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Shape matters: animal colour patterns as signals of individual quality

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Colour patterns (e.g. irregular, spotted or barred forms) are widespread in the animal kingdom, yet their potential role as signals of quality has been mostly neglected. However, a review of the published literature reveals that pattern itself (irrespective of its size or colour intensity) is a promising signal of individual quality across species of many different taxa. We propose at least four main pathways whereby patterns may reliably reflect individual quality: (i) as conventional signals of status, (ii) as indices of developmental homeostasis, (iii) by amplifying cues of somatic integrity and (iv) by amplifying individual investment in maintenance activities. Methodological constraints have traditionally hampered research on the signalling potential of colour patterns. To overcome this, we report a series of tools (e.g. colour adjacency and pattern regularity analyses, Fourier and granularity approaches, fractal geometry, geometric morphometrics) that allow objective quantification of pattern variability. We discuss how information provided by these methods should consider the visual system of the model species and behavioural responses to pattern metrics, in order to allow biologically meaningful conclusions. Finally, we propose future challenges in this research area that will require a multidisciplinary approach, bringing together inputs from genetics, physiology, behavioural ecology and evolutionary-developmental biology.

1. Introduction

Animal coloration is widely involved in mate choice, intra-sexual competition, dominance relationships and other social interactions, playing a central role in quality signalling [1]. Most research on colour-based signals of quality has focused on pigment-based traits (especially carotenoids, but also melanins). Under the assumption that pigment bioavailability is the main constraint in colour expression, most emphasis has been placed on the acquisition, metabolism and allocation trade-offs of each pigment or its precursors [1]. Derived from this marked interest in 'quantity-dependent' colour expression, most studies have focused on measuring the size or colour intensity/hue of colour patches as proxies of individual quality, irrespective of their production mechanism. However, coloured patches often vary among conspecifics in the shape, distribution and connectivity of their constituent units (e.g. spots, stripes and other heterogeneous markings; figure 1). That is, the actual two- or three-dimensional pattern of a colour trait can be highly variable among individuals. Such variability in patterning is largely independent of the area or colour intensity of the patch, and may therefore be subject to other functional constraints, allowing alternative—but not mutually exclusive—signalling pathways and reliability mechanisms for visual traits. Understanding the quality-signalling potential of visual patterns requires a conceptual and empirical change to our approach to animal coloration, addressing how they can be linked to individual quality, how animals perceive them, and what specific tools can be used to quantify these patterns.

Here, we review the main examples of quality-signalling colour patterns across animal taxa (§2); propose potential mechanisms by which patterns may reliably signal several aspects of individual quality (§3); summarize
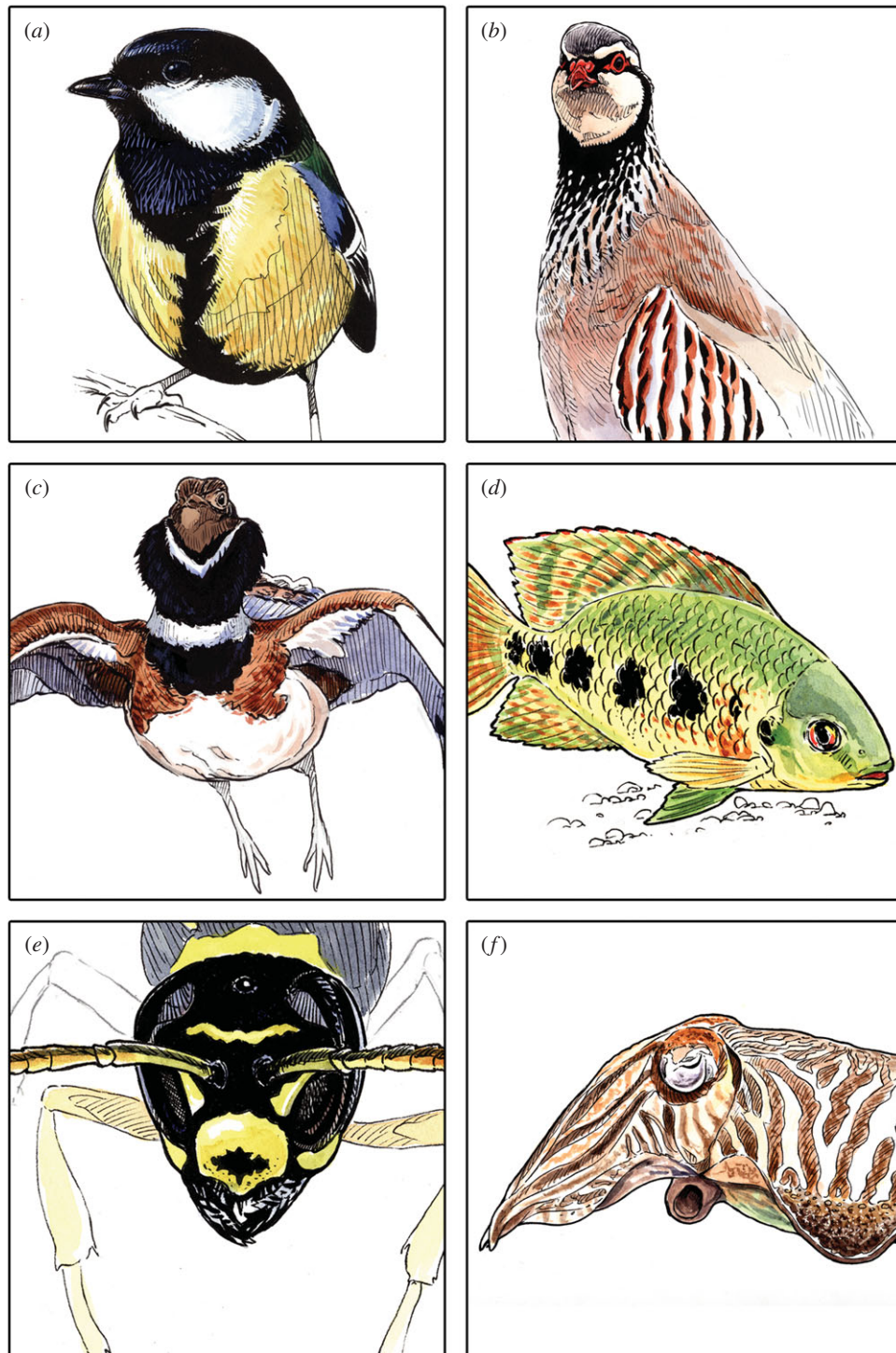
Figure 1. Six examples of colour patterns for which empirical evidence supporting quality-signalling potential has been reported: (*a*) white cheek patch of great tit (*Parus major*), (*b*) black spotted bib of the red-legged partridge (*Alectoris rufa*), (*c*) black V-shaped foreneck collar of little bustard (*Tetrax tetrax*), (*d*) black body patterning of tilapia (*Tilapia mariae*), (*e*) black clypeal spot of female paper wasps (*Polistes dominula*) and (*f*) body patterning of common cuttlefish (*Sepia officinalis*). Further details are given in table 1. Illustrations courtesy of Francisco J. Hernández. (Online version in colour.)

relevant analytical tools for objective quantitative descriptions of colour patterns (§4); identify aspects of pattern perception mechanisms that must be considered to interpret the biological relevance of pattern features (§5); and identify future challenges in this research area (§6).

2. Empirical evidence of quality-signalling colour patterns

Several studies using more holistic pattern descriptions than simply measuring the area or the number of constituent elements (e.g. number of spots or stripes) support the relevance of visual patterns in signalling contexts (figure 1 and table 1; see the electronic supplementary material, table S1, for a more complete list). Most evidence comes from birds, but a foremost example is the clypeal black patch of paper wasps (*Polistes dominula*; table 1 and figure 1), where shape is used in dominance signalling and is linked to developmental condition and other individual physiological variables. Cichlids provide among the best fish examples, with fast changes among discrete colour patterns reflecting the motivational state of the bearer or the outcome of social interactions (electronic supplementary material, table S1). The same applies to

Table 1. Illustrative examples of colour patterns of species from different taxa for which evidence compatible with quality signalling role has been provided (further examples are provided in the electronic supplementary material, table S1). Patterns are shown in figure 1.

species	colour pattern feature	evidence of its role as quality signal	ref.
great tit (*Parus major*)	regularity of the white cheek patch borders	Assortative mating according to the pattern, which also determines social status and survival. The pattern is also positively related to breeding investment and offspring quality	[2–5]
red-legged partridge (*Alectoris rufa*)	fractal dimension of the black bib	the pattern reflects male condition and immunocompetence	[6]
little bustard (*Tetrax tetrax*)	symmetry of the V-shaped foreneck collar	males with more symmetric patterns occupy more competitive leks and are preferred by females	[7,8]
tilapia (*Tilapia mariae*)	variable black patterning across the body	pattern expression mediates male's behavioural responses to opponents and reflects motivational state	[9,10]
paper wasp (*Polistes dominula*)	irregularity of the black clypeal spot	pattern reflects dominance status, nutrition during early development and juvenile hormone levels at adulthood; it also predicts overwinter survival and breeding success; it is negatively related to parasite prevalence at the population level	[11–17]
common cuttlefish (*Sepia officinalis*)	variable colour patterning across the body	certain colour patterns reflect motivational state and mediate agonistic interactions	[18,19]

cephalopods, which also rely on skin chromophores to display variable colour patterns that can change within seconds and may reflect dominance relationships in agonistic interactions (electronic supplementary material, table S1). Scant evidence is available for mammals and reptiles, where camouflage, predator–prey communication, thermoregulation or warning signalling are the most commonly suggested adaptive functions attributed to colour patterning. However, interspecific studies suggest that quality signalling is also a likely function in these taxa [20–22], thus encouraging empirical studies at the specific level in candidate mammal and reptile species.

3. Quality-dependent expression of colour patterns

Assessing the quality-signalling role of colour patterns requires an understanding of the factors determining differential expression between high- and low-quality individuals; that is, addressing the information a receiver can extract from the signal and the factors ensuring signal reliability. Different colour patterns probably entail different reliability mechanisms according to their own architecture, complexity, production mechanism, stage of ontogeny when they are generated, and the particular life history and ecology of the species. Below we suggest four non-mutually exclusive main pathways that may link individual quality to the expression of colour patterns. While melanin is responsible of most colour patterning found in animals, these pathways are potentially applicable to patterns resulting from any production mechanism (either pigmentary or structural).

(a) Conventional signals of social status

Traits mediating intraspecific social interactions often evolve as conventional signals, or badges of status [23,24]. These traits do not necessarily involve significant production costs, but target

receivers penalize the mismatch between sender quality and its signal level through agonistic interactions [24]. Given that the reliability of conventional signals is based on a consensus among senders and receivers, signal form is not necessarily constrained by a linkage between production mechanism and information conveyed [24]. Thus, any colour pattern could, in principle, evolve as a badge of status. However, for reasons of signalling efficiency, we would expect patterns used as badges of status to be simple and thus easily discriminable by the receiver (see §4). In fact, most examples of this kind of trait consist of simple colour patches that mainly vary in size between high- and low-quality individuals [23]. However, there are some examples where more complex pattern features work as a badge of status, like the uniformity of the cheek patch of great tits, the black spots of paper wasps, or the rapidly variable and state-dependent patterns displayed by cichlids and certain marine taxa (table 1; electronic supplementary material, table S1).

Nevertheless, some degree of condition-dependence can also be expected in badges of status because signal expression, agonistic behaviour and condition are likely interrelated, and displaying a certain level of the signal implies a prime physiological state to face the social costs associated with it [25]. The mechanisms invoked to link physiological state and dominance signalling via colour intensity or size of badges of status often involve endocrine or energetic constraints [23], but the potential effects of these factors on the spatial features of a colour patch are yet to be elucidated. For instance, evidence from paper wasps indicates that the shape of the clypeal spot is subject to social control by conspecifics, but is also influenced by body condition during early development and is correlated to juvenile hormone levels (an invertebrate analogous to testosterone), thus supporting the existence of such links. In any case, carefully designed experimental set-ups [23] are required to tease apart the relative importance of social costs and physiological constraints on the production of colour patterns used as badges of status.

(b) Indices of developmental homeostasis

Developmental homeostasis (including developmental stability and canalization) buffers small perturbations that can cause alterations in the normal developmental process of individuals, leading to fitness reductions [26–28]. In organisms with bilateral symmetry, fluctuating asymmetry is the most commonly used estimate of this phenomenon [26,28] and is often assumed to behave as a reliable index of individual quality [28]. However, most studies on fluctuating asymmetry have focused on morphological traits, but rarely on colour pattern features (but see the electronic supplementary material, table S1, for exceptions). This is surprising since morphological traits are likely under strong stabilizing selection, as even subtle asymmetries in any structural traits would entail significant viability costs [28]. By contrast, fluctuating asymmetry of colour traits is less likely to entail viability costs. This probably relaxes the selection for tight control over their symmetry, increasing sensitivity to environmental and genetic stress, and allowing them to better reflect developmental stability.

Beyond fluctuating asymmetry of symmetric traits, the capacity of individuals to express a given pattern can also reveal an individual's developmental homeostasis [26]. The pathway to produce a colour pattern form involves many different steps that must be synchronized at very different temporal and spatial scales (figure 2; e.g. [29,30]). Genetic and environmental perturbations can affect this process at different levels, causing cumulative deviations from the target pattern, which can be reliable indicators of the incapacity of the individual to buffer the developmental process. This is highlighted by a trait architecture that involves the imbrication of different units, like feathers, hairs or scales (figure 2). However, the same basic mechanism applies to taxa lacking these structures (e.g. invertebrates and amphibians), as the maturation, migration and arrangement across the body of their main coloration units—chromatophores—are equally sensitive to the same stressors [31].

Sharp and uniform borders, as well as regular repetition of elements (i.e. bars and spots) probably represent challenges for developmental buffering mechanisms, particularly in complex forms. Thus, uniformity, regularity and complexity are likely candidates as signals of developmental homeostasis. However, in most cases, identifying the optimum display *a priori* would be difficult. To avoid using arbitrary criteria, the best approach would be to rely on behavioural data (e.g. mate choice or dominance tests) to identify the pattern features positively selected under signalling scenarios. Identifying the factors deviating patterns from these optima would then be the next step.

Trait sensitivity to alterations of developmental homeostasis varies across ontogeny [26,28], and this is probably the case for pattern capacity to mirror individual quality. This implies that stressful conditions will only impact pattern expression at certain developmental windows that will vary among species or traits. This is particularly relevant for traits in animals that undergo one or multiple moulting processes. In these cases, pattern sensitivity to individual physiological state during moult can be restricted to early development or remain open at every moulting event, depending on the lability of the precise mechanisms implicated in the expression of each pattern feature. Colour patterns fixed during early development, even though insensitive to physiological state afterwards, are indeed good candidate indices of quality, as stressful conditions early in life often have long-lasting effects on individual viability [31].

(c) Amplifiers of cues of somatic integrity

The wear of plumage, skin or pelage is often related to suboptimal performance, senescence or overall somatic deterioration [2,32,33]. Parasites impose significant fitness costs to the individual, and in the case of ectoparasites, their action often damages external host appearance. In addition, damage, scars and broken or missing feathers or scales are usually the result of close encounters with predators or outcomes of agonistic interactions from which the individual did not escape unscathed. It is therefore not surprising that all these alterations of somatic integrity can be used as cues for individual quality assessment (e.g. [32,34]).

Cues of somatic integrity would be amplified by certain colour patterns [35]. In fact, this potential role of some plumage decorations was originally selected by Hasson to illustrate the concept of an 'amplifier' (i.e. a trait that increases the resolution of a signal, enhancing the discrimination power of the receiver) [36], and some empirical evidence supports this. For instance, in great tits (*Parus major*), cheek patch irregularities often reveal the presence of ectoparasites or injuries caused by conspecifics [2,5]. Similarly, the lateral barred pattern of the red-legged partridge (*Alectoris rufa*), resulting from the perfect alignment of flank feathers (figure 1b), is conspicuously altered by feather loss [37]; interestingly, replacement feathers do not perfectly fill these gaps, leaving traces of traumatic events [37].

This somatic integrity role of colour patterns should not be confounded with the handicapping role of certain markings that increase the risk of damage, abrasion or degradation by bacteria or ectoparasites, as typically proposed for some plumage traits [33]. Whereas the latter role is dependent on the size or location of the markings, the amplifying function of somatic integrity is mostly based on the shape of the pattern and the particular architecture of the trait. We propose that traits composed of multiple units and whose imbrication produces a regular pattern of repeated elements (bars and spots) evenly distributed across a given body region are particularly prone to evolve under this amplifying function.

(d) Amplifiers of cost-added signals of maintenance activities

Preening and grooming activities are essential to remove ectoparasites and maintain the insulating and signalling properties of external teguments. Animals, and particularly vertebrates, spend considerable time and energy in maintenance behaviour [38,39], trading off with other behaviours, such as feeding and vigilance. Given that these grooming and preening activities are particularly important to enhance the conspicuousness of ornamental traits [39], it has been suggested that they function as cost-added signals of individual quality revealing that the bearer can afford a high day-to-day investment [39].

The effective execution of these maintenance activities would be amplified by certain colour patterns. As in the previous case, composite patterns whose correct display involves an optimal arrangement of multiple units probably require higher investment. Combinations of highly contrasting colours, and predominance of white markings, may be
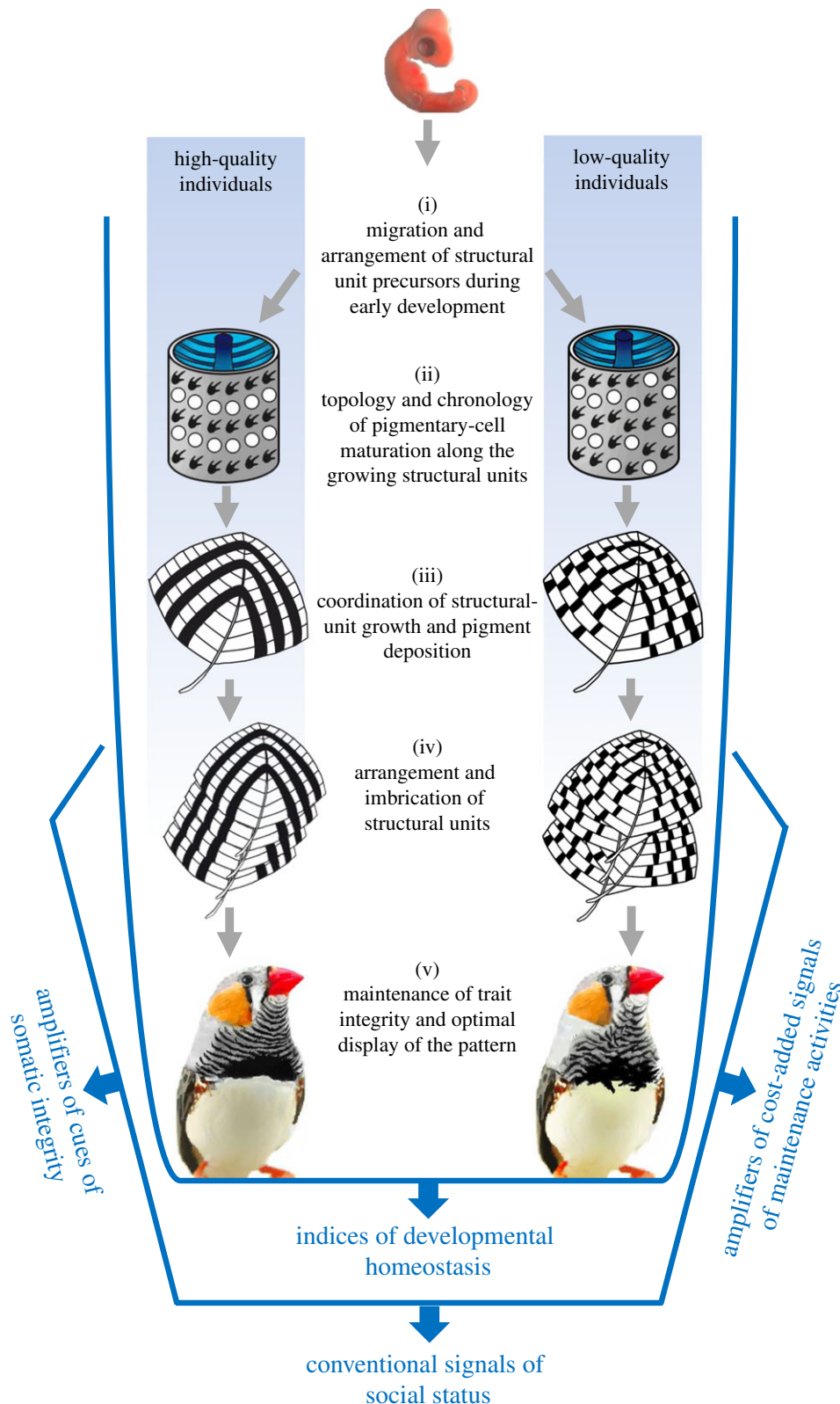
Figure 2. Schematic of the developmental process of colour pattern formation and how this relates to the four reliability mechanisms discussed in §3. A melanin-based pattern expressed in a plumage trait has been selected as an illustrative example, although the general scheme can be easily translated to other types of traits (skin-, hair- or scale-based). Pattern expression depends on the developmental control of processes that take place at different scales and that require a tight spatio-temporal coordination. These include, for instance, the arrangement during early embryonic development of structural units (feather germs) and pigmentary cell precursors (melanocytes) across the body according to the general pattern layout (i). During structural unit growth, the topology and maturation of undifferentiated (white circles) into differentiated melanocytes (black symbols) must be coordinated with structural unit growth (ii). A correct synchronization between melanosome production by differentiated melanocytes and their transfer to proliferating keratinocytes is required to elaborate the within-unit pattern adequately (iii). Furthermore, these structural units must be developed, arranged and perfectly imbricated to fully display the composite pattern resulting from their combined effect (iv). Stressors altering all these steps will exert cumulative effects on the final pattern, which would be gradually deviated from its optimum. Individual capacity to buffer such deleterious effects will differ among high- and low-quality individuals, making colour pattern expression a reliable index of developmental homeostasis (§3b). Beyond these factors affecting pattern development, individual wearing an undamaged, immaculate and well-groomed plumage, coat or skin will be able to better display their colour pattern (v), which would then act as an amplifier of somatic integrity (§3c) and investment on maintenance activities (§3d). Finally, overall pattern appearance would elicit variable responses from conspecifics, mediating the reliability of colour pattern features as conventional signals of status (§3a). (Online version in colour.)

particularly used by receivers to assess the signaller's ability to keep their pelage, skin or plumage in good shape.

4. Methods for quantifying colour patterning

One of the main factors to have hampered our understanding of the functions of colour patterns is the difficulty in quantifying overall pattern appearance. As a simple holistic solution, some studies have relied on qualitative classifications of the patterns (electronic supplementary material, table S1). This is a reasonable method for clearly distinguishable and discrete forms, such as the state-dependent patterns of many cichlid fishes (table 1). However, this is not advisable for more continuous traits, or when discrete categories are in fact a summary of different independent traits that may signal different aspects of individual quality (§3). In recent years, an increasing number of analytical tools and methodological approaches for capturing different aspects of colour patterns have become available. Although in some cases their application to animal colour markings is still pending, they constitute promising venues for objectively describing patterns and thus exploring their potential biological function.

(a) Barred patterns and regularity analysis

Barred patterns (i.e. those composed by lines or stripes) are widespread across taxa. In those groups where the barred pattern results from lighter and darker elements placed side by side, pattern regularity is one of the most evident trait features. The freely accessible software developed by Gluckman & Cardoso [40] analyses barred patterns by aligning the coloured bars, and then quantifying deviations from an ideal pattern, where all bars are uninterrupted, of constant widths and with smooth borders between colours. This measure only allows comparisons between equivalent patches among individuals of the same species, but not among different patches or species, because this measure is affected by the gross morphology of the pattern (e.g. the width of the bars) [41]. So far, this method has only been applied to the plumages of a few bird species [40]. In common waxbills (*Estrilda astrild*), it has provided compelling evidence that the regularity of their barred plumage would serve as a quality signal, as revealed by its sex-by-age variability and its link to body condition [41].

(b) Colour adjacency analysis

Built on the basis of colour analyses and visual modelling, the colour adjacency method [42] provides a framework based upon transitions between colour patches that make it possible to estimate pattern parameters like colour diversity, complexity or aspect ratio. The adjacency analysis relies on collecting colour characteristics—either by spectrophotometric methods or digital photography—as in conventional coloration studies. Instead of collecting colour samples in a single patch, they are collected in a large number of points ordered in a grid covering the entire body of the animal or the body region of interest. This grid is aligned with a reference body axis, so that colour measures are encoded into a zone map that allows subsequent adjacency analyses. These allow quantifying patch size and the number and orientation of transitions across colour patches, thus providing indices of pattern elongation, regularity and complexity, while also considering the particularities of the visual system of the study

species. No specific software has been released for this method, although all procedures can be carried out in R or MATLAB (functions are available from the author) [42].

Adjacency analyses have been used to address the study of the highly variable colour patterning of poison frogs [43,44]. This approach allowed summarizing frogs' dorsal patterns in a few descriptive variables, like the relative contribution of each colour to the forms or pattern complexity and elongation, which have been shown to be useful to understand their biological function [43,44]. However, while this approach is a statistically useful avenue to analyse patterns, it does not resemble the way that visual systems process pattern information.

(c) Spotted patterns and Fourier and granularity analyses

Substantial earlier work revealed a number of properties of early spatial vision processing across a range of animals, including the presence of receptive fields that respond to contrast, edges and shape information, including in particular orientations (e.g. [45,46]). Such features are often processed at different spatial frequencies (e.g. pattern sizes) [47]. The advent of image analysis tools opened up a wide range of avenues with regards to quantifying patterns, many of them based on spatial frequency techniques, especially Fourier analysis. Here, a given pattern can be quantified in terms of its contrast, spatial frequency, phase and orientation.

In nature, many patterns are not lines and gratings (e.g. stripes), but rather composed of spots and 'blobs' of different sizes. A comparatively recent approach to quantify these has been through 'granularity' analysis, whereby images of a given object pattern or scene are Fourier-processed followed by bandpass filtering to create a subset of images containing information at a number of spatial frequency bands, ranging from high (small markings) to low spatial frequency (large markings). Following this, the amount of 'energy' at each band can be measured, with higher energy corresponding to more prominent markings. A plot of energy versus spatial frequency produces a 'granularity spectrum', from which a number of descriptive metrics can be obtained, including marking size, contrast and diversity. This approach has successfully been implemented in various studies describing types of cuttlefish camouflage markings [48,49], as well as pattern mimicry and rejection behaviour of cuckoo-host eggs [50]. It is likely that animals respond to multiple metrics derived from such analyses, but that the specific features used vary with species and context. For example, hosts of brood parasites base their egg rejection behaviour on assessing mimicry with regard to egg marking size, contrast, variability and dispersion, but the specific features used and their relative importance varies with species [50,51]. However, to our knowledge, the application of these approaches to the study of quality-signalling patterns is still pending. These granularity approaches are freely available in a recently released image calibration and analyses toolbox [52].

There are at least two other approaches here to quantify spot-type patterns. First, recent work has used an approach called Scale Invariant Feature Transform (SIFT), which is essentially a computer vision approach for object and feature recognition at different angles and scales. This has been successfully applied to analysing cuckoo-host egg markings [53]. Another complementary approach used by some authors is

to threshold patterns into binary black and white images, and then measure the distribution and coverage of markings over different regions of an object [54]. A recent set of functions called 'SpotEgg' [55] have also been published that allow adaptive thresholding of images to cope with differences in illumination and object shape, while providing information about spot size, distribution, shape and other features such as fractal dimension (see below).

(d) Fractal geometry

Fractals are mathematical objects that are self-similar across scales and whose shape is too complex to be described by Euclidean geometry [56]. Many natural objects are not strictly self-similar, but can be considered 'statistical fractals' and their shape can be successfully described by fractal geometry [56].

There are several types of fractal analyses, but all of them rely on some type of 'fractal dimension', which estimates pattern complexity as a scaling rule comparing how a pattern's detail changes with the scale at which it is considered. Fractal dimension is often calculated by box-counting methods, which proceed by overlaying the studied pattern by meshes of different cell side lengths, subsequently counting the number cells occupied by the pattern for each mesh size. The scaling rule of cell size over the inverse of the number of cells occupied by the pattern (both in logarithmic scale) determines its fractal dimension [56]. Fractal dimension can be calculated on lines, surfaces or volumes, capturing the space-filling capacity of the pattern, which is closely related to different properties such as the number, length, tortuosity and connectivity of its elements. Importantly, fractal dimension may be sensitive to different trait features for different types of patterns. Therefore, understanding the meaning of the fractal dimension for each pattern requires a case-by-case exploration [6]. However, irrespective of the particular pattern studied, it should be noted that the applicability of this method does not imply that animals are able to detect fractal dimension itself; rather, this measure captures variations in certain pattern features that animals can detect, but that are difficult to quantify objectively by other methods.

Fractal dimension is the simplest and most popular fractal analysis, but not the only one. Multifractal analysis provides a much more detailed description of a pattern, where the arrangement (mass distribution) of the pattern is analysed at different scales by the 'singularity spectrum'. 'Lacunarity' is another useful concept from fractal geometry that quantifies the gappiness and heterogeneity of a given pattern, as well as its rotational invariance. Performing most of these analyses is relatively straightforward by using freely available software (e.g. Fractaldim, HarFa, FracLac).

Fractal geometry techniques are particularly suitable for addressing intricate, complex and heterogeneous patterns. By measuring the continuity of a pattern through scales, it somehow mirrors the inherent architecture of many animal colour traits composed by different units (scales, feathers and hairs), and is thus an interesting tool to capture the variability resulting from such multi-scaled construction of the trait. However, to date, their application to animal colour patterning has been limited [57]. In a recent experimental study, fractal dimension of the black bib of the red-legged partridge (figure 1b) was particularly useful to distinguish between individuals with a smooth or a sharp transition from the plain black to the spotted areas of the bib. This trait feature predicted individual body condition and immune

responsiveness, a relationship that remained unnoticed when using simpler measures of the trait [6]. Also, although not from the perspective of quality-signalling, fractal geometry has proved useful to describe butterfly wing patterns [58], and the cranial and shell sutures in mammals and ammonoid taxa [59,60]. The latter examples support the usefulness of fractal dimension to quantify the integrity and regularity of whole colour patches or their borders.

(e) Geometric morphometrics

Geometric morphometrics is the analysis of morphological structures using Cartesian geometric coordinates rather than linear, areal or volumetric variables. One of the main advantages of this tool is that it allows capturing the shape of an object independent of its size, position and orientation. Object shape is translated into a series of derived coordinates that are easy to interpret and represent, and amenable to a wide array of statistical approaches [61,62].

Geometric morphometrics is based on 'landmarks' (i.e. homologous points that represent the same biological location across specimens). Once identified and digitized, landmarks can be processed by different geometric approaches, of which the Procrustes superimposition method is the most widespread [61,62]. The homology requisite of landmarks is usually fulfilled by using clearly identifiable points like cusps, invaginations or intersections.

There are several issues that make geometric morphometrics a particularly interesting tool for colour patterning analysis. For instance, it allows describing both in two- and three-dimensional shapes. This is particularly useful to capture colour patterns displayed in tridimensional structures, like legs, wings or non-flat areas of the body, providing these are digitized in a natural display manner. Also, geometric morphometrics allow controlling for potential allometric effects, or for a covariance between body and pattern shape. Another interesting feature of geometric morphometrics is its unique potential to capture several types of symmetry, from matching or object symmetry to more complex configurations, like reflection, rotational, translational or spiral symmetries [27]. It also addresses what specific pattern features are contributing most to symmetry deviations, which is of great interest for understanding the subjacent mechanisms linking pattern expression and individual quality (§5).

There are several freely available software tools and R packages for data digitalization, conversion, visualization and analysis of geometric morphometric data (see life.bio. sunysb.edu/morph). Despite the advantages of geometric morphometrics and availability of free and user-friendly software, to our knowledge no study has applied this set of powerful tools to the study of colour patterns in the context discussed here.

5. The need to consider the visual properties of the receiver

In recent years, the study of animal coloration has advanced considerably with the widespread use of objective measures of colour and models of animal vision. Unlike colour perception, which varies considerably across and even within species [63], many of the general features determining pattern vision seem to be similar even across taxa (at least in low-level vision [64]). This makes modelling certain aspects of

pattern vision and producing widely relevant techniques potentially highly tractable.

A number of approaches to quantifying animal patterns have been based on the idea of approximately resembling visual processing, most notably Fourier and granularity analyses (see above; though note that these algorithms do not mimic real visual systems exactly, but rather broad principles). Other approaches include techniques for quantifying the edges of objects and patterns (e.g. [65]), although again how exactly edge detection is undertaken by real visual systems is unclear and many models exist [64]. Ultimately, any model used needs to be validated with behavioural data to determine its relevance. In theory, it is possible to come up with a highly sophisticated model of high-level pattern vision, yet if this misses some key step or process found in real visual systems then this may produce inaccurate results. By contrast, comparatively simple models of pattern assessment could produce very effective metrics. The latter is broadly the case for granularity and edge detection approaches, whereby derived pattern metrics do effectively predict behavioural responses [50]. Other models may not mimic visual processing pathways closely (e.g. fractal analysis) but still derive information that is closely akin to that acquired and used by the receiver.

Ultimately, just as with metrics of colour, we need to test that the values and variation among individuals in pattern metrics coincide with a response by the receiver; that is, that the receiver actually sees and responds to that information. This is the key consideration for any pattern quantification tool. If on top of that the model is aimed at mimicking principles of visual processing, then this also allows us to potentially understand the visual mechanisms involved. Note, however, that to make more realistic models of pattern vision, further precise information on pattern processing is needed, as well as more information on things such as display behaviour and angle and distance of viewing by the receiver to the signaller. For example, visual acuity (the ability to resolve features of a given sized object) varies considerably with species' visual system and observation distance, and this will affect how well a receiver can see aspects of pattern. Furthermore, owing to features of receptive fields and spatial frequency processing (see above), animals differ in their ability to detect different spatial frequencies at different contrast levels, which can be characterized with a so-called 'contrast sensitivity function' (CSF) [47]. CSFs can describe and compare visual performance at different levels of pattern scale and contrast among species. As such, incorporating CSF and acuity information (which are available for a range of species) into models of pattern vision should, in principle, provide a more accurate approach to determining the information available from animal markings to the receiver, and can allow other information to be considered (such as viewing distances). At present, information on acuity and CSF are rarely incorporated into analyses of animal colour patterns, yet this information could be valuable in determining receiver responses to patterns of different contrast and size from different viewing distances.

6. Concluding remarks and future research directions

In this review, we have highlighted the potential of animal colour patterning, beyond size and colour intensity, to play a relevant

role as reliable signals of individual quality. Available evidence supports this signalling role in a wide array of taxa. The reliability of quality-signalling colour patterns might involve several mechanisms, like social control, impaired developmental homeostasis, somatic deterioration or reduced investment on self-maintenance. Although methodological limitations have hampered the research of these patterns for a long time, these are no longer a major constraint, as currently available analytical methods allow an objective and accurate quantification of different pattern features. However, the use of these tools must consider relevant aspects of the visual system of the model species and (crucially) behavioural responses, in order to allow biologically meaningful conclusions.

The different reliability mechanisms proposed here are not mutually exclusive. Indeed, colour patterns may (and probably do) act as 'multicomponent signals', where different features of a given pattern may inform about different aspects of the bearer or act as back-ups [66]. For instance, the symmetry and uniformity of the markings composing a given plumage pattern could indicate the stress levels suffered by the individual during early development. But once developed, the ability of the individual to keep undamaged and perfectly arranged all the feathers composing the display would amplify its capacity to keep its soma in prime conditions and allocate resources to self-maintenance. If the pattern behaves as a badge of status, the social costs derived from agonistic interactions can also be added to the system. The specific weight of each reliability pathway will depend on the ecology of the species and the particular architecture of the trait. Experiments would be needed to disentangle the relative importance of each signalling pathway.

A quality-signalling capacity does not preclude the same colour patterns from simultaneously being used in other functions, such as thermoregulation, anti-glare, concealment, individual recognition or aposematism [67]. This would be the case, for instance, of the facial masks and other common head markings of birds often assumed to provide anti-glare protection or gaze concealment to predators or opponents [67], but whose expression (regularity of borders, symmetry) might also reflect individual quality (e.g. [2,8]). This polyvalent conception of colour patterns can conciliate, for instance, a signalling function and a role in predation avoidance via camouflage or aposematism for a single trait. In the latter case, this would help to explain the apparently paradoxical variability in aposematic patterns observed within a given species [43].

Understanding the information content of colour patterns requires a deep knowledge of the main factors constraining its expression. This is particularly pertinent in the case of amplifiers of developmental homeostasis (§3b), as the reliability of the colour pattern is intrinsically linked to its production mechanism. Understanding how each pattern feature can reflect the homeostasis of the developmental process is therefore a major challenge. In this sense, reaction–diffusion models provide a useful framework for studying pattern formation, both within structural units and across the whole body (e.g. [68,69]). According to these models, increasing pattern complexity requires controlling a higher number of morphogens and regulatory parameters to achieve the target pattern [68,69]. Such complexity derived from theoretical models predicts the evolutionary pathways and key ecological aspects of patterns in different taxa [70,71]; however, addressing whether increased pattern complexity implies higher

lability during development is still pending. This task requires a multidisciplinary approach, combining inputs from genetics, biochemistry, physiology and evolutionary developmental biology. Incorporating other reliability mechanisms into the equation (§3) would require behavioural tests and comparative approaches. Unfortunately, to date, evidence of the different reliability mechanisms discussed here is fragmentary, and comes from very different study models. Bringing together behavioural and mechanistic approaches in the same study system is a pressing task to fully assess the quality-signalling role of colour patterns.

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Table S1. Overview of colour patterns from for which evidence compatible with quality signalling role has been provided. We detail the trait studied, the method used to quantify it, the evidences compatible with a signalling role reported, the study conditions (i.e. wild or captive), the type of study (i.e. observational or experimental) and the corresponding references. [Pérez-Rodríguez L, Jovani R, Stevens M (2017). Shape matters: animal colour patterns as signals of individual quality. *Proc. R. Soc. B-Biol. Sci.]*

Species	Studied trait	Measurement method	Evidence of its role as quality signal in social interactions	Conditions	Type of study	Ref.
Birds						
Harris's sparrows (*Zonotrichia querula*)	Plumage "studliness", defined on the basis the presence of unflecked and sharply defined black bibs	14-point subjective "studliness" score	Birds with higher scores are dominant in winter flocks	Wild	Obs	[1]
Mallard (*Anas platyrhynchos*)	Deviations from an ideal ("unblemished" or "bright") nuptial plumage of collar, head, chest, flanks, speculum and tail	Composite score based on the presence/absence and severity of blemishes, uneven, jagged borders, interruptions, fleckings in each plumage patch	Males with higher scores were preferred by females	Captivity	Obs, Exp	[2, 3]
Zebra finch (*Taeniopygia guttata*)	Symmetry of the barred chest plumage	Fluctuating asymmetry of the barred chest pattern	Females prefer males with more symmetric patterns	Captivity	Exp	[4]
	Deviations from the natural uniform barred chest plumage	Classification as normal vs. abnormal chest pattern (i.e. presence of melanic areas)	Greater proportion of juveniles with pattern abnormalities among those experiencing poor nutritional conditions	Captivity	Exp	[5]
House finch (*Haemorhous mexicanus*)	Symmetry of the carotenoid based pigmentation of the crown plumage	5-point score of symmetry	Birds with more symmetric crown pigmentation are redder (being plumage redness and indicator of overall quality in this species) and have higher mating success	Wild	Obs	[6, 7]
Black-capped chickadee (*Poecile atricapillus*)	"Raggedness" of the black bib , defined by the presence of irregular and interdigitated borders	Continuous variable derived from perimeter-to-area relationship	Age-related differences (yearlings >adults) consistent with a status signalling role. Indirect evidence of some environmental determination.	Wild	Obs	[8]
Red-legged partridge (*Alectoris rufa*)	Fractal dimension of the black bib, determined by a gradual vs sharp transition from the solid to the spotted area of the bib	Fractal dimension	Bib fractal dimension reflects male condition and immunocompetence	Captivity	Obs, Exp	[9]
Great tit (*Parus major*)	White cheek "immaculateness", determined by regularity of the patch borders	Continuous variable derived from an *ad hoc* algorithm relating perimeter and area of the patch	Assortative mating according to cheek immaculateness. Trait also positively related to breeding investment and heightened offspring quality. Immaculateness determines social status in males and is related to overwinter survival.	Wild	Obs, Exp	[10-13]
Red-necked nightjar (*Caprimulgus ruficollis*)	"Contrast" and "conspicuousness" of the tail and wing white patches, defined by the sharpness of their edges and their uniformity within a patch	Composite measures based on scores and subsequent classification into discrete categories	Age- and sex-related variations consistent with role in social signalling	Wild	Obs	[14]

Species	Trait	Measurement	Finding	Origin	Method	Ref
Little bustard (*Tetrax tetrax*)	Symmetry of the V-shaped foreneck collar	Classification of individuals either as symmetric or asymmetric	Higher proportion of symmetric individuals in large (i.e. more competitive) leks. Symmetric collars result more attractive to females	Wild	Obs, Exp	[15, 16]
Shelduck (*Tadorna tadorna*)	"Immaculateness" of the red-brown chest patch, determined by the uniformity of the plumage colour and the regularity of the borders	8-point score based on the presence and frequency of white specks and smoothness of the borders	Sexual dimorphism (males>females) and assortative mating on the basis of the trait. More immaculate males are more successful at holding a territory and producing offspring	Wild	Obs	[17]
Peacock (*Pavo cristatus*)	Symmetry in the number of ocelli of the train	Fluctuating Asymmetry of the trait	Males with more elaborate trains also show higher asymmetry in the distribution of ocelli	Capt	Obs	[18]
Common waxbill (*Estrilda astrild*)	Regularity of the barred contour plumage	Software specifically designed to measure barred pattern regularity and contrast (19)	Age- and sex-related differences consistent with a quality signalling role (i.e. yearlings <adults; females<males). Pattern regularity positively related to body condition.	Wild	Obs	[19]
Barn swallow (*Hirundo rustica*)	Roundness of the white spots of tail feathers	Spot perimeter statistically controlled for spot area as a covariate	Sexual dimorphism in spot shape: male spots were more variable in shape and overall less rounded than females'. Spot roundness was negatively related to condition during feather growth	Wild	Obs	[20]
Common chaffinch (*Fringilla coelebs*)	Symmetry of the white wing eppaulettes	Discrete classification either as symmetric or asymmetric	Intruders with asymmetric epaulettes receive more direct aggressions from territory owners	Wild	Exp	[21]
Black grouse (*Lyrurus tetrix*)	Frequency and location in the feather (vane vs. tip) of black spots in the undertail white cover plumage of males	Presence and location of spots in the undertail feathers	Higher frequency of spots in the feather tips is negatively related to male survival, fighting rate and reproductive success	Wild	Obs	[22]
Eurasian jay (*Garrulus glandarius*)	Regularity of the barred pattern of the alula, primary coverts and outer greater coverts	Qualitative classification	Age-related differences consistent with a quality signalling role (1st-year< older individuals)	Wild	Obs	[23]
Mammals						
Killer whale (*Urcinus orca*)	Saddle patch asymmetry	Fluctuating Asymmetry of the trait	More inbreed populations exhibit higher levels of patch asymmetry	Wild	Obs	[24]
Amphibians						
Fire salamander (*Salamandra salamandra*)	Dorsal spotted pattern	Circularity of dorsal spots	Dorsal spots become more irregularly shaped with age (size used as a proxy)	Wild	Obs	[25]
Spotted salamander (*Ambystoma maculatum*)	Dorsal spotted pattern	Fluctuating asymmetry of the pattern	Fluctuating asymmetry of the pattern is negatively related to body condition, being also higher Individuals grown in more degraded habitats as compared to those from more conserved areas	Wild	Obs	[26, 27]
Fishes						
Mbuna malawian cichlids (*Labeotropheus fuelleborni*)	Gross colour pattern across the body	Categorical classification of the pattern based on the presence, abundance, shape and size of colour patches	Gross colour pattern mediates the male´s agonistic responses to opponents	Capt	Exp	[28]

Tilapia (*Tilapia mariae*)	Black patterning across the body	Categorical classification of patterns based on the presence, abundance, shape and size of colour patches	Colour pattern mediates the male´s behavioural responses to opponents and reflects motivational state	Capt	Obs, Exp	[29, 30]
Texas cichlid (*Cichlasoma cyanoguttata)*	Black patterning across the body	Categorical classification of patterns based on the presence, number, shape and contrast of spots and stripes	Colour pattern mediates the male´s behavioural responses to opponents	Capt	Exp	[31]
Günther's mouthbrooder (*Chromidotilapia guentheri*)	Black patterning across the body	Categorical classification of patterns based on the presence, number, shape and contrast of spots and stripes	Different colour pattern are used as signals in social interactions (i.e. courting and agonistic displays)	Capt	Obs	[32]
Insects						
Paper wasp (*Polistes dominula*)	"Brokenness" of the black clypeal spot, defined by its irregularity and likeliness to be split in separate units	*Ad hoc* image processing method that quantifies the variability in pigment distribution across the area of interest	Pattern brokenness reflects dominance status, nutrition during early development and juvenile hormone levels at adulthood; it also predicts overwinter survival and breeding success. It is negatively related to parasite prevalence at the population level	Wild, Capt	Obs, Exp	[33- 39]
	The irregularity –or "blobbiness"- of the yellow dorsal abdominal spots	A Spot Shape Index derived from an *ad hoc* algorithm relating perimeter and area of the spot	Males with elliptically shaped spots were more dominant over male rivals and were more preferred by females than males with irregularly shaped spots.	Capt	Obs, Exp	[40]
Molluscs						
Common cuttlefish (*Sepia officinalis*)	Yellow, red, brown and white patterning across the body	Categorical classification of colour patterns	Colour patterns mediates the agonistic interactions	Capt	Obs	[41-42]
Indo-pacific cuttlefish (*Sepia latimanus*)	Yellow, red, brown and white patterning across the body	Qualitative description of different body patterns	Colour patterns mediates the agonistic interactions	Wild	Obs	[43]
Veined squid (*Loligo forbesii*)	Yellow, red, brown and white patterning across the body	Asymmetry in the number and location of chromatophores	Fluctuating asymmetry in chromatophore number and topology reflects thermal stress during embryonic development	Capt	Exp	[44]
Cape Hope squid (*Loligo reynaudii*)	Yellow, red, brown and white patterning across the body	Categorical classification of colour patterns	Certain colour patterns mediate agonistic interactions	Wild	Obs	[45]
Southern reef squid (*Sepioteuthis australis*)	Yellow, red, brown and white patterning across the body	Categorical classification of colour patterns	Certain colour patterns mediate agonistic and mating interactions	Wild	Obs	[46]
Long-finned squid (*Loligo pealei*)	Yellow, red, brown and white patterning across the body	Categorical classification of colour patterns	Colour patterning associated to a wide array of behaviours, including mating and agonistic interactions	Wild, Capt	Obs	[47]
Arrow squid (*Doryteuthis plei*)	Yellow, red, brown and white patterning across the body	Categorical classification of different colour patterns	Colour patterns mediates mating and agonistic interactions	Capt	Obs	[48, 49]

Common octopus (*Octopus vulgaris*)	Clear and dark patterning across the body	Qualitative description of different body patterns	Colour patterning associated to courtship display	Capt	Obs	[50]
Day octopus (*Octopus cyanea*)	Clear and dark patterning across the body	Qualitative description of different body patterns	Colour patterning associated to courtship display	Capt	Obs	[50]

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