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LETTER

Rudolph the red nosed reindeer had a very bioluminescent nose. A reply to van der Hoven *et al.* 2012

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Research published in Deinsea by van der Hoven *et al.* (2012) identifies the cause of Rudolph's infamous red nose to be the consequence of hyperemia of the nasal mucosa induced by the exertion of pulling a heavy load. Van der Hoven *et al.* (2012) claim that the excessive stresses endured whilst flying with Santa Claus and the sleigh in tow resulted in cerebral and bodily hyperthermia, overworking the nasal cooling system, causing the nose to glow. Whilst we recognise van der Hoven *et al.*'s (2012) central tenet of highly vascularized nasal mucosa in reindeer (*Rangifer tarandus* Linnaeus, 1758) helping regulate nasal heat exchange, we concluded that this is unlikely to be the causal factor of Rudolph's particularly iridescent appendage for multiple reasons, detailed below.

Selection

Van der Hoven *et al.* (2012) fail to take into account that Rudolph was selected to lead the team prior to the circumnavigation undertaken on Christmas Eve. It is therefore unlikely that the onset of hyperemia of the nasal mucosa would have been identified prior to this. In fact, in the first documented account of Rudolph, May (1939) states that Rudolph was excluded by his peers due to his unusually large, red nose, suggesting that the nose remained red under normal conditions and not only under the working stresses described by van der Hoven *et al.* (2012).

Distance and altitude

The distance required to travel in the restricted time-frame available would suggest that Rudolph and his colleagues would have to fly at both altitude and speed. A press release from the Federal Aviation Administration noted that clearance was given for Santa Claus to cruise at 50,000 feet before descending to the rooftops to deliver presents (FAA 2012). Given the nature of nasal heat exchange and its comparison to the mechanisms of a car radiator, it is impractical to dismiss the combined cooling effects of the altitude and speed required to deliver presents globally in a timely manner. As with all animals that travel long-distances the minimisation of travel time and energy expenditure are important evolutionary drivers of migratory behaviour (Duerr *et al.* 2012). Flying at altitude can be advantageous if avoiding lengthy detours (e.g. flying around mountains) or when utilising horizontal air currents to increase speed (Tucker 1968). Flight at altitude has also been shown to be more energy efficient due to reduced air density leading to lower drag (Altshuler & Dudley 2006). This issue of how Rudolph and the other reindeer cope with the decreased oxygen levels at altitude is not clear, although research has shown that under exercise at lower ambient temperatures oxygen consumption was reduced in *Rangifer tarandus* (Nilssen *et al.* 1990). This suggests that at higher altitudes, where the temperature is greatly reduced the oxygen requirements for reindeer may be significantly less than at ground level. Given the fact that these

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reindeer are also exceptional specimens able to cope with extreme workloads, flying at altitude seems a likely scenario for Rudolph.

Flight formation

Rudolph was part of a team of nine reindeer, each of which would have contributed to the effort of pulling Santa Claus and the sleigh. It is well documented that only Rudolph exhibited a glowing nose and if the theory of van der Hoven *et al.* (2012) is to be accepted it would seem reasonable to assume that the other reindeer would have also exhibited a red nose under the same work pressures. Whilst V-formation flying in pelicans (*Pelecanus onocrotalus*) has been shown to reduce individual's heart rate and wingbeat frequency and therefore reduce individual energy expenditure (Weimerskirch *et al.* 2001), more recent work on flocks of pigeons (*Columba livia domestica*) has shown trailing individuals significantly increase flapping frequency and therefore energy expenditure when flying directly behind lead individuals (Usherwood *et al.* 2011). As noted from the figures in May's account (1939) the reindeer exhibit a linear flying formation with no evidence of limb anti-phase whilst flying (Fig. 1). It therefore seems likely that Dasher, Dancer, Prancer, Vixen, Comet, Cupid, Donner and Blitzen would have struggled to avoid each other's, and Rudolph's, downwash and therefore be subject to similar levels of exertion as the lead individual; unlike v-formation flyers such as the northern bald ibis (*Geronticus eremita*; Portugal *et al.* 2014).

Vision

Finally, research into the vision of reindeer has also brought into question the validity of this hypothesis. It could be more reasonably argued that the red nose could actually be an aid to navigation when used in conjunction to the adapted eyesight of *R. tarandus* and this seems a more plausible account for the occurrence of a red nosed reindeer.

ULTRAVIOLET ADAPTATIONS

Reindeer have been shown to detect ultraviolet light (Hogg *et al.* 2011), which is a rarity in mammals and an adaptive response to living in an environment with extreme changes in light level. It is suggested that this is advantageous as it provides a high contrast for objects that absorb UV light. Tyler *et al.* (2014) suggest that UV light may enhance the ability of reindeer to distinguish plants in snow, whilst Petzold and Goward (1988) revealed that a major food item of reindeer, the reindeer lichen (*Caldonia rangifera*) absorbs UV light making it more visible against the snow. The same has been suggested for the fur of one of the main predators of reindeer, the Arctic wolf (*Canis lupus arctos*). The fur has been shown to absorb a high level of UV light (Reynolds & Lavigne 1981) purportedly making them more visible to reindeer. A further adaptation allows reindeer to change their tapeta lucida from a gold colour in summer to a blue colour in winter, increasing UV detection (Stokkan *et al.* 2013). Reindeer have the ability to adapt the tapetum lucidum using a layer of spaced collagen fibres (Greanya 2015) allowing the eyes to cope with darkness in winter and therefore enhance sensitivity to light (Stokkan *et al.* 2013). However, even in cloudy or foggy conditions the vision of the reindeer would be limited, despite the constant dilation of the pupils noted throughout the Arctic winter months. Thus increased light availability would be beneficial.

A more plausible explanation for Rudolph's red nose is the provision of additional light for navigation through the night sky in conjunction with adapted vision. This would indicate a more permanent feature to that proposed by van der Hoven *et al.* (2012). It is more likely that the "glow" from Rudolph's nose is a commonly encountered natural phenomenon. Biofluorescence is one such possibility and has been described in a number of organisms. Most extensively described in scleractinian corals (Salih *et al.* 2000), bioflouorescence is increasingly being discovered in a range of other organisms, including many fish species (Sparks *et al.* 2014, Gruber *et al.* 2015). Red fluorescence in fish is common and serves to increase vision in dark waters (Meadows *et al.* 2014). Despite the presence of red biofluorescence in many species (Meadows *et al.* 2014, Sparks *et al.* 2014) it is unlikely that biofluorescence can be attributed to the glow of Rudolph's nose due to the fact that it is invisible to humans under normal light conditions.

BIOLUMINESCENCE FOR IMPROVED VISUAL ACUITY

Bioluminescence is found in eleven phyla and over 600 genera, primarily of marine origin, but has also been identified in a number of terrestrial species (Hastings & Morin 1991). Blue

Figure 1 Illustration from May's original account showing the linear formation employed during flight and, as indicated in the inset text, the effectiveness of the light produced in foggy flying conditions. [courtesy of Rauner Special Collections Library, Dartmouth College, reproduced with kind permission from The Rudolph Company, L.P.]

(Mittag & Hastings 1996) and green (Tsien 1998) bioluminescence are most common, although red bioluminescence does occur (Widder *et al.* 1984, Denton *et al.* 1985). Red bioluminescence is relatively rare, although more common than flying reindeer, of which only nine have previously been described from an isolated population in the Arctic circle (May 1939). Red bioluminescence as a consequence of the catalysis of luciferase has been described in three genera of dragon fishes (*Aristostomias*, *Pachystomias* and *Malacosteus*) (O'Day & Fernandez 1974, Widder *et al.* 1984, Campbell & Herring 1987, Partridge & Douglas 1995, Douglas *et al.* 1999, Douglas *et al.* 2000) as well as in the terrestrial railroad worm (*Phrixothrix* spp.; Viviani 2002).

Although not previously described in mammals, the ability to evolve bioluminescence features is not unfeasible. It has been suggested that bioluminescence may have already evolved independently up to 30 times (Hastings 1983); evidence for important selective advantages for organisms able to bioluminesce. Adaptive evolution could explain the presence of bioluminescence in Rudolph, especially given the other important trait (flying), which has only previously been recorded in mammals of the order Chiroptera. As with biofluorescence, there is evidence that certain species may use red bioluminescence for improved visual acuity. Several genera of deep-sea fishes have been shown to bioluminesce, reportedly to improve vision in dark environments. *Aristostomias*, *Malacosteus* and *Pachystomias* have pigments which allow them to detect their own bioluminescence, guiding them to prey items. The use of the red light emitted from Rudolph's red nose used in conjunction with adaptive night vision in reindeer could enable precise, high speed travel required for circumnavigation of the globe.

CONCLUSION

The fact that Rudolph's nose glows red has previously been noted as being advantageous in foggy conditions (Dominy 2015), since it is the most visible colour in foggy conditions (Granath & Hulbert 1929). May (1939) noted that Rudolph's "glowing" nose aided Santa Claus in his Christmas Eve preparations when a thick fog descended. This would suggest that Rudolph was specifically chosen because of this adaptive trait and would suggest that, far from being caused by excessive strain from pulling Santa Claus and the sleigh, his red nose was in fact caused by bioluminescence to aid in navigation.

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