



Wintering Snowy Owls *Bubo scandiacus* integrate plumage colour, behaviour and their environment to maximize efficacy of visual displays

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For a comprehensive understanding of the evolution of animal signals, it is necessary to understand how the performance of visual displays is maximized to get the most possible attention from receivers. We assessed whether the white plumage of Snowy Owls *Bubo scandiacus* functioned as a social signal and, if so, how coloration and behavioural adaptations enhance signal efficacy. Signalling theory predicts that: (1) the colour properties of plumage should vary across the body, with the brightest parts being those involved in visual display performance; (2) specific displays calling attention to or enhancing detection or conspicuousness to conspecifics should be evident; and (3) location of the signalers should be such that signal efficacy is optimized. All three predictions were supported. The brightest areas of the plumage (particularly the face, throat and upper breast) were always unspotted, and white is particularly effective in open habitats characteristic of this species. The birds displayed a specific posture and orientated toward the sun preferentially on sunny days, and Owls with the whitest (least spotted) plumage displayed more and signalled more frequently from perches on the ground, where albedo from the snow may enhance the visual display. Snowy Owls integrate coloration, behaviour and environment through habitat selection to maximize the efficacy of their visual displays.

Keywords: display, orientation to sun, perch height, Saskatchewan, social signalling.

Key to understanding the evolution of animal visual signals is the efficacy with which the signal's information is conveyed (Rowe & Skelhorn 2004). The tactical aspects of signals that deal with this efficacy in eliciting a response from receivers have been much less studied than the strategic aspects, which are often used to classify signals as handicaps, symbols, etc., depending on the information they give (Hurd & Enquist 2005). However, understanding how the performance of visual displays is maximized to get the most possible attention from receivers is necessary for a comprehensive understanding of signal evolution (Marchetti 1993, Rowe & Skelhorn 2004, Galván 2008).

Ambient light plays a particularly important role in determining the efficacy of signals because it affects how colours and patterns are perceived (Endler 1993, Marchetti 1993). The evolutionary consequences of these effects can be seen in associations between different signal forms and spatial and temporal light environments, as demonstrated by interspecific comparisons (Marchetti 1993, McNaught & Owens 2002, Gomez & Théry 2004, Galeotti & Rubolini 2007) or revealed by the active habitat selection of individuals (e.g. Endler & Théry 1996). Behavioural adaptations to optimize colour displays have received little attention (however, see Galván 2008), and most examples come from tropical forest birds (Endler & Théry 1996, Heindl & Winkler 2003). These studies have shown that birds can change their display location depending on ambient light conditions. Penteriani *et al.* (2010) found Eagle Owls *Bubo bubo* take advantage of moonlight conditions to increase the conspicuousness of their white throat patch during

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vocal displays, and Campioni *et al.* (2010) found territorial Eagle Owls chose signalling posts that were more visible than those chosen by non-territorial birds. Most studies have ignored fine-tuned behavioural adaptations, such as changes in body orientation, to cope with variation in the light environment. Orientating the body or plumage colour patches according to physical attributes of the environment (Doucet & Montgomerie 2003) or to the position of the sun (Hamilton 1965, Dakin & Montgomerie 2009, Olea *et al.* 2010) has been suggested to be an adaptive response to maximize the efficacy of visual displays. Solar orientation in particular may be expected to be a common adaptive response because, with the exception of some animals able to produce light chemically, all visual displays use the light provided by the sun. However, the only study to date showing both location and orientation of displays according to position of the sun is Dakin and Montgomerie's (2009) study of the Peafowl *Pavo cristatus*, a species with iridescent plumage whose perception depends on the angle at which it is observed. Olea *et al.* (2010) found that Great Bustards *Otis tarda* orientate their white undertail parts toward the sun, but only in the morning and during the most elaborate components of their displays on the lek. Evidence of solar orientation from other species and colour types is lacking.

Most research on the function of bird coloration has focused on plumage and bare parts generated by carotenoid and melanin pigments (Hill & McGraw 2006a, 2006b) and, more recently, on other pigments, iridescence and feather structures (Shawkey *et al.* 2005, Galván *et al.* 2009, Meadows *et al.* 2009, Negro *et al.* 2009). By contrast, predominantly white plumages have always been problematic (Tickell 2003, Bortolotti 2006), although the intensity and size of white patches are known to transmit information such as signaller presence or quality and affect the efficacy of visual displays (Galván 2008 and references therein). White, too, is a structural colour, and bright white feathers are known to have special morphological adaptations (Dyck 1979). Most research on white birds has focused on the heat-loading effect of solar radiation rather than on the perception of the colour (Bortolotti 2006). However, white acts as an effective long-distance signal, especially in open habitats (Bortolotti 2006, Galván 2008, Schön 2009, Olea *et al.* 2010). As it is expected that in such habitats, brighter plumage maximizes

contrast over long distances (McNaught & Owens 2002), and white is created by reflectance of light in all wavelengths, white plumage probably acts as a long-distance signal because of the efficacy of white in open environments.

The Snowy Owl *Bubo scandiacus* has a predominantly white plumage but is enigmatic in that, unlike other species of owls except the Barn Owl *Tyto alba* (Roulin *et al.* 1998), there is considerable variation in coloration related to age, sex and individual patterning (Josephson 1980). The proportion of the body covered by black spots and barring varies from zero to approximately 50% (G. R. Bortolotti pers. obs.), although the face, throat and upper breast are invariably white (see below). Snowy Owls in North America winter primarily in open habitats of the Great Plains (Kerlinger *et al.* 1985, Kerlinger & Lein 1988). They perch during daylight hours in conspicuous locations, generally the top of power poles, but also on other structures or on small rises on the ground. While other authors have interpreted elevated perches as functioning in foraging (Keith 1964, Hohn 1973, Boxall & Lein 1989), the birds often perch for several hours without showing any of the typical behaviours (e.g. scanning the ground) that suggest they are hunting (G. R. Bortolotti, M.J. Stoffel pers. obs.). Furthermore, our observations suggested that the birds habitually faced the sun (see Results). Thus, perching behaviour may be part of a display whereby Snowy Owls transmit information to conspecifics. The aim of this study is to assess how the white plumage of Snowy Owls might function as a social signal and, if so, to identify possible adaptations that enhance signal efficacy in relation to solar orientation.

If the white plumage of Snowy Owls is used in communication, then signalling theory predicts that: (1) the colour properties of plumage should vary across the body, with the brightest parts being those involved in visual display performance; (2) specific displays calling attention to or enhancing detection or conspicuousness to conspecifics should be evident; and (3) the location of the signallers should be such that signal efficacy is optimized (Endler 1993, Hasson 1997). Therefore, we predicted that signalling Snowy Owls should adopt a posture whereby their frontal, unspotted surface, which should be the brightest area of the plumage, is orientated towards the sun. Furthermore, as white coloration is used in long-distance communication, such a display should be

performed on the top of poles rather than on the ground to optimize signal efficacy. We test these predictions in an area where Snowy Owls winter in large numbers.

METHODS

Study area and species

We studied Snowy Owls over 10 winters in 1999–2000 and 2008–2009 in an area of southern Saskatchewan, Canada, from approximately just north of Saskatoon to Swift Current. This and adjacent areas of Saskatchewan have one of the highest wintering densities of this species in North America (Kerlinger & Lein 1988). The habitat is flat and almost entirely agricultural, with a mean daily average temperature in January of -13°C (high) and -23°C (low). Birds are present from late October to early April, but local densities vary among years and over the course of the winter. Like most of the other regular winter sites studied (Keith 1964, Hohn 1973, Boxall & Lein 1989), at least a proportion of the population is territorial. However, given that the local population varies considerably over the course of the winter, we suspect many birds may just exclude competitors from their immediate proximity rather than maintaining long-term territories *per se* (see also Boxall & Lein 1982).

Variation in plumage colour of the Snowy Owl is to some degree indicative of age and sex (Josephson 1980), with young birds and females being more heavily pigmented. However, there is considerable individual variation, and it is only possible to use criteria to delineate age/sex (including body size) in the hand (D. Holt pers. comm. and G. R. Bortolotti unpubl. data). Therefore, it was not possible reliably to attribute age or

sex in the field. We classified plumage colour variation using a simple, subjective three-score system that was appropriate for our field conditions: 1 = white (or only a few spots), 2 = moderate spotting and 3 = heavy spotting (Fig. 1). To avoid observer bias, only those scores from one observer (M.J.S.) were used.

Behaviour observation

We made no attempt to survey the number of birds in our area, but it was clear they were not evenly distributed across the landscape as they tended to cluster in areas with power poles. It was not uncommon to see two to five Snowy Owls simultaneously without the aid of optics. Owls were found by systematically driving around the countryside and scanning the ground and all elevated perches, as in previous studies (e.g. Lein & Webber 1979). Birds were generally detected at distances of up to 1.5 km. Upon sighting a bird we recorded the orientation of the front of the body as being directed exactly toward the sun or not, and whether the sun was shining or not at that moment. We did not measure the angle of deviation from sun orientation and subsequently analyse the data with circular statistics. Because the orientation behaviour was so strong (see Results) we saw little point in estimating angles; therefore, we adopted a test of independence whereby birds either faced the sun directly or did not. This is a very conservative test as the *a priori* probabilities are strongly weighted against detecting orientation to the sun, and so any positive result would indicate an extreme preference. We also recorded whether there were other Snowy Owls within sight using binoculars, and we often attempted to capture the bird using baited nets, bal-chatris or



Figure 1. Plumage colour classification for wintering Snowy Owls: 1 = white (or only a few spots), 2 = moderate spotting, and 3 = heavy spotting (photos by G. R. Bortolotti).

bow nets. We assume our observation points to be independent, i.e. individuals were not knowingly sampled repeatedly as we varied our survey route over this large area, and we know from the sudden appearance and disappearance of birds in an area, as well as band recoveries, that the Owls are very mobile. Our trapping results also suggest independence among years as we have only recaptured three individuals over the 10 years and 225 captures.

Snowy Owls perched at one of three height categories: on the ground (typically on a small rise); on a pole (power line); or on a perch of intermediate height such as a fence post, hay bale or road sign. While intermediate perches were abundant and ubiquitous, they were used infrequently in our area. Each of these perch height categories is expected to have a different value for a signalling bird.

Colour measurements

To characterize the colour properties of the plumage of Snowy Owls, spectrophotometric analyses were performed on eight frozen birds and five live birds from the Saskatoon area during November and December 2007. Data were collected in the laboratory using an Ocean Optics USB2000 spectrophotometer (range 250–800 nm) with ultraviolet (deuterium) and visible (tungsten-halogen) lamps and a bifurcated 400- μm fibre-optic probe (Dunedin, FL, USA). The fibre-optic probe provided both illumination and obtained light reflected from the sample, and had a reading area of approximately 1 mm². The measurements were taken at a 90° angle to the plumage surface of birds. The spectrometer measured reflectance in 0.36-nm increments. All measurements were relative to a white 'Spectralon' tablet (WS-1-SS; Ocean Optics), and reference measurements were made frequently. The spectral curves were generated by using OOIBASE software (Ocean Optics, Dunedin, FL, USA). To cover as much heterogeneity in the colour of the plumage patches as possible, three readings were obtained on different points of the patches, moving the probe by at least 5 mm before taking each new reading, but always following the same order (from upper to lower patch). The measurements were taken at the white plumage of four different patches to explore possible variation in colour variables: face, throat, breast and back. In addition, we measured reflectance at three black plumage spots chosen at random in

those individuals that presented them to illustrate the contrast generated by differences in brightness between black and white of the feathers. The colour of the black spots was measured at two body parts: breast and back. Total brightness (i.e. sum of reflectance between 300 and 700 nm) and UV chroma (i.e. sum of reflectance between 300 and 400 nm divided by total brightness) were then calculated. In all cases, the mean values of three measurements were used.

RESULTS

Variation in colour among body parts

The reflectance spectra of the white plumage of Snowy Owls showed considerably high reflectance values across the entire range of wavelengths as expected for white feathers, and a characteristic well-defined UV peak was observed in all plumage patches (Fig. 2). By contrast, the reflectance spectra obtained for the black spots showed relatively low reflectance values that progressively increased from low to high wavelengths, and a lack of defined peaks of reflectance, as is typical of melanin-based plumage traits (Fig. 2; McGraw 2006).

A repeated-measures ANOVA showed significant differences in the total brightness of the white face, throat, breast and back plumage patches ($F_{3,30} = 4.73$, $P = 0.008$). *Post-hoc* LSD tests showed that these differences were due to higher reflectance of the face compared with the throat

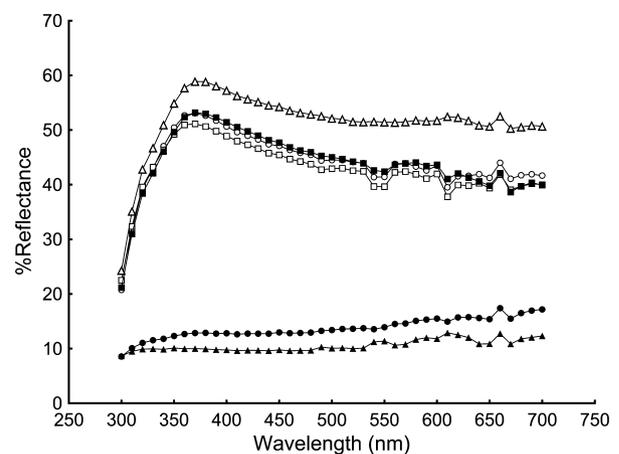


Figure 2. Reflectance spectra of Snowy Owls at six different plumage patches. Open circles: white throat; open triangles: white face; open squares: white breast; solid circles: black breast spots; solid triangles: black back spots; solid squares: white back ($n = 13$ Owls).

($P = 0.003$), the breast ($P = 0.004$) and the back ($P = 0.006$) (Fig. 3). White plumage patches also differed in UV chroma ($F_{3,30} = 6.53$, $P = 0.001$) but in the opposite direction of total brightness, as UV chroma were lower in the face than in the throat ($P = 0.002$), breast ($P < 0.001$) and back ($P = 0.008$). Other differences in these variables among plumage patches were not significant (all $P > 0.2$; Fig. 3).

Solar orientation

Consistent with the second prediction, Snowy Owls appeared to display by adopting a posture that emphasized the bright white and unspotted face, throat and upper breast (Fig. 4). The body was held erect, even to the point of appearing stretched, with head up and breast out. We made no attempt to quantify the frequency of this body posture as it was always associated with facing the sun, which was easier to quantify unequivocally.

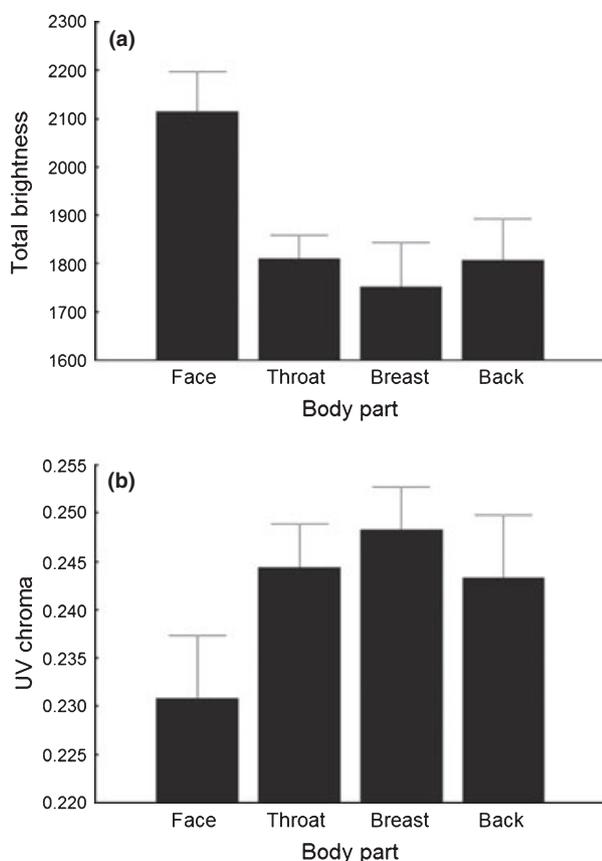


Figure 3. Means + se of total brightness (a) and UV chroma (b) of white feathers of 13 Snowy Owls from different body parts.

There was no difference in the frequency of orientating to the sun in the am vs. pm hours ($\chi^2 = 0.010$, $df = 1$, $P = 0.921$, $n = 198$ Owls). However, there was a highly significant association between this orientation behaviour and whether it was sunny or cloudy at the time ($\chi^2 = 98.703$, $df = 1$, $P < 0.0001$). Of 191 Owls sighted on sunny days, 91% were orientated toward the sun, as opposed to 11% of 28 Owls seen on cloudy days. The bright white feathers and unspotted nature of the face, throat and breast made the birds strikingly conspicuous when orientated to the sun on a sunny day, but the degree of spottiness overall did not appear to alter our detectability of plumage types (sunny vs. cloudy days, $\chi^2 = 4.109$, $df = 2$, $P = 0.123$). Although the birds were orientated towards the sun on sunny days without other Owls being present in the surroundings of the focal individual (86% of 71 observations), that proportion increased significantly to 94% of 108 occasions ($\chi^2 = 3.828$, $df = 1$, $P = 0.050$) when other Owls were present. There is little doubt that the focal Owls were not only aware of, but responded to, these neighbours. More Owls were captured when no other Owl was in view than when there was an Owl in view ($\chi^2 = 5.537$, $df = 1$, $P = 0.019$). We believe these birds presented with



Figure 4. Display posture of a Snowy Owl (photo: G. R. Bortolotti).

an opportunity to attack prey were concerned with competitors, and Snowy Owls are one of the few species regularly seen in our area. On several occasions we, and others (D. Zazelenchuk pers. comm.), have observed two Snowy Owls in aggressive, physical conflicts over our lures. Collectively, these findings suggest that orientation towards the sun is involved in communication, and hereafter we refer to it as signalling behaviour.

We observed birds of all degrees of plumage spotting to display. Although most birds orientated on sunny days, plumage category and signalling were not independent because, of 191 Owls seen when it was sunny, 97% of white, 83% of moderately spotted and 86% of heavily spotted Owls orientated toward the sun ($\chi^2 = 7.562$, $df = 2$, $P = 0.023$). On overcast days there was no difference ($\chi^2 = 0.124$, $df = 2$, $P = 0.940$) as most birds were not signalling.

Use of perches

As white is particularly effective in signalling at long distances, we assessed whether perch height was independent of the Owl's signalling behaviour for each of the three plumage types. Heavily spotted birds clearly preferred the tallest category; 71% of 65 birds were seen on poles regardless of whether the Owl was orientated to the sun or not ($\chi^2 = 0.898$, $df = 2$, $P = 0.638$). For moderately spotted Owls, there was a modest shift to the ground when the birds were displaying; 35% of 26 signalling, but none of 12 non-signalling, birds were perched on the ground ($\chi^2 = 6.657$, $df = 2$, $P = 0.036$). However, the most significant change in perch height was for white Owls; 58% of 67 birds that were signalling were seen on the ground, as opposed to nine of 10 non-signalling birds which were perched on poles ($\chi^2 = 14.328$, $df = 2$, $P = 0.001$).

DISCUSSION

All three of the general predictions of signalling theory were supported by our results. Alternatively, although unlikely, the proposed display posture and perching behaviour in Snowy Owls could serve a thermoregulatory function. However, the sun-facing orientation would not be necessary for, nor would it maximize, exposure to solar radiation. Indeed, Lustick *et al.* (1978) showed that the sun orientation of the white breast of Herring Gulls *Larus argentatus* functioned to reduce heat

load. Furthermore, thermoregulation cannot explain the variation in behaviour demonstrated by the different plumage colours. Snowy Owls are extremely well insulated and have evolved physiological adaptations that allow them to live at very low temperatures (Gessaman 1972). It appears that generally the role of colour in thermoregulation in birds is relatively minor (Bortolotti 2006). The only areas of the body of Snowy Owls that are always unpigmented, i.e. the face, throat and upper breast, are always visible on perched, displaying birds. We believe their lack of spots and the high reflectance of the face (Figs 1 and 2) are indicative of enhancement for signalling, and that plumage colour variation influences the size of the signal (Fig. 1). In a comparison of species of owls, Galeotti and Rubolini (2007) concluded that head ornaments (ear tufts, eyebrows, throat patch, etc.) evolved to serve a communication function, and were influenced by the light environment of the species during their daily activity period.

The orientation preference by signalling Snowy Owls at first seemed paradoxical, as bright sunshine and albedo from the snow is painfully blinding to humans. Snowy Owls typically squint as they face the sun; however, their facial disc may also have a unique adaptation. Numerous and long bristles and other feathers protrude outward from the facial disc (Fig. 5). This may reduce glare, as other species of northern owls that are similarly exposed to snow and low temperatures, but inhabit forests, lack these feathers (our pers. obs.). Facing the sun also does not appear to be a characteristic behaviour of owls or birds in general. In the winter of 2008–2009 we observed three Great-horned Owls *Bubo virginianus*, one Great Gray Owl *Strix nebulosa* and eight Northern Hawk Owls *Surnia ulula* perched in conspicuous locations on sunny days, and none was orientated to the sun. At the same time, we observed 29 perched Common Ravens *Corvus corax* and only six were orientated towards sun. However, Eagle Owls display during specific hours of the day to optimize signal transmission of their white throat patch (Penteriani & Delgado 2009).

The importance of sunshine to Snowy Owl behaviour became obvious when on three occasions we were observing birds under cloudy conditions; the sun came out and the birds immediately shifted position approximately 45° to face directly into the sun in typical display posture. After the first time we noted this shift, the birds

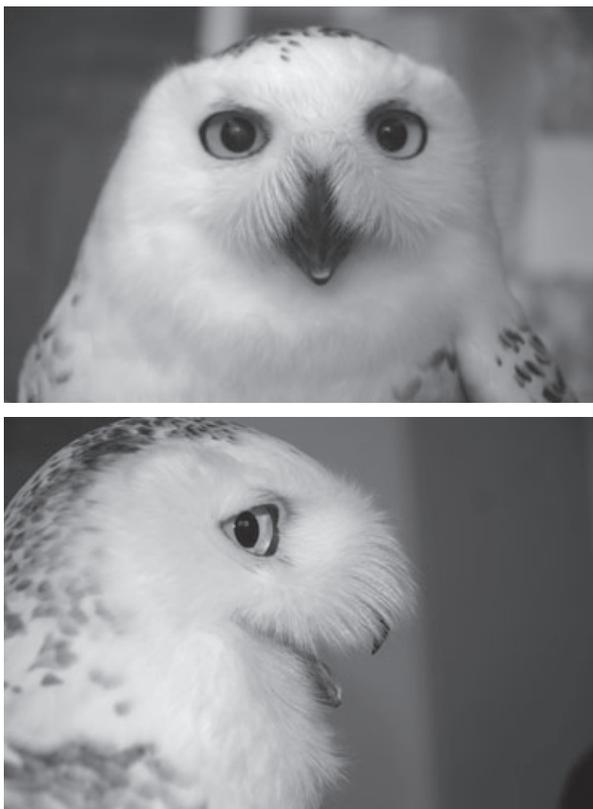


Figure 5. View of a Snowy Owl's facial disc from the front (top) and from the side (bottom) (photos: G. R. Bortolotti).

that we observed always shifted when the sun came out. On a separate occasion, we made observations in late afternoon. It was only after hours of continuous observation that we noticed that the body had in fact changed from its original position and that it must have gradually and imperceptibly reorientated to maintain its posture relative to the sun. What was unexpected was that the Owls did not orientate towards conspecifics, but always toward the sun. Multiple birds could be seen with identical orientation, so perhaps it is more important to maximize the signal quality that some birds are likely to see than orientate to a specific individual. The observing bird need not be directly in front of the signaller as the rounded body of the Owl when shone upon is visible from a wide angle. In addition, the highly flexible rotation of the head allows birds to view others in all directions. It would be interesting to study settlement and perching behaviours of Snowy Owls relative to one another to determine how individuals take advantage of sunshine, or perhaps put competitors at a signalling disadvantage.

It was not possible to determine perch site preference in relation to availability. In theory, the ground was always an option to perch on, and intermediate perches were abundant, as there were fence posts along virtually every road we travelled. Yet 60% of the birds overall were detected on power poles, which were not available on all, or even most, search routes. While we cannot rule out a visibility bias, this finding is consistent with those of intensive behavioural studies, which show the heavy use of poles for perches (Boxall & Lein 1982, 1989). Contrary to the intuitive expectation that high perches might be chosen for signalling, there was a preference for displaying from the ground, as both white and moderately spotted Owls were more likely to be on higher perches when it was not sunny and hence they were not signalling. The fact that the heavily spotted birds did not change their perching behaviour in the presence or absence of sunshine may be due to the fact that such birds were likely to be juveniles (Josephson 1980) and so may not have even been territorial or of a high enough quality to be competitive. Lein and Webber (1979) found Snowy Owls tended to use elevated perches such as trees and utility poles early in the morning and towards sunset (apparently most often the time for hunting), and to perch on or near the ground in mid-day. Similarly, and consistent with our interpretation of communication, Keith (1964) observed Snowy Owls typically roosting at mid-day on ice or Muskrat *Ondatra zibethicus* lodges, a behaviour 'pattern most pronounced on clear sunny days'. It may be that high perches were not necessary to convey the signal. Ground perches were almost invariably on a small rise or clump of snow, which may have afforded an uninterrupted sight line in this open habitat. We propose that the ground was preferentially used on sunny days, especially by white birds, to enhance the brightness of the signal from the albedo of the snow. Thus, Snowy Owls may maximize the reflectance properties of their plumage through an active selection of highly reflective display sites, as described for different species of tropical birds (e.g. Endler & Théry 1996, Heindl & Winkler 2003), because brighter plumages in open habitats like those used by wintering Snowy Owls maximize contrast over long distances (McNaught & Owens 2002). Counterintuitively, even pure white Snowy Owls were very conspicuous when perched on snow. We observed an extreme case of signalling from the ground, and

one that suggests a broader function to the signal than territoriality, during spring migration (27 March). At that time, there were only discrete patches of snow covering < 50% of the ground. In one scan of a field using a spotting scope we observed 29 Snowy Owls, 24 of which were on the ground. Of the total, 19 were classified as white birds; 18 were on the ground and always located on snow patches, and all were facing the sun regardless of the proximity or orientation of other Owls. This micro-habitat selection is again complemented by the solar orientation behaviour of birds likely to increase signal efficacy. In sharp contrast, only six of 10 birds with some degree of spotting were seen on the ground, all of them on grass or bare soil.

The fact that whiter birds were more likely to signal was undoubtedly biased by age and sex, as whiter birds are more likely to be older males. However, Snowy Owls of both sexes are known to be territorial, and we observed birds spanning the entire plumage colour range to signal. The change in perching behaviour according to plumage is less obviously accounted for. Similar to the question posed by Olea *et al.* (2010) – why don't all males signal – we question why perch site preference should vary with colour, especially if signal transmission may be enhanced, as we propose, on the ground. Olea *et al.* (2010) point out that the display behaviours of bustards are costly and so signalling may indicate condition. Cost to Snowy Owls is unlikely to be associated with the energetics of the display, but it could be influenced by predators and competitors. Although perhaps not at a great risk of mortality, ground perching would leave the birds vulnerable to disturbance by such animals as canids, which are common in our area. Perhaps only higher quality individuals may pay the energetic or other costs associated with harassment.

Although our results strongly support a signalling function for the white plumage of Snowy Owls, at this stage we can only speculate about what information the birds transmit during displays. In some species, stressful conditions determine the size or the brightness of white plumage patches that are associated with individual quality (Qvarnstrom 1999, Hanssen *et al.* 2006, Ferree 2007, McGlothlin *et al.* 2007), perhaps because only high-quality individuals have access to diets rich in some nutrients needed for feather growth (McGlothlin *et al.* 2007). Thus, Snowy Owls may be signalling their quality to conspecifics in their surroundings, which may be a form of territoriality.

However, if Snowy Owls signal individual quality when facing the sun, and the albedo of the snow maximizes plumage brightness, why do heavily spotted birds avoid displaying on the ground? The answer may concern some pattern of covariation between plumage spottiness and quality. Heavily spotted birds may be individuals of low quality trying to avoid the enhancing effect of the albedo in revealing quality through the colour properties of the white plumage, and thus plumage spottiness in Snowy Owls may act as an attenuator (Hasson 1997). If this were the case, low-quality, heavily spotted birds would still signal because it is always better to obtain poor resources through signalling low quality than not signalling at all. Although future studies should test these possibilities, our results show that Snowy Owls integrate coloration, behaviour and environment to maximize the efficacy of their visual displays. It has been previously shown that the interaction between colour and behaviour (movement complexity) is essential to understand the evolution of visual displays (Galván 2008, Penteriani *et al.* 2010), and the possibility that the environment (habitat selection) also has a role in this system clearly increases the complexity of our view of animal visual signals.

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