maratus* males display at varying distances depending on the species, but during the majority of the courtship period that includes lifting and displaying the abdomen, males are quite close to the females (between 5 mm and 50 mm, personal observation, MCH). *M. spicatus*, for example, first lift their abdomen at an average distance of 27 mm before moving closer towards the female (Hardenbicker & Tedore, 2023). Assuming the spiders' vision is in sharp focus at this distance, the spiders would be able to resolve a maximum of 26.5 cycles/mm, which is slightly higher than the maximum spatial frequency analysed (i.e., 24.4 cycles/mm). Although *Maratus'* small size compared to *P. fimbriata* makes this an optimistic upper limit for the details *Maratus* can resolve, peacock spiders' intricate visual courtship displays at short distances from the female suggest that they may indeed have relatively high spatial acuities at close distances.

Finally, in calculating the spectral slope, to account for the log-scaled x-axis, where high frequencies are more closely spaced and therefore have more weight, we averaged the mean amplitude of frequencies used for calculating the slope in nine evenly spaced bins.

Figure 3.1: Computational filter images (matching the spectral sensitivity of the salticid green receptor that peaks at 530 nm) of the abdomens of male and female *Maratus* species (one example per species and sex). Squares indicate the area that was cropped from the image (yellow for females and blue for males) and used in the analysis to calculate the spectral slope.

3.2.3 Statistical Analysis

We fitted a Bayesian linear mixed-effects model with two submodels using the `brm` function from the `brms` R package, version 2.20.1 (Bürkner, 2017). Fitting the two submodels jointly within a multivariate framework enabled us to directly compare posterior estimates while accounting for shared variance and potential confounding factors.

In the first submodel, *spectral slope* as a continuous response variable was predicted by slopes measured for male and female *Maratus*, using *sex* as a predictor variable. For this analysis we only included species with data for both sexes

($N = 137$; for sample sizes per species and sex see Supplementary Data Table S1). We fitted species (18 levels) as a hierarchical grouping term to account for repeated observations per species, but we allowed species to vary by sex (model formula: `spectral slope ~ sex + (sex|species)`).

Since female abdomens were typically larger than males', the number of pixels making them up was also larger. This meant that, although the same range of frequencies in units of cycles per millimetre was used between males and females of the same species, the number of discrete frequencies this range was broken into was typically larger in females. We therefore assessed whether the number of discrete spatial frequencies used in the analysis should be included alongside sex in the model.

We conducted a pre-model comparison using 10-fold cross-validation with stratified sampling by species. We compared several candidate models, including models with number of frequencies as a main effect, an interaction term, and varying random slopes by species. The model including only sex and a random slope by species showed nearly identical predictive performance to more complex models, and substantially outperformed models including number of frequencies alone. Given the strong correlation between the number of frequencies and sex, and no improvement in predictive power when including this parameter, we retained the simpler model using only sex as a fixed effect in the multivariate model (for full model comparison results, see Supplementary Data Table S3; for a plot showing the relationship between number of frequencies and spectral slope, see Supplementary Data Figure S5).

In a second submodel, spectral slope was predicted by our natural scenes data with `region` (Skåne /Queensland) as predictor variable ($N = 41$; see Supplementary Data Table S2). We initially considered including `habitat` as an additional covariate, but due to its strong correlation with region and the substantial imbalance in sample sizes across habitat levels, its inclusion prevented the model from converging. We therefore excluded `habitat` from the final analysis.

The multivariate model was implemented using the Hamiltonian Monte Carlo (HMC) algorithm as Markov Chain Monte Carlo (MCMC) sampling method, specifically the No-U-Turn Sampler (NUTS). Since our response variables followed a Gaussian distribution and their relationship with the predictors was linear, we specified `family` as gaussian with an identity link function. We ran the model with four chains, each consisting of 5000 iterations and a warm-up period of 2500 iterations. We set `adapt_delta` to 0.999 with a maximum tree depth of 10 to avoid false positive divergences. Since we had no specific prior information, priors were set as weakly informative with the default flat distributions for gaussian models.

The model successfully converged ($\hat{R}$ values = 1.00) and the Effective Sample Sizes (ESS) were > 1000 for all parameters, indicating that estimates are reliable.

We report posterior estimates (ES) and standard deviations (SD), as well as 95% credible intervals (CrI). If the CrI of the effect size (Δ) does not cross zero, we interpret this as credible evidence for an effect of the predictor.

3.3 Results

We measured male and female spectral slopes as well as spectral slopes of images of natural scenes (only ground shots). Male slopes ranged from -2.15 to -0.79 with a mean slope of -1.5 ± SD: 0.28. Slopes of females and natural scenes were distributed very similarly, with females ranging from -1.43 to -0.91 (mean: -1.17 ± SD: 0.13) and natural scenes from -1.35 to -0.80 (mean: -1.09 ± SD: 0.14; Figure 3.2).

In our model, the spectral slopes estimated for males differed substantially from those estimated for females with $\Delta = -0.31$ (SD: 0.05; CrI: $[-0.4, -0.21]$; posterior estimates for each species: Figure 3.3). The slope for natural scene images, averaged over both regions, was estimated at -1.09 (SD: 0.02; 95% CrI: $[-1.14, -1.05]$). Female slopes did not differ from spectral slopes of natural scene images ($\Delta = -0.06$; SD: 0.04; CrI: $[-0.13, 0.01]$), whereas male slopes did ($\Delta =$ -0.37 ± SD: 0.07, CrI: $[-0.5, -0.24]$).

3.4 Discussion

Peacock jumping spiders are small (~2 to 6 mm) and live in cluttered environments like leaf litter and grass plants. Females usually hide in their surroundings and move very little, which makes them difficult to detect (MCH, JS and CT, personal observations). Since jumping spiders react to a moving stimulus by orienting towards it (Land, 1971; Zurek et al., 2010), males can increase their chance of finding a female by triggering such a response. A conspicuous signal that catches female attention leads to the female orienting towards that signal. This movement then enables the male to locate the female (MCH, JS and CT, personal observations). Standing out is therefore of great importance to males, not only during courtship, but also in the process of finding females, whereas female behaviour suggests that their main concern is blending in.

Our analysis of photos of male and female abdomens revealed a consistent pattern in 18 different species of *Maratus*, in that the spectral slopes of male ornaments diverge from the slopes of natural scenes, whereas female patterns

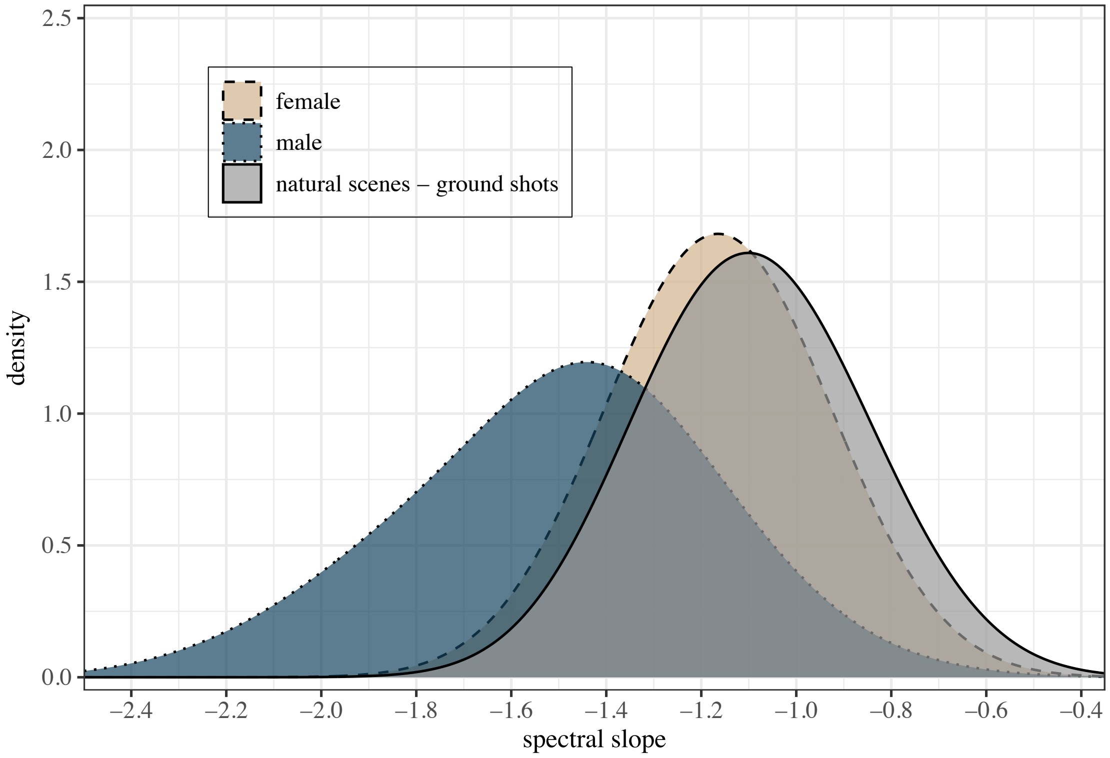

Figure 3.2: Distribution of spectral slopes of male and female *Maratus* from all species pooled (density plot based on raw data; SD of smoothing kernel = 0.2; females: $N_{\text{species}} = 18$, $N_{\text{individuals}} = 49$; males: $N_{\text{species}} = 21$, $N_{\text{individuals}} = 94$) compared to the distribution of slopes of natural scene images picturing the ground ($N = 41$).

have slopes close to the slope of natural scenes. These results would seem to indicate that male colour patterns evolve to have contrasting image statistics, which would increase their conspicuousness, and that female colour patterns evolve to have matching image statistics, making them better camouflaged in the natural environment. We did not find evidence for a processing bias influencing the form of *Maratus* sexual signals; i.e., an influence of a preference for image statistics of natural scenes on the evolution of colour patterns relevant in courtship. The results of this study are in line with the findings of previous studies (Godfrey et al., 1987; Hardenbicker & Tedore, 2023; Hulse et al., 2022; Zylinski et al., 2011), and provide more evidence for second-order image statistics playing a role in colour pattern evolution.

Deviating from the spectral slope of the natural surroundings would seem to be an effective way to improve signal efficacy. However, there is evidence that visual systems are tuned to the image statistics of the natural environment and process visual input that possess the same properties more efficiently, leading to a preference for such statistics (Hardenbicker & Tedore, 2023; Redies, Hänisch, et al., 2007; Redies, Hasenstein, & Denzler, 2007; Spehar et al., 2015). Yet, to date, no

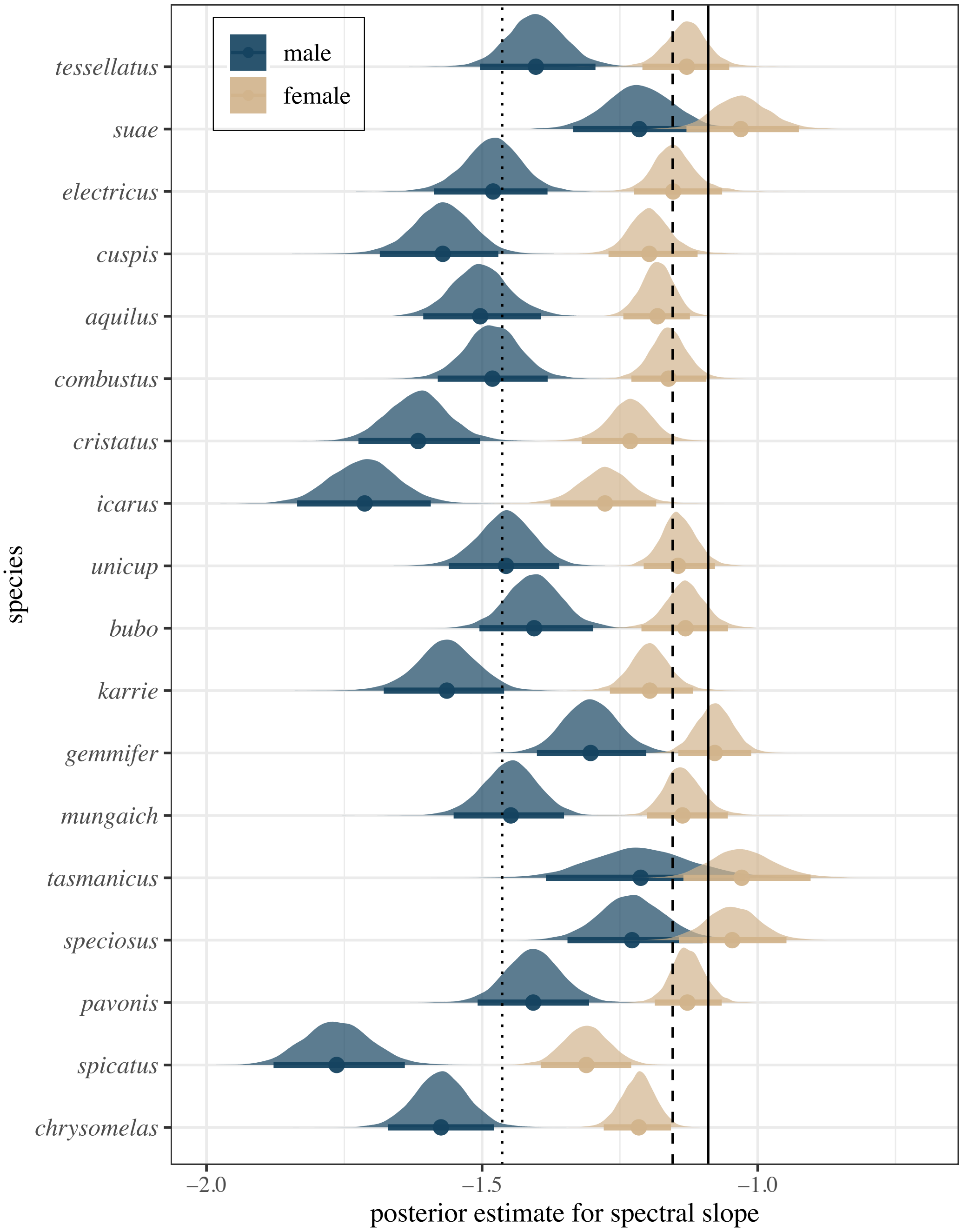

Figure 3.3: Distribution of posterior estimates for spectral slopes of male and female abdomens of 18 different *Maratus* species (Bayesian linear mixed-effects model). Means per species and credible intervals are shown in a darker shade. Vertical lines represent means (dotted = males, dashed = females, solid = natural scenes; for boxplots of raw data, see Supplementary Data Figure S6; for sample sizes per species, see Supplementary Data Table S1).

unequivocal evidence for sexual signals evolving to exploit this preference has been found. Still, the evolution of sexual signals could be influenced by the tuning of the visual system to the natural spectral slope, in that the range of spectral slopes that colour patterns evolve is limited by what can be perceived by the targeted visual system. Visual information might become distorted and not processable if it diverges too much from what the visual system is tuned to, making visual signals less likely to be seen. Hence, there could be a trade-off between the need to stand out in front of the background and the risk of not being perceived because the signal deviates too far from what the eye is adapted to see. In our study system, male spectral slopes were always steeper than the natural slope/female slope, but usually just outside the range of slopes we measured for natural ground images, which could potentially be attributed to such a trade-off.

Female slopes of some species (e.g., *M. spicatus*, *M. chrysomelas*, *M. icarus* and *M. cristatus*) seem to diverge from the slope measured for natural scenes, although we have to account for low sample sizes per species, which makes it difficult to test for an effect of species on the spectral slope of male and female spiders. Regardless, sex differences across all species pooled together are strong, as is the similarity of female slopes to the natural slopes compared to male slopes. The variation that we observed among the spectral slopes of different species could potentially be explained by the spiders being adapted to the image statistics specific to their respective microhabitats. Since we did not measure the spectral slope of each species' microhabitat, we do not know whether there is significant variation among them. However, even though we only analysed natural scene images picturing the ground, we found a similar distribution of slopes to those found in previous studies for a variety of terrestrial habitats, supporting previous studies showing that the "natural slope" of -1 is prevalent across different scales and habitats (Balboa & Grzywacz, 2003; Field, 1987; van der Schaaf & van Hateren, 1996). Moreover, *M. spicatus* preferring random noise images that represented a slope of -1 (Hardenbicker & Tedore, 2023) would make the most sense if this were the slope characteristic of their natural habitat. Female spectral slopes, when pooled, had a strikingly similar distribution to those of natural scenes, suggesting that variation in female slopes follows the natural variation of the "natural slope". Male slopes were distributed much more broadly, which suggests that other factors besides the advantage of pattern-background contrast may be driving this variation.

Our results show quite a clear pattern, but it is important to keep in mind that we are singling out one trait of a courtship display that consists of multiple traits that target more than one sensory modality. Courtship displays of Australian peacock jumping spiders are complex and involve other visual traits like colour and movement as well as vibrational and potentially chemical cues (Girard et al., 2015). There are several studies showing that multimodal signals can be more than the sum of their parts, due, for example, to temporal association between modalities (reviewed by Mitoyen et al., 2019). Consequently, caution is warranted when interpreting the evolutionary significance of single parts of a multimodal display, since it might be the composition of different traits that is selected for. With our study, we showed that male slopes deviate from the natural slope, but to confirm that contrasting spectral slopes actually increase female attention and with that the chance to mate, behavioural tests are needed. It is also worth noting that contrasting spectral slopes may not be selected for in their own right, but rather, could be a by-product of other selective forces, such as the level of detail resolvable by different colour receptors in the spiders' eyes. All salticids measured so far have densely-packed green receptors and sparsely-distributed UV receptors (Blest et al., 1981; De Voe, 1975; Land, 1969), which means that to resolve a pattern with UV-green contrast, the pattern would need to be made up of low spatial frequencies. Selection for UV-green colour contrasts alone could therefore produce patterns dominated by lower spatial frequencies without a particular spectral slope being selected for per se.

In conclusion, the results of our study provide insight into the complex processes of colour pattern evolution in the *Maratus* genus. We identified a strong sexual dimorphism in spectral slope, showing that female slopes match the slope of the natural environment whereas male slopes diverge and are more variable between species. With this study, we add to the large body of literature showing that conspicuousness achieved by colour patterns contrasting to the background is a major driver in the evolution of visual courtship signals (reviewed by Caves et al., 2024).

Supplementary Data

Supplementary material can be found at onlinelibrary.wiley.com. Analyses reported in this article can be reproduced using the data and codes provided at doi.org/10.5061/dryad.4f4qrfjnb.

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4

Signal–Background Contrast in Spectral Slope Modulates Female Attention

Understanding how neural costs and benefits shape mating preferences is crucial for uncovering the mechanisms driving sexual selection. Signal detectability plays a central role in the evolution of courtship displays, as easily detectable signals can reduce the cognitive costs of mate assessment. Jumping spiders of the genus *Maratus* prefer images that reflect the statistical properties of the natural world, likely because they can be more efficiently processed. Yet, males do not seem to exploit this bias as the intricately patterned courtship ornaments of male peacock spiders deviate from the "natural spectral slope". As *Maratus* females exhibit body patterns that closely match the image statistics of their environment, presumably as a function of camouflage, we ask whether male patterns may elicit female preference through enhanced detectability via contrasting spectral slopes. Here, we test whether spectral slope contrast between male displays and background influences female attention in *M. spicatus*. We conducted behavioural trials in which males courted females against random noise backgrounds differing in spectral slope: one matched male colour patterns (-1.7), one resembled natural scenes (-1.0), and one was steeper (-2.3). Females tracked males significantly longer when they were courting in front of backgrounds with contrasting spectral slopes compared to backgrounds matching the male slope. Assuming that increased attention reflects female preference, detectability via spectral slope contrast may increase mating success. These results suggest that signal detectability, mediated by contrasting image statistics, may play a key role in shaping mating preferences and the evolution of courtship signals in visually complex environments.

4.1 Introduction

From the elaborate dances of birds of paradise (Frith & Beehler, 1998; Scholes, 2008), to the diverse colour patterns of darters (Mendelson, 2003; Page, 1983), and the multimodal courtship performances of wolf spiders (Stratton, 2005; Uetz & Roberts, 2002), animals that invest heavily in courtship are widespread across taxa. Regardless of form or sensory modality, traits that make up such elaborate displays typically share the common feature of being highly salient, whether through vibrant coloration, complex movement patterns, acoustic elements, or substrate-borne vibrations. A major component of attractiveness in a mating context thus appears to lie in the level of conspicuousness, making it a frequent target of sexual selection (Andersson, 1994; Endler, 1992).

Signal detection theory provides a framework for understanding the evolution of such conspicuous traits by proposing that signals are selected to maximize detectability to the receiver against a noisy environment. It models decision-making under uncertainty, where receivers face a trade-off between detecting true signals and avoiding false alarms. Signals that can be readily detected reduce the cognitive and energetic costs of mate assessment, and thus may be favoured by selection, even if exaggerated or arbitrary (Wiley, 2006; Wiley, 2013). Detectability is typically enhanced by within-pattern contrast, for example through sharp colour boundaries and/or by contrasting against the natural background (Brumm & Todt, 2002; Clark et al., 2011; Endler & Thery, 1996; Fleishman, 1992; Kirschel et al., 2009; Marshall & Stevens, 2014; Uetz et al., 2011; White et al., 2020). In addition to contrast-based conspicuousness, signal efficacy, i.e, the capacity of a signal to propagate reliably through the environment to reach the receiver, also shapes signal form (Guilford & Dawkins, 1991). In the jumping spider *Habronattus dossenus*, males that signal on substrates that enhance the propagation of their seismic courtship signals are more successful when trying to copulate with a female, indicating that transmission efficacy directly affects mating success (Elias et al., 2004). However, the efficacy of a signal depends not only on its physical transmission properties, but also on how it interacts with the sensory and cognitive architecture of the receiver (Ryan & Cummings, 2013). In surfperch, for instance, divergence in male colour signals matches species-specific visual sensitivities shaped by habitat light properties, illustrating how receiver sensory tuning directly influences the efficacy of signal design (Cummings, 2007).

While signal detection theory emphasizes detectability under uncertainty, favouring contrast and efficacy to overcome environmental noise, alternative frameworks suggest that signals may also evolve by exploiting inherent preferences resulting from perceptual biases. Such biases can originate from ecological contexts like, for example, preferences for traits resembling food items (e.g., Rodd et al., 2002), or to reflect sensory system organisation and amplify perceptual stimulation (Ryan & Rand, 1990). Processing bias hypothesis proposes that preferences emerge from neural processing architecture, which has likely evolved to efficiently encode environmental information by adapting to the statistical properties of natural scenes (Barlow, 1961; Warrant, 2016; Wehner, 1987). Signals that mirror the natural statistics may be preferred, because they can be processed more efficiently and at lower energetic cost (Dibot et al., 2023; Héjja-Brichard et al., 2024; Reber et al., 2004; Renoult & Mendelson, 2019; Winkielman et al., 2003).

Among the environmental features that shape sensory systems, the statistical properties of natural scenes have emerged as particularly important determinants of perceptual tuning, especially at early stages of visual processing (Field, 1987; Olshausen & Field, 1996; Simoncelli, 2003). Natural scenes are characterized by consistent spatial regularities, described by second-order statistics, calculating the interaction of neighbouring pixels in an image. Averaged over orientation, the amplitudes of spatial frequencies f typically fall linearly with $1/f$, with a so called spectral slope around -1 in images picturing terrestrial habitats (when plotted in a log-log plane, Balboa & Grzywacz, 2003; Burton & Moorhead, 1987; Field, 1987; Pamplona et al., 2013; Párraga et al., 2000; Tolhurst et al., 1992; van der Schaaf & van Hateren, 1996). This “natural spectral slope“ has been linked to an aesthetic sense in humans and is suspected to underlie similar preferences across the animal kingdom. Specifically, humans tend to prefer images that posess the statistics of the natural world (Isherwood et al., 2021; Spehar et al., 2015), a tendency that also manifests in the recurring natural slope in visual artwork across different cultures and historical periods (Graham & Redies, 2010; Redies, Hänisch, et al., 2007; Redies, Hasenstein, & Denzler, 2007). A recent study found that the Australian peacock spider *Maratus spicatus* exhibits a similar preference for images matching the spectral slope of natural scenes (Hardenbicker & Tedore, 2023). However, male colour patterns diverge from natural statistics, while female patterns align more closely with the background (Hardenbicker et al., 2025), suggesting that conspicuousness and camouflage, rather than processing bias, drive signal evolution (regarding spatial content) in this species.

A similar pattern has been observed in darters (*Etheostoma spp.*). An analysis of colour patterns across multiple species found that although male pattern statistics were correlated with those of their habitat backgrounds, they were systematically offset, with male patterns showing an increased emphasis on lower spatial frequencies (Hulse et al., 2020). In contrast, female pattern statistics showed no such relationship to habitat backgrounds. These results were further supported by a later study using deep neural networks to model visual similarity between darters and their habitats, with male patterns plotted farther from habitat textures in feature space than female patterns (Hulse et al., 2022). The findings indicate that sexual signals in darter males, too, are shaped by the need to maximize conspicuousness rather than to blend in with environmental statistics. Previous studies on camouflage also highlight the role of matching or contrasting image statistics in managing detectability. Cuckoo eggs have evolved to closely mimic the spatial statistics of host eggs, making it more difficult for hosts to detect parasitism (Stoddard & Stevens, 2010). Similarly, cuttlefish adjust their body patterns to match the spectral properties of surrounding substrates when attempting to blend in, but actively shift to high-contrast patterns, thereby enhancing conspicuousness, when engaging in social signaling (Barbosa et al., 2008; Zylinski et al., 2011).

While these studies reveal intriguing correlations between image statistics, background matching, and signal design, experimental evidence directly linking contrasting image statistics to increased attention or attractiveness in a mating context remains lacking. To address this gap, we test whether background image statistics influence female attention during courtship interactions in *M. spicatus*. Given recent evidence that male colour patterns in *M. spicatus* diverge from the spatial statistics of natural backgrounds with a spectral slope of -1.7 (Hardenbicker et al., 2025), we ask whether background matching at the level of image statistics affects signal salience during courtship and consequently female attention. Like all peacock spiders, *M. spicatus* males perform elaborate multimodal courtship displays that include complex motion with substrate-borne vibratory signals, but primarily engage the visual modality (Girard et al., 2011, 2021), consistent with the highly developed visual system of salticids (Land, 1969). A prominent component of the display is a colourful abdominal fan, which males raise and orient toward females during courtship. While vibratory and visual elements are often tightly synchronized, previous work suggests that visual features, such as display duration and pattern contrast, are especially influential in modulating female attention and receptivity (Girard et al., 2018). We measure female attention as a proxy for mate attraction while males are courting against random noise backgrounds that either match or diverge from the spectral slope of their courtship displays. We predict that female attention is greater when males court against backgrounds with image statistics that diverge from their own spectral slope, thereby enhancing contrast and detectability. Conversely, we expect lower female attention when males display against backgrounds that match their spectral slope, resulting in reduced visual salience.

4.2 Methods

4.2.1 Study Subjects

All male and female *M. spicatus* were hatched and reared in the laboratory. After maturation, individuals were housed individually in plastic containers (14.5 × 11 × 7 cm), each fitted with plastic mesh-covered cut-outs to ensure airflow and opaque dividers to prevent visual contact between spiders. In each box, there was a paper towel on the ground, an accordion-shaped piece of black paper for shelter and some wood wool to provide structure. Spiders were kept at 25°C and 55% humidity under a 14:10 light:dark cycle and fed *Drosophila melanogaster* ad libitum twice a week, as well as sprayed with water 6 days a week.

We tested 24 pairs of spiders, each consisting of a virgin male and a virgin female. At the time of testing, males ranged in age from 7 to 45 days post-maturation (Mean: 17.32 ± SD: 11.06) and females from 12 to 43 days (Mean: 43 ± SD: 7.76). Each female was used only once and had never encountered a male prior to the experiment. Due to limited sample size, males were tested in up to two trials, with a minimum interval of one week between tests (multiple testing of males was taken into account in the statistical model).

4.2.2 Experimental Design

We tested each pair over three 60-minute trials on consecutive days, with each trial featuring a different background. Background stimuli consisted of chromogenic prints displaying random noise patterns characterized by one of three distinct slopes: the average natural slope of −1.0 (Balboa & Grzywacz, 2003; Pamplona et al., 2013), the slope typical of *M. spicatus* males, −1.7 (Hardenbicker & Tedore, 2023), and a steeper slope of −2.3. We generated two versions of each image stimulus following the methodology described by Hardenbicker and Tedore (2023), which were randomized across trials.

Trials were conducted inside one of two identical arenas, consisting of a 3 mm thick quartz glass tube with an inner diameter of 60 mm and 50 mm height. Random noise backgrounds were affixed to the outer surface of the tube so that they would cover the entire circular wall. The arena floor was made from gray painted granite to prevent the transmission of vibratory signals. A female was placed inside a smaller quartz glass tube (1 mm thickness, 8 mm inner diameter, 50 mm height) positioned at the center of the arena while the male was introduced into the surrounding outer ring. This setup allowed the male to move around freely and court the female in front of the stimulus background, while the female could observe but not physically interact with the male (see Figure 4.1). Separating male and female by a glass wall also ensured that interactions during courtship were not affected by directional chemical cues, thus only visual cues were available.

The distance between the background and the inner wall of the smaller tube was 27 mm, matching the average distance at which *M. spicatus* males typically initiate visual courtship by raising their fans (Mean: 26.69 mm ± SD: 3.73 mm, $N = 15$, Hardenbicker & Tedore, 2023). To prevent the spiders from escaping the arena, we applied nano coating (CleanglaS, Unterschleissheim, Germany) to the quartz glass surfaces. The arena was evenly illuminated by three LED strips (realUV 365 nm and 395 nm and ABSOLUTE SERIES 6500K, Waveform Lighting, Vancouver, WA, USA), mounted onto a removable 3D-printed framework placed atop the arena with the lights tilted inward. This produced a spectrum closely resembling natural light (see Supplementary Data by Hardenbicker and Tedore (2023) for irradiance spectrum). A heating plate beneath the arena maintained a constant temperature of 30°C. After each trial, the arena was cleaned with 70% ethanol to remove any chemical residues. Trials were recorded from above using an iPhone SE (2nd generation; HD resolution, 30 fps).

Behavioural analysis was performed using BORIS software (Friard & Gamba, 2016). We scored five different behaviours. As a proxy for female attention, we measured the time the female was oriented towards the male (*track*). We approximated an angle of 30° when measuring if the male was in the female's field of view, which is similar to that of the principal eyes when typical retinal movements are considered (Land, 1969). Tracking was considered to stop when the male was out of the female's field of view for more than one second, as females tracking a moving male often exhibit a brief delay in body rotation. We also recorded the time the male was displaying his fan towards the female (*fan raise*) as well as two additional behaviours that are components of the male courtship dance: *run* and *wiggle* (for complete ethogram see Table 4.1). Quick movements such as wiggle and run usually occurred when the female stopped tracking the male, and often resulted in her turning towards him again, suggesting males use these behaviours to regain female attention. When the male was displaying within 5 mm of the outside of the female's tube (i.e., touching or almost touching the wall), we interpreted this as an attempt to mount the female. During *close courtship*, it was often difficult to reliably score individual courtship behaviours due to limited visibility, so only the duration of close approaches was recorded. If either spider managed to climb the glass walls, we paused the trial and resumed behavioural recording only after returning them to the arena. These brief interruptions resulted in minimal variation in total trial length, which we accounted for in the statistical analysis.

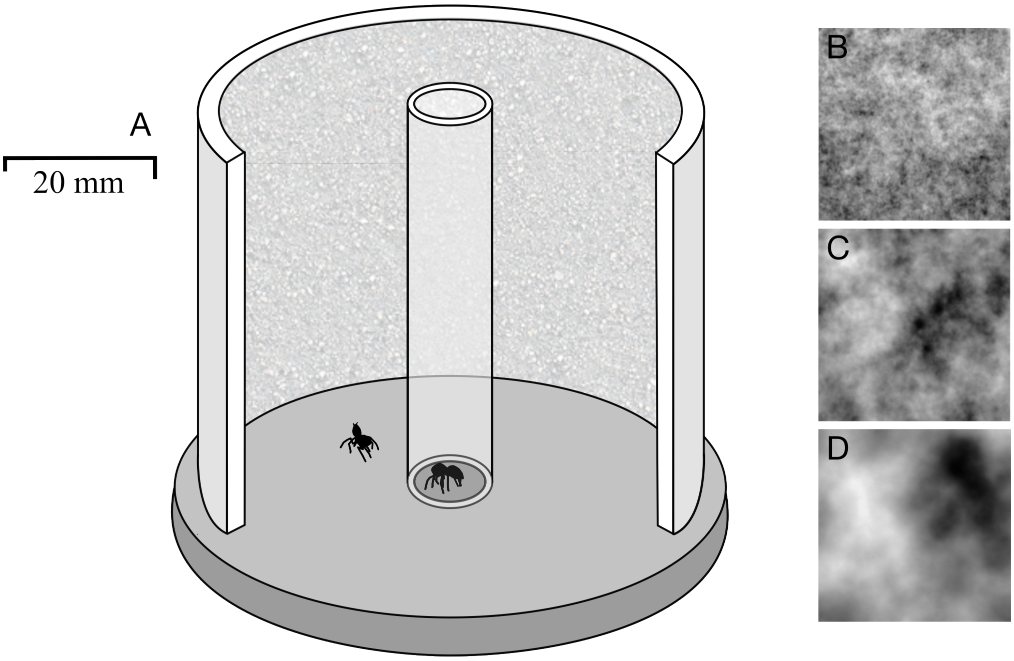

Figure 4.1: **A** Schematic of testing arena. Random noise backgrounds (**B** −1.0, **C** −1.7, **D** −2.3) were affixed to the outer wall of a larger quartz glass cylinder with random noise backgrounds. Female was constrained by a smaller quartz tube in the center. Within the outer ring males could freely court the female in front of the background.

In addition to behavioural recordings, we quantified the distance at which males displayed using a custom Python script to automatically track the male's distance from the arena center throughout each trial. Distances were recorded every tenth frame and categorized into three equal zones within the arena: outer, middle, and inner area. By overlapping these data with the behavioural recordings, we were able to analyse male courtship and female attention in relation to the distance between the pair and the male's proximity to the background.

Due to technical difficulties, four video recordings were lost, resulting in a total of 68 analysed trials (20 pairs with three trials each and four pairs with two trials each).

4.2.3 Statistical Analysis

We fitted multiple submodels with correlated response variables in two multivariate Bayesian beta regression models using the brm function from the brms R package (version 2.20.1, Bürkner, 2017), which implements hierarchical modeling and the No-U-Turn Sampler (NUTS). Trials were excluded from the respective submodels if normalization values were unavailable; for example, if a male did not raise his fan, the duration of female tracking behaviour during fan raise was treated as missing rather than zero. The hierarchical structure allowed the model to handle

Table 4.1: Behavioural categories used for video analysis

Subject	Behaviour	Interpretation	Metric
female	*track*	female tracks male	female's gaze follows male; body axis deviates for no more than one second; male remains within a 30° viewing angle
male	*fan raise*	male courts the female	male raises abdomen above horizontal (i.e., higher than parallel to the ground)
male	*wiggle*	male uses fan movement to get female's attention	male rapidly moves raised fan side to side when elevated to 90°
male	*run*	male runs a short distance to get female's attention	male runs quickly sideways for >1.5 cm, then stops abruptly and raises fan
male	*close courtship*	male attempts to copulate with female	male is within 5 mm of the inner tube wall (partially obscured); movements such as wiggling, running, and fan raising are unclear, but female following is still recorded

unbalanced data structures through partial pooling, so pairs with missing trials could still be included. Modelling all responses as submodels jointly within a multivariate model accounted for shared variance resulting from correlations and dependecies between responses.

In the first model, we tested for an effect of spectral slope background (3 levels) on female tracking behaviour at trial-level. Tracking was measured using four proportional response variables: (1) total tracking duration relative to trial duration, (2) tracking during *courtship display* relative to courtship display duration, (3) tracking during *close courtship* relative to close courtship duration , and (4) tracking during *fan raise* (excluding the time spent in close courtship) relative to duration fan was raised outside of close courtship. *Courtship display* refers to the total duration the fan was raised, including the time male spent in *close courtship* (when in close courtship fan was always raised). These analyses were conducted using per-trial data, excluding area-level effects.

In a second multivariate model, we tested for an interaction effect of slope and area (3 levels) on two proportional response variables: (1) total tracking duration per area relative to the time male spent in the respective area and (2) tracking during *courtship display* per area relative to duration of courtship display in the respective area. Since fan raise and close courtship were highly correlated with area, we did not test for area-level effects on tracking during these behaviours separately.

Each response variable was fitted in a beta regression submodel with slope (or slope × area) as predictor, and pairID as well as maleID as random intercepts to account for repeated measures. To address heteroskedasticity, we modeled the beta distribution precision parameter (φ) as a function of the log-transformed normalisation factor, allowing response variability to scale with behaviour duration.

Covariates for each submodel were selected via K-fold cross-validation, comparing model performance (ELPD difference), fit (Bayes R^2), and mean predictive variance (CV). We tested combinations of covariates including male and female age (days since hatching), male and female maturation age (days since maturation), male and female body weight (on the day of the third trial), and low-level random effects such as testing order (3 levels), observer (3 levels), time of day (3 levels), arena (2 levels), and image stimuli version (2 levels). All age-related predictors were z-transformed to facilitate model convergence. Courtship effort was defined by combining number of wiggles, number of runs, and duration of fan raise using PCA on z-scaled values (Supplementary Data S1). Close courtship duration (z-scaled) was added as additional separate measure of effort, as wiggles and runs were not recorded when the male was courting in a 5 mm radius of the female.

None of the tested low-level random effects improved model fit without causing overfitting and were thus excluded. Male maturation age and female age were removed due to multicollinearity. All models showed no signs of overdispersion, and predictor-response relationships were linear. For φ of response (1) total tracking duration in the first multivariate model, we specified a `normal(0, 1)` prior for fixed effects and `a normal(2, 1)` prior for the intercept, to stabilize estimation under variable trial durations. For all other parameters and submodels, we retained default priors as implemented in brms (i.e., `student_t(3, 0, 2.5)` for intercepts and standard deviations; `gamma(0.01, 0.01)` for φ, reflecting weak prior knowledge of the size or direction of effects.

To estimate the overall effect of spectral slope we averaged posterior samples of slope parameters across submodels within each of the two multivariate models. By using the joint posterior distribution to compute pooled estimates, we treated the slope effect as a latent shared influence across multiple behavioural responses, allowing us to preserve both uncertainty and correlation among responses. Rather than analysing each response separately or averaging estimates post hoc, this approach uses all available information at once, keeping the relationships between behaviours intact and giving a more reliable estimate of the overall effect.

We ran models with four MCMC chains, each with 4000 iterations (2000 warm-up) with `adapt_delta` = 0.999 and `max_treedepth` = 14, showing good convergence diagnostics ($\hat{R} = 1.00$ for all parameters; all ESS > 1800).

We report posterior means (μ) and standard deviations (SD), along with 95% credible intervals (CrI) for all models (logit scale). If the CrI of the difference in posterior means ($\Delta = \mu_1 - \mu_2$) does not include zero, we interpret this as evidence for a credible difference.

4.3 Results

There was no credible difference in female tracking behaviour depending on the spectral slope of the background in any of the individual submodels of the first multivariate model (Figure 4.2; Table 4.2). During fan raise (submodel 4), females tracked males less when they performed more runs (Δ = -0.28 ± SD: 0.13, CrI = [-0.54, -0.02]). The number of wiggles had a weakly positive effect on tracking during courtship display, but its CrI slightly overlapped with zero (Δ = 0.27 ± SD: 0.14, CrI = [0, 0.54]). Male age or courtship effort had no effect in any of the submodels (Table 4.2).

When treating slope as a latent variable there was an overall effect on tracking behaviour, in that females tracked males less in front of backgrounds with a spectral slope of -1.7 compared to a slope of -1.0 (Δ = 0.28 ± SD: 0.12, CrI = [0.04, 0.52]) and a slope of -2.3 (Δ = 0.25 ± SD: 0.11, CrI = [0.02, 0.47]), while there was no difference between slopes -1.0 and -2.3 (Δ = 0.03 ± SD: 0.12, CrI = [-0.19, 0.27]; Figure 4.4).

In the second multivariate model, there was no effect of spectral slope × area on female tracking behaviour, as none of the slope contrasts were credibly different from zero (Figure 4.3; Table 4.2). However, females showed higher total tracking duration (submodel 1) in the inner area compared to the middle area (Δ = 0.66 ± SD: 0.34, CrI = [0.04, 1.32]). Additionally, courtship effort had a positive effect on tracking across areas (Δ = 0.11 ± SD: 0.05, CrI = [0.02, 0.21]). For tracking during courtship display within areas (submodel 2), no effects reached credibility (Table 4.2).

When modelling slope × area as a latent interaction term in a meta-analysis framework, there were no credible differences in female tracking behaviour across

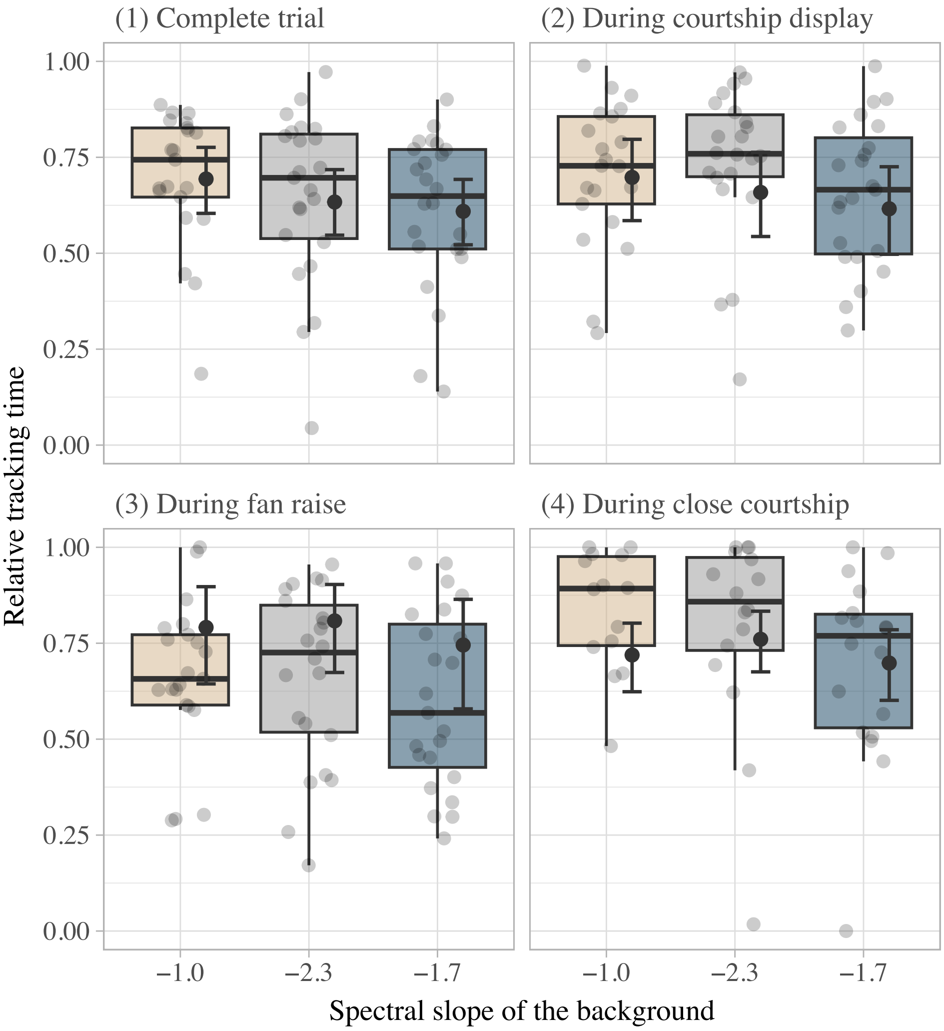

Figure 4.2: Proportion of time females tracked males in front of random noise backgrounds with varying spectral slopes: (1) total tracking time relative to trial duration, (2) tracking time during *courtship display* (including close courtship) relative to courtship display duration, (3) tracking time during *close courtship* relative to close courtship duration, (4) tracking time during *fan raise* relative to fan raise duration (excluding close courtship). Horizontal bars on top of boxplots represent posterior means and 95% credible intervals from Bayesian multivariate modeling (backtransformed from logit scale to proportions).

any pairwise spectral slope contrasts within any of the three areas (Figure 4.5; Table 4.2).

The dispersion parameter (φ) was significant in all submodels except submodels 1 (total tracking duration (per area) relative to trial duration (per area); Table 4.2), indicating meaningful variation in response precision across trials.

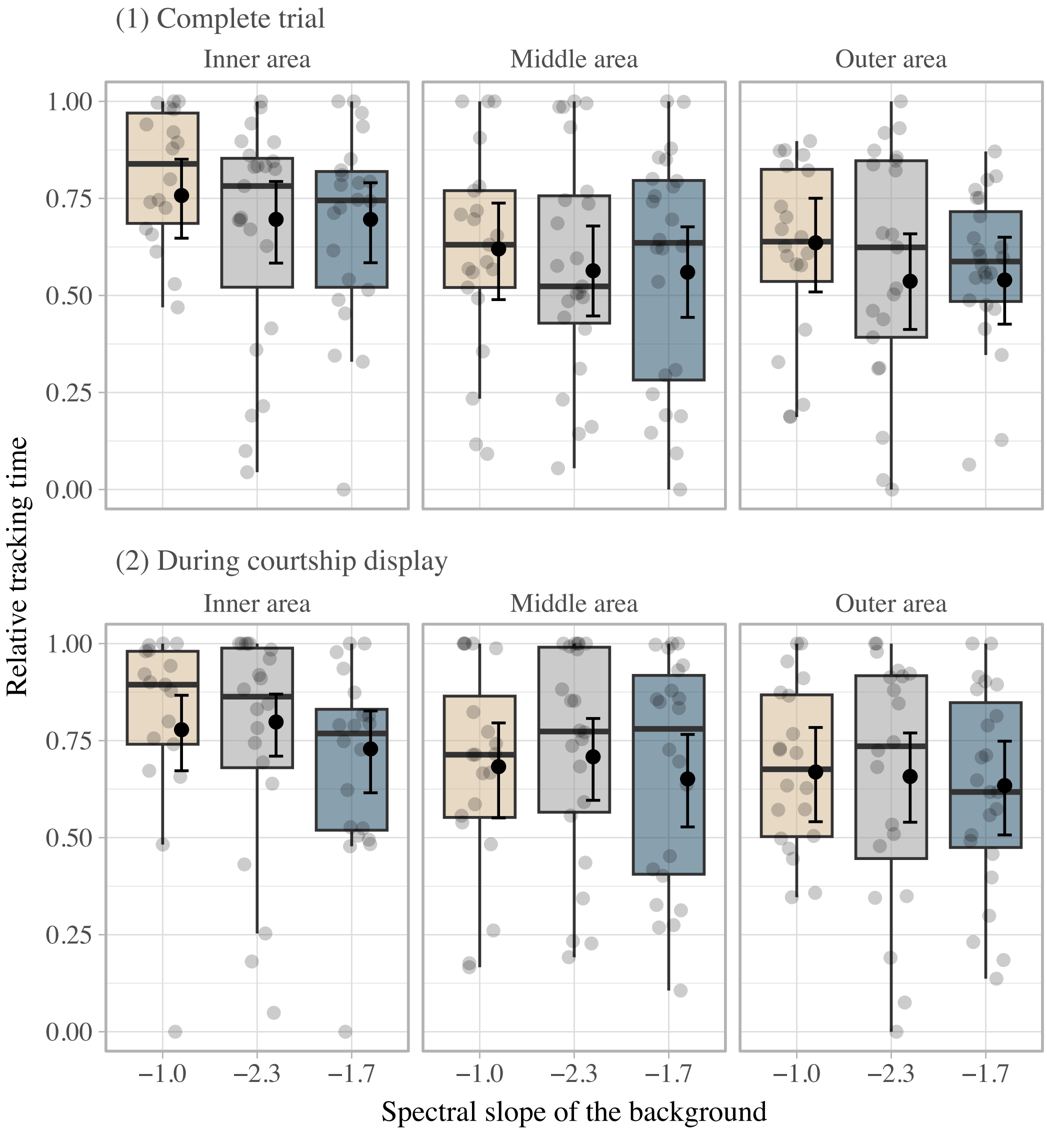

Figure 4.3: Proportion of time females tracked males in front of random noise backgrounds with varying spectral slopes analysed by male proximity to the female (scored as three equal zones within the arena): (1) total tracking time relative to trial duration, (2) tracking time during *courtship display* (including *close courtship*) relative to *courtship display* duration. Horizontal bars on top of boxplots represent posterior means and 95% credible intervals from Bayesian multivariate modeling (backtransformed from logit scale to proportions).

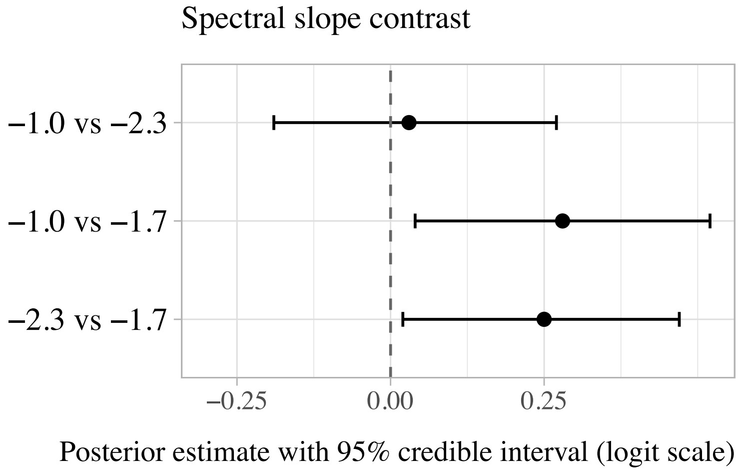

Figure 4.4: Mean posterior estimates for the difference in relative time females tracked males in front of random noise images with varying spectral slopes. Estimates are averaged posterior samples from a multivariate model with four submodels, each testing the effect of spectral slope on relative female tracking time during different male behaviours.

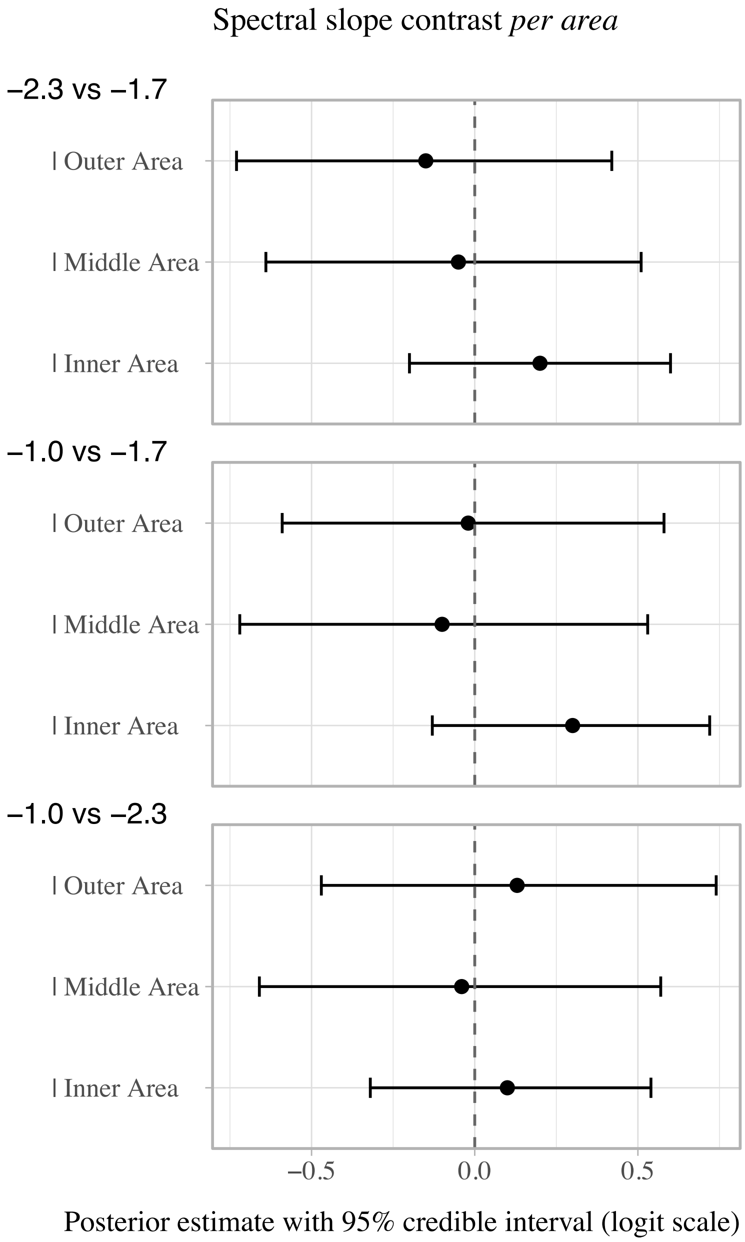

Figure 4.5: Mean posterior estimates and 95% credible intervals for the difference in relative time females tracked males at varying differences in front of random noise images with different spectral slopes. Estimates are are averaged posterior samples from a multivariate model with two submodels, each testing the effect of spectral slope × distance (area) on relative female tracking time during different male behaviours.

Table 4.2: Posterior estimates from multivariate Bayesian beta regression models (logit scale). Model 1: trial-level effects of spectral slope background on relative total tracking duration (submodel 1), tracking during *courtship display* (submodel 2), tracking during *close courtship* (submodel 3), and tracking during *fan raise* (submodel 4). Model 2: Interaction effects of slope and area on relative total tracking duration per area (submodel 1) and tracking during *courtship display* per area (submodel 2).

		Model 1				**Model 2**	
Predictor		Submodel 1	Submodel 2***	Submodel 3***	Submodel 4***	Submodel 1	Submodel 2***
-1.0 vs -2.3		0.27 ± 0.26 [−0.24, 0.78]	−0.21 ± 0.20 [−0.61, 0.19]	−0.11 ± 0.25 [−0.58, 0.41]	0.18 ± 0.24 [−0.30, 0.66]		
	Inner Area					0.32 ± 0.33 [−0.29, 1.00]	−0.12 ± 0.31 [−0.71, 0.49]
	Middle Area					−0.08 ± 0.44 [−0.97, 0.75]	−0.00 ± 0.45 [−0.88, 0.86]
	Outer Area					0.10 ± 0.45 [−0.83, 0.97]	0.17 ± 0.43 [−0.68, 1.01]
-1.0 vs -1.7		0.38 ± 0.25 [−0.11, 0.87]	0.10 ± 0.21 [−0.29, 0.52]	0.27 ± 0.27 [−0.24, 0.80]	0.37 ± 0.24 [−0.10, 0.83]		
	Inner Area					0.32 ± 0.32 [−0.31, 0.96]	0.27 ± 0.32 [−0.35, 0.91]
	Middle Area					−0.07 ± 0.44 [−0.94, 0.78]	−0.13 ± 0.45 [−1.03, 0.78]
	Outer Area					0.09 ± 0.44 [−0.78, 0.94]	−0.12 ± 0.44 [−0.99, 0.74]
-2.4 vs -1.7		0.10 ± 0.23 [−0.34, 0.57]	0.32 ± 0.20 [−0.07, 0.70]	0.37 ± 0.23 [−0.09, 0.84]	0.19 ± 0.23 [−0.26, 0.64]		
	Inner Area					0.00 ± 0.29 [−0.57, 0.57]	0.39 ± 0.29 [−0.19, 0.96]
	Middle Area					0.01 ± 0.41 [−0.80, 0.80]	−0.12 ± 0.42 [−0.95, 0.71]
	Outer Area					−0.01 ± 0.41 [−0.83, 0.77]	−0.29 ± 0.42 [−1.09, 0.55]
Number of *wiggles***					0.27 ± 0.14 [−0.00, 0.54]		
Number of *runs***					−0.28 ± 0.13 [−0.54, −0.02]		
Courtship effort*		0.10 ± 0.07 [−0.04, 0.24]				0.11 ± 0.05 [0.02, 0.21]	
Male age**		0.09 ± 0.13 [−0.16, 0.35]	0.09 ± 0.17 [−0.23, 0.43]		−0.01 ± 0.19 [−0.39, 0.36]		
Female weight**							
Precision (φ)		−0.68 ± 0.90 [−2.45, 1.09]	0.93 ± 0.36 [0.26, 1.65]	0.45 ± 0.19 [0.08, 0.82]	−0.15 ± 0.29 [−0.71, 0.44]	0.29 ± 0.06 [0.18, 0.41]	0.40 ± 0.06 [0.29, 0.52]
Mean ± SD [CrI lower, CrI upper]							

Notes:

* PCA1 (number of *wiggles***, number of *runs***, duration *fan raise***) + duration *close courtship***

** z-scaled

*** corrected for beta-regression

4.4 Discussion

In peacock jumping spiders, males are highly conspicuous in colour and movement patterns, while female patterns are cryptic. This is reflected even at the level of second-order image statistics: male spectral slopes diverge from those of natural scenes, while female patterns closely match the spectral slope of their presumed natural background (Hardenbicker et al., 2025). In the present study, we provide evidence for the evolutionary relevance of spectral slope as a means of enhancing conspicuousness through background contrast, thereby increasing female attention and, presumably, mating success. We found that *M. spicatus* females responded more attentively when males courted against backgrounds that diverged from the spectral slope of the colour pattern on their fans, compared to when males displayed in front of a background with a matching spectral slope. These results suggest that signal-background contrast at the level of second-order image statistics increases visual salience and, consequently, attractiveness.

In Model 1 there was an overall effect of background spectral slope on female attention, in that females tracked males more when they were courting against random noise images with spectral slopes of -1.0 and -2.3 compared to -1.7. Event though none of the individual submodels detected a credible effect, the multivariate approach leverages shared information across correlated behaviours, improving sensitivity to detect subtle but consistent patterns. This is especially useful in behavioural studies, where individual measures are often noisy, yet high sample sizes are sometimes difficult to obtain (McElreath, 2020).

Our results support the idea that contrast in spectral slope enhances visual detectability and are in line with predictions derived from signal detection theory, in that signal-detectability drives female preference because it reduces the costs of decision-making (Wiley, 2006; Wiley, 2013). Signals that stand out from background noise are easier to detect, which may reduce the cost of mate assessment. A background with a similar slope to the male's pattern may reduce signal salience, hence, displaying in front of a background with contrasting spectral slope increases male attractivness byincreasing conspicuousness. Although we did not measure mating outcomes directly, female attention in salticids is a reliable indicator of reproductive success (Clark et al., 2002; Girard et al., 2015; Hebets & Maddison, 2005). Our results add to a growing body of research on visual properties including colour and luminace, showing that sexual selection favours signals that stand out from their environmental background (eg., Brumm & Todt, 2002; Clark et al., 2011; Kirschel et al., 2009; Marshall & Stevens, 2014; White et al., 2020).

We cannot exclude the possibilty that the background slope alone influences female behaviour, independent of its relationship to the male slope. *M. spicatus* show a preference for random noise images with a spectral slope of -1.0 (Hardenbicker & Tedore, 2023). Being exposed to the natural spectral slope may have a positive effect on females, conceivably enhancing receptivity or redirecting focus by reducing the need to escape. Yet, females show the same level of attention for males in front of backgrounds with a spectral slope of -2.3, which they did not show a preference for in the aformentioned study. If preference for the background slope alone would be causing the difference in tracking behaviour, we would expect increased tracking only on -1.0 backgrounds. This makes it more likely that the effect we observed was indeed based on how the male pattern interacted with the background, rather than the background alone.

Peacock spiders inhabit visually complex environments such as leaf litter and dense ground vegetation, where visual clutter makes it difficult for a small, visually guided animal to locate a mate. Since females are usually well camouflaged and remain still, males may struggle to locate them, given that salticids rely heavily on visual motion cues (Land, 1971; Zurek et al., 2010). Conspicuous display might provoke a female to orient reflexively toward the stimulus, resulting in the male seeing the female in turn (MCH, personal observation). In this context, visual conspicuousness may become critical not only for persuading a female to mate, but as an initial mechanism for overcoming camouflage and triggering detection. Moreover, during courtship, females appear easily distracted, requiring males to continually regain their attention (Girard et al., 2015; Girard et al., 2011), further emphasising the importance of effective visual contrast in maintaining engagement.

Model 2 found no interaction effect between spectral slope and the distance at which the male was displaying, indicating that how the male spectral slope was perceived in front of the background slope was consistent across distances. Previous work showed that spectral slopes of male peacock spider displays can vary depending on spatial scale. Using a different frequency range to calculate the spectral slope shifted the slope from the previously reported slope of -1.7 (Hardenbicker & Tedore, 2023) to a slightly steeper slope of -1.9 (Hardenbicker et al., 2025). Our results suggest that, within the spatial scale tested here, such distance-dependent variation does not significantly modulate female responses. One possible explanation is that the overall difference in slope between the male display and the background was sufficiently large to remain perceptually meaningful across distances. Alternatively, spectral slope contrast might not be relevant at all scales but function to attract females only at a specific distance, presumably at which contrast is highest. Females of the dipmorphic jumping spider *Maevia inclemens* chose mates according to which male attracts their attention first regardless of male morphology (Clark & Uetz, 1992). Interestingly, the two male morphs vary in successfully attracting female attention depending on the distance at which are are displaying. One morph was consistently more effecitve at a closer distance whereas the other morph attracted female attention first at a further distance (Clark & Morjan, 2001). In this system, first contact is sufficient to elicit female preference. Alternatively, *Maratus* females may not assess detectability continuously at all scales, but instead focus on different features depending on distance or context. Event though our results suggest that conspicuousness and detectability are driving female preference, different mechanisms may take effect in shaping female preference and consequently males' signals.

Males were surprisingly stable in their behavioural patterns across experimental conditions, even when confronted with different females (within-male Euclidean distances across all trials of behaviours relative to trial duration: median = 0.19, IQR = 0.03 – 0.35, Supplementary Data S2. This indicates that male coutship behaviour is consistent and independant of the female target. Cross-validation also showed that including trial order did not improve model performance, which is somewhat surprising. One might expect a habituation effect, such as reduced tracking in later trials, simply because the stimulus becomes familiar or less engaging. Either the spiders did not remember seeing each other the day before, or their behaviour is highly stereotyped.

In summary, our results show that females pay more attention to males when they are presented against backgrounds that differ in spectral slope from the male's display. This suggests that second-order image statistics, such as spectral slope, contribute to signal salience in a courtship context and are likely under selection. Contrast in spectral slope may represent an overlooked but important mechanism for increasing conspicuousness in visually complex environments in order to respond to a sensory bias towards signals that can be easily detected.

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Supplementary Data

S1: PCA of Courtship Effort

We performed a principal component analysis (PCA) on three male courtship behaviours, using the R base function `prcomp(scale. = TRUE)`. Behaviours included fan raise duration, number of wiggles, and number of runs per trial. All variables were z–scaled to unit variance. We retained only the first principal component (PC1), which had an eigenvalue > 1 and captured the majority of variance (60.1%).

Table 4.3: PCA summary statistics (left) and loadings (right) for courtship behaviours.

Component	SD	% Variance	Cumulative %
PC1	1.3433	60.1	60.1
PC2	0.9054	27.3	87.5
PC3	0.6130	12.5	100.0

Behaviour	PC1	PC2	PC3
display	0.657	0.127	0.743
wiggle	0.595	0.518	-0.615
run	0.463	-0.846	-0.265

S2: Within–Male Behavioural Consistency

To quantify within–male consistency across trials, we first converted all male behaviours (close courtship duration, fan raise duration, number of wiggles, and number of runs) into proportions by dividing by total duration for each trial. We then computed all pairwise Euclidean distances among these variables vectors using `dist(..., method = "euclidean")` in base R. Malespecific dispersions were extracted using the vegan package's`betadisper()` on the distance object, grouping by male. We summarize each male's dispersion by the median and interquartile range (IQR) of its within-male distance (0.193, IQR = 0.034–0.351).

5

General Discussion

Understanding the evolutionary forces that give rise to extreme and often seemingly arbitrary courtship signals remains one of the most intriguing challenges in behavioural ecology. While classical theories such as indicator models or the good genes hypothesis have provided robust frameworks in some contexts (Andersson, 1994; Griggio et al., 2010; Mcglothlin et al., 2008; Stuart-Fox & Ord, 2004; Zahavi, 1977), the adaptive nature of mating preferences has been hotly debated. For many sexual traits, adaptive mate choice theories alone may not fully explain the origin or spread of exaggerated and seemingly arbitrary displays (McCoy et al., 2019; reviewed by Jones & Ratterman, 2009). Sexual selection pressure must be potent enough to counteract the costs imposed by natural selection (such as predation risk), which often come with highly conspicuous signals (Heinen-Kay et al., 2015; Johnson & Candolin, 2017). A large body of theory has emerged, emphasising the evolution of non-adaptive mating preferences in the classical sense. In particular, the idea that mating preferences can arise from sensory biases has become a powerful framework to explain the evolution of arbitrary sexual traits (Endler & Basolo, 1998; Enquist & Arak, 1993; Prum, 2017; Prum, 2010, 2012; Renoult & Mendelson, 2019).

In this thesis, I explored how biases in visual information processing may shape sexual preferences and, in turn, influence the evolution of male courtship signals. Specifically, I focused on how the statistical properties of visual input may influence female choice. My investigations were guided by two theories that predict contradictory outcomes. The processing bias hypothesis posits that neural systems are adapted to efficiently process the natural world and elicit positive responses to stimuli that match these natural statistics (Redies, 2007; Renoult & Mendelson, 2019). According to this framework, mating preferences arise not from mate quality indicators but from the perceptual system's efficiency in coding redundancies. The second theory is based on assumptions from signal detection theory and predicts that traits are considered attractive when they are easy to detect, because it allows the receiver to make quick decisions in a noisy, unpredictable environment, thereby reducing metabolic energy. Here, preference is not for familiarity but for contrast, as more conspicuous signals increase detectability (Wiley, 2006; Wiley, 2013).

The Role of Natural Image Statistics in the Evolution of Courtship Signals

Perhaps what intrigued me most when I began this thesis was the idea that there may be a universal mathematical formula underlying our perception of beauty. Human psychophysical studies show a general preference for the *natural spectral slope* in random noise images (Isherwood et al., 2017; Spehar et al., 2015), suggesting that a simple mathematical property can elicit aesthetic responses. Such a preference may reflect a prossessing bias and thus drive the evolution of courtship signal design.

The results of my thesis do not support the idea of such a processing bias driving the evolution of colour patterns in male *Maratus* spiders. Male patterns differed significantly from those of natural scenes; however, female colour patterns matched closely with the natural slopes (Chapter 3). For male *M. spicatus*, we measured spectral slopes of -1.7 and -1.9 (Chapter 2 and Chapter 3, respectively), diverging significantly from the average slope we measured for images of natural scenes: -1.1 (Chapter 3), which closely matches the natural slope of -1.0 ($\pm\,0.2$) found in previous studies (Field, 1987; Pamplona et al., 2013; Párraga et al., 2000; Tolhurst et al., 1992; van der Schaaf & van Hateren, 1996). From cuttlefish, it is known that matching the spectral slope with the slope of the background enhances camouflage, while contrasting spectral slopes enhance signal salience (Barbosa et al., 2008; Zylinski et al., 2011). A similar principle seems to be operating in the *Maratus* genus. While males express traits that are boldly coloured and visually prominent, female traits and behaviours suggest that their main concern is blending in, aligning with the results of our spectral slope analyses. Female spectral slopes closely matching those of natural scenes further suggest that the natural slope of approximately -1.0 is indeed representative of *Maratus* habitats and supports the notion that this slope is prevalent in the natural world. Though we cannot rule it out, it is unlikely that diverging male spectral slopes reflect habitat-specific image statistics, as suggested by Hulse et al. (2020). However, there may be a trade-off between detectability and responding to the tuning of the visual system, such that slopes evolved to be just distinct enough from the background to enhance detectability without deviating so far as to become too costly to process.

Though I could not confirm that *Maratus* spectral slopes underlie a potential processing bias, I did find evidence that a general preference for the natural slope, as exhibited in humans, is also present in *M. spicatus*. Male, female, and juvenile *M. spicatus* spent more time oriented towards random noise images with a slope of -1.0 compared to a slope of -1.7 (representative of the male colour pattern in this species). When presented with the male slope versus a steeper slope of -2.3, however, they showed no preference (Chapter 2). This suggests that efficiently coded signals do elicit a preference, yet males do not seem to exploit this by evolving signals that match the preferred statistics. With these results, I provide the first evidence that a preference for efficiently coded signals exists in a species other than humans. However, to confirm whether -1.0 is the peak preference, follow-up experiments that include a finer resolution in the spectral slopes are needed. Even if not reflected in the evolution of courtship signals, finding evidence for such a preference based on efficient coding is very intriguing and warrants further testing in other species.

Additionally, Chapter 4 provides evidence that the spectral slope of male displays is indeed relevant in a mating context, in that signal–background contrast increases female attention, thereby potentially enhancing the male's chance of mating (Chapter 2). Although effects were subtle, females tracked males less when they were courting against matching backgrounds with a slope of -1.7 compared to contrasting backgrounds with slopes -1.0 and -2.3. Female attention has been linked to mating success in other salticid species (Clark et al., 2002; Girard et al., 2015; Hebets & Maddison, 2005) and seems to be a reliable indicator of preference. However, ideally, this relationship should be confirmed in *M. spicatus* by directly testing actual mating outcomes. Still, my findings contribute to the broader body of literature on sexual selection favouring signals that contrast with their environment (Brumm & Todt, 2002; Clark et al., 2011; Endler & Thery, 1996; Fleishman, 1992; Kirschel et al., 2009; Marshall & Stevens, 2014; White et al., 2020). Spectral slope likely represents another, less commonly studied factor contributing to selection for conspicuousness in visual sexual signals. Whether this is a general feature of sexual signalling across the animal kingdom, or specific to certain evolutionary contexts (such as being small and operating in visually cluttered habitats) remains unclear, pointing to the need for further studies across a wider range of taxa and ecological conditions.

Broader Implications: Mating System and Evolutionary Pressures

Throughout my PhD journey, I developed a deep appreciation for these tiny but extraordinary spiders. My initial curiosity about the evolution of their seemingly extravagant courtship displays gradually expanded into a broader fascination with their natural history and mating ecology. One memorable field experience involved locating *M. karrie* at a site where males were densely aggregated, displaying at very close distances. This unusual clustering led me to suspect that *Maratus* might exhibit lekking behaviour, i.e., that males aggregate in display sites to compete for females.

Although evidence remains anecdotal, *Maratus* may exhibit several characteristics associated with lekking systems: (1) elaborate and diverse male courtship displays, (2) female-only mate choice, (3) high variance in male mating success, and (4) absence of male parental investment (Bradbury et al., 1986; Bradbury, 1977). Conspicuousness and signal complexity seem to be key determinants of mating success in lekking systems, as males must compete for limited female attention. Birds of paradise that display in classic leks have greater color richness, corresponding to the increased strength of sexual selection on males to stand out visually when being evaluated simultaneously in lekking contexts (Ligon et al., 2018). Despite strong sexual selection, examples like birds-of-paradise show that lekking does not necessarily preclude species diversity, but rather that it can foster both exaggerated signal diversity and high rates of speciation (Irestedt et al., 2009), patterns that are consistent with the remarkable diversity observed in the *Maratus* genus.

My own experience with breeding *Maratus* in the lab further supported this idea as despite considerable effort, establishing breeding populations proved difficult. Females were extremely choosy, and in species other than *M. spicatus*, mating rarely occurred, if at all. In lekking species, mating success is typically skewed toward a small number of males, and females are exposed to a wide array of displaying males to choose from (Emlen & Oring, 1977). One-on-one mating encounters may therefore be unfamiliar, potentially reducing female willingness to mate. Notably, even under controlled laboratory conditions, females showed considerable variation in moult intervals (2 to 12 weeks) and in the number of moults (4 to 7), suggesting asynchrony in female receptivity. This variation may further promote lekking as a mating strategy, as asynchronous and short-lived female receptivity is thought to favour male aggregation and facilitate female choice during narrow fertile windows (Emlen & Oring, 1977).

Another noteworthy observation was the lack of cannibalism. Based on my experiences, the popular depiction of *Maratus* males “dancing for their lives” does not appear to be very accurate. Even after rejecting males multiple times, females were rarely aggressive. On the rare occasions when a female jumped at a male, it never resulted in cannibalism, suggesting that such behaviour is not typical in this species. In the lab, females were well-fed, so their responses might vary depending on hunger levels. However, given the abundance of prey in their natural environment, this seems unlikely.

Taken together, these behavioural and reproductive patterns in *Maratus* strongly hint at a lek-like mating system, which may help explain the exceptional diversity and signal elaboration observed in the genus. However, this hypothesis remains highly speculative. Investigating whether *Maratus* truly conform to a lekking mating system represents a promising avenue for future research.

Methodological Reflection: Limitations of the Spectral Slope

This discussion of my thesis also provides an opportunity to critically evaluate the relevance of spectral slope as a feature for investigating the link between visual input and neural adaptations that reduce processing costs. The consistent preference for natural spectral slopes observed in humans and *Maratus* spiders, alongside its prevalence in aesthetically pleasing human art, suggests that efficient processing may indeed influence the perception of beauty (Hardenbicker & Tedore, 2023; Isherwood et al., 2017; Redies et al., 2007; Spehar et al., 2015).

However, the relationship between the spatial statistics of male colour patterns and female perception is likely more complex than spectral slope alone can capture. Although scale did not affect female behaviour in our experiments (Chapter 3), viewing distance may alter the range of spatial frequencies accessible to the female, potentially changing the relative strength of these frequencies and thus the perceived contrast with the background. A spectral slope of -1.0 is traditionally considered scale-invariant, implying equal energy across spatial frequencies (e.g., Field, 1987). Adjusting the frequency range in our analyses led to slight shifts in spectral slope, hinting that scale invariance may not hold for slopes differing from -1.0. Additionally the discrete nature of the 2-dimensional Fourier transform used for digital images imposes limitations: the number of sampling orientations increases exponentially as a function of frequency: lower frequencies are sampled less than higher frequencies, meaning information may be incompletely captured in lower frequencies.

Some authors argue that it is physiologically unrealistic to assume visual processing operates the same way a Fourier transform does(e.g., Troscianko & Osorio, 2023). Instead, oriented Gabor filters, which resemble the receptive fields of retinal ganglion cells and simple cells in the mammalian visual cortex, may provide a more biologically plausible framework for modeling efficient coding (Olshausen & Field, 1996). While I found evidence for a preference for natural spectral slopes, attributing this preference solely to processing efficiency remains speculative, as the true nature of spider visual processing is unknown, and current assumptions rest on correlational evidence.

Additionally, *M. spicatus* exhibits relatively stationary courtship displays, but other *Maratus* species employ complex movement patterns that likely influence temporal perception of spatial frequencies. The presence of multiple pairs of eyes, whose functions and integration remain poorly understood, further complicates our understanding of spider vision. Thus, while spectral slope is a useful starting point, a comprehensive understanding of signal perception in these spiders will require methodologies that better reflect the structure and function of their visual systems.

Conclusion

This thesis offers novel insights into how visual preferences may shape the evolution of courtship signals. Across behavioural experiments and comparative image analyses, I showed that *Maratus* spiders exhibit a general preference for natural image statistics, yet male colour patterns diverge from these statistics, suggesting that sexual selection acts predominantly on detectability rather than efficient processing. Ultimately, this work contributes to a growing understanding that signal evolution results from a negotiation between the sender's need to be seen and the receiver's capacity to perceive, all shaped by environmental constraints. The *Maratus* genus, with its vibrant diversity, provides a rich model for future studies on how information processing and selection pressures interact to sculpt the spectacular displays we observe in nature.

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