



Emerging Issues

Cryptic Impact: Visual Detection of Corona Light and Avoidance of Power Lines by Reindeer

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ABSTRACT Assessing the impact of human development on animals is complicated by the fact that overt effects may have covert causes. Cryptic impacts (*sensu* Raiter et al. 2014) can arise where sensory stimuli to which species respond fall outside the human sensory range. Ultraviolet (UV) light, which is detected by a range of nonprimate mammals, is a potential example. We review evidence that dark-adapted eyes of reindeer–caribou *Rangifer tarandus* can detect light at 330–410 nm emitted by electrical corona on high-voltage power lines, which is necessarily barely visible to humans. Based on this, we suggest that the superior ability of *Rangifer* to detect corona UV light may partly account for the tendency of the animals to avoid power lines. *Rangifer* has UV-permissive ocular media that transmit approximately 15 times more corona light than human eyes. Retinal irradiance under full dilation is in the order of 7 times greater in *Rangifer* compared with humans. Seasonal transformation of the tapetum lucidum substantially increases retinal sensitivity in this species in winter. Threshold distances of detection of corona by *Rangifer* are in the order of hundreds of meters. Displays of corona may catch the animals' attention, and plume coronas, in particular, may induce the illusion of motion (the phi phenomenon), thereby falsely signaling the presence of potential predators. Both features are likely to increase wariness and cause animals to withdraw from the source of the stimulus. We suggest that spatial and temporal variability of corona contributes to substantial variation observed in the strength and persistence of avoidance responses in *Rangifer* at these structures. © 2016 The Wildlife Society.

KEY WORDS Arctic, barrier effects, environmental impact, *Rangifer tarandus*, tapetum lucidum, ultraviolet light, vision.

Assessing the impact of human development on animals in natural habitat is complicated by the fact that overt effects may have covert causes. “Cryptic impacts” (*sensu* Raiter et al. 2014) arise, for instance, where anthropogenic stimuli to which species respond fall outside the human sensory range and are, therefore, liable to be overlooked because of divergence in the sensory abilities of animals and man. Ultraviolet (UV) light, which is detected by a range of large, nonprimate mammals (Douglas and Jeffery 2014), is a potential example. In this paper we argue 1) that dark-adapted eyes of reindeer–caribou (*Rangifer tarandus*; hereafter, “*Rangifer*”) can detect light emitted by corona discharges on high-voltage power lines, which is barely visible to humans; and 2) that threshold distances of detection are in the

order of hundreds of meters. The corona effect is described below. In this paper the term “power line” includes masts (also known as “towers” or “utility poles”), insulators and cables (wire conductors) but does not include linear clearings (also known as “utility corridors” or “easements”) cut where power lines pass through dense vegetation. We do not distinguish power lines by operating voltage but refer to all lines ≥ 66 kV as “high-voltage” power lines. Based on this, we suggest that avoidance of power lines by *Rangifer* in open terrain—where it cannot be attributed to modification of habitat—may be linked with the ability of the animals to detect corona UV light. Further, we suggest that inherent unpredictability of the occurrence of corona on power lines causes substantial variation in the strength and persistence of avoidance responses observed in *Rangifer* at these structures.

AVOIDANCE OF LINEAR INFRASTRUCTURE: INDIRECT AND DIRECT CAUSES

Linear infrastructure, including fences, forestry, gas pipelines, high-voltage power lines, railways, and roads, is a common

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source of disturbance to wildlife (Forman and Alexander 1998, Berger 2004, Fahrig and Rytwinski 2009). Such structures disrupt movement and patterns of dispersion of animals across a broad range of taxa, including amphibians, birds, fish, insects, mammals, and reptiles, and have a major influence on use of habitat and the connectivity of ecosystems (Keller and Largiadèr 2003, Wilcove and Wikelski 2008, Laurance et al. 2009, Benítez-López et al. 2010).

Linear infrastructure may influence movement through barrier effects (i.e., hindrance to passage) and avoidance (i.e., a behavioral response induced by the sight, sound, or smell of humans or human artifacts either directly perceived or associated through learning with infrastructure; Dyer et al. 2001, Barber et al. 2011, Brown et al. 2012, Shannon et al. 2014, and Supporting Information). Power lines cause both effects (e.g., Joyal et al. 1984, Strevens 2007; see also Supporting Information, Table S1), but animal responses at these structures are paradoxical: rows of masts at intervals of tens or hundreds of meters connected by cable conductors, usually suspended >3 m above ground, are neither a barrier to the passage of terrestrial animals nor are necessarily associated with traffic. Barrier effects have nevertheless been recorded at power lines standing in isolation (*Rangifer*: Reimers et al. 2007) and at those near other infrastructure (*Rangifer*: Vistnes and Nellemann 2008; Tibetan antelope [*Pantholops hodgsonii*]: Xia et al. 2007). Avoidance occurs at power lines near other infrastructure (Mongolian gazelle [*Procapra gutturosa*] and Asiatic wild ass [*Equus hemionus*]: Ito et al. 2013. Note: while Xia et al. 2007 and Ito et al. 2013 do not specifically mention power lines they were evidently present: power line masts are clearly apparent beside the railway lines in Google Earth® images of the study sites.), at power lines in clear-cut corridors in forest or jungle, which involve major changes in the structure and composition of arboreal and understory vegetation (e.g., bush rat [*Rattus fuscipes*] and brown antechinus [*Antechinus stuartii*]: Strevens 2007) and at power lines on grassland prairie (e.g., lesser prairie chicken [*Tympanuchus pallidicinctus*], greater prairie chicken [*T. cupido*], greater sage grouse [*Centrocercus urophasianus*]: Pruett et al. 2009 but see Tryjanowski et al. 2014) and on taiga-tundra (*Rangifer*: Nellemann et al. 2001; Vistnes and Nellemann 2001, 2008) where vegetation is hardly altered. Zones of avoidance in *Rangifer* extend from 2.5 km to 4 km from power lines standing alone (Nellemann et al. 2001, Vistnes and Nellemann 2001) and up to 5 km from those associated with other infrastructure (Nellemann et al. 2001, Vistnes and Nellemann 2008, Vistnes et al. 2008 [Fig. 1; Table 1]). In common with other infrastructure (Mahoney and Schaefer 2002, Schaefer 2003, Joly et al. 2006, Ito et al. 2013, Panzacchi et al. 2013a), barrier effects and avoidance of power lines may persist for years (Nellemann et al. 2003, Reimers et al. 2007) or even decades after construction (Vistnes and Nellemann 2001, Vistnes et al. 2004).

Explanations of avoidance at power lines fall into 2 classes according to whether the effects are direct or indirect. Indirect effects have been documented extensively. Most involve species' responses to changes in the environment

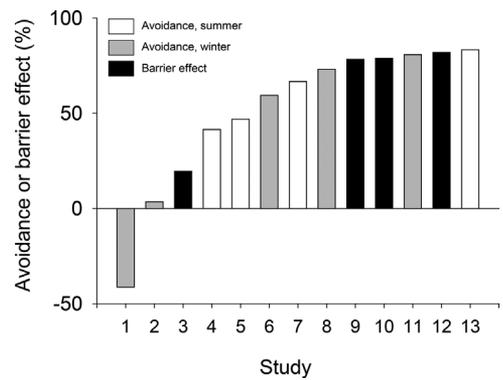


Figure 1. Levels of avoidance and barrier effects at power lines, either alone or in conjunction with other infrastructure, by reindeer (*Rangifer tarandus*) in Norway. Data for each study, by numbers, are given in Table 1.

concomitant with the erection and maintenance of power lines rather than with the structures (masts and cables) themselves (e.g., Willyard et al. 2004, Clarke and White 2008, Strevens et al. 2008, Pohlman et al. 2009, Carthew et al. 2013). Thus, changes in the composition and structure of vegetation may result in the loss of features that forest-dwelling animals require (e.g., Wilson et al. 2007, Asari et al. 2010) or in invasion by competitors (Goosem and Marsh 1997) or predators (James and Stuart-Smith 2000). The fact that such changes may sometimes attract animals (i.e., negative avoidance [e.g., Johnson et al. 1979, Loft and Menke 1984, Clarke et al. 2007, Neumann et al. 2013, Rytwinski and Fahrig 2013, see also Bartzke et al. 2014]) simply illustrates how important habitat structure is for animal distribution. Reduced density of ground-nesting birds near power lines has similarly been attributed to predation hazard following the invasion of raptors that use masts as perches (Lammers and Collopy 2007, Pruett et al. 2009). In all these cases the response drivers are evident and the causal relationships are obvious. It is, therefore, not surprising that the properties of the power lines themselves have generally been considered immaterial except by implication where the dimensions of masts influence the width of clear cuttings.

The avoidance of power lines in open country (Nellemann et al. 2001, 2003; Vistnes and Nellemann 2001, 2008; Vistnes et al. 2008) presents a different situation. Avoidance in the absence both of clearings and traffic has directed attention to sensory input emanating from power lines themselves. Studies of the effects on *Rangifer* of low-frequency electromagnetic fields and both wind and corona auditory noise have been inconclusive owing to a lack of knowledge of signal strength and sensory threshold (Flydal et al. 2009). Recently, however, Tyler et al. (2014) advanced the hypothesis that avoidance might be linked with the ability of animals to detect UV light emitted by corona. This hypothesis, based on integration of information on vision in *Rangifer* and the spectral characteristics of corona, represents a potential example of a “cryptic impact” (Raiter et al. 2014), where the stimulus that causes disturbance falls outside the human sensory range. Here, we expand the original analysis

Table 1. Summary of research on avoidance and barrier effects at power lines, either alone or in conjunction with other infrastructure, by reindeer (*Rangifer tarandus*) in Norway. For graphical presentation of studies, by numbers, see Figure 1.

Descriptive variable	Study												
	1	2	3	4	5	6	7	8	9	10	11	12	13
Location	Setesdal-Ryfylkeheiene	Setesdal-Ryfylkeheiene	North Ottadalen	Setesdal-Ryfylkeheiene	Setesdal-Ryfylkeheiene	Setesdal-Ryfylkeheiene	Nordfjella	Repparfjord	North Ottadalen	Snohetta	Nordfjella	Nord Ottadalen	Setesdal-Ryfylkeheiene
Date	Nov-Apr	Nov-Apr	Feb-Mar	May-Oct	May-Oct	Nov-Apr	Jun-Aug	May	Feb-Mar	Feb-Apr	Feb-Apr	Feb-Apr	May-Oct
Phase of annual cycle	Restricted availability of forage	Restricted availability of forage	Minimum availability of forage	Growing season	Growing season	Restricted availability of forage	Growing season	Calving	Minimum availability of forage	Minimum availability of forage	Minimum availability of forage	Minimum availability of forage	Growing season
Infrastructure ^a	Roads (closed), 300 and 420 kV, dam	Road (closed), 300 kV	66 kV	Road (closed), 300 and 420 kV	Road (closed), 300 and 420 kV	Road (closed), 300 and 420 kV	Power lines, minor roads	66 kV	66 kV	132, 300 kV, winter closed road	300 and 420 kV, road, ski trails	66, 300 kV, winter closed road	Roads (closed), 300 and 420 kV, dam
Phase of development	Post-development	Early development	Post-development (1994-2004)	Mid-development	Early development	Mid-development	Post-development	>30 yr after construction	Post-development (1974-1993)	2-17 yr post-construction	Post-development	2-17 yr post-construction	Post-development
Effect	Avoidance	Avoidance	Barrier	Avoidance	Avoidance	Avoidance	Avoidance	Avoidance	Barrier	Barrier	Avoidance	Barrier	Avoidance
Method	Ground count	Ground count	Aerial survey (fixed wing)	Ground count	Ground count	Ground count	Aerial survey (fixed wing)	Ground count	Aerial survey (fixed wing)	Aerial survey (fixed wing)	Aerial survey (fixed wing)	Aerial survey (fixed wing)	Ground count
Comparison	<4 vs. >4 km	<4 vs. >4 km	North vs. South side	<4 vs. >4 km	<4 vs. >4 km	<4 vs. >4 km	0-2.5 vs. >5 km	<4 vs. >4 km	North vs. South side	2-5 km either side of barrier	0-2.5 vs. 2.5-5 km	2-5 km either side of barrier	<4 vs. >4 km
Result (%) ^b	-41.4	3.5	19.5	41.5	46.9	59.4	66.7	73.1	78.4	78.9	80.8	82.0	83.4
Control	Before-after	Before-after	n.a.	Before-after	Before-after	Before-after	Altitude	Terrain ruggedness	n.a.	Snow, altitude	Altitude	Snow, altitude	Before-after
Source	Nellemann et al. (2003)	Nellemann et al. (2003)	Reimers et al. (2007)	Nellemann et al. (2003)	Nellemann et al. (2003)	Nellemann et al. (2003)	Vistnes and Nellemann et al. (2008)	Vistnes and Nellemann (2001)	Reimers et al. (2007)	Vistnes et al. (2004)	Nellemann et al. (2001)	Vistnes et al. (2004)	Nellemann et al. (2003)

^a kV = operating voltage of power lines.

^b Indicates the level of avoidance within, or the strength of the barrier effect between, the zone(s) indicated ("Comparison"). A negative value indicates attraction. n.a., not applicable.

and provide a more detailed explanation of the sensory mechanisms involved. We also consider the likelihood that other species of ungulates may detect corona UV light.

CORONA DISCHARGE ON POWER LINES

“Corona” or “corona discharge” is a light-emitting phenomenon associated with alternating current or direct current energized electrical devices, including high-voltage power lines. It occurs when the electric field close to a conductor becomes sufficiently strong to create dielectric breakdown of the air locally. The result is ionization of air creating a region of plasma in which electrons and positive ions recombine and release photons of light.

The spectrum of the corona discharge emission in air includes several discrete peaks within the range of 230–440 nm (Grum and Costa 1976, Machala et al. 2007, Muhr and Schwarz 2009, Shimizu et al. 2010, Czech et al. 2011; Fig. 2). The strongest peaks occur at 317, 337, and 357 nm in the near-ultraviolet spectrum and are not visible to humans. Medium strong peaks at 380 and 405 nm, however, fall close to or just within the human visual range (400–700 nm) and these 2 bands may consequently be visible to our species:

If potential is applied between the smooth conductors of a transmission line . . . and gradually increased, a voltage is finally reached at which a hissing noise is heard, and if it is dark, a pale violet light can be seen to surround the conductors. This voltage is called the critical visual corona point (Peek 1920:38).

Corona light appears in 3 forms: as a glow discharge running along conductors; and, at higher local electric field strengths, as localized brush or plume discharges that occur either in steady state or as flashing points with plumes, in particular, extending to ≥ 10 cm from source. Brush discharges generate audible hissing or “frying” noise, whereas plume discharges may generate an intense snapping sound; glow discharge is usually not associated with audible noise. All 3 forms can be visible to the naked eye (Anonymous 2004).

The dielectric breakdown that results in corona is primarily a function of voltage and the radius of curvature of the

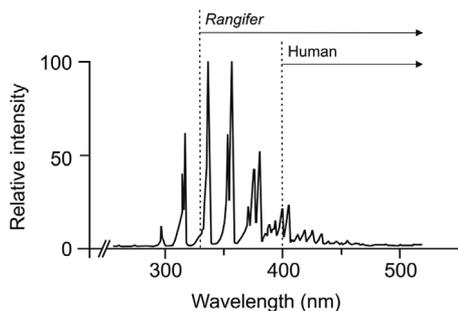


Figure 2. Spectrogram of corona discharge emission in air (210–500 nm). Band heads at 317, 337, 357, 380, and 405 nm are clearly apparent. Vertical dashed lines indicate the approximate lower limit of the visual range in reindeer (*Rangifer tarandus*) and humans, respectively. Redrawn from Grum and Costa (1976).

electrode. However, the strength of the electric field—and, hence, both the incidence and the intensity of corona—is also strongly affected by substrate and environmental conditions. High humidity, which increases the conductivity of air, water droplets, ice crystals, inorganic and organic matter, irregularities (cracks or corrosion) on conductors, insulators, or other components of the line all intensify the electric field locally. Hence, they may serve both as points at which corona initiates at high frequency and may generate considerable temporal and spatial variation in the incidence of coronas (Maruvada 2000, Matthews 2012). They may also account for the occurrence of glow discharge in relatively small systems such as on 20-kV power lines with small-diameter conductors at coastal sites in Norway (V. Dahle, NTE Nett AS, personal communication).

MAMMALIAN VISION IN THE UV RANGE

It was formerly held that the visual range of most mammals was 400–700 nm and did not, therefore, extend into the UV (< 400 nm). This view was based on extrapolation from our own species, in which UV light is blocked in the anterior eye (Stark and Tan 1982). Consistent with this, UV-specific photopigments (opsins) are rare in mammals, being largely confined to bats and rodents (Bowmaker 2008). It has recently been demonstrated, however, that the anterior eye of a variety of large, nonprimate mammals is UV-permissive at 310–400 nm (Douglas and Jeffery 2014). The lens of artiodactyla ($n = 10$ species including *Rangifer*) transmits on average (median) 19% of UV light within this range compared with 34.6% in rodents but just 0.4% in primates. Crucially, opsins have a broad response range in which 50% spectral sensitivity (λ_{50}) typically extends 50 nm around peak value (λ_{max} ; Bowmaker 2008). It follows that UV light that enters the eye may be detected by opsins in rods ($\lambda_{max} = 498$ nm) and blue cones ($\lambda_{max} = 420$ nm), potentially extending the visual range of species lacking UV-specific opsins. This is nicely exemplified in *Rangifer*, which responds to 372 and 330 nm LEDs (Hogg et al. 2011 and C. R. Hogg, unpublished data). Moreover, because the electrophysiological corneal recording techniques used by these authors are approximately 3 log units less sensitive than psychophysical measurements of the perceptual act (Ruseckaite et al. 2011), their results demonstrate only an ability to detect light; they are poor indicators of visual threshold and they underestimate visual sensitivity.

CAN RANGIFER DETECT CORONA LIGHT ON POWER LINES? PHYSIOLOGICAL ADAPTATIONS AND FUNCTIONAL CONSTRAINTS

The probability of an animal detecting corona UV light emitted from a power line depends on 1) signal strength, and 2) distance from the source. We consider these in turn.

Detection of Signal

The mammalian eye has a dynamic range of approximately 9 log units and, at maximum sensitivity, is theoretically capable

of responding to a single photon. This condition is probably rarely realized outside the laboratory, but visual sensitivity under low luminance is nevertheless enhanced by a number of factors. These include the size of the eye; the area of the pupil; the adaptive state of photoreceptors; neuronal retinal mechanisms; and the presence of a reflective surface called the tapetum lucidum (TL), which lies directly behind the retinal pigmented epithelium in the central one-third of the retina (Johnson 1968). The TL reflects light not absorbed on its first pass through the photoreceptors and returns it for a second pass, consequently increasing both the probability of it being absorbed by photopigment and, hence, retinal sensitivity (Johnson 1968). The TL is present in many species of mammal, including ungulates and carnivores, but not in rodents and primates (Johnson 1968). Structural differences between these 2 groups (Ollivier et al. 2004) indicate the TL evolved independently in each.

The premise for assessing the ability of *Rangifer* to detect corona light on high-voltage power lines is that humans may just barely see it (e.g., Peek 1920:38, Silva et al. 2004). Indeed, prior to the development of sensitive spectrographic devices, visual assessment with binoculars or the naked eye was the accepted method for recording the presence of corona on such structures (e.g., Chartier et al. 1995). Two authors of the present paper (CN and AIV) confirm having seen corona on power lines from approximately 20 m in a snowy landscape and on foggy nights, respectively. They both report repeated, independent observations made on different power lines over several years, in every case several years before the present study was conceived. Clearly, therefore, the strength of the signal in that part of the corona spectrum that overlaps the lower end of the human visual range (i.e., ≥ 400 nm; Fig. 2) may exceed the threshold of detection by the human eye. It follows that the likelihood of *Rangifer* being able to detect corona may be examined by comparing the visual system of the 2 species.

Rangifer have large eyes in which the pupils dilate to a diameter of approximately 21 mm (C. R. Hogg, unpublished data) compared with approximately 8 mm in humans. The integrated irradiance over the retina under full dilation—which is likely to be the permanent condition of the pupil during the extended twilight of the boreal winter—is likely, therefore, be in the order of 7 times greater in *Rangifer* than in humans. Prolonged dilation of the pupil in *Rangifer* has, moreover, a second consequence for its visual system. The dilated pupil restricts aqueous flow from the anterior eye, causing an increase in intra-ocular pressure. This, in turn, reduces the spacing of TL collagen fibers, shifting the wavelength of reflected light (Bragg's Law) and augmenting shorter wavelengths, which scatter more than longer wavelengths (the Rayleigh effect; Stokkan et al. 2013). The resulting scattering of light among the outer segments of photoreceptors, rather than reflecting it directly back, enhances photon capture and contributes approximately 30% to an increase in retinal sensitivity of approximately 3 log units from summer to winter in *Rangifer* (Stokkan et al. 2013; C. R. Hogg, unpublished data).

Both of these features increase visual sensitivity in winter and, hence, the ability of *Rangifer* to detect those wavelengths of corona light that humans may see (i.e., approx. 400–410 nm; Fig. 2). This, however, understates the visual capacity of the animals. Four major peaks of the spectral output of corona (337, 357, 380, and 405 nm) fall within the visual range of *Rangifer* compared with only one (405 nm) in humans (Fig. 2). It follows, based on summation of the peaks, that the integrated retinal irradiance by corona light may be approximately 15 times greater in *Rangifer* than in humans. On this basis alone the animals would be expected to be more sensitive to corona than humans under scotopic conditions. Neither species will, of course, detect corona on power lines under photopic conditions because the intensity of corona light (≤ 410 nm) will never normally exceed the intensity of daylight within the range 410–700 nm, and corona will, therefore, always be masked by daylight. This may, in fact, at least in part explain purportedly lower rates of avoidance of power lines by *Rangifer* in summer compared with winter; see Tyler et al. 2014).

Our argument for superior ability of dark-adapted *Rangifer* to detect corona UV light compared with humans rests on 3 differences in visual function between the 2 species: extension of the visual range, greater integrated retinal irradiance, and seasonal adaptation of the TL in *Rangifer*. Each represents a strong independent argument for improved rate of photon capture and, hence, higher retinal sensitivity in the mesopic–scotopic (low light) range in *Rangifer*. Their effects, moreover, are likely to be additive. We have not considered this because the integration is complex and beyond the scope of the present study. It is sufficient to note that our evaluation of differences in visual function between the 2 species is deliberately conservative.

Over What Distance Can *Rangifer* Detect Corona Light on Power Lines?

The distance of detection of signal is a function of 4 factors: the intensity, spatial distribution, and spectral content of the light source; the rate of attenuation of the emitted light with distance; the integrating area for collection of light by the eye; and the sensitivity of the photoreceptors for the relevant spectral distribution. In the absence of complete spectral-sensitivity data for *Rangifer*, we are unable to use data on the corona spectrum to calculate threshold distances of detection. An estimate may, however, be made by extrapolation from humans given that 1) people may see corona glow on conductors from approximately 20 m (CN and AIV, personal communication); 2) the lens and pupil of *Rangifer* transmits approximately 15 times more corona light; and 3) the retina of winter-adapted *Rangifer* is at least twice as sensitive as the human retina (and probably very considerably more so). Corona glow has cylindrical symmetry and the integrated intensity of its discharge will therefore attenuate at the rate of $1/r$ (where r is the distance from source to the point of observation). The same applies for brush corona, at least where the distance between adjacent structures is small. Extrapolation on this basis, from the estimate of 20 m in

humans, suggests that *Rangifer* may detect corona glow and brush corona from several hundreds of meters. Plume coronas have spherical symmetry and the integrated intensity of the signal therefore attenuates at the rate of $1/r^2$. Threshold distances of detection for these structures are therefore likely to be correspondingly lower.

Such estimates are, however, only abstractions. The probability of animals detecting corona light is influenced by a range of variables not considered here. Dilation of the pupil in winter increases the ability of the animals to sample the visual field on the peripheral retina, which is sensitive, in particular, to brief stimuli. Second, the eyes of *Rangifer*, like many other species of ungulates, are arranged laterally and sample a much wider visual field than in humans. The visual field of the animals is approximately 280–300° compared with only 160° in humans, which have a forward binocular visual field. This, too, enhances the ability of *Rangifer* to detect visual signals in the peripheral retina. Third, the illuminance of corona is enhanced in winter by snow, which strongly reflects UV light (Shcherbakov et al. 2006, Wuttke and Seckmeyer 2006). Fourth, the heuristic models used here to assess visual performance in *Rangifer* were founded on evidence that adult humans can see power line corona from approximately 20 m. Transmission of shorter wavelengths declines with age, however, owing to progressive reduction in the clarity of the optic media (Brainard et al. 1999), and the effect, moreover, is likely to be less pronounced in *Rangifer* than in humans owing to the preponderance of young animals in most populations (strong positive skew in the age distribution—wild: Miller [1974]; feral: Leader-Williams [1988]; semidomesticated: N. J. C. Tyler, unpublished data). It is an important consideration because an increase of only 10 m in the estimate (i.e., from 20 m to 30 m) to compensate for the age effect would more than double the theoretical threshold distance of detection of brush and plume corona in *Rangifer*. The probability of detection of corona light thus involves integration of animal and environmental variables across multiple temporal and spatial scales and it is for this reason unrealistic to elaborate the threshold distances of detection beyond stating that these are likely to be in the order of hundreds of meters for glow and brush corona but less for plume corona.

EFFECT OF CORONA LIGHT ON *RANGIFER*

Rangifer are characteristically active around the clock including during mesopic–scotopic conditions; indeed, activity under such conditions is inevitable in the boreal winter when the photoperiod approaches zero (Erriksson et al. 1981; van Oort et al. 2005, 2007). The animals fall prey to a variety of crepuscular–nocturnal predators (see Supporting Information for a list of relevant species) and mesopic–scotopic conditions therefore represent a “high-risk situation” (*sensu* Lima and Bednekoff 1999) for the animals. They are likely to be both wary and vigilant under these conditions (see Underwood 1982) and, of the 3 senses that they use to detect predators, vision (unlike hearing and smell) is compromised by neither the level nor the direction of wind,

and is, therefore, presumably often the sense upon which they chiefly rely.

The dark-adapted animal may be affected by corona in various ways. Unpredictable illumination of what are normally dark, passive structures is likely to promote wariness. Potentially more potent is the likelihood that adjacent plume coronas recurring at the appropriate phase and frequency may induce the illusion of motion. This effect (the phi phenomenon; Dimmick 1920) is commonly observed in our everyday life in light-bar displays on emergency services and works’ vehicles. When active, the flashes of stationary lights in the left and right sides of such bars appear to jump from one side to the other; we experience a strong and convincing perception of movement even though we know that nothing actually moves. Adjacent brush or plume discharges flashing rapidly but out of phase may falsely signal movement in the same way. The illusion—interpreted as the presence of another animal, potentially a predator—is likely to increase wariness in prey animals, causing them to withdraw from (i.e., avoid) its source. This model has an important corollary: it potentially accounts for the remarkable persistence of avoidance behavior (Vistnes and Nellemann 2001, Vistnes et al. 2004). Corona light is selectively neutral and the probability of animals’ responding to it would therefore normally be expected to decrease over time. However, real movement and, in particular, real movement associated with predator attack, will presumably provide strong reinforcement for the response, thereby delaying the process of habituation. Such reinforcement, moreover, would be likely to continue for as long as prey fail to distinguish illusory from real movement.

VARIATION IN THE LEVEL OF AVOIDANCE

The ability to detect UV light adds a causal dimension to, and hence a direct explanation for, wide variation in the strength and persistence of avoidance behavior displayed by *Rangifer* at power lines. In contrast with ecological correlates that have been invoked in this respect, our hypothesis permits variation in avoidance to be interpreted in terms of a stimulus (i.e., corona UV light) rather than merely a response. Levels of avoidance by *Rangifer* at power lines range from strong to weak (Fig. 1; Table 1) and they may decrease after a few years (Reimers et al. 2007) or persist for decades (Vistnes and Nellemann 2001, Nellemann et al. 2003, Vistnes et al. 2004). Neither the strength nor the persistence of such responses is well understood. Variation in the former has been attributed to differences in ecological settings (Panzacchi et al. 2013a) and methodology (Tyler et al. 2015). Studies vary with respect to biotic variables including 1) the sex and age of animals; 2) the distribution, abundance, and quality of forage; and 3) animals’ imperative to approach and cross power lines (which is likely to vary with season). They also vary with respect to abiotic variables such as 4) the structure and, hence, ease of passage across the terrain, and 5) the presence of other infrastructure or other forms of disturbance (Reimers and Colman 2006; Reimers et al. 2007; Panzacchi et al. 2013a,b). They also vary with

respect to method; some studies have examined continuous records of movement in small numbers of animals (usually of one particular age and sex class) tracked using Global Positioning System devices (e.g., Panzacchi et al. 2013a), whereas others have evaluated single sample or interval patterns of distribution of entire herds (including both sexes and all age classes) in relation to infrastructure (e.g., Vistnes and Nellemann 2001, 2008; Vistnes et al. 2001, Nellemann et al. 2003). All these factors contribute to differences in patterns of dispersion of animals at power lines but they are also all independent of the source of the disturbance that they are recruited to explain. Conceptualizing avoidance as a response to corona UV light has the singular virtue of addressing the heterogeneity of the response in terms of its cause. Power line corona varies in terms of form (glow, brush, and plume), incidence (temporal component), site (spatial component), and intensity. All 4 qualities vary within and between power lines—including those operating at the same voltage—owing to the 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 4 physical dimensions prior to consideration of any ecological or socio-biological imperatives. This is a potent reason for expecting large variation in the strength of responses.

DETECTING POWER LINE CORONA: OTHER UNGULATES

Power line corona may be assumed visually salient in species that possess UV-sensitive opsins (including certain rodents, bats, and birds; Bowmaker 2008; Lind et al. 2013, 2014). Detection of UV light in species, such as *Rangifer*, with UV-permissive ocular media but lacking UV opsins will depend on 1) the energy of the signal within the functional range of opsins in rods and blue cones, and 2) aspects of visual anatomy upon which we have concentrated here. The visual range extends into the UV in several species of ungulates, including okapi (*Okapia johnstoni*), cattle (*Bos taurus primigenius*), and sheep (*Ovis aries*; Douglas and Jeffery 2014), and possibly also white-tailed deer (*Odocoileus virginianus*) and fallow deer (*Dama dama*; Jacobs et al. 1994). Given that the mammalian retina is well conserved, with retinal processing and neuronal adaptation varying little among species (Rodieck 1998), it is reasonable to assume that these species will also detect power line corona when dark-adapted. There is one important caveat: none of them, so far as is known, shows a blue shift in the TL similar to that observed in *Rangifer* in winter. This might, indeed, be unlikely given that seasonal transformation of the TL in *Rangifer* appears to be a result of prolonged exposure to low luminance (Stokkan et al. 2013). Sub-boreal species might, therefore, be less sensitive to UV light than *Rangifer*. Such a conclusion, however, may be premature. The TL has been little-studied beyond the descriptive analysis of Johnson (1968) and in the study of *Rangifer* by Stokkan et al. (2013); it would be interesting to know whether it has dynamic

properties in other species adapted to low-luminance environments, such as forest ungulates.

CONCLUSION

Knowledge of sensory capacity is central to understanding the ways in which animals respond to anthropogenic disturbance (e.g., Martin 2011, Lima et al. 2015). It is necessary to know what types of information underlie the behavioral decisions animals make at infrastructure and the thresholds of detection for each type. Both aspects are indispensable not only for anticipating but also for mitigating impact of infrastructure.

Hogg et al. (2011) demonstrated that the visual range of *Rangifer* extends into the UV. To this is now added evidence that the retinal sensitivity of these animals in the mesopic–scotopic range far exceeds that of humans. From these 2 facts arises the general conclusion that dark-adapted *Rangifer* is likely to detect corona light on power lines considerably better than humans. Integration of this information with the physical characteristics of corona discharges on power lines indicates that detection of corona light may account, at least in part, not only for avoidance behavior *per se* but also for both the persistence and the high degree of variation of avoidance responses displayed by *Rangifer* at these structures. Corona light on power lines is, thus, clearly a cryptic impact: it belongs to that class of impacts that “elude detection and may be overlooked because of inherent limitations of impact evaluations, but [which] can be substantial” (Raiter et al. 2014:637). Recent work suggesting that UV sensitivity is widespread in birds (Lind et al. 2014) and nonprimate mammals (Douglas and Jeffery 2014) opens, in this respect, a new perspective in the sensory ecology of environmental conservation.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site. This includes a definition and description of barrier effects and avoidance, including effects at high-voltage power lines, and a list of crepuscular and/or nocturnal mammalian predators of *Rangifer*.

Table S1. Documented incidences of barrier effects and avoidance involving mammals at high-voltage power lines.