

IRIDESCENT DUNG BEETLES: A DIFFERENT ANGLE

KEVINA VULINEC

Entomology & Nematology Department, University of Florida
Gainesville, Florida 32611

ABSTRACT

Iridescence, in both the visible and ultraviolet (UV) spectra, is produced by various means and may serve several functions in different animals. In insects, such colors are often considered as anti-predator adaptations, either crypsis or aposematism, or a means of thermoregulation. A less explored alternative is social signaling. Iridescent colors are particularly useful in this context because they are brightest from certain directions and body orientation could be employed to direct a visual signal to particular receivers. In phanaeine dung beetles the head and prothoracic shield reflect a visible-light and UV iridescence that is best seen from a position facing the insect. The less iridescent male horn is silhouetted against the prothoracic shield. Since horn size is indicative of male size, such a display may be directed to sexual competitors in agonistic interactions. Broad and reflective prothoracic surfaces on males might also be preferred by females choosing a mate, who will cooperate in future brood care, since they would make infestations of kleptoparasitic flies more obvious.

Key Words: Scarabaeidae, mate choice, intrasexual selection, ultraviolet reflectance, phanaeine

RESUMEN

La iridiscencia, en ambos espectros, visible y ultravioleta (UV), es producida de diversas maneras y puede ejercer diversas funciones en diferentes especies animales. En insectos, dichos colores generalmente son considerados como adaptaciones biológicas para protegerse de sus depredadores por mecanismos crípticos o de aposematismo, o como una forma de termoregulación. Otra alternativa, menos estudiada, es la iridiscencia como un medio de comunicación social. Los colores iridiscentes son particularmente útiles en este contexto porque son demasiado brillantes desde ciertas direcciones y la orientación corporal pudiera ser empleada para dirigir una señal visual a receptores particulares. En los escarabajos de estiércol (Phanaeine), la cabeza y la coraza protorácica reflejan una luz visible y una iridiscencia ultravioleta que se observa mejor desde una posición de frente al insecto. El cuerno de los machos, un poco menos iridiscente, forma una silueta contra la coraza protorácica. Si consideramos que el tamaño del cuerno del macho refleja el tamaño corporal, este mecanismo pudiera ser dirigido a competidores sexuales en interacciones agonistas. Las superficies protorácicas anchas y reflejantes presentes en los machos, pudieran también ser preferidas por hembras eligiendo su pareja sexual, quienes cooperarán en el cuidado futuro de su progenie, puesto que pudieran hacer más obvias las infestaciones de moscas cleptoparasitas.

Iridescence is found in many organisms, but among terrestrial animals it is most highly developed in two groups, birds and insects. Perhaps not coincidentally, these classes also exhibit well developed visual systems, and protean body coverings. The two groups frequently interact; birds are among the principal predators of insects, and iridescent species of both are largely diurnal, suggesting that these colors are used in interspecific and/or intraspecific communication. In this paper, the mechanics of iridescence are briefly described, as are some of the different structures that cause iridescence. Different

hypotheses are then proposed for the evolution of iridescent coloration, and each hypothesis is considered in relation to iridescence in dung beetles (Coleoptera: Scarabaeidae).

Animal coloration often correlates with a species' visual capabilities. Mammals are typically colored with shades of brown and black, the hues of melanin. Most apparently do not see color, or do not respond to color stimuli. Primates are an exception, and not only respond to color but are often brightly colored themselves, e.g., the faces and rumps of mandrills, (*Mandrillus sphinx*). Humans generally see wavelengths between 400 and 790 nm (referred to from this point as the "visible" spectrum; Endler 1990). Birds perceive not only the colors visible to humans, but also detect ultraviolet colors with wavelengths shorter than 400 nm (Goldsmith 1980; Parrish et al. 1984). Bees perceive wavelengths from the UV range up to 650 nm, but do not distinguish orange (600-650 nm) from yellow (550-600 nm), or blue (400-480 nm) from violet (380-400). Other insects' visual systems vary. For example, the absorbance maxima of the photo pigments in some moth eyes are 345, 440 and 520, while the peaks in *Heliconius* butterflies are 350, 460 and 550 (Endler 1990). These differences may be due to differences in available light and other components of their respective environments (e. g., Lall et al. 1980).

Browns, reds, and yellows in animals are almost always formed by pigmentation, and can be washed out of the underlying structure with solvents. Blue and green colors are usually structural and cannot be permanently changed unless the structure itself is crushed.

Structural colors can be produced in two ways. One is through diffusion, i.e., the scattering of short wave colors, blue and violet, by submicroscopic particles, that results in Tyndall blue. The blues of the sky and human eyes are formed this way (Simon 1971), as are some blues on butterfly scales (Huxley 1976).

The other structural means of color production is through interference, which causes the brilliant changing hues common in iridescent insects. Thin films, such as oil on water, reflect some incoming light from their shiny top surfaces. The rest of the light enters the film and is refracted by the film's greater density compared to air. This light then slows as it passes through the film, and when it reaches the lower surface, is reflected back. When it rejoins the light reflected off the upper surface, it has been traveling slower, and is thus out of phase with the reflected beam of light. If the phase difference between the two beams equals one full wavelength, or a multiple thereof, the color of that particular wavelength will be reinforced. If the amplitudes (crests and troughs) of the two light beams are equal, reinforcement will be strongest, and the color purest. All other wavelengths are either weakened, if they are out of phase, or eliminated if the crest of one beam meets the trough of the other. If the angle of incident light is changed, a different color will appear. Changing the width of the film will also select for different wavelengths, and thus different colors (Simon 1971).

Thin films are not the only way to obtain interference colors. Thin slits arranged equidistant from each other, called diffraction gratings, also cause iridescence (Hinton 1973). Additionally, a structure called a space lattice, where minute particles suspended in a medium are arranged in layers stacked on top of each other, produces iridescent reflections. The microscopic structure of iridescent bird feathers are made up of stacks of melanin rods within layers of keratin, creating a space lattice (Simon 1971).

A SURVEY OF IRIDESCENCE

Feathers

Of all soft body coverings bird feathers are the most strikingly iridescent. Many birds are largely iridescent, such as the Resplendent Quetzal (*Pharomachrus mocino*). Others are dull, but exhibit patches of iridescent feathers. These patches, in

otherwise dull-colored birds, also strongly reflect ultraviolet wavelengths (Radwan 1993). As will be seen in insects, iridescent patches are highly directional, appearing brightest from particular angles of view.

Butterfly scales

In butterflies, several types of iridescent scales have been described. The average lepidopteran wing has rows of alternate long and short scales. The longer are cover scales, which arch over and hide the short, ground scales. In iridescent patches, the cover scales are specialized, but the ground scales are usually undifferentiated. Iridescence may arise from "lamellar thin-film iridescent" scales, "microrib thin-film iridescent" scales, "laminar thin-film iridescent" scales, or "diffraction lattice" scales, whose interiors are filled with crystals of a cubic lattice that produces a diffraction color (Ghiradella 1985). These various ways of producing iridescence can be readily modified, as demonstrated by ultraviolet reflectance in *Colias*, where the lamellar thin-film color is inherited at a single locus (Silberglied & Taylor 1973). Because of this plasticity and that several scale types can be found in taxa without any particular correlation to phylogenetic associations, iridescence in butterflies probably evolves in response to selection (Ghiradella 1985).

Some butterflies have intense UV reflection caused by interference, and produced in the same manner as visible iridescence. This ultraviolet reflectance can overlay visible colors (Silberglied 1979). Additionally, most iridescent scales also contain melanin, which absorbs much of the light not reflected by the iridescence and enhances the brilliance of the color (Nijhout 1991). The intensity of most colored surfaces varies linearly with the angle between the light source, the reflecting surface, and the observer (Endler 1990). With interference colors, reflectance at a given wavelength "cuts on" and "cuts off" more abruptly, and the peak wavelength (that is, the color), shifts with changes in the angle (Silberglied 1979). Additionally, at certain angles the reflected light will be highly polarized. When flying *Colias eurytheme* and other species are observed through a UV-viewing device, they resemble flashing beacons (Silberglied 1979). Crane (1954) writes: "With every wingbeat, a flying *Morpho* butterfly changes the angle of light incidence through the entire possible range. To the human eye, a *Morpho* in flight is simply a flickering flash of varying tints of blue. However, to another *Morpho*, in sunlight, there should be a brilliant shift from blue-green or blue to ultraviolet, then momentary extinction and back again through the spectral arc; conceivably this may be an exceptionally potent stimulus. The well known dipping of these butterflies to blue papers and other objects suggests strongly that the wing color may prove to be a sign stimulus in inter-male or courtship behavior."

Beetles

In some beetles that live under bark the microsculpture in the cuticle may produce a type of iridescence. This microsculpture has a characteristic orientation and asymmetrical sculpture, and is thought to be a by-product of the frictional properties of the cuticle (Crowson 1981). The more common bright iridescence seen in many Coleoptera is produced from light interference in thin films in the endocuticle. As with iridescence in feathers, and butterfly scales, these colors vary with the direction of incident light. The most frequent color is metallic green, but blue, red, gold, and purple are also common (Hinton 1973).

Colors are often a result of an animal's relation to activity and habitat. Green iridescence typically occurs in diurnal, leaf feeding beetles (Crowson 1981). Beetles that

are obligate cave dwellers are pale brown, not black, suggesting that this shade is the natural color when no selection for color occurs. Generally, nocturnal beetles are black (Crowson 1981).

One group of new world, scarab dung beetles, the phanaeinae, is known for iridescent colors, diurnal habits, and conspicuous behavior (e.g., Edmonds 1994). A conventional interpretation for this suite of characters is that the beetles may be bad tasting, and advertise their unpalatability to bird predators who subsequently avoid them (Arrow 1951). However, evidence for this hypothesis is minimal, and several other arguments for the adaptive benefit of iridescence in these beetles can be invoked with equal conviction.

ADAPTIVE HYPOTHESES

Not all examples of iridescence in animals may be adaptive. For example, some fly larvae infected with a particular virus become iridescent. Unless iridescence attracts new hosts or agents of dispersal, such coloration is probably an artifact and has no selective advantage. But given the striking apparancy of iridescence in diurnal dung beetles and other insects, it is reasonable to investigate adaptive hypotheses for their coloration.

Thermoregulation

Dung beetles of many species perch on leaves in tropical forests. While much of this behavior is related to foraging, one beetle species is thought to perch as a way of regulating body temperature (Young 1984). This beetle, however, is dull black. Bright, large scarabs probably possess internal mechanism that allow for large increases in body temperature prior to flight, and sun-basking in these beetles is not necessary (Young 1984). Further, iridescence reflects light, rather than absorbing it. Possibly, iridescence might serve to prevent overheating, allowing diurnal insects to forage in open habitats. Brilliantly colored species of phanaeinae are found in both forests and more open habitats (Edmonds 1994).

Distracting glare

Hinton (1973) argues that diffraction gratings can produce warning colors, and because some of the light reflected is of the complete spectrum, will also produce intense glare. This glare might prevent a predator from judging the exact distance of the animal.

Crypsis

Endler (1990) stressed that the conspicuousness of an animal in its environment is a function of the receiver's visual system, and the intensity, hue, saturation, and degree of contrast between different patches on the animal and its environment. What may be described as bright when seen out of context by humans may actually be cryptic in its environment. Many bright green iridescent leaf beetles could be cryptic to avian predators; e.g., the iridescence might resemble dew on leaves (Crowson 1981).

Visual signals

Colors can be used to pass information visually from one organism to another. In the case of insect iridescence, signals are most likely directed at either conspecifics or

at diurnal predators. Bats do not use vision in hunting, and generally, defense against these predators involves interference with their sonar, or evasive action (Dunning & Roeder 1965). Nocturnal mammals usually hunt by smell, and most diurnal mammals are not thought to have color vision. The main predators that would encounter visual signals from prey are birds, some reptiles, and other insects (Crowson 1981).

The physiology of bird sight is well known, but behavioral responses to specific colors are not. For example, there have been a number of studies examining birds' reaction to signals in the ultraviolet spectra. Birds have been known to have receptors sensitive to UV wavelengths for over 20 years (Bennett et al. 1996), but controlled studies to determine if they respond behaviorally to these frequencies are rare. Birds can distinguish between visible light that differs only in the presence or absence of the UV component (Goldsmith 1980). Studies using filters that screen out particular wavelengths in choice experiments reveal that female zebra finches respond preferentially to males that are displayed behind filters that allow transmittance of both UV and visible light as opposed to those that only allowed in visible light (Bennett et al. 1996). Because birds make mate choices based on UV reflectance, it might not be surprising to find that they perceive and react to UV reflectance in insects (see Parrish et al. 1984).

A—Aposematism: Bright colored insects, including certain dung beetles, are often thought to be aposematic. Arrow (1951) recorded an instance where one of the African ball-rolling beetles *Gymnopleurus virens*, which is bright green, blue, or crimson, was shown to induce nausea in a captive baboon. Furthermore, this beetle is usually found in association with 2 other similarly colored species, which are presumed to be Batesian mimics.

On Barro Colorado Island (BCI), two diurnal ball-rolling species, *Canthon c. sallei* and *C. moniliatus* are also brightly colored and conspicuous, flying slowly at 15-30 cm above the ground (Gill 1991). *Canthon c. sallei* produces a secretion that repels blowflies from its food (Bellés & Favila 1984), and these beetles captured in flight have an unpleasant aroma. *Canthon angustatus* displays with pygidium raised when threatened. The secretion of the exposed gland has been shown to repel assassin bugs (Gill 1991). Staphylinids and assassin bugs are known to eat other dung beetles. Small, metallic colored dung beetles like *Ateuchus*, and some *Canthon*, made up 74% of the captures by a robber fly on BCI (Shelly, cited in Gill 1991). Bats are also known to occasionally eat dung beetles (Bellwood, pers. comm.). Burrowing owls are a persistent predator of north American Phanaiines (Woodruff 1971), and other birds have been seen to eat them (Sivinski, pers. comm.).

Aposematism in other iridescent beetles has been more convincingly demonstrated. Many cicindelids are iridescent, and a number of these have been shown to be distasteful (Acorn 1988). One tiger beetle species appears to mimic an iridescent sympatric blister beetle species. Others are thought to be Mullerian mimics of each other. There is also a purported Mullerian complex of tiger beetles and mutillid wasps in Africa (Acorn 1988). Whether the iridescent colors of dung beetles are aimed at aposematic deterrence of predation remains to be demonstrated.

B—Social signaling: If the brilliant colors of some dung beetles are used in signaling conspecifics, the conspecifics must be able to detect either the colors or some aspect of them. The eyes of most Scarabaeidae are of the eucone type believed to make possible the discrimination of colors, and of polarized light (Horridge 1975). Electrophysiological evidence for color sensitivity has been found in some Cetoniinae (Scarabaeidae) (Mazokhin-Porshnyakov 1964).

Most insects appear capable of seeing ultraviolet reflectance. Their visual system often has one absorbance maximum around 350 nm (Silberglied 1979). Many species of butterflies use UV for communication (Silberglied 1979). In a number of butterflies,

ultraviolet patterns and iridescence are not related to the visible wing patterns (Silberglied & Taylor 1973), whereas UV reflectance patterns in birds often parallel the visible patterns (Bleiweiss 1994; Bennett et al. 1996).

To examine iridescent coloration in dung beetles, several species of *Phanaeus* and related genera were photographed at various angles and under different lighting conditions. Because insect perception is vastly different than ours, naturally, the inferences made about the photographs must be made with caution (Endler 1990). Photographs were taken from the front to simulate a beetle's eye view of another, interacting, beetle, with 100 ISO Fuji daylight slide film and a Cokin ring flash with color temperature 5600 K. Iridescent reflectance changed dramatically with the angle and intensity of the light, as is typical with interference coloration. The iridescence on the horn and clypeus disappears when not directly illuminated. The same light reflected onto the subject completely changes the pattern on the prothorax. A front view of *Sulcophanaeus imperator* reveals iridescent spots on either side of the head that resemble large red eyes. This is unlikely to be the region of the beetle typically encountered by attacking predators. Photographing an iridescent beetle, *Phanaeus mexicanus*, with daylight film under flash and UV lights yields even more psychedelic color patterns; i.e., the insect fluoresces by absorbing UV light and reemitting it in the visible spectrum. Finally, photographing phanaeines under UV light (Spectroline model MB100, peak wavelength 365 nm), with a Kodak UV 18A Wratten filter (passes only wavelengths between 310 and 400 nm), and a Panasonic AG-150 videocamera with a TV Zoom lens (6-54 mm; 1:1.4) (Eisner et al. 1988; Bleiweiss 1994; Van der Kerkovan, pers. comm.), demonstrated UV reflectance from various iridescent areas of the beetles, notably the front of the pronotum which forms an expansive shield (Fig. 1a and b). The UV reflectance could be seen only at specific light angles, and small changes of light source direction extinguished it. These dramatic and abrupt changes in light reflectance due to angle (in both the visible and ultraviolet spectra) could be a potentially efficacious method of communication, either between or within the sexes.

Beetle horns are thought to be used in combats between males for access to females or over resources that attract females. However, male-male encounters are rarely seen in the phanaeines (Halfpter & Lopez 1977; Rasmussen pers. comm.; but see Otronen 1988). Fighting requires energy and may lead to injury or at least the loss of a mating opportunity (see Sivinski this symposium). As an alternative to fighting, I suggest that males assess other males, particularly their size, by the appearance of the horn, and that this presentation is enhanced by iridescence. While the horn itself is less reflective, it is highlighted against the backdrop of a bright pronotal shield (Fig 1b). The relationship between horn size and body size in *Phanaeus* spp. can be complex and polymodel, however the two characters are generally positively and allometrically correlated (J. Sivinski unpublished data; see also Otte & Stayman 1979). Allometry may be characteristic of structures designed to transmit visual signals concerning male body size (e.g., Green 1992; see Sivinski this symposium).

In some phanaeines, such as *Diabroctus mimas*, male horns are small but the prothoracic shield is massive (Edmonds 1972), and may provide a broad signaling surface. The various bosses, projections, horns, sculpturing and textures that occur on phanaeines might be due to adaptations for signaling in different environments or even result from selection for species isolation through different patterns of reflective points. There is some intriguing evidence that color patterns in phanaeines may have simple inheritance patterns similar to that in the butterfly *Colias*. The blue and green morphs of *Phanaeus difformis* were bred in the laboratory with results consistent with Mendelian ratios in the offspring (Blume & Aga 1976).

Horns and prothoracic shields could also be used in male - female signaling. Females may choose males on the basis of many criteria (Arnold 1983). Hamilton and

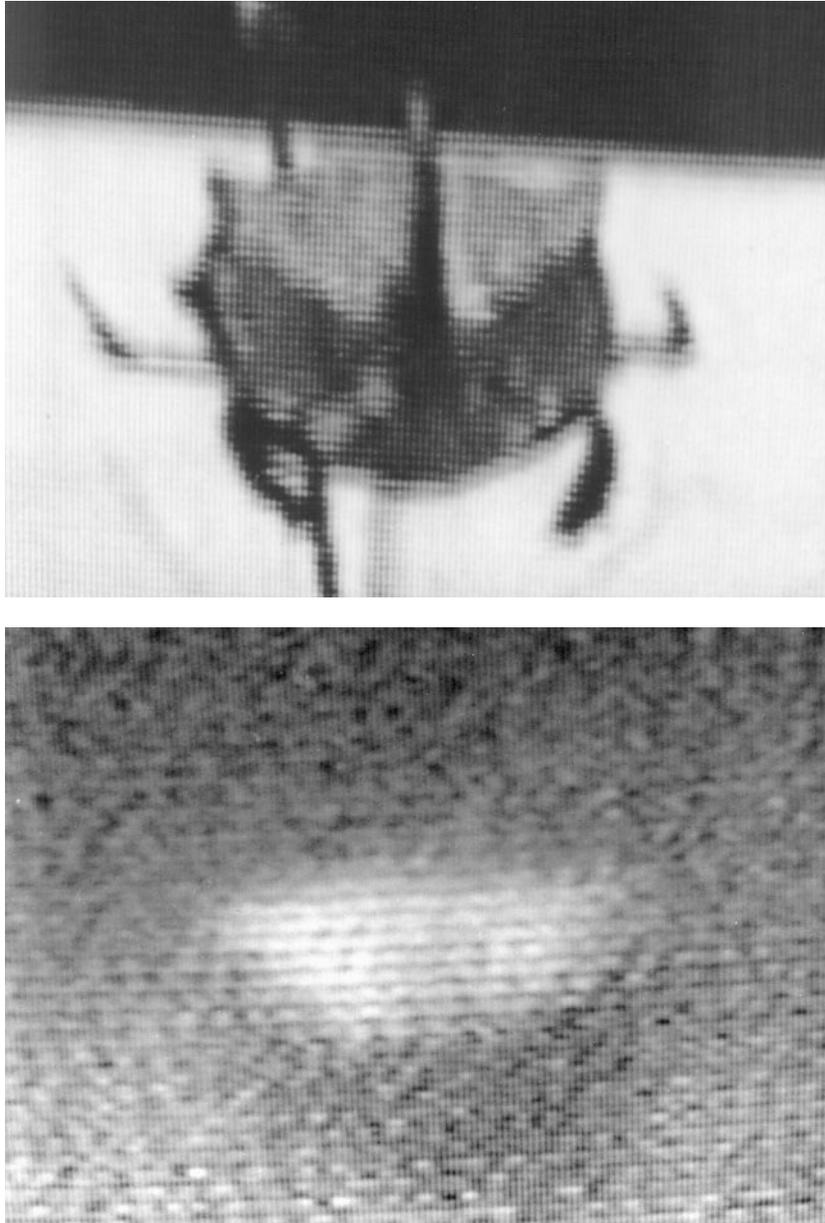


Fig. 1a—A photograph of a male *Phanaeus vindex* taken from a video screen displaying the specimen video-taped under light produced by a tungsten bulb.

b—The same specimen video-taped with a camera fronted by an ultraviolet filter and illuminated only by ultraviolet light. Note the strong UV reflectance of the prothoracic shield.

Zuk (1982) proposed that parasites can influence the evolution of sexually selected traits. Individuals increase their net fitness by choosing mates with high genetic resistance to parasites. This model assumes that heritable variation in fitness is maintained in host-parasite coevolution. Hosts will select mates based on condition-dependent traits that indicate parasite loads. For example, parasites in brightly colored birds may cause dulling in the plumage, or a change in courtship displays.

Many birds signal with patches of feathers that reflect UV and/or are iridescent in the visible spectrum (Radwan 1993). Male hummingbirds have iridescent patches on head and neck that can be seen only from certain angles (Tyrrell & Tyrrell 1990). In pigeons, iridescent feathers around the neck region have been hypothesized to inform potential mates of the health of the bird (Hamilton & Zuk 1982). Birds with little or no louse infestations are expected to show less iridescence. However, louse damage doesn't affect the distal end of the feather, which is the part visible on an intact bird. One study on mate choice in pigeons with artificially enhanced louse loads demonstrated that females are less likely to mate with males which have high louse loads (Clayton 1990). However, to human observers there is no difference between the birds. Unfortunately, these birds were not examined under ultraviolet light, and feather reflectance patterns may be affected in those wavelengths. Clayton hypothesizes that females see louse infestations during close encounters during courtship. Further, Clayton presents an alternative to the Hamilton-Zuk "good genes" hypothesis that mates are chosen for their genetic resistance to parasites. He argues that choosiness may be explained more parsimoniously by a female's aversion to contracting lice herself or passing them to offspring.

The bright triangular pronotum of *Phanaeus vindex* and related species can be occupied and partially obscured by phoretic kleptoparasitic flies (Sphaeroceridae), such as *Norbommia frigipennis*. The flies ride scarabs down into their subterranean chambers and deposit eggs in the fecal food-masses and brood balls, where the fly larvae develop (Sivinski 1983). The dung consumed by rapidly developing fly larvae may decrease the fitness of the slower developing beetle larvae. Because *Phanaeus* forms pair bonds and the pair cooperate in long periods of nest construction (Haftler & Edmonds 1982), it would be advantageous for a female to determine, prior to mating, that a male carries flies that might be deleterious to her offspring. Females may choose males that exhibit traits which clearly demonstrate their freedom from kleptoparasites.

The plausibility of the male-advertisement/female-mate choice hypothesis is affected by the absence of obvious behaviors that suggest female comparison of mating partners in phanaeine dung beetles (Arrow 1951; Otte & Stayman 1979). However, females of most species are turtle-shaped, and difficult for a male to mount. Furthermore, the female's genital opening is covered by a plate that would be difficult for a male to pry open. Such a structure suggests the possibility of covert female choice at the time of pair formation (Otronen 1988). Arrow (1951) suggests that female beetles have inadequate vision to assess male horn size. Iridescent and ultraviolet reflective surfaces, that change radically with small increments in angle of view, may serve as signal enhancement for the visually impaired.

Since males participate in securing provisions for their offspring they may also prefer mates without phoretic kleptoparasites. However, females appear to present fewer opportunities for males to discern an infestation. While females are typically the same color as males they are generally not horned and often have a less developed prothoracic shield. Exceptions are the nearly sexually monomorphic *Coproghanaeus lancifer* and *ensifer* (Edmonds 1972). These are extremely large insects that form brood masses from carrion. Perhaps in keeping with their nocturnal habits they are among the darkest colored of their tribe. Female horns are used in combats with other females and males in competitions over cadavers (Otronen 1988).

The hypotheses that iridescent surfaces are due to sexual selection through mate choice and intrasexual competition are not necessarily mutually exclusive. Neither does the use of iridescent characters in sexual contexts preclude the hypothesis that iridescent dung beetles may also be aposematic to diurnal predators or even cryptic in certain habitats. Iridescence in insects may be influenced by numerous selective pressures. The least explored is the hypothesis of social signaling, and male - male competition and perhaps intersexual assessment could be important in the evolution of iridescence in dung beetles. If so, the bright flashing patterns of still other iridescent insects may more often be territorial or sexual displays rather than aposematic or disruptive predator defenses (Crane 1954).

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