

The ontogeny and distribution of countershading in colonies of the naked mole-rat (*Heterocephalus glaber*)

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Abstract

Most naked mole-rats *Heterocephalus glaber* are countershaded, with purple-grey dorsal but pale pink ventral skin. The exceptions to this coloration pattern are uniformly pink, and include newborn pups, most queens and breeding males, and very old animals. Countershading begins to appear at 2–3 weeks of age and begins to disappear at *c.* 7 years of age. Countershading may provide camouflage when young naked mole-rats are above ground attempting to disperse. Therefore, reproductives and older workers may lose this coloration once they are unlikely to leave the burrow. Alternative hypotheses for pigmentation that we considered include: thermoregulation, and protection from abrasion or from damaging ultraviolet radiation. These hypotheses are not necessarily mutually exclusive, but do lead to different predictions regarding the development of pigmentation and which colony members should be countershaded.

Key words: *Heterocephalus glaber*, naked mole-rat, countershading, adaptive coloration

INTRODUCTION

Naked mole-rats *Heterocephalus glaber* (Bathyergidae) are fossorial and eusocial mammals (Jarvis, 1981; Sherman, Jarvis & Alexander, 1991; Braude & Lacey, 1992; Sherman, Jarvis & Braude, 1992) that live in extensive burrows in the semi-arid desert of East Africa. Colonies range in size from pairs of adults up to families of 300 animals (Brett, 1986). Virtually all colonies contain only one breeding female, known as the queen. She breeds with only one or a few of the males. All of the other individuals are non-breeding workers, performing tasks related to burrow excavation and maintenance, foraging, colony defence, and pup care (Sherman, Jarvis & Alexander, 1991). One such task relevant to the current study is called ‘volcanoing’, in which an individual kicks soil up out of the tunnel system forming a mole hill with the appearance of a miniature active volcano (Braude, 1991). In doing so, the animal’s back, tail, and rear limbs are exposed to the light.

As their name implies, naked mole-rats are nearly hairless. Hair is restricted to tactile hairs around the face

and tail, rows of brushes between the toes, and scattered bristles (Thigpen, 1940; Daly & Buffenstein, 1998). Thigpen (1940) noted that in preserved specimens the dorsal skin is slightly bluish owing to dark pigment cells, while the ventral skin is whitish-yellow and has far fewer pigment cells, which are light brown or yellowish. Daly & Buffenstein (1998) concluded that the skin colour of naked mole-rats results from a combination of melanin and the presence of blood vessels, and suggested that the ability to vary the amount of blood flow near the surface of the skin aids in thermoregulation. However, these explanations did not consider the development and function of countershading in this species.

Countershading has been proposed to be a form of camouflage in many species (e.g. Cott, 1940; Heran, 1976; but see Kiltie, 1988), by making the dorsum and shadow of an individual less conspicuous under various lighting situations. This adaptation has been best demonstrated in cephalopods and freshwater fish that swim upside-down (Ferguson & Messenger, 1991; Chapman, Kaufman & Chapman, 1994; Ferguson, Messenger & Budelmann, 1994). For aquatic species seen from above, the background colour is often the dark of murky lake beds or deep water, and when seen from below, the background colour is the light sky.

Countershading also occurs in many terrestrial animals. The darker dorsal coloration may make young

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or small animals less conspicuous to aerial predators, while the lighter colour of the underside may serve to decrease the intensity or visibility of the shadow the animal's body makes against the ground (Thayer, 1896; but also see Kiltie, 1989). This pattern of camouflage would also benefit adult animals by making them less conspicuous to their predators or to their prey (Gotmark, 1987).

Countershading may also result when dorsal pigmentation is adaptive while the lack of ventral coloration occurs simply because ventral surfaces are generally hidden and so pigmentation is not wasted there (as opposed to the contrast itself being an adaptive trait). This possibility has resulted in some confusion over the use and meaning of the term countershading (Kiltie, 1988). We use the term here as a description of the darker dorsal and lighter ventral coloration of most naked mole-rat workers regardless of the mechanism by which this may provide camouflage or other advantage.

In addition to camouflage, Burt (1981) has summarized various physiological functions of animal coloration. Animals may benefit from the protection pigmentation provides from the ultraviolet radiation in sunlight and Tucker (1981) found that exposure to sunlight causes the skin of naked mole-rats to darken. Naked mole-rat body temperatures vary with the ambient temperature (Buffenstein & Yahav, 1991), and countershading may aid in the maintenance of an optimal temperature if the concentration of coloration in one part of the body increases the efficiency of behavioural thermoregulation. Finally, melanin may strengthen skin, providing protection from abrasion. Alternatively, countershading seen today could be a remnant of the colour pattern of naked mole-rats' surface-dwelling ancestors.

METHODS

Animals in this study are part of 2 ongoing studies of naked mole-rat demography and behaviour in Meru National Park, Kenya (field) and at the University of Michigan Museum of Zoology, Ann Arbor (laboratory).

Field

More than 30 colonies of naked mole-rats have been captured, marked and released in the 6 km² area between the Mulika and Bwatherongi rivers in Meru National Park. Most of the colonies have been recaptured at least once and many colonies have been captured repeatedly since 1987. Upon capture, mole-rats in the Meru demographic study are weighed, sexed, marked by toe-clipping[†] and examined for reproductive

Table 1. Colours of captive naked mole-rats as determined by comparison to the colour samples in *The Methuen handbook of colour* (Kornerup & Wanscher, 1978). See text for explanation of hue, tone and saturation codes. There were no animals 3–8 or 12–16 years of age

Colour			No. of animals in each age cohort		
Hue	Tone	Saturation	3 months– 3 years	8–12 years	≥ 16 years
8	3	2			2
9	3	2			2
9	4	2	1		
9	5	3	8		
9	5	4	1		
9	5	5	1		
9	5	6	1		
10	2	2			1
10	3	2		2	11
10	3	3		1	
10	4	3	2	2	1
10	5	2	2		
10	5	3	26	3	
10	5	4	15		
11	3	2			3
11	4	2	1		
11	4	3	4		
11	5	3	4		
11	5	4	17	2	
12	4	2		1	

development. Since 1988, extreme pink dorsal coloration has been reported in the field notes when observed.

Laboratory

Captive animals at the University of Michigan (UM) were trapped in 1979 near the town of Mtito Andei, 200 km south of Meru, or have since been born in captivity. Precise ages of animals born in the laboratory are known; the minimum age of field-captured animals was 17 years at the time of this study. The breeding status of males was determined by observation of mating behaviours (Jarvis, 1991; Lacey *et al.*, 1991). Between May 1993 and April 1996, 20 successful litters were born in the UM colonies, resulting in 116 pups being raised. The ontogeny of skin pigment acquisition was recorded for 12 of these litters, containing 69 pups.

Dorsal skin colours of 114 captive animals comprising five colonies (A, B, C, E, F; see Table 1) were evaluated on 29 September 1996 by an observer with no knowledge of the age, sex, or breeding status of the animals, nor of the hypotheses being addressed. Skin colour was measured in 2 ways: by comparing each animal to the 1260 colour samples provided in the *Methuen handbook of colour* (Kornerup & Wanscher, 1978) and by simply ranking the animals from darkest to lightest.

Colour sample measurement

The animals were placed individually in a clear plastic

[†] Alternative marking techniques were tested for this species (Braude & Ciszek, 1998). Toe-clipping was found to result in better survivorship than marking with implantable transponder chips. Marking with ear tags is not possible in this species because there is almost no external ear pinna.

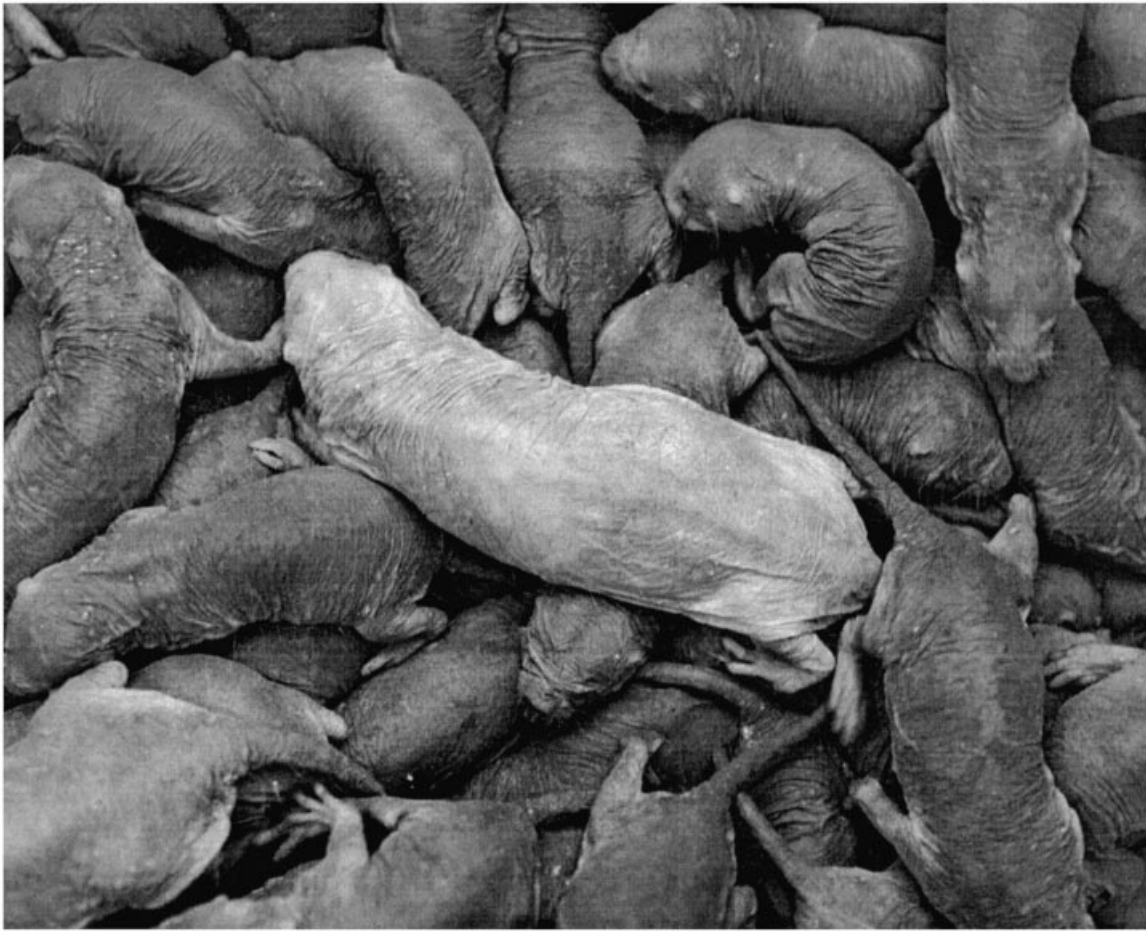


Fig. 1. Naked mole-rat queens are typically pink in contrast with the darker grey dorsal coloration of most workers.

open box. Lighting was from a large fluorescent ceiling fixture. The observer slid the box across the colour plates until she located the colour sample most similar to the dorsal skin immediately anterior to the base of the tail (c. 1 cm²).

The colour samples are quantified along 3 axes, which vary with hue, tone, and saturation, respectively (Kornerup & Wanscher, 1978). Hue refers to the colour along the visible spectrum. The hues observed in naked mole-rats ranged from orange/brownish-red (8) to bluish-red (12). Tone is the amount of grey in the sample scaled from 1 to 9, with 9 being completely black. Saturation is the colour intensity, scaled from 1 to 8, with 8 indicating maximum intensity.

Colour ranking

Animals were placed in individual dark grey open boxes. Colonies were evaluated separately. For each colony, the observer shuffled the boxes until the animals were, in her opinion, ranked in order from darkest to lightest dorsal coloration. There was no time limit. Researchers (DC and NS) were in the room during this process, but did not watch or note the order of the animals until after the observer stated that she was finished.

There was a possible source of bias owing to the method of marking some of the subjects. The 20 oldest animals (17%) had tattoos on the left and right side of the abdomen. These animals had been tattooed by earlier researchers in 1983 and 1985. However, after data collection was completed the observer was questioned, and replied that she had noticed tattoos on only a few animals, and had not perceived any correlation between tattoos and dorsal skin colour.

Statistics

All statistics (simple linear regressions and the Mann–Whitney *U*-test) were performed using the program SYSTAT (SYSTAT, Inc. 1992). For the regressions, the exact ages of animals born in the laboratory were used, and 17 years taken as the age of wild-caught animals. Tables 1 & 2 group animals into age cohorts for clarity of presentation of results, but these groupings were not used in the calculations. For analysis of skin colours as determined using Kornerup & Wanscher (1978), each individual's values for tone and saturation were added together, giving an estimate of degree of pigmentation. For the regression of colour rank against age, each colony was analysed separately.



Fig. 2. Naked mole-rat workers are countershaded, with purple-brown-grey dorsal and pink ventral skin.

RESULTS

Field

The differences in coloration within colonies of wild naked mole-rats was first noted by NB in 1988. When looking into a basin full of recently captured animals she observed that the queen was pink while all the other naked mole-rats were dark grey (Fig. 1). Upon closer examination of the workers, it was noted that the grey pigment is restricted to the dorsal surface while the ventrum remains pink (Fig. 2).

Queens are easily identified by their elongated bodies, prominent nipples and swollen genitals (Jarvis, 1991). Queens in all of the established wild colonies were pink and not countershaded. Queens and their mates in newly formed, 'nascent' colonies had not yet lost their countershading. Ten wild adults other than queens observed from 1990 to 1995 were also noted as pink and lacked countershading. Six of these animals were non-breeding females and four were males; all were among the largest 10% in their colony but their ages are unknown. Two of the males were noted as possible breeding males because of their body morphs (long and thin) and their protruding penises.

Pups as small as 2–3 g were captured if present in a colony. These animals were always pink and not countershaded. As the precise birthdates and ages of animals in the wild population is unknown it is impossible to pinpoint at what age countershading develops in wild naked mole-rats.

The observation of countershading in a fossorial species suggests some above-ground activity. This is supported by several observations reported to us: C. Mann and T. Heaton first noted a naked mole-rat walking on the surface within the Meru study site in August 1974 (Heaton, 1998); in the early 1980s J. Hebrard (pers. comm.) also found a naked mole-rat walking above ground at night while camping in the Meru study site; more recently, assistant wardens of Meru National Park have reported sightings of two

naked mole-rats above ground – F. Mwenda saw a naked mole-rat walking on a road in Meru National Park at 22:00 on 15 January 1987, and H. Muhindi found a naked mole-rat that had fallen into a concrete drain trough behind his house at Meru Park headquarters on 20 January 1987. All of these animals were probably dispersers (Braude, 2000).

Laboratory

Pups are pink when born. This pink is darker than the colour of very old, uncountershaded individuals. Colour seems to vary with their hydration level, such that pups not being nursed become a very dark, almost red colour. The distal end of the tail is the first part of the body to become shaded, changing from pink to grey. The earliest this change was observed was in a litter of nine pups at 9 days of age (this conforms with the timing reported by Jarvis, 1991); the latest it was recorded as a first occurrence was at 41 days of age, in a litter of 10 pups. The timing of colour changes ranged widely between litters, but within litters the changes in the pups' coloration patterns were always synchronous. The grey coloration spreads down the tail to the lower back, while the colour deepens to the purplish-greyish-brown that is characteristic of the dorsa of most naked mole-rats (Table 1). The earliest appearance of coloration on the back was at 18 days of age. The ventral surface, legs, and feet do not darken. Full dorsal/ventral countershading was evident in all litters by *c.* 3 months of age. The skin over the shoulders sometimes remains a lighter colour than that of the back and head for a varying length of time.

Often a distinct but jagged line runs down the sides of the body, separating the dorsal colour from the lighter ventrum (Fig. 2). In countershaded adults as well as juveniles the tail is darker than the skin of the dorsum, and it is not countershaded, being darkly coloured throughout its circumference. The animals' front and rear lower legs and feet are light pink. The skin covering

Table 2. Results of the regression of colour rank against age. A 'blind' observer ranked the animals in each colony from darkest to lightest dorsal coloration. There were no animals 3–8 or 12–16 years of age

Colony	No. in age cohort			r^2	P
	3 months–3 years	8 years–12 years	≥ 16 years		
A	23	1	1	0.371	0.001
B	11	2	11	0.784	<0.001
C	0	5	6	0.753	0.001
E	15	2	1	0.374	0.007
F	34	1	1	0.142	0.023

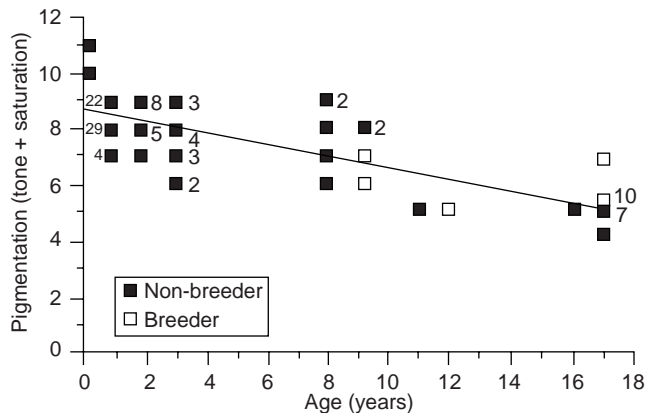


Fig. 3. Degree of pigmentation (combined tone and saturation values) is plotted against age ($r^2=0.714$, $P<0.001$, $y=-0.210x+8.67$). The value next to a data marker indicates the number of data points plotted at that coordinate, if >1 ; 10 breeders and seven non-breeders are all plotted at the single coordinate 17, 5. For animals aged 1–3 years, ages are rounded off to the year for graphical clarity, but exact ages were used in the regression.

the abdomen is translucent, and to some extent transmits the colour of internal organs. In pups, the dorsal skin is also somewhat translucent, which can result in confusion regarding dorsal coloration in juveniles.

As adults age they lose dorsal pigmentation (Table 2), such that the dorsum fades until it becomes the same pink colour as the feet and ventrum. For the 114 captive naked mole-rats combined, degree of pigmentation (estimated as the sum of the values for tone and saturation) decreased significantly with age ($r^2=0.714$, $P<0.001$; Fig. 3). However, there is some variation in colour that is not explained by age. Animals aged 8–12 years expressed a wide range of pigmentation values (Fig. 3). Also, in colony B, two of the wild-caught animals (one male, one female) were still slightly countershaded. The oldest laboratory-born animal (a 16-year-old male from colony B) had entirely lost countershading, and was ranked as lighter in colour than five of colony B's 10 wild-caught animals.

The queen and male breeder(s) were always among the oldest individuals in their laboratory colony, and were generally light in colour. However, among animals aged 8 years and older there was no significant difference in pigmentation level between breeders and non-breeders

(Mann–Whitney $U=144$, $P=0.245$). There was no apparent effect of sex on degree of pigmentation at any age.

DISCUSSION

Our data on the development, distribution, and loss of countershading in naked mole-rat colonies provide an opportunity to evaluate functional hypotheses about this coloration pattern. These hypotheses involve protection from ultraviolet light, thermoregulation, abrasion resistance, and camouflage. These hypotheses are not mutually exclusive but can be contrasted with the neutral alternative that countershading is not adaptive and serves no current function in these fossorial animals. We first consider the neutral alternative and then each of the other hypotheses.

Neutral hypothesis

The surface-dwelling ancestor of the bathyergids may have been countershaded, suggesting the possibility that the coloration pattern in naked mole-rats is a vestige of an ancestral trait. However, the epigeal ancestor would have been covered with fur, and the coloration of fur and skin develop by different mechanisms. In *Cryptomys damarensis*, a furred bathyergid that is dark brown except for a large white patch on the head, the skin colour of shaved animals is the same on the head as on the rest of the body (B. Goldman, pers. comm.).

It could also be suggested that the loss of coloration in older naked mole-rats is merely a consequence of a finite population of melanocytes spread over a larger area as animals grow. However, in both the laboratory and the field there are both pigmented and unpigmented large animals. This explanation also fails to address the specific pattern of pigment acquisition and the lack of pigment on the ventral surface.

Protection from ultraviolet light

Naked mole-rats may benefit from the protection from ultraviolet light provided by dorsal pigmentation of the skin more than would species protected by fur. Since naked mole-rats kick loose soil out of open volcanoes

during daylight hours (Braude, 1991) they are occasionally exposed to sunlight. The hypothesis that dorsal pigmentation protects naked mole-rat workers from ultraviolet radiation is also consistent with the development and distribution of pigment on the body. The tail and posterior dorsum are the body parts most exposed when the animal kicks soil and are the first to become pigmented. The head is next to acquire pigment and is occasionally exposed when a volcano turns and looks up out of the hole. The shoulders are the least exposed and are the last to become pigmented. In addition, pups and reproductives rarely perform this task, and are not countershaded.

However, the rear legs and feet are also exposed to sunlight during volcanoing, yet are not pigmented. Also, Braude (1991) found that the largest workers in a colony were among the most likely to volcano and these are also likely to be among the oldest animals in the colony. This observation is, therefore, inconsistent with the ultraviolet protection hypothesis.

It is unlikely that dorsal pigmentation provides protection from ultraviolet light to the animals who disperse above ground because all reported cases of naked mole-rat activity above ground have been during darkness, and naked mole-rats would have difficulty withstanding the intense heat during daylight hours in East Africa (Jarvis, 1978). Even their subterranean activity is greatly reduced during the hottest hours of the day.

Thermoregulation

Naked mole-rats control their body temperature by modifying their behaviour. Daly & Buffenstein (1998) suggest that skin coloration functions in heat transfer, via melanocytes or blood flow or both. However, this does not explain why queens and their mates lose pigmentation. In fact a queen may have even greater need to gain heat during pregnancy and nursing.

Protection from abrasion

Burt (1981) suggests that melanin makes feathers more abrasion-resistant by forming disulfide crossbridges with keratin. If melanin also strengthens skin, the pigmentation of naked mole-rats would function to protect their skin from abrasion resulting from scraping against soil and rocks in their underground tunnels. A prediction of this hypothesis is that the parts of the body most prone to abrasion should contain the most melanin.

A mole-rat's dorsal skin may scrape against the top or sides of the tunnel when it squeezes over another mole-rat in the burrow (termed 'passing over'; Lacey *et al.*, 1991) and, indeed, the back is highly pigmented in most individuals. However, dominant animals, which tend to be older than most animals in the colony, are more likely to pass over others (Rymond, 1991) yet have

less dorsal pigmentation. In particular, pregnant queens scrape heavily against the tunnel surface as they attempt to turn around or pass over other animals, and queens always become unpigmented. Also, the tail of a countershaded mole-rat is always at least as dark as its dorsum, but does not scrape against the tunnels. Finally, the soles of the feet, which suffer the most abrasion, are not pigmented (they are protected by *c.* 20 layers of epidermis, while the dorsal skin has four to seven layers and the ventrum only one or two: Tucker, 1981). On the whole our results do not support the abrasion protection hypothesis.

In addition, it is possible that the pigment in naked mole-rats is not melanin. Thigpen (1940) reports pigment cells but Tucker (1981) found no evidence of melanin granules in the skin of the naked mole-rats he studied. However, this may have been a limitation of the available techniques.

Camouflage

The most widely accepted explanation for countershading is camouflage (Gould & Lewontin, 1979). Yet, how could a fossorial rodent benefit from camouflage? Wild naked mole-rat workers disappear from their colonies at such high rates that the worker class is almost completely replaced every 3 or 4 years. Some of these animals are known to be dispersing above ground (Braude, 2000) but the precise percentage is unknown. Dispersers would benefit significantly from darker coloration if it decreased their visibility to predators. Of 16 known wild dispersers, the average age at dispersal was 2.3 years; the maximum was 5 years (S. Braude, pers. obs.). If the relationship between age and degree of pigmentation is similar for captive and wild mole-rats, then these dispersers would have had an average pigmentation level of *c.* 8.5 according to Fig. 3.

The only documented predation on naked mole-rats has been by snakes who enter their burrows (Jarvis & Bennett, 1991; Aggundey, 1997). However, dispersers would be more vulnerable to nocturnal avian predators because most snakes would be less active at night. All four of the documented sightings of naked mole-rats above ground occurred at night. The exact dates of two of these sightings are known (15 and 20 January, 1987) and occurred during full and waning three-quarter moon phases. Thus, visual camouflage against avian predators would have been extremely beneficial to these animals (Kaufman, 1974; Edmunds & Dewhurst, 1994). The degree to which grey dorsal coloration is more difficult for an avian predator to detect than lighter pink against the orange-brown soil typical of north-eastern Kenya has not been tested.

We have presented the first detailed information on the development and pattern of coloration within individuals and within colonies. Although the four functional hypotheses we have considered are not mutually exclusive, the evidence most strongly fits the camouflage hypothesis.

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