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Living in the dark does not mean a blind life: bird and mammal visual communication in dim light

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For many years, it was believed that bird and mammal communication 'in the dark of the night' relied exclusively on vocal and chemical signalling. However, in recent decades, several case studies have conveyed the idea that the nocturnal world is rich in visual information. Clearly, a visual signal needs a source of light to work, but diurnal light (twilight included, i.e. any light directly dependent on the sun) is not the only source of luminosity on this planet. Actually, moonlight represents a powerful source of illumination that cannot be neglected from the perspective of visual communication. White patches of feathers and fur on a dark background have the potential to be used to communicate with conspecifics and heterospecifics in dim light across different contexts and for a variety of reasons. Here: (i) we review current knowledge on visual signalling in crepuscular and nocturnal birds and mammals; and (ii) we also present some possible cases of birds and mammals that, due to the characteristics of their feather and fur coloration pattern, might use visual signals in dim light. Visual signalling in nocturnal animals is still an emerging field and, to date, it has received less attention than many other means of communication, including visual communication under daylight. For this reason, many questions remain unanswered and, sometimes, even unasked.

This article is part of the themed issue 'Vision in dim light'.

1. Introduction

Animals use elaborate signalling to communicate with conspecifics and heterospecifics in different contexts and for a variety of reasons. For example, social interactions (e.g. warning displays), mate choice and intrasexual competition (e.g. territoriality) may be the result of information transferred by visual communication [1]. Though the study of communication is a complex field of research, it has been widely explored in diurnal animals [1–4], as it was believed that visual communication was a prerogative of daylight. Scientists have long believed that crepuscular and nocturnal animals forgo such visual signals and rely solely on sound. Yet, many animals seem to indicate otherwise. If nocturnal vision allows animal displacements through a world of obstacles, and guides them to locate food sources, nests and dens, to select suitable mates, and to find new habitats, why should it not allow for visual communication also?

Twilight and nocturnal light (moonlight and starlight) may have acted as an evolutionary force shaping different methods of visual communication among a broad range of mammals and birds. Yet, as highlighted by Warrant [5, p. 786]: 'Our own rather limited ability to see at night, coupled to unwarranted feelings of sensory superiority, have clouded our expectations concerning the visual powers of other animals. In a sense this is quintessentially human, and it has happened before'. Our understanding of bird and mammal visual signalling in dim light has been further hampered by the fact that: (i) the assessment of

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Figure 1. Some examples of visual signals in crepuscular and nocturnal birds (upper photos) and mammals (lower photos). From left to right and up to down: the white badge on the eagle owl *Bubo bubo* throat (V. Penteriani), which is inflated during vocalizations; the white patches on the throat, wings and tail of a common nighthawk *Chordeiles minor* (123RF royalty free stock photos, http://www.123rf.com, image ID 35701390, copyright: Steve Byland), particularly visible during flying displays at twilight; the white feathers exhibited by the great bustard *Otis tarda* during displays at dusk and dawn (123RF royalty free stock photos, http://www.123rf.com, image ID 37058799, copyright: byrdyak); the mask of a European badger *Meles meles* (123RF royalty free stock photos, http://www.123rf.com, image ID 28445502, copyright: Michael Lane); the combination of black-and-white marks in the fur of the striped skunk *Mephitis mephitis* (123RF royalty free stock photos, http://www.123rf.com, image ID 7734416, copyright: Shirley Palmer); and the contrasting neck and tail of the Indian civet *Viverra zibetha* (123RF royalty free stock photos, http://www.123rf.com, image ID 9220957, copyright: panda3800).

coloration function necessarily hinges on the assumption that animals view the world in approximately the same manner as humans [6], which is not necessarily true; and (ii) moonlight may modulate the conspicuousness of visual signals, creating spatial (e.g. orientations of surfaces in a scene, as the source of light—the moon—changes position) [7,8] and temporal (e.g. full versus new moon, clear versus cloudy or foggy nights) patterns in their use. The irradiance spectra of sunlight and moonlight are similar, although full moon night light levels are approximately one million times dimmer [9] and on moonless nights illumination is provided by starlight only.

There is every reason to suspect that visual signalling is more widely employed by nocturnal animals than previously thought. Visual signals are produced by specialized morphological adaptations, pigment cells and musculature [10], and factors influencing their evolution include the perceptual systems of individuals receiving the signal, the nature of the conveyed information and the properties of the physical environment in which the signal is generated [11]. Indeed, if visibility of colour patterns depends on the background in which they are seen, species living in darker conditions may evolve brighter coloration to enhance visual display [11]. In daylight, variability in coloration is a particularly common signal, and bird plumage is one of the best examples. In diurnal birds, this type of information is generally conveyed through a wide range of carotenoid- and melanin-based colours, as well as structural colours (e.g. blue, violet, ultraviolet and white patches). Although there is little information on bird and mammal thresholds of colour vision, it is known that owls may use colours for signalling [12] and some diurnal birds have evolved more sensitive colour vision in dimmer light [13]. In dim light, however, colours could become progressively more indistinguishable. Indeed, a number of nocturnal species bear achromatic patches of feathers and fur, i.e. those showing pigment-free white feathers or fur and/or variability in the amount of melanin, which are ideal for signalling in dim light, when contrasts seem important (figure 1). Many nocturnal species have been found to be habitually active around sunset and sunrise [14], when specific conditions of ambient light may facilitate visual communication by white patches, and several other crepuscular species present contrasting visual signals associated with crepuscular displays, such as *Burhinus* spp. [14], the great snipe *Gallinago media* [15], the little bustard *Tetrax tetrax* [16] and the nightjar *Caprimulgus ruficollis* [17]. Thus, the need for nocturnal species to convey information to conspecifics by visual communication may have promoted convergent evolution towards white visual signals at twilight in distantly related groups of nocturnal species. Unlike acoustic signals, which may reach the receiver even if the sender's view is obstructed, visual signals only work when the sender positions itself in a conspicuous location, e.g. a visible place where the detectability of the signal is increased by the contrast between the signaller and its background [1,10]. For example, the setting or rising sun forms the best light angle for using a white patch as a high-contrast signal against a dark background [18,19]. Moreover, the light level under which birds are active also has a strong influence on eye shape and other aspects of the visual system [20]: nocturnal and crepuscular species have eye shapes that are optimized for visual sensitivity, showing larger corneal diameters and axial lengths than do diurnal birds [20]. That is, nocturnal birds exhibit eye shapes that are optimized for both increased image brightness and heightened visual acuity [20].

Our review on visual signalling in crepuscular and nocturnal birds and mammals presents the current state of knowledge in this field. We show that visual signalling in dim light is an emerging field and, to date, there is still little evidence concerning what these animals are exactly communicating and under what circumstances they may rely on visual signals. As many questions remain unanswered and, sometimes, even unasked, we also highlight some possible cases of birds and mammals that, due to features of their feather and fur coloration patterns, might use visual communication in dim light.

2. Visual signalling in birds

For many years, it was believed that crepuscular and nocturnal bird species only use vocal communication. Yet, a growing body of literature has recently provided new insights into how important visual signals also are for these species [21]. It is well known that: (i) birds use very specific light environments for their displays where plumage characteristics are maximized because of the ambient light and background properties [18,19] and (ii) the light environment plays a role in the evolution of colour patterns and signals [19,22,23]. Thus, we can easily expect that any visual signal used around twilight by crepuscular and nocturnal bird species should maximize the use of the scarce light available. This was experimentally demonstrated by Penteriani & Delgado [24] when studying the patterns and functionality of the white patch of the eagle owl *Bubo bubo* throat: the variability in the total amount of light reflected by throat feathers is exploited as a high-contrast signal both at twilight and on bright nights. Notably, the white throat of eagle owls is repeatedly exposed (inflated and deflated) at each call, following a pattern of switched on–off that may be related to the idea that birds should mostly communicate with dynamic signals [25].

Visual communication in crepuscular and nocturnal bird species may be modulated by lunar cycles [26]. Iida [27] reported that the display flight of the Latham's snipe *Gallinago hardwickii* usually has peak periods shortly before sunrise and shortly after sunset, as well as at midnight during full-moon periods. Indeed, the number of displays increases on full-moon nights. The increase of displays may be related to the fact that males can easily locate females in clear moonlight because of their white marks. Penteriani *et al.* [28] also showed that call displays of eagle owls, which are associated with the exposure of their white badge, are strongly related to the moon phase, as silent nights are more frequently darker nights than brighter nights. Moreover, call posts chosen by displaying owls are higher on nights with moonlight than without, suggesting that nocturnal birds may take advantage of any source of natural light to increase the effectiveness of their visual communication.

Achromatic plumage has been shown to present individual variability in size or design, as well as status-related variability and sexual dichromatism in the amount of total intensity of the light spectrum. For example, previous research on the barn owl *Tyto alba* showed how plumage coloration (number of black spots) was positively correlated to female quality in terms of immunocompetence [29,30]. The same authors suggest that the trait may be under intersexual selection (male mate choice) because: (i) males that mate with highly spotted females obtain more immunocompetent offspring [31], (ii) males consistently choose to mate with such females in different breeding seasons and (iii) their male offspring also prefer highly spotted females as mates [32]. Along the same line, eagle owls also show female-biased dichromatism in the brightness of their badges [33]. The eagle owl is a resident, territorial and apparently plumage monomorphic species characterized by relatively strong mate bonds and female contribution to territorial defence. Such characteristics suggest that higher reflectance in females may be due to intersexual selection (male mate choice). In fact, in some monogamous species with biparental care, males seem to select their mate in the same manner as females, as the fitness of the former is also affected by female quality [31,32,34]. As an additional or alternative explanation, sexual dichromatism in eagle owls could have also emerged from female–female competition for both a mate and a territory. In eagle owls, due to the subtle sexual size dimorphism, colour variability in the white badge may be used as a signal of female quality related to body size. In fact, a significant correlation was detected between female forearm size and brightness [33]. In this way, the variability in the female white badge could have arisen as a means to evaluate rivals. As female body size has been related to fertility in different raptor species (e.g. larger females produce more and larger eggs) [35], males could benefit from choosing mates based on this trait.

Thus, signal conspicuousness in nocturnal birds may be an effective way of distinguishing between potential mates. This might also be the case for the red-necked nightjar *C. ruficollis*, a nocturnal bird in which the variation of white bands on the wings and tail is related to sex and age, being larger in males and adults [17]. This variation potentially allows individuals to evaluate others in aggressive or reproductive contexts. In the great snipe, males have white spots on their tails, and females choose the males with the whitest signals [15]. As stressed by Aragonés *et al.* [17], nightjars are birds that rely on crypsis (as one of the most efficient antipredator mechanisms), while visual communication requires the conspicuousness of signals. Thus, visual cues in nocturnal birds may be the outcome of an appropriate balance between these two selection forces, and for this reason, these signals are generally hidden under cryptic feathers and only visible during displays.

It is at sunset and sunrise when little bustard males [36] perform wing-flash displays at their lekking sites. Such displays have been suggested to play a role in the context of male–male competition and mate choice [16]. These assumptions are respectively supported by two facts. First, the probability that a male used a wing-flash display increased with lek size. Second, the wing-flash display was most likely performed when a female visited the display site. Further, vegetation height also affected the probability of wing-flash displays, and it is likely that in habitats that preclude the propagation of visual cues (e.g. high vegetation) males will not invest in such displays. Wing-flash displays have been observed in other bird species too, as in the case of the pennant-winged nightjar *Semeiophorus vexillarius* that shows the white markings on its wings while displaying at twilight [37]. Similarly, Allan [38] observed that male advertisements in the Ludwig's bustard *Neotis ludwigii* include spectacular visual displays from prominent positions at twilight, which involve the inflation of their large neck to the maximum extent and the exhibition of their upper chest plumage.

In an attempt to understand whether the white feathers of the eagle owl throat patch could function as a signal towards conspecifics, Penteriani *et al.* [39] evaluated the performance of this white badge during contests by simulating territorial intrusions. They analysed the reactions of territory owners towards a taxidermic mount with a control badge (i.e. normal brightness treatment) or a brightness-reduced badge, with both male and female territorial calls. Different reactions to different badge treatments indicated the importance of visual cues in owl conspecific communication. The results of this study provide the first experimental support for the hypothesis that the white badge of eagle owls plays an important role in visual communication during contests, also being the first time that it has been possible to establish an active role of visual signalling in a nocturnal species. The dynamics of the contests were consistent with the idea that the brightness of the white badge was used as a status-signalling trait. The responses ranged from ritualized calls to direct attacks. Consequently, the eagle owl's white badge might be considered a phenotypic signal that reliably informs opponents about their asymmetries in fighting skills, minimizing the risk of wasteful and potentially injurious fights. Indeed, visual signalling may have coevolved to maximize the effectiveness of social communication such as the dusk/dawn chorus, when several favourable conditions for conspecific communication coincide (e.g. proximity of individuals to their nest sites—territory owners generally have their diurnal roosts close to the nest) [40]. The results regarding owl badge characteristics as a signal of individual quality fit well with the remarks of Johnstone & Norris [41], who stated that badges which serve to settle conflicts should also constitute honest indicators of individual condition. As far as we know, there is no evidence concerning the direct physiological cost of producing achromatic traits. However, honest signalling may also be preserved by honesty-maintaining mechanisms (i.e. costs induced by social interactions), which would prevent cheating because only high-quality dominant individuals could stand the cost of aggression [42,43].

The potential assortative mating pattern found in eagle owls by Bettega *et al.* [44] may also support a role for their white feathers as a signal of individual quality. Assortative mating, which may occur through a variety of behavioural mechanisms [45], has been observed in both structurally coloured species and species exhibiting white marks. For example, assortative mating may be the result of individuals' mutual preference for similar phenotypes [46] and/or by intrasexual competition for nest sites. This competition may result in high-quality individuals gaining access to the best territories and pairing with high-quality mates. Following Kose & Møller [47], there are at least two potential costs associated with using white plumage for signalling. First, melanization strengthens feathers; non-melanized feathers are more likely to break due to their greater structural weakness. Second, if feathers without melanin are particularly susceptible to breakage, it is also possible that feather parasites may display a preference for the melanin-free parts of feathers. Although the costs associated with the brightness of white feathers is a topic in need of further research, these results suggest a definite relationship between bright, white plumage and an individual's physical state. This relationship is a prerequisite for the use of white markings as a signal of individual quality, supporting previous evidence from Gustafsson *et al.* [48] and McGlothlin *et al.* [49].

Importantly, colours may also play a role in social and sexual signalling in nocturnal birds. When studying the colour variation, and potential signalling, of the yellow bill in females of the little owl *Athene noctua*, Avilés & Parejo [50] found that the yellow-red chroma of the bill was highly variable between individuals. Females with brighter bills were larger in size and produced larger owlets, suggesting that the yellow part of the bill may indicate female quality and potentially be used as a quality signal in intra and intersexual contexts [51].

Visual signals can also play an important role in parent–offspring communication during feeding. For example, during the post-fledging dependence period [50], control eagle owl fledglings were in better condition than fledglings with brightness-reduced mouths, suggesting parental preference based on visual cues. Parejo *et al.* [52] showed that the cere of scops owl (*Otus scops*) nestlings reflects UV, with the level of reflectance related to body mass. In their experiment, the authors observed that parents biased food allocation towards nestlings that presented UV levels typical of nestlings with small body size. Further, Avilés & Parejo [50] recently demonstrated that owlet bill coloration advertizes quality and influences parental feeding behaviour in little owls. Until quite recently, the only recognized way in which owl chicks communicated with parents was via the vocalizations associated with begging, an activity designed to solve family conflicts over parental feeding. However, in most avian species, begging may involve several different signals such as posturing and plumage features [53–55]. The combination of the vocal and visual components of begging might provide parents with additional information concerning the state of the offspring and/or reflect different aspects of offspring condition [53]. The different elements involved in begging displays may interact synergistically—in particular, visual cues may increase parental response to vocal cues [56]. Lastly, offspring detectability by parents can be enhanced by brightness contrast between the white fleshy borders of the gape and its dark surroundings [57].

Finally, crepuscular and nocturnal birds may mark focal elements of their home ranges with different conspicuous visual signals as a defence against predators and to attract potential mates [58]. During the pre-laying period and throughout the nestling period, large quantities of visible white faeces and prey feathers appear on posts and at plucking sites in the vicinity of the nest site, which may signal breeding status to conspecifics [59]. As would be expected for a signalling behaviour that has evolved to maximize signal strength relative to the background environment, the data in this study suggest that eagle owls preferentially leave white faeces on the darkest and most detectable surfaces, and preferentially leave prey species with conspicuous plumage at highly visible plucking sites. Some of the faecal marks are only visible from nests, suggesting that they may also signal the owl's reproductive state or function in mate–mate communication (e.g. choice of nest placement). In such a context, the authors did not exclude the possibility that the faecal markings provide a signalling function similar to that conveyed by the transport of green material to the nest (especially for owls that do not carry nesting materials), which in some bird species serves as an intersexual signal for nest occupation. These signs might also contain useful information for predators. Indeed, there is another study suggesting that birds can use visual cues during the night to deter predators. This is the case for male malachite sunbirds *Nectarinia famosa*, which display pectoral tufts only while sleeping at night. As they appear in the dark as 'eyes' to humans, Wellmann & Downs [59] suggested that this nocturnal display in male malachite sunbirds may deter predators.

3. Visual signalling in mammals

Since researchers first tried to explain the function of coloration in mammals, they have debated the significance of black-and-white coats [6]. However, the possibility that such a contrasting mix of dark and white patches of fur might have a visual signalling function in dim light have frequently been overlooked (but see [60–62]). As a consequence, there has not been systematic attempts to test different theories of coloration with respect to black-and-white pelage in mammals, especially crepuscular and nocturnal species, although Caro [6] reported that many species of terrestrial mammals have contrasting black (or dark) and white (or light) patches of fur on their heads, bodies, legs or tails.

Compared with birds, mammals show a smaller variety of colour patterns, being generally limited to various shades of brown and tan to grey and black and white [62], with the exception of primate families that may show more elaborate coloration [6,62]. Some prevalently crepuscular and nocturnal species of mammals have distinct contrasts in markings, as is the case for the conspicuous markings in the facial region of a group of mesopredators that includes 36 species from four families of Carnivora [62] (figure 1), i.e. *Mustelidae* (e.g. European badger *Meles meles*, American badger *Taxidea taxus*, marbled polecat *Vormela peregusna*), *Procyonidae* (e.g. raccoon *Procyon lotor*), *Canidae* (e.g. raccoon dog *Nyctereutes procyonoides*) and *Viverridae* (e.g. African civet *Civettictis civetta*). Among other possible functions, a communication role based on the combination of black-and-white marks may be possible, especially as patterns of contrasting brightness in the pelage are particularly useful in dim-light communication [63], i.e. at times when all these carnivores are active. These masks mainly occur in a select group of medium sized mammalian carnivores that coexist with larger carnivores and suffer from intraguild predation [64], meaning that this group of mesopredators has the capacity (because of their aggressiveness and scent defences) to deter predatory advances by attacking and harming larger carnivores. Newman *et al.* [62] used natural history and semiquantitative data to suggest that these facial masks may represent an aposematic coloration, i.e. a warning signal to deter predation by larger carnivores. Indeed, these authors showed that facial masks could be a visual signal warning predators that an attack would be answered by a counter attack that potentially could be harmful to the perpetrator and/or discharge noxious odours from anal scent glands. Implicitly, this means that such mammals have evolved a way to communicate in dim light, signalling their ability to respond to an aggressor. Although experimental tests are lacking, we believe that this might represent one of the most striking and well-supported cases of interspecific visual communication in crepuscular and nocturnal mammals ever reported, as these species provide a crucial example supporting the existence of visual communication using coloration by mammals in dim light. Similarly, the facial markings of the slow loris (*Nycticebus* spp.) of Southeast Asia might be a form of aposematic coloration (slow lorises are the only primates that harbour toxins) or a form of Müllerian mimicry of spectacled cobras (*Naja* sp.) to protect adults and young against predators, an adaptation that can also be used for intersexual competition [65].

Caro [6] suggested that aposematism cannot apply to all face masks, because these masks may also function as signals of dominance or condition (i.e. intraspecific communication) at night. This might be the case for some small nocturnal species such as the feather-tailed possum *Distoechurus pennatus*, the garden dormouse *Eliomys quercinus*, the fork-marked dwarf lemur *Phaner furcifer* and the night monkey *Aotus*, that display these fur patterns at dawn and dusk. As found in several species of diurnal lemurs, which use black-and-white fur patterns for conspecific signalling [6], these nocturnal species might take advantage of contrasting fur patterns for social communication. In some cases, however, fur patterns are puzzling. This is the case for fossorial blesmols or African mole rats (Bathyergidae), which have poor vision [66] but which possess white markings on their face or head. However, the presence of these patterns of coloration may nonetheless indicate the need to communicate in dark environments [6]. The same can be suggested for the white-and-black facial bars of the plains viscacha *Lagostomus maximus*, in which facial marks may provide an aposematic or pursuit deterring signal. That is, independent of the receiver of the signal (a conspecific or a predator), all these species seem to have evolved similar visual signals for information transmission in dim light. Among the 5000 species described by Caro [6], many crepuscular and nocturnal species have contrasting patches on their body that might potentially be used for visual communication in dim light, but their function is still unclear, because no experimental studies have been attempted. As examples we can mention here those species that have contrasting necks and chests (e.g. European pine martens *Martes martes*, grisons *Galictis vittata*) or a black body with white spots (e.g. spotted pinto bats *Euderma maculatum*, black pacaranas *Dinomys branickii*). As a general remark, which may also serve as additional support for the hypothesis that contrasting fur patterns might allow for visual communication in dim light, we agree with one of Caro conclusions [6] that areas of the face, neck and chest are most likely viewed upclose by conspecifics and thereby have the potential to be involved in intraspecific communication.

Although detailed research in this area is still lacking, it has been suggested that visual recognition by means of facial markings between conspecifics may be important in Strepsirrhini [67], a suborder of primates that includes the lemuriform primates, among which are the lemurs [60,61]. These are cathemeral species (i.e. animals that can have both diurnal and nocturnal activity [68]) that possess distinctive facial markings (i.e. patterns of light and dark fur on the face) that might enable them to distinguish between species and individuals by sight in dark environments. Moreover, dark rings around the face that are surrounded by a light area may function as a startle display against predators [61], particularly in poor light conditions [60].

Finally, it is important to briefly mention another peculiarity of crepuscular and nocturnal mammals, namely ultraviolet vision. Ultraviolet light sensitivity was discovered in mammals only two decades ago [69] and it is probably typical of small-sized species: imaging errors caused by chromatic aberration in the ultraviolet region increase with the size of the eye, and this would no doubt be particularly disturbing for larger species [70]. Additionally, ultraviolet sensitivity is restricted to small, night-active mammals [69,71]. The possible adaptive function of ultraviolet vision in mammals may be to enhance visual contrast perception [72] of ultraviolet light-reflecting body patches during the twilight phase of the day, when the spectrum is shifted towards short wavelengths [73], i.e. when the ozone attenuates middle wavelengths disproportionately because solar elevations are low. Thus, although twilight can be rich in short and long wavelengths initially, short wavelengths will eventually dominate. Ultraviolet light sensitivity may thus represent an additional but unexplored adaptation for communication at twilight when light conditions favour patches of fur that contrast well in this part of the spectrum.

4. Visual communication in dim light, an overlooked way to communicate

This synthesis of our current knowledge on visual signalling in crepuscular and nocturnal avian and mammalian species highlights several lines of evidence showing that visual communication has been an overlooked communication channel, although it does not seem to be as general as vocal communication. As a consequence, an interesting question arises: why have not all nocturnal animals evolved visual communication? This is particularly remarkable if we consider that one of the more obvious properties of visual signals is the ease of identifying sender location: if the signal is visible, the location of the sender is known. This could be potentially important in dim light, when the perception of the surroundings and its elements is limited. Most nocturnal species communicate via their voice, which is the reason why we have thought for decades that most of them rely exclusively on vocal signalling. In addition, many mammals have glands that allow for chemical communication, but few of them seem to have evolved visual communication. Such an adaptation in a narrow range of species might indicate that very specific conditions and/or needs are required for visual signals to evolve in nocturnal birds or mammals. However, why visual signalling has evolved in these nocturnal species remains a mystery.

A lack of experimental evidence prevents us from suggesting the conditions under which some species developed visual signalling in dim light. But now that we know that visual communication is an effective way for birds and mammals to communicate 'in the dark of the night', this communication channel provides a very promising field for future research. However, we still lack the wider body of data necessary to support and better understand the evolution, characteristics and mechanisms of visual communication in dim light. Further, we also need to (i) improve our understanding of the way visual signals respond to ambient light conditions and (ii) better understand the visual systems of those nocturnal species that communicate in this silent but conspicuous manner. Obviously, understanding visual signalling starts by understanding how animal eyes are adapted to see and interpret such signals. Both behavioural and physiological approaches are therefore needed. Because the environment plays a major role in animal communication, it is also crucial to understand the success of behavioural strategies as a function of environmental conditions [74]. Understanding how animals perceive natural environments at night will allow us to gain insights into how they have adapted their communication to dim light conditions. The dim nocturnal world seems to be much richer in visual information than we have previously given it credit for [5].

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