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Color Change



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Color change in animals is a taxonomically widespread type of phenotypic plasticity, in which the body coloration of an individual is altered over the course of seconds, minutes, days, seasons, or a lifetime. This within-individual change can be induced by external (e.g., social interactions) or intrinsic factors (e.g., circadian rhythms), may or may not be adaptive, and may or may not be reversible. Color change can refer to a change in the spectral reflectance of the entirety of an individual's body, only a small portion of the body surface, or anything in between, including changes in patterns or mottling of all or part of the body surface. Adaptive color change can serve a variety of functions, such as thermoregulation, communication, and camouflage. Mechanisms of color change are nearly as diverse as the types of color change themselves, illustrating a diversity of evolutionary strategies converging to achieve similar goals. Color change can influence the persistence of animal populations in an increasingly anthropogenically altered world by differentially affecting key life functions, including predator avoidance, thermoregulation, and mate attraction, in human-altered habitats.

Types of Color Change

Animal color change can be broadly grouped into two categories: morphological and physiological. Both morphological and physiological color change rely on a diversity of pigment cells (chromatophores), particularly in ectotherms. Chromatophores include melanophores (brown or black pigment), xanthophores (yellow), erythrophores (red/orange), and iridophores (iridescent), among others. Blue and some green colors in animals are typically produced structurally (e.g., via diffraction gratings or crystal fibers). Some animal colors are produced by a combination of pigments and structural colors.

Morphological (chromogenic) color changes are driven by the creation or degradation of pigments and the number or type of chromatophores, which effectively alter pigment concentration in the skin. Morphological color change can be reversible or irreversible. Long-term cyclic changes, such as seasonal increases in melanin that permit improved solar heat absorption in snakes during colder months, are common examples of morphological color change. Most ontogenetic color changes, which occur as individuals age, are also examples of morphological color change, though these tend to be irreversible changes associated with accruing sexual coloration or altering coloration to maximize camouflage from juvenile to adult habitats.

Physiological (chromomotor) color changes occur much more rapidly, in seconds to minutes, and are typically driven by the dispersal and reaggregation of pigments in chromatophores or by rapid changes in the orientation and consequently the light reflectance of crystalline plates. Mechanisms of physiological color changes have been well studied in lizards. The rapid dispersal of melanin following stressful social encounters in many *Anolis* lizards produces a color change from green to brown within seconds (Greenberg 2002). The structural colors of *Urosaurus* lizards likewise change rapidly: reducing the spacing between adjacent iridosomes decreases long-wavelength radiation scattering, which increases “blueness” of abdominal tissue with temperature (Morrison et al. 1996).

A third class of animal color change could be considered behavioral, as it relies on the choice of an individual to utilize substances to alter its coloration. Greater flamingos, for instance, produce carotenoid-rich oily secretions that are actively spread over their plumage as “makeup” during mating seasons (Amat et al. 2011), and bearded vultures stain their plumage with iron oxide from soil, likely to advertise dominance (Negro et al. 1999). Though mechanistically distinct, these behaviorally driven color changes appear to serve similar roles in species’ ecologies as do morphological and physiological color changes.

Functions of Color Change

Color change can provide a wide variety of adaptive functions. Though not all color change is adaptive (e.g., color change induced by pathogen or parasite infection), color change can serve innumerable beneficial roles related to survival and reproduction across animal taxa. Change in color, brightness, and pattern of an animal’s body surface is widely used for predator avoidance. The circadian rhythm-driven color change of horned ghost crabs evolved to optimize background matching in both day and night lighting conditions. Many cephalopods rapidly alter their coloration and pattern to provide maximum concealment via either background matching or

disruptive coloration to mask their body outline, depending on the substrate. Predation pressure is not the only force selecting for camouflage-related color change; crab spiders utilize color change to conceal themselves within inflorescences of variable colors to deceive their prey (Anderson and Dodson 2015). In lieu of camouflage, some species use color change to deceive predators or prey via mimicry: for example, the dusky dotyback (*Pseudochromis fuscus*) can alter its coloration to mimic that of surrounding schooling fish and thereby increase prey capture success while simultaneously reducing detection by its own predators (Cortesi et al. 2015).

A variety of species exhibit body coloration changes over maturation. Juveniles of some lizard species bear bright tails to direct predator attacks to a more expendable body region, whereas adults lose bright tail coloration as their activity patterns and habitat use (and concomitant selective pressures) change with maturity. Ontogenetic color change can also be used as a strategy to avoid mating harassment. Some female damselfishes (*Ischnura senegalensis*) use immature-specific coloration to deter costly male attention, wearing “mature” colors only at sexual maturation (Takahashi et al. 2012).

Short-term alterations in social state are often conveyed by reversible changes in color. Chameleons, a lizard group popularly recognized for their color-changing abilities, rapidly darken their skin to communicate subordination in male-male contests or heighten conspicuous coloration during courtship and male combat (Stuart-Fox and Moussalli 2008). Male cichlids (*Astatotilapia burtoni*) alternate among blue, yellow, and cryptic color morphs depending on hormone concentrations associated with success in agonistic encounters (Korzan et al. 2008). Other social functions of color change include, but are not limited to, seasonal mate advertisement, mating or parental status, and honest indicators of quality or parental ability. Due to the speed and reversibility of physiological color change, many of these messages are conveyed to conspecifics in real time.

Color change is also widely used to protect individuals from abiotic pressures. One important abiotic selective pressure driving color change

is solar irradiation. Many species evolved color change as a protective mechanism against excessive heat absorption (in which colors tend to lighten to maximize reflectance) and to permit more rapid warming in cooler temperatures (in which colors tend to darken). For example, some *Uca* fiddler crabs adjust carapace brightness depending on temperature as a thermoregulatory mechanism. Photoprotection is another abiotic driver of color change. Some species, such as the Kerry spotted slug (*Geomalacus maculosus*), increase melanization in response to ultraviolet light exposure to reduce the risks associated with ultraviolet radiation (O’Hanlon et al. 2017).

Color-changing species may experience conflicting color optima, particularly in species in which coloration is used both for crypsis and communication. In the western rainbow fish (*Melanotaenia australis*), subordinate males that darken their body coloration for substrate matching subsequently experience greater attacks from dominant male conspecifics, as increased melanization is also used to communicate dominance in this species (Kelley et al. 2016).

Despite its advantages, the ability to change color can also be physiologically costly. Pigments are either derived from the environment (e.g., carotenoid pigments obtained from food) or synthesized directly (e.g., melanin), either method involving energy expenditure. For example, guppies induced to change color require greater food intake compared to those not induced to change color (Rodgers et al. 2013). In addition, some pigments required for color change are also used for other vital functions, namely immunity, exacting a potentially costly trade-off.

Animal Coloration and Global Change

How global change interacts with animal color change will increasingly become a focus for investigation. Though color change can provide individuals with the ability to respond to natural abiotic and social changes in their habitats, if and the extent to which color change enables species to cope with anthropogenic stressors is unclear. New evidence suggests that some

color-changing species may fare particularly poorly due to mismatch with current climate patterns. The white-brown springtime fur transition of snowshoe hares (Zimova et al. 2016) is now asynchronous with the current timing of the seasonal melting of snowpacks and has demonstrable fitness costs; these observations are likely repeatable in species that similarly evolved seasonal snow-related camouflage. With increasing average global temperatures, species that use color change for thermoregulation may likewise experience costs. Body color lightening in lizards for thermoregulatory purposes can conflict with body color darkening for camouflage, leading to a sub-optimal balance between thermoregulation and predator avoidance as habitats warm globally. When body color lightening is a sexually selected trait used primarily during courtship, as it is in *Uca* male fiddler crabs that temporarily lighten their carapaces during mating displays, natural selection for lighter carapaces for thermoregulatory benefits in a warming world could reduce the strength of sexual selection for lighter carapaces, with unknown population-level consequences. Anthropogenic stress can also strongly affect color-changing sexual signals, as illustrated by the duller sexual colors of European tree frogs following exposure to traffic noise (Troianowski et al. 2017).

Cross-References

- ▶ [Camouflage](#)
- ▶ [Communication](#)
- ▶ [Cryptic Coloration](#)
- ▶ [Disruptive Coloration](#)
- ▶ [Intersexual Selection](#)
- ▶ [Intrasexual Selection](#)
- ▶ [Thermoregulation](#)

References

- Amat, J. A., Rendón, M. A., Garrido-Fernández, J., Garrido, A., Rendón-Martos, M., & Pérez-Gálvez, A. (2011). Greater flamingos *Phoenicopterus roseus* use uropygial secretions as make-up. *Behavioral Ecology and Sociobiology*, 65, 665–673.

- Anderson, A. G., & Dodson, G. N. (2015). Colour change ability and its effect on prey capture success in female *Misumenoides formosipes* crab spiders. *Ecological Entomology*, *40*, 106–113.
- Cortesi, F., Feeney, W. E., Ferrari, M. C. O., Waldie, P. A., Phillips, G. A. C., McClure, E. C., Sköld, H. N., Salzburger, W., Marshall, N. J., & Cheney, K. L. (2015). Phenotypic plasticity confers multiple fitness benefits to a mimic. *Current Biology*, *25*, 949–954.
- Greenberg, N. (2002). Ethological aspects of stress in a model lizard, *Anolis carolinensis*. *Integrative and Comparative Biology*, *42*, 526–540.
- Kelley, J. L., Rodgers, G. M., & Morrell, L. J. (2016). Conflict between background matching and social signalling in a colour-changing freshwater fish. *Royal Society Open Science*, *3*, 160040.
- Korzan, W. J., Robison, R. R., Zhao, S., & Fernald, R. D. (2008). Color change as a potential behavioral strategy. *Hormones and Behavior*, *54*, 463–470.
- Morrison, R. L., Sherbrooke, W. C., & Frost-Mason, S. K. (1996). Temperature-sensitive, physiologically active iridophores in the lizard *Urosaurus ornatus*: An ultrastructural analysis of color change. *Copeia*, *1996*, 804–812.
- Negro, J. J., Margalida, A., Hiraldo, F., & Heredia, R. (1999). The function of the cosmetic coloration of bearded vultures: When art imitates life. *Animal Behaviour*, *58*, F14–F17.
- O'Hanlon, A., Feeney, K., Dockery, P., & Gormally, M. J. (2017). Quantifying phenotype-environment matching in the protected Kerry spotted slug (Mollusca: Gastropoda) using digital photography: Exposure to UV radiation determines cryptic colour morphs. *Frontiers in Zoology*, *14*, 35.
- Rodgers, G. M., Gladman, N. W., Corless, H. F., & Morrell, L. J. (2013). Costs of colour change in fish: Food intake and behavioural decisions. *Journal of Experimental Biology*, *216*, 2760–2767.
- Stuart-Fox, D., & Moussalli, A. (2008). Selection for social signalling drives the evolution of chameleon colour change. *PLoS Biology*, *6*, e25.
- Takahashi, Y., Morimoto, G., & Watanabe, M. (2012). Ontogenetic colour change in females as a function of antiharassment strategy. *Animal Behaviour*, *84*, 685–692.
- Troianowski, M., Mondy, N., Dumet, A., Arcanjo, C., & Lengagne, T. (2017). Effects of traffic noise on tree frog stress levels, immunity and color signaling. *Conservation Biology*, *31*, 1132–1140.
- Zimova, M., Mills, L. S., & Nowak, J. J. (2016). High fitness costs of climate change induced camouflage mismatch in a seasonally colour moulting mammal. *Ecology Letters*, *19*, 299–307.