Review

Technicolour deceit: a sensory basis for the study of colour-based lures

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The study of deceptive signalling has provided compelling insights into evolutionary and ecological processes. Aside from mimicry, however, research into the use of colour as a deceptive instrument has progressed largely without an explicit theoretical basis. This is especially true for colour-based prey lures, that is, displays of colour used by predators to actively attract and deceive prey. Such lures are widespread and phenotypically diverse, and a valuable body of research has laid the foundation for novel tests of evolutionary theory in these systems. In this review, we aim to cast the study of colour-based luring under a theoretical framework centred on sensory drive, and outline hypotheses and predictions that may guide future work. We first discuss the principles of sensory drive theory, and briefly review its relevance and use in colour lure research. Notably, although rarely framed in explicit sensory drive terms, many studies consider questions highly relevant to this theory, such as the influence of signalling environments on lure evolution. We then highlight how hypotheses drawn from sensory drive theory may guide the study of intriguing features of colour lure systems. To that end, we review the empirical literature with a focus on two key areas: signal function and the evolution and maintenance of polymorphism. We examine the predictions of the relevant model of signal function, sensory traps, against the limited literature evidence in orb-web spiders, and find little support, at present, for the common contention that lures act as sensory traps via floral mimicry. Finally, we suggest that just as a more explicit consideration of sensory drive theory may allow new or broader insights into colour lure evolution, the study of lure systems offers unique opportunities to test theory in visual ecology, predator–prey dynamics and the evolution of polymorphism.

Our understanding of evolutionary and ecological processes such as adaptation and speciation has been greatly advanced through the study of biological coloration (Dyer et al., 2012; Hugall & Stuart-Fox, 2012; Hughes, Houde, Price, & Rodd, 2013). By examining the signalling role of colour across contexts, this work has, for example, demonstrated the adaptive value of colour traits in mate assessment through their encoding of genetic and phenotypic information (Grether, Cummings, & Hudon, 2005; Taylor, Clark, & McGraw, 2011) and the role of pollinator visual ecology in driving angiosperm diversification (Burd, Stayton, Shrestha, & Dyer, 2014; Dyer et al., 2012). Valuable insights, such as the ubiquity of perceptual biases in shaping sexual signal evolution (Ryan & Cummings, 2013), have been gained through consideration of how such signals involve an element of deception or exploitation. Colour has also been studied as a dedicated instrument of deception, perhaps most comprehensively and famously in regard to crypsis

and mimicry (Bates, 1862; Cott, 1940), and this work has played a role in the development of fundamental evolutionary theories including Batesian and Müllerian mimicry (Bates, 1862; Cott, 1940; Rettenmeyer, 1970; Ruxton, Sherratt, & Speed, 2004). In contrast, studies of colour-based deception in other contexts, such as the luring of prey, have often proceeded without a consistent conceptual basis (as discussed below). This work has, however, yielded extremely valuable system-specific knowledge, and a more consolidated basis of theory may allow such knowledge to directly feed back into theoretical development (sensu Christy, 1995; Endler & Basolo, 1998; Endler, 1993a). Furthermore, in colour lure systems, ongoing discussions of signal function (Bush, Yu, & Herberstein, 2008; Bennett & Ellison, 2009; Schaefer & Ruxton, 2009; Vaclav & Prokop, 2006) and the drivers of phenotypic diversity (Kemp, Holmes, Congdon, & Edwards, 2013; Tso, Tai, Ku, Kuo, & Yang, 2002) may be resolved through studies based more explicitly on theory.

Colour-based prey lures are a widespread class of deceptive signal (Fig. 1). They encompass a diversity of colours and patterns (Schaefer & Ruxton, 2008; Tso, Huang, & Liao, 2007), are used by both animals and plants (Hauber, 2002; Schaefer & Ruxton, 2008)

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Figure 1. The intra- and interspecific diversity of colour-based prey lures: (a) *Gasteracantha fornicata* (photo: Thomas White); (b) *Thomisus spectabilis* (photo: Felipe Gawryszewski); (c) *Gasteracantha quadrispinosa* (photo: Darrell Kemp); (d) *Nepenthes ventricosa* (photo: Alastair Robinson); (e) *Nephila pilipes* (photo: Darrell Kemp); (f) *Argiope keyserlingi* (photo: Anne Wignall); (g) *Gasteracantha fornicata* (photo: Thomas White); (h) *Thomisus spectabilis* (photo: Felipe Gawryszewski); (i) *Leucauge* sp. (photo: Darrell Kemp).

and exist throughout terrestrial and aquatic environments (Pietsch & Grobecker, 1978). Intriguingly, prey lures are often phenotypically variable, plastic or polymorphic (Chuang, Yang, & Tso, 2007; Kemp et al., 2013). The bulk of empirical work has focused on spiders, particularly orb-web spiders, whose conspicuous colours on the body or web are known to attract arthropod prey (Bush et al., 2008; Hauber, 2002; Herberstein, Craig, Coddington, & Elgar, 2000; Peng, Blamires, Agnarsson, Lin, & Tso, 2013; Tso et al., 2007, 2002). Owing to lingering controversy regarding the function of these signals (Bush et al., 2008; Foot, Rice, & Millett, 2014; Schaefer & Ruxton, 2008; Vaclav & Prokop, 2006), the field has been largely focused on testing 'proof of function' hypotheses (Hauber, 2002; Hoese, Law, Rao, & Herberstein, 2006; Schaefer & Ruxton, 2008). Given the extensive groundwork that has established a luring function across several taxa (Table 1), and the advantages of lure systems over traditional signalling contexts (such as sexual systems, discussed below), colour lure systems are well suited for testing broader theory in visual ecology and signal evolution.

In this review we aim to consolidate the study of colour-based prey deception within sensory drive theory. This theory has relevance to sensory-based deception regardless of modality (visual, olfactory, auditory, etc.), but the relevant literature is especially well developed in regard to visual signals, and in particular those based on colour (see e.g. Endler, 1992, 1993a,b, 2012). For heuristic reasons, we develop the argument largely in reference to the most popularly studied and best characterized empirical context: colour-based prey lures in orb-web spiders (Table 1). Our review proceeds in three stages. First, we outline the key principles of sensory drive, define a relevant sensory-based model of signal function (sensory traps) and discuss the relevance of these principles to prey lure systems. Second, we draw upon this framework to review the extensive literature on colour-based prey lures (with a focus on signal structure, signalling environments and identifying relevant receivers), and discuss the empirical insights that may be possible through a more explicit consideration of sensory drive theory. Here we focus on two points: (1) the evolution of signal function and (2) the evolution of extreme variation and polymorphism. Finally, we highlight the reciprocal opportunities that colour lure systems offer for testing and extending theory, and conclude by outlining promising directions for future research.

WHAT IS SENSORY DRIVE?

The theory of sensory drive attempts to explain the evolution of signalling system efficacy (Endler & Basolo, 1998; Endler, 1992). It contends that elements of signalling systems, including signal

Table 1
Known colour-based prey lures in nature

Classification	Species	Habitat	Receiver(s)	Colour	Polymorphic	Activity	Method	Function(s)	Source
Angiosperm (Eudicot: Caryophyllales)	*Drosera rotundifolia*	Large gap	Diptera>Collembola, Hymenoptera>Araneae, Hemiptera	Red	N	D/N	Manipulative (field)	Unknown. Not prey lure or camouflage	Foot et al. (2014)
Angiosperm (Eudicot: Caryophyllales)	*Nepenthes ventricosa*	Large gap, woodland shade	Diptera>Homoptera, Acari>Hymenoptera>Araneae	Red and green	N	D/N	Manipulative (field)	Prey lure	Schaefer and Ruxton (2008)
Angiosperm (Eudicot: Ericales)	*Sarracenia purpurea*	Large gap, woodland shade	Hymenoptera>Diptera>Collembola, Araneae	Red and green	N	D/N	Manipulative (field)	Unknown. Not prey lure	Bennett and Ellison (2009)
Arthropoda (Insecta: Diptera)	*Arachnocampa* spp.	Caves	Diptera, Isopoda, Hymenoptera, Myriapoda, Gastropoda	White	N	D/N	Manipulative (field)	Prey lure	Broadley and Stringer (2001); Willis, White, and Merritt (2011)
Arthropoda (Arachnida: Araneae)	*Argiope argentata*	Large gap, woodland shade	Hymenoptera, Diptera, Coleoptera, Orthoptera, Homoptera	Silver and UV dorsum, yellow & black striped ventrum	N	D/N	Manipulative (field), observational	Prey lure, crypsis	Craig and Ebert (1994); Robinson and Robinson (1978)
Arthropoda (Arachnida: Araneae)	*Argiope bruennichi*	Small gap	Hymenoptera>Diptera, Coleoptera	Yellow and white stripes	N	D	Manipulative (field)	Prey lure, crypsis	Bush et al. (2008); Vaclav and Prokop (2006)
Arthropoda (Arachnida: Araneae)	*Argiope keyserlingi*	Forest shade	Hymenoptera, Diptera, Coleoptera	Yellow & black stripes	N	D	Manipulative (lab)	Crypsis	Defrize et al. (2010)
Arthropoda (Arachnida: Araneae)	*Gasteracantha cancriformis*	Woodland shade, small gaps	Diptera, Lepidoptera, Coleoptera	Yellow (m1), white (m2) or black and white (m3)	Y	D	Manipulative (field)	Unknown	Gawryszewski and Motta (2012); Muma (1971)
Arthropoda (Arachnida: Araneae)	*Gasteracantha fornicata*	Woodland shade	Diptera, Hymenoptera>Hemiptera, Coleoptera	White (m1) or yellow (m2), with black stripes	Y	D	Manipulative (field)	Prey lure	Hauber (2002); Kemp et al. (2013)
Arthropoda (Arachnida: Araneae)	*Gasteracantha quadrispinosa*	Forest shade	?	Red or orange	Y	D	None	Prey lure (hypothesised)	Personal observation
Arthropoda (Arachnida: Araneae)	*Micrathena gracilis*	Small gap	Diptera>Hymenoptera	White with some yellow ventrally	N	D	Manipulative (field)	Unknown	O'Hanlon, Herberstein, and Holwell (2014); Uetz and Hartsock (1987); Vanderhoff, Byers, and Hanna (2008)
Arthropoda (Arachnida: Araneae)	*Neoscona punctigera*	Woodland shade, large gap	?	White ventral spots	N	D/N	Manipulative (field)	Prey lure	Blamires et al. (2012); Chuang et al. (2008)
Arthropoda (Arachnida: Araneae)	*Cyrtaphora moluccensis*	Forest shade, woodland shade	Lepidoptera, Blattodea, Hymenoptera, Orthoptera, Hemiptera, Diptera	White, orange and yellow	N	D/N	Manipulative (field)	Prey lure	Blamires et al. (2014)
Arthropoda (Arachnida: Araneae)	*Heteropoda venatoria*	Forest shade	Lepidoptera >	Brown with white stripe	N	N	Manipulative (field)	Prey lure	Zhang et al. (2015)
Arthropoda (Insecta: Mantodea)	*Hymenopus coronatus*	Small gap, woodland shade	Hymenoptera>Diptera, Lepidoptera	White, some UV (juveniles only)	N	D	Manipulative (field), observational	Prey lure	O'Hanlon et al. (2014a); O'Hanlon et al. (2014b); O'Hanlon et al. (2013)
Arthropoda (Arachnida: Araneae)	*Nephila pilipes*	Forest shade	Orthoptera, Diptera, Coleoptera, Lepidoptera>Hymenoptera, Odonata	Yellow bands and spots with UV (m1), dark with less UV (m2)	Y	D/N	Manipulative (field), observational	Prey lure, crypsis	Chiao et al. (2009); Chuang et al. (2007); Fan et al. (2009); Tso et al. (2002); Tso et al. (2004)
Arthropoda (Malacostraca: Decapoda)	*Macrobrachium crenulatum*	Freshwater	Cyprinodontiformes	Orange	N	?	Manipulative (lab)	Prey lure	De Serrano et al. (2012)
Arthropoda (Arachnida: Araneae)	*Leucauge magnifica*	Large gap	?	Yellow, silver and black stripes	N	D/N	Manipulative (field), observational	Prey lure	Tso et al. (2007), (2006)
Arthropoda (Arachnida: Araneae)	*Argyrodes fissifrons*	Forest shade, woodland shade	Hymenoptera	Silver	N	D	Manipulative (field)	Prey lure	Peng et al. (2013)

Table 1 (*continued*)

Classification	Species	Habitat	Receiver(s)	Colour	Polymorphic	Activity	Method	Function(s)	Source
Arthropoda (Arachnida: Araneae)	*Diadea lactea*	Large gap	Lepidoptera, Hymenoptera>Diptera	White to yellow with UV	N	D	Manipulative (lab)	Prey lure	Herberstein et al. (2009)
Arthropoda (Arachnida: Araneae)	*Rucinia elongata*	Large gap	Lepidoptera, Hymenoptera>Diptera	White to yellow with UV	N	D	Manipulative (lab)	Prey lure	Herberstein et al. (2009)
Arthropoda (Arachnida: Araneae)	*Sidymella rubropunctata*	Large gap	Lepidoptera, Hymenoptera>Diptera	White to yellow with UV	N	D	Manipulative (lab)	Prey lure	Herberstein et al. (2009)
Arthropoda (Arachnida: Araneae)	*Thomisus spectabilis*	Large gap	Lepidoptera, Hymenoptera>Diptera	White to yellow with UV	N	D	Manipulative (lab), observational	Prey lure, crypsis	Gawryszewski, Llandres, and Herberstein (2012); Heiling, Cheng, and Herberstein (2004); Heiling and Herberstein (2004); Heiling, Cheng, Chittka, Goeth, and Herberstein (2005); Heiling, Chittka, Cheng, and Herberstein (2005); Heiling, Herberstein, and Chittka (2003); Heiling, Cheng, and Herberstein (2006); Llandres, Gawryszewski, Heiling, and Herberstein (2011); Llandres and Rodriguez-Girones (2011)
Arthropoda (Arachnida: Araneae)	*Verrucosa arenata*	Forest shade, small gap	Hymenoptera, Diptera	Yellow (m1), white with some UV (m2)	Y	?	Manipulative (field)	Prey lure	Rao et al. (2014)
Chordata (Actinopterygii: Lophiiformes)	*Antennarius* sp.	Deep ocean	Gadiformes, Perciformes	?	N	?	None	Prey lure (hypothesized)	Pietsch and Grobecker (1978)
Chordata (Actinopterygii: Lophiiformes)	*Lophius* sp.	Deep ocean	?	?	N	?	None	Prey lure (hypothesized)	Gudger (1945)
Cnidaria (Hydrozoa: Siphonophorae)	*Erenna* sp.	Deep ocean >1600 m	?	Blue-green to orange-red fluorescence	N	?	None	Prey lure (hypothesised)	Haddock, Dunn, Pugh, and Schnitzler (2005)

Includes summary information on the ecological factors central to the sensory drive framework (e.g. habitats and putative receivers). Studies that tested for but did not find a prey-luring function, and those that present prey luring as a hypothesis, are included. Habitat: categorized as per Endler (1993) where appropriate, based on qualitative descriptions from the literature. Receiver(s): putative targets of the signal, inequalities indicate relative abundance where reported. Colour: the hues displayed by the animal described in human terms (UV-absent unless otherwise specified); morphs (m1, m2, m3) are indicated in parentheses. Polymorphic: whether polymorphism has been described. Activity: activity period. Method: the method by which a function has been determined. Source refers to studies that either focus on signal function or provide information on the signalling ecology of the given species.
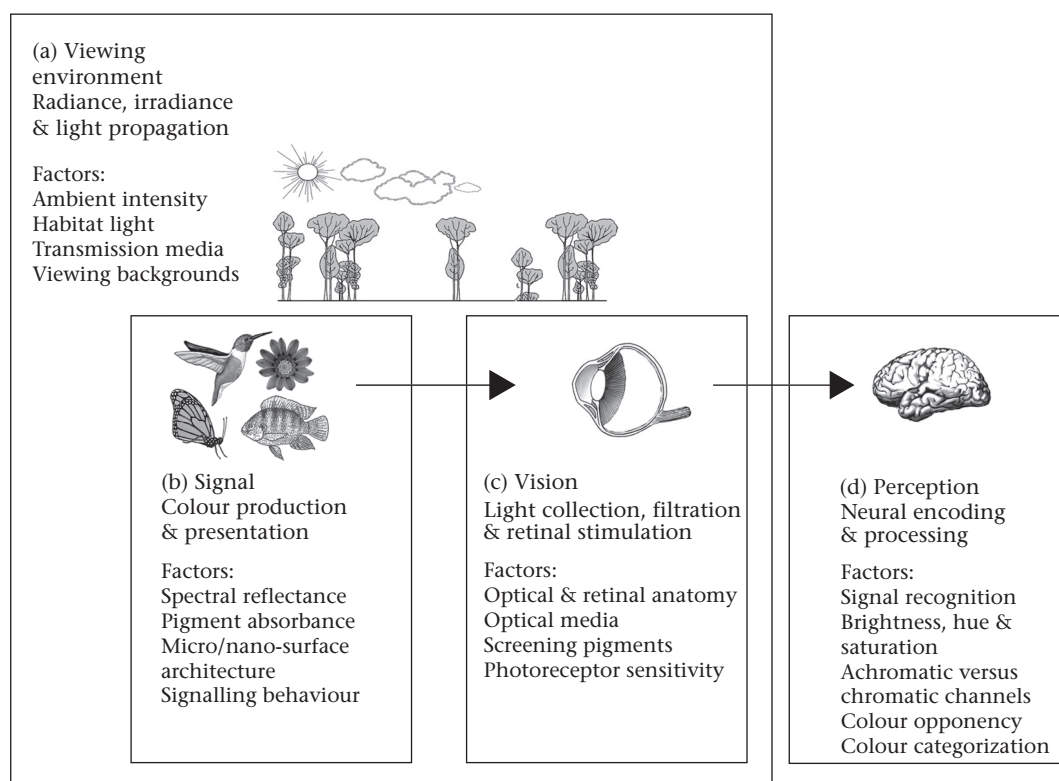
design, presentation and receiver sensory biology, should evolve to maximize signal transmission against background noise (irrespective of signal modality; Endler, 1992). Visual signal design (Fig. 2b) encompasses the chromatic and achromatic features of individual colour patches (i.e. colour and luminance components; Osorio & Vorobyev, 2005), the relative size and adjacency of such elements (Endler & Mielke, 2005; Endler, 2012) and additional properties such as iridescence and polarization (Douglas, Cronin, Chiou, & Dominy, 2007; Kelber, 1999; Sweeney, Jiggins, & Johnsen, 2003; Vukusic, Sambles, Lawrence, & Wootton, 2001). Signal presentation (Fig. 2a, b) refers to the behavioural context of display, which includes the mechanics of how signals are presented (Dakin & Montgomerie, 2009; Sicsu, Manica, Maia, & Macedo, 2013; White, Zeil, & Kemp, 2015) as well as strategic choices about when and where to display (Endler & Thery, 1996; Endler, 1991). Reception is determined by the complex (and often little-understood) processes of vision and perception (Fig. 2c, d), for which we refer readers to excellent recent reviews (Kelber & Osorio, 2010; Kelber, Vorobyev, & Osorio, 2003; Kemp et al., 2015; Osorio & Vorobyev, 2008).

Signals are transmitted and received in 'noisy' visual environments, and many factors are involved in the production, transmission and reception of visual signals (summarized in Fig. 2; also see Endler, 1993a, 1993b). These factors interact in complex ways. Sensory drive emphasizes the potential for coevolution among components of signalling systems to maximize salience (Endler & Basolo, 1998; Endler, 1992, 1993a). An excellent example of such coevolutionary potential is illustrated by sexual signal evolution and speciation among cichlid fish in Lake Victoria. The lake is home to dozens of species that inhabit heterogeneous environments with

respect to water clarity and, hence, ambient light (Seehausen, Alphen, & Witte, 1997). Natural selection is thought to have driven divergence in the long-wave sensitive photoreceptors of populations across a depth gradient, with longer-wavelength sensitivity favoured at depth where the attenuation of red light is lower (Maan et al., 2004; Terai et al., 2006). Seehausen et al. (2008) suggested that sexual selection for conspicuousness in the eyes of females then drove divergence in male nuptial coloration, and concurrent selection on female vision and male coloration generated linkage disequilibrium between each candidate set of genes. The reduced fitness of offspring with mismatched colour phenotypes generated disruptive selection that ultimately led to sympatric speciation (Seehausen et al., 2008). Thus populations ultimately diverged because of the need to maintain signal efficacy, a key principle of sensory drive (Endler, 1992).

The theory of sensory drive has broad explanatory power, but its interpretation varies across the literature (Schaefer & Ruxton, 2009; Endler & Basolo, 1998; Stevens, 2013). There are conflicting views regarding, for example, the evolutionary lability of signal preferences (Holland & Rice, 1998), the importance of the environment in driving signal evolution (Fuller, Houle, & Travis, 2005) and the relationship of sensory drive to other models of signal evolution (Endler & Basolo, 1998; Stevens, 2013). As we explain below, we consider sensory drive as a generalizing framework that subsumes models such as sensory bias and sensory traps, which emphasize the evolution of signals that exploit sensory and perceptual biases in receivers (Basolo, 1990; Christy, 1995; Ryan, 1990). Sensory drive subsumes these models because it broadly integrates receiver perception, including biases (regardless of how

(a) Viewing environment
Radiance, irradiance & light propagation

Factors:
Ambient intensity
Habitat light
Transmission media
Viewing backgrounds

(b) Signal
Colour production & presentation

Factors:
Spectral reflectance
Pigment absorbance
Micro/nano-surface architecture
Signalling behaviour

(c) Vision
Light collection, filtration & retinal stimulation

Factors:
Optical & retinal anatomy
Optical media
Screening pigments
Photoreceptor sensitivity

(d) Perception
Neural encoding & processing

Factors:
Signal recognition
Brightness, hue & saturation
Achromatic versus chromatic channels
Colour opponency
Colour categorization

Figure 2. The visual ecology of colour signalling, highlighting some of the features of signalling systems that may be shaped by sensory drive. The viewing environment (a) provides the scene and setting for which a colour (b) is viewed, the eye (c) determines what is detected and neurally encoded for processing in a viewer's brain (d). Sensory drive theory contends that components of signalling systems should evolve to maximize the signal-to-noise ratio in signalling systems and, given the myriad processes and interactions involved in signal production, transmission and reception, we should expect complex coevolutionary feedback between such features.

they arise), with the suite of potential influences on signal generation, presentation and propagation (Fig. 2).

Signal Function and Sensory Traps

The sensory trap model (Christy, 1995) is one of several closely related models concerned with understanding the adaptive basis of signal design (see Endler & Basolo, 1998, for a more precise treatment of these models). Roughly speaking, these models seek to explain how receiver sensory psychology can generate 'biases' that favour particular stimuli, and which may subsequently shape the trajectories of signal evolution. Such receiver biases have been shown to influence signal evolution in a range of contexts, including sexual signalling (as in the cichlid example), mimicry (e.g. mantids; O'Hanlon, Holwell, & Herberstein, 2014a) and prey luring (see below). Equally, sensory biases may define the potential avenues for species to minimize their conspicuousness to predators and/or prey (Barry, White, Rathnayake, Fabricant, & Herberstein, 2014; Cronin et al., 2003; Cummings, Rosenthal, & Ryan, 2003).

The term 'sensory trap' refers to signals thought to exploit receiver biases that may have arisen in several ways. These include biases that once had a function that is now lost, those that developed as an idiosyncratic consequence (or an emergent property) of sensory system construction or, in particular, neural biases (whether reflexive and peripheral or higher-level cognitive processes) that are adaptive in unrelated contexts (Christy, 1995; Endler & Basolo, 1998). A classic example is given by the sand hoods constructed by mate-seeking male fiddler crabs, *Uca musica*. Evidence suggests that these structures evolved to exploit a tendency in females to spontaneously approach potential shelters, especially under perceived predation risk (Christy, Backwell, & Schober, 2003; Christy, Baum, & Backwell, 2003). The hoods themselves play no role in the female assessment of mate quality per se, yet building them indirectly increases male mating success. As this example highlights, responding to sensory traps need not be costly for receivers. In the context of prey luring, however, receiver responses are exclusively maladaptive (given that predation is the ultimate potential consequence).

In a general sense, colour-based lures are thought to attract prey because they are mistaken for something they are not (e.g. a food source or reproductive resource, or simply an object of potential interest). For this reason they may be considered to function as sensory traps, and a key question then becomes why a given colour lure system is effective. The ecological and evolutionary features of lure systems vary along several interrelated axes (Table 2). These include the nature of the bias that is exploited, the evolutionary lability of signals and receiver preferences and the source and maintenance of polymorphism in such signals. At one hypothetical extreme, for example, lies a sensory trap selected to target some general preference for a colour in receivers. This would be analogous to the red nuptial coloration displayed by male three-spined sticklebacks, *Gasterostaus aculeatus*, that exploits a female preference thought to have arisen in the context of foraging (Smith, Barber, Wootten, & Chittka, 2004). At another hypothetical extreme lies a lure that produces out-of-context cognitive responses in receivers (which is more analogous to a model–mimic relationship) through a close similarity to otherwise rewarding stimuli, as in the case of the resemblance of the orchid mantis, *Hymenopus coronatus*, to the local floral resources of pollinating insects (O'Hanlon et al., 2014a; O'Hanlon, Holwell, & Herberstein, 2014b). As we explore in detail below, the sensory traps concept provides a useful framework for the study of colour lures, as knowledge of one or more of the features of a given system (Table 2), and particularly of the underlying receiver biases being exploited, will allow researchers to generate and test specific hypotheses about signal function and evolution. Identifying how lure systems function in perceptual terms is central to understanding how features of sensory, neural and perceptual systems shape the evolution of lure phenotypes (as per the extensive work on receiver biases and male sexual traits; reviewed in Ryan and Cummings, 2013).

Sensory Drive as a Framework for Studying Colour-based Lures

Sensory drive offers a valuable framework for examining colour-based lures because lures are conspicuous physical displays that evolved to manipulate the behaviour of a receiver (Maynard Smith & Harper, 2003). They are often displayed at specific times and places, transmitted through variable environments, and ultimately perceived by a suite of viewers whose behavioural responses define the effectiveness of the signal. The deceptive nature of lures probably pertains only to the identity of the signaller (i.e. signal recognition or classification). This contrasts

Table 2
Features of colour lure systems under the sensory traps model

Feature	
Mechanism	Signallers manipulate receivers through the exploitation of biases that may have arisen in several ways. These include sensory or neural biases that are incidental, neutral or no longer functional, or those that have evolved to be adaptive in an unrelated context. A signal may move from the exploitation of one bias to another through evolutionary time (e.g. from the targeting of general colour-preferences to the mimicry of specific stimuli)
Evolutionary lability	Signals and receiver biases may be relatively labile, for reasons that vary depending on the bias being exploited. If biases are not strongly relevant in another context then signals and receivers may be relatively free to antagonistically coevolve. Where signals more closely mimic specific stimuli, their evolutionary trajectory may be tied to both models and receivers, which may coevolve as both model and receiver populations diverge
Ecology	Depending on the degree to which lures resemble specific stimuli, both the trap and putative models may be expected to target the same receivers with overlapping distributions. Receivers should also encounter lures less frequently than models
Polymorphism	Polymorphism may evolve via the exploitation of multiple biases (e.g. innate wavelength preferences) or biases in multiple receivers. In systems in which lures more closely resemble specific stimuli, polymorphism may evolve through matching multiple models or the models of multiple receivers. Spatial and/or temporal variation in any component may shape signal evolution
Colour palette	The lure colour palette will largely be defined by the biases of receivers, and will be relatively broad due to the large number of potential perceptual targets. In the case of more specific mimicry, however, the palette of lures may be delimited by model/s coloration, although signals may also exploit open-ended preferences to become elaborated to the point of model-mimic mismatch if models are restricted (e.g. through physiological constraints) and the sensory trap is not

Sensory traps describes the evolution of signals that exploit receiver biases that may have arisen in several ways, such as biases that once had a function that is now lost, those that developed as an idiosyncratic consequence (or an emergent property) of sensory system construction or, in particular, those that exploit psychosensory responses that serve adaptive roles in unrelated contexts. The evolutionary and ecological properties of systems together describe the origin and function of signals, and information about any one or more features of a given system (particularly the underlying biases being exploited) may guide hypotheses and predictions about other features.

with sexual signals, for example, which often carry additional information about mate quality (Hill, 2006; Kemp & Rutowski, 2011). This makes them particularly well suited for tests of sensory drive theory, as they are free from other potential confounds of information exchange, such as demands of signal honesty (Zahavi, 1975). That is, the costs of signalling in lure systems are primarily, although not exclusively, efficacy based (the principal domain of sensory drive; Endler, 1992a) rather than strategy based (Ryan & Cummings, 2005). At a functional level, the traps model is particularly relevant given that colour lures are, by nature, deceptive and antagonistic. The most effective lures will be those that best manipulate potential receivers through effective signal production, transmission and perception, leading ultimately to mistaken categorization by receivers (Table 2).

Sensory Drive and the Colour Lure Literature

Our understanding of the function and evolution of colour lure systems is in its infancy, and most studies to date have explored the fundamental question of whether a given phenotype enhances foraging success (Blamires et al., 2012; Gawryszewski & Motta, 2012; Tso et al., 2007; Tso, Liao, Huang, & Yang, 2006; Vaclav & Prokop, 2006). This work has done much to dispel the idea that common luring groups, such as orb-web spiders, are essentially passive predators, and has proven particularly valuable in clarifying the ecology of colour lure systems. With regard to the theoretical context of these studies, among the 36 direct examinations of colour lure systems to date (Table 1), 13 explicitly reference sensory drive or aspects thereof (broadly defined to include some mention of sensory traps, bias or exploitation, as well as mimicry). An interesting example is seen in the interaction between the predatory prawn *Macrobrachium crenulatum* and the guppy, *Poecilia reticulata*, in freshwater Trinidadian streams. Female guppies show strong preferences for small orange-coloured stimuli, a common and variable feature of male sexual signals in conspecific males (Endler & Houde, 1995; Gotanda & Hendry, 2014; Grether, Kolluru, Rodd, De la Cerda, & Shimazaki, 2005), which incidentally may have evolved to exploit a female preference for orange-coloured food items (Rodd, Hughes, Grether, & Baril, 2002). De Serrano et al. (2012) presented evidence that the orange pincer spots of *M. crenulatum* similarly act to lure guppies, although whether the effectiveness of these spots is governed by their direct resemblance to male sexual signals, or through the convergent exploitation of a general female preference for orange objects (i.e. whether prawns and male guppies are setting the same trap), remains unclear. Here (as discussed further below), knowledge of the historical patterns of signal and preference evolution may be very useful for understanding how this system works.

Although studies of colour lure systems are rarely framed in an explicit sensory drive context, concepts that are central to this theory are regularly considered in the literature. Several researchers, for example, have explored questions of signal perception under dramatically varying light conditions (such as the broad contrast of night and day; Blamires, Hou, Chen, Liao, & Tso, 2014; Chuang et al., 2007; Chuang et al., 2007) and by specific viewers (Defrize, Théry, & Casas, 2010; Fan, Yang, & Tso, 2009). Some researchers have also applied visual modelling to great effect (e.g. Chiao, Wu, Chen, & Yang, 2009; Chuang et al., 2007; Tso, Lin, & Yang, 2004). As discussed below, the sit-and-wait ecology of many colour-luring species means that the signalling context (including light environments and receivers) may be readily appraised. As a general point, precisely quantifying these factors (as emphasized by the sensory drive framework; Fig. 2) would be extremely valuable in future work.

THEORY-DRIVEN INSIGHTS INTO COLOUR LURES

Colour lure systems across taxa express a number of notable general features that need to be explained. For one, the breadth of colours expressed within and between species is considerable, with short- (UV, blue), mid- (green, yellow) and long-wavelength (orange, red) colours all having been identified. There is, however, a curious overrepresentation of mid- to long-wavelength (i.e. >500 nm) hues (particularly 'yellow'), with 15 of the 24 described systems showing such colours, at least in part (Herberstein, Heiling, & Cheng, 2009). Polymorphism is also a conspicuous feature of several systems, with five studied species exhibiting at least two discrete morphs (and up to eight morphs, as in *Gasteracantha cancriformis*; Levi, 1978). Qualitative evidence suggests that the incidence of polymorphism among colour-luring species may be considerably higher (see Appendix).

There is also great diversity in the habitats in which colour lures are displayed. In terrestrial environments, these range from open and/or directly sunlit areas to spectrally complex environments under and around forest canopies. The spectral environments presented across this range have been characterized in discrete terms (e.g. as per the terms 'open/cloudy/large gaps', 'woodland shade', 'forest shade' and 'small gaps' by Endler 1993; summarized in Table 1), although such variation largely defies neat categorization (Cronin, Johnsen, Marshall, & Warrant, 2014). The broader point is that there is a range of spectral environments under which colour lures are illuminated, potentially influencing their appearance. Limited evidence suggests that colour lures exist throughout aquatic habitats, which also present a diversity of illumination/viewing environments (Lythgoe, 1988).

The known viewers of lures also encompass variation in sensory capacity, with some 16 orders across three phyla having been documented to date (although with a bias towards arthropods owing to the extensive work on spiders; Table 1). Common receivers include trichromatic honeybees (Hempel de Ibarra, Vorobyev, & Menzel, 2014), potentially tetrachromatic flies (Lunau, 2014), and butterflies, which possess one of the most complex terrestrial colour vision systems known (Kelber & Pfaff, 1999; Kinoshita, Shimada, & Arikawa, 1999; Koshitaka, Kinoshita, Vorobyev, & Arikawa, 2008).

Sensory drive, with its emphasis on signal design, transmission and reception (Fig. 2), is thus well poised to inform this diversity of signals, signalling environments and receivers, as well as their complex interactions. We suggest there are two general areas in which sensory drive may guide empirical work on visual lures: signal function and the maintenance of signal diversity.

Lure Function and Evolution: Sensory Traps

One key outstanding question in the study of colour lure systems is the ultimate (evolutionary) basis of signal function. The sensory trap model offers a potential explanation (Christy, 1995), and examination of the features that define a given system as informed by this model (Table 2) may guide questions and hypotheses for future research. An improved understanding of signal function, in turn, may offer insight into the history and direction of evolution, the coevolutionary interactions between signallers, receivers and potential models, and macroscale patterns of phenotypic variation (such as the commonality of polymorphism, discussed below) in such systems. Studies aimed at exploring the particular receiver biases being targeted (i.e. the underlying mechanism; Table 2) would be particularly valuable for guiding future work. If a lure is found to act as a sensory trap, for example, via a specific resemblance to a food resource (e.g. floral mimicry in the orchid mantis; O'Hanlon et al. 2014a), then

information about the temporal and spatial dynamics of putative model(s) would be necessary to understand the evolutionary history and trajectory of lure evolution. If a lure serves to exploit more general perceptual biases, however, then studies of receiver biases (e.g. innate, spontaneous and/or learned colour preferences; ten Cate & Rowe, 2007) would be more important for understanding signal diversification. Establishing the workings of a given system (Table 2) will prove challenging, particularly in cases where the potential biases being targeted are not immediately clear (e.g. the yellow or white stripes of *Gasteracantha fornicata*; Hauber, 2002; Kemp et al., 2013). For this reason, phylogenetically controlled comparative analyses are likely to have great value. The sequence of trait evolution in related species can potentially address the question of whether a lure has evolved convergently alongside profitable signals (e.g. food resources) to exploit a common pre-existing receiver bias, or has subsequently evolved to co-opt receiver responses to otherwise profitable stimuli (i.e. mimicry).

We explore the value of this model in reference to the common suggestion that the lures of orb-web spiders have evolved to mimic flowers (Chiao et al., 2009; Tso et al., 2007, 2006, 2004). Given the nature of the available evidence, here we consider the most restrictive formulation of the sensory traps model (i.e. specific mimicry), which makes several clear predictions (Table 2). First, because signallers and model(s) target common receivers, the conspicuous colours displayed by orb-web spiders should be aimed at the pollinators whose food resources they apparently mimic. Hymenoptera and Diptera, two of the largest pollinating insect groups, are the primary captures of many colour-luring spiders (Blamires et al., 2014; Hauber, 2002). It should be noted, however, that the primacy of Hymenoptera and Diptera as prey items is often simply assumed (Rao, Castañeda-Barbosa, Nuñez-Beverido, & Díaz-Fleischer, 2014; Tso et al., 2004). While such an assumption may be justified with reference to prey composition data from nonluring species, it should be regarded with caution given the potential for receiver targeting and selectivity in colour lure systems. Where more precise data exist, the taxonomic spread of captured prey can be diverse, even within and among similarly coloured species (Austin & Anderson, 1978; Bush et al., 2008; Harvey, Austin, & Adams, 2007; Tso et al., 2002; Vaclav & Prokop, 2006). In some cases, captures of Orthoptera and Hemiptera comprise the majority of a luring species' diet (Austin & Anderson, 1978; Bush et al., 2008; Harvey et al., 2007). Given that visually mediated behaviour in such insect taxa is shaped by selection in contexts unrelated to floral foraging (such as host plant detection and sexual signalling; Döring & Chittka, 2007), there is little reason to expect floral mimicry would offer the best strategy for attracting these species. It is of course always likely that a range of incidental species will be captured in orb webs, but under the strictest trap explanation, spider fitness should be supplemented to an adaptively significant degree by active prey attraction. Lures that capture a greater breadth of prey may function instead by exploiting more general features of insect sensory and perceptual systems (Table 2).

A second sensory trap prediction is that the appearance of lures and models should converge to produce an indistinguishable perceptual response in viewers (Christy, 1995). Again, this is only the case in the strictest formulation of the model as is being discussed here. A mismatch between signaller and model phenotypes may be expected in cases where receiver preferences are spectrally broad, where the lure has evolved away from the model to exploit an 'open ended' preference, or where there has not been enough evolutionary time for close convergence (Christy, 1995). Behavioural studies offer good evidence that the colours of both orb-web spiders (e.g. Hauber, 2002; Chuang, Yang, & Tso, 2008; Bush et al.

2008) and flowers (Briscoe & Chittka, 2001; Chittka & Menzel, 1992) are equivalently attractive to insects. Indirect evidence gained via sensory modelling in Hymenoptera and Lepidoptera also suggests that spiders and flowers present equivalent visual contrasts against vegetative backgrounds (Chuang et al., 2007). This, along with subjective human judgements regarding shape and colour (e.g. Chiao et al., 2009; Prokopy & Owens, 1983; Tso et al., 2007, 2004), has been extended in indirect support of a strict sensory trap model. To further resolve this question, observational studies coupling sensory modelling and detailed morphometric analysis (to account for the combined colour, shape and patterning) of spiders and co-occurring flowers would be useful. Because the crucial issue is whether (and under what conditions) insect prey misclassify spider lures as potential food resources, carefully controlled behavioural experimentation will prove essential. Examination of how putatively targeted pollinators react across subtle ranges of deviation in spider appearance (both colour and morphology) therefore presents an intriguing direction for future research.

Finally, strict sensory trap-based explanations predict that deceptive signals and models should covary both spatially and temporally, and that prey should encounter lures less frequently than models. These predictions pose interesting untested opportunities, requiring spatial and temporal surveys of the interactions between colour-luring spiders, coincident floral communities and putatively targeted insect pollinators.

The possibility that orb-spider lures act as sensory traps via floral mimicry is intriguing, and studies that are explicitly directed at testing the predictions of models of signal function (as discussed above; Table 2) offer exciting experimental opportunities. As an example of how research may progress in testing the traps model in orb-spider systems, in line with our suggestions given above, we refer readers to recent work on a putative sensory trap (via floral mimicry) in the orchid mantis. By exploring the relative attractiveness (O'Hanlon et al., 2014a), morphological resemblance (O'Hanlon et al., 2014b; O'Hanlon, Li, & Norma-Rashid, 2013) and signalling ecology (O'Hanlon et al., 2014b) of the mimic and potential models, this work suggests that mantids are indeed deceiving pollinators through a multifaceted resemblance to local flowers.

Visual Signal Polymorphism

Considerable intraspecific variation is a striking feature of prey lures (Fig. 1). Such variation runs counter to naïve expectation that phenotypes should converge on a single optimum, and sensory drive has been implicated as one of several drivers of large-scale variation in signal-related traits, including polymorphism (Boughman, 2002). Evidence for such a role in sexual systems includes covariation between local light environments and male coloration in fish (Seehausen et al., 2008), covariation between male song and acoustic conditions in Amazonian birds (Tobias et al., 2010), species-specific solutions to sensory trade-offs and correlated changes in male sexual signals in surfperch (Cummings, 2004, 2007) and variation in feeding ecology and signal morphology in the swordtail characin (family Characidae; Kolm, Amcoff, Mann, & Arnqvist, 2012). It also encompasses variation in sexual signal design across diverse environments reported for lizards (Stuart-Fox, Moussalli, & Whiting, 2007; Leal & Fleishman, 2004), butterflies (Douglas et al., 2007) and birds (Marchetti, 1993; McNaught & Owens, 2002).

When applied to colour lure systems, sensory drive theory makes several nonexclusive predictions as to the maintenance of adaptive polymorphism. First, if such signals act as sensory traps through the mimicry of specific stimuli, then polymorphism may be

maintained if there are multiple profitable models. Alternatively, if such signals are tuned to lure particular prey species or groups due to more general sensory, neural or perceptual biases (e.g. innate or learned spectral preferences), then polymorphism may be favoured by multiple receiver biases. This is probable, because lures are often viewed by diverse suites of potential receivers and, hence, diverse visual systems. An interesting possibility is that morphs of a luring species may each be tuned to exploit distinct biases via, for example, both resource mimicry (as in the guppy example cited above; Rodd et al., 2002) and the targeting of simple detection biases (as in surfperch; Cummings, 2007). The tuning of lures to different receivers may also generate variation if there were multiple optima in the trade-off between the benefits of increased prey capture and any costs of increased conspicuousness (due, for example, to increased predation). Evidence suggests that such a trade-off maintains polymorphism in the body coloration of *Nephila* spiders (Tso et al., 2002), wherein a yellow morph attracts more prey than a rarer melanic morph, but consequently suffers greater predation (Tso et al., 2002).

Variation in signalling environments at micro- or macroscales may maintain signal polymorphism if phenotypes are locally adapted. Such variation has been implicated as a driver of the yellow to white variation in webs of the orb-web spider *Nephila clavipes*, with yellower webs seen in more open, spectrally rich environments (Craig, Weber, & Bernard, 1996). Similarly, correlative evidence suggests that macroscale climatic variation (the incidence of cloudy versus sunny skies) may drive a geographical cline in the frequency of yellow/white morphs in *G. fornicata* (Kemp et al., 2013). As these cases imply, variation in any individual component of signalling system efficacy or function could be relevant. This also includes fluctuations in the relative abundance of potential models, receivers with varied sensory physiology (e.g. insect pollinators), or variation in signalling environments across microhabitat, macrohabitat, geographical scales, diel and/or seasonal timeframes.

COLOUR LURE SYSTEMS AS A TESTING GROUND FOR THEORY

Just as sensory drive may aid our understanding of the function and diversity of colour lures, such systems pose empirical opportunities for testing and refining theory. A central point here is that sensory drive and its subsidiaries (such as sensory traps) have been largely tested and elaborated in the context of sexual signalling (Basolo, 1990; Endler, 1980, 1982; Ryan & Rand, 1990). Such work has confirmed the importance of sensory system structure as a driver of phenotypic evolution (for reviews see Fuller et al. 2005; Arnqvist, 2006; Ryan & Cummings, 2013), including the role of biases (Arnqvist, 2006; Fuller et al., 2005; Grether, Kolluru, et al., 2005; Rodd et al., 2002; Ryan & Cummings, 2013). The focus in this context is typically on the way in which male ornaments evolve to 'exploit' features of female sensory and perceptual systems or, conversely, how female physiology biases the trajectory of male ornament evolution.

In sexual systems, communication between sender and receiver is mostly (if not partly) mutualistic in the broad sense that each party shares the common goal of reproduction (not entirely, because optimal strategies often differ between the sexes; Parker, Blum, & Blum, 1979). Signals contain information about the identity of the signaller and, often, individual phenotypic and/or genetic quality (e.g. Kemp & Rutowski, 2007; Keyser & Hill, 1999). The structure of sexual signals will therefore result from selection for signalling efficacy (for detection and species or mate recognition) and potentially for the communication of a more subtle level of information at the level of individual phenotypes. The latter may introduce phenotypic constraints

imposed by the demands of honest signalling (Zahavi, 1975), runaway (Kirkpatrick & Ryan, 1991) or chase-away selection (Holland & Rice). Colour lure systems, in contrast, are entirely antagonistic in the sense that signallers attempt to elicit maladaptive responses from potential receivers. The deceptive content of colour-based lures is centred upon identity or recognition, so signalling costs in lure systems are likely to be weighted towards efficacy rather than strategy (Ryan & Cummings, 2005). Thus, a key benefit of colour lure systems is that they afford researchers the opportunity for more sensitive tests of hypotheses about signal design per se (Endler & Basolo, 1998).

The maintenance of adaptive polymorphism in the face of strong selection remains an unresolved theme in evolutionary biology (Bond, 2007; McLean & Stuart-Fox, 2014; Wellenreuther, Svensson, & Hansson, 2014). In sexual systems, processes such as assortative mating (Pryke, 2010) and alternative reproductive tactics (Sinervo & Lively, 1996) are known drivers of colour polymorphism. Theoretical and empirical evidence has also demonstrated the potential for sensory drive to maintain variation, including polymorphism, in sexual signalling systems (Chunco, McKinnon, & Servedio, 2007; Kawata, Shoji, Kawamura, & Seehausen, 2007; Kolm et al., 2012; McNaught & Owens, 2002; Seehausen et al., 2008). There is of course no reason to expect the influence of sensory drive to apply exclusively or disproportionately to sexual signalling systems. For example, a general prediction of sensory drive is that species inhabiting complex, heterogeneous environments should be more likely to be polymorphic because variability in signalling environments over small scales may favour multiple evolutionary optima (Endler, 1992, 1993b). This prediction is a consequence of the fact that illumination in open, terrestrial environments is roughly constant during daylight hours, whereas in closed environments, particularly dense, tropical forests, the filtering effects of vegetation dramatically alter the colour and intensity of available light over small spatial and temporal scales (Cronin et al., 2014; Endler, 1993b). The greater availability of signalling niches in complex light environments should engender higher potential for polymorphic solutions in species that inhabit them, as opposed to less-complex signalling habitats. In colour lure systems, the extreme phenotypic variation on show across diverse light environments (Table 1) offers untapped potential for exploring the strength and generality of sensory drive as a diversifying agent, outside of the sexual signalling context in which it was developed. Indeed, preliminary evidence suggests such a prediction may be supported in colour lure systems (see Appendix).

A further advantage of colour lure systems is that many core principles of the sensory drive framework, including signal structure, signalling environments and the physiology of receivers (Endler, 1992, 1993a), are uniquely well defined. At least in the case of orb-weaving spiders, this is because colour luring is associated with a sit-and-wait hunting style (Table 1). The relevant viewing environments are easily defined and quantifiable through the measurement of irradiance (Endler, 1993b), which allows for studies of light environments over fine temporal and spatial scales, variation in which may partly drive the considerable inter- and intraspecific variation in signal structure (e.g. the spider genus *Gasteracantha*). Signal structure may be analysed using well-established methods such as reflectance spectrometry (Tso et al., 2004), photography (Chiao et al., 2009) and colour patch adjacency (Endler, 2012). The size and morphology of many species also allow direct manipulation of phenotypes (Chuang et al., 2007; Tso et al., 2006) and/or the use of artificial models (Fan et al., 2009). In combination with often short generation times, these features offer opportunities for closely controlled experimental research in both laboratory and field settings: a potential that has been

fruitfully exploited in many studies to date (Table 1). The visual ecology of the main prey groups of many luring species, such as Hymenoptera, Diptera and Lepidoptera (Table 1), is also relatively well understood (Hempel de Ibarra et al., 2014; Lunau, 2014; Rutowski, 2003), and a suite of tools for representing colour vision and/or perception are available for these groups (Chittka, 1992; Endler & Mielke, 2005; Johnsen et al., 2006; Kelber, 2001; Troje, 1993; Vorobyev & Osorio, 1998). Finally, the phylogenetic history of key luring species (such as orb-web spiders) is relatively well characterized (Blackledge et al., 2009; Bond et al., 2014; Griswold, Coddington, Horminga, & Scharff, 1998; Kuntner, Arnedo, Trontelj, Lokovšek, & Agnarsson, 2013; Scharff & Coddington, 1997), which provides great opportunities for comparative tests of sensory drive hypotheses.

CONCLUSIONS

Here we have sought to illustrate the potential value of approaching the study of colour-based prey lures through the lens of sensory drive. Sensory drive theory (Endler & Basolo, 1998; Endler, 1992) and its subsidiary models (Christy, 1995; Ryan, 1990) offer clear potential for expanding our understanding of the puzzling features of colour lure systems, and these systems offer reciprocal benefits for testing and extending evolutionary theory by virtue of their novelty and tractability.

Efforts to reconcile lure function according to models such as sensory traps (Table 2) would have immediate value for informing broader patterns of phenotypic diversity in these systems. To this end, surveys of micro- (e.g. spatial, diel) and macro- (e.g. seasonal) scale variation in light environments and captured prey will be necessary to identify potential drivers of signal design evolution. Given that lures are typically targeted at suites of potential receivers, and are presented in highly variable spectral environments (hence, influencing potential signal appearance), there is a need for fine- spatial and temporal scale data. Observational tests of the more restrictive formulation of the traps model through surveys of colour-luring species and coincident communities of potential 'models' (e.g. orb spiders and flowers) would be relatively simple, and offer a useful route for establishing signal function. If the colour palette of luring species is locally distinct and/or there is no ecological overlap with any putative 'models', for example, then the traps model in its strictest formulation could be discounted.

The psychosensory basis of lure attractiveness to ecologically relevant receivers (once identified) presents an intriguing area for future research. For example, receiver colour preferences may be innate (colour naïve), spontaneous (colour experienced, but 'untrained' as to rewarding stimuli) and learned/cognitive (colour experienced and 'trained' to rewarding stimuli; Ryan & Cummings, 2013; ten Cate & Rowe, 2007). Experimental tests of perceptual biases, their relative strength and their interaction in determining the attractiveness of lure phenotypes, especially in polymorphic species, may inform questions of macroscale diversity, such as the seemingly biased distribution of lure phenotypes (Table 1). Such knowledge carries great promise for extending our understanding of how biases shape visual signal evolution outside of sexual signalling contexts.

Acknowledgments

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APPENDIX

Visual signal polymorphism: a heuristic test

We illustrate the potential for colour lure systems to extend tests of sensory drive theory using colour polymorphism as an example. We tested whether species inhabiting complex, heterogeneous environments should be more likely to be polymorphic because variability in signalling environments over small scales may favour multiple evolutionary optima (see main text; Endler, 1992, 1993).

We explored this hypothesis using spider colour lures, which are known to be polymorphic, and displayed in diverse light environments (Table 1, main text). There is a deep evolutionary history of web building in spiders (Eberhard, 1990; Penney & Ortuño, 2006; Bond et al. 2014), and the use of coloration as a lure appears highly evolutionarily labile (demonstrated, for example, by the diversity of coloration within genera such as *Gasteracantha*). We extracted data on coloration, habitat and colour polymorphism for 245 species of web-building spider from the literature as well as print and online field guides (data available via figshare: http://dx.doi.org/10.6084/m9.figshare.1371150). Given that few studies actually demonstrate or quantify the occurrence of colour polymorphism, we judged polymorphism in most cases qualitatively, by inspecting photographs where available. A species was designated polymorphic if there was evidence of substantial discrete colour variation among individuals whose sex and species had been positively identified. Assessments were made conservatively, such that species in which there was clear potential for continuous variation (such as between yellow and off-white individuals), or evidence of purely ontogenetic colour change, were deemed monomorphic. Species were categorized as inhabiting 'simple' or 'complex' environments (which map approximately to open and closed environments), based on the twice-repeated blind assessment of qualitative habitat descriptions.

Of the 245 species sampled, 44 were designated as polymorphic, with 13 and 31 occurring in 'simple' and 'complex' habitats, respectively. A chi-square test for homogeneous frequencies of polymorphism with respect to habitat type proved significant ($\chi^2_1 = 12.071$, $P < 0.001$), suggesting that polymorphism may be more prevalent in species known to inhabit complex signalling environments. Although this is an informal test, these data are entirely consistent with the notion that the greater availability of niches (or the greater amount of 'noise') in complex signalling environments may create relatively higher potential for polymorphic solutions in species that inhabit them (Endler, 1992). This is a central prediction of sensory drive theory, and aligns with evidence from sexual systems (McNaught & Owens, 2002; Chunco et al., 2007; Seehausen et al., 2008). These data tentatively suggest that sensory drive has a role in driving signal diversification outside of sexual signalling systems, the evidence for which is otherwise limited. A more comprehensive, phylogenetically informed test of this hypothesis would be interesting.