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Trends in Parasitology

Opinion

Colorful parasites: an overlooked frontier in animal coloration research

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The diverse coloration of animals has fascinated researchers over the past centuries. A growing body of evidence has documented the many functions of animal coloration, ranging from mate attraction to predator avoidance. Yet, the adaptive functions of parasite coloration have been largely neglected in this context, despite the fact that many parasites across diverse taxonomic groups exhibit colorful body patterns. In this opinion article, we discuss the potential adaptive functions of color in parasites. We first summarize some potential functions of parasite coloration based on an intensive review of the existing literature. We then propose several possible ecological, evolutionary, and biogeographical hypotheses regarding patterns in parasite coloration and outline future directions for this intriguing study frontier.

Highlights

Research on animal coloration has become a dynamic and growing study area, yet parasites have been largely neglected in this context.

Contrary to the common assumption, macroparasites exhibit diverse color patterns, many of which may have adaptive functions such as camouflage and mimicry. Similar to the coloration of free-living organisms, both biological factors (e.g., predation pressure from cleaners and hosts) and environmental factors (e.g., UV exposure) may play important roles in driving and maintaining coloration patterns in parasites.

Understanding the selective pressures and resulting functions of parasite coloration can lead to new insights, such as identifying the underlying drivers of macroecological patterns in coloration.

We call for more studies to quantify and describe parasite coloration patterns and to test their functions.

Animal coloration studies: are parasites left behind?

Nature is colorful: wherever you go in the natural world, you can see the diversity of colors in animals. Most people know from documentaries or personal experience that birds, amphibians, and butterflies living in tropical forests have very colorful bodies. When you dive into the ocean, especially on tropical coral reefs, you are invariably amazed by the many types of colorful fishes. Rather than being bright, the coloration of some animals, such as insects, matches that of the background on which they live, helping them blend into the landscape. Over the past centuries, the diversity of animal coloration has attracted the interest of many leading naturalists (e.g., [1]), and a wide range of researchers, from evolutionary biologists to engineering scientists, have actively investigated the mechanistic underpinnings and functions of animal coloration [2–8]. Indeed, diverse animals have evolved coloration in many ecological contexts over a long evolutionary history. For instance, animals with conspicuous coloration often use it to warn predators that they are poisonous (**aposematism**, see Glossary) or to attract individuals of the opposite sex. Animals often mimic the coloration of the background on which they live to blend into the environment and avoid detection (**camouflage**). These adaptive functions of animal coloration have been well documented and summarized in previous reviews [2–8].

Despite the fact that many studies have explored the adaptive functions of animal coloration, very few studies have focused on parasitic organisms (Figure 1). Yet, parasites have often been considered in the context of animal coloration studies, but almost always only as factors affecting host coloration in the context of sexual selection (Figure 1). This research question has been particularly prominent since the proposal of the Hamilton–Zuk hypothesis [9], which argued that bright colors in animals, especially in males, are an 'honest signal' to attract females because bright coloration indicates high-quality immune systems and disease resistance [9] (Figure 1). In contrast, studies on parasite coloration itself remain extremely limited (Figure 1). This may be because the body coloration of parasites is almost universally assumed to be dull and without function, as parasites are very small and cryptic. However, parasites do

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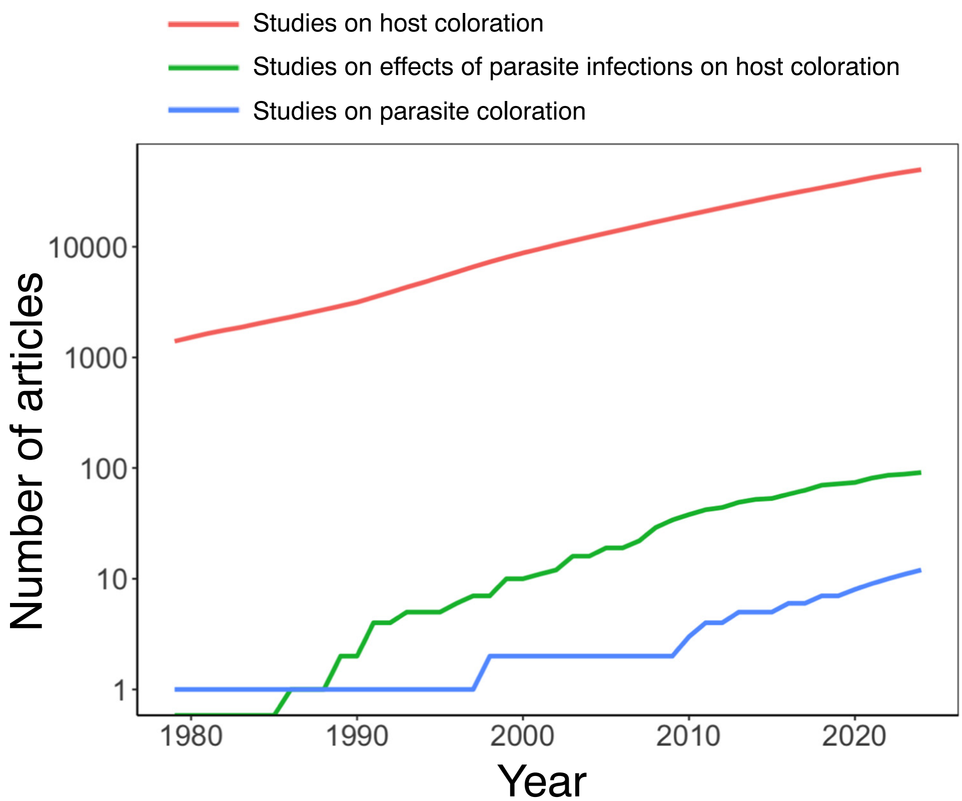

Figure 1. Historical overview of research on animal coloration including parasites. Cumulative number of articles on animal coloration published since 1980. Data were obtained from a search of Web of Science in August 2025, using the search string ('animal*' OR 'vertebrate*' OR 'invertebrate*') AND ('colour*' OR 'color*' OR 'background-matching' OR 'camouflage*' OR 'mimic*' OR 'aposemat*' OR 'masquerad*' OR 'countershading' OR 'crypsis') in the first instance. The same string was then used with additional terms about parasites ('parasit*' OR 'macroparasit*' OR 'ectoparasit*' OR 'endoparasit*' OR 'endohelminth*' OR 'helminth*' OR 'digenea*' OR 'trematod*' OR 'nematod*' OR 'cestod*' OR 'tapeworm*' OR 'acanthocephala*' OR 'monogenea*' OR 'lice' OR 'louse' OR 'glochid*' OR 'leech*' OR 'copepod*' OR 'tick*' OR 'flea*' OR 'mite*' OR 'isopod*'). Publications retrieved by the first search are represented by the red line, whereas those from the second search were categorized into either 'Studies on effects of parasite infections on host coloration' (green line) or 'Studies on parasite coloration' (blue line), based on screening their title and abstract. Note the logarithmic scale on the *y*-axis; numbers of articles published before the 1980s were summed due to their small number.

show considerable variation in their body coloration (Figure 2). In this opinion article, we first summarize the potential adaptive functions of parasite coloration, drawing on the limited existing evidence and hypotheses. Then, we propose several conceptual frameworks and unanswered (or even unasked) questions to encourage future study in this emerging research frontier.

Adaptive functions of parasite coloration: hypotheses and evidence

In many cases, the color of parasites may simply be a nonadaptive byproduct. For example, in the total darkness of the gastrointestinal tract of vertebrates, any coloration shown by helminths serves no possible function in signaling and communication. Instead, it may simply reflect the presence of pigments in the host's food that are absorbed by the parasite [10–12]. In what follows, we focus on situations where the body coloration of parasites may have an adaptive role and where some studies indicate and show such evidence.

Glossary

Aggressive mimicry: a strategy in which organisms resemble a harmless model (e.g., their prey), which entice their prey to approach them and be captured.
Aposematism: a defensive strategy in which toxic or unprofitable prey use warning signals to inform or deter potential enemies (e.g., predators or parasites).
Background matching: a type of crypsis in which organisms adjust their coloration to match their typical background.
Camouflage: all forms of concealment strategies that reduce the likelihood of detection (crypsis, see next) or recognition (masquerade, see next) from enemies.
Cercaria: a short-lived and free-living infective stage of trematodes' life cycle, released from the first intermediate hosts (generally mollusks, such as snails).
Countershading: a type of camouflage in which the dorsal surface, exposed to light, is darker and the ventral surface is lighter or lacking in pigmentation, allowing the organism to reduce visual cues from shadows and 3D shape, making the body appear flatter and less detectable by enemies.
Crypsis: a type of camouflage in which organisms use their coloration to prevent detection by enemies.
Cystacanth: a larval stage of acanthocephalans' life cycle that infects the first intermediate hosts, generally small crustaceans such as amphipods and isopods.
Gloger's rule: an ecogeographical rule that states that animals tend to be more darkly colored in warm and humid regions, underpinned by several nonexclusive factors such as UV exposure, humidity, and temperature.
Masquerade: a type of camouflage in which organisms use their coloration to prevent recognition by enemies, typically by resembling inedible or inanimate objects (e.g., stones, leaves) that are of no interest to enemies.
Sexual ornamentation: a morphological or behavioral trait, such as bright nuptial coloration, that increases the probability of successful mating by attracting the opposite sex or by providing an advantage over same-sex individuals in competition.
Sporocyst: an asexual stage of trematodes' life cycle, infecting the first intermediate hosts, that lacks a mouth and digestive system.

Trophically transmitted parasite: parasites that utilize predation of prey (intermediate hosts) by predators (definitive hosts) to complete their complex life cycle.

Blending into the environment: camouflage functions

Under numerous selective pressures, parasites have evolved traits that maximize their own fitness. One of the major selective pressures they face is the parasite removal behavior of host individuals [13–15]. Animals relying on visual cues often attempt to remove parasites by preening (in birds) and grooming (in mammals), during which they try to kill or remove ectoparasites from their bodies [13–15]. Since the frequency of preening and grooming is relatively high [15], these behaviors have driven the evolution of many parasite traits, such as sites of attachment and body size [13]. Thus, it is likely that these behaviors also influence the body coloration of parasites. **Crypsis**, especially **background matching**, would be effective in helping parasites escape from removal, and indeed, a few pioneering studies clearly showed that avian feather lice evolved background-matching coloration against preening by their host birds using evolutionary comparative analyses [10] and experimentally induced evolution under laboratory conditions [16,17] (Figure 2). Although these are the only clear cases showing the evolution of parasite coloration driven by the hosts' parasite removal behaviors, we hypothesize that the evolution of color, especially background matching, also occurs in other host–parasite systems. For instance, some parasitic copepods, mainly those infecting other crustaceans, adopt the shape and coloration of host eggs [18,19]. **Masquerading** as eggs may help them escape from the self-grooming of their hosts [18,19], although it remains to be confirmed whether these host use vision to detect parasites, and whether this coloration is simply a byproduct of their morphological mimicry (Figure 2). Some species of fish and reptiles attempt to remove parasites by scraping their bodies against available substrates [20,21]. Although these host responses can be triggered not only by visual detection but also by physical recognition (i.e., irritation), these behavioral responses could promote the evolution of background-matching coloration if visual detection plays a role in initiating the responses.

Another possible selective pressure likely to influence parasite coloration is predation by cleaner organisms [22]. Cleaning symbioses are common in both terrestrial and aquatic ecosystems [22–25], and predation pressure from cleaners is estimated to be very high [22,24,26]. For instance, a single cleaner wrasse *Labroides dimidiatus*, probably the best-studied cleaner in aquatic ecosystems, inspects nearly 2300 client fish and consumes over 1200 gnathiid isopods (common ectoparasites of reef fish) per day [26]. Monogeneans, another common prey item of cleaner fish [22], are thought to have evolved background matching as a counteradaptation against this predation pressure [11,27–31]. Some monogeneans, such as *Anoplodiscus australis*, occasionally contain bright-colored pigment (yellow, blue, and green), which may be ingested from their host's surfaces [28] and could help match their coloration to their site of attachment [22,29]. Similarly, transparent coloration, commonly observed in monogeneans and parasitic copepods (e.g., *Caligus* spp.), may function as crypsis [22,30] or potentially as **masquerade** if their potential predators can detect them but ignore them. However, there is still no robust experimental evidence confirming whether these colorations effectively help parasites escape from cleaners. Only one experiment found that smaller monogeneans, which are generally white-pigmented (matching the coloration of their attachment sites), suffered less from cleaner's predation than larger worms, suggesting that not only their body size but also their coloration is effective for escaping from cleaners [31].

Symbiotic cleaning interactions have also been well documented in terrestrial ecosystems [24,32]. Oxpeckers (*Buphagus* spp.), for instance, are among the best-known cleaner birds; they remove ectoparasites, such as ticks, from large-bodied mammals [24,32]. Predation pressure by these cleaners is high, and indeed, they are major drivers of parasite population dynamics [24]. Given this high predation pressure, we expect similar camouflage coloration to evolve in terrestrial ectoparasites as seen in aquatic ectoparasites, and indeed, some studies

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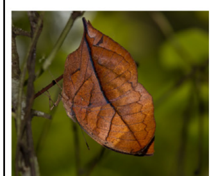
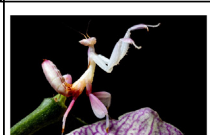
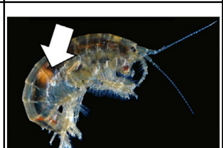
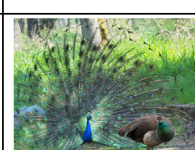
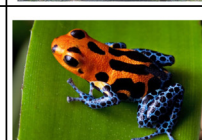
Potential function	Subcategories	Examples of parasites		Examples of free-living animals	
Camouflage	Crypsis (including background matching)		Feather lice parasitizing bird evolved background matching coloration to avoid host preening [10, 16].		Many owls adjust their coloration to match the background to avoid detection by their prey [66].
	Countershading (shadow concealment)		The parasitic isopod *Anilocra physodes* exhibits countershading coloration, with one longitudinal half of its dorsum being dark, while the opposite half light-colored) [36].		Countershading is a common strategy in both terrestrial and aquatic animals, particularly pelagic fishes.
	Masquerade		Parasitic copepod *Choniomyzon inflatus* masquerades as eggs of its host to escape from the host self-grooming [19].		Butterflies in the genus *Kallima* resemble a dead leaf, both in terms of their coloration as well as shape, in order to avoid recognition by predators [76].
Mimicry	Protective mimicry (including Batesian & Mullerian mimicry)	No studies			Many beetle species (e.g. family Cerambycidae) Batesian mimicry, in which they mimic poisonious wasps to avoid predation attack [77].
	Aggressive mimicry		Trematodes of the genus *Leucochloridium* attract their definitive bird host, using their caterpillar-like coloration [41-44].		The coloration of flower mantis (e.g. genus *Hymenopus*) can function to attract pollinating insects as prey [78].
Photoprotection			Orange-yellow coloration in acanthocephalan cystacanths may function as protection against UV radiation [47, 52].		Melanin-based pigmentation can function as photoprotection in the glass field whip snakes *Hierophis viridiflavus* [57].
Sexual ornamentation			Colorful patterning of male hard ticks (left, family Ixodidae), such as *Amblyomma variegatum*, may function as sexual ornaments [33].		Bright plumage coloration in male peacock functions to attract females [79].
Aposematism		No studies			Aposematic coloration is widely used in poison frogs (family Dendrobatidae) [80].

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(See figure legend at the bottom of the next page.)

hypothesized that the brownish and dark coloration of ticks may represent a counteradaptation against cleaner predation [33]. However, again, there is no empirical evidence supporting these hypotheses.

Countershading is another example of camouflage to avoid detection from predators, in which dorsal pigmentation is dark, but ventral pigmentation is light or absent [34]. While the strategy has been well documented in many animal taxa (e.g., [34,35]), to our knowledge, only one study suggested the possibility of countershading in parasites. Körner [36] found that the parasitic isopod *Anilocra physodes*, which infects marine fishes, showed unique asymmetric color patterns in its dorsal pigmentation; one longitudinal half of its back was dark, while the opposite half was light-colored (Figure 2). The dark side corresponded with the upward-facing (dorsal) side when it attached to the side of its host fish [36]. The author hypothesized that this coloration pattern was a form of countershading that served to escape from predators (e.g., cleaner fishes), although they did not carry out any empirical tests [36]. Similarly, a possible camouflage function has been suggested for the isopod *Nerocila japonica*, which exhibits symmetric coloration patterns (dark blue with two faint pale submedian longitudinal bands) [37]. Such longitudinally or latitudinally symmetrical banded patterns are common among ectoparasitic isopods (cf. [37,38]) and copepods (cf. [39]), and thus further tests are required to investigate their actual function.

In all previous examples, we focused on parasites living on hosts, but parasites also face strong predation pressures during their free-living or infectious stages [40]. For instance, free-living stages of trematodes, **cercariae**, and nematodes are frequently preyed upon by many types of nonhost organisms [40]. In this context, it would not be surprising if they had evolved cryptic coloration to reduce the risk of predation by nonhost organisms. Indeed, cercariae of many trematode species show inconspicuous coloration (e.g., black or brownish), potentially serving for crypsis, although there is no empirical test of this hypothesis (but see next for potential functions related to host attraction).

Attracting hosts: potential aggressive mimicry to enhance transmission success

Many **trophically transmitted parasites** with a two- or three-host life cycle have evolved their transmission strategy to maximize lifetime reproductive fitness. In this context, some parasites are hypothesized to utilize their coloration to increase their transmission success. The most famous examples involve trematodes of the genus *Leucochloridium* (Figure 2), which use land snails and birds as intermediate and definitive hosts, respectively [41–43].

When **sporocysts** invade the snails' antennae, their bodies adopt a caterpillar-like coloration, which may attract birds visually searching for food [41–43]. This has been considered as an example of **aggressive mimicry**, although this assumption has yet to be clearly tested and remains in doubt [43,44], as not only coloration but also wormlike movements and their combination may effectively attract bird hosts [42,43]. A similar hypothesis has been tested in fish–acanthocephalan systems, where it has been hypothesized that the carotenoid-based yellow–orange coloration (Box 1) of acanthocephalan **cystacanths**, seen through

Figure 2. Plausible adaptive functions and their examples in parasite coloration. Several adaptive functions that can plausibly apply to parasites are shown, along with known examples from free-living animals. Note that most examples about parasites and some examples of free-living animals lack empirical tests, and some adaptive functions are achieved not only through their coloration itself but also through their posture, body shape, and/or their combination e.g., 76–80. Photo credit: Feather louse; Dr Sarah E. Bush, Masquerading copepod; this figure includes a photograph reproduced (with modification) from Wakabayashi *et al*. (2013) *Systematic Parasitology*. Permission to reuse was obtained from Springer. Snail infected with *Leucochloridium passeri*; Dr Takashi Iwaki, Ticks: Dr Ryo Nakao and Dr Ernest Teo, Amphipod *Gammarus pulex* infected by a cystacanth of *Pomphorhynchus laevis*; Dr Nicolas Kaldonski, and the members of the Laboratory Biogéosciences (Dijon, France). All other images are from iStock.

Box 1. Mechanisms underpinning parasite coloration

Mechanisms underlying the production of animal colors are largely divided into pigments and nanostructures, and their combination [6]. Here, we summarize the major known and possible coloration mechanisms of parasites, by focusing on pigment coloration.

Carotenoid-based coloration

Carotenoids are a group of organic pigments, composed of eight isoprene units (i.e., tetraterpenes) producing yellow, orange, and red colors. Depending on their chemical features, they are broadly divided into xanthophylls (containing oxygen) and carotenes (containing no oxygen). As animals cannot synthesize carotenoids *de novo*, they generally obtain these from their diet (especially from plants and algae) [45,46]. Parasites can obtain carotenoids from their hosts [47,48]. Although at least more than 750 types of carotenoids have been recorded from nature [46], only a few types have been identified from parasites. Cystacanths and adult acanthocephalans contain lutein, β-carotene, and astaxanthin [49,50]. The rediae of some trematodes contain β-carotene [48,51]. Some copepods and cestodes also contain unidentified carotenoids [52,53].

Melanin-based coloration

Melanins are also very common pigments in natural systems. They are divided into eumelanin (responsible for black and gray coloration) and pheomelanin (responsible for brown and reddish coloration) [54]. Animals can synthesize these pigments within chromatophores (e.g., melanocyte or melanophore) and this production process is regulated by hormones (melanocortins), which are genetically determined [54]. For instance, the tendency toward black coloration in head-attaching avian lice may be genetically determined [10,16,17]. Some parasites, such as monogeneans, can obtain this pigment from host tissues [11,27].

Other pigment sources

As with carotenoids and melanins, parasites often obtain their coloration (pigments) from hosts; however, some of these pigment types have not yet been identified. For instance, gnathiid isopods often exhibit colorful body patterns, from yellow to blue [12,55,56], based on compounds which may have been obtained from fish plasma [12].

their semitransparent crustacean intermediate hosts, may attract definitive hosts to prey on them [47,57,58] (Figure 2). Two experimental studies tested this and found supporting evidence [57, 58]. Later, however, this was revisited by Kaldonski *et al.* [47] using a more rigorous experimental design, and the authors rejected the possibility of host attraction. Nonetheless, carotenoid-based coloration is widely observed in acanthocephalans, trematodes, and cestodes [48–51,59], and this pigment may have other functions such as photoprotection [50, see next].

Although direct empirical evidence is lacking, infectious stages of many parasites may use their coloration as aggressive mimicry, potentially enhancing transmission success. The cercariae of some trematode species have long tails and unique swimming behaviors and often exhibit bright coloration (yellow, red, and brown), which may attract fish, their definitive hosts [60,61]. Some parasitic isopods mimic the behaviors of their hosts' prey and successfully attach to the hosts' bodies when the latter approach them [62]. In addition to this behavioral mimicry, we speculate that their darkly pigmented coloration may also play an important role in increasing the attraction of hosts.

Protection against harmful light, including UV

Ultraviolet (10–400 nm) radiation from sunlight affects most ecosystems on Earth, and the fitness of organisms can deteriorate under UV exposure [63]. Therefore, many types of animals have black melanin pigments (Box 1), which play important roles in UV protection [64]. Many studies focusing on free-living animals have shown effective protection from UV provided by dark coloration, mainly through melanin-based pigmentation (e.g., [64,65]) (Figure 2), whereas very few studies have mentioned or tested this in parasites. Bush *et al.* [10] found that lice attached to the heads of birds were more likely to have dark coloration compared with those attached to feathers, suggesting that melanin-based dark coloration may serve for UV protection, as parasites on the heads of birds are exposed to higher amounts of UV. Carotenoids also play key roles in protection from UV [65], and indeed, many parasites have this pigment (Acanthocephalans [47,50], Trematodes [48,51], Cestodes [59], and Copepods [53]), suggesting that it may play an important role in photoprotection. This pigment would be particularly effective for photoprotection when infected hosts (and their parasites) remain in open habitats (e.g., near the water surface) where they are exposed to higher levels of UV radiation [47,50]. This prediction was partly supported by Perrot–Minnot *et al*. [50], using several acanthocephalan species. Nonetheless, widely recognized ecological patterns may also support this prediction; many intestinal parasites, such as helminths, are colorless, generally pale or white in color. Not only would color play no role in protection from predation or host attraction for adult helminths but also there is no UV exposure inside the definitive host. Since synthesizing, obtaining, and/or maintaining these pigments is very costly [66], similar pigment or coloration loss can be seen in other free-living animals under dark conditions, such as cave fishes [67].

Attract opposite sex: sexual ornamentation

Sexual selection is a major driver of animal coloration [9]. In many taxa, males exhibit brighter coloration, i.e., **sexual ornamentation**, to attract females. This may also be true in some ticks (Figure 2). The colorful body patterns of hard ticks (family Ixodidae) have long been known (e.g., [68]). Some researchers have hypothesized that this coloration may function as ornamentation; however, this has never been specifically tested, and it may instead serve other functions, such as thermoregulation (reviewed by Schachat *et al.* [33]). Therefore, future studies that explicitly identify its actual functions are strongly needed.

Scaling up from microhabitat to macroecological patterns

Although most of the evidence summarized previously remains hypothetical and therefore requires proper empirical testing, it indicates that many selective pressures can influence parasite coloration, as well as host coloration. A parasite's color is directly influenced by environmental factors (e.g., cleaners' predation and UV exposure) and also indirectly via host coloration, which itself can also be influenced by environmental factors (Figure 3A). Based on these points and the facts discussed previously, we propose several testable ecological and evolutionary hypotheses by focusing on distinct biological levels, from micro- to macroecological scales.

Host individual patterns

Given that many ectoparasites have specific attachment sites, we hypothesize that background matching varies among different parasite species depending on attachment sites, even within the same host individual (Figure 3B, left). This would occur through two nonexclusive mechanisms in which either coloration is genetically determined or it results from the host tissues ingested by parasites at their attachment sites. Indeed, this pattern has been observed in parasitic copepods, monogeneans, and scale worms, such as *Gastrolepidia clavigera* [22,69,70], although the underlying mechanisms remain unexplored. Another easily predicted pattern is that closely related parasites that use different host species adapt their coloration to each host species, as shown by Bush *et al*. [10,16]. These hypotheses on parasite coloration could be tested using phylogenetically controlled comparative analyses.

Regional and macroecological level

When scaling up, we hypothesize that coloration patterns differ among habitat types. In terrestrial ecosystems, some habitats are more exposed to sunlight than others (e.g., forested vs. deforested areas). Because UV can be a strong determinant of parasite coloration, darker or more pigmented coloration that protects from UV would be more adaptive in open habitats (Figure 3C). This pattern

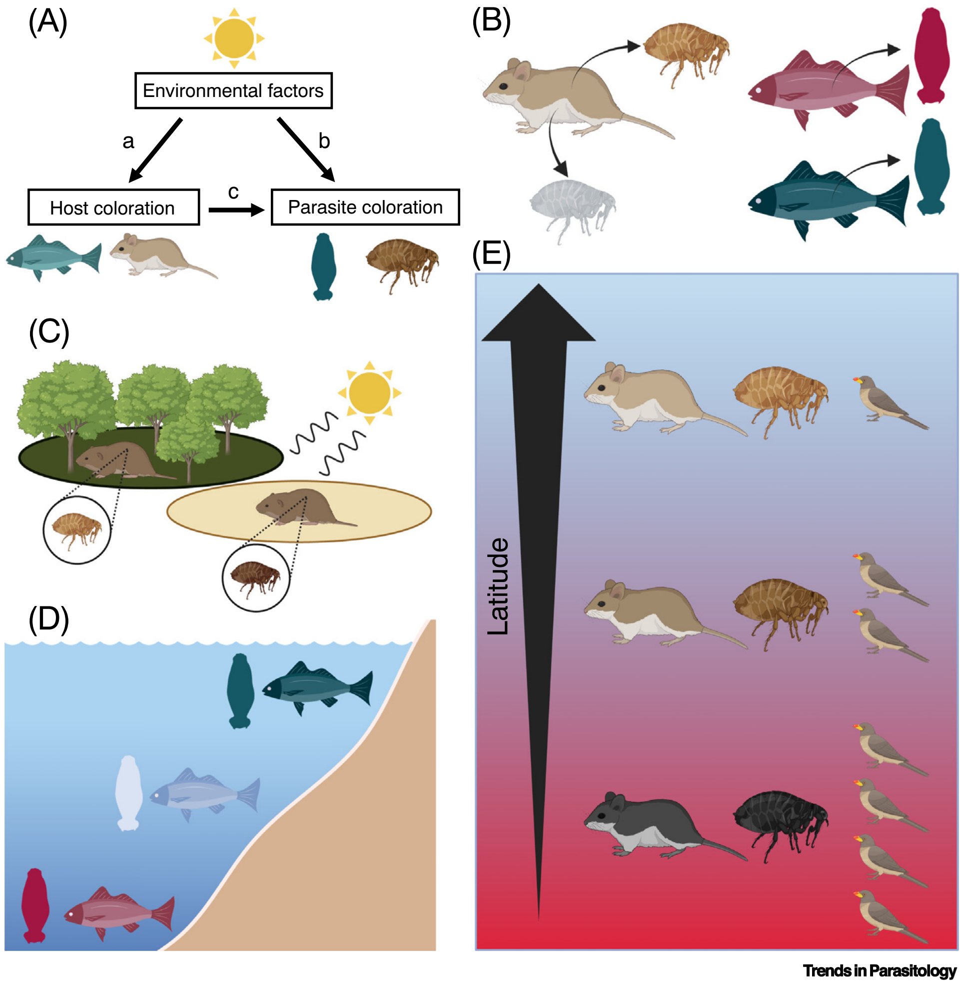

Figure 3. Some testable ecological and evolutionary patterns in parasite coloration. (A) Conceptual framework for understanding the patterns and processes of parasite coloration. Environmental factors, such as UV, strongly influence host and parasite coloration (arrows, a, b), but parasite coloration can also be influenced by host coloration (c). (B) Patterns of parasite coloration at host individual level. Coloration should differ among parasite species preferentially attaching to different sites of attachments on the same host (left) (e.g., abdomen vs. dorsal areas) or those exploiting different host species that are phylogenetically closely related with each other but differ in coloration patterns (right). (C) Different coloration patterns are expected among habitats with different openness gradients, such as forested versus deforested areas. (D) In aquatic habitats, such as ocean or deep lakes, parasite coloration should change along a depth gradient. (E) Based on Gloger's rule, which states that darker coloration is more common in humid and warm environments (conditions generally occurring in lower latitudes), a latitudinal gradient in parasite coloration is also plausible. This pattern may be exacerbated by the abundance of cleaner organisms, which also shows the latitudinal gradient (right side of the figure). Figure created with BioRender.com.

has often been reported for host coloration [64,71], and such changes in host coloration may also influence parasite coloration (see above section, Figure 3A). Similar patterns can also be expected in aquatic ecosystems. Because the intensity of sunlight decreases with depth due to absorption and scattering, red or black coloration is most common in mesopelagic areas, whereas white to red coloration is common in deeper areas [72]. These patterns are well described in fishes (e.g., [73]), but similar patterns may also be common among parasites (Figure 3D).

Patterns on a much wider scale can also be predicted, such as latitudinal clines. One relevant pattern, **Gloger's rule**, which has yet to be tested in parasites, states that animals living in warm and wet habitats (generally at lower latitudes) tend to be darker than those living in cooler and drier habitats [74]. This rule has been widely supported across many taxa, mainly mammals and birds [74,75,81], albeit with exceptions (e.g., [82]). If parasites adapt their coloration to that of their hosts, they would inevitably follow the same rules (Figure 3E). Moreover, the frequency and intensity of cleaning interactions appear to be greater at lower latitudes than at higher latitudes in both terrestrial [83] (Figure 3E) and aquatic environments [84]. This latitudinal gradient of cleaning interactions can produce a latitudinal gradient in the frequency of cryptic or background-matching coloration in parasites (Figure 3E).

Concluding remarks

Our review of the existing literature suggests several testable hypotheses. Critically, it must be noted that most studies propose hypotheses, whereas only a few provide actual experimental or field evidence for the function of parasite coloration. Furthermore, it should be noted that, in many cases, the mechanisms underlying coloration (e.g., whether parasite coloration has a genetic basis) remain unclear. Therefore, we call for more studies to rigorously test the mechanisms and adaptive function of parasite coloration or to explore wider ecological and evolutionary patterns in parasite coloration in nature (see Outstanding questions). To this end, databases of photographs and related information on parasite coloration would be invaluable, although the number of articles reporting data on parasite coloration is extremely limited at present (Figure 1). Nonetheless, as coloration patterns themselves can be useful traits to identify parasite species (e.g., [85]), recording and analyzing coloration (ideally using standardized quantification methods such as photographs with color charts or spectrophotometry) is also valuable from a taxonomic perspective, and thus, we strongly recommend that authors specifically describe parasite coloration or submit color photos of parasites as part of species descriptions for future studies on the adaptive functions in parasite coloration. Additionally, in this context, citizen science platforms such as iNaturalist (https://www.inaturalist.org/) may be useful for investigating global or regional patterns in parasite coloration. We sign off by calling for more attention to be directed toward this most understudied trait and what it may reveal about parasite ecology and evolution.

Outstanding questions

Does the coloration of parasites influence their fitness?

Is the coloration of parasites an inherent (genetically determined) trait or an acquired trait (derived from the host)? Does this differ among parasite taxa?

Does the coloration of parasites change ontogenetically (i.e., across their development and lifetime), and if so, why does this occur and how common is the pattern?

Which factors most strongly determine parasite coloration: host coloration or external environmental conditions, such as UV exposure?

Does coloration show convergence among distinct parasite taxa exploiting the same host species (i.e., distinct monogeneans or copepods on the same fish host species)?

Do recent environmental changes, such as deforestation and eutrophication, influence the evolution of parasite coloration? Have parasite populations living in habitats impacted by such environmental changes already evolved different coloration?

Does the conspicuous coloration of parasites make their hosts vulnerable to predation? Under such conditions, does this benefit parasites by increasing their transmission success?

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Declaration of interests

The authors declare no competing interests.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used ChatGPT in order to correct grammatical errors in some sentences. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

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