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What If I Told You Camouflage is a Myth? Animal Coloration is Mainly A-biotic and not Biotic (Camouflage)

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ABSTRACT

In the present article, the author posits that the perception that animals apparently display a strategy of avoiding detection by means of camouflage—i.e., by disguising themselves in the natural colours of their environment—is not the actual case in nature but, rather, merely anecdotal. **Animal coloration is mainly a-biotic** (eco-physiological) **and not biotic** (camouflage). The contention regarding the absence of the phenomenon of camouflage among animals as a common evolutionary response is based on three arguments: 1) that reflecting the natural colours of the environment is linked to ecophysiology; 2) that predator and prey constitute "an evolutionary pair" and, accordingly, they know how to identify one another (in order to survive they employ different strategies, of which camouflage is not one of them); and 3) that the approach of relating animal camouflage to reflecting the colours of the environment is an anthropocentric one. Rather than the accepted biotic-ethological approach (colour camouflage), the present article suggests the recognition of a-biotic and eco-physiological conditions as a distinct research field, whose title "Reflection of environmental colours by animals", along with this article, calls for eco-physiologists to demonstrate that this approach indeed offers a special contribution to the understanding of colouration in animals.

Keywords: A-biotic; Anthropocentrism; Camouflage; Eco-physiology; Ethology; Evolution; Reflection

1. Material and methods

A survey of the literature from ancient times (4th century BCE, Aristotle [1]) to present days [2] was done in order to claim that the perception that animals apparently display a strategy of avoiding detection by means of camouflage is not the actual case in nature.

2. Introduction

Camouflage, even if not this precise term, has

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been recognised as such since ancient times; and already in the 4th century BCE Aristotle carried out observations on the active changes in colour performed by the octopus and squid to resemble stones and the surrounding habitat for the purpose of concealment. Erasmus Darwin [3], one of the forefathers of biological research, documentation and the systematics of animals in nature, wrote in his book *Zoonomia* (1794–1796): "Many animal species have adapted in various ways to ensure their own security by developing hard shells or camouflage" (*Zoonomia I, p. 505).* His grandson, Charles Darwin, did not use the term "camouflage", but a similar one—"resemblance" [4]. It seems that since then researchers have always related to the phenomenon of camouflage in nature as inbuilt and, so too, have books devoted to the subject [2,5–8]. There is abroad literature on the subject of camouflage and many surveys have been published in recent years [9–12] as well as studies of the evolutionary aspects of camouflage [13] and camouflage and mimicry through colour in fossils [14]. Where there is disagreement among researchers, it focuses on the mechanisms behind the phenomenon of camouflage but does not question its existence [15–17].

In this article I would like to quote the words of the first documented researcher to write on the subject, over 2,300 years ago: "It can change its colour to make it resemble the colour of its habitat" (Aristotle 4th century BCE [1]); as well as the opening words of Endler's [15] article: "It has long been known that the general colors and tones of animals tend to match their background". Here, however, I shall present a different rationale to theirs and contend that the phenomenon is not usually an abiotic response—that is, a similarity to the environment, background matching or camouflage, performed in order to deceive other animals. Rather, it is an a-biotic, eco-physiological response: in other words, a projection of the environment's colours in order to gain eco-physiological advantages.

I base my contention regarding the non-existence of animal camouflage as a common evolutionary solution on three arguments: radiating the colours of the environment is linked to eco-physiology; predator and prey constitute "an evolutionary pair" and, accordingly, they know how to identify one another and the possible anthropocentrism of those who insist that camouflage is very common in nature.

3. Results and discussion—The three arguments

According to the life-dinner principle [18] and the dicey dinner dilemma [19], the prey needs to attempt every way possible in order to prevent being devoured. The present article, however, contends that camouflage is generally not one of these ways—neither for the prey nor for the predator. In the following, I shall contend that the colours ascribed to camouflage are in fact colours that serve the a-biotic needs of the animals.

3.1 Argument A—The reflection of environmental colours is an eco-physiological solution

I would like to suggest that the issue of the colour of the body cover that "wraps" the animals be examined not from the biotic perspective, "vision", but from the a-biotic one: in other words—"the eco-physiological suitability to the characteristics of the habitat", with emphasis on the conditions of reflection.

A connection between physiology and colour and body orientation was already noted by Schmidt-Nielsen in his classic book [20]. Mendelssohn also stated this in regard to his experience in the deserts of the Middle East, where he found that large desert mammals, predators and prey, are light-coloured like their surroundings in order to reflect solar radiation [21]. The phenomenon, termed 'maxithermal strategy' [22], has also been widely studied in reptiles [23].

Beyond the issue of any particular animal, a number of rules explain the a-biotic, eco-physiological influence on animals, such as Bergmann's rule, dealing with the connection between body weight and geographical region [24];

and Allen's rule on the connection between length of bodily appendages (length of ears, tail, limbs, beak, etc.) and temperature [25,26]. Two rules link animal colouration with climate: Gloger's rule (darker colouration where wet and warm [27]) and Bogert's rule (darker colouration where cold, see the seemingly opposing effects in Delhey et al. survey [28] of passerine birds).

While the above enables the advocates of camouflage to claim that the species in the tropical rain forest are darker than their conspecifics that inhabit cold, dry regions, because the darker colour offers a good camouflage in the forest, the present article subscribes, rather, to the a-biotic explanation as the factor influencing the animal's colour.

If this is so, then for the camel, leopard, hyena, bear, moth and others it is more reasonable to seek an explanation for their colours as reflecting those of their habitat, rather than as camouflage—i.e., as eco-physiological. Following are a number of examples—not camouflage but a reflection of the colours of the habitat**.**

Cephalopods: Colour change versatility is probably no better developed in the animal kingdom than in the coleoid cephalopods (octopus, squid, cuttlefish). According to Hanlon et al. [29]: These marine molluscs possess…sophisticated visual system that controls body patterning for communication and camouflage… cephalopods have evolved a different defense tactic: they use their keen vision and sophisticated skin—with direct neural control for rapid change and fine-tuned optical diversity—to rapidly adapt their body pattern for appropriate camouflage against a staggering array of visual backgrounds: colourful coral reefs, temperate rock reefs, kelp forests, sand or mud plains, seagrass beds and others.

The ability of coleoid cephalopods to change colour according to their environment, although highly impressive, is not proof of biotic reason—i.e., to avoid the danger of predation or of preparation for predation; and if in place of the word "camouflage" we write "reflection of the colour of the habitat", it is still an impressive ability, with the animals' anatomy having been and still being studied in depth in order to understand this ability [30,31]. Similarly, because the animal has the ability to project the colour of its environment—i.e., a variety of colours, it exploits this ability also for interspecific communication [32] as is known in chameleons (see below).

Insect: The famous peppered moth is active by night and during the daytime hours it rests beneath horizontal branches in the tree canopy [33]. It is no wonder therefore that the birds searching for food above the branches do not discern it (see similar criticism in Majerus's book about Industrial Melanism [34]). Nonetheless, there is a need for an explanation of the moth's dark colour, such as it's reflecting of its polluted environment. Indeed, Wells [33] suggests looking in the a-biotic direction, such as "thermal melanism". The subject is controversial and Mallet [35] summaries it with the question "What and who do you believe?"

The study by Walton and Stevens [36], who performed an artificial predation experiment, does not provide proof that reflecting the habitat background is biotic response of camouflage but, rather, even intensifies the need to focus on the a-biotic possibility, as can be learned also from the impressive research on the bogongmoth in Australia [37].

Spiders: Spiders display a wealth of mechanisms by which to produce colour [38] and, accordingly, there are reports of spiders camouflaged inside flowers [39], inside egg cartons [40] and even camouflaging their own webs [41]. It seems, however, that neither their predators nor their prey are influenced by the "camouflage" because they perceive UV radiation on the spiders' webs, which helps the predators to detect them, while also attracting the prey to them [41]. Figon and Casas [42] note:

Crab spiders can be spectacularly invisible to our eyes when they match the colour of the flower on which they hunt, however, there is still no evidence for colour matching as being beneficial in catching more prey, this result might rely on the fact that flower-matching crab spiders are actually not invisible to bees and flies, their most abundant preys in the field.

Because the prey discerns the contrast created by the UV radiation, it is drawn towards the "camouflaged" spider and in fact prefers spider-occupied flowers [43].

Fish: The behaviour of juvenile sole (flatfish) includes a preference for a background similar to their body colour [44], and even though their matching to the sand is not perfect, they still bury themselves in the sand [45]. Moreover, their predators at this age are crabs (See [46] and Figure 1 in [47]). All the above attest to camouflage not being the system used to avoid detection. Crabs are short in height and, therefore, when the fish is in close contact with the sandy ground the crab perceives it mainly against the background of seawater and not that of the sand on which the crab is standing. The sole's ability to change its body colour to that of the surrounding environment attests to the activity of the sensors that the animal is expected to possess in order to project a colour like that of the surroundings, as contended in this article.

Reptile: The chameleon serves as a classic example for those who claim the use of camouflage, and is even noted by Aristotle [1], although only the fact of this ability to change colour without providing an explanation for this; and, indeed, studies have revealed that the majority of colour changes in chameleons are connected to inter-species communication [48,49].

In a study in which Stuart-Fox and Moussalli [50] examined 21 species of dwarf chameleons, they found "that the remarkable ability for chromatic change in dwarf chameleons is likely to have evolved to facilitate social signalling rather than background matching." In contrast, when they examined the presence of predators near the chameleons, in connection with colour changes for camouflage [50], the authors repeatedly attempted to bridge the incompatibility between the expected and the observed, perhaps due to their having examined the colour changes in connection with biotic variable, the predator, rather than with the a-biotic conditions, such as environmental reflectance.

Stuart-Fox and Moussalli in a study on chameleons published in 2008 [48], contended: "Our results suggest that the evolution of the ability to exhibit striking changes in colour evolved as a strategy to facilitate social signalling and not, as popularly believed camouflage." Following this statement, another expert in the field of camouflage contended: "No one has ever shown that the chameleon's special ability provides camouflage" [51].

Mammals: It is incorrect to claim that camouflage colour is what enables the Polar bear to stealthily approach its prey, in light of the fact that the main prey of this bear is the seal pup [52], a prey found beneath the ice floes [53]. In order to catch its prey, the Polar bear collapses the roof of the seal pup's icy hiding place [54]. In other words, the Polar bear's body colour is evolutionarily suited to contending with the a-biotic (eco-physiological) conditions and not with the biotic (camouflage) ones, as has indeed been shown:

The polar bear evolved an efficient optical nano-technology for **energy harvesting and energy conservation…** harnessing solar radiation to heat the subcutaneous and skin surface layers [55] and also convert ultraviolet rays into thermal energy [56].

The spotted hyenas live in a clan system [57] and they attack their prey in large and loudly vocal packs [58]. In other words, there is no concealment and their intention can be clearly discerned by the potential prey. Therefore, we should interpret the advantage of this hyena's brown-yellow colour interspersed with black spots as an a-biotic, eco-physiological solution, rather than as biotic need linked to the "predator-prey" relationship.

In all of the above examples, what was written about the spider appears also to be correct here: "**Camouflage** profits from such a relationship, but **may not be the driving force"** [41,59].

Light wave reflectance of the environment as a physiological strategy ("the eco-physiological approach")

Based on the one hand, the "automatic" changes in colour of the chameleon or the octopus, to match the new background when they move to a different habitat [60], and based on the grey colour characterising large animals such as the elephant and rhinoceros [61] on the other hand, I would like to present a rational hypothesis regarding the meaning of "colour of the environment" that not only characterises predators and prey in nature, but also those animals that are not in danger of predation, such as fowl and large reptiles on isolated islands.

I propose to examine the fact of "similarity" between an animal's colour and that projected by its environment, focusing on the physiological factors as manifested in expressing the spectrum of solar radiation on animals and their natural environment. In other words, in terms of "natural selection" there may be some physiological advantage to this, with the body covering radiating colours similar to those radiated by the environment, in what appears to us as matching the environment, as 'camouflage'.

There are a number of examples, including the elephant and the rhinoceros, whose body colour is grey and prominent in almost every habitat (the camouflage advocates can base this on these animals spending the hot hours in the shade, and claim that they are there for the sake of camouflage). I seek to examine the significance of their colour, however, on the basis of the "eco-physiological approach"; i.e., to contend that they reflect the light waves that the average environment reflects (perhaps grey is the best average colour) for these large herbivores that roam in a variety of ecological niches [13]. This colour thus provides an average "physiological answer" for all the habitats in which these animals roam and forage for existence.

The hippopotamus too, being very large and in various shades of grey, seemingly offers the best answer regarding a physiological matching to the environment, as does the grey colour of the largest of all mammals, the whale.

The camel has few natural predators in the sandy deserts [62,63], and even if it did have many predators, it is doubtful, due to its large size, whether camouflage would conceal it from them (it produces a sufficient shadow to reveal it to the predator both by day and by moonlight). However, colour matching to the light waves radiating from the environment could be significant to this large animal, dwelling in a habitat so exposed and arid.

Mammals avoided competition with the dinosaurs by being nocturnal [61] and, accordingly, most of them lost the ability to perceive colours (on the minority with colour vision [64]), which is not necessary for animals functioning in a dark environment [54]. Indeed, most of these mammals' representatives are small-bodied and dark-coloured, although those among them that also hunt during daylight, when all the colours of the rainbow can be seen, are colourful species, despite most of them, and their prey, having no ability to perceive these colours. This serves to strengthen the "eco-physiological approach", confirming that the bodily colour of an animal does not provide biotic, visual, solution intended to impede its discernment by an onlooker; but, rather, it is an a-biotic physiological solution (conserving body heat, energy, etc.) and, accordingly, it functions as "non-visual selection" [33].

Regarding the issue of an animal's colouring, the "eco-physiological approach" suggested in the present article contends that even in the absence of another species in the habitat, it is beneficial for an animal to reflect similar light waves to those of its environment. In other words, an animal's colour is not an answer to a problem whose source is biotic (i.e., how not to be seen by another animal, or ostensibly "camouflage"); but, rather, **body colour is a physiological response** to an a-biotic problem and an evolutionary development independent of the presence of additional animals. Thus, even if during the evolutionary process only one species of animal developed, it is reasonable to assume that its colour would have been that of its habitat, due to eco-physiological reasons.

A prominent example of animal colouration as an eco-physiological solution is that of those species whose colour differs greatly from that of their environment, leading researchers to carry out in-depth studies and to an eco-physiological explanation (see, e.g., the black Bedouin goat [65]; and the ladybird beetle [33]).

Physics and physiology of radiation/energy

In physics radiation and energy are one and the same, with energy taking many forms, such as light, heat and electromagnetic waves [66]. In biology, there is an existential importance to energy which, as a component of the environment, is transferred between the environment and the organism, also by means of radiation [67]. That is: there is a relationship between the animal and its environment, of which radiation and energy exchange are a part.

Despite the claims of misconception regarding the perceptible and imperceptible colours, in connection with their contribution to energy exchange between animals and their environment [68], colour reflectance in an animal should be examined in accordance with the environmental reflection, as an eco-physiological component in the matching of the animal to its environment, apparently as part of the law of conservation of energy [69]. It is thus also necessary to determine the energy savings or at least energy balance [70], as well as when the animal's colour differs from that of its environment, as in the Bedouin goat [65] and in desert arthropods [71].

Light waves that the environment and the animals reflect as colour

In order to examine the expected physiological advantage for the animal from reflecting the same light waves as those radiating from the environment, as this study asks eco-physiologists to do, it is necessary to engage with the issue of the light waves projected by the environment, and with the fact that animals do not absorb them but, rather, reflect them back to the environment.

The physical explanation of the seeming camouflage, derives from the following characteristics: the environment absorbs various light waves (electro-magnetic), with the "colour" of the environment being that of those same light waves that are not absorbed but, rather, reflected, emitted from the environment and reaching our eyes. If the light rays that reach our eyes lie within our spectrum of "the visible", we discern their "colours" [72]. However, if these rays that we discern are emitted from an animal and integrate with those emitted by the environment, it is customary to say that "the animal is camouflaged in its environment".

Thus, for example in the desert, the sand reflects light waves of the yellow colour and so too are the light waves reflected by the camel. In icebergs and snow the substrate reflects light waves perceived as white and so even the light waves reflected from the body of a Polar bear in the Arctic present it as white. In the forest the dominating colours are a mixture of dark shades and light ones, and so too are the light waves reflected from the coat of the leopard. The grasshopper too, dwelling among the leaves that emit a green reflection, emits the same green colour.

Animals received the ability to permanently adapt or temporarily change their color to match the background colors of the environment in the same evolutionary process in which plants and animals developed every other ability.

Over the course of time such abilities were also perfected by mutations, of which those that best fit the environmental conditions tended to survive [73–75]. Regarding animals whose body color pattern is fixed or changing, it can be assumed that evolution "chose" the color they are born in and that the color may change until they reach maturity and, if required, also later. The animals, however, are not required to mentally/cognitively identify the characteristics of the colors in their habitat. Rather, sensors (senses) on their bodies detect these (color sensors and/or energy sensors, temperature sensors, etc.) and the animal's color changes accordingly. Using a variety of senses, other animals can recognize an animal that has the color of the environment [12,76]. The call at the end of this article to conduct research on the subject also refers to the expansion of studies on the evolution and sense directions.

This article contends that when we find that the animal "covers itself" in the colors of the environment, in most cases the reason for this is not for camouflage (biotic reason) but for an eco-physiological reason (an abiotic reason). However the understanding of the animal's color patterns is not yet complete and it is clear that some of these patterns are intended for internal use (eco-physiological) while others relate to the environment—the biotic environment (e.g., visual communication between animals), and yet others may refer to the physical environment (avoidance of creating changes in its stability). An example of the latter is that of Ectotherm insects that rely on color for thermoregulation [77].

Moreover, due to the trade-off problem—between the animal and its environment [78] the issue of eco-physiology is complex and the mutual effects are not always completely clear. Since the contention of the present article is that the reflection of environmental colours in animals in nature is mainly an a-biotic (eco-physiological) solution and not biotic (camouflage) one, it is consequently proposed that eco-physiology researchers will examine different a-biotic environments, based on the different colour projections they emit, and thereby determine the energetic advantage to the animal that reflects the same light waves.

3.2 Argument B—Predator and prey identify one another

The pair "predator-prey" is a "pair" from the evolutionary perspective and cannot be separated from one another by a temporary mechanism such as camouflage. I term camouflage a "temporary mechanism" because it perhaps seems to be useful during the first few encounters between the two (See different examples of how predators "learned to see cryptic forms" [79]). However, camouflage cannot be an answer in the life history of an animal, in which the predator knows the prey and the prey knows the predator [80,81]. Indeed, in over 50 years of study of a "camouflaged" animal, no proof has ever been provided that the predator failed because the prey was camouflaged (the famous case of the peppered moth and industrial melanism [33]).

The predator is experienced in finding a suitable diet, making the seeming camouflage meaningless from its perspective. My contention is that detecting the prey is performed by means of skillful identification, including familiarity with a large variety of its characteristics (see the use of smell or vision, the five main steps and the importance of the ecology-in predator-prey interactions [76] introduction and the functional trait approach [82] and not only through differentiating between these and other colours. In other words, there exist different mechanisms in the evolutionary pair of "predator-prey" that prevent one from preying and the other from being preyed upon; and when one of these "partners" is unfit from the point of view of the functioning of these mechanisms, that is the moment when, biologically, it must pay the price.

Thus, the assumption that camouflage is indeed a mechanism linking the "cunning" (the camouflaged) and the "foolish" (the other individual) or between the "decorated" and the "cannot distinguish details", is an approach that should be rejected out of hand. In other words, we need to relate more seriously to the detection ability of the predator and the alertness to detection of the prey. It is incumbent upon us to make a greater effort to uncover and understand the more complex mechanisms and factors determining the predator's success/failure as well as those of the potential prey, and not merely to remain satisfied with the argument of "camouflage".

Note: I do not wish to be drawn into the claim that if the "camouflage" of the prey does not serve to protect against the predator specialising in that prey, it at least, serves to protect against the generalist predators [83]. It is hard to accept that despite the cost of "camouflage", its entire role is solely to avoid an animal that does not specialise. If this was so, the generalists, the "non-specialists", would be satisfied by eating the "non-camouflaged", but no more than that required for their existence and, in any case, not all the "non-camouflaged" would be preyed upon—so why the camouflage? In other words, this mechanism too, of a relationship between "non-specialist" and "non-camouflaged" would reach equilibrium over the course of evolution without the need for "camouflaged" (on the equilibrium between generalist predators and prey [84]; and for predation equations by generalist predators [85].

3.3 Argument C—"Camouflage" and the anthropocentric effect

It is an anthropocentric error to relate to such a great extent to the visual acuity of animals when, for example, applauding the ability of the pigeon to detect a seed from a great height, while at the same time relating so little to the visual acuity of

Arctic rodents when they need to identify a snow fox approaching against a background of the sky.

In situations of contradiction, an individual usually prefers her/his own perception [86] and humanizes nature (the moon smiles at me, the elephant loves me, the chameleon is worried about me) and so on, from film to photography and the new media, Anthropocentrism is the dominant worldview [86].

It is possible that the anthropocentric effect also influences our understanding of the colour projected by animals, and thus our enthusiasm for the fascinating concept of "camouflage", despite our own ability to distinguish a Polar bear walking on the ice several kilometres away; a camel lying on the desert sand; and a chameleon walking along a leafy branch.

Researchers of dogs [87], dolphins [88] and many other animals [86,89] have already demonstrated the characteristics of the anthropocentric and anthropomorphic effect [90] and, consequently, we need to take this into consideration and assign less importance to its effect when setting out tore-examine the reflection of colour of the environment in animals, and adopt the a-biotic, eco-physiological approach, in order to more correctly understand colouration in animals.

4. Conclusions

"It is known in a general way that the patterns and forms of animals are similar to their background" [15]. The present study suggests negating the idea of abroad existence of camouflage colour in nature, and seeks instead to ask researchers to search for another reason for the animal resembling its environment in colouration—as an "ecological morph" [91], i.e., it emits light waves like those emitted by its environment and thus possesses colour patterns similar to those of the environment.

Following the three arguments presented in this study—that projection of the colour by the animal is linked to its eco-physiology; that the predator and prey constitute an "evolutionary pair" and consequently know how to identify one another and that the limitations imposed by anthropocentrism influence the discussion on the existence of colour camouflage in nature—the present article suggests that the physiological aspect should be examined as a possible explanation of the fact that the colouration of many animals resembles that of the background of their habitat.

According to the "**eco-physiology approach" to explaining an animal's colour**, it is beneficial for the animal to emit the same light wavelengths as those that its environment emits. Accordingly, a nocturnal animal benefits from being dark coloured for eco-physiological reasons. I do not contend that "nocturnal animals benefit from appearing as dark-coloured", as the eco-physiological approach to the issue of animal colouration does not locate the visual system of the "watcher" (predator or prey) as an evolutionary factor in determining these animals' colour. Rather, it is **the animals' physiological needs** that have evolutionarily **shaped their colours in nature**; and apparently, in particular, the physiology of conserving energy.

In other words, if only one single species of animal (vertebrate or invertebrate) existed in the world—for example, the camel—as a result of a-biotic conditions, i.e., eco-physiological ones, its colour would be the colour of the desert sand, reflecting the shade of yellow so familiar to us.

This article constitutes a sort of "call for submissions" for eco-physiology researchers to focus their studies on the a-biotic approach as a distinct field of research, whose title is "Projection of the colour of their environment by animals". Such studies will greatly contribute on the one hand to refuting the "biotic, ethological approach" that claims the widespread existence of "colour camouflage in nature"; and on the other hand, they will further illuminate the great importance of light wave emissions from the animal's body as an eco-physiological component contributing to the animal's survival.

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Data Availability statement

Data not available- Mendelssohn, H. 1974

References

[1] The History of Animals [Internet]. [cited 2024 Mar 19]. Available from: http://classics.mit.edu/Aristotle/history_anim.mb.txt

[2] Parker, S., 2021. Camouflage: 100 masters of disguise from the animal kingdom. Ivy Press: Brighton.

[3] Zoonomia, or, The Laws of Organic Life [Internet]. [cited 2024 Mar 19]. Available from: http://darwin-online.org.uk/converted/pdf/1794_Zoonomia_A967.1.pdf

[4] Darwin, C., 1872. The origin of species with introduction, notes and illustrations. P.F. Collier & Son Press: New York.

[5] Thayer, G.H., 1909. Concealing-Coloration in the Animal Kingdom. Macmillan Publishers: New York.

[6] Cott, H.B., 1957. Adaptive coloration in animals. Methuen & Co Ltd: London.

[7] Owen, D., 1982. Camouflage and mimicry. University of Chicago Press: Chicago.

[8] Tildes, P.L., 2020. Animals in camouflage. Charlesbridge Pub.: Watertown.

[9] Osorio, D., Cuthill, I., 2015. Camouflage and perceptual organization in the animal kingdom. The Oxford handbook of perceptual organization. Oxford University Press: Oxford. pp. 843–862. DOI:https://doi.org/10.1093/oxfordhb/9780199686858.013.044

[10] Endler, J.A., Mappes, J., 2017. The current and future state of animal coloration research. Philosophical Transactions of the Royal Society B: Biological Sciences. 372(1724), 20160352. DOI:http://dx.doi.org/10.1098/rstb.2016.0352

[11] Hughes, A., Liggins, E., Stevens, M., 2019. Imperfect camouflage: how to hide in a variable world?. Proceedings of the Royal Society B. 286(1902), 20190646. DOI:http://dx.doi.org/10.1098/rspb.2019.0646

[12] Galloway, J.A., Green, S.D., Stevens, M., et al., 2020. Finding a signal hidden among noise: How can predators overcome camouflage strategies?. Philosophical Transactions of the Royal Society B. 375(1802), 20190478. DOI:http://doi.org/10.1098/rstb.2019.0478

[13] Merilaita, S., 2003. Visual background complexity facilitates the evolution of camouflage. Evolution. 57(6), 1248–1254. DOI:https://doi.org/10.1111/j.0014-3820.2003.tb00333.x

[14] Kácha, P., Petr, V., 1995. Camouflage and mimicry in fossils I: general part. Acta Musei nationalis Pragae, Series B–Historia Naturalis. 51(1–4), 53–82.

[15] Endler, J.A., 1978. A predator's view of animal color patterns. Evolutionary Biology. Springer: Boston. pp. 319–364. DOI:https://doi.org/10.1007/978-1-4615-6956-5_5

[16] Merilaita, S., Lyytinen, A., Mappes, J., 2001. Selection for cryptic coloration in a visually heterogeneous habitat. Proceedings of the Royal Society of London. Series B: Biological Sciences. 268(1479), 1925–1929. DOI:https://doi.org/10.1098/rspb.2001.1747

[17] Lev-Yadun, S., Dafni, A., Flaishman, M.A., et al., 2004. Plant coloration undermines herbivorous insect camouflage. BioEssays. 26(10), 1126–1130. DOI:https://doi.org/10.1002/bies.20112

[18] Dawkins, R., Krebs, J.R., 1979. Arms races between and within species. Proceedings of the Royal Society of London. Series B. Biological Sciences. 205(1161), 489–511. DOI:http://doi.org/10.1098/rspb.1979.0081

[19] Humphreys, R.K., Ruxton, G.D., 2020. The dicey dinner dilemma: Asymmetry in predator–prey risk-taking, a broadly applicable alter-

native to the life-dinner principle. Journal of Evolutionary Biology. 33(3), 377–383. DOI:https://doi.org/10.1111/jeb.13585

[20] Schmidt-Nielsen, K., 1997. Animal physiology: Adaptation and environment. Cambridge University Press: Cambridge.

[21] Mendelssohn, H. 1974. Adaptation of animals to live in deserts. Symposium Israel – France: Ecological research on developing of arid zones (Mediterranean deserts) with winter precipitation, 39: 181- 191.

[22] Hamilton, W.J., 1973. Life's color code. McGrew-Hill: New York.

[23] Pearson, O.P., 1977. The effect of substrate and of skin color on thermoregulation of a lizard. Comparative Biochemistry and Physiology Part A: Physiology. 58(4), 353–358. DOI:https://doi.org/10.1016/0300-9629(77)90154-2

[24] Campbell, M.D., Schoeman, D.S., Venables, W., et al., 2021. Testing Bergmann's rule in marine copepods. Ecography. 44(9), 1283–1295. DOI:https://doi.org/10.1111/ecog.05545

[25] Nudds, R.L., Oswald, S.A., 2007. An interspecific test of Allen's rule: Evolutionary implications for endothermic species. Evolution. 61(12), 2839–2848. DOI:https://doi.org/10.1111/j.1558-5646.2007.00242.x

[26] Ryding, S., Klaassen, M., Tattersall, G.J., et al., 2021. Shape-shifting: Changing animal morphologies as a response to climatic warming. Trends in Ecology & Evolution. 36(11), 1036–1048. DOI:https://doi.org/10.1016/j.tree.2021.07.006

[27] Delhey, K., 2019. A review of Gloger's rule, an ecogeographical rule of colour: Definitions, interpretations and evidence. Biological Reviews. 94(4), 1294–1316. DOI:https://doi.org/10.1111/brv.12503

[28] Delhey, K., Dale, J., Valcu, M., et al., 2019. Reconciling ecogeographical rules: Rainfall and temperature predict global colour variation in the largest bird radiation. Ecology Letters. 22(4), 726–736. DOI:https://doi.org/10.1111/ele.13233

[29] Hanlon, R.T., Chiao, C.C., Mäthger, L.M., et al., 2011. Rapid adaptive camouflage in cephalopods. Animal camouflage: Mechanisms and functions. Cambridge University Press: Cambridge. DOI:https://doi.org/10.1017/CBO9780511852053.009

[30] Guidetti, G., Levy, G., Matzeu, G., et al., 2021. Unmixing octopus camouflage by multispectral mapping of Octopus bimaculoides' chromatic elements. Nanophotonics. 10(9), 2441–2450. DOI:https://doi.org/10.1515/nanoph- 2021-0102

[31] Hadjisolomou, S.P., El-Haddad, R.W., Kloskowski, K., 2021. Quantifying the speed of chromatophore activity at the single-organ level in response to a visual startle stimulus in living, intact squid. Frontiers in Physiology. 12, 675252. DOI:https://doi.org/10.3389/fphys.2021.675252

[32] Allen, J.J., Akkaynak, D., Schnell, A.K., et al., 2017. Dramatic fighting by male cuttlefish for a female mate. The American Naturalist. 190(1), 144–151. DOI:https://doi.org/10.1086/692009

[33] Second Thoughts about Peppered Moths. This Classical Story of Evolution by Natural Selection Needs Revising [Internet]. [cited 2024 Mar 19]. Available from: https://www.discovery.org/a/590/

[34] Majerus, M.E.N., 1998. Melanism: Evolution in action. Oxford University Press: Oxford.

[35] Mallet, J., 2004. The peppered moth: A black and white story after all. Genetics Society News. 50, 34–38.https://www.ucl.ac.uk/taxome/jim/pap/malletgensoc03.pdf

[36] Walton, O.C., Stevens, M., 2018. Avian vision models and field experiments determine the survival value of peppered moth camouflage. Communications Biology. 1, 118.

DOI:https://doi.org/10.1038/s42003-018-0126-3

[37] Stavenga, D.G., Wallace, J.R., 2020. Bogong moths are well camouflaged by effectively decolourized wing scales. Frontiers in Physiology. 11, 95.
DOI:https://doi.org/10.3389/fphys.2020.00095

[38] Hsiung, B.K., Shawkey, M.D., Blackledge, T.A., 2019. Color production mechanisms in spiders. The Journal of Arachnology. 47(2), 165–180.
DOI:https://doi.org/10.1636/JoA-S-18-022

[39] Chittka, L., 2001. Camouflage of predatory crab spiders on flowers and the colour perception of bees (Aranida: Thomisidae/Hymenoptera: Apidae). Entomologia Generalis. 25(3), 181–187.
DOI:https://doi.org/10.1127/entom.gen/25/2001/181

[40] Eberhard, W., 2003. Substitution of silk stabilimenta for egg sacs by Allocyclosa bifurca (Araneae: Araneidae) suggests that silk stabilimenta function as camouflage devices. Behaviour. 140(7), 847–868.
DOI:https://doi.org/10.1163/156853903770238346

[41] Théry, M., Casas, J., 2009. The multiple disguises of spiders: Web colour and decorations, body colour and movement. Philosophical Transactions of the Royal Society B: Biological Sciences. 364(1516), 471–480.
DOI:https://doi.org/10.1098/rstb.2008.0212

[42] Figon, F., Casas, J., 2018. Morphological and physiological colour changes in the animal kingdom. eLS. John Wiley & Sons, Ltd: Chichester.
DOI:https://doi.org/10.1002/9780470015902.a0028065

[43] Heiling, A.M., Chittka, L., Cheng, K., et al., 2005. Colouration in crab spiders: substrate choice and prey attraction. Journal of Experimental Biology. 208(10), 1785–1792.
DOI:https://doi.org/10.1242/jeb.01585

[44] Ryer, C.H., Lemke, J.L., Boersma, K., et al., 2008. Adaptive coloration, behavior and predation vulnerability in three juvenile north Pacific flatfishes. Journal of Experimental Marine Biology and Ecology. 359(1), 62–66.
DOI:https://doi.org/10.1016/j.jembe.2008.02.017

[45] Spinner, M., Kortmann, M., Traini, C., et al., 2016. Key role of scale morphology in flatfishes (Pleuronectiformes) in the ability to keep sand. Scientific Reports. 6, 26308.
DOI:https://doi.org/10.1038/srep26308

[46] Vinagre, C., França, S., Cabral, H.N., 2006. Diel and semi-lunar patterns in the use of an intertidal mudflat by juveniles of Senegal sole, *Solea senegalensis*. Estuarine, Coastal and Shelf Science. 69(1–2), 246–254.
DOI:https://doi.org/10.1016/j.ecss.2006.04.017

[47] Maia, A., Vinagre, C., Cabral, H.N., 2009. Impact of a predator in the foraging behaviour of *Solea senegalensis*. Journal of the Marine Biological Association of the United Kingdom. 89(3), 645–649.
DOI:https://doi.org/10.1017/S002531540800266X

[48] Stuart-Fox, D., Moussalli, A., 2008. Selection for social signalling drives the evolution of chameleon colour change. PLoS Biology. 6(1), e25.
DOI:https://doi.org/10.1371/journal.pbio.0060025

[49] Keren-Rotem, T., Levy, N., Wolf, L., et al., 2016. Male preference for sexual signalling over crypsis is associated with alternative mating tactics. Animal Behaviour. 117, 43–49.
DOI:https://doi.org/10.1016/j.anbehav.2016.04.021

[50] Stuart-Fox, D., Moussalli, A., 2009. Camouflage, communication and thermoregulation: Lessons from colour changing organisms. Philosophical Transactions of the Royal Society B: Biological Sciences. 364(1516), 463–470.
DOI:https://doi.org/10.1098/rstb.2008.0254

[51] There's No Hiding This Camouflage. Chameleons Change Color to Stick out, not to Disappear [Internet]. Science. [cited 2024 Mar 19].

Available from: https://www.science.org/content/article/theres-no-hiding-camouflage

[52] Best, R.C., 1985. Digestibility of ringed seals by the polar bear. Canadian Journal of Zoology. 63(5), 1033–1036. DOI:https://doi.org/10.1139/z85-155

[53] Smith, T.G., 1980. Polar bear predation of ringed and bearded seals in the land-fast sea ice habitat. Canadian Journal of Zoology. 58(12), 2201–2209. DOI:https://doi.org/10.1139/z80-302

[54] Chinery M.1990. Predators- Killers of the wild, strategies and techniques of predation in the natural world. Bedford Editions, London, UK, 224p.

[55] Khattab, M.Q., Tributsch, H., 2015. Fibre-optical light scattering technology in polar bear hair: A re-evaluation and new results. Journal of Advanced Biotechnology and Bioengineering. 3(2), 38–51.

[56] Jia, H., Guo, J., Zhu, J., 2017. Comparison of the photo-thermal energy conversion behavior of polar bear hair and wool of sheep. Journal of Bionic Engineering. 14, 616–621. DOI:https://doi.org/10.1016/S1672-6529(16)60427-4

[57] Frank, L.G., 1986. Social organization of the spotted hyaena (*Crocuta crocuta*). I. Demography. Animal Behaviour. 34(5), 1500–1509. DOI:https://doi.org/10.1016/S0003-3472(86)80220-2

[58] Kruuk, H., 1972. The spotted hyena: A study of predation and social behavior. The University of Chicago Press: Chicago.

[59] Sever, Z., 2005. The resemblance to the environment is not necessary for camouflage. Israel Journal of Ecology & Evolution. 51, 80.

[60] Burton, M., 1983. The new larousse Encyclopedia of Animal life. Hamylan Pub: Middlesex.

[61] Macdonald, D., 1984. The encyclopedia of mammals. Oxford University Press: Oxford.

[62] Kaczensky, P., Adiya, Y., von Wehrden, H., et al., 2014. Space and habitat use by wild Bactrian camels in the Transaltai Gobi of southern Mongolia. Biological Conservation. 169, 311–318. DOI:https://doi.org/10.1016/j.biocon.2013.11.033

[63] Camelus Dromedaries, Linnaeus, 1758 [Internet]. GBIF. [cited 2024 Mar 19]. Available from: https://www.gbif.org/species/144101237

[64] Carroll, J., Murphy, C.J., Neitz, M., et al., 2001. Photopigment basis for dichromatic color vision in the horse. Journal of Vision. 1(2). DOI:https://doi.org/10.1167/1.2.2

[65] Dmi'El, R., Prevulotzky, A., Shkolnik, A., 1980. Is a black coat in the desert a means of saving metabolic energy?. Nature. 283(5749), 761–762. DOI:https://doi.org/10.1038/283761a0

[66] Energy=Light=Radiation=Temperature [Internet]. ESA. [cited 2024 Mar 19]. Available from: https://www.esa.int/Science_Exploration/Space_Science/Energy_light_radiation_temperature

[67] Gates, D.M., 1968. Energy exchange and ecology. Bioscience. 18(2), 90–95. DOI:https://doi.org/10.2307/1294057

[68] Nussear, K.E., Simandle, E.T., Tracy, C.R., 2000. Misconceptions about colour, infrared radiation, and energy exchange between animals and their environments. Herpetological Journal. 10(3), 119–122.

[69] Conservation of Energy [Internet]. [cited 2024 Mar 19]. Available from: https://www.feynmanlectures.caltech.edu/I_04.html

[70] Porter, W.P., Gates, D.M., 1969. Thermodynamic equilibria of animals with environment. Ecological Monographs, 39(3), 227–244. DOI:https://doi.org/10.2307/1948545

[71] Hadley, N.F., 1979. Recent developments in ecophysiological research on desert arthropods. Journal of Arid Environments. 2(3), 211–218. DOI:https://doi.org/10.1016/S0140-1963(18)31772-5

[72] The Evolution of Color Vision [Internet]. The Talk Origins Archive. Available from: http://www.talkorigins.org/faqs/vision.html

[73] Tomasi, T.E., Anderson, B.N., Garland Jr, T.,

2019. Ecophysiology of mammals. Journal of Mammalogy, 100(3), 894–909.
DOI:https://doi.org/10.1093/jmammal/gyz026

[74] Feder, M.E., 2002. Plant and animal physiological ecology, comparative physiology/biochemistry, and evolutionary physiology: Opportunities for synergy: An introduction to the symposium. Integrative and Comparative Biology. 42(3), 409–414.
DOI:https://doi.org/10.1093/icb/42.3.409

[75] Ackerly, D.D., Dudley, S.A., Sultan, S.E., et al., 2000. The evolution of plant ecophysiological traits: Recent advances and future directions: New research addresses natural selection, genetic constraints, and the adaptive evolution of plant ecophysiological traits. Bioscience. 50(11), 979–995.
DOI:https://doi.org/10.1641/0006-3568(2000)050[0979:TEOPET]2.0.CO;2

[76] Fischer, S., Oberhummer, E., Cunha-Saraiva, F., et al., 2017. Smell or vision? The use of different sensory modalities in predator discrimination. Behavioral Ecology and Sociobiology. 71, 143.
DOI:https://doi.org/10.1007/s00265-017-2371-8

[77] Clusella-Trullas, S., Nielsen, M., 2020. The evolution of insect body coloration under changing climates. Current Opinion in Insect Science. 41, 25–32.
DOI:https://doi.org/10.1016/j.cois.2020.05.007

[78] Wikelski, M., 2009. Physiological ecology: Animals. The Princeton guide to ecology. Princeton University Press: Princeton.
DOI:https://doi.org/10.1515/9781400833023.14

[79] Dawkins, M., 1971. Perceptual changes in chicks: Another look at the 'search image' concept. Animal Behaviour. 19(3), 566–574.
DOI:https://doi.org/10.1016/S0003-3472(71)80113-6

[80] Crawford, B.A., Hickman, C.R., Luhring, T.M., 2012. Testing the threat-sensitive hypothesis with predator familiarity and dietary specificity. Ethology. 118(1), 41–48.
DOI:https://doi.org/10.1111/j.1439-0310.2011.01983.x

[81] Crane, A.L., Ferrari, M.C., 2017. Patterns of predator neophobia: A meta-analytic review. Proceedings of the Royal Society B: Biological Sciences. 284(1861), 20170583.
DOI:https://doi.org/10.1098/rspb.2017.0583

[82] Schmitz, O., 2017. Predator and prey functional traits: Understanding the adaptive machinery driving predator–prey interactions. F1000Research. 6, 1767.
DOI:https://doi.org/10.12688/f1000research.11813.1

[83] Symondson, W.O.C., Sunderland, K.D., Greenstone, M.H., 2002. Can generalist predators be effective biocontrol agents?. Annual Review of Entomology. 47, 561–594.
DOI:https://doi.org/10.1146/annurev.ento.47.091201.145240

[84] Hassell, M.P., May, R.M., 1986. Generalist and specialist natural enemies in insect predator-prey interactions. The Journal of Animal Ecology. 55(3), 923–940.
DOI:https://doi.org/10.2307/4425

[85] Rogers, D., 1972. Random search and insect population models. The Journal of Animal Ecology. 41(2), 369–383.
DOI:https://doi.org/10.2307/3474

[86] Creed, B., Reesink, M., 2015. Animals, images, anthropocentrism. NECSUS. European Journal of Media Studies. 4(1), 95–105.
DOI:https://doi.org/10.25969/mediarep/15174

[87] Horowitz, A., Hecht, J., 2014. Looking at dogs: Moving from anthropocentrism to canid umwelt. Domestic dog cognition and behavior: The scientific study of Canis familiaris. Springer: Berlin. pp. 201–219.
DOI:https://doi.org/https://doi.org/10.1007/978-3-642-53994-7_9

[88] White, T.I., 2013. Humans and dolphins: An exploration of anthropocentrism in applied environmental ethics. Journal of Animal Ethics. 3(1), 85–99.
DOI:https://doi.org/10.5406/janimalethics.3.

1.0085
[89] Furlong, E., Silver, Z., Furlong, J., 2018. Anthropocentrism as cognitive dissonance in animal research?. Animal Sentience. 12(11). DOI:https://doi.org/10.51291/2377-7478.1366
[90] Wynne, C.D.L., 2007. What are animals? Why anthropomorphism is still not a scientific approach to behavior. Comparative Cognition & Behavior Reviews. 2, 125–135. DOI:https://doi.org/10.3819/ccbr.2008.20008
[91] The Influence of Environment upon Coloration and Size in Tortoise Populations [Internet]. Tortoise Trust Web. [cited 2024 Mar 19]. Available from: https://www.tortoisetrust.org/articles/golden.htm