Open Journal of Animal Sciences, 2017, 7, 356-363
http://www.scirp.org/journal/ojas
ISSN Online: 2161-7627
ISSN Print: 2161-7597

Peri-Ocular Eye Patterning (POEP): More than Meets the Eye

Noam Josef[1,2]

[1]Mote Marine Laboratory, Sarasota, Florida, USA
[2]Institute for Human & Machine Cognition, Pensacola, Florida, USA
Email: njosef@mote.org

How to cite this paper: Josef, N. (2017) Peri-Ocular Eye Patterning (POEP): More than Meets the Eye. *Open Journal of Animal Sciences*, 7, 356-363.
https://doi.org/10.4236/ojas.2017.73027

Received: April 8, 2017
Accepted: July 25, 2017
Published: July 28, 2017

Abstract

Spatial body patterning is widely observed throughout the phylogenetic tree and is used for a variety of functions. Body colours in general and camouflaging patterns in particular have been extensively studied for their role in stealth and crypsis. Particular interest has focused on the diverse skin patterns surrounding animals' eyes (Peri-Ocular Eye Patterning-POEP). These patterns have been suggested to aid in high brightness conditions, help camouflage an organism's eyes or ornament and emphasize bright head colorations. In this work I demonstrate the apparent widespread use of POEP among various marine and terrestrial organisms (both vertebrates and invertebrates) and discuss the trait's abundance, variations, and possible roles.

Keywords

Eyes, Camouflage, Body Patterning, Malar Stripes

1. Introduction

Numerous studies have addressed the evolution, comparative physiology, and functions of animal body patterning [1]-[6]. Documented functions of organism's body patterning include: camouflage [7] [8] [9], visual communication, including warning coloration [10] [11] [12] [13] [14], insect avoidance [15] and even assistance with thermal regulation [16].

Camouflage can take several forms: crypsis (avoiding detection) [17], mimicry (resembling a defended organism) [18] and masquerading (resembling an inedible object) [19]. Crypsis is an adaptation developed by many organisms seeking to minimize detection [6] [8] [20] [21] [22] [23]. One example of such adaptation is *disruptive coloration*-a set of markings that creates the appearance of false edges and boundaries and hinders the detection or recognition of an object's or part of an object's true outline and shape [22].

In their various forms, eyes have evolved and regressed multiple times throughout the evolutionary process [24]. Their function, optics and physiological constraints have shaped and preserved the eye's location and overall appearance, establishing eyes as an important facial feature in visual search-pattern analysis, facial recognition and even individual identification [25]-[32]. Given eyes' prominent role, concealing eye structure through body patterning may be of significant evolutionary benefit which may have driven development of eye camouflage and obliterating eye-lines [33]. Nevertheless, many animals, ranging from birds [34] to fishes [35], have prominent and even ornamented eyes. Walls [36] suggested that since eyes are so difficult to conceal, some vertebrates have gone the alternate route of incorporating dramatic periocular ornamentation.

Given that eyes are visual targets of many visual search patterns, animals appear to have developed eye camouflage, ornamentation, false eyes and eye-masks as means of avoiding recognition or deterring opponents [33] [35]. Indeed, Barlow found an ecological association between the stripes and fish habitat and even provided four examples of teleost's eyes camouflage: 1) Eye Inclusion – black surrounding includes the dark eye; 2) Mottling-mottled pattern distracts the observer from the eye; 3) Radiating lines-disruptive patterning; and 4) Eye lines-body patterns running through and over the eyes.

"Malar stripes" are another important facial marking; these dark stripes are located immediately beneath the eye. Malar stripes are known to aid in reducing glare in high light intensity conditions, as sought by athletes when applying black paint below their eyes. While Malar stripes serve as an important distinguishing feature between species or individuals (e.g. ornithology), their dark colour and their infraorbital facial location distinguish them from POEP which usualy surround the eye in a radial manner or across the eye and over the pupil in particular. POEP comes in many colours on the eye's periphery, typically in patterns that cross the pupil or in a periorbital POEP (**Figure 1(B)** and **Figures 1(D)-(F)**). In some cases, both periorbital POEP and infraorbital Malar stripes can be found in the same organism (**Figure 1(C)**). The application of this phenomenon is not yet fully understood but coloration surrounding animal's eyes seems to have a wider, more significant purpose then originally thought. Helping visual acuity in high illumination conditions is just one example, but the recurring shapes, colours and patterns suggests a possible mechanistic function.

Based on previous but limited examples, this work presents a wider spectrum of animals from diverse taxa that express various types of eye patterning. Although in many cases these patterns seem to be helpful in camouflaging the eyes, their true nature and benefits clearly require additional inquiry. I believe the additional evidence offered below suggests an evolutionary emphasis on eye patterning across the phylogenetic tree.

2. Methods

As a means of demonstrating the prevalence of the POEP trait, I have identified as many examples as possible within the animal kingdom. These examples were

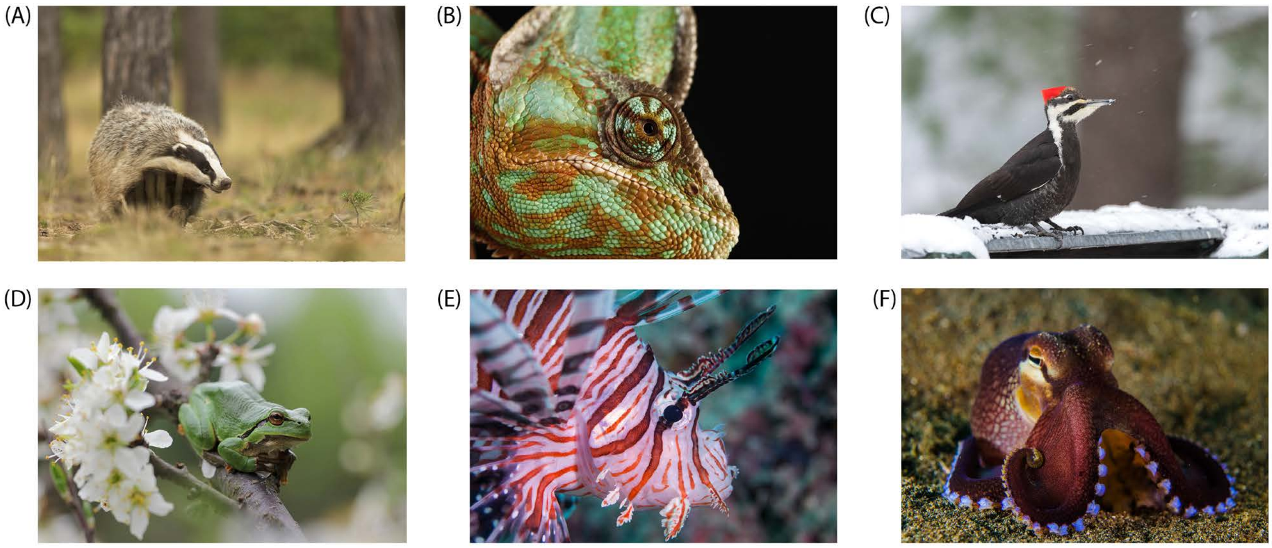

Figure 1. Examples of the POEP in a variety of animals: (A) European badger (*Melesmeles*) is a mammalian example of the eye-inclusion pattern. (B) Veiled chameleon (*Chameleo calyptratus*) is a dynamically camouflaging reptile that displays the radial-lines pattern. (C) Pileated woodpecker (*Dryocopus pileatus*) expressing both eye-lines and Malar stripes; the latter is the lower mark, extend from the base of the bill to the side of the neck. (D) European tree frog (*Hylaarborea*) provides an example for eye-lines in amphibians. (E) Lionfish (*Pterois miles*) display eye-lines; this image provides just one example of the many fish that express POEP. (F) The Veined octopus (*Amphioctopus marginatus*) is a dynamically camouflaging mollusc that expresses all four POEP types in different scenarios-in this case, a horizontal eye-line. All photos are legally purchased adobe stock©.

obtained by searching several image bases including personal photo libraries, permitted photographers libraries (Adobe stock©), Internet photo search and the classic literature. The objective of the species examples presented here is to offer evidence of the trait's prevalence as well as support for my hypothesis as to possible POEP convergence.

3. Results

In this section, I document examples of POEP, emphasizing the variety of phyla in which the POEP can be found as well as the trait's versatility. As can be seen in Figure 1 it is clear that the POEP phenotypic trait's is eminent in mammals, reptiles, birds, amphibians, fish and even molluscs.

In the enclosed table (Table 1), I list various examples of POEP types expressed in a variety of organisms from across the phylogenetic tree. I also include some examples of the Malar stripes known to assist in vision acuity at high light intensity [37].

Obviously, there are many animals (e.g. Grevy's zebra-*Equusgrevyi* and Mandarin fish *Synchiropussplendidus* which express body and head patterns which are ambiguous and do not appear to represent either POEP or Malar stripes (Figure 2(A) and Figure 2(B)). In some other examples, it was unclear whether an observed eye patterning represented a "Malar stripe" or a POEP (e.g. Cheetahs *Acinonyx* or the Thomson's gazelle, *Eudorcas thomsonii* presented in Figure 2(C) and Figure 2(D)). In such situations, a literature review was performed to discern how previous studies addressed the markings in question.

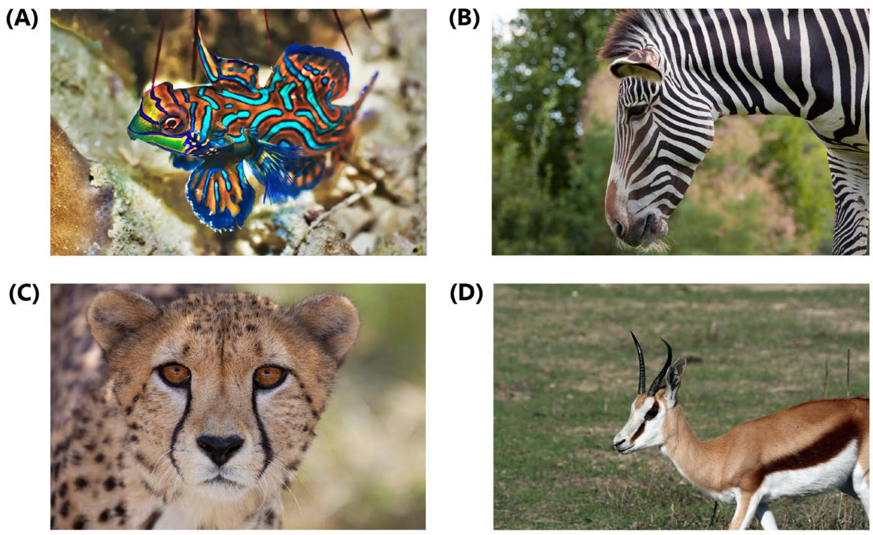

Figure 2. Examples for eye patterning which are not representative of what I perceive to be POEP. The first two examples are of undetermined categories (A) Mandarin fish-*Synchiropussplendidus* and (B) Gravy's zebra (*Equusgrevyi*). The following two examples are of Malar striping, believed to decrease glare in high light intensity conditions in the (A) Thompson's gazelle (*Eudorcas thomsonil*) and (B) Cheetah (*Acinonyxjubatus*). All photos are legally purchased adobe stock©.

4. Conclusions

Eyes structure, colour and the shape have been the focus of many studies [24] [38] [39]. Although previously mentioned in Barlow's work, the development of various periocular patterns has been primarily addressed in the context of individual fish species. It was only when I considered looking for patterns outside of fish species that I came to realize the extent of this phenotype. Hopefully, the short survey presented here will document the apparent frequency of this phenotype. While not necessarily novel, I believe this work demonstrates that POEP can be found in many taxa and that it is surprisingly common across the phylogenetic tree.

The sheer fact that the POEP trait can be found among different mammals, fish, birds, reptiles and even molluscs would seemingly validate the trait's prominence and its importance across the phylogenetic tree and in many different light conditions. Intriguingly, POEP can be found among marine and terrestrial animals, carnivores and herbivores, static and dynamic camouflagers and in a variety of landscape complexity. Therefore, it seems reasonable to assume that this attribute has developed independently several times along the evolutionary process.

When a phenotypic trait is eminent in such a wide diversity of animals, it is clearly designed to answer a fundamental requirement throughout the evolution process. As such, its optical and cryptic functions should be further examined. Future questions could address various issues including (but not limited to): 1) Does POEP truly aid in eye camouflage?; 2) Does POEP offer any optical benefit to its bearer?; and 3) How does POEP type change with environmental properties?".

Table 1. POEP types expressed in various species.

	Scientific name	Common name
Eye inclusion	*Ailuropodamelanoleuca*	Giant panda
	Pomacanthus imperator	Emperor angelfish
	Taxideataxus	American badger
	Dendrobatesauratus	Dart frog
	Paracanthurushepatus	Palette surgeonfish
Eye lines	*Dendroicachrysoparia*	Golden warbler
	Hylatomuspileatus	Pileated woodpecker
	Varanuspanoptes	Yellow-spotted monitor
	Zonotrichialeucophrys	White-crowned sparrow
	Pteroisvolitans& miles	Lionfish
	Siganusdoliatus	Rabbit fish
	Spizellapasserina	Chipping sparrow
	Aulostomusmaculatus	Trumpetfish
	Pterapogonkauderni	Banggaicardinalfish
Radial lines	*Choerodonfasciatus*	Harlequin tuskfish
	Psammophilusdorsalis	Peninsular rock agama
	Dendrochirusbrachypterus	Shortfin turkeyfish
	Hippocampus breviceps	Short head seahorse
	Canthigastersolandri	Blue spotted pufferfish
	Histiophrynepsychedelica	Psychedelic frogfish
	Barchatuscirrhosus	Toadfish
	Cymbacephalusbeauforti	Crocodile fish
Dynamic pattern	*Octopus vulgaris*	Common octopus
	Furciferpardalis	Panther chameleon
Malar stripes	*Falco mexicanus*	Prairie falcon
	Acinonyx	Cheetah
	enospizabaileyi	Sierra Madre sparrow
	Eudorcasthomsonii	Thompson's gazelle

Since a human observer did the decision as to which animals express POEP, there is clearly an element of subjectivity in the current study. That said, given the qualitative nature of this work, such subjectivity should not impair the overall conclusions presented in this communication.

Acknowledgements

I would like to thank Dr. Aaron Fink and Andy Dietch for the English editing and photographic materials, Erin Petrino for her technical contribution and assistance in searching and identifying POEP in big online datasets, Gal Eyal and Dr. Gil Koplovitz for their generous agreement of using their underwater photographs.

References

[1] Poulton, E.B. (1890) The Colours of Animals: Their Meaning and Use, Especially Considered in the Case of Insects. D. Appleton and Company, New York. https://doi.org/10.5962/bhl.title.69899

[2] Ogle, W. (1882) On the Parts of Animals. K. Paul, Trench & Company, London.

[3] Endler, J.A. (1978) A Predator's View of Animal Color Patterns. *Journal of Evolutionary Biology*, **11**, 319-364. https://doi.org/10.1007/978-1-4615-6956-5_5

[4] Mallet, J. and Joron, M. (1999) Evolution of Diversity in Warning Color and Mimicry: Polymorphisms, Shifting Balance, and Speciation. *Annual Review of Ecology and Systematics*, **30**, 201-233. https://doi.org/10.1146/annurev.ecolsys.30.1.201

[5] Butcher, G.S. and Rohwer, S. (1989) The Evolution of Conspicuous and Distinctive Coloration for Communication in birds. In: Power, D.M., Ed., *Current Ornithology*, Vol. 6, Plenum Press, New York, 51-108. https://doi.org/10.1007/978-1-4757-9918-7_2

[6] Cott, H. (1940) Adaptive Coloration in Animals. Methuen, London.

[7] Darwin, C. (1859) On the Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life. John Murray, United Kingdom, London, 502.

[8] Stevens, M. and Merilaita, S. (2011) Animal Camouflage: Mechanisms and Function. Cambridge University Press, Cambridge. https://doi.org/10.1017/CBO9780511852053

[9] Stevens, M. and Merilaita, S. (2011) Animal Camouflage: An Introduction. In: Stevens, M. and Merilaita, S., Eds., *Animal Camouflage: Mechanisms and Function*, Cambridge University Press, United States of America by Cambridge University Press, New York, 1-16. https://doi.org/10.1017/CBO9780511852053.001

[10] Hailman, J.P. (1977) Optical Signals: Animal Communication and Light. Indiana University Press, Bloomington, IL.

[11] Moynihan, M. (1985) Communication and Non-Communication in Cephalopods. Indiana University Press, Bloomington, IL.

[12] Guilford, T. (1990) The Evolution of Aposematism. In: Evans, D.L. and Schmidt, J.O., Eds., *Insect Defenses*: *Adaptive Mechanisms and Strategies of Prey and Predators*, State University of New York Press, Albany, New York, 23-61.

[13] Grant, J. (2007) Ontogenetic Colour Change and the Evolution of Aposematism: A Case Study in Panic Moth Caterpillars. *Journal of Animal Ecology*, **76**, 439-447. https://doi.org/10.1111/j.1365-2656.2007.01216.x

[14] Merilaita, S. and Ruxton, G. (2007) Aposematic Signals and the Relationship between Conspicuousness and Distinctiveness. *Journal of Theoretical Biology*, **245**, 268-277.

[15] Egri, Á., Blahó, M., Kriska, G., Farkas, R., Gyurkovszky, M., Åkesson, S. and Horváth, G. (2012) Polarotactictabanids Find Striped Patterns with Brightness and/or Polarization Modulation Least Attractive: An Advantage of Zebra Stripes. *Journal of Experimental Biology*, **215**, 736-745. https://doi.org/10.1242/jeb.065540

[16] Cloudsleythompson, J. (1984) How the Zebra Got His Stripes-New Solutions to an Old Problem. *Biologist*, **31**, 226-228.

[17] Stevens, M. and Merilaita, S. (2009) Introduction. Animal Camouflage: Current Issues and New Perspectives. *Philosophical Transactions of the Royal Society*, *Series B*, **364**, 423-427. https://doi.org/10.1098/rstb.2008.0217

[18] Speed, M.P. (1993) Muellerian Mimicry and the Psychology of Predation. *Animal Behaviour*, **45**, 571-580.

[19] Skelhorn, J., Rowland, H.M., Speed, M.P. and Ruxton, G.D. (2010) Masquerade: Camouflage without Crypsis. *Science*, **327**, 51. https://doi.org/10.1126/science.1181931

[20] Stevens, M., Cuthill, I., Windsor, A. and Walker, H. (2006) Disruptive Contrast in Animal Camouflage. *Proceedings of the Royal Society, Series B*, **273**, 2433-2438. https://doi.org/10.1098/rspb.2006.3614

[21] Stevens, M. (2007) Predator Perception and the Interrelation between Different Forms of Protective Coloration. *Proceedings of the Royal Society of London, Series B*, **274**, 1457-1464. https://doi.org/10.1098/rspb.2007.0220

[22] Stevens, M. and Merilaita, S. (2009) Defining Disruptive Coloration and Distinguishing Its Functions. *Philosophical Transactions of the Royal Society, Series B*, **364**, 481-488. https://doi.org/10.1098/rstb.2008.0216

[23] Stevens, M. and Merilaita, S. (2011) Crypsis through Background Matching. In: Stevens, M. and Merilaita, S., Eds., *Animal Camouflage*: *Mechanisms and Function*, Cambridge University Press, New York, 17-33. https://doi.org/10.1017/CBO9780511852053

[24] Land, M.F. and Nilsson, D.-E. (2012) Animal Eyes. Oxford University Press, Oxford. https://doi.org/10.1093/acprof:oso/9780199581139.001.0001

[25] Tanaka, J.W. and Farah, M.J. (1993) Parts and Wholes in Face Recognition. *The Quarterly Journal of Experimental Psychology Section A*, **46**, 225-245. https://doi.org/10.1080/14640749308401045

[26] Maurer, D. and Young, R.E. (1983) Newborn's Following of Natural and Distorted Arrangements of Facial Features. *Infant Behavior and Development*, **6**, 127-131.

[27] Ellis, H.D., Shepherd, J.W. and Davies, G.M. (1979) Identification of Familiar and Unfamiliar Faces from Internal and External Features: Some Implications for Theories of Face Recognition. *Perception*, **8**, 431-439. https://doi.org/10.1068/p080431

[28] Tanaka, J.W. and Sengco, J.A. (1997) Features and Their Configuration in Face Recognition. *Memory & Cognition*, **25**, 583-592. https://doi.org/10.3758/BF03211301

[29] Hermer, L. and Spelke, E.S. (1994) A Geometric Process for Spatial Reorientation in Young Children. *Nature*, **370**, 57-59. https://doi.org/10.1038/370057a0

[30] Hsu, R.-L., Abdel-Mottaleb, M. and Jain, A.K. (2002) Face Detection in Color Images. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, **24**, 696-706. https://doi.org/10.1109/34.1000242

[31] Keil, M.S. (2009) "I Look in Your Eyes, Honey": Internal Face Features Induce Spatial Frequency Preference for Human Face Processing. *PLoS Computational Biology*, **5**, e1000329. https://doi.org/10.1371/journal.pcbi.1000329

[32] Haig, N.D. (2013) The Effect of Feature Displacement on Face Recognition. *Perception*, **42**, 1158-1165. https://doi.org/10.1068/p130505n

[33] Barlow, G.W. (1972) The Attitude of Fish Eye-Lines in Relation to Body Shape and to Stripes and Bars. *Copeia*, **1972**, 4-12. https://doi.org/10.2307/1442777

[34] Smith, N.G. (1966) Evolution of Some Arctic Gulls (Larus): An Experimental Study of Isolating Mechanisms. *Ornithological Monographs*, No. 4, 1-99. https://doi.org/10.2307/40166680

[35] Thresher, R.E. (1977) Eye Ornamentation of Caribbean Reef Fishes. *Zeitschrift für Tierpsychologie*, **43**, 152-158.

[36] Walls, G.L. (1942) The Vertebrate Eye and Its Adaptive Radiation.

[37] De Broff, B.M. and Pahk, P.J. (2003) The Ability of Periorbitally Applied Antiglare Products to Improve Contrast Sensitivity in Conditions of Sunlight Exposure. *Archives of Ophthalmology*, **121**, 997-1001. https://doi.org/10.1001/archopht.121.7.997

[38] Stubbs, A.L. and Stubbs, C.W. (2016) A Novel Mechanism for Color Vision: Pupil Shape and Chromatic Aberration Can Provide Spectral Discrimination for Color Blind Organisms.

[39] Akkaynak, D., Allen, J.J., Mathger, L.M., Chiao, C.C. and Hanlon, R.T. (2013) Quantification of Cuttlefish (*Sepia officinalis*) Camouflage: A Study of Color and Luminance Using *in Situ* Spectrometry. *Journal of Comparative Physiology A*, **199**, 211-225. https://doi.org/10.1007/s00359-012-0785-3