

REVIEW

Visual Ecology in Challenging Environments

Vision at high latitudes: High sensitivity without specific boreal adaptations in photoreception in reindeer (*Rangifer tarandus* L.)Nicholas J. C. Tyler^{1,2}  | Robert A. E. Fosbury^{3,4} | David Hazlerigg⁵ | Christopher Hogg³¹Centre for Saami Studies, UIT The Arctic University of Norway, Tromsø, Norway²Department of Agriculture, Lincoln University, Christchurch, New Zealand³Institute of Ophthalmology, University College London, London, UK⁴European Southern Observatory, Munich, Germany⁵Department of Arctic and Marine Biology, UIT The Arctic University of Norway, Tromsø, Norway

Correspondence

Nicholas J. C. Tyler

Email: nicholas.tyler@uit.no

Handling Editor: Sara Stieb

Abstract

1. The light climate at high latitudes, in particular the extended twilight of winter and the reduced diel variation in light level in midsummer and midwinter, potentially constrains visual function and the synchronisation of temporal organisation in polar species.
2. In this paper, we describe the temporal pattern and variation in the spectral composition and brightness of skylight (daylight, twilight, moonlight, starlight, airglow and aurorae) at high latitudes and review photoreception of reindeer/caribou (*Rangifer tarandus*; '*Rangifer*') which is one of the few polar resident species for which data are available.
3. Experimental data indicate that the rods of *Rangifer* may be stimulated by levels of ambient light lower than those occurring during astronomical twilight (solar angle <math><-18^\circ</math>).
4. Several features of the eyes of *Rangifer* contribute to their visual capability under extended twilight. These include transmission of UV through the optical media, which enables the animals to exploit the shorter wavelengths characteristic of twilight, and a shift in the peak spectral reflectance of the *tapetum lucidum* (TL) from around 640 nm in summer to around 450 nm in winter, which increases retinal illumination at short wavelengths.
5. Enhanced sensitivity to short wavelengths is likely to enhance the contrast of some objects and hence the ability of *Rangifer* to discriminate forage plants and to detect other animals (conspecifics or predators) against a snowy background under low illuminance.
6. There is, nevertheless, currently no evidence of any specific boreal adaptation in their visual system: (i) The eyes of *Rangifer*, and by inference the area of the dilated pupil, are no larger than expected based on the allometry of eye size in ruminants. (ii) There is no evidence of a change in the spectral sensitivity of photoreceptors associated with detection of UVa. (iii) Transmission of UV through the anterior eye is not unique to *Rangifer*. (iv) The blue shift in the reflectance of the winter TL appears to be a passive response to prolonged dilation of the pupil and there is no a priori reason not to predict the same response in other large ungulates exposed

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2024 The Author(s). *Functional Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

to low light levels. (v) There is no conclusive evidence of a seasonal shift in absolute retinal sensitivity in *Rangifer*. (vi) Weak circadian organisation in *Rangifer* has tentatively been linked to mutations within the circadian molecular clockwork but it remains unclear to what extent this represents a specific adaptation to high latitude.

KEYWORDS

light–dark cycle, *Rangifer tarandus*, reindeer, spectral irradiance, *tapetum lucidum*, twilight, UV, visual adaptation

1 | INTRODUCTION

The light climate influences animals directly in two ways. First, they need light to see and visual appreciation of the environment is therefore constrained by both the spectral sensitivity and the dynamic range of their eyes. They also need to synchronise their physiology, activity and behaviour with daily and seasonal environmental cycles and they use predictable diel (24 h, [Box 1](#)) and annual (365 day) variation in light level as cues to achieve this. The extended twilight of winter and the reduced variation in light level across the diel in both summer and winter at high latitudes ([Box 2](#)) therefore potentially represent major constraints on the visual function and temporal organisation in polar species.

Low ambient illuminance between sunset and sunrise clearly limits visual function in our species: humans are almost wholly dependent on artificial light for pursuing outdoor activity after sunset. Many species of mammal, including many large herbivores, by contrast, are principally active around dawn and dusk (Cox & Gaston, 2023; Tyler et al., 2020): for these, activity in low illuminance (civil twilight, [Box 2](#)) is normal. Indeed, most eutherian mammals and marsupials retain the rod dominated retinae and have limited colour vision, both redolent of ancestral low light lifestyles (Borges et al., 2018; Bowmaker, 2008; Gerkema et al., 2013). The spectral sensitivity of mammals also varies between species in ways that reflect selective pressures derived from the characteristics of the light climate in which their visual systems evolved. Some, for instance, have become cone monochromats. Thus, many aquatic mammals have lost their short wavelength sensitive cones and have very restricted colour sensitivities: for them the sea is not blue (Bowmaker, 2008; Peichl et al., 2001). Here we examine how the eyes of reindeer/caribou (*Rangifer tarandus*, hereafter '*Rangifer*') respond, and how the regulation of temporal organisation in this species has responded, to prolonged levels of high and low light characteristic of summer and winter, respectively, at high latitude.

2 | ADAPTATION TO LOW ILLUMINANCE

Adaptation to the extended twilight of the polar winter has both functional and temporal dimensions. Functionally, we may distinguish

BOX 1 Glossary

Airglow	The emission of faint light from the upper atmosphere at night from energy stored in atoms and molecules excited or ionised by solar ultraviolet radiation during the day or by cosmic-rays and chemiluminescence
Aurora	Aurorae are high latitude light emissions resulting from disturbances in the Earth's magnetosphere caused by the incoming solar wind
Astronomical twilight	Level of light when solar elevation is -12° to -18° relative to the horizon. Beyond this is 'darkness'
Boreal	Of northern regions including the Arctic and sub-Arctic climatic zones
Chappuis band	A broad spectral absorption band in the visible region (450–650 nm) due to ozone gas in the stratosphere. While much weaker than the very strong shorter wavelength Hartley and Huggins absorption bands in the UV that protect the biosphere from molecular radiation damage, the Chappuis band becomes the dominant visible light absorber when the Sun is close to or below the horizon. It results in the deep metallic purple of twilight that is entirely different from the Rayleigh scattering blue of the clear daytime sky
Chionophile	Organism that thrives in cold winter conditions
Civil twilight	Level of light when solar elevation is 0° to -6° relative to the horizon
Colour temperature	A shorthand for describing the spectral distribution of source of light in terms of the temperature (measured in Kelvin) of a thermal (Planckian) radiator that exhibits the same perceived colour. This is useful for natural sources of environmental light such as sunlight or moonlight but can be misleading for non-thermal emitters such as the twilight sky

BOX 1 (Continued)

Darkness	Level of light when solar elevation is less than -18° relative to the horizon
Dichromat	Animal possessing two types of cone receptors
Diel	Period of 24 h associated with one rotation of the Earth. The diel (24 h) cycle of light can be considered in terms of its photoperiod. The light portion of the 24 h cycle is denoted 'day' or 'photophase' while the dark portion is denoted 'night' or 'scotophase'
Diurnal	Activity or event occurring between dawn and dusk
Illuminance	The total luminous flux incident on a surface, per unit area. The unit is lux (lx) and the quantity is wavelength-weighted to correspond to human visual perception
Insolation	Solar radiation energy input received at the surface of the Earth per unit area per unit time integrated over the spectral range reaching the ground
Irradiance, spectral	Energy received by a flat surface per unit time, per unit area and per unit wavelength or frequency. When dealing with the interactions between photons and biology, it is more appropriate to use photon number rather than energy, for example, photons per second per m^2 per nm. Photon spectral irradiance increases by the factor of the wavelength towards longer wavelengths compared to energy irradiance
LED	Light emitting diode
Light climate	The intensity, spectrum, and duration of light in a given period at a given location
Light-dark (LD) cycle	Diel cycle of light intensity across one diel ('day-night cycle')
Lux (lx)	A lux is one lumen per square metre ($\text{lm}\cdot\text{m}^{-2}$)
Lumen (lm)	The lumen is the unit of luminous flux, a measure of the total quantity of visible light emitted by a source per unit of time
Luminance	The incident energy of light in a given direction
Mesopic	Light level in which both rods and cones are active (see also 'photopic' and 'scotopic')
Nocturnal	Activity or event occurring between dusk and dawn
Nautical twilight	Level of light when solar elevation is -6° to -12° relative to the horizon
Photoperiod (PP)	The duration of the photophase of one diel
Photophase	The light portion of the 24 h cycle (diel) during which photopic vision occurs
Photopic	Light level in which cones are principally active (see also 'mesopic' and 'scotopic')
Polar day	Period of the year during which the Sun remains above the horizon throughout the diel, that is solar elevation remains $>0^\circ$ through the entire 24 h cycle

BOX 1 (Continued)

Polar night	Period of the year during which the Sun remains below the horizon throughout the diel, that is solar elevation remains $<0^\circ$ through the entire 24 h cycle
Scattering	Scattering of light is the redirection of a photon, usually without a change of wavelength, when it encounters a change in refractive index
Scotophase	The dark portion of the 24 h cycle during which there is scotopic vision
Scotopic	Dim light in which rods but not cones are active (see also 'mesopic' and 'photopic')
Scotopic threshold response (STR)	A corneal negative deflection elicited in the fully dark-adapted eye to dim stimuli which and appears to originate in the inner retina
Solstice	Event when the Sun appears to reach its most northerly or southerly excursion relative to the celestial equator and hence when, in either hemisphere, there is most or least sunlight of the year (summer and winter solstice, respectively). The summer solstice occurs around June 21st and the winter solstice around December 21st
Spectral quality	The difference between the spectral distribution of sunlight outside the atmosphere and that reaching the ground is the result of both the scattering and the absorption of photons by atmospheric constituents in processes that have different wavelength dependencies. These spectral changes are most extreme during twilight
Sward	Mat of grass and similar growth forms on the surface of the ground
Tapetum lucidum (TL)	An intraocular reflecting structure behind the retina that influences the light sensitivity capabilities of the eye
$\text{Td}\cdot\text{s}^{-1}$	Trolands per second. A Troland is the retinal illuminance occasioned by 1 mm^2 of pupil being illuminated by $1\text{ cd}\cdot\text{m}^{-2}$
Twilight	Level of light when the Sun is below the horizon. See: 'civil', 'nautical' and 'astronomical' twilight
UV (ultraviolet light)	The region of the electromagnetic spectrum with wavelengths between 100 and 400 nm: UVa (315–400 nm), UVb (280–315 nm) and UVc (100–280 nm)
$\text{W}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$	An integral measure of energy occurring in a short duration flash
Zeigeber	A periodic environmental signal that entrains some biological rhythm
Zodiacal light	Light from the scattering of sunlight off dust particles, the remnants of the formation of the Solar-system, orbiting in the plane of the ecliptic

between modulation of the amount of light enters the eye and the processing of light once it has been captured. Temporally, we distinguish between short term, dynamic responses that occur within seconds or minutes, and structural adaptation that has developed across an evolutionary timescale.

The principle short term response to a reduction in illuminance is dilation of the pupil which increases the amount of light entering the eye. *Rangifer* have large eyes and their fully dilated pupil has a diameter of approximately 21 mm (C. Hogg, unpublished data) compared to just 8 mm in the adult human (Spector, 1990). Consequently, under full dilation—which is likely to be the permanent condition for much of the boreal winter—the eyes of *Rangifer* admit approximately seven times more light than the eyes of humans, thus giving them substantially greater potential for absorption of photons. (Note: The relative increase in retinal illumination will be slightly less than seven times owing to light being spread over a greater area in the larger eyes of *Rangifer*.)

A second short term response is the progressive change from cone to rod dominated vision, that is a transition from the photopic, through the mesopic and into the scotopic range of retinal function. This transition can be detected from changes in the waveform of the electroretinogram (ERG). Thus, the scotopic threshold response (STR) of the ERG gives the first electrically recordable indication of retinal activity originating in the retinal ganglion cells and driven by the dark-adapted rods (Frishman, 2006; Saszik et al., 2002). The luminance level required for the STR in *Rangifer* in winter is $8 \cdot 10^{-8} \text{ W} \cdot \text{s}^{-1} \cdot \text{m}^{-2}$ at 525 nm (C. Hogg, unpublished data). It follows that the rods of *Rangifer* are likely to be stimulated at levels of ambient light through and even below astronomical twilight (i.e. at luminance levels $\leq 10^{-7} \text{ W} \cdot \text{m}^{-2}$; Figure 3). This conclusion is emphasised by the fact that the ERG threshold, the STR, underestimates visual sensitivity by approximately 3 log units when compared psychophysical measurements of the perceptual act, at least in humans (Ruseckaite et al., 2011).

The shift from cone to rod vision involves considerable metabolic activity: indeed, the rod driven dark-adapted retina has the highest specific metabolic rate of any tissue in the mammalian body (Wong-Riley, 2010). This is due in part to synthesis of new outer segment discs at the base of the rod outer segments and the phagocytosis and removal of waste products from old ones through the retinal pigment epithelium (Rodieck, 1998). These processes are mediated by the daily light/dark cycle (Rodieck, 1998), and it is not clear how they are regulated in winter when this cycle is weak or absent. It may be that the outer segments increase somewhat in length and that the resulting accumulation of outer segment discs enhances photon capture and hence retinal sensitivity. Unlimited accumulation of active and shed discs, however, would normally be expected to limit the flow of blood between the retinal pigment epithelium and the outer retina and hence the transport of nutrients to, and waste products from, the photoreceptors.

The variation in illuminance across the diel is accompanied by a significant change in the spectral composition light reaching the

eye (Box 2), which many species appear able to exploit owing to the characteristics of spectral transmission through their ocular media. Twilight, which is a principal characteristic of the boreal winter (Box 2), includes a substantially greater proportion of shorter wavelengths than daylight owing to the attenuation by the atmosphere of the longer wavelengths (a shift towards the blue end of the spectrum at around 350–500 nm; Figure 4). The UVa (315–400 nm) component of twilight is almost entirely beyond the lower limit of the adult human visual range (approximately 390 nm; Bowmaker, 2008) and therefore contributes nothing to our visual capacity. The anterior eye of *Rangifer* by contrast, is UVa permissive and the retina responds electro-physiologically to the output of narrow band LEDs at both 372 nm and 330 nm which increases the amount of light/energy entering the eye (Hogg et al., 2011). Note: LED devices have narrow spectral output, typically ± 10 –15 nm (50%) but, owing to the broad spectral range of cones, it is reasonable to assume that the eyes of the animals are sensitive to light across this entire range; Bowmaker, 2008). The magnitude of this effect is difficult to estimate, owing to the number of variables involved, but the 50% bandwidth of the light available to *Rangifer* evidently extends from 400 nm upwards into the near infrared in summer while in winter, when the available light at its predominant wavelength is reduced by 4 log units, its 50% bandwidth shifts downwards to 320–500 nm (Figure 4). The effect of this change is to shift the visual input to the rods and, to some extent, to the short wavelength cones.

A major structural adaptation to low illuminance has been the evolution, in species from many taxa, of a reflective surface behind the central retina called the *tapetum lucidum* (TL; Johnson, 1968; Walls, 1942). The TL functions as a mirror that reflects back through the retina photons not absorbed during their first pass, returning them for a second pass and thus a further opportunity for absorption by the photoreceptors. The TL, plainly apparent by the way the eyes of many mammals shine when caught in car headlights at night, differs fundamentally between groups. In carnivores the reflective property of the TL is based on crystalline structures but in large herbivores it is based on collagen fibres (Ollivier et al., 2004; Walls, 1942). The TL thus appears to be an instance of the convergent evolution of different structures to a similar function (Schwab et al., 2002). Irrespective of its structural basis, in most species the central region of the TL appears golden in colour (Johnson, 1968) indicating that the TL preferentially reflects the wavelengths in the middle of the visual range. (Note: Images of the TL of five species of large ungulates published by Ollivier et al. (2004) are turquoise-blue). The apparent colour of TL observed in vivo, however, is likely to be modified by absorption in the retina through which it is normally observed. The colour of the TL can only be properly characterised by spectroscopy analysis of preparations stripped of overlying tissue.) In *Rangifer*, both by contrast and also uniquely so far as currently is known, the spectral reflectance of the TL changes across the annual cycle (Fosbury & Jeffery, 2022; Stokkan et al., 2013). In summer it appears golden,

BOX 2 The light climate at high latitude

The light climate in polar regions is determined by the same atmospheric scattering and absorption processes that occur at all latitudes. The specific property of high latitudes is the geometry of the path taken by sunlight as it traverses the atmosphere to reach the ground. This is closer to tangential than to radial and so is generally longer on average, with a higher column density, than at lower latitudes. The path, furthermore, is modulated across the year by the tilt of the Earth's equator with respect to the plane of its orbit (23.5°; [Figure 1](#)) which generates temporal variation in the annual cycle of daily insolation, culminating in continuous day in midsummer and continuous night in midwinter ([Figure 2a](#)).

Temporal variation in the light climate

Daylength at any point on the surface of the Earth—save at the Equator—traces an annual cycle between an annual maximum at the summer solstice and an annual minimum at the winter solstice. The amplitude of this cycle, and hence daylength at the solstices, increases away from the Equator until, at latitudes in excess of 66° N/S, the Sun remains above the horizon across the diel for at least 1 day at the summer solstice and, correspondingly, below it for at least 1 day at the winter solstice ([Figure 2a](#)). These two events, the polar day (photoperiod (PP) = 24 h) and the polar night (PP = 0 h), respectively, increase in duration by approximately 7 days with each degree of latitude. Thus, the polar day lasts ~2 months at 68° N and ~4 months at 78° N while the polar night lasts ~1 month at 68° N and ~4 months at 78° N and the visual environment is correspondingly predominantly mesopic-scotopic for an extended period in winter ([Figure 2a](#)).

The term 'polar night' and the associated characterisation 'PP = 0 h', however, are misleading insofar as they imply a constant state. This is not the case. The solar angle of elevation, though continually negative, continues to describe a diel cycle, ascending to a minimum at midday and descending to a maximum at midnight ([Figure 2a](#)), thereby generating a corresponding diel cycle of light intensity. This, by convention, is recognised at four levels congruent with the amount of light scattered into the upper atmosphere from the Sun at varying degrees below the local horizon. These are 'civil twilight' when solar elevations are between the horizon and 6° below the horizon, 'nautical twilight' at solar elevations from 6° to 12° below the horizon, 'astronomical twilight' at solar elevations from 12° to 18° below the horizon and, beyond this, there is 'darkness'. Consequently, even in midwinter at 78° N there are approximately 8 h astronomical twilight in the middle of the day ([Table 1](#)).

Spectral (wavelength) and brightness variations

We first consider the variations of the environmental light produced by the changing solar altitude measured in degrees from the local refracted horizon (<https://gml.noaa.gov/grad/solcalc/calcdetails.html> for explanations and mode of calculation used in this paper).

Direct sunlight is the principal contributor to skylight at solar altitudes above approximately 5°. Below this, indirect sunlight provides the illumination by scattering from the atmosphere (twilight), reflection from the Moon (moonlight) and, at a much lower level, by scattering from dust occupying the Solar System in the plane of the ecliptic. The latter contribution is generally called the 'zodiacal light' and the material scattering the light is the continuously evolving debris left over from the formation of our planetary system about 4.6 billion years ago. Low surface brightness notwithstanding, it is a prominent and easily recognisable feature in a dark sky and a potential aid in animal navigation near dawn and dusk.

Additional contributions come from starlight. This provides a low-level background that is modulated by the position of the plane of our Galaxy in the sky which varies through the night and the year. It is accompanied by a visually faint and time-variable airglow originating in the high atmosphere from energy stored in the atmospheric gases during the day and released slowly during the night. The aurora, which may occasionally reach much brighter levels, will often contribute at high latitudes. These contributors and their brightness ranges are illustrated in [Figure 3](#).

Daytime

On a clear day the sky irradiance changes by a factor of a few hundred between sunset/rise and noon. In the visible spectrum, this corresponds to a change from about 400 to 100,000 lx. In the presence of a heavy overcast and a low Sun, this factor can increase to several thousand. When the Sun is below the horizon, however, the natural range of irradiance increases dramatically to a total factor of a billion from a truly dark sky to full sunlight.

The spectral quality of the visible sunlight reaching the ground during the day is determined almost entirely by two scattering processes. The first of these is the Rayleigh scattering of solar photons by the molecular constituents of the air, mostly N₂ and O₂. For such scatterers that are much smaller than the wavelength of light, the scattering power increases rapidly towards the blue as the inverse fourth power of the wavelength. It is this Rayleigh scattering that forms the blue of a cloudless sky by redirecting, in a single scattering event, predominantly short wavelength light from the column of air carrying sunlight to the ground.

BOX 2 (Continued)

The sky, however, is not always clear and other particles with sizes more comparable to the light wavelength scatter light with a wavelength dependence (colour) that depends on their shape, size and refractive index. This process (Mie scattering) produces a much less saturated scattered blue light than Rayleigh. Altering the combination of these two scattering processes change the appearance of the sky from a crisp deep blue to a palette of soft pastel colours.

Twilight

When the Sun drops below the horizon, the twilight irradiance in the absence of moonlight, driven by indirect sunlight scattered from the atmosphere above the observer, drops by almost a factor of a million (from 10 to approximately $10^{-5} \text{ W}\cdot\text{m}^{-2}$; [Figure 3](#)). This large range becomes extremely pertinent at high latitudes owing to its occupying such a large fraction of the diel ([Figure 2](#)). The twilight is in addition accompanied by a marked change in spectral composition due to the deep metallic purple colour of ozone gas that occupies a layer between around 12 to 40 km over the ground.

The ozone layer in the upper atmosphere that strongly absorbs (and therefore protects the surface of the Earth from harmful UVB and UVC radiation) also absorbs in the visible spectrum. Absorption in the Chappuis band becomes apparent around sunset and sunrise when the sunlight grazes the atmosphere. The selective removal of a substantial fraction of the green/yellow, orange and red light leaves a deep blue-purple spectrum and creates the deep metallic blue twilight which is extended in time at high latitudes ([Figure 4](#), [Table 1](#)). The blueness of twilight is unaffected by cloud conditions because the ozone absorption takes place well above the cloud layer and acts as a sky-spanning filter affecting everything below it. This absorption however leaves the UVA and the near-infrared (NIR) regions of the spectrum almost untouched. This effect of ozone in twilight is illustrated in [Figure 3](#) where the ozone column density represents the transition between civil and nautical twilight.

Moonlight

A full moon has an illuminance in the visible spectrum of approximately 0.25 lx. This corresponds to the brighter part of the range of nautical twilight ([Figure 3](#)) and hence adds a small but significant dose of reflected sunlight to the twilight sky. The lunar surface is not quite uncoloured (grey): it reflects about half as much blue as it does red light and so has a brownish tint. The level of illuminance varies across both the lunar and the diel cycle. Variation across the lunar cycle reflects the change in visible illuminated surface area associated with the waxing and waning of the moon and the backscattering of light off lunar dust which causes a full moon to be approximately six times brighter than first or last quarter rather than just twice. Variation across the diel reflect the fact that lunar illuminance varies with its altitude. During darkness (i.e. solar elevation $< -18^\circ$), the full moon reaches its highest altitude at local midnight when it can create the illuminance approximately equivalent to late (i.e. sunset) civil twilight ($\approx 1 \text{ lx}$). The spectral irradiance then contains a weaker blue signature of ozone absorption and the light will be yellower than twilight. In the twilight phase of the diel, by contrast, the full moon is always at a low altitude and its contribution to the irradiance is smaller because of the cosine factor of altitude and the atmospheric extinction. In practice this means that the lunar light contribution remains approximately constant at $\sim 2 \times 10^{-4} \text{ W}\cdot\text{m}^{-2}$ (on the irradiance scale used in [Figure 3](#)) when its disk is more than 50% illuminated (Palmer & Johnsen, 2015).

Starlight, airglow and aurorae

The remaining contributors to natural skylight are the astronomical background, consisting of direct and scattered starlight, some small fraction coming from the far reaches of the Universe. The major contributor to this is our own Galaxy, the Milky Way, the centre of which is seen best from the southern hemisphere. Its colour is a little redder than sunlight, contributed by a huge number of faint red stars in the Galaxy.

The airglow is faint but can be seen as the shadow of an object seen against the sky on a dark, moonless night. It derives from molecules and atoms in the atmosphere that are excited or ionised by sunlight during the day and which slowly release this energy at night, mostly in the green, red and far-red regions of the spectrum.

The aurora shows a rather similar spectrum to the airglow but it is excited instead by high speed particles from the Sun interacting with the Earth's magnetic field which guides them towards the magnetic poles where they collisionally excite light emissions from the atmosphere. The aurora can be much brighter than the airglow and can rival and even exceed the irradiance of the full Moon.

The colour of natural skylight changes continuously from full Sun to the darkest night, most conspicuously around sunset. As the Sun approaches the horizon, the irradiance becomes redder than the 'white' of daylight while the extinction-reddened Sun remains dominant. Before it reaches the horizon, the scattered light from the sky takes over from the dimming Sun and moves the colour towards the blue. As soon as the Sun sets, there is a rapid increase in blueness as the ozone Chappuis band absorption asserts its influence. This trend increases and becomes a deep 'metallic' purple during nautical twilight. Finally, as the light fades towards darkness, the

BOX 2 (Continued)

influence of starlight and the airglow moves the colour towards the red again. The inverse sequence occurs during sunrise of course. When the Moon is present at its brighter phases, it dilutes these colour changes by adding a dose of slightly reddened sunlight to the mix.

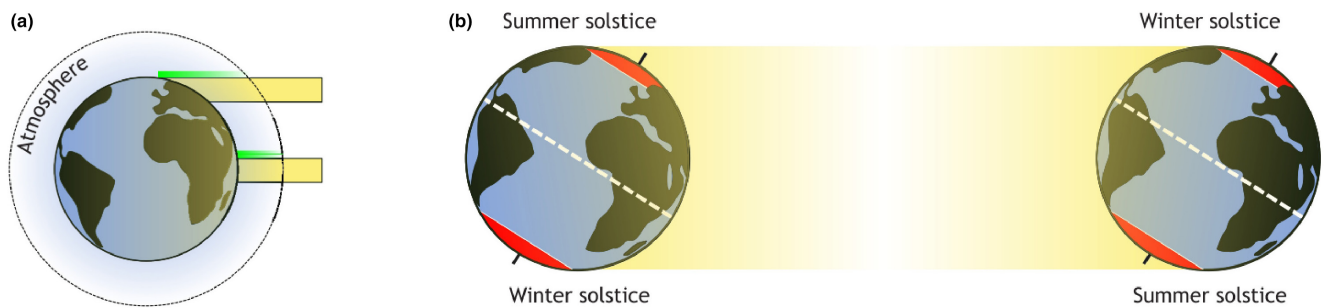


FIGURE 1 The polar light climate. (a) At high latitudes the path taken by sunlight as it traverses the atmosphere to reach the ground is closer to tangential than to radial and so is generally longer on average, with a higher column density, than at lower latitudes. (b) Exposure of the Earth's surface to sunlight is modulated across the year by the tilt of the Earth's equator with respect to the plane of its orbit (23.5°). This generates temporal variation in the annual cycle of daily insolation, culminating in continuous day in midsummer and continuous night in midwinter (Figure 2a). After Hazlerigg et al. (2023).

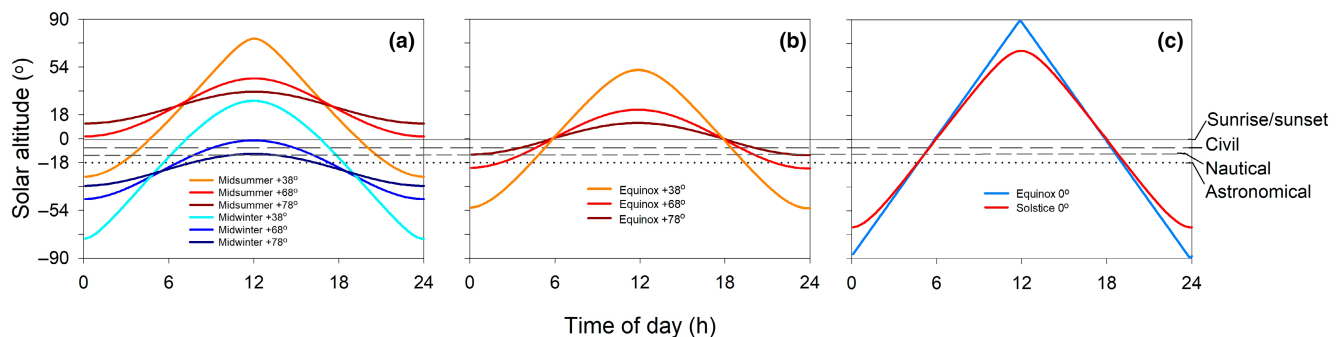


FIGURE 2 Representations of solar altitude across the diel illustrating latitudinal variation in the duration of twilight and darkness at different times of year. (a) Summer and winter solstices at latitudes +38°, +68° and +78°. (b) Equinox at latitudes +38°, +68° and +78°. (c) Equinox and solstice at the equator. Dashed and dotted horizontal lines indicate the lower limits of civil (0 to -6°), nautical (-6 to -12°) and astronomical (-12 to -18°) twilight, respectively. Data from NOAA_Solar_Calculations_day.xls.

TABLE 1 Effect of latitude on the duration (h) of different levels of light (h/24 h) at the winter solstice.

Solar angle (°)	Light level	Latitude		
		38° (h)	68° (h)	78° (h)
>0	Daylight	9.6	0	0
0 to -6	Civil twilight	1.2	5.5	0
-6 to -12	Nautical twilight	1.2	3.1	0
-12 to -18	Astronomical twilight	1.2	2.2	8.4
< -18	Darkness	10.8	13.2	15.6

like the TL of other large herbivores (e.g. European mouflon (*Ovis aries musimon*) and domestic cattle (*Bos taurus*; Johnson, 1968), and it displays peak spectral reflectance around 640nm with a saddle extending to around 320nm (Figures 5 and 6). In winter, by contrast, it appears blue owing to a shift in peak spectral reflectance to 450nm (Figure 6).

The blue shift in the spectral reflectance of the TL of *Rangifer* in winter appears to be a consequence of prolonged dilation of the pupil (Stokkan et al., 2013). This is a progressive response. When the pupil is fully dilated, the iris folds over and obstructs the trabecular meshwork through which fluid in the anterior chamber of the eye (between the cornea and the lens) drains. Restriction of flow causes

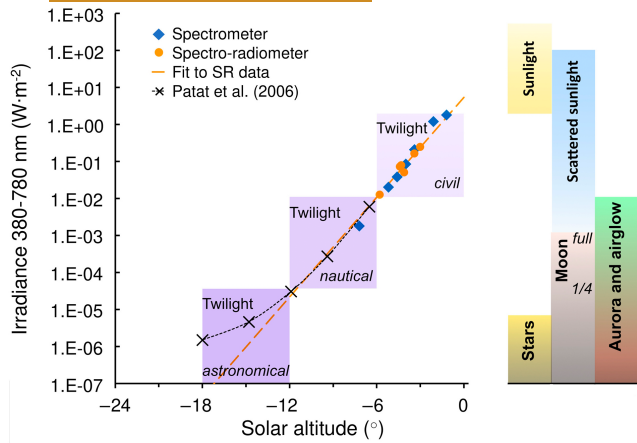


FIGURE 3 Diagrammatic representation of the sky irradiance from daylight (solar altitude $>0^\circ$) to darkness ($<-18^\circ$) and showing the range of the contribution from sources discussed in the text. The irradiances on the ordinate are computed as the integral of measured spectral irradiances over a wavelength range from 380 to 780 nm. Empirical spectroradiometer data from Patat et al. (2006) are included for comparison. The diagram covers the level of irradiance across the visual dynamic range of humans. The graph was constructed from a combination of our own measurements of the twilight sky spectral irradiance at 52° N with published measurements from the European Southern Observatory's Paranal VLT site in northern Chile. The upper data points (orange circles) are from measurements of clear sky twilights since 2018 using a Sekonic C-7000 spectroradiometer which gives absolute spectral irradiance measurements in the visible spectrum. The blue diamond measurements are made with an Ocean Insight Maya2000Pro spectrometer which has a relative wavelength-brightness calibration that has been referred to the absolute scale of the Sekonic radiometer.

an increase in intraocular pressure which it is proposed reduces the amount of fluid within the TL, and thus the spacing between the collagen fibres, causing them selectively to reflect light of shorter wavelengths and hence the TL to appear blue (Figure 5; Fosbury & Jeffery, 2022).

The seasonal change in the colour of the TL in *Rangifer* seems to be an adaptive response to the seasonal change in the spectral irradiance of environmental light. The reflective characteristics of the winter TL match the blue-dominated spectrum of the twilight winter sky (Box 2): the TL appears, in effect, to be seasonally tuned to the animals' visual environment. This results in an increase in retinal illumination at the shorter wavelengths which predominate in winter and contributes to the enhancement of visual function across the mesopic range evident from an increase in retinal sensitivity of up to 3 log units below the summer threshold (Hogg et al., 2011).

3 | ARE THERE SPECIAL ADAPTATIONS IN RANGIFER TO THE LIGHT CLIMATE AT HIGH LATITUDES?

Three features of the eyes of *Rangifer* contribute to the visual capability of the animals during the prolonged twilight of the Arctic winter: their large pupils, transmission of UV through the anterior eye and the blue shift in the TL. None of these features, or the putative extension of rod outer segments, however, can be considered a specific evolutionary adaptation to the light climate of the boreal zone.

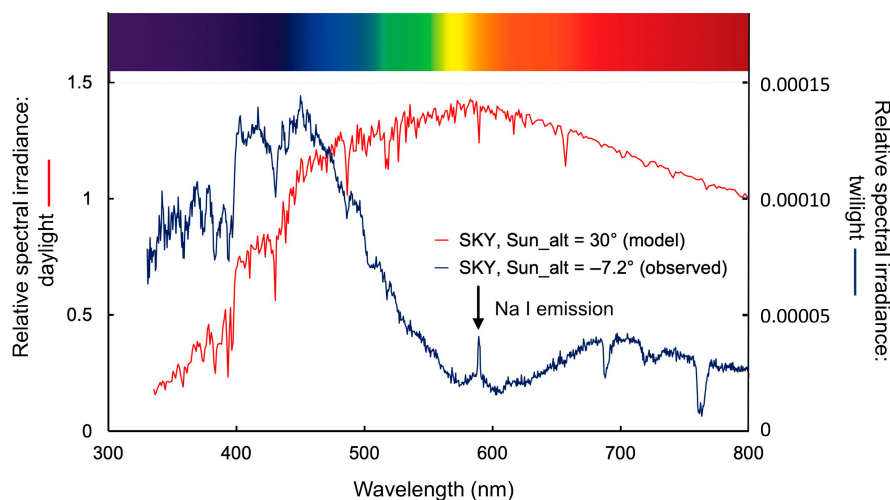


FIGURE 4 Changes in the spectral composition of light across the diel. Spectral irradiance of a clear daylight sky and that near the beginning of nautical twilight (solar altitude -12° ; Figure 3) where ozone has its maximum effect on colour. The red line shows a model of sunlight at a solar altitude of 30° which includes the effects of Rayleigh and aerosol scattering but without any molecular absorption. The blue line is a measurement of a clear sky with the Sun 7.2° below the horizon. This includes the dominant molecular absorption in the Chappuis band of ozone which removes much of the green to orange/red region of the spectrum; it also shows other absorption bands of water vapour and oxygen which appear at wavelengths longer than 600 nm. The data indicate the enormous relative amplification of the blue at the peak of 'the blue hour' around the onset nautical twilight. Note that these twilight spectral data appear as the lowest blue diamond point in Figure 3 and have been scaled up in brightness by more than four orders of magnitude to illustrate the qualitative comparison here. The marked narrow orange emission peak is sunlight scattered by sodium atoms from ablated meteors at altitudes of around 100 km.

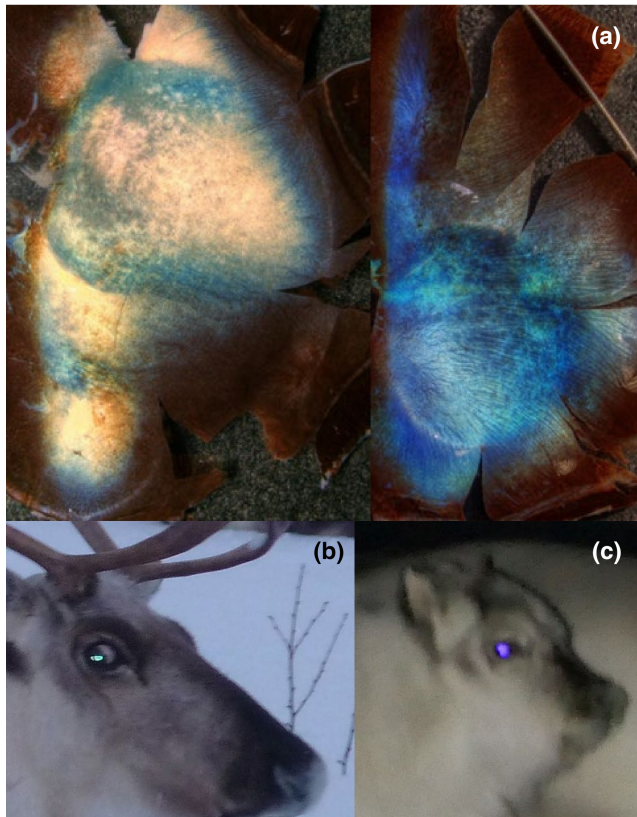


FIGURE 5 The tapetum lucidum (TL) of *Rangifer*. (a) Reflections of daylight from whole mounted tapeta collected in summer (Left) and winter (Right). The reflection from the summer specimen is largely golden with turquoise at the edges. The winter specimen reflects blue. The tissues were fixed with 10% formalin and flat mounted in phosphate buffer. In both cases the reflective surfaces reside only in central retinal position and are absent from the periphery. (b) The TL of an adult free-living reindeer (*R. t. tarandus*) reflecting a camera flash (March). (c) The same in a juvenile (5 mo.) free-living Svalbard reindeer (*R. t. platyrhynchus*; November). Photographs by (a) Robert Fosbury and (b, c) Nicholas Tyler.

First, the large area of the dilated pupil in *Rangifer* is in part a consequence of their having large eyes but their eyes are no larger than expected based on the allometry of eye size in tropical and temperate zone ruminants (Figure 7). Hence, there is no evidence that exposure to the boreal light climate resulted in selection for increased eye size and, by inference, an associated increase in the area of the pupil in this species. This contrasts with the situation in birds and primates in which there are well-established associations between ambient light levels and the size of the eye (Pearce & Dunbar, 2011). Particularly relevant among these is a positive association between latitude and orbital volume in humans which, insofar as the orbit predicts the size of the eye in our species, has been interpreted specifically as an adaptive response to low light (Pearce & Dunbar, 2011). The difference between humans and *Rangifer* in this respect may be due at least in part to the absence of a TL in the former which consequently elevated the responsive significance of increased eye and hence pupil size.

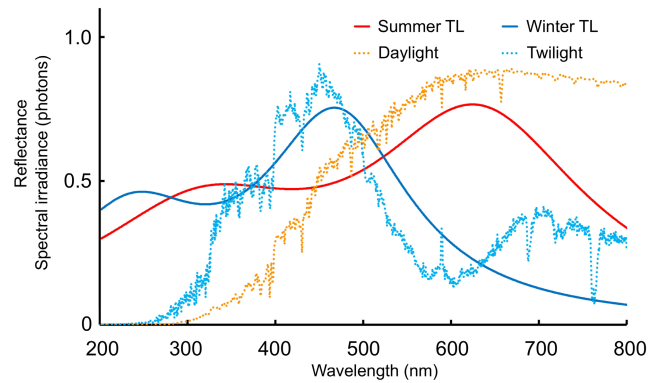


FIGURE 6 Transformation of the reflectance spectrum of the *Rangifer* tapetum between summer and winter. The measurements were made from preparations like those shown in Figure 5a. The change in reflectance is the result of changes in the spacing of the constituent collagen fibres in the tapetum. Peak of reflectance occurs around 640 nm in summer and 450 nm in winter. Although the summer reflectance appears largely golden, a long saddle in the response (≈ 500 to ≈ 320 nm) indicates that the tapetum reflects across the animals' visual range into the UV (≤ 400 nm). The winter reflectance is tighter and closely matches the spectral composition of the winter twilight sky (see text) and a greater proportion of the reflectance spectrum is located in the UV range.

Second, retinal RNA extraction and in vitro opsin expression has produced no evidence of a change in the spectral sensitivity of photoreceptors associated with the detection of UVa. The response to UVa in *Rangifer* is mediated by short wavelength sensitive cones which have a peak spectral sensitivity around 439 nm (Carvalho et al., 2006; Cottrill et al., 2009). This is above the UVa band (Box 1) but the spectral profile of cones extends substantially either side of peak sensitivity: they will therefore respond across a range of wavelengths provided stimuli are sufficiently strong (above). Moreover, transmission of UV through the anterior eye is not unique to *Rangifer*. The optics of many non-primate species of mammals are UV permissive (Douglas & Jeffery, 2014). The rate of transmission of UV through the lens of *Rangifer* (26.5%) is substantially above the median value for 11 species of large herbivores (15.2%) but nevertheless substantially below that of the okapi (*Okapia johnstoni*, 53%; Douglas & Jeffery, 2014) which is a tropical species. No explanation for the high rate of transmission in the okapi has been offered.

Third, the seasonal increase in intraocular pressure proposed to be responsible for the blue shift in the reflectance of the winter TL is a passive response to prolonged dilation of the pupil (above). If this is indeed the cause, there can be no objection to the mechanism extending to other large ungulates and therefore to these expressing a similar shift in response to extended exposure to twilight. This has not to our knowledge been tested. Interestingly, darkness initiates a similar kind of response in humans: the human pupil dilates during sleep and there is a corresponding increase in intraocular pressure of 4%–40% (Liu et al., 1999, 2015): no function for this response, however, has been proposed.

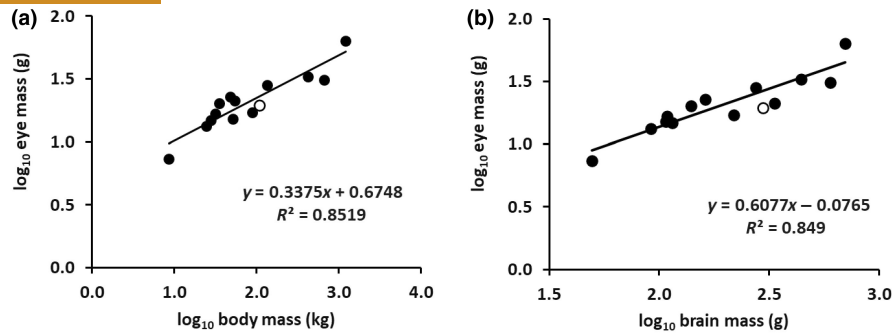


FIGURE 7 Allometry of eye size in ruminants. Correlation between the mass of one eye (\log_{10} g) and the mass of (a) the body (\log_{10} kg) and (b) the brain (\log_{10} g) in 14 species of ruminants, including 9 tropical and 4 temperate zone species and reindeer/caribou *Rangifer tarandus* (white circle). The standardised residual of the mass of the eye of *Rangifer tarandus* was in each case <3.5 , NS. Similar results were obtained using axial length of the eye in place of eye mass (Howland et al., 2004). Data from Burton (2006).

Finally, there is a strong indication but as yet no conclusive evidence for a seasonal shift in absolute retinal sensitivity in *Rangifer*. Nor, as a matter of principle, could such evidence easily be obtained. *Rangifer* is a boreal species and, with the exception of animals at the southern border of the species' global range (Tyler et al., *In press*), their eyes are never normally exposed to darkness ($<10^{-7} \text{W}\cdot\text{m}^{-2}$; Figure 3) in summer and the STR of the summer phenotype is therefore a functional abstraction. A mean STR of $2.6 \cdot 10^{-6} \text{W}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ at 525 nm recorded in June appears to indicate lower retinal sensitivity in summer compared to winter (mean STR $8 \cdot 10^{-8} \text{W}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ at 525 nm; C. Hogg, *in prep.*) but the difference is probably spurious: the summer measurements were made following just 45 minutes' dark adaptation (the normal experimental standard) whereas natural dark adaptation in winter is likely to be the sum of multiple adjustments that develop over a period of weeks.

Taken together, the data show that *Rangifer* have normal mammalian visual capabilities and there is currently no evidence of the boreal light climate having promoted evolution of novel structures or mechanisms in their visual system. We cannot, of course, exclude the possibility that these exist but none to date are known.

4 | WHAT DO RANGIFER SEE IN WINTER TWILIGHT?

A central question is what *Rangifer* actually see in the low illumination of the boreal winter (i.e. at irradiance levels of $10\text{--}10^{-7} \text{W}\cdot\text{m}^{-2}$; Figure 3). This cannot satisfactorily be addressed. Measurements of retinal sensitivity indicate to what level of light an animal's retina responds but reveal nothing about visual perception. The macaque STR ($1.5 \cdot 10^{-11}$ scotopic $\text{Td}\cdot\text{s}^{-1}$; Frishman, 2006) indicates sensitivity well beyond astronomical twilight yet another primate—ourselves—has very limited visual perception at this level of luminance. Current understanding of the vast range of visual function in mammals, represented by differences in colour perception, visual acuity and light sensitivity, is almost wholly based on sensitive visual psychophysical and other methodologies that can readily be applied in humans but

are barely practicable in animals. We can therefore only speculate about what *Rangifer* perceive visually in winter.

Rod dominated vision means that they perceive their world in monochrome and have only coarse spatial resolution. It is unlikely, for instance, that they can differentiate by colour the edible parts of the diminutive Arctic plants on which they feed: selective foraging in twilight must involve a combination of vision and other senses. Moreover, it is not inconceivable that rod dominance in *Rangifer*, as in humans (Arden & Hogg, 1984), is accompanied by inhibition of cones which would further reduce the likelihood of colour discrimination under low light. Increased sensitivity to short wavelengths, on the other hand, is likely to enhance the contrast of some objects and hence improve the ability of the animals to discriminate plants and animals (conspecifics or predators) against a snowy background as well as enabling them to detect certain forms of anthropogenic activity (Box 3). Above all, their ability to detect available light in the dark-adapted state, enhanced by the large aperture of their pupil, the reflective action of the TL and their extended spectral range, almost certainly results in their world appearing brighter than it does to humans under similar conditions, and presumably also enhances what they perceive at very low levels of contrast.

5 | NON-VISUAL PHOTORECEPTION IN RANGIFER

In mammals, non-visual photoreception refers to photosensing by retinal cells which does not contribute to vision, instead serving to modulate behaviour and physiology to match the changing light environment (Doyle & Menaker, 2007). Given the rhythmical essence of solar illumination (Box 2), non-visual photoreception is strongly associated with the temporal organisation of behaviour, which may be shaped by a combination of direct light effects ('masking') and *Zeitgeber* effects mediated via entrainment of biological time-keeping (chronobiological) processes operating at diel (circadian) or annual (circannual) timescales (Bittman, 2021; Bruce, 1960; Mrosovsky, 1999). Longstanding interest in how adaptation to life

BOX 3 Functional aspects of UV vision in *Rangifer*

UV and visual salience of plants and predators

Visual sensitivity to UV wavelengths is a feature of species in many taxa, among them insects, birds, fish and non-primate mammals (Aidala et al., 2012; Chittka et al., 2013; Douglas & Jeffery, 2014; Harosi & Hashimoto, 1983). A variety of functions have been attributed to it: navigation and orientation appear to be associated with scattering and polarisation of UV wavelengths while signalling, foraging and detection of predators have been associated with enhanced levels of contrast between features of interest and their background (Aidala et al., 2012; Cronin & Bok, 2016; Newman & D'Angelo, 2024; Tovée, 1995).

Consistent with the latter, Hogg et al. (2011) and Stokkan et al. (2013) suggested that extension of the visual range into the UV in *Rangifer* (main text) might confer selective advantage by enhancing image formation in low but relatively UV-enriched levels of illuminance characteristic of the extended twilight of high latitudes (Box 2). Their suggestion rested on the assumption that forage plants and other biologically important elements of their environment are visually salient under natural UV illuminance. This, however, is not self-evident. Most organic material strongly absorbs UV, including vascular plants and many species of lichens (Dominy et al., 2023; Gausman et al., 1975; Petzold & Goward, 1988; Robberecht et al., 1980) and swards are therefore likely to form dark, low-contrast images with reduced visual information when viewed in the UV range. Snow, however, completely alters this situation. Snow strongly reflects UV and organic material on or in it will therefore normally be expected to stand out in high contrast against its UV-reflecting (i.e. light) background. This is clearly the case for large structures (e.g. seals on snow: Lavigne & Øritsland, 1974) but the situation is different for small ones like the diminutive tundra plants on which *Rangifer* feed in winter (e.g. Mathiesen et al., 2000). Small structures are likely to be closely surrounded and even partially covered by snow and heterogeneous angular scattering of UV off randomly orientated snow crystals will potentially reduce contrast and hence their visual salience.

Tyler et al. (2014) examined visual salience of *Rangifer* forage in snow and demonstrated how several species of vascular plants in situ on natural pasture showed in substantially greater contrast against their snow background when viewed in UV (Figure 8). Importantly, their study was based on natural UV illumination. Most studies of, or exploiting, visual salience in the UV range have used artificial sources of UV (e.g. Burkhardt, 1982, 1989; Church et al., 1998; Honkavaara et al., 2008; Kellie et al., 2004; Viitala et al., 1995). This complicates the interpretation of results. The salience of an object under artificial UV potentially differs significantly from its salience under the UV component of natural solar light owing to the latter being of lower energy and broader spectral range. Thus, Lind et al. (2013) were unable to replicate in sunlight the enhancement of chromatic contrast of organic material observed under artificial UV. The use of natural UV by Tyler et al. (2014) added realism to their measurements and hence credence to the suggestion that vision in the UV range may enhance achromatic contrast for *Rangifer* of vascular plants in snow under low light conditions.

The situation for forage lichens is complicated because while some, including *Cladina stellaris*, *Cladonia arbuscula*, *Ophioparma* spp., *Stereocaulon paschale* and *Usnea hirta* strongly absorb UVa others, including *Cladonia rangiferina* and *C. portentosa*, display high reflectance at the upper end of the UVa range (Dominy et al., 2023; Petzold & Goward, 1988). Presumably the contrast of the latter in the UV range may be enhanced where they are observed against a background of vascular plants or earth but reduced against a background of snow (Dominy et al., 2023).

UV and avoidance of power lines

Expansion of infrastructure into pasture is a problem for both wild herbivores and pastoralism across the globe (Tyler et al., 2021). Infrastructure disrupts movement through barrier effects and reduces animals' use of habitat through avoidance behaviour (Benítez-López et al., 2010; Keller & Largiadèr, 2003; Laurance et al., 2009; Wilcove & Wikelski, 2008). Power lines cause both effects. *Rangifer* and other ungulates tend to avoid ground ≤ 4 km from power lines and barrier effects associated with them may persist for years (Tyler et al., 2016). These responses are paradoxical, however, because rows of masts spaced tens or hundreds of meters apart and linked by cable conductors suspended usually > 3 m above ground are neither a barrier to passage nor are associated with human activity in the post-construction phase. Attention therefore turned to the suggestion that the responses might be linked some feature of the structures themselves. Studies of the effects on *Rangifer* of low frequency electromagnetic fields and wind and corona auditory noise have been inconclusive (Flydal et al., 2009) and Tyler et al. (2014) therefore suggested that avoidance might be linked to the emission of UV light from corona discharges on cables and insulators (Supporting Information).

The ability of *Rangifer* to detect corona light on high-voltage power lines in the dark has not been measured directly but corona discharges may just be visible to humans (e.g. Peek, 1920, p. 38, Silva et al., 2004) which indicates that the strength of the signal at 405 nm (which overlaps the lower end of the human visual range at ≈ 400 nm) may exceed the threshold of detection by the human eye. This provides a baseline for assessing the corresponding performance of *Rangifer*.

BOX 3 (Continued)

Rangifer are likely to be visually more sensitive to corona discharges than humans for several reasons. First, in contrast to humans, their optical media are more permissive to the transmission of the three principal peaks of corona spectral output (337, 357 and 380nm; [Supporting Information](#)). Second, their retinal sensitivity is maximised in winter owing, in particular, to seasonal tuning of the tapetum to short wavelengths (main text). Third, their eyes are larger than those of humans which results in greater image size and increased light gathering (main text), consequently increasing retinal sensitivity. Together, these observations represent a strong independent argument for improved rates of photon capture and the animals therefore being more sensitive to corona than humans (Tyler et al., 2014). Added to this, *Rangifer* are prey to a variety of cathemeral–nocturnal predators (e.g. wolves (*Canis lupus*), brown bears (*Ursus arctos*) and lynx (*Lynx lynx*); COSEWIC (Committee on the Status of Endangered Wildlife in Canada), 2015; Mattisson et al., 2011) and are presumably both wary and vigilant under low light conditions. Unpredictable, flickering illumination of normally dark structures is presumably also likely to promote wariness in the dark-adapted animal hence causing it to withdraw.

The ability to detect UV light potentially accounts in part not only for avoidance of power lines per se but also for wide variation in the strength and persistence of the response (Tyler et al., 2016). Variation in the strength of the response in *Rangifer* has been attributed to differences in ecological settings (Panzacchi et al., 2013) which, however, are necessarily independent of the source of the disturbance they are recruited to explain. Conceptualising avoidance as a response to corona UV light addresses the heterogeneity of the response in terms of its cause. Power line corona varies in form, incidence, location and intensity. All four qualities vary within and between power lines owing to technical and environmental factors that influence the phenomenon (Maruvada, 2000; Matthews, 2012). It follows that the decision-making process for an animal confronted by corona must involve integration of visual stimuli across the four physical dimensions prior to consideration of any ecological or socio-biological imperatives and is therefore a potent reason for expecting large variation in the strength of responses.

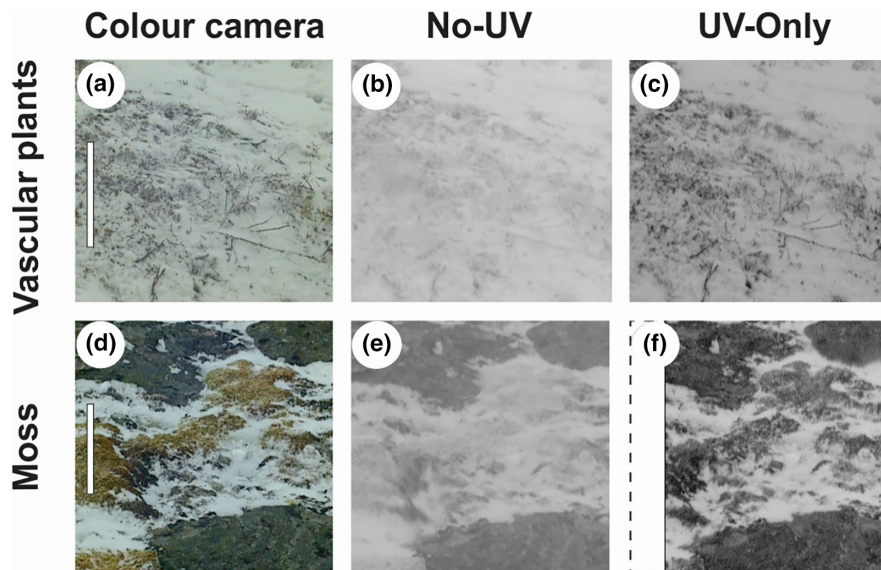


FIGURE 8 Visual salience under natural UV illumination of vegetation in situ on *Rangifer* pasture in winter. (a–c) Mosaic of vascular plants in snow. Species present include *Betula nana* × *pubescens*, *Dryas octopetala*, *Empetrum nigrum*, *Festuca ovina*, *Vaccinium uliginosum* and *V. vitis-idaea*. (d–f) A patch of moss *Racomitrium lanuginosum* (light brown) between rocks. Each scene is presented in three ways: Full chromatic range (a, d); monochrome 400–750 nm (No-UV; b, e); monochrome 350–390 nm (UV-Only; c, f). The full chromatic range represents the image apparent to humans but not to *Rangifer* which are dichromats. Each UV-Only image had significantly greater Michelson contrast than its corresponding No-UV image (see Tyler et al., 2014 for details). Trials were conducted between two and three hours after sunrise in late winter (2nd March 2011) when the local ambient UV (350 to 400 nm) incident on, and reflected from, snow $\approx 6.5 \cdot 10^{-2} \text{ W} \cdot \text{m}^{-2}$; Tyler et al., 2014). Scale bars: 25 cm. After Tyler et al. (2014).

at high latitudes impacts on chronobiology reflects the fact that increased annual variation in the daily pattern of solar illumination at high latitudes increases the range of daily light exposure patterns that internal timing processes must accommodate (Hazlerigg

et al., 2023). Clearly, polar latitudes represent the extreme framing of this problem, giving rise to long periods when the Sun remains above (polar day) or below (polar night) the horizon (Box 2). These solstitial periods potentially constitute periods of reduced *Zeitgeber*

strength owing to the reduced amplitude of daily changes in light intensity and spectral composition. This, however, is contingent on evolved sensitivity of light sensing pathways in species living in such environments, and neither the polar day nor the polar night can be equated to experimental 'constant conditions' used in laboratory chronobiology experiments.

Rangifer is one of a few species in which attempts have been made to explore the impact of the polar light climate on temporal organisation (Lu et al., 2010; van Oort et al., 2005, 2007). These studies have revealed a picture of weak circadian organisation, with direct masking effects apparently shaping both behaviour and melatonin secretion (Lu et al., 2010). *Rangifer* show little or no diel patterning of behaviour during both the polar day and the polar night but instead display a strong ultradian pattern that is probably based on the cycle of rumination. The limited molecular evidence suggests that mutations within the circadian molecular clockwork may underlie these overt behavioural characteristics (Lin et al., 2019; Lu et al., 2010) but since almost all of our understanding of mammalian circadian organisation stems from study of nocturnal rodents with highly robust circadian clocks (Hazlerigg & Tyler, 2019), it remains unclear to what extent the case in *Rangifer* represents an example of high latitude adaptation, or a phylogenetic contrast between rodents and ruminants. Whether these chronobiological attributes of *Rangifer* are linked to functional differences in non-visual photoreception remains an entirely open question, but there are no clear a priori reasons for predicting adaptation at this level.

AUTHOR CONTRIBUTIONS

All four authors conceived, wrote and reviewed all drafts of the paper.

ACKNOWLEDGEMENTS

We are grateful to many colleagues for discussion during the preparation of this paper and to one anonymous referee for critical appraisal of the manuscript.

FUNDING INFORMATION

None.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

None.

ORCID

Nicholas J. C. Tyler  <https://orcid.org/0000-0002-7074-9135>

REFERENCES

- Aidala, Z., Huynen, L., Brennan, P. L. R., Musser, J., Fidler, A., Chong, N., Machovsky Capuska, G. E., Anderson, M. G., Talaba, A., Lambert, D., & Hauber, M. E. (2012). Ultraviolet visual sensitivity in three avian lineages: Paleognaths, parrots, and passerines. *Journal of Comparative Physiology. A*, 198, 495–510. <https://doi.org/10.1007/s00359-012-0724-3>
- Arden, G. B., & Hogg, C. R. (1984). Rod-cone interactions and analysis of retinal disease. *British Journal of Ophthalmology*, 69, 404–415.
- Benítez-López, A., Alkemade, R., & Verweij, P. A. (2010). The impacts of roads and other infrastructure on mammal and bird populations: A meta-analysis. *Biological Conservation*, 143, 1307–1316. <https://doi.org/10.1016/j.biocon.2010.02.009>
- Bittman, E. L. (2021). Entrainment is NOT synchronization: An important distinction and its implications. *Journal of Biological Rhythms*, 36, 196–199. <https://doi.org/10.1177/07487304209728>
- Borges, R., Johnson, W. E., O'Brien, S. J., Gomes, C., Heesy, C. P., & Antunes, A. (2018). Adaptive genomic evolution of opsins reveals that early mammals flourished in nocturnal environments. *BMC Genomics*, 19, 121. <https://doi.org/10.1186/s12864-017-4417-8>
- Bowmaker, J. K. (2008). Evolution of vertebrate visual pigments. *Vision Research*, 48, 2022–2041.
- Bruce, V. G. (1960). Environmental entrainment of circadian rhythms. *Cold Spring Harbour Symposia on Quantitative Biology*, 25, 29–48. <https://doi.org/10.1101/SQB.1960.025.01.005>
- Burkhardt, D. (1982). Birds, berries and UV: A note on some consequences of UV vision in birds. *Die Naturwissenschaften*, 69, 153–157.
- Burkhardt, D. (1989). UV vision: A bird's eye view of feathers. *Journal of Comparative Physiology. A*, 164, 787–796.
- Burton, R. F. (2006). A new look at the scaling of size in mammalian eyes. *Journal of Zoology*, 269, 225–232.
- Carvalho, L. d. S., Cowing, J. A., Wilkie, S. E., Bowmaker, J. K., & Hunt, D. M. (2006). Shortwave visual sensitivity in tree and flying squirrels reflects changes in lifestyle. *Current Biology*, 16, R81–R83.
- Chittka, L., Stelzer, R. J., & Stanewsky, R. (2013). Daily changes in ultraviolet light levels can synchronize the circadian clock of bumblebees (*Bombus terrestris*). *Chronobiology International*, 30, 434–442. <https://doi.org/10.3109/07420528.2012.741168>
- Church, S. C., Bennett, A. T. D., Cuthill, I. C., & Partridge, J. C. (1998). Ultraviolet cues affect the foraging behaviour of blue tits. *Proceedings of the Royal Society of London B: Biological Sciences*, 265, 1509–1514.
- COSEWIC (Committee on the Status of Endangered Wildlife in Canada). (2015). *COSEWIC assessment and status report on the Peary Caribou Rangifer tarandus pearyi in Canada* (xii + 92 pp). Committee on the Status of Endangered Wildlife in Canada.
- Cottrill, P. B., Davies, W. L., Semo, M., Bowmaker, J. K., Hunt, D. M., & Jeffery, G. (2009). Developmental dynamics of cone photoreceptors in the eel. *BMC Developmental Biology*, 9, 71.
- Cox, D. T. C., & Gaston, K. J. (2023). Cathemerality: A key temporal niche. *Biological Reviews of the Cambridge Philosophical Society*, 99, 329–347. <https://doi.org/10.1111/brv.13024>
- Cronin, T. W., & Bok, M. J. (2016). Photoreception and vision in the ultraviolet. *Journal of Experimental Biology*, 219, 2790–2801. <https://doi.org/10.1242/jeb.128769>
- Dominy, N. J., Hobaiter, C., & Harris, J. M. (2023). Reindeer and the quest for Scottish enlivenment. *Perception*, 14(6), 1–6. <https://doi.org/10.1177/20416695231218520>
- Douglas, R. H., & Jeffery, G. (2014). The spectral transmission of ocular media suggests ultraviolet sensitivity is widespread among mammals. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20132995. <https://doi.org/10.1098/rspb.2013.2995>
- Doyle, S., & Menaker, M. (2007). Circadian photoreception in vertebrates. *Cold Spring Harbor Symposia on Quantitative Biology*, 72, 499–508. <https://doi.org/10.1101/sqb.2007.72.003>
- Flydal, K., Korslund, L., Reimers, E., Johansen, F., & Colman, J. E. (2009). Effects of power lines on area use and behaviour of semi-domestic reindeer in enclosures. *International Journal of Ecology*, 2009(1), 340953. <https://doi.org/10.1155/2009/340953>

- Fosbury, R. A. E., & Jeffery, G. (2022). Reindeer eyes seasonally adapt to ozone-blue Arctic twilight by tuning a photonic *tapetum lucidum*. *Proceedings of the Royal Society B: Biological Sciences*, 289, 20221002. <https://doi.org/10.1098/rspb.2022.1002>
- Frishman, L. J. (2006). Origins of the Electroretinogram. In J. R. Heckenlively & G. B. Arden (Eds.), *Principles and practice of clinical electrophysiology of vision* (2nd ed., pp. 139–183). Massachusetts Institute of Technology.
- Gausman, H. W., Rodriguez, R. R., & Escobar, D. E. (1975). Ultraviolet radiation reflectance, transmittance, and absorbance by plant leaf epidermises. *Agronomy Journal*, 67(5), 720–724.
- Gerkema, M. P., Davies, W. I. L., Foster, R. G., Menaker, M., & Hut, R. A. (2013). The nocturnal bottleneck and the evolution of activity patterns in mammals. *Proceedings of the Royal Society B: Biological Sciences*, 280, 20130508. <https://doi.org/10.1098/rspb.2013.0508>
- Harosi, F. I., & Hashimoto, Y. (1983). Ultraviolet visual pigment in a vertebrate: A tetrachromatic cone system in the dace. *Science*, 222, 1021–1023.
- Hazlerigg, D. G., Appenroth, D., Tomotani, B. M., West, A. C., & Wood, S. H. (2023). Biological timekeeping in polar environments: Lessons from terrestrial vertebrates. *Journal of Experimental Biology*, 226, jeb246308. <https://doi.org/10.1242/jeb.246308>
- Hazlerigg, D. G., & Tyler, N. J. C. (2019). Activity patterns in mammals: Circadian dominance challenged. *PLoS Biology*, 17(7), e3000360. <https://doi.org/10.1371/journal.pbio.3000360>
- Hogg, C., Neveu, M., Stokkan, K.-A., Folkow, L., Cottrill, P., Douglas, R., Hunt, D. M., & Jeffery, G. (2011). Arctic reindeer extend their visual range into the ultraviolet. *The Journal of Experimental Biology*, 214, 2014–2019.
- Honkavaara, J., Åberg, H., & Viitala, J. (2008). Do house mice use UV cues when foraging? *Journal of Ethology*, 26, 339–345. <https://doi.org/10.1007/s10164-007-0068-6>
- Howland, H. C., Merola, S., & Basarab, J. R. (2004). The allometry and scaling of the size of vertebrate eyes. *Vision Research*, 44, 2043–2065.
- Johnson, G. L. (1968). Ophthalmoscopic studies on the eyes of mammals. *Philosophical Transactions of the Royal Society of London. B: Biological Sciences*, 254(794), 207–220.
- Keller, I., & Largiadèr, C. R. (2003). Recent habitat fragmentation caused by major roads leads to reduction of gene flow and loss of genetic variability in ground beetles. *Philosophical Transactions of the Royal Society of London. B: Biological Sciences*, 270, 417–423. <https://doi.org/10.1098/rspb.2002.2247>
- Kellie, A., Dain, S. J., & Banks, P. B. (2004). Ultraviolet properties of Australian mammal urine. *Journal of Comparative Physiology. A*, 190, 429–435. <https://doi.org/10.1007/s00359-004-0507-6>
- Laurance, W. F., Goosem, M., & Laurance, S. G. W. (2009). Impacts of roads and linear clearings on tropical forests. *Trends in Ecology & Evolution*, 24, 659–669.
- Lavigne, D. M., & Øritsland, N. A. (1974). Ultraviolet photography: A new application for remote sensing of mammals. *Canadian Journal of Zoology*, 52, 939–941.
- Lin, Z., Chen, L., Chen, X., Zhong, Y., Yang, Y., Xia, W., Liu, C., Zhu, W., Wang, H., Yan, B., Yang, Y., Liu, X., Sternang Kvie, K., Røed, K. H., Wang, K., Xiao, W., Wei, H., Li, G., Heller, R., ... Li, Z. (2019). Biological adaptations in the Arctic cervid, the reindeer (*Rangifer tarandus*). *Science*, 364, 1154.
- Lind, O., Mitkus, M., Olsson, P., & Kelber, A. (2013). Ultraviolet sensitivity and colour vision in raptor foraging. *The Journal of Experimental Biology*, 216, 1819–1826.
- Liu, J. H. K., Kripke, D. F., Twa, M. D., Hoffman, R. E., Mansberger, S. L., Rex, K. M., Girkin, C. A., & Weinreb, R. N. (1999). Twenty-four-hour pattern of intraocular pressure in the aging population. *Investigative Ophthalmology & Visual Science*, 40, 2912–2917.
- Liu, J. H. K., Mansouri, K., & Weinreb, R. N. (2015). Estimation of 24-hour intraocular pressure peak timing and variation using a contact lens sensor. *PLoS One*, 10(6), e0129529. <https://doi.org/10.1371/journal.pone.0129529>
- Lu, W., Meng, Q.-J., Tyler, N. J. C., Stokkan, K.-A., & Loudon, A. S. I. (2010). A circadian clock is not required in an Arctic mammal. *Current Biology*, 20, 533–537.
- Maruvada, P. S. (2000). *Corona performance of high-voltage transmission lines*. Research Studies Press Ltd. ISBN 0 86380 254 0.
- Mathiesen, S. D., Haga, Ø. E., Kaino, T., & Tyler, N. J. C. (2000). Diet composition, rumen papillation and maintenance of carcass mass in female Norwegian reindeer (*Rangifer tarandus tarandus*) in winter. *Journal of Zoology (London)*, 251, 129–138.
- Matthews, J. C. (2012). The effect of weather on corona ion emission from AC high voltage power lines. *Atmospheric Research*, 113, 68–79.
- Mattisson, J., Odden, J., Nilssen, E. B., Linnell, J. D. C., Persson, J., & Andren, H. (2011). Factors affecting Eurasian lynx kill rates on semi-domestic reindeer in northern Scandinavia: Can ecological research contribute to the development of a fair compensation system? *Biological Conservation*, 144, 3009–3017.
- Mrosovsky, N. (1999). Masking: History, definitions, and measurement. *Chronobiology International*, 16, 415–429. <https://doi.org/10.3109/07420529908998717>
- Newman, B. A., & D'Angelo, G. J. (2024). A review of Cervidae visual ecology. *Animals*, 14, 420. <https://doi.org/10.3390/ani14030420>
- Ollivier, F. J., Samuelson, D. A., Brooks, D. E., Lewis, P. A., Kallberg, M. E., & Komáromy, A. M. (2004). Comparative morphology of the *tapetum lucidum* (among selected species). *Veterinary Ophthalmology*, 7, 11–22.
- Palmer, G., & Johnsen, S. (2015). Downwelling spectral irradiance during evening twilight as a function of the lunar phase. *Applied Optics*, 54, B85–B92. <https://doi.org/10.1364/AO.54.000B85>
- Panzacchi, M., van Moorter, B., Jordhøy, P., & Strand, O. (2013). Learning from the past to predict the future: Using archaeological findings and GPS data to quantify reindeer sensitivity to anthropogenic disturbance in Norway. *Landscape Ecology*, 28, 847–859. <https://doi.org/10.1007/s10980-012-9793-5>
- Patat, F., Ugolnikov, O. S., & Postlyakov, O. V. (2006). UVBRI twilight sky brightness at ESO-Paranal. *Astronomy & Astrophysics*, 455, 385–393. <https://doi.org/10.1051/0004-6361:20064992>
- Pearce, E., & Dunbar, R. (2011). Latitudinal variation in light levels drives human visual system size. *Biology Letters*, 8, 90–93. <https://doi.org/10.1098/rsbl.2011.0570>
- Peek, F. W. (1920). *Dielectric phenomena in high voltage engineering*. McGraw-Hill Book Company, Inc.
- Peichl, L., Behrmann, G., & Kröger, R. H. H. (2001). For whales and seals the ocean is not blue: A visual pigment loss in marine mammals. *The European Journal of Neuroscience*, 13, 1520–1528.
- Petzold, D. E., & Goward, S. N. (1988). Reflectance spectra of subarctic lichens. *Remote Sensing of Environment*, 24(3), 481–492. [https://doi.org/10.1016/0034-4257\(88\)90020-X](https://doi.org/10.1016/0034-4257(88)90020-X)
- Robberecht, R., Caldwell, M. M., & Billings, W. D. (1980). Leaf ultraviolet optical properties along a latitudinal gradient in the Arctic-Alpine life zone. *Ecology*, 61(3), 612–619. <https://doi.org/10.2307/1937427>
- Rodieck, R. W. (1998). *The first steps in seeing*. Sinauer.
- Ruseckaitė, R., Lamb, T. D., Pianta, M. J., & Cameron, A. M. (2011). Human scotopic dark adaptation: Comparison of recoveries of psychophysical threshold and ERG b-wave sensitivity. *Journal of Vision*, 11, 2. <https://doi.org/10.1167/11.8.2>
- Saszik, S. M., Robson, J. G., & Frishman, L. J. (2002). The scotopic threshold response of the dark-adapted electroretinogram of the mouse. *Journal of Physiology*, 543(3), 899–916. <https://doi.org/10.1113/jphysiol.2002.019703>
- Schwab, I. R., Yuen, C. K., Buyukmichi, N. C., Blankenship, T. N., & Fitzgerald, P. G. (2002). Evolution of the tapetum. *Transactions of the American Ophthalmological Society*, 100, 187–200.
- Silva, J. M., Fleischmann, H. H., & Shih, C. H. (2004). Transmission line corona and X-rays. *IEEE Transactions on Power Delivery*, 19(3), 1472–1482.

- Spector, R. H. (1990). The pupils. In H. K. Walker, W. D. Hall, & J. W. Hurst (Eds.), *Clinical methods: The history, physical, and laboratory examinations* (3rd ed.). Butterworths. Chapter 58. <https://www.ncbi.nlm.nih.gov/books/NBK381/>
- Stokkan, K.-A., Folkow, L., Dukes, J., Neveu, M., Hogg, C., Siefken, S., Dakin, S. C., & Jeffery, G. (2013). Shifting mirrors: Adaptive changes in retinal reflections to winter darkness in Arctic reindeer. *Proceedings of the Royal Society of London B: Biological Sciences*, 280, 20132451. <https://doi.org/10.1098/rspb.2013.2451>
- Tovée, M. J. (1995). Ultra-violet photoreceptors in the animal kingdom: Their distribution and function. *Trends in Ecology & Evolution*, 10(11), 455–460.
- Tyler, N. J. C., Forchhammer, M. C., Fortin, D., Gunn, A., Leblond, M., & Panchenko, D. (In press). Chapter 51. Reindeer/Caribou (*Rangifer tarandus* L. 1758). In M. Melletti & S. Focardi (Eds.), *Deer of the world. Ecology, conservation and management*. Springer Nature.
- Tyler, N. J. C., Gregorini, P., Parker, K. L., & Hazlerigg, D. G. (2020). Animal responses to environmental variation: Physiological mechanisms in ecological models of performance in deer (Cervidae). *Animal Production Science*, 60, 1248–1270. <https://doi.org/10.1071/AN19418>
- Tyler, N. J. C., Hanssen-Bauer, I., Førlund, E. J., & Nellemann, C. (2021). The shrinking resource base of pastoralism: Saami reindeer husbandry in a climate of change. *Frontiers in Sustainable Food Systems*, 4, 585685. <https://doi.org/10.3389/fsufs.2020.585685>
- Tyler, N. J. C., Stokkan, K.-A., Hogg, C. R., Nellemann, C., & Vistnes, A. I. (2016). Cryptic impact: Visual detection of corona light and avoidance of power lines by reindeer. *Wildlife Society Bulletin*, 40, 50–58. <https://doi.org/10.1002/wsb.620>
- Tyler, N. J. C., Stokkan, K.-A., Hogg, C. R., Nellemann, C., Vistnes, A.-I., & Jeffery, G. (2014). Ultraviolet vision and avoidance of power lines in birds and mammals. *Conservation Biology*, 28(3), 630–631.
- van Oort, B. E. H., Tyler, N. J. C., Gerkema, M. P., Folkow, L., Blix, A. S., & Stokkan, K.-A. (2005). Circadian organisation in reindeer. *Nature (London)*, 438, 1095–1096.
- van Oort, B. E. H., Tyler, N. J. C., Gerkema, M. P., Folkow, L., & Stokkan, K.-A. (2007). Where clocks are redundant: Weak circadian mechanisms in reindeer living under polar photic conditions. *Die Naturwissenschaften*, 94, 183–194.
- Viitala, J., Korpimäki, E., Palokangas, P., & Koivula, M. (1995). Attraction of kestrels to vole scent marks visible in ultraviolet light. *Nature*, 373, 425–427.
- Walls, G. L. (1942). *The vertebrate eye and its adaptive radiation*. Hafner.
- Wilcove, D. S., & Wikelski, M. (2008). Going, going, gone: Is animal migration disappearing? *PLoS Biology*, 6(7), e188. <https://doi.org/10.1371/journal.pbio.0060188>
- Wong-Riley, M. (2010). Energy metabolism of the visual system. *Eye and Brain*, 2, 99–116.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Spectrogram of corona discharge emission in air indicating band heads at 317, 337, 357, 380, and 405 nm. Vertical dashed lines indicate the approximate lower limit of the visual range in reindeer (*Rangifer tarandus*) and humans, respectively. Purple shading indicates UV wavelengths. After Grum and Costa (1976).

How to cite this article: Tyler, N. J. C., Fosbury, R. A. E., Hazlerigg, D., & Hogg, C. (2024). Vision at high latitudes: High sensitivity without specific boreal adaptations in photoreception in reindeer (*Rangifer tarandus* L.). *Functional Ecology*, 00, 1–15. <https://doi.org/10.1111/1365-2435.14669>