

# Carotenoid ornamentation of adult male Common Redpolls predicts probability of dying in a salmonellosis outbreak

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## Summary

1. Conditional handicap models of sexual selection predict that ornamentation should be positively associated with an individual's ability to withstand challenges to their health.
2. We assessed whether levels of carotenoid ornamentation were related to the probability of adult male Common Redpolls, *Carduelis flammea*, dying in a salmonellosis epidemic by comparing the ornamentation of surviving adult male redpolls to those found dead. Hosts suffering from salmonellosis shed bacteria in faeces, and new individuals are typically infected when they ingest faeces-contaminated food.
3. The proportion of adult males in the sample of dead birds was significantly higher than in the sample of living birds.
4. Among adult males, probability of survival was significantly predicted by the expression of their carotenoid signals: brightly ornamented adult males were more likely to die in the epidemic.
5. A probable hypothesis for these results is that if carotenoid ornamentation in redpolls functions as a status badge of dominance, bright males would have had priority access to highly preferred, and contaminated, food patches.

*Key-words:* *Carduelis*, carotenoid-dependent plumage colour, Common Redpolls, conditional handicap, honest advertisement, salmonellosis, status badge

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## Introduction

Conditional handicap models of sexual selection state that preferences for secondary sexual traits can evolve if the trait is condition-dependent, because preferences for such traits can provide fitness benefits to choosy females (Zahavi 1977; Grafen 1990). The key mechanism of this idea is that only males in good condition can afford to invest in costly non-functional traits (handicaps) and survive. Considerable empirical support for this idea has been found in birds, where plumage ornaments are thought to indicate the bearer's health state; this is particularly true for carotenoid-based plumage coloration.

Carotenoid pigments typically are red, orange or yellow, and can be acquired by animals only through ingestion (Brush 1990). There are primarily two reasons why carotenoid ornaments may be honest indicators of quality (reviewed in Olson & Owens 1998): (1) carotenoid availability may be limited by an individual's

foraging efficiency (Endler 1980); and (2) carotenoids are required for self-maintenance (Lozano 1994). The second explanation reasons that because carotenoids stimulate the immune system and have antioxidant properties, there is a potential trade-off between allocating carotenoids to self-maintenance *vs* producing an ornament (Lozano 1994; von Schantz *et al.* 1999). This trade-off has been demonstrated experimentally (Blount *et al.* 2003; Faivre *et al.* 2003; McGraw & Ardia 2003), and carotenoid signal expression has repeatedly been linked with aspects of condition (Hill & Montgomerie 1994; Hill 2000; McGraw & Hill 2000a; Saks *et al.* 2003). From this body of work, it appears that carotenoid ornaments support the conditional-handicap model.

Although controlled studies have built a strong case for the role of carotenoid signals in indicator models, there have been few studies that examine natural selection events in a population, and compare how carotenoid ornamentation relates to survivorship during, for example, a disease outbreak. Notably, Nolan, Hill & Stoehr (1998) compared the characteristics of a House Finch (*Carpodacus mexicanus*) population before and after an epidemic of mycoplasmal conjunctivitis.

Demographic changes in the study population suggested that large males, and males with drab carotenoid ornamentation, were less likely to survive, resulting in a female-biased population with unusually small and brightly ornamented males (Nolan *et al.* 1998). Here, we compare the ornamentation of adult male Common Redpolls (*Carduelis flammea*) that died during an outbreak of salmonellosis with those that survived. If ornamentation is indicative of male quality, then we would expect that males with highly developed ornaments would be more likely to survive the die-off.

## Materials and methods

### SALMONELLOSIS

Salmonellosis is a disease caused by *Salmonella* bacteria, and affects a wide range of taxa including birds (Friend 1999). The disease agent, usually *Salmonella enterica* serovar Typhimurium in songbirds, is shed in faeces by infected individuals and is propagated by ingestion of contaminated food items (Friend 1999; Refsum *et al.* 2002, 2003). Occurrences of *Salmonella* outbreaks appear to be cyclical (Refsum *et al.* 2002) and may be increasing (Friend 1999). Salmonellosis results in a multitude of pathological symptoms including poor body condition, enlarged spleen and necrosis of various gastrointestinal organs (Friend 1999; Refsum *et al.* 2003).

### STUDY SPECIES

Common Redpolls are a circumpolar finch species that breeds in the arctic and spends the winter foraging in large transient flocks further south (Knox & Lowther 2000). In our area, winter flocks forage in birch (*Betula papyrifera*) and alder trees (*Alnus crispa*), and are commonly seen at bird feeders or gritting on sanded roads. *Carduelis* finches, including Common Redpolls, Eurasian Siskins (*C. spinus*), Pine Siskins (*C. pinus*) and Greenfinches (*C. chloris*), appear to be highly vulnerable to salmonellosis (Friend 1999; Refsum *et al.* 2002, 2003). Adult male Common Redpolls have extensive red carotenoid (equinone and lutein) plumage ornaments on their breast and rump (Troy & Brush 1983) that are variable both in size and colour (Seutin 1994). In Greenfinches, carotenoid ornaments are associated with social dominance, and also confer a mating advantage (Eley 1991, cited in Lindström & Lundström 2000).

### DISEASE OUTBREAK, AND SAMPLING OF DEAD AND LIVING REDPOLLS

During late winter of 2002, a severe salmonellosis outbreak occurred in the interior of north-central British Columbia, Canada (53°N, 122°W). Dead birds were collected from 24 February to 28 March in the city of Prince George and surrounding areas. Common Redpolls were by far the most commonly collected species ( $n = 79$ ), followed by Pine Siskins ( $n = 10$ ). Several raptor

species were also collected, but these were later found to have died from causes other than salmonellosis. During this period, the weather was seasonably cold with temperatures being consistently below freezing (average hourly temperature =  $-7.3\text{ }^{\circ}\text{C} \pm 0.32\text{ }^{\circ}\text{C SE}$ ). Infected birds showing visible signs of lethargy were commonly seen resting near feeders. Dead redpolls were found in a frozen state, usually lying in feeders or on the snow pack nearby. Specimens were stored in air-tight plastic bags at  $-20\text{ }^{\circ}\text{C}$ . Birds were later thawed and processed (see below), and then refrozen before being shipped to the Western College of Veterinary Medicine at the University of Saskatchewan for necropsy.

Of the Common Redpolls ( $n = 79$ ) and Pine Siskins ( $n = 10$ ) submitted for necropsy, bacterial cultures were performed on liver tissues of a subsample of 10 birds, and *Salmonella* bacteria were isolated in large numbers from all samples (G. A. Wobeser, unpublished data). We are reasonably confident that all dead redpolls succumbed to salmonellosis, given that they were all collected from within or beneath feeders. Moreover, members of the public repeatedly reported observing redpolls in a lethargic state, with puffed-up plumage, resting near food sources such as bird feeders; these signs are consistent with salmonellosis (see Friend 1999). Similarly, salmonellosis was confirmed in redpolls from our area through a sample submitted for necropsy to the provincial animal health agency (D. J. Wilson, BC Ministry of Water, Land and Air Protection, personal communication).

Simultaneously to collecting dead birds, we captured live redpolls ( $n = 57$ ) at two locations within Prince George ( $n = 23$  and  $34$ , respectively); as redpolls are highly transient (Knox & Lowther 2000), we saw little reason to sample over a wide area. Birds were trapped from 12 March to 19 March using potter traps baited with black oil sunflower seeds. Birds were leg-banded so that recaptures ( $n = 2$ ) could be identified and omitted from the analysis.

For both dead and living redpolls, we measured mass (nearest 0.25 g) using a 50 g spring balance, and lengths of wing chord, ninth primary feather and tail (nearest 0.5 mm) using a ruler. Adult males were identified by the presence of red plumage patches, which are absent, or highly reduced, in females and juvenile males (Pyle 1997). Furcular fat was scored using a 6-point scale (after Gosler 1996). To measure the areas of carotenoid pigmentation, two high-resolution photographs (2 580 000 pixels/photograph), one of the breast and one of the rump, were taken of each bird using a tripod-mounted digital camera (Cybershot® model DSC-F505V, Sony Corp., Tokyo, Japan) with the lens positioned 60 cm above the bird. To get comparable data from photographs birds were positioned in a standard way by the same observer. We also subjectively classified the colour of the breast and rump of each bird into one of three groups: little to no redness, pink or bright red. To objectively measure colour (see below), we collected a single representative feather from the centre of

the breast, and another from the centre of the rump. The fifth right rectrix was collected to assess nutritional status of the birds during their last moult using ptilochronology (Grubb 1995), and the length of this feather was also measured using digital callipers (nearest 0.1 mm).

To compare body size among redpolls, we collapsed the four measures of body size (lengths of wing, ninth primary, tail and fifth rectrix) into a single variable using principal components analysis (PCA). All four factors loaded strongly and positively (0.83, 0.83, 0.80, 0.82, respectively) into the first component (PC1), which had an eigenvalue of 2.69 and explained 67% of the total variation in the data.

Adult redpolls undergo complete moult at the end of summer (Pyle 1997), and size of alternating dark and light bands (growth bars) on tail feathers may reflect nutritional status from the time of year when carotenoid signals were produced (Grubb 1995). Tail feathers were mounted on black construction paper, and holes were inserted through the card at the leading edge of each growth bar. Seven to 10 growth bars centred on the distal two-thirds of the feather shaft were measured, and average growth bar size was calculated. To ensure reliability, we analysed data only from cases with distinct growth bars.

#### SCORING CAROTENOID SIGNALS

Carotenoid plumage signals vary in both size and colour, so we measured the area of carotenoid plumage patches for each bird from the photographs, and colour from the feather samples, for both the breast and the rump. The area of red pigmentation was calculated from photographs using the polygon tool in ImageJ software, version 1.3 (US National Institutes of Health, Bethesda, MD, USA). Breast and rump feathers were mounted on white paper and digitized by scanning an image at 2400 dpi. Scanned images were of sufficient resolution to sample colour on individual feather barbs. Using the tools in Adobe Photoshop 6.0, we recorded values of colour components red, green and blue (RGB system). RGB measures give equal scores to each component colour when sampling white (high scores) or black (low scores) colours. The hue of a colour is determined by the relative difference in component colours (red, green or blue). For example, bright, highly saturated red colours score high in the red component relative to either the green or blue, whereas colours that are less red in hue will have a larger green and/or blue component, relative to the red component. We calculated 'redness' of the colour by subtracting the average of green and blue scores from the red score. By using this relative difference, we were essentially measuring hue, while also capturing variation in saturation. We took four measurements of colour from each feather, and we used the average in analyses. We are confident that this methodology adequately described the colour of the feathers, as the breast feather redness score calculated this way differed

among our three subjectively classified groups for breast colour in the predicted direction (ANOVA,  $F_{2,122} = 356.63$ ,  $P < 0.0001$ ), and was correlated with size of the breast patch size ( $r = 0.91$ ,  $n = 126$ ,  $P < 0.0001$ ).

Our four distinct measures of carotenoid signals (breast patch area, breast colour, rump patch area and rump colour) were collapsed into a single variable using PCA. All four measures were correlated and loaded strongly and positively in PC1 (factor loadings were 0.96, 0.93, 0.98 and 0.86, respectively), which had an eigenvalue of 3.28, and explained 82% of the total variance. Data from a random subset of nine birds, with signal area re-measured from photographs and redness scores measured from a second set of feathers, showed that these composite signal scores were highly repeatable (repeatability  $r = 0.97$ ; see Lessells & Boag 1987).

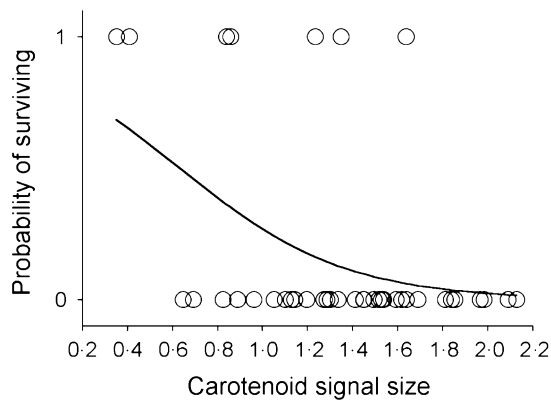
## Results

#### SALMONELLOSIS AND BODY CONDITION

Common Redpolls that were found dead were generally emaciated and had very little breast muscle. Body mass of dead birds was 22% lower than live birds (living =  $13.69 \pm 0.25$  g, dead =  $10.05 \pm 0.30$  g; ANOVA,  $F_{1,133} = 85.22$ ,  $P < 0.0001$ ), and fat scores were also drastically reduced in dead birds (living =  $1.70 \pm 0.15$ , dead =  $0.17 \pm 0.12$ ; ANOVA,  $F_{1,133} = 65.30$ ,  $P < 0.0001$ ). The extreme reduction in body mass and lack of fat stores were not unexpected as these are normal clinical signs associated with salmonellosis. It is possible that some mass reduction was due to postdeath water loss; however, owing to the ambient winter conditions this effect would have been minimal as birds were frozen immediately following death.

#### CONDITION-DEPENDENCE OF THE CAROTENOID SIGNAL

Among adult male redpolls, carotenoid signal scores (PC1) were not correlated with growth bar size ( $r = 0.09$ ,  $n = 37$ ,  $P = 0.61$ ) or body size ( $r = 0.14$ ,  $n = 39$ ,  $P = 0.39$ ). It is possible that the signal was more reliable in one body region compared with another, or that colour measures are more reliable than area of pigmentation, as has been seen in other studies (e.g. Badyaev *et al.* 2001); however, when we individually analysed the four raw variables that were used to derive our carotenoid signal score, we did not find any association with growth bar size or body size (all  $P$ -values  $> 0.10$ ). To test whether carotenoid signal score of adult males was related to fat scores or body condition, we included only living birds in analyses because salmonellosis had such dramatic impacts on body mass and fat reserves (above). We estimated body condition by using residuals from a regression of body mass on body size ( $F_{1,5} = 9.31$ ,  $P = 0.03$ ). We could detect no significant relationship between carotenoid signal score and either our index of body condition ( $r = -0.23$ ,



**Fig. 1.** The probability of adult male Common Redpolls surviving during an outbreak of *Salmonella* decreased if they had larger carotenoid plumage ornaments. Carotenoid signal values (PC1) are plotted for living (1) and dead (0) male redpolls.

$n = 7$ ,  $P = 0.62$ ) or fat score ( $r = -0.07$ ,  $n = 7$ ,  $P = 0.89$ ). Although sample sizes were very small in these analyses, the patterns were not at all suggestive.

#### DEMOGRAPHY OF THE DIE-OFF

The dead sample had a larger proportion of adult males (32/76) compared with the live sample (7/43;  $G_1 = 8.45$ ,  $P < 0.01$ ), and hereafter our analyses include only adult males. After removing non-significant effects of growth bar size and body size from models, logistic regression revealed that the probability of adult males dying was significantly predicted by the carotenoid plumage score, where bright individuals were less likely to survive ( $\chi_1^2 = 3.89$ ,  $n = 37$ ,  $P = 0.049$ ). This relationship was strengthened when two additional cases were added which had been removed for the previous analysis due to missing growth bar data ( $\chi_1^2 = 5.26$ ,  $n = 39$ ,  $P = 0.02$ ; Fig. 1).

#### Discussion

In this study we examined whether carotenoid signaling in Common Redpolls was associated with the probability of surviving a disease epidemic. Under the theory of honest advertisement (Zahavi 1977), we predicted that individuals with extensive carotenoid ornamentation would have greater chances of survival because they may have stronger resistance to diseases. In contrast with this idea, we found that carotenoid ornamentation was negatively associated with the probability of survival, whereby the most ornamented individuals were uncommon among the survivors, and abundant in the sample of dead birds (Fig. 1).

A skewed demographic die-off pattern was seen at two levels in our study: (1) adult males were disproportionately abundant in the dead sample compared with the live sample, and (2) among adult males, those that were highly ornamented were more likely to die than

less ornamented adult males. Although possible, it is unlikely that these results reflect sampling bias. A relationship between ornamentation and the probability of dying could occur if highly ornamented dead birds were preferentially collected over those that were less ornamented. This seems unlikely as carcasses were found in feeders, or lying on the snow nearby, and were therefore easily seen regardless of their colour. Moreover, as all adult males were reasonably bright red in colour, it would be unlikely that the relatively subtle differences among adult males had a large impact on their probability of being collected. Second, the tendency for adult males to be less abundant in the live sample could arise if they were more difficult to capture. Such a bias would cause a skew to exist only in the capture data, since probability of dying is presumably independent of our trapping efforts. However, 42% of dead birds were adult males, which is a high proportion if we assume that the sex ratio is 50:50 (Knox & Lowther 2000) and that juvenile males should constitute about 50% of males (Seutin 1994). As such, our data from capture of live redpolls (16% adult males) seems to more closely reflect the expected proportion of adult males in a population compared with the sample of dead birds. Therefore, we believe that capture bias is also unlikely to explain our findings. Instead, we believe that these two unusual demographic skews are biologically driven.

We found that carotenoid ornamentation of Common Redpolls was not correlated with past condition as measured with growth bars, or with present body condition. While these results may suggest that carotenoid ornamentation is not an honest signal in redpolls, the two demographic patterns described in our study can be readily explained under the hypothesis that competitive interactions among free-living Common Redpolls cause differential exposure to the disease among dominance ranks. The tendency for adult and brightly ornamented males to die in a *Salmonella* outbreak may arise if these individuals are dominant over other members of the population (e.g. females, young males and dull adult males), and thereby have priority access to the most heavily contested, and heavily contaminated, food sources. Although some finch species are known to have reversed dominance hierarchies (e.g. McGraw & Hill 2000b), members of the *Carduelis* genus are known to display carotenoid ornaments in aggressive interactions (e.g. Greenfinches, Lindström 2000; Pine Siskins, H. van Oort, personal observation). This suggests that these ornaments may function as status signals in this genus, although this has only been confirmed with the Greenfinch (Eley 1991, cited in Lindström & Lindström 2000). Even if plumage ornaments do not act as status badges, it is possible that older males are dominant to, and more brightly ornamented than, younger males; this hypothesis could also explain our results. These dominance-based exposure mechanisms are biologically reasonable hypotheses for explaining our observations; however, because dominance

has not been studied in Common Redpolls, further studies would be needed to verify this idea.

It is unlikely that the immunosuppressive effects of testosterone can explain our findings. The immunocompetence handicap hypothesis (Folstad & Karter 1992) predicts that healthy males can afford to have higher levels of circulating testosterone without suffering from a compromised immune system, compared with less healthy males, resulting in visible differences in sexual signaling. Furthermore, testosterone levels are unlikely to be elevated during winter months, and testosterone does not appear to be associated with plumage ornamentation in redpolls (Romero *et al.* 1997).

We are confident in concluding that ornamentation is not positively related to survival of redpolls in *Salmonella* epidemics, as might be predicted by indicator models of sexual selection. Indicator models suggest that highly ornamented males generally have more effective immune defences; as such, these individuals should have greater survivorship in disease outbreaks, as demonstrated by Nolan *et al.* (1998). Although our results appear to contradict these ideas, they are perhaps less surprising when one considers that redpolls appear to have extremely low resistance to this disease (Friend 1999; Refsum *et al.* 2002, 2003), perhaps as a consequence of their feeding habits (Refsum *et al.* 2003). Consequently, exposure to the disease may be a far more important factor predicting survivorship than immunocompetence. If we are correct in suggesting that social dominance explains our findings, *Salmonella* epidemics appear to remove highly competitive individuals from the population that may typically have greater phenotypic quality. In terms of impacts to a population and its gene pool, this is a more serious type of die-off compared with other disease epidemics where individuals with less ornamentation, and therefore lower phenotypic quality, are more likely to die (e.g. Nolan *et al.* 1998).

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### References

Badyaev, A.V., Hill, G.E., Dunn, P.O. & Glen, J.C. (2001) Plumage color as a composite trait: development and functional integration of sexual ornamentation. *American Naturalist* **158**, 221–235.

Blount, J.D., Metcalfe, N.B., Birkhead, T.R. & Surai, P.F. (2003) Carotenoid modulation of immune function and sexual attractiveness in zebra finches. *Science* **300**, 125–127.

Brush, A.H. (1990) Metabolism of carotenoid pigments in birds. *FASEB Journal* **4**, 2969–2977.

Endler, J.A. (1980) Natural selection on color patterns in *Poecilia reticulata*. *Evolution* **34**, 76–91.

Faivre, B., Grégoire, A., Prévault, M., Cézilly, F. & Sorci, G. (2003) Immune activation rapidly mirrored in a secondary sexual trait. *Science* **300**, 103.

Folstad, I. & Karter, A. (1992) Parasites, bright males, and the immunocompetence handicap. *American Naturalist* **139**, 603–622.

Friend, M. (1999) Salmonellosis. *Field Manual of Wildlife Diseases: General Field Procedures and Diseases of Birds* (eds M. Friend & J. C. Franson), pp. 99–109. US Department of the Interior, Madison, WI.

Gosler, A.G. (1996) Environmental and social determinants of winter fat storage in the great tit *Parus major*. *Journal of Animal Ecology* **65**, 1–17.

Grafen, A. (1990) Biological signals as handicaps. *Journal of Theoretical Biology* **144**, 517–546.

Grubb, T.C. (1995) Ptilochronology: a review and prospectus. *Current Ornithology* **12**, 89–114.

Hill, G.E. (2000) Energetic constraints on expression of carotenoid-based plumage coloration. *Journal of Avian Biology* **31**, 559–566.

Hill, G.E. & Montgomerie, R. (1994) Plumage color signals nutritional condition in the House Finch. *Proceedings of the Royal Society of London Biology B* **258**, 47–52.

Knox, A.G. & Lowther, P.E. (2000) Common redpoll (*Carduelis r. flamma*). *The Birds of North America*, no. 543 (eds A. Poole & F. Gill). The Birds of North America, Inc., Philadelphia, PA.

Lessells, C.M. & Boag, P.T. (1987) Unrepeatable repeatabilities: a common mistake. *Auk* **104**, 116–121.

Lindström, K. (2000) *Bird-parasite interactions: using Sindbis virus as a model system*. PhD Thesis, University of Uppsala, Uppsala.

Lindström, K. & Lundström, J. (2000) Male greenfinches (*Carduelis chloris*) with brighter ornaments have higher virus infection clearance rate. *Behavioural Ecology and Sociobiology* **48**, 44–51.

Lozano, G.A. (1994) Carotenoids, parasites, and sexual selection. *Oikos* **70**, 309–311.

McGraw, K.J. & Ardia, D.R. (2003) Carotenoids, immunocompetence, and the information content of sexual colors: an experimental test. *American Naturalist* **162**, 704–712.

McGraw, K.J. & Hill, G.E. (2000a) Differential effects of endoparasitism on the expression of carotenoid- and melanin-based ornamental coloration. *Proceedings of the Royal Society of London B* **267**, 1525–1531.

McGraw, K.J. & Hill, G.E. (2000b) Carotenoid-based ornamentation and status signalling in the house finch. *Behavioral Ecology* **11**, 520–527.

Nolan, P.E., Hill, G.E. & Stoehr, A.M. (1998) Sex, size and plumage redness predict house finch survival in an epidemic. *Proceedings of the Royal Society of London B* **265**, 961–965.

Olson, V.A. & Owens, I.P.F. (1998) Costly sexual signals: are carotenoids rare, risky or required? *Trends in Ecology and Evolution* **13**, 510–514.

Pyle, P. (1997) *Identification Guide to North American Birds, Part I*. Slate Creek Press, Bolinas, CA.

Refsum, T., Handeland, K., Baggesen, D.L., Holstad, G. & Kapperud, G. (2002) Salmonellae in avian wildlife in Norway from 1969 to 2000. *Applied Environmental Microbiology* **68**, 5595–5599.

Refsum, T., Vikøren, T., Handeland, K., Kapperud, G. & Holstad, G. (2003) Epidemiologic and pathologic aspects of *Salmonella typhimurium* infection in passerine birds in Norway. *Journal of Wildlife Diseases* **39**, 64–72.

- Romero, L., Soma, K., O'Reilly, K., Suydam, R. & Wingfield, J. (1997) Territorial behavior, hormonal changes, and body condition in an arctic-breeding song bird, the redpoll (*Carduelis flammea*). *Behaviour* **134**, 727–747.
- Saks, L., Ots, I. & Hõrak, P. (2003) Carotenoid-based plumage coloration of male greenfinches reflects health and immunocompetence. *Oecologia* **134**, 301–307.
- von Schantz, T., Bensch, S., Grahn, M., Hasselquist, D. & Wittzell, H. (1999) Good genes, oxidative stress and condition-dependent sexual signals. *Proceedings of the Royal Society of London B* **266**, 1–12.
- Seutin, G. (1994) Plumage redness in redpoll finches does not reflect hemoparasitic infection. *Oikos* **70**, 280–286.
- Troy, D.M. & Brush, A.H. (1983) Pigments and feather structure of the redpolls, *Carduelis flammea* and *C. hornemanni*. *Condor* **85**, 443–446.
- Zahavi, A. (1977) The cost of honesty (further remarks on the handicap principle). *Journal of Theoretical Biology* **67**, 603–605.

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