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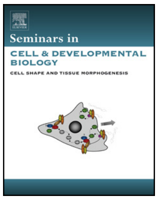

Review

Genetics and evolution of colour patterns in reptiles

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ABSTRACT

The study of coloration in the polyphyletic reptilians has flourished in the last two decades, in particular with respect to the underlying genetics of colour traits, the function of colours in social interactions, and ongoing selection on these traits in the wild. The taxonomic bias, however, is profound: at this level of resolution almost all available information is for diurnal lizards. Therefore, we focus on case studies, for which there are as complete causal sequences of colour evolution as possible, from phenotypic expression of variation in colour, to ongoing selection in the wild. For work prior to 1992 and for a broader coverage of reptilian coloration we refer the readers to Cooper and Greenburg's (Biology of the Reptilia, 1992) review. There are seven major conclusions we would like to emphasise: (a) visual systems in diurnal lizards are broadly conserved but among the wider range of reptiles in general, there is functionally important variation in the number and type of photoreceptors, spectral tuning of photopigments and optical properties of the eye; (b) coloration in reptiles is a function of complex interactions between structural and pigmentary components, with implications for both proximate control and condition dependence of colour expression; (c) studies of colour-variable species have enabled estimates of heritability of colour and colour patterns, which often show a simple Mendelian pattern of inheritance; (d) colour-polymorphic lizard species sometimes, but not always, show striking differences in genetically encoded reproductive tactics and provide useful models for studying the evolution and maintenance of polymorphism; (e) both male and female colours are sometimes, but not always, a significant component of socio-sexual signalling, often based on multiple traits; (f) evidence for effects of hormones and condition on colour expression, and trade-offs with immunocompetence and parasite load, is variable; (g) lizards show fading of colours in response to physiological stress and ageing and are hence likely to be appropriate models for work on the interactions between handicaps, indicator traits, parasitology and immunoecology.

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1. Introduction

Studies of lizards have been instrumental for our current understanding of some important principles of evolutionary biology, such as sexual selection and parental investment. Gladwyn Noble's early work on lizard mating behaviour in a framework of sexual selection was truly pioneering [1]. It was followed by the first detailed sex-specific analyses of lizard reproductive success in free-ranging populations by Robert Trivers, including effects on, and of, coloration [2]. Since then, molecular tools have become available for assigning paternity in the wild and identifying genes underlying colour vision [3,4]. Relatively cheap spectrometry equipment has become available for objective quantification of colours in the field and the resolution of electroretinography and microspectrometry has increased [5]. These developments have opened up a new world of possibilities to study the complex, integrated evolutionary biology of colour vision and coloration in the wild. In this article, we review these topics for reptiles.

We start with a brief introduction to the primary components of lizard vision and how integumental colours are produced, including mechanisms of colour change. These topics, and the functional significance of reptile coloration, are well covered in the extensive review by Cooper and Greenburg [6] and our ambition here is largely to cover the development in the field since their seminal contribution. Our intention is not to exhaustively review all work but to target select areas that we find have been particularly well addressed using reptilian models. We review studies addressing the inheritance of colours and colour patterns and their molecular genetic basis. We then discuss the evolution and maintenance of colour polymorphism and associated alternative reproductive tactics, an area in which reptiles provide numerous models and are one of the most intensively studied taxa. In a section on reptilian sexual selection, we focus primarily on evidence that colour signals can indicate male fighting ability or resource holding potential but we also address the evolution of female-specific coloration. Finally, we review studies assessing the relationship between coloration and immunocompetence, parasite load, oxidative stress, ageing and life-history components. We conclude by identifying areas for future research where reptiles are likely to be suitable models.

2. Colour vision and mechanisms of colour production

2.1. Vision in reptiles

Variation in coloration is only biologically meaningful if it can be perceived by signal receivers (conspecifics, predators and prey). For this reason, we begin with an overview of vision. Comparative visual ecology of reptiles is still in its infancy but the available data suggest both phylogenetic conservatism and ecologically relevant variation, sometimes between closely related species. Most vertebrates have a dual or duplex retina, so called because they have two types of photoreceptors: rods used for vision in low light conditions and cones used for vision in bright light conditions [7]. In lizards, the dual retina has been lost and the retina in most cases contains only cones [8], although these may be morphologically rod-like or express rod-specific opsins (photopigment proteins) in some nocturnal geckos [9,10]. A few examples of rod-like cells or pigments have been reported in diurnal lizards, although to date there is no evidence that they function physiologically as rods. In diurnal lizards, the visual system is broadly conserved, the retina having five classes of cones. Four of these are single cones used for colour vision, each containing a different visual pigment or photopigment, which are ultraviolet sensitive (UVS), short wavelength sensitive (SWS), medium wavelength sensitive (MWS) and long wavelength sensitive (LWS) [5,11]. Comparison of the signal from these four photoreceptor types by neurons in the visual system enables colour vision within a broad wavelength range, including the ultraviolet (approx. 300–700 nm). The fifth cone class is the double cones, comprising a principal and accessory member containing a LWS visual pigment. The double cones are often the most abundant in the retina and are most likely used for tasks requiring achromatic (luminance) discrimination [12]. Despite this broad conservatism, visual sensitivities may vary significantly depending on the relative abundance of photoreceptors. For example, in the cordylid lizard, *Platysaurus broadleyi*, sensitivity in the ultraviolet (UV) is approximately three-fold that of other lizards due to a relatively higher number of UVS photoreceptors [5]. This heightened UV sensitivity reflects the importance of UV social signals in this species [13,14].

The visual system of geckos differs from that of other lizards. Nocturnal geckos have three types of visual pigment sensitive to ultraviolet, blue and green wavelengths of light respectively [15]. Nocturnal geckos have a number of visual adaptations to enable colour vision in low light conditions, because the appearance of an object can change dramatically depending on illumination. The change in appearance is greater with respect to an object's intensity than its colour. Therefore, colour vision may be important under low light conditions to improve object constancy and recognition [7]. Behavioural experiments support the ability of geckos to discriminate objects based on colour cues alone under low light conditions [16] and colour patches appear to be used as social signals in some species (*e.g.*, [17]). Nocturnal geckos have additional optical adaptations for vision in low light. In particular, their cones are much larger and more light sensitive, their pupil is large and focal length is short [7]. These features would result in blurring of the retinal image without zones of different refractive power (multi-focal optical system), which were recently confirmed for the nocturnal helmet gecko, *Tarentola chazaliae*, and are absent in the diurnal Madagascar giant day gecko, *Phelsuma madagascariensis grandis* [8]. In nocturnal geckos, the ultraviolet sensitive photoreceptors are sparse (<10% of photoreceptors in the retina) and given this, and the low levels of UV radiance (particularly at night), pattern discrimination in the UV range is likely to be very poor [15]. However, the UV photoreceptors may contribute to colour constancy for colours primarily distinguished by the other two photoreceptor classes [15].

All snakes studied to date have three types of visual pigment with some variation in their sensitivities (SWS with λ_{max} of approx. 357–365 nm, MWS 482–495 nm and LWS 535–560 nm). In sea snakes, however, the SWS photopigment peak sensitivity is shifted to approximately 430 nm, potentially because UV light attenuates rapidly with increasing water depth [18]. The MWS visual pigment may be contained within photoreceptors that morphologically resemble rods, cones or an intermediate [18]. Basal henophidian snakes, such as the Colombian boa, *Boa constrictor imperator*, and the ball python, *Python regius*, have rods making up approximately 90% of photoreceptors (λ_{max} of approx. 495 nm) and two types of single cones containing the SWS and LWS visual pigments, respectively (λ_{max} of approximately