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The evolution of colouration in parrots (Psittaciformes).

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The evolution of colouration in parrots (*Psittaciformes*).

Abstract:

The aim of this study is to investigate the colouration of parrots in an evolutionary context utilising novel metrics for the quantification of colour pattern. Previously, the study of animal colouration has been limited by its inability to produce statistically robust and objective measures of pattern. We propose the use of image correlograms, a method adapted from the field of computer science where it is used in the indexing and retrieval of images for search engines, in order to evaluate the whole colour pattern of parrot species as taken from field guides. This is the largest study of parrot colouration in terms of number of species included in the study (403) and includes the ancestral reconstruction of the original parrot's colouration as well as how colouration has changed over time. Finally, the information gained on the parrots' colouration is applied to an issue of pressing concern for those studying the conservation of parrots, how differences in colour pattern relates to conservation status.

Introduction:

Body colouration has been found to underpin a wide variety of animal communication, as evidenced by the expansive list of papers published on the subject (Osorio and Vorobyey, 2008). Numerous reviews cover important behaviours such as predator avoidance by employing camouflage (Kelman et al., 2008; Stevens and Merilaita, 2008; Stuart-Fox and Moussalli, 2008) or aposematic warnings (Merilaita and Kaitala, 2002; Summers et al., 2015) as well as the mimicry of these signals by less dangerous animals (Cuthill and Bennett, 1993). There has also been much investigation into the role of colouration in sexual selection (Bennett et al., 1994; Roulin and Bize, 2007; Wellenreuther et al., 2014).

What this work demonstrates is that the use of colour and pattern is repeatedly integral to the communication behaviours of many visual animals (Cuthill et al., 2017). With such a number and variety of examples, it is unsurprising that the importance of understanding differences in the colouration of animals has long been recognised. Detailed measurements of the colouration animals display are needed in order to gain a full understanding of its diversity. However, until recently, the most common method of quantifying a colour pattern has been the use of subjective classifications, such as a butterflyfish having different sized spots and stripes (Kelley et al., 2013) or a snake's patterning being defined as containing either longitudinal or transverse stripes (Jackson et al., 1976). Another study looked at the presence or absence of conspicuous eye spots in the colouration of lizards, manually categorising the spots as conspicuous when they contrasted with the lizard's background body colouration based on an observer's visual inspection of spectrograms (Pérez et al., 2016). This type of

dichotomous classification can be useful for answering specific questions about variation in animal colouration, such as differences in male and female colouration (Marchetti, 1998) but it inevitably removes any variation within a category and as such limits the power of an analysis to detect evolutionary changes (Allen et al., 2013).

In an effort to overcome these limitations, more comprehensive measures of quantifying colour patterns have been proposed. Kiskowski, et al (2019) quantified the spot pattern within a specific circular zone on the head of eight leopard geckos.

Measures included the mean size, area and roundness of the spots within the pattern, as well as the mean area of dark (melanistic) pixels within the image for each gecko and the average distance between pattern elements. Although more sophisticated in how the pattern is quantified, the analysis was restricted to a single analogous area on the head of the geckos. Continuing with the study of reptile patterns, a measure combining both the length and contrast of longitudinal and transverse stripes in snakes, as well as the presence and absence of spots was proposed to quantify the “stripedness” of a snake’s pattern (Brodie, 1992). This is a step in the right direction in that what resulted was a continuous measure of an animal’s pattern, however the selection of specific elements of the pattern is based on the author’s perception and so it is possible that so far unidentified biologically relevant pattern traits are ignored (Tanaka and Mori, 2007).

Endler and Mielke (2005), recognised that the colour pattern of an animal, in this case birds, is made up of patches of different size, shape, colour, brightness and position that fit together to create a mosaic image. For this reason, most studies on the colouration of birds are limited by the traditional approach of concentrating on the

analysis of only a small number of patches, often only one or two and ignoring the rest of the pattern (Andersson and Andersson, 1998; Pearn et al., 2001; Siitari et al., 2007). In this study, plots of the percentage of light reflected at each colour wavelength (reflectance spectra), of each patch within an image was recorded. These were used to calculate the four photon capture values (the amount of energy captured by each of the four cones in a bird's retina) of each patch. This results in a matrix of values where the photon capture value of each cone makes up a row and the number of columns is equal the number of patches sampled. Storing the colour information of an image thus allows for the statistical comparison of two entire colour patterns, each containing multiple different colour patches.

While this method enables the comparison of colour patterns, the photon capture matrix cannot be used to investigate differences in the location of colour patches relative to each other within a pattern. This limitation was addressed in a 2012 paper (Endler, 2012) that again used reflectance spectra, this time collected in a grid. This resulted in an analysis that considered not only the colours of a pattern, but also which patches appeared adjacent to each other, referred to as the geometry of the pattern. From the data collected, metrics for quantifying colouration were developed, including "transition density", a measure of complexity based on the number of transitions from one colour to another within a pattern.

In this study we aim to combine the sophisticated quantification of colour pattern with the principles of colour pattern geometry in order to analyse the whole-body colouration of parrots (Psittaciformes).

Considering the utility of being able to compare the whole pattern of an animal as a continuous variable, we propose the use of image correlograms (see Chapter Two) in order to store and analyse colour information. Image correlograms are used in computer science to store the colour and spatial data of an image for indexing and retrieval in search engines (Kunttu et al., 2003). Similar to a histogram, they consist of the information on hue and number of pixels within an image, as well as their relative positions. This added spatial dimension is what will enable us to overcome the limitations of previous studies investigating the whole-body colouration of animals discussed at the beginning of this section.

In this study, I have used parrots as model group in order to investigate the evolution of colour patterns. The order Psittaciformes, consisting of the superfamilies Psittacoidea ("true" parrots), the Cacatuoidea (cockatoos), and the Strigopoidea (New Zealand parrots) exhibit some of the most striking examples of colouration in the natural world (Forshaw, 1989; Juniper and Parr, 1998). The order morphologically distinct from other bird lineages and as such are easily recognised by characteristic shared features such as their hooked bills with a fleshy cere, zygodactyl feet and colourful plumage (Hackett et al., 2008). These features, along with the ability of some species to mimic human voices, make them a very charismatic order that have also long been popular as pets and are traded both legally and illegally worldwide (Shephard, 1994). Parrots are also of special conservation concern globally with 56% of all species in decline and 112 at risk of extinction (Juniper and Parr, 1998). Many areas of Psittaciform biology have been studied closely (Forshaw, 1989; Juniper and Parr, 1998). However, regardless of a trend towards the study of avian colouration

generally, the number of papers on the colouration of parrots is sparse. Consequently, we currently have surprisingly little understanding of the evolution and ecology of their colouration. Compared to other lineages, such as the Passeriformes (song birds), the processes behind the diversity of parrot colouration are not yet well understood. Reviews on the evolution of colouration of many different bird groups, both on its function and the mechanisms behind it, have been published in the last ten years (McGraw and Hill, 2006; Bennett and Théry, 2007; Protas and Patel, 2008) but these often focus on the song birds, with little attention given to parrots. The pigmentation of parrot feathers is different to all other birds. As well as structural colouration and melanin, the parrots utilise a suite of unique pigments called psittacoflavinins (McGraw, 2006; Berg et al., 2019), named as such because they have only been found in the parrots. Differences in the production, development and evolution of colouration means that knowledge of one group of birds can not necessarily be applied to other groups. This study will add to our understanding of avian colouration by investigating the evolution and distribution of Psittaciform colouration.

The following chapter will focus on how field guide plate illustrations were used for the collection of colour data and how these data were applied to the reconstruction of the colouration of parrots' common ancestor. This will be the first time colour data from such a large set of extant species (n= 404) will be used in such a way, and will contribute to evidence of the root ancestor's appearance and life history. Chapter Two will address the problem of quantifying animal colouration by detailing the creation of three colour metrics from the novel use of image correlograms in the study of animal

colouration. These can then be applied to estimating how the colour patterns of parrots have changed over evolutionary time. Finally, Chapter Three will apply the knowledge gained about the colouration of extant species to a real-world problem by investigating the relationship between a species' colouration and its conservation status.

Chapter One: The ancestral reconstruction of parrot colour patterns.

Introduction:

Parrots are one of the most diverse groups of birds (Toft and Wright, 2015). As well as the variation in the colours and patterns they display, they also range in size from around 10g for the pygmy parrots (*spp. Micropsitta*) to the giant macaws (*spp. Anodorhynchus*), over 100g (Juniper and Parr, 1998). Despite this variation in colouration and body size, the parrots are also one of the most physically homogeneous groups of birds. Characteristic features such as the curved upper beak with a fleshy cere, large head and stout body (Forshaw, 1998) unite the Psittaciformes and separate them from other bird lineages. This morphological distinctiveness, diversity of colouration, and the amount of colour information available from field guides make the parrots a textbook model for studying how evolution can lead to the diversification of colour pattern from an ancestral root.

The importance of evolution's role in colouration has been recognised since the time of Darwin and Wallace (Beddall, 1972). Animal colouration provided valuable early evidence for evolution by natural selection, at a time when very little evidence was available. Colour patterns often fall into two categories; bright and contrasting, as seen many parrot species (Dawkins and Guilford, 1997), the macaws (*Ara*) being a familiar example; or dull and cryptic colouration. In order to understand the adaptive significance of an animal's colouration we need to know about their evolutionary history, specifically how certain colour patches and patterns come to be; how often they evolve and how they differ from ancestral species.

Currently there are no examples of attempts to recreate an image of the appearance of the most primitive parrot species, those at the root of the Psittaciformes phylogeny, in the literature. This is likely due to the different methods used to reconstruct ancestral forms and their limitations (Toft and Wright, 2015).

One of the simplest methods involves looking at the “most primitive” extant species, the one most directly related to the root ancestor (Crisp and Cook, 2005; Amemiya et al., 2013). This method is based on the assumption that an early splitting clade would more closely resemble the ancestor species. However, observing the branch lengths of most phylogenies show that all existing parrots would have had roughly the same amount of time to evolve differences from their common ancestor (Felsenstein, 1988). Generally, one extant species does not provide more information about the appearance of the common ancestor than any other within the clade (Toft and Wright, 2015).

Fossil records are also used to aid reconstruction but the conditions for fossilisation and preservation are rare, especially in birds due to their fragile bones, resulting in large gaps in the fossil record. Indeed, of the few fossils that are confidently classified as Psittaciformes, we only have very small fragments (Stidham, 1998 & Waterhouse, 2006). Were there fossils to be studied, they would not be practical for the investigation of colouration of parrots. Recent work has been done on the analysis of the structural colouration of fossilised bird and dinosaur feathers (Vinther et al., 2009) but as pigments are not preserved, they can tell us very little about an animal’s colouration other than the presence of structural colouration (the physical properties of the feather, utilised to refract and reflect light at different wavelengths).

Another method considers the current traits of extant species and, uses an existing phylogeny as a scaffolding on which to build estimates of how those traits came to be, with the minimum amount of change from the common ancestor to the present-day descendants, in a process called ancestral state reconstruction (Cunningham, 1999). This method benefits from being able to draw from larger datasets than the fossil record as measurements from photographs, museum specimens and illustrated field guides can be used. Rather than focussing on one descendant to estimate appearance, this method utilises information from all extant species that share the root ancestor, weighted by the branch length data of the phylogeny (Omland, 1999).

Ancestral state reconstruction has been used before to study the colouration of birds, lizards (Stuart-Fox et al., 2004; Perez and Font, 2016 & Murali et al., 2018) and fish (Kelley et al., 2013). These studies often involve the classification of different colour patches or pattern types, for example the presence or absence of lateral stripes (Murali et al., 2018). A major disadvantage of presence or absence data is the difficulty of classifying intermediate states, for example in the Murali study (2018) stripes were only classified as present if stripes they “were clearly visible and occurred throughout [the lizards’ colouration], from the tip of the snout to tail base”. This definition would presumably discount faint markings or shorter stripes, calling into question the accuracy of the subsequent reconstruction as gradual changes in pattern are not considered. This methodology is useful for the ancestral state reconstruction of particular elements of an animal’s colouration but would not produce a complete image of what an ancestor would be estimated to have looked like.

In order to produce detailed images of ancestral reconstructions we propose a method of using colour plates from parrot field guides and taking the colour value of each pixel for each species images in order to build ancestral state reconstructions pixel by pixel. This would negate the need for the subjective classifications of colouration, allow for the inclusion of subtle changes in colouration and the analysis of the whole colour pattern.

Methodology:

Constructing phylogeny

A representatively average tree for use in the phylogenetic analysis and ancestral reconstruction of colouration and shape was obtained by calculating the median of 10,000 trees from birdtree.org. Using the “treedist” function in the R package phangorn (Schliep et al., 2017), the branch score distances (Kuhner and Felsenstein, 1994) between the trees were calculated and the ‘middle’ or median tree is the one with the smallest distance to all other trees. This is similar to building a consensus tree, except that this method allows us to retain the branch length information needed to carry out any ancestral reconstruction of traits. The phylogeny of the parrots is a fairly robust one, based on several studies utilising molecular dating and biogeographic patterns (Wright et al, 2008; Groombridge et al, 2004; Ribas and Miyaki, 2004; Cracraft, 2001). As such the branching pattern for the major groups of parrots is well established with differences between hypothesised trees revolving mostly around rearrangements of species within larger clades.

Extinct species were dropped from the tree and subspecies added using 'ape' (Paradis et al., 2004) and 'phytools' (Revell and Revell, 2019) packages in R v. 3.6.0 (The R Foundation for Statistical Computing, 2019 <http://www.R-project.org>)

respectively. Where multiple subspecies were attributed to a parent species, they were attached to the parental species first, and then randomly to one another at half the distance of the parent species to the next node. Once complete our time-calibrated phylogeny consisted of 403 nodes (including species and subspecies).

Colour and shape data

High-resolution scans (4936 x 3520 pixels) of colour plates from *Parrots of the World* (Forshaw, 1998) were converted to TIFF files and used for subsequent analyses.

Handbook illustrations are created to facilitate the identification of species based on their appearance. For this purpose, the parrots are illustrated as accurately as possible in order to depict the typical colouration and patterning of each species. The use of plates over live specimens is much more space and time effective. A single live specimen may also not be representative of the species as a whole, particularly if comparing a captive bred bird to its wild counterparts.

Thirteen landmarks (Figure 1a) were selected to define the outline of the parrot by encompassing characteristic features: five points around the beak, one in the centre of the eye, four around the wing and another three to mark the tail.

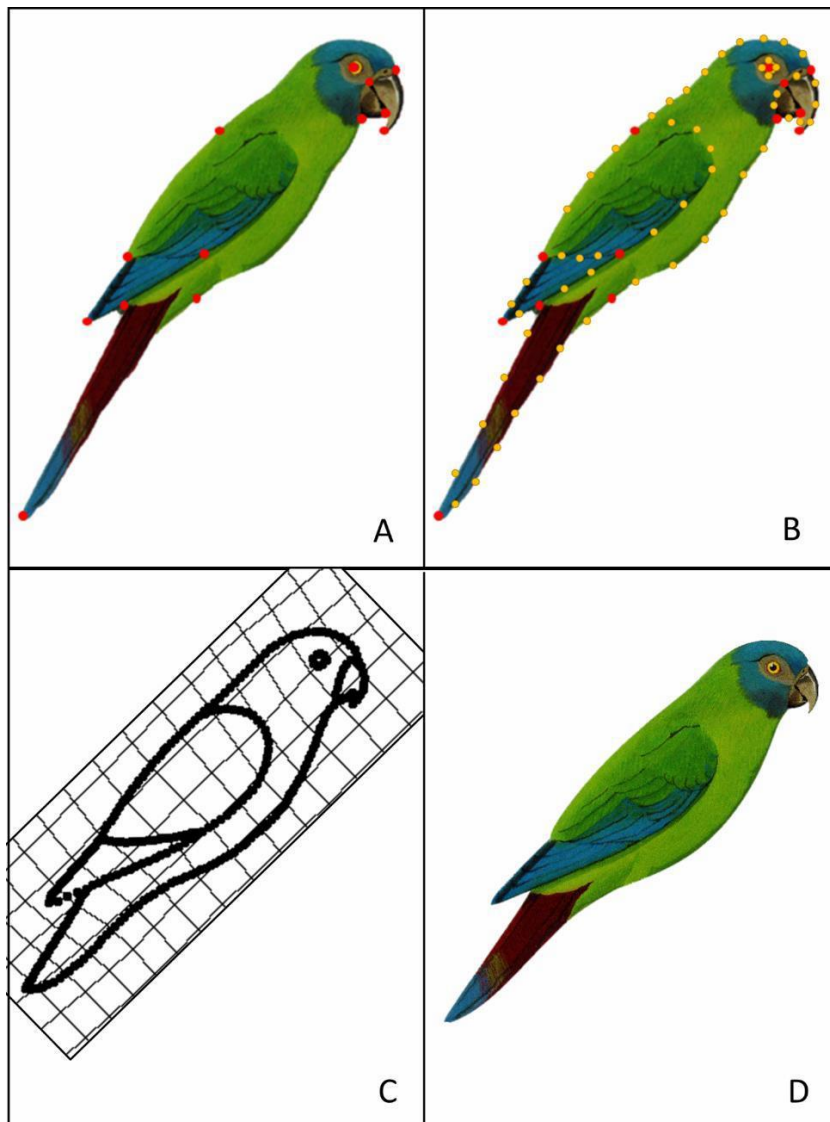


Figure 1: An example of how the colour pattern of a parrot species (*Prioniturus couloni*) was warped into an average parrot shape. Starting with the selection of 13 landmarks (A) shown in red, which are then connected to build an outline of the parrot (B).

The landmark positions were manually inputted using a custom Matlab graphical user interface (GUI) which also allowed the researcher to fill in the outline with an indeterminate amount of points (Figure 1b). The software then used the outline indicated by the researcher to generate a set of 300 equally spaced coordinates for the shape of each parrot.

To account for size and orientation differences in the original images, a procrustes fit was performed on the coordinate data using the “gpagen” function of the ‘geomorph’ (Adams and Otárola-Castillo, 2013) package in R. The outlines are resized, shifted into the same position and rotated to the same orientation. From this, principal component scores were calculated from the transformed coordinates, the principle components are dimensionally transformed coordinates that allow for the multifactor shape variables to be plotted into 2-dimensional morphospace, whilst retaining as much information as possible. The colour patterns of each parrot were then warped onto the average parrot shape (Figure 1d), so that for each species there was an equal number of pixels. Having all the species being the same size and with the same orientation allows us to compare differences in the colour pattern using the homologous pixels in specific areas across all species and subspecies in our dataset.

To enable a valid comparison between the images, plates that did not show a species in full lateral aspect were discarded. Males and females of sexually monochromatic species were generally represented by one image ($n = 270$). When the sexes of a species were represented by two illustrations, the male was more often prominent on the page and obscured regions of the female or else only a partial image showing the dichromatic colour patch was given. In these cases, only the male parrot’s image was used ($n = 134$). In total, the landmark coordinates of 416 parrot images were collected, twelve of which were later found to be extinct and so were dropped from the data set.

Ancestral reconstruction

We reconstructed the maximum likelihood ancestral colouration, shape and size of the parrots at each internal node ($n = 403$) of our phenology using the “ace” function of the ‘ape’ package in R and the branch length data contained within the tree.

For the colouration, the ancestral RGB values of each pixel in the warped images were computed pixel by pixel, separately for each colour channel (red, green and blue) and mapped onto an empty average shape image in order to produce a complete ancestral colour pattern, along with 95% confidence interval images. This method produces reconstructed images with a more detailed and intricate colour pattern than previous studies that categorise pattern types (Lanzua and Font, 2016), reconstruct the image region by region or perform analysis on the presence or absence of specific colour patches. To complete the reconstructions, the PC scores of body shape were used to calculate the estimated ancestral shape at each internal node, onto which the corresponding reconstructed colour patterns were superimposed.

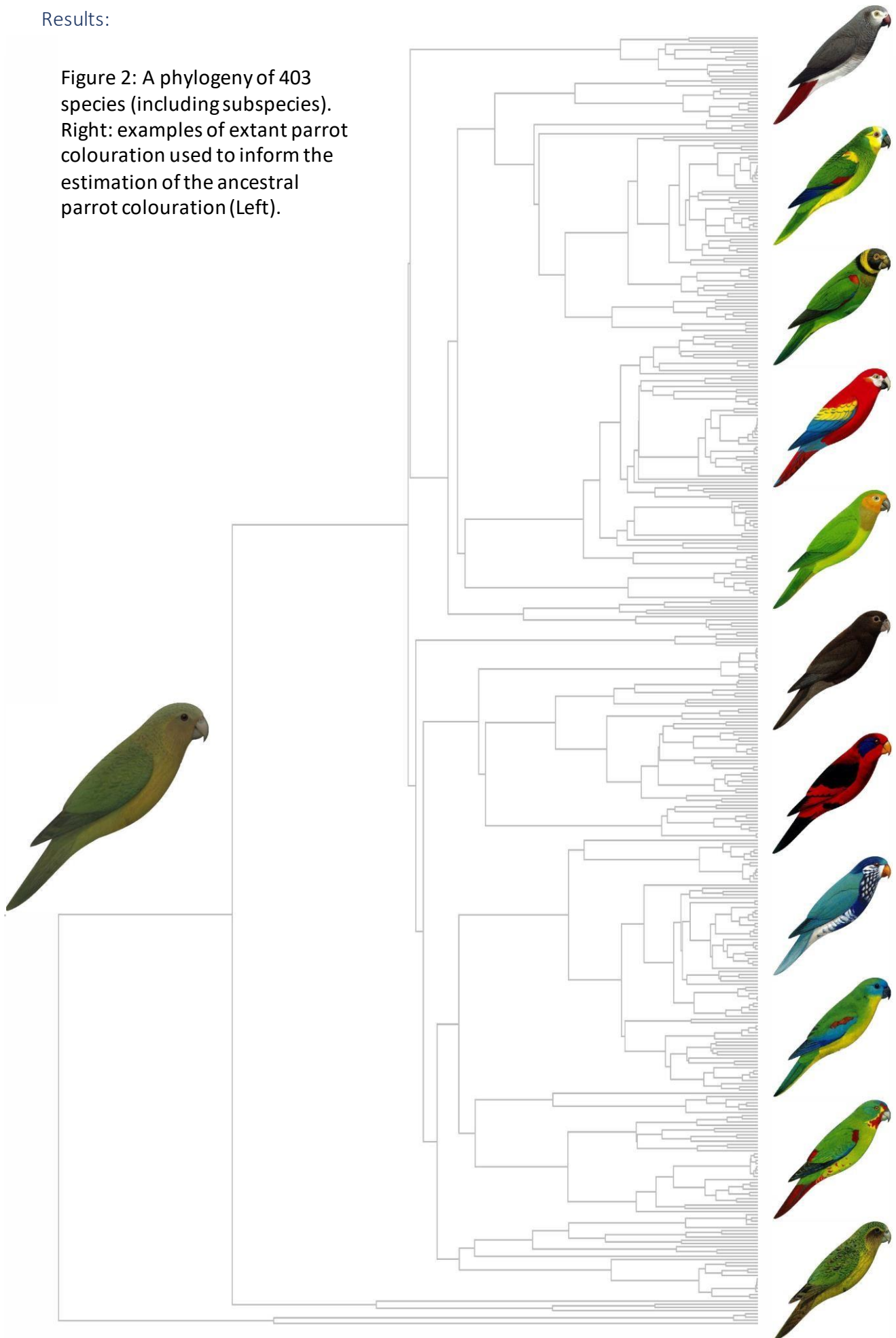
Estimating phylogenetic signal

The effect of phylogeny on the differences between the RGB values of the same pixels across the extant species was accounted. Pagel’s lambda is a measure of phylogenetic signal (Pagel, 1999) which ranges from 0, indicating that the evolution of the colouration is phylogenetically independent and not a result of the relatedness of species; to 1, a strong phylogenetic signal predicting the accumulation of traits over time in direct proportion to the length of the phylogeny’s branches (Brownian motion).

An image containing the phylogenetic signal of each pixel was generated in R using the 'geiger' (Harmon et al., 2007) package pixel by pixel, for each colour channel.

Results:

Figure 2: A phylogeny of 403 species (including subspecies).
Right: examples of extant parrot colouration used to inform the estimation of the ancestral parrot colouration (Left).



Ancestral reconstruction of the root species produced a detailed image of a squat, mottled green and brown parrot with a dull grey beak, brown iris and no colourful eye-ring (Figure 3).



Figure 3: The estimated ancestral state of the Psittaciformes' root ancestor as a result of a pixel by pixel reconstruction of the colour values.

The pixel by pixel reconstruction of each node allowed for the accumulation of colour patches to be observed over time. As an example, the root ancestor for the Amazona genera (Figure 4a) is a green parrot with a blue wing tip and a small red patch on the outside edge of the wing; at one of the next nodes, the radiation of the five Amazona

Ochrocephala subspecies (Figure 4b), the blue and red of the wing is more vibrant and the red patch is larger. The cap of the Ochrocephala root was yellow, whereas the earlier ancestor's head was green with a paler green patch on the cap.



Figure 4: A: The estimated reconstructed state of the common ancestor of Amazona. B: and Amazona ochrocephala.

Phylogenetic signal

Figure 5a depicts the effect of phylogeny on the RGB values of each pixel using a grey scale to represent the lambda value. Lighter regions have a lambda value closer to 1, meaning that there is an effect of phylogeny on the colouration of these regions. Black indicates a pixel with a lambda value of 0, meaning there is no phylogenetic signal. Our results indicate a stronger phylogenetic signal on the beak, forehead and belly. Regions with less phylogenetic signal include the cap of the head, the throat and the lower wing.

Figure 5b depicts the significance of the lambda values shown in 5a, pixels with a lambda value significantly different from 0 are coloured black. The white pixels on the wing and the iris indicate regions where the colouration does not have a lambda value significantly different from 0.

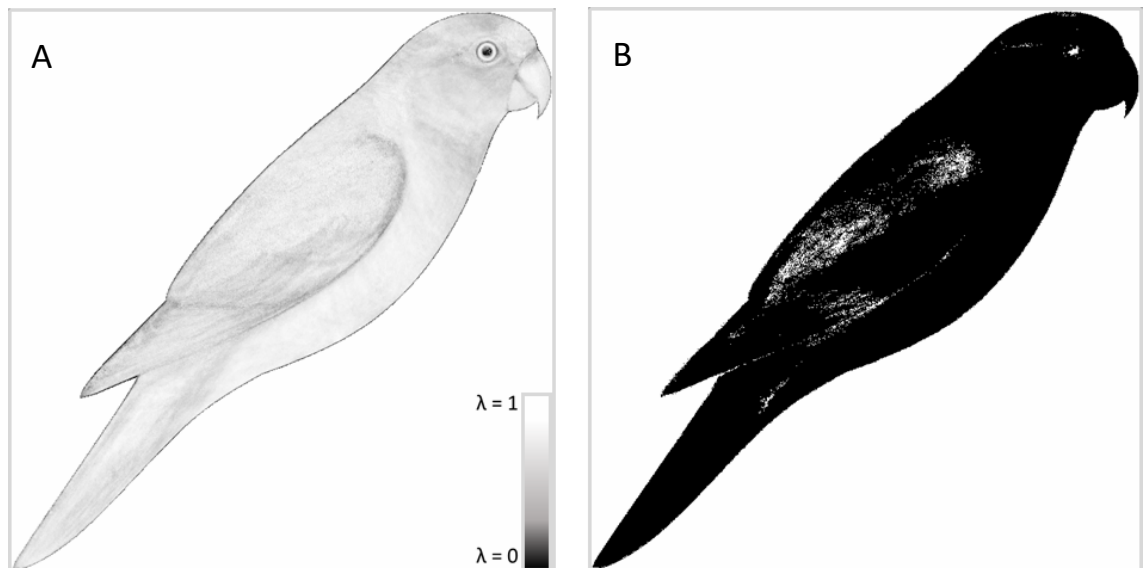


Figure 5: A and B both show an 'average' parrot shape. A: depicts the value of lambda. B: shows the p-value of lambda at each pixel location (black = lambda significantly different from 0).

Discussion:

We have shown that our method of building an ancestral reconstruction of colouration pixel by pixel is effective at producing clear and detailed estimates of ancestral parrots. The estimated colouration of the root ancestor of the Psittaciformes is relatively dull compared to the vibrant and often complex colouration of some of its descendants. This movement towards diversity of appearance is to be expected from a radiation as

rapid as that of the parrots (Wright, 2008) into a wide range of habitat, dietary and behavioural niches.

The kakapo (*Strigops habroptila*) and the nestor genus being the most direct descendants of the first parrot, share some features of their colouration. The dabbled green colouration of the root is somewhat similar to that of the kakapo (Juniper and Parr, 1998) that helps to camouflage it in the mossy understory of its New Zealand forest habitat (King et al., 2015). That the first parrot species is estimated to share this colouration, suggests it may have lived in a similar habitat (Stevens and Merilaita, 2015).

Neither the kaka (*Nestor meridionalis*) nor the kea (*Nestor notabilis*) bear a strong anatomical resemblance to the root species. Despite being very closely related to the first parrot, both are far from primitive. They are highly adapted to their environments, one noticeable feature being their large hooked beak indicative of their omnivorous diet (McNab and Salisbury, 1995). This is further evidence that the number of branching points between a descendant and its ancestor, does not determine how closely they will resemble each other.

Figure 2 demonstrates how the use of our method overcomes the limitations of presence/absence ancestral reconstruction by showing how different elements of colouration likely became more prominent over evolutionary time. Reconstruction of the yellow cap for example, using a presence/absence method would lead a series of ancestors without yellow colouration, followed by its sudden appearance when a certain threshold is reached. The gradual accumulation or loss of colour patches will

allow us to better make inferences about a species' evolutionary history based on their colouration.

Being able to look at different colour patches in one image and how they interact with each other is also valuable and can offer insights into the use of complex colour signals in many different animal behaviours.

From our results it appears that the areas of the body where colouration is most influenced by the species' ecology is the cap, cheek, throat and some areas of the wing (Figure 5a). One explanation for difference in interspecific plumage colouration in birds is to enable the recognition of species, thus reducing the risk of hybridisation of sympatric populations (Wallace, 1889; Grant and Grant, 1992). This would mean that colour differences between closely related species of birds would be caused by the character displacement of colouration used in reproductive signalling (Pfennig and Pfennig, 2009). The location of colour patches where phylogenetic signal is low, namely the head and face area could lend support to this explanation because of their conspicuousness. An alternative explanation is that interspecific variation in plumage colour is an adaptive response to variation in light environments across habitats (Endler and Mielke, 2005).

An area of interesting further study would be to look at the relationship between the parrots' colouration and elements of their ecology, in order to determine the mechanism driving the variation in colouration. Some parrots are also capable of perceiving ultraviolet light, and ultraviolet colour patches have been discovered to be present in the colour patterns of budgerigars (*Melopsittacus undulates*) and to influence female mate choice (Pearn et al, 2001). Further investigation into other

species that may possess ultraviolet colouration and incorporating more of the colour spectrum visible parrots into our analysis of colour pattern could add to our current knowledge on the purpose and origin of such patches.

The following chapter will demonstrate how this method of analysing the whole colouration can be developed to produce a set of colour metrics for quantifying the colouration of animals. Which is then applied to calculate shifts in the evolution of patterns.

Chapter Two: Quantifying parrot colouration.

Introduction:

Most previous studies that aim to classify the colouration of animals do so by using discrete categories. However, this method has a number of limitations such as the bias of human observers when assessing the colouration of animals meaning that some characteristics of the pattern that are salient to the animal are ignored in the analysis. Discrete categories also inevitably ignore the presence of intermediate colouration creating further bias as these are forced into binary categories.

Efforts have been made to treat colouration as a continuous trait. Brodie (1992) used the completeness of stripes as well as the presence of spots in the colouration of snakes to create a measure of “stripedness”. Another study looked at the presence of lateral or dorsal stripes in lizards, plus the presence of contrasting eye spots to investigate the “conspicuousness” of lizards (Perez and Font, 2016). Evaluating the colouration of animals by combining the several heterogeneous elements of the pattern also has its problems. Firstly, there is the issue of treating different elements of the colouration as independent components when in reality the different parts of the pattern interact with each other both in their evolution and in how they are perceived. A further limitation of this method is that the selection of pattern components for analysis is often subjective due to the influence of human visual biases. The importance of particular pattern components in the evolutionary history of the animal’s colouration maybe overestimated because they are particularly salient to human researchers. In order to overcome these problems, the colouration of an animal should be evaluated as a whole and on a continuous scale.

We achieved this by designing three separate colour metrics to quantify the colour pattern of parrots by colourfulness, the abundance and distribution of colour in a pattern; complexity, a measure of the amount of transition from one colour to another and uniqueness, how dissimilar a parrot's colouration is from the colouration of its most similar species. By adopting a method of storing the colour and spatial information of an image, image correlograms (see. Methodology), we can evaluate the whole colouration of an animal. The development of the three continuous variables gives power to different statistical analyses and allows us to investigate changes in the colouration of parrots over evolutionary time.

Rates of phenotypic evolution change throughout the evolutionary time, producing different levels of diversity among groups, the colouration of parrots is an interesting example of this. The evolutionary history of parrots and their diversification has been of interest to biologists for decades, identifying changes in the rate of the evolutionary process behind a trait is a key step towards forming hypotheses about what causes them (Ackerly, 2009; Mahler et al., 2010).

Methodology:

Colour metrics

To investigate the variation in colour pattern between species we created three colour metrics to quantify the colourfulness and complexity of the colour pattern as well as how unique the colouration among parrots.

In order to calculate these metrics, a colour correlogram (Figure 1) for each species was created that contains information on the RGB (red, green, blue) values of each pixel that are quantified into eight colour categories (m), in this case the colours are

white/light grey, blue, green, cyan, magenta, red, yellow and black/dark grey. So far this is similar to a colour histogram that captures the colour distribution in an image but does not include any spatial correlation information. The spatial dimension of a colour correlogram is achieved by calculating the probability that, given a pixel of colour c_i another pixel at distance k will be of colour c_j (when i and j are one of the quantified colours m).

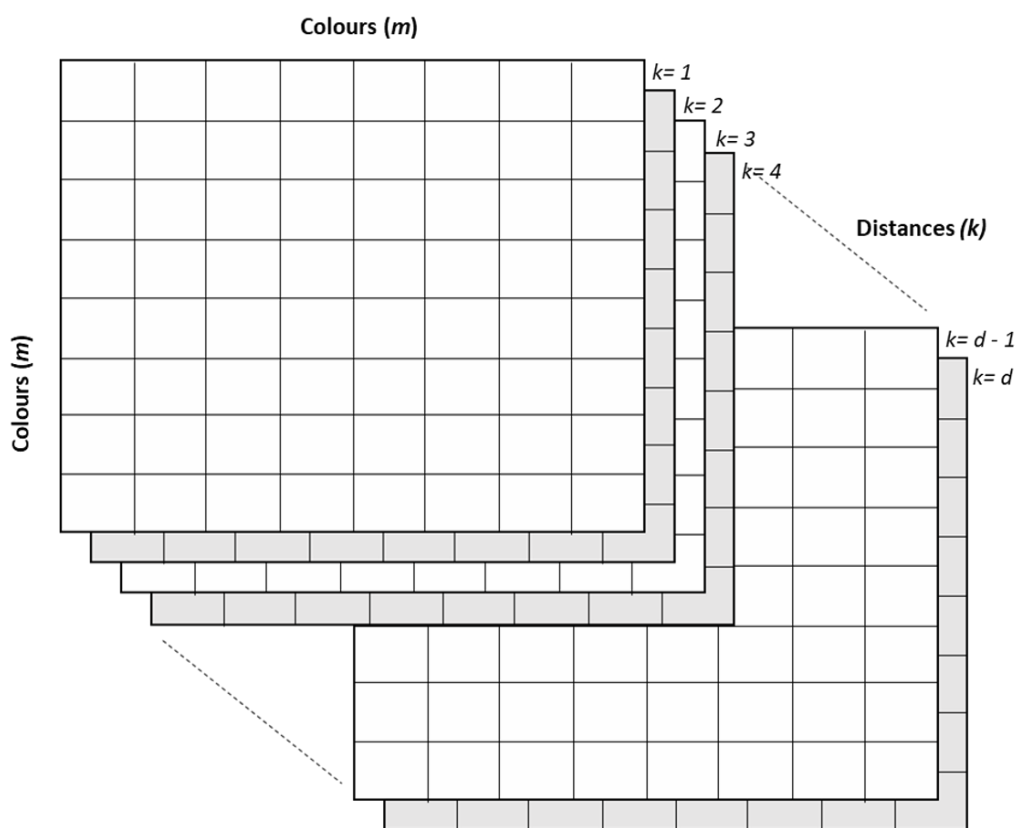


Figure 1: A visual representation of how colour and spatial information is stored in a correlogram (adapted from Talib et al., 2013). It shows a table of probabilities for finding the spatial correlation of a colour (m) with the other colours within an image at different distances (k).

Therefore, the spatial information contained in the correlogram is expressed as the correlation of pairs of colours at different distances in an image.

This method of compiling the colour and position of pixels within an image was developed in the field of computer science, specifically for its use in image database indexing and retrieval (Huang et al, 1997). Its use in the study of animal colouration will allow us to make more robust comparisons of the entire colour pattern of animals as they are seen by conspecifics and allospecifics.

From the computed correlograms we were then able to calculate the colourfulness, complexity and uniqueness values of each species' colour pattern. These terms will be defined in the following sections.

Colourfulness

Colourfulness is a measure of the relative abundance of different coloured pixels, quantified as the Shannon entropy of values within each category of the colour correlogram, divided by the largest possible entropy. The output is therefore a value between 0 and 1 based on the number and ratio of the different colours within the image. A value of 1 would mean that all eight colours are represented equally in the parrot's colouration (Figure 2 demonstrates this with two colours), and 0 would denote completely homogenous colouration, i.e. a parrot displaying only one solid colour. This metric is similar to that used by Endler and Mielke (2005), who quantified the colouration of animals based on the number and proportion of different colour patches.

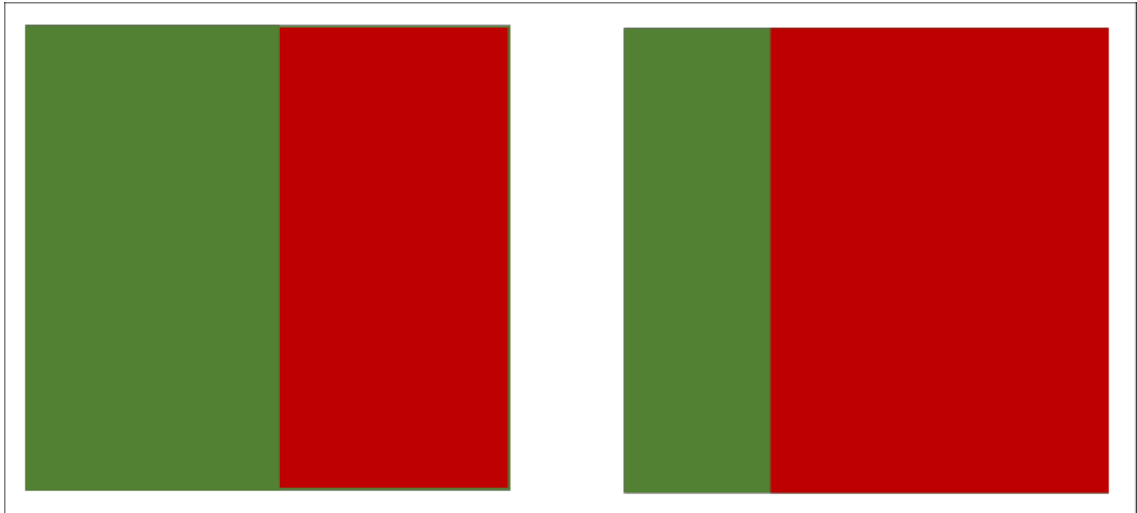


Figure 2: Both images consist of the same two colours (red and green) and the same number of transitions between colours (1). However, the first square is considered more colourful than the second because the colours are equally distributed rather than being a mostly red image with some green.

Complexity

Our second metric (Figure 3) uses the probability of one random pixel being the same colour as another random pixel within the same image in order to quantify the complexity of the colour pattern. As described above the pixels of the image are assigned a colour category based on their RGB value. Each image is then separated into ten regions and the probability of a pixel in one region being the same colour as one in each of the nine other regions is calculated. A value of 0 would again represent a homogenous colour pattern as there would be no transitions between colours. 1 would indicate that the all pixels sampled each region are different colours, a value of 1 is not possible given that there are ten regions and only eight colours. This method overcomes the limitations of previous measures of colour pattern geometry in its

ability to encompass the relationship of each colour patch to all other colour patches in the pattern, rather than being limited to those adjacent to each other (Endler, 2012).

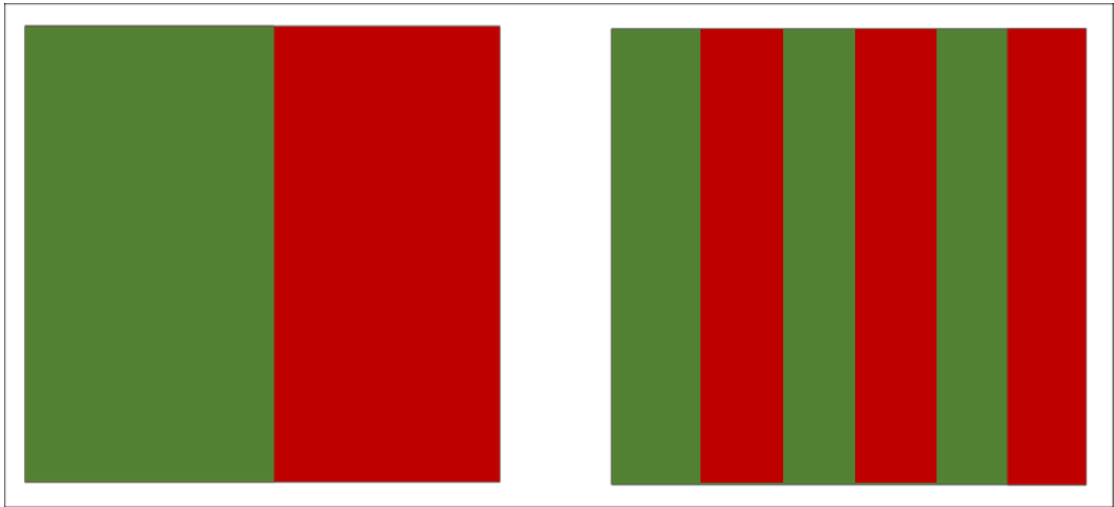


Figure 3: Both images consist of an equal number of red and green pixels. The second image is the most complex due to the number of transitions between colours (5 as opposed to 1 in the first image).

Uniqueness

The uniqueness of a parrot's colouration was calculated by first determining the correlogram distance between each pair of species, as simply the summed difference between each species' colour correlograms (Huang 1997), so that species with identical colour patterns would have a distance of 0, and the distance would increase as colour patterns became increasingly different. The results of this are represented in a dissimilarity matrix (Figure 4).

The mean distance of a species from its three most similar species is then calculated to give the uniqueness of that species. For example, the species at position A (Figure 4)

will have a lower uniqueness value than that at position at B as it is in a closely grouped cluster of other species.

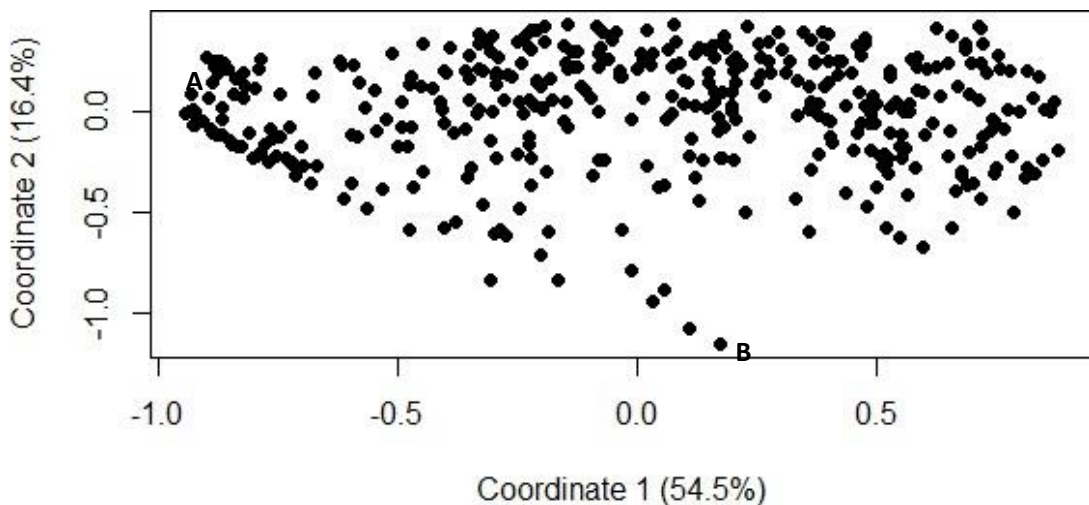


Figure 4: A plot of the position of each parrot species ($n = 403$) in colour correlogram space. Two species with different uniqueness scores are labelled A (low uniqueness) and B (high uniqueness).

Calculating rate shifts

Using the R package “auteur” (Eastman et al., 2011), the rate at which colouration, complexity and uniqueness changes within the time calibrated tree was estimated. Previously to the development of this method, shifts in the evolutionary process of a trait had to be known beforehand in order to run a calculation of the rate of evolutionary change (e.g., Butler and King, 2004; O'Meara et al., 2006; Revell and Collar, 2009). Auteur uses the metric values of the 403 terminal nodes contained in our phylogeny to inform uncertainty in the estimated evolutionary process (Bayesian posterior probability) by sampling across a broad set of possible trait (colourfulness,

complexity and uniqueness of colouration) evolution scenarios, considering models containing local rate shifts at differing positions and numbers within the tree.

Trait evolution is modelled according to Brownian-motion, which is considered to be an adequate approximation of the evolutionary process in many lineages (Harmon et al., 2010). Under the modelled random-walk process, the direction of trait evolution and the size of any shifts is independent of the current value of the metric. Variance in traits is assumed to accumulate in proportion to the branch length and number of internal nodes (Revell et al., 2008). For example, using this method we would expect there to be less variation between two sister species that recently diverged than between two species separated by a branching event much further back in the phylogeny.

A reversible-jump Markov Chain Monte Carlo (Hastings, 1970) was then used (iterations = 5 million, sample frequency = 500) to calculate the posterior probability of a shift occurring within the tree. This reversible-jump approach assesses the fit of models of differing complexity, which in this case refers to the number of shifts in the phylogeny.

In the results section of this chapter the output of these analyses is presented in a colour coded phylogeny for each metric. Each tree contains the rate of the evolutionary process relative to the background rate for either colourfulness, complexity or uniqueness and the Bayesian posterior probability of a shift occurring at the internal nodes.

Results:

The results of the Markov chain Monte Carlo for the colourfulness and complexity of the parrot colouration both showed relatively recent accelerations in the rate of evolutionary process and often at the same locations on the tree (Figures 5 and 6).

There were many upturns in the rate of evolutionary process, most often at the species level in the phylogeny. As well as occurring further back in the phylogeny, often genus level or earlier, there was also a large downturn in the direction of the evolution of uniqueness resulting in a section of the tree where the rate of the evolutionary process was less than the background rate. The same phenology of 403 parrots was used in the creation of the following three figures (5, 6 and 7). Images on the right of the figures are examples of the variation in colour pattern within the phenology.

Figure 5: A phylogeny of 403 species. The rate of the evolutionary process for colourfulness is shown by the colour of the branches: Grey indicates the background rate. Relative to this, red shows an accelerated rate and blue shows a decelerated rate. Circles indicate the presence of a shift: Red denotes an upturn and blue a downturn. The size of the circle relates to the estimated Bayesian posterior probability.

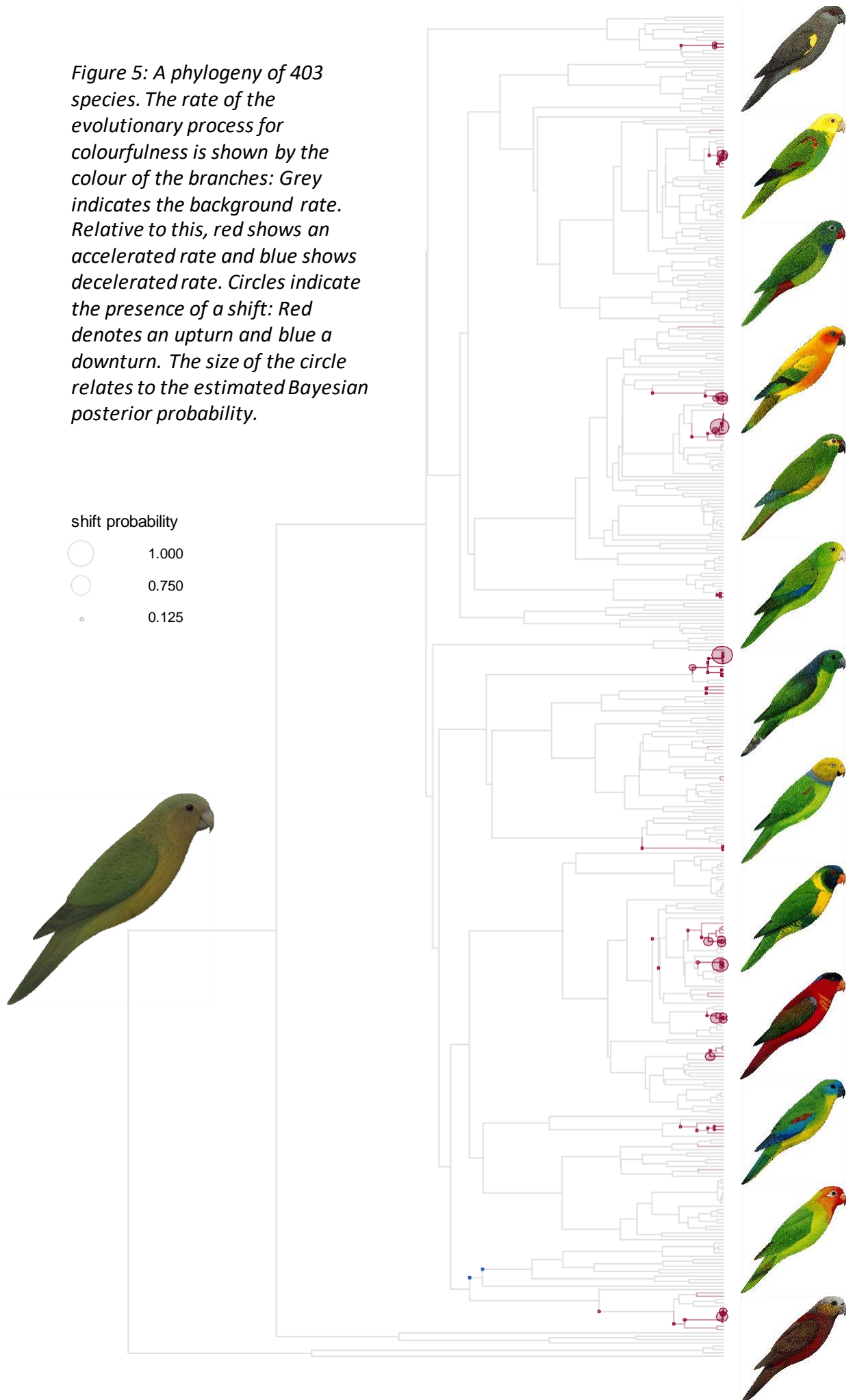


Figure 6: A phylogeny of 403 species. The rate of the evolutionary process for complexity is shown by the colour of the branches: Grey indicates the background rate. Relative to this, red shows an accelerated rate and blue shows decelerated rate. Circles indicate the presence of a shift: Red denotes an upturn and blue a downturn. The size of the circle relates to the estimated Bayesian posterior probability.

shift probability

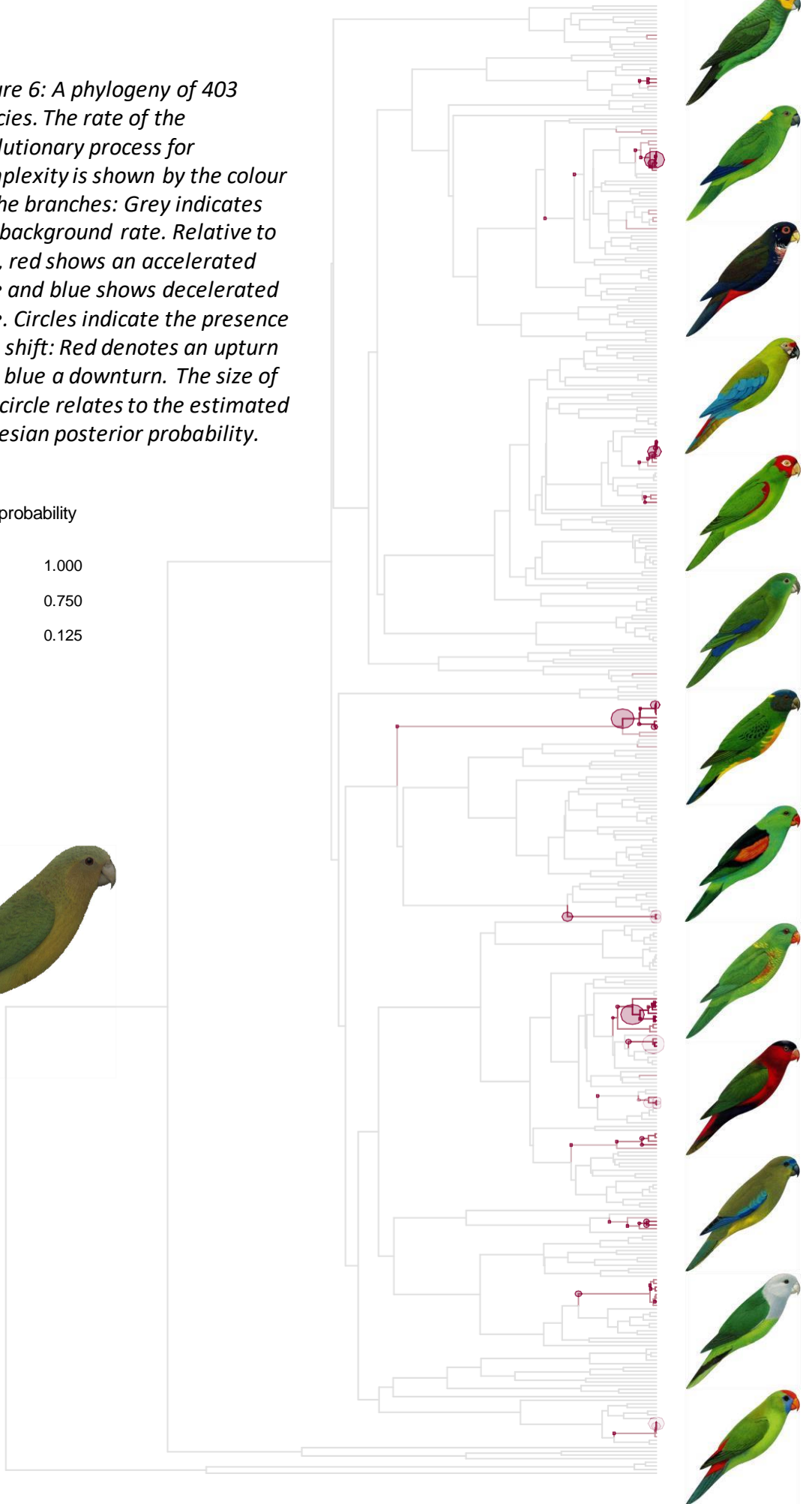
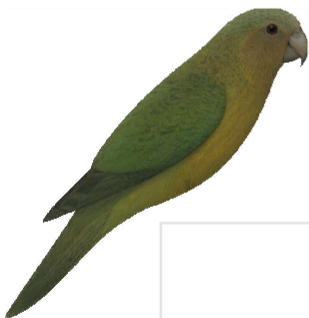
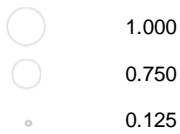
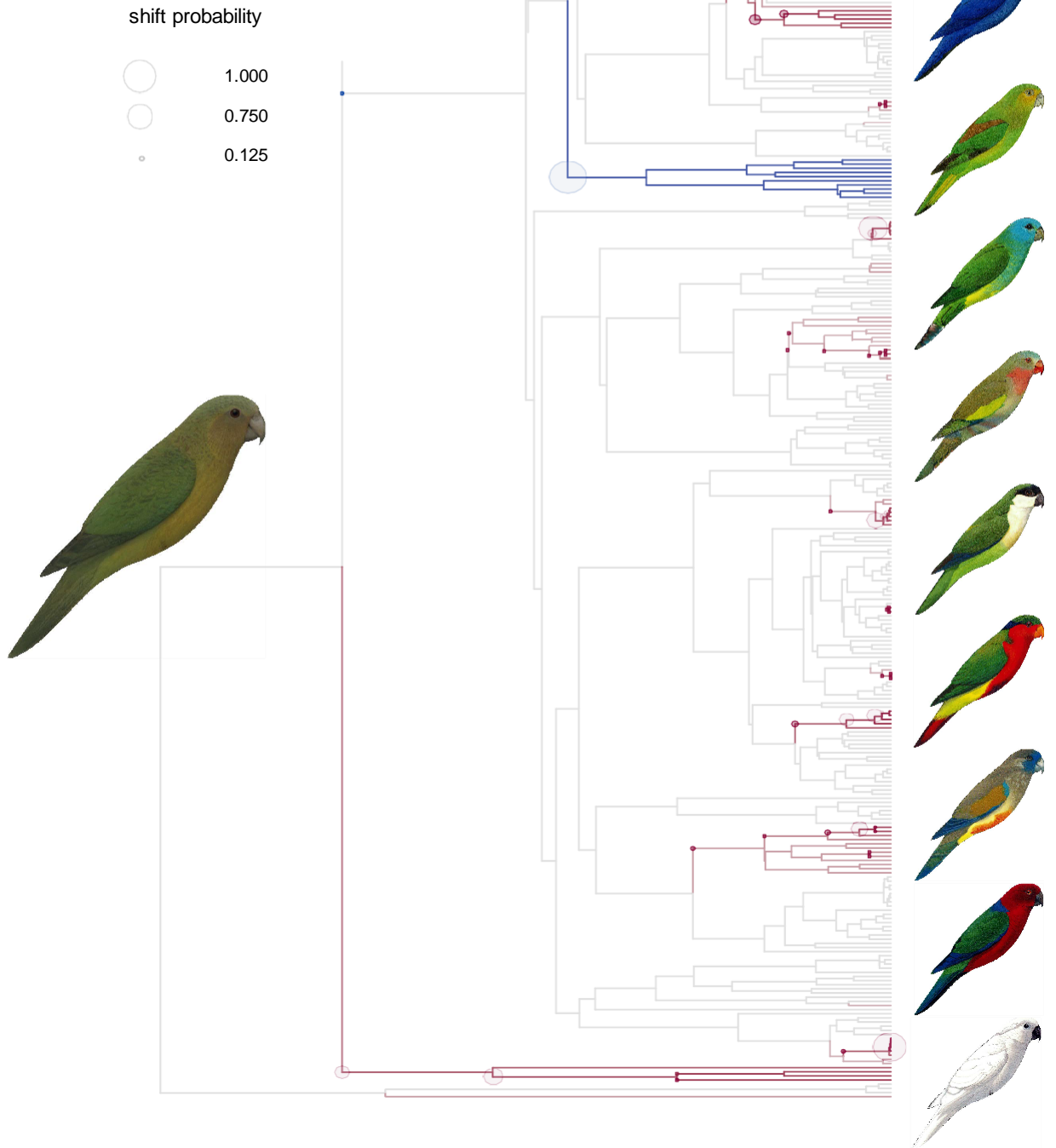


Figure 7: A phylogeny of 403 species. The rate of the evolutionary process for uniqueness is shown by the colour of the branches: Grey indicates the background rate. Relative to this, red shows an accelerated rate and blue shows decelerated rate. Circles indicate the presence of a shift: Red denotes an upturn and blue a downturn. The size of the circle relates to the estimated Bayesian posterior probability.



Discussion:

Despite the high amount of complexity and colourfulness, green was highly conserved among the parrots with 371 of 403 species expressing the colour. This is likely due to the forest habitat of many parrots and the role of colouration in their camouflage.

More work is needed to investigate the relationship between a parrot's colour and its ecology to form hypotheses on why differences occur.

The recent acceleration of colourfulness and complexity could be a result of the rapid radiation of the parrots into a wide range of niches (Wright et al., 2008). These metrics are unavoidably linked in the way they are measured, for example the addition of more colours in a pattern (increasing colourfulness) will lead to a larger number of transitions between colours (increasing complexity). For this reason, it is unsurprising that the pattern of evolutionary change was similar for both. What is interesting is where these metrics differ, by analysing these differences it may be possible to gain insights into how different elements of colouration are utilised by the parrots and any relationship between they may have with life history traits.

Chapter Three: Conservation Status and Colouration.

Introduction:

Parrots contain the highest proportion of endangered species of any other avian order (Olah et al, 2016) and of the 398 recognised species, 112 are considered to be globally endangered (that is, facing a very high risk of extinction in the wild) and a further 60 are classed as near threatened, meaning that they are likely to be threatened by extinction in the near future. In fact, overall 56% of parrot species are thought to have declining populations (IUCN, 2014). Because of this, there has been a significant amount of research done into the external factors that contribute to the extinction risk of parrots (Pimm et al, 2006; Owens and Bennet, 2000; Olah et al., 2016; Melbourne and Hastings, 2008). Threats include, but are not limited to, disease (Fogell and Groombridge, 2018), shrinking habitat ranges due to climate change (Hermes et al., 2018), habitat loss from deforestation (Pimm et al., 2006; Gosling et al., 2017) and the removal of individuals from the wild for the legal and illegal pet trade (Wright et al., 2001; Pain et al., 2006).

The latter two impacts namely, habitat loss and trade are considered by most to be the factors that have the greatest contribution to the decline of most and ultimate extinction of many parrot species (Clarke and Rolf, 2013). There has been much debate over which factor is of most concern when planning the conservation of parrots (Wright et al, 2001). While habitat loss undoubtedly puts more species at risk, the removal of vast numbers of parrots through poaching, historically combined with hunting, has led to more species becoming extinct in the wild (Pires, 2012; Berkunsky et al., 2017).

At least two parrot extinctions have been directly connected to habitat loss. The Carolina parakeet (*Conuropsis carolinensis*) a former native of the riverine hardwood forests in North America, and probably that of the glaucous macaw (*Anodorhynchus glaucus*) whose range was within the Rio Paraguay Basin where they lived in yatay palms (Collar, 1997). Conversely, some parrot species have shown a remarkable ability to adapt to habitat change or loss. For example, the ring-necked Parakeet (*Psittacula krameria*) has adapted well to urban habitats in its native Africa and India after significant deforestation and has even become well established in the U.K., the Netherlands, and Japan (Strubbe and Matthysen, 2007; 2009). Habitat loss occurs wherever humans have settled but is occurring at an elevated rate in the neotropical regions of Africa and South America, where parrots have suffered from both poaching and rapid habitat loss (Wright and Muller-Landau, 2006). Forest clearing is well documented in the countries of the Neotropics, and although large clearings by European settlers date back to the 1600's (Herrera and Hennessey, 2007) it wasn't until around the 1960s that rapid deforestation of vast areas occurred on the scale seen today (Cantu et al., 2007; Gastañaga et al., 2010).

The destruction of a habitat has a high impact factor that has received a great deal of conservation attention from activists, charities and policy makers for good reason: it is a highly visible problem with over-arching consequences for all species within the affected ecosystems (Andren, 1994; Huxel and Hastings, 1999; Deane and He, 2018). However, habitat loss at the scale it is today is a relatively recent problem. Many bird extinctions occurred after their discovery by European explorers due to their overexploitation through hunting and collecting; either live birds as pets or for private menageries, or mounted specimens and skins for museums and private collections, a

notable example being the Dodo (*Raphus cucullatus*) of Mauritius that went extinct only 64 years after its first recorded sighting by Dutch sailors in 1598 (Roberts and Solwol, 2003). At around the same time (c.1693) the Raven Parrot (*Lophopsittacus mauritianus*), also native of Mauritius became extinct; in fact, of the eight or so parrot species native to the Mascarene archipelago, including the Rodrigues parrot (*Necropsittacus rodricanus*) and Newton's parrot (*Psittacula exsul*), only the Echo Parrot (*Psittacula eques*) remains extant (Gosling et al, 2017).

This pattern has been repeated around the world and dates even further back than first presumed. Prior to European expansion, fossil records and animal remains suggest that many parrot species were wiped out by Aztec travellers exploring the islands of the Pacific as early as the 16th century (Hargrave, 1965). Parrots were hunted for their meat as well as their feathers, being valued for their colourful plumage that has been used in the ceremonial dress of many Amazonian tribes. An example being the wings of the hyacinth macaw that were used to create the traditional headdresses of the Kayapo tribe of Southern Brazil; recent concern has been raised that these headdresses, once only used in religious ceremonies, have become a popular tourist commodity, with the wings of up to ten of the critically endangered macaws being used to create just one headdress (Wild for Life, n.d.). It can be assumed that many were taken alive as ornamental pets and status symbols back to the explorers' native lands (Collar and Juniper, 1992).

In recent decades the removal of parrots from the wild has become heavily restricted, starting with a complete ban by the U.S.A. of removals of native American parrots as well as the import of wild caught parrots from other countries (Cooney and Jepson, 2006). While there has not been a complete ban by the Mexican, Peruvian and Bolivian

governments, it has been restricted with the use of licences and strict quotas. However, conservationists argue that rather than preventing poaching, these measures have led to a massive increase in the illegal trade of parrots on the black market; indeed, a report by the USA's Department of Criminal Justice found that as of 2012 the trade of parrots continues unabated by policy changes (Pires, 2012). The World Wildlife Fund (WWF) estimated that between 1991 and 2000, up to 1 million wild caught parrots were traded on the global market (Gastañaga et al., 2011). This is thought to be a severe underestimation, given that this number does not include those caught and sold within the same country, a significant sum when it is considered that parrots are the most common household pet in the neotropics (Pires, 2015). The WWF's estimate also ignores the number of parrots that die before they can be sold, the fatality rate of parrots being smuggled is between 60% and 75% of all birds harvested (Cantu et al., 2007).

Poaching is not a problem restricted to South America. A paper by Olah et al. (2017) found that after logging, poaching had the largest negative impact on parrot species of Oceania. In this area, as in South America, parrots were more likely to be threatened in less developed countries with high unemployment rates. Here the majority of poaching is carried out by opportunistic local villagers who will keep the parrots until a trader passes through to pass them on to larger illegal markets (Wright et al., 2001; Pain et al., 2006; Barré et al., 2010). Illegal trade is not restricted to less affluent countries; Australia, despite having some of the strictest border control in the world struggles with the illegal trade of its endemic parrot species (Vall-Ilosera and Cassey, 2016).

Between 2005 and 2011 it is estimated that in Singapore alone up to 20,000 parrots of 27 Australian species were imported for sale to an international market (Low, 2014).

The rarity of these birds and their unavailability elsewhere make them extremely valuable on the black market; for example, the endemic Black Cockatoo (*spp. Calyptorhynchus*) can fetch as much as AU \$30,000 (Barry, 2011).

As poaching continues at these rates, more parrots are put under increasing threat of extinction; 66 species are directly threatened by illegal trade (Gastañaga et al., 2011).

The most recent and high-profile loss of a species is Spix's Macaw (*Cyanopsitta spixii*), a large blue parrot native to the Amazon Basin where the last individual monitored by conservationist disappeared in 2000, following a severe decline due to unsustainable harvesting for the pet trade (Juniper, 2004). Much of the effect of poaching on parrot decline is attributed to the relatively slow reproductive rate and small clutch size shared by the majority of the family (Clarke and de By, 2013; Berkunsky et al., 2017; Murphy et al., 2017) making it difficult to replenish their numbers after the adults are taken or, more commonly, nestlings and eggs are poached from nests (Wright et al., 2001; Pires, 2012).

Similarly, to habitat loss poaching does not impact on all species equally (Owens and Bennet, 2000). Understanding the specific characteristics that put certain species more at risk and that ultimately underlie extinction is fundamental to conservation. To this end, several studies have investigated what species-specific characteristics make some parrots more attractive to poachers than others (Melbourne and Hastings, 2008; Tella and Hiraldo, 2014; Murphy et al., 2017). Pires and Clarke (2012) looked at a group of 22 Mexican species to determine if those with the highest export rates fit into the CRAVED paradigm (Clarke, 1999) of species, explicitly whether they are concealable, removable, available, valuable, enjoyable and disposable. They found that species with large population sizes and in close approximation to human settlements were traded

in the largest numbers. However, those that were more enjoyable (most attractive) fetched the highest price. This finding was repeated in Tella and Hiraldo's (2014) study, where they found that Amazons (*Amazona* spp.) and Macaws (*Ara* spp.) (grouped together based on their higher "attractiveness") were disproportionately caught based on their availability. By using the export figures as a proxy for how at risk the parrot species are, both studies were limited by the underestimation of numbers referred to above. Additionally, in both studies the parrot's attractiveness was determined by a simple measure of how many "bright" colours were displayed in the parrots' plumage and its body size. This is a sensible, if rather subjective, measure of attractiveness given the results of a previous study that found these features were preferred by European pet owners (Frynta et al., 2010), however this approach may overlook some of the more subtle differences between the whole-body colouration of different parrot species. Such as where certain colours are exhibited on the body and in which combinations or patterns.

For this study we propose the use of three separate colour matrices; colourfulness, complexity and uniqueness in order to objectively test the relationship between colouration ("attractiveness") and extinction risk. Our first hypothesis is that species with higher colourfulness and complexity values will be classified at a greater risk of extinction because their aesthetic appeal to potential buyers will mean that they are preferentially selected to be removed from the wild by poachers. Secondly, more uniquely coloured parrots will also be more threatened and are likely to have a greater monetary value than those with more common colouration, and that having a high proportion of certain (comparatively rare) colours, such as blue and white, will also contribute negatively to threat status.

Methods:

Extinction risk

In order to test the relationship between the conservation status of a species and its colouration, we collated data from the International Union for Conservation of Nature (IUCN) website (<http://www.iucnredlist.org/>) into our parrot database. Based on a list of criteria including rate of decline, population size, area of geographic distribution, and degree of population and distribution fragmentation, the IUCN sorts each species with adequate data into five categories, two non-threatened categories (Least Concern and Near Threatened), and three threatened categories (Vulnerable, Endangered and Critically Endangered). In total, the conservation status of 433 species and subspecies in our data set was recorded; those classified as extinct or data deficient were dropped (n = 27). For this study threatened species were grouped together (n = 81) and all others remained as either near threatened (n = 51) and least concern (n = 260).

Colour metrics

The parrot colour data was collected from colour plates in Forshaw's field guide and used to calculate the complexity and colourfulness of each parrot species as described in Colour Metrics (Chapter One). An additional measure of uniqueness was employed to quantify how dissimilar a parrot is to its three most similar species in terms of colour patterns (i.e. the three species with the smallest distance to each focal species within our colour correlogram space).

Colour categories

Based on their RGB values, in the colour correlograms the colour pixels of an image are divided into eight colour categories: red, magenta, blue, green, cyan, yellow, white/light grey and black/dark grey, and recorded as the relative proportion of colours falling within each category.

Analysis

Following the calculation of the average value of colourfulness, complexity, uniqueness and the eight colours for each IUCN category, we evaluated the support of any identified relationship between species' traits and IUCN status using phylogenetically corrected Bayesian ordinal regression models implemented in the procedure MCMCgmm (Hadfield, 2010) in R. We modelled IUCN status as an ordinal response (family = "ordinal") and included the median tarsus size of each species as a proxy for body size in order to control for its effect on IUCN status.

The phylogeny used was a median tree with 403 terminal nodes, included as a random factor. For the priors, we fixed the residual variance to 1 (R-component, $V = 1$, $\text{fix} = 1$), the random effect variance was set to 10 with a low credibility (i.e. a noninformative prior; G-component, $V = 10$, $\text{fix} = 1$) (Gonzalez-Voyer et al., 2016).

Because we assume that Red List status reflects continuous variation in vulnerability to extinction, the modelled categories represent a latent continuous variable, and a generalised linear model is fit between the latent continuous variable (with a probit link modification) and the independent variables. We ran the chain for 10,000 iterations, thinning of 10, and burn-in of 1000. In the results section of this chapter the

output of these models is presented, including the estimated regression coefficients (β), 95% credible intervals (95% CI), and MCMC p-values (pMCMC).

Results:

With regards to our first hypothesis, that species with higher colourfulness and complexity will have a higher risk of extinction, the relationships between conservation status and colour showed a very similar pattern for both metrics, with colourfulness and complexity being elevating in the near threatened species, compared to those that are classified as threatened or least concern (Figure 1A-B), although not significantly. Generalised linear models using a Markov Chain Monte Carlo (MCMC), found that the IUCN status of a species was not significantly predicted by either colourfulness ($\beta = 2.26$, 95% CI = -0.37 to 4.7, pMCMC = 0.09) or complexity ($\beta = 1.5$, 95% CI = -1.86 to 4.81, pMCMC = 0.34).

Hypothesis 2 looked to investigate if the uniqueness of a species from its most similar species, in terms of its colour patterns, had a bearing on its risk of extinction.

Uniqueness (Figure 1C) increased as the threat of extinction increased, with the species of least concern possessing the lowest uniqueness score in both cases. The results of MCMC generalised linear model showed that uniqueness significantly predicted a species' IUCN status ($\beta = 1.81$, 95% CI = 0.73 to 3.16, pMCMC <0.001).

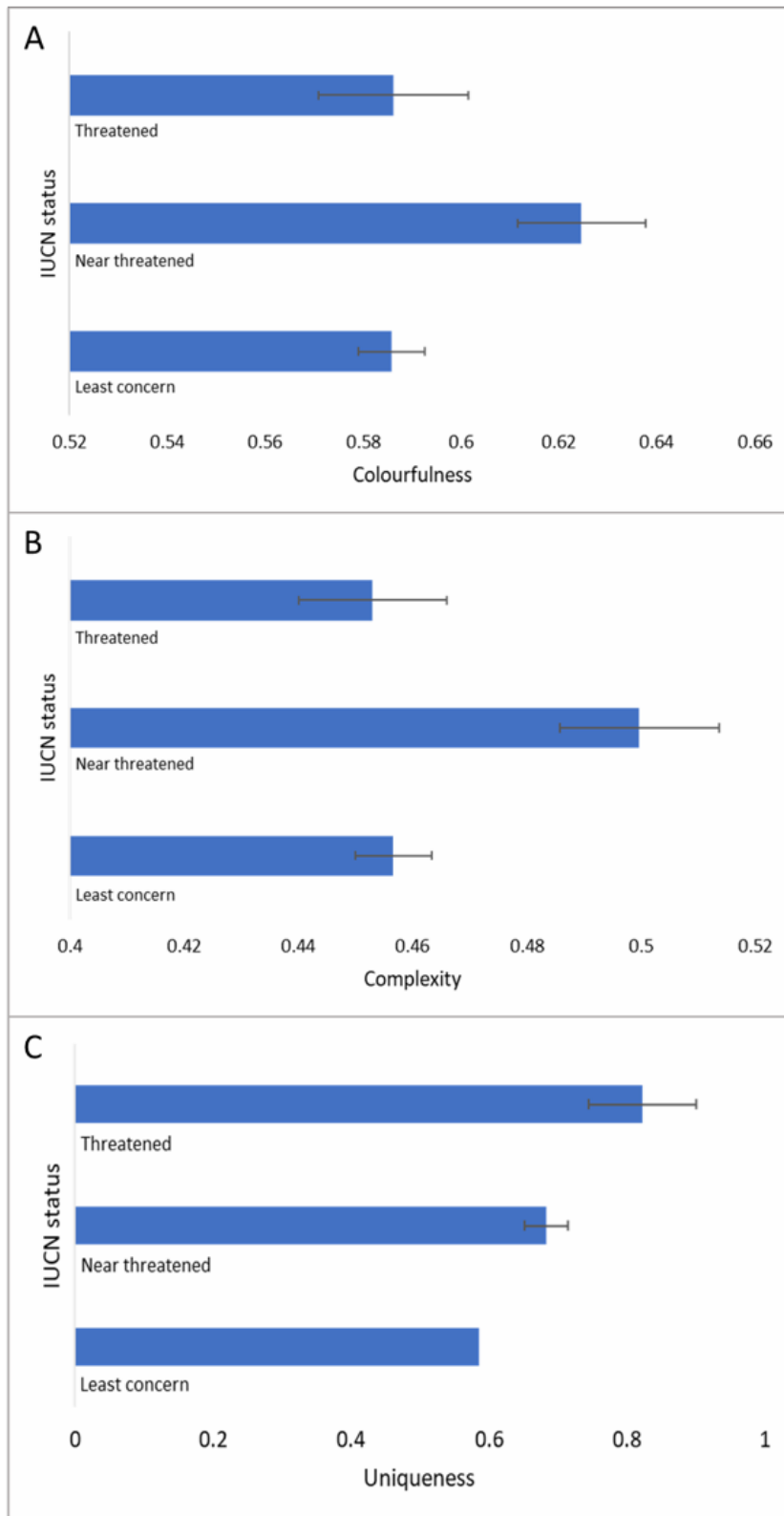


Figure 1 The mean \pm SE values of each colour metric, colourfulness (A), complexity (B) and uniqueness (C), for species classified as least concern ($n= 81$), near threatened ($n= 51$) and threatened ($n= 260$).

Considering the relative proportions of colours in each of the eight colour categories, only cyan ($\beta = 44.72$, 95% CI = 13.21 to 78.42, pMCMC <0.001), light grey/white ($\beta = 6.23$, 95% CI = 1.42 to 12.47, pMCMC = 0.01) and red ($\beta = -5.88$, 95% CI = -10.33 to -2.43, pMCMC <0.001) were significant predictors of the IUCN status of parrots, although in opposite directions (Figure 2). Specifically, parrots with a greater relative proportion of cyan or white were more likely to be classified as Threatened, while those with a greater proportion of red were more likely to be of Least Concern. Dark grey/black ($\beta = -0.76$, 95% CI = -2.12 to 0.66, MCMC = 0.3), blue ($\beta = 7.33$, 95% CI = -3.28 to 19.02, pMCMC = 0.18), green ($\beta = -1.48$, 95% CI = -3.24 to 0.34, pMCMC = 0.1), magenta ($\beta = -332.63$, 95% CI = -993.27 to 413.17, pMCMC = 0.34), and yellow ($\beta = 2.31$, 95% CI = -1.26 to 5.51, pMCMC = 0.11) were not significant predictors of IUCN status (Figure 2).



Figure 2 Mean \pm SE proportions of colours falling within each of the 8 discrete colour categories for parrot species classified as least concern (LC), near threatened (NT) and threatened (T).

Discussion:

Our results show that there are some elements of the colouration of parrots that are able to significantly predict the IUCN status, or extinction risk, of a species. Species with predominately white or cyan colouration were most likely to be categorised as threatened. This could be a result of poachers preferentially targeting blue and white species because of a higher demand for parrots with these colours, as they are more attractive to potential customers and so are more valuable (Frytna et al., 2010). For example, the only white parrot in our dataset was the white cockatoo (*Cacatua alba*), which is considered endangered due to its removal from the wild for the pet trade and as such is protected by appendix II of the CITES (The Convention on International Trade in Endangered Species) list by restricting export and import of wild-caught birds (IUCN, 2018). The next four most unique parrots were the hyacinth macaw (*Anodorhynchus hyacinthinus*), Spix macaw (*Cyanopsitta spixii*), Lear's macaw (*Anodorhynchus leari*) and ultramarine lorikeet (*Vini ultramarina*); the only predominately blue/cyan parrots. This suggests that rather than the actual colour being the factor that most attracts buyers and so inevitably poachers, it is also the rarity of the colouration that is found to be most attractive as has been previously found in the trade of reptiles and amphibians (Tapley et al., 2011). All these species came under the threatened category, with the Spix macaw thought to be extinct in the wild, the popularity of unique colouration puts a disproportionate amount of pressure on the few species of parrot that possess it.

Interestingly, the highest colourfulness and complexity values were not in the threatened category as predicted but were most common amongst the species of parrot considered near threatened by the IUCN. This is contrary to one study that

found more aesthetically pleasing species were more often poached in the Bolivian market (Pires and Clarke, 2011). However, given the history of poaching and removal of parrots from the wild based on their colouration for pets and decoration it is possible that many of the most colourful parrot species have already become extinct and so were not included in our data set. This seems a plausible explanation based on several extinct species, for example the Cuban macaw (*Ara tricolor*) and the Carolina parakeet (*Conuropsis carolinensis*), both very colourful parrots that are believed to have been hunted to extinction for their plumage (Clarke and Rolf, 2013). The remaining most colourful parrots are predominately near threatened most likely due to other extrinsic ecological factors such as large population sizes and not being restricted to island habitats meaning they are not as vulnerable to the effects of poachers (Cantu et al., (2007).

The results of this study present an exciting opportunity to improve our understanding of what put makes certain parrot species more vulnerable to poachers. The proportion of white and blue colouration, as well as the uniqueness of colour pattern can be utilised in current models of risk such as Pires and Clarke's (2012) CRAVED as additional measures of attractiveness making the criterion more objective and robust overall. This will be particularly useful to criminologists tackling the problem of illegal trade as well as for directing the efforts of conservationists towards the most popular species. As more emphasis is placed on the problem of habitat and conserving areas of forest, the impact of poaching can only increase. Restricting species to protected fragments of habitat will result in the accessibility of different species to the poachers becoming more similar, making intrinsic species-specific factors such as colouration more relevant when predicting a species vulnerability (Wright et al., 2001).

The process of collecting the colour data of a species is largely automated once high-quality images of the animal, such as those in field guides, have been digitalised. This allows for the colour data of much larger numbers of species to be collected and compared relatively quickly. Our methodology could be applied to other taxa threatened by poaching, especially those valued for their colouration such as ornamental fish. Although they are largely captive bred, significant numbers of fish are removed from the wild for the pet trade (Andrews, 1990). For example, the red-lined torpedo barb (*Puntius denisonii*) have suffered large population declines in the last 20 years due to their removal from the wild for the pet trade and as such are classed as endangered on the IUCN red list (Raghavan et al., 2013). It remains to be seen if the same features of colouration prized in parrots by customers valued by those that collect other colourful animals.

Discussion:

The aim of this study was to investigate the evolution of the colouration of Psittaciformes. This was achieved with the construction of a phylogeny of parrots that included species and subspecies and the extraction of colour data from field guides. Chapter One details how this information was used to reconstruct the ancestral parrot including its shape and colouration. This is a significant contribution to our understanding of parrot evolution as such a complete image of the appearance of the original Psittaciform has not been created until now (Wright et al., 2008; Russello and Amato, 2004). Insights into the appearance of the early parrots are valuable in the testing of evolutionary and ecological hypothesis, and, if correlation between habitat type and colouration are supported, may be particularly useful in the when examining the geographical origin of the parrots; a question that has so far drawn several opposing theories (Waterhouse et al., 2008; Wright et al, 2001; Schweizer et al., 2010). Our method of pixel-by-pixel ancestral state reconstruction, was utilised with the aim of overcoming limitations of previous studies such as the subjective selection of isolated traits, reconstructed in the ancestor as being either present or absent. We hope that the successful reconstruction of parrot colouration may encourage the adoption of the same method in the study of other orders. This could allow for the origin of pattern traits to be more accurately placed, such as stripes in lizards, to better understand their function and development. It may also reveal changes in colour pattern and colouration previously overlooked when traits for study are selected. Building on this, the rate at which metrics of the parrot pattern evolved was calculated. This information is central to the formation of any future hypothesis on the diversity of parrot colouration. Quantifying colouration with three continuous

measures overcomes the limitations of previous attempts to analyse colour patterns by enabling the objective evaluation of the whole pattern, removing any bias of selecting particular elements to study. The results of this chapter showed a wide variation in the colourfulness, complexity and uniqueness of parrot colouration. Visual observation of parrots tells us that there is a large amount of superficial variation simply by the number of different colours expressed by different species. The creation of these metrics allows a much deeper analysis of colour pattern, helping to overcome observer bias and unpicking variation in the make-up of a pattern independent of colour. The results of this study show a wide variation in colouration properties, explanation of this variation can now be investigated by comparing metric values to the ecology and life history traits of the parrots.

Given the rate at which parrot populations are declining around the world, it was prudent to investigate how this variation in colouration may relate to the conservation status of different parrot species. We found that more unique parrots were considered to be threatened by the IUCN. This, we suggest, is related to the appeal of rarer coloured species, such as blue and white, to poachers due to the higher price they can fetch on the illegal markets. Future research should combine these measures of attractiveness with other factors known to impact on the conservation status of parrots, such as habitat size and rate of loss. It is possible that the attractiveness of a species is weighted depending on context (Liu et al., 2011; Kahler and Gore., 2012), for example the colouration of a species maybe less important as than its abundance and accessibility. Understanding more about the risk factors associated with the endangerment of species, allows for more efficient conservation effort. These involve stricter legislation and physical protection of more attractive species, or more targeted

education programmes aimed at consumers of the pet trade and the communities that rely on it for income.

Bibliography:

Introduction

1. Andersson, S., Örnborg, J. and Andersson, M., 1998. Ultraviolet sexual dimorphism and assortative mating in blue tits. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 265(1395), pp.445-450.
2. Bennett, A.T. and Théry, M., 2007. Avian color vision and coloration: multidisciplinary evolutionary biology. *the american naturalist*, 169(S1), pp.1-6.
3. Bennett, A.T.D., Cuthill, I.C. and Norris, K.J., 1994. Sexual selection and the mismeasure of color. *The American Naturalist*, 144(5), pp.848-860.
4. Berg, M.L., Knott, B., Ribot, R.F., Buchanan, K.L. and Bennett, A.T., 2019. Do glucocorticoids or carotenoids mediate plumage coloration in parrots? An experiment in *Platycercus elegans*. *General and comparative endocrinology*.
5. Brodie III, E.D., 1992. Correlational selection for color pattern and antipredator behavior in the garter snake *Thamnophis ordinoides*. *Evolution*, 46(5), pp.1284-1298. Cuthill, I.C. and Bennett, A.T., 1993. Mimicry and the eye of the beholder. *Proc. R. Soc. Lond. B*, 253(1337), pp.203-204.
6. Cuthill, I.C., Allen, W.L., Arbuckle, K., Caspers, B., Chaplin, G., Hauber, M.E., Hill, G.E., Jablonski, N.G., Jiggins, C.D., Kelber, A. and Mappes, J., Marshall, J., Merrill, R., Osorio, D., Prum, R., Roberts, N.W., Roulin, H.M., Sherratt, T.N., Skelhorn, J., Speed, M.P., Stoddard, M.C., Stuart-Fox, D., Talas, L., Tibbetts, E., and Caro, T., 2017. The biology of color. *Science*, 357(6350).
7. Endler, J.A. and Mielke, P.W., 2005. Comparing entire colour patterns as birds see them. *Biological Journal of the Linnean Society*, 86(4), pp.405-431.

8. Endler, J.A., 2012. A framework for analysing colour pattern geometry: adjacent colours. *Biological Journal of the Linnean Society*, 107(2), pp.233-253.
9. Hackett, S.J., Kimball, R.T., Reddy, S., Bowie, R.C., Braun, E.L., Braun, M.J., Chojnowski, J.L., Cox, W.A., Han, K.L., Harshman, J. and Huddleston, C.J., 2008. A phylogenomic study of birds reveals their evolutionary history. *science*, 320(5884), pp.1763-1768.
10. Juniper, T. and Parr, M., 1998. Parrots. *A guide to the parrots of the world*. Pica, Sussex.
11. Kelley, J.L., Fitzpatrick, J.L. and Merilaita, S., 2013. Spots and stripes: ecology and colour pattern evolution in butterflyfishes. *Proc. R. Soc. B*, 280(1757), p.20122730.
12. Kelman, E.J., Osorio, D. and Baddeley, R.J., 2008. A review of cuttlefish camouflage and object recognition and evidence for depth perception. *Journal of Experimental Biology*, 211(11), pp.1757-1763.
13. Kiskowski, M., Glimm, T., Moreno, N., Gamble, T. and Chiari, Y., 2019. Isolating and quantifying the role of developmental noise in generating phenotypic variation. *PLoS computational biology*, 15(4), p.e1006943.
14. Kunttu, I., Lepistö, L., Visa, A. and Rauhamaa, J., 2003. Image correlogram in image database indexing and retrieval. In *Digital Media Processing for Multimedia Interactive Services* (pp. 88-91).
15. Marchetti, K., 1998. The evolution of multiple male traits in the yellow-browed leaf warbler. *Animal Behaviour*, 55(2), pp.361-376.
16. McGraw, K.J. and Hill, G.E., 2006. Mechanics of carotenoid-based coloration. *Bird coloration*, 1, pp.177-242.,
17. McGraw, K.J., 2006. Mechanics of uncommon colors: pterins, porphyrins, and psittacofulvins. *Bird coloration*, 1, pp.354-398.

18. Merilaita, S. and Kaitala, V., 2002. Community structure and the evolution of aposematic coloration. *Ecology Letters*, 5(4), pp.495-501.
19. Osorio, D. and Vorobyev, M., 2008. A review of the evolution of animal colour vision and visual communication signals. *Vision research*, 48(20), pp.2042-2051.
20. Pearn, S.M., Bennett, A.T. and Cuthill, I.C., 2001. Ultraviolet vision, fluorescence and mate choice in a parrot, the budgerigar *Melopsittacus undulatus*. *Proceedings of the Royal Society of London B: Biological Sciences*, 268(1482), pp.2273-2279.
21. Pérez I de Lanuza, G. and Font, E., 2016. The evolution of colour pattern complexity: selection for conspicuousness favours contrasting within-body colour combinations in lizards. *Journal of evolutionary biology*, 29(5), pp.942-951.
22. Protas, M.E. and Patel, N.H., 2008. Evolution of coloration patterns. *Annual review of cell and developmental biology*, 24, pp.425-446.
23. Roulin, A. and Bize, P., 2007. Sexual selection in genetic colour-polymorphic species: a review of experimental studies and perspectives. *Journal of Ethology*, 25(2), pp.99-105.
24. Shephard, M., 1989. *Aviculture in Australia: keeping and breeding aviary birds*. Prahran, Victoria: Black Cockatoo Press.
25. Siitari, H., Alatalo, R.V., Halme, P., Buchanan, K.L. and Kilpimaa, J., 2007. Color signals in the black grouse (*Tetrao tetrix*): signal properties and their condition dependency. *the american naturalist*, 169(S1), pp.S81-S92.
26. Stevens, M. and Merilaita, S., 2008. Animal camouflage: current issues and new perspectives. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1516), pp.423-427.

27. Stuart-Fox, D. and Moussalli, A., 2008. Camouflage, communication and thermoregulation: lessons from colour changing organisms. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1516), pp.463-470.
28. Summers, K., Speed, M.P., Blount, J.D. and Stuckert, A.M.M., 2015. Are aposematic signals honest? A review. *Journal of evolutionary biology*, 28(9), pp.1583-1599.
29. Wellenreuther, M., Svensson, E.I. and Hansson, B., 2014. Sexual selection and genetic colour polymorphisms in animals. *Molecular ecology*, 23(22), pp.5398-5414.

Chapter One: The ancestral reconstruction of parrot colour patterns

1. Adams, D.C. and Otárola-Castillo, E., 2013. geomorph: an R package for the collection and analysis of geometric morphometric shape data. *Methods in Ecology and Evolution*, 4(4), pp.393-399.
2. Amemiya, C.T., Alföldi, J., Lee, A.P., Fan, S., Philippe, H., MacCallum, I., Braasch, I., Manousaki, T., Schneider, I., Rohner, N. and Organ, C., 2013. The African coelacanth genome provides insights into tetrapod evolution. *Nature*, 496(7445), p.311.
3. Beddall, B.G., 1972. Wallace, Darwin, and Edward Blyth: Further notes on the development of evolution theory. *Journal of the History of Biology*, 5(1), pp.153-158.
4. Beddall, B.G., 1972. Wallace, Darwin, and Edward Blyth: Further notes on the development of evolution theory. *Journal of the History of Biology*, 5(1), pp.153-158.
5. Cracraft, J., 2001. Avian evolution, Gondwana biogeography and the Cretaceous–Tertiary mass extinction event. *Proceedings of the Royal Society of London B: Biological Sciences*, 268(1466), pp.459-469.
6. Crisp, M.D. and Cook, L.G., 2005. Do early branching lineages signify ancestral traits?. *Trends in Ecology & Evolution*, 20(3), pp.122-128.

7. Cunningham, C.W., 1999. Some limitations of ancestral character-state reconstruction when testing evolutionary hypotheses. *Systematic Biology*, 48(3), pp.665-674.
8. Dawkins, M.S. and Guilford, T., 1997. Conspicuousness and diversity in animal signals. In *Communication* (pp. 55-75). Springer, Boston, MA.
9. Endler, J.A. and Mielke JR, P.W., 2005. Comparing entire colour patterns as birds see them. *Biological Journal of the Linnean Society*, 86(4), pp.405-431.
10. Felsenstein, J., 1988. Phylogenies and quantitative characters. *Annual Review of Ecology and Systematics*, 19(1), pp.445-471.
11. Forshaw, J.M., 1998. *Parrots of the World*. Princeton University Press.
12. García-Martínez, R., Marín-Moratalla, N., Jordana, X. and Köhler, M., 2011. The ontogeny of bone growth in two species of dormice: reconstructing life history traits. *Comptes Rendus Palevol*, 10(5-6), pp.489-498.
13. Grant, P.R. and Grant, B.R., 1992. Hybridization of bird species. *Science*, 256(5054), pp.193-197.
14. Groombridge, J.J., Jones, C.G., Nichols, R.A., Carlton, M. and Bruford, M.W., 2004. Molecular phylogeny and morphological change in the Psittacula parakeets. *Molecular phylogenetics and evolution*, 31(1), pp.96-108.
15. Guilford, T. and Dawkins, M.S., 1991. Receiver psychology and the evolution of animal signals. *Animal behaviour*, 42(1), pp.1-14.
16. Harmon, L.J., Weir, J.T., Brock, C.D., Glor, R.E. and Challenger, W., 2007. GEIGER: investigating evolutionary radiations. *Bioinformatics*, 24(1), pp.129-131.
17. I de Lanuza, G.P., Font, E. and Monterde, J.L., 2013. Using visual modelling to study the evolution of lizard coloration: sexual selection drives the evolution of sexual dichromatism in lacertids. *Journal of evolutionary biology*, 26(8), pp.1826-1835.

18. Juniper, T. and Parr, M., 1998. Parrots. A guide to the parrots of the world. Pica, Sussex.
19. Kelley, J.L., Fitzpatrick, J.L. and Merilaita, S., 2013. Spots and stripes: ecology and colour pattern evolution in butterflyfishes. *Proc. R. Soc. B*, 280(1757).
20. Kuhner, M.K. and Felsenstein, J., 1994. A simulation comparison of phylogeny algorithms under equal and unequal evolutionary rates. *Molecular biology and evolution*, 11(3), pp.459-468.
21. McNab, B.K. and Salisbury, C.A., 1995. Energetics of New Zealand's temperate parrots. *New Zealand Journal of Zoology*, 22(3), pp.339-349.
22. Murali, G. and Kodandaramaiah, U., 2017. Body size and evolution of motion dazzle coloration in lizards. *Behavioral Ecology*, 29(1), pp.79-86.
23. Omland, K.E., 1999. The assumptions and challenges of ancestral state reconstructions. *Systematic biology*, 48(3), pp.604-611.
24. Pagel, M., 1999. Inferring the historical patterns of biological evolution. *Nature*, 401(6756), p.877.
25. Paradis, E., Claude, J. and Strimmer, K., 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20(2), pp.289-290.
26. Pearn, S.M., Bennett, A.T. and Cuthill, I.C., 2001. Ultraviolet vision, fluorescence and mate choice in a parrot, the budgerigar *Melopsittacus undulatus*. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 268(1482), pp.2273-2279.
27. Pérez I de Lanuza, G. and Font, E., 2016. The evolution of colour pattern complexity: selection for conspicuousness favours contrasting within-body colour combinations in lizards. *Journal of evolutionary biology*, 29(5), pp.942-951.

28. Pérez I de Lanuza, G. and Font, E., 2016. The evolution of colour pattern complexity: selection for conspicuousness favours contrasting within-body colour combinations in lizards. *Journal of evolutionary biology*, 29(5), pp.942-951.
29. Pfennig, K. and Pfennig, D., 2009. Character displacement: ecological and reproductive responses to a common evolutionary problem. *The Quarterly Review of Biology*, 84(3), pp.253-276.
30. R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
31. R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.Rproject.org/>
32. Revell, L.J. and Revell, M.L.J., 2019. Package 'phytools'.
33. Ribas, C.C. and Miyaki, C.Y., 2004. Molecular systematics in Aratinga parakeets: species limits and historical biogeography in the 'solstitialis' group, and the systematic position of *Nandayus nenday*. *Molecular phylogenetics and evolution*, 30(3), pp.663-675.
34. Schliep, K., Potts, A.A., Morrison, D.A. and Grimm, G.W., 2017. *Intertwining phylogenetic trees and networks* (No. e2054v1). PeerJ Preprints.
35. Stevens, M. and Merilaita, S., 2008. Animal camouflage: current issues and new perspectives. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1516), pp.423-427.
36. Stidham, T.A., 1998. A lower jaw from a Cretaceous parrot. *Nature*, 396(6706), p.29.
37. Stuart-Fox, D.M. and Ord, T.J., 2004. Sexual selection, natural selection and the evolution of dimorphic coloration and ornamentation in agamid lizards. *Proceedings of the Royal Society of London B: Biological Sciences*, 271(1554), pp.2249-2255.

38. Toft, C.A. and Wright, T.F., 2015. Parrots of the wild: A natural history of the world's most captivating birds. Univ of California Press.
39. Toft, C.A. and Wright, T.F., 2015. Parrots of the wild: A natural history of the world's most captivating birds. Univ of California Press.
40. Vinther, J., Briggs, D.E., Clarke, J., Mayr, G. and Prum, R.O., 2009. Structural coloration in a fossil feather. *Biology Letters*, p.rsbl20090524.
41. Wallace, A.R., 1889. *A narrative of travels on the Amazon and Rio Negro: with an account of the native tribes, and observations on the climate, geology, and natural history of the Amazon valley* (No. 8). Ward, Lock.
42. Waterhouse, D.M., 2006. Parrots in a nutshell: the fossil record of Psittaciformes (Aves). *Historical Biology*, 18(2), pp.227-238.
43. Wright, T.F., Schirtzinger, E.E., Matsumoto, T., Eberhard, J.R., Graves, G.R., Sanchez, J.J., Capelli, S., Müller, H., Scharpegge, J., Chambers, G.K. and Fleischer, R.C., 2008. A multilocus molecular phylogeny of the parrots (Psittaciformes): support for a Gondwanan origin during the Cretaceous. *Molecular biology and evolution*, 25(10), pp.2141-2156.

Chapter Two: Quantifying parrot colouration

1. Ackerly, D., 2009. Conservatism and diversification of plant functional traits: evolutionary rates versus phylogenetic signal. *Proceedings of the National Academy of Sciences*, 106(Supplement 2), pp.19699-19706.
2. Brodie III, E.D., 1992. Correlational selection for color pattern and antipredator behavior in the garter snake *Thamnophis ordinoides*. *Evolution*, 46(5), pp.1284-1298.

3. Butler, M.A. and King, A.A., 2004. Phylogenetic comparative analysis: a modeling approach for adaptive evolution. *The American Naturalist*, 164(6), pp.683-695.
4. Endler, J.A. and MIELKE JR, P.W., 2005. Comparing entire colour patterns as birds see them. *Biological Journal of the Linnean Society*, 86(4), pp.405-431.
5. Endler, J.A., 2012. A framework for analysing colour pattern geometry: adjacent colours. *Biological Journal of the Linnean Society*, 107(2), pp.233-253.
6. Harmon, L.J., Losos, J.B., Jonathan Davies, T., Gillespie, R.G., Gittleman, J.L., Bryan Jennings, W., Kozak, K.H., McPeck, M.A., Moreno-Roark, F., Near, T.J. and Purvis, A., 2010. Early bursts of body size and shape evolution are rare in comparative data. *Evolution: International Journal of Organic Evolution*, 64(8), pp.2385-2396.
7. Hastings, W.K., 1970. Monte Carlo sampling methods using Markov chains and their applications.
8. Huang, J., Kumar, S.R., Mitra, M., Zhu, W.J. and Zabih, R., 1997, June. Image indexing using color correlograms. In *Computer Vision and Pattern Recognition, 1997. Proceedings., 1997 IEEE Computer Society Conference on* (pp. 762-768). IEEE.
9. Kunttu, I., Lepistö, L., Visa, A. and Rauhamaa, J., 2003. Image correlogram in image database indexing and retrieval. In *Digital Media Processing For Multimedia Interactive Services* (pp. 88-91).
10. Mahler, D.L., Revell, L.J., Glor, R.E. and Losos, J.B., 2010. Ecological opportunity and the rate of morphological evolution in the diversification of Greater Antillean anoles. *Evolution: International Journal of Organic Evolution*, 64(9), pp.2731-2745.
11. O'Meara, B.C., Ané, C., Sanderson, M.J. and Wainwright, P.C., 2006. Testing for different rates of continuous trait evolution using likelihood. *Evolution*, 60(5), pp.922-933.

12. Pérez I de Lanuza, G. and Font, E., 2016. The evolution of colour pattern complexity: selection for conspicuousness favours contrasting within-body colour combinations in lizards. *Journal of evolutionary biology*, 29(5), pp.942-951.
13. Revell, L.J. and Collar, D.C., 2009. Phylogenetic analysis of the evolutionary correlation using likelihood. *Evolution: International Journal of Organic Evolution*, 63(4), pp.1090-1100.
14. Revell, L.J., Harmon, L.J. and Collar, D.C., 2008. Phylogenetic signal, evolutionary process, and rate. *Systematic Biology*, 57(4), pp.591-601.
15. Talib, A., Mahmuddin, M., Husni, H. and George, L.E., 2013. Efficient, compact, and dominant color correlogram descriptors for content-based image retrieval. In *Proceedings of the Fifth International Conferences on Advances in Multimedia, Venice, Italy* (pp. 52-61).

Chapter Three: Conservation Status and Colouration

1. Andrews, C., 1990. The ornamental fish trade and fish conservation. *Journal of fish Biology*, 37, pp.53-59.
2. Barberena, J.B., 2017. Current threats faced by Neotropical parrot populations. *Biological Conservation*, 214, pp.278-287.
3. Barré, Nicolas, et al. "Exponential population increase in the endangered Ouvéa Parakeet (*Eunymphicus uvaeensis*) after community-based protection from nest poaching." *Journal of Ornithology* 151.3 (2010): 695-701.
4. Barry, C., 2011. Rogue traders; A suprising variety of endangered Australian wildlife is up for grabs on the black market. *Australian Geographic*.

5. Berkunsky, I., Quillfeldt, P., Brightsmith, D.J., Abbud, M.C., Aguilar, J.M.R.E., Alemán-Zelaya, U., Aramburú, R.M., Arias, A.A., McNab, R.B., Balsby, T.J.S. and
6. Cantu, J.C.G., Saldana, M.E.S., Grosselet, M. and Gamez, J.S., 2007. The illegal parrot trade in Mexico: a comprehensive assessment. *Mexico and Washington, DC: Defenders of Wildlife*.
7. Clarke, R. V. and de By, R. A (2013) Poaching, habitat loss and the decline of neotropical parrots: a comparative spatial analysis. *J. Exp. Criminol.* 9: 333 – 353.
8. Clarke, R.V., 1980. Situational crime prevention: Theory and practice. *Brit. J. Criminology*, 20, p.136.
9. Collar, N.J. (1997). Family Psittacidae (parrots). In J. de Hoyo, A. Elliott, and J. Sargatal (Eds.), *Sandgrouse to cuckoos, handbook of the birds of the world, vol.* (pp. 280-477). Barcelona: Lynx.
10. Collar, N.J. and Juniper, A.T., 1992. Dimensions and causes of the parrot conservation crisis. *New World parrots in crisis: solutions from conservation biology*, pp.1-24.
11. Cooney, R. and Jepson, P., 2006. The international wild bird trade: what's wrong with blanket bans?. *Oryx*, 40(1), pp.18-23.
12. Deane, D.C. and He, F., 2018. Loss of only the smallest patches will reduce species diversity in most discrete habitat networks. *Global change biology*, 24(12), pp.5802-5814.
13. Fogell, D.J. and Groombridge, J.J., 2018. Detection of Beak and feather disease virus in native and introduced parrots and consequent implications for conservation and the pet bird trade. *Conservation Biology*.
14. Frynta, D., Lišková, S., Bültmann, S. and Burda, H., 2010. Being attractive brings advantages: the case of parrot species in captivity. *PloS one*, 5(9), p.e12568.

15. Gastañaga, M., MacLeod, R., Hennessey, B., Nunez, J.U., Puse, E., Arrascue, A., Hoyos, J., Chambi, W.M., Vasquez, J. and Engblom, G., 2011. A study of the parrot trade in Peru and the potential importance of internal trade for threatened species. *Bird Conservation International*, 21(1), pp.76-85.
16. Gonzalez-Voyer, A., González-Suárez, M., Vilà, C. and Revilla, E., 2016. Larger brain size indirectly increases vulnerability to extinction in mammals. *Evolution*, 70(6), pp.1364-1375.
17. Gosling, W.D., de Kruif, J., Norder, S.J., de Boer, E.J., Hooghiemstra, H., Rijdsdijk, K.F. and McMichael, C.N., 2017. Mauritius on fire: Tracking historical human impacts on biodiversity loss. *Biotropica*, 49(6), pp.778-783.
18. Hadfield, J.D., 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software*, 33(2), pp.1-22.
19. Hargrave, L.L., 1965. Identification of feather fragments by microstudies. *Memoirs of the Society for American Archaeology*, pp.202-205.
20. Hermes, C., Keller, K., Nicholas, R.E., Segelbacher, G. and Schaefer, H.M., 2018. Projected impacts of climate change on habitat availability for an endangered parakeet. *PloS one*, 13(1), p.e0191773.
21. Herrera, M. and Hennessey, B., 2007. Quantifying the illegal parrot trade in Santa Cruz de la Sierra, Bolivia, with emphasis on threatened species. *Bird Conservation International*, 17(4), pp.295-300.
22. Human impacts on the rates of recent, present, and future bird extinctions. *Proceedings of the National Academy of Sciences*, 103(29), pp.10941-10946.
23. Huxel, G.R. and Hastings, A., 1999. Habitat loss, fragmentation, and restoration.
24. IUCN (2018). *Cacatua alba*. *IUCN Red List of Threatened Species. International*

25. IUCN. (2016). *IUCN Annual Report*. IUCN Redlist of Threatened Species. Available from <https://www.iucn.org/about/programme-work-and-reporting/annual-reports> [accessed 29 October 2018].
26. Juniper, T., 2004. *Spix's Macaw: the race to save the world's rarest bird*. Simon and Schuster.
27. Low, B.W., 2014. Corrigendum to: The global trade in native Australian parrots through Singapore between 2005 and 2011: a summary of trends and dynamics. *Emu*, 114(4), pp.389-390.
28. Melbourne, B.A. and Hastings, A., 2008. Extinction risk depends strongly on factors contributing to stochasticity. *Nature*, 454(7200), p.100.
29. Murphy, S.A., Austin, J.J., Murphy, R.K., Silcock, J., Joseph, L., Garnett, S.T., Leseberg, N.P., Watson, J.E. and Burbidge, A.H., 2017. Observations on breeding Night Parrots (*Pezoporus occidentalis*) in western Queensland. *Emu Austral Ornithology*, 117(2), pp.107-113.
30. Olah, G., Butchart, S.H., Symes, A., Guzmán, I.M., Cunningham, R., Brightsmith, D.J. and Heinsohn, R., 2016. Ecological and socio-economic factors affecting extinction risk in parrots. *Biodiversity and Conservation*, 25(2), pp.205-223.
31. Olah, G., Theuerkauf, J., Legault, A., Gula, R., Stein, J., Butchart, S., O'Brien, M. and Heinsohn, R., 2018. Parrots of Oceania—a comparative study of extinction risk. *Emu Austral Ornithology*, 118(1), pp.94-112.
32. Owens, I.P. and Bennett, P.M., 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proceedings of the National Academy of Sciences*, 97(22), pp.12144-12148.

33. Pain, D.J., Martins, T.L.F., Boussekey, M., Diaz, S.H., Downs, C.T., Ekstrom, J. M.M., Garnett, S., Gilardi, J.D., McNiven, D., Primot, P. and Rouys, S., 2006. Impact of protection on nest take and nesting success of parrots in Africa, Asia and Australasia. *Animal Conservation*, 9(3), pp.322-330.
34. Pimm, S., Raven, P., Peterson, A., Şekercioğlu, Ç.H. and Ehrlich, P.R., 2006.
35. Pires, S. and Clarke, R.V., 2012. Are parrots CRAVED? An analysis of parrot poaching in Mexico. *Journal of research in crime and delinquency*, 49(1), pp.122-146.
36. Pires, S.F. and Clarke, R.V., 2011. Sequential foraging, itinerant fences and parrot poaching in Bolivia. *The British Journal of Criminology*, 51(2), pp.314-335.
37. Pires, S.F., 2012. The illegal parrot trade: a literature review. *Global Crime*, 13(3), pp.176-190.
38. Raghavan, R., Dahanukar, N., Tlustý, M.F., Rhyne, A.L., Kumar, K.K., Molur, S. and Rosser, A.M., 2013. Uncovering an obscure trade: threatened freshwater fishes and the aquarium pet markets. *Biological Conservation*, 164, pp.158-169.
39. *Restoration Ecology*, 7(3), pp.309-315.
40. Roberts, D.L. and Solow, A.R., 2003. Flightless birds: when did the dodo become extinct?. *Nature*, 426(6964), p.245.
41. Strubbe, D. and Matthysen, E., 2007. Invasive ring-necked parakeets *Psittacula krameri* in Belgium: habitat selection and impact on native birds. *Ecography*, 30(4), pp.578-588.
42. Strubbe, D. and Matthysen, E., 2009. Experimental evidence for nest-site competition between invasive ring-necked parakeets (*Psittacula krameri*) and native nuthatches (*Sitta europaea*). *Biological Conservation*, 142(8), pp.1588-1594.
43. Tapley, B., Griffiths, R.A. and Bride, I., 2011. Dynamics of the trade in reptiles and amphibians within the United Kingdom over a ten-year period. *The Herpetological Journal*, 21(1), pp.27-34.

44. Tella, J.L. and Hiraldo, F., 2014. Illegal and legal parrot trade shows a long-term, cross-cultural preference for the most attractive species increasing their risk of extinction. *PLoS One*, 9(9), p.e107546.
45. *Union for Conservation of Nature*. Available from <https://www.iucnredlist.org/species/22684789/131915204> [accessed 19 October 2018].
46. Vall-Ilosera, M. and Cassey, P., 2017. 'Do you come from a land down under?' Characteristics of the international trade in Australian endemic parrots. *Biological conservation*, 207, pp.38-46.
47. Wild for Life (undated) Hyacinth Macaw. Wild for Life. Available from <https://wildfor.life/species/hyacinth-macaw> [accessed 12 November 2018].
48. Wright, S.J. and Muller-Landau, H.C., 2006. The Future of Tropical Forest Species *Biotropica: The Journal of Biology and Conservation*, 38(3), pp.287-301.
49. Wright, T.F., Toft, C.A., Enkerlin-Hoeflich, E., Gonzalez-Elizondo, J., Albornoz, M., Rodríguez-Ferraro, A., Rojas-Suárez, F., Sanz, V., Trujillo, A., Beissinger, S.R. and Berovides, V., 2001. Nest poaching in Neotropical parrots. *Conservation Biology*, 15(3), pp.710-720.

Discussion

1. Liu, C., White, M. and Newell, G., 2011. Measuring and comparing the accuracy of species distribution models with presence–absence data. *Ecography*, 34(2), pp.232-243.
2. Kahler, J.S. and Gore, M.L., 2012. Beyond the cooking pot and pocket book: Factors influencing noncompliance with wildlife poaching rules. *International Journal of Comparative and Applied Criminal Justice*, 36(2), pp.103-120.

3. Wright, T.F., Toft, C.A., Enkerlin-Hoeflich, E., Gonzalez-Elizondo, J., Albornoz, M., Rodríguez-Ferraro, A., Rojas-Suárez, F., Sanz, V., Trujillo, A., Beissinger, S.R. and Berovides, V., 2001. Nest poaching in Neotropical parrots. *Conservation Biology*, 15(3), pp.710-720.
4. Wright, T.F., Schirtzinger, E.E., Matsumoto, T., Eberhard, J.R., Graves, G.R., Sanchez, J.J., Capelli, S., Müller, H., Scharpegge, J., Chambers, G.K. and Fleischer, R.C., 2008. A multilocus molecular phylogeny of the parrots (Psittaciformes): support for a Gondwanan origin during the Cretaceous. *Molecular biology and evolution*, 25(10), pp.2141-2156.
5. Waterhouse, D.M., Lindow, B.E., Zelenkov, N.V. and Dyke, G.J., 2008. Two new parrots (Psittaciformes) from the lower Eocene fur formation of Denmark. *Palaeontology*, 51(3), pp.575-582.
6. Russello, M.A. and Amato, G., 2004. A molecular phylogeny of Amazona: implications for Neotropical parrot biogeography, taxonomy, and conservation. *Molecular phylogenetics and evolution*, 30(2), pp.421-437.
7. Schweizer, M., Seehausen, O., Güntert, M. and Hertwig, S.T., 2010. The evolutionary diversification of parrots supports a taxon pulse model with multiple trans-oceanic dispersal events and local radiations. *Molecular phylogenetics and evolution*, 54(3), pp.984-994.

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