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The function of lichen flakes and white spider cocoons on the outer surface of birds' nests

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The predictions from two hypotheses for the adaptive significance of the application of lichen flakes and white silk cocoons to the outer surface of bird nests are compared. The hypotheses are: (a) concealment by resemblance to the branches to which the nest is attached, and (b) concealment by light reflection to make the nest dissolve into the background beyond the site of attachment. The predictions are tested with evidence obtained from a sample of 42 Long-tailed Tit (*Aegithalos caudatus*) nests and 64 Blue-grey Gnatcatcher (*Polyoptila caerulea*) nests, and from examination of single nests of over 50 other species. Little evidence is found to support branch matching although this hypothesis may partly or wholly explain the external application of lichen to the nests of some species. The hypothesis of concealment by light reflection is supported by the data, in particular by the general absence of lichen on branches to which lichen-covered nests are attached and the substitution in some species of pieces of white man-made materials for pieces of lichen or white silk cocoons. Thus concealment by light reflection is probably an important method of nest camouflage for a range of species of small bird.

KEYWORDS: Bird, nest, cryptic, lichen, spider cocoon.

Introduction

Bird nests with an outer layer that incorporates lichen flakes or white cocoons are sufficiently common that descriptions of them are given in field guides to nest identification, e.g. Long-tailed Tit (*Aegithalos caudatus* Linnaeus), Pygmy Sunbird (*Anthreptes platurus* Vieillot) and Chaffinch (*Fringilla coelebes* Linneaus) (C. Harrison 1985) and the Vireo *Vireo solitarius* Wilson (H. H. Harrison 1979).

Some authors also discuss the function of the decoration; Perrins (1979) describes the covering of 'greyish lichens' on the nest of the Long-tailed Tit as rendering it 'beautifully camouflaged, especially against a tree trunk'. What is apparently the same mechanism is more fully expressed by Collias and Collias (1984) as 'camouflage of the exterior of the nest to resemble the immediate environment', who give examples including the Ruby-throated Hummingbird (*Archilocus colubris* Bourcier and Mulsant) and the Blue-Grey Gnatcatcher (*Polyoptila caerulea* Linnaeus). They also state that: 'often lichen-covered nests of various birds are saddled on a branch and look like a knot on that branch'.

This explanation of camouflage by appearing to be part of the tree is regarded by Robinson (1981) as a type of mimicry because the object is seen but not recognized, while he uses crypsis to describe objects that blend into the background. Starrett (1993) calls both these types of concealment, crypsis while agreeing that they may be perceived

differently. Endler (1981) refers to resemblance to part of a plant as 'masquerade', reserving the term 'crypsis' for resemblance to 'a random sample of the background' as perceived by predators.

The explanation of Collias and Collias (1984) for the attachment of lichens to the nest surface is therefore a masquerade hypothesis, referred to here as 'branch matching'. However, examination of nests in museum collections over the last three years suggested to me that crypsis (Endler, 1981) is a possible alternative explanation for an external nest covering of either lichen or white silken cocoons and that the crypsis is achieved through their ability to reflect light (Hansell, 1993). The argument is that the surface of a solid object seen against a lighter background can be made to blend with it by having a light reflecting surface. Some bird species, however, apply only a few relatively large lichen flakes or white spider cocoons scattered over the nest exterior. I suggest that these are light reflecting spots which, on the surface of a darker solid object, create the appearance of light passing through an insubstantial object unworthy of a predator's attention. This would be included by Cott (1940) as disruptive camouflage because the solid shape of the nest is broken up but it is specifically achieved by the use of light reflecting patches. Cott himself describes this effect using the example of the white spots on the body of the forest dwelling Bush Buck *Tragelaphus scriptus* Pallas.

This paper examines nests of > 50 different species to assess evidence in support of either the branch matching hypothesis (masquerade) or light reflecting hypothesis (crypsis) for the function of lichen flakes or white spider cocoons attached to the external surfaces of nests. Crypsis depends on the background context of the object (Endler, 1990), a factor which can only be judged indirectly in this study on collected nests. However, this study in addition to being based on nests of over 50 species, tests clear predictions of the two hypotheses which can be tested using collected nests. These are:

	Branching matching	Light reflection
(1)	Lichens on a nest will be associated with lichens on the nest attachment site and the lichen on the two of them will be of similar colour.	Lichens on the nest may occur even in the absence of any lichen at the attachment site
(2)	Materials other than lichens (including man-made materials) applied to the nest exterior will tend to make them similar in appearance to the attachment site	Materials other than lichens may be applied to the nest exterior to enhance light reflection
(3)	Nests coated with lichens will be attached to branches of similar or larger diameter to themselves.	Such nests may be attached to branches much narrower than the nest diameter.

Methods

The three predictions were tested in the following manner:

The presence of lichens on branches bearing lichen-covered nests

(*a*) Long-tailed Tit (*Aegithalos caydatus*): an appeal launched in BTO News (Hansell, 1993) asked readers who had photographs of nests of this species to report the nature of the nest site and whether any lichen occurred at the site of the nest attachment. This produced information on 45 nests including copies

of the photographs of 11 of them. As these results had to be judged second-hand, the scoring method was kept as simple as possible with lichen being recorded as present even if the description sent in suggested that it was only in small amounts. Not all these reports indicated whether or not lichen was present on the nests themselves; however, since none of the more than 70 Long-tailed Tit nests was without external lichen, it was assumed always to be present.

(*b*) Blue-grey Gnatcatcher (*Polyoptila caerulea*): a large sample of the lichen-bearing nests of this species attached to their original branches were found in the Western Foundation of Vertebrate Zoology (California). These were examined and scored for the presence of lichen on the branches to which they were attached, provided that at least 18 cm of branch was included with the specimen (Mean nest diameter = 6·6 cm). Sixty-four nests satisfied this criterion. The presence of lichen was scored on a four-point scale (0 = no lichen present, 3 = branch surface largely or wholly covered). The amount of lichen on the nest also varied and was scored on the same four-point scale.

(*c*) Other species: as part of a wider study of nests in museum collections (including Western Foundation of Vertebrate Zoology, California; National Museum of Natural History, Washington DC and British Museum (Natural History, Tring), single nests of species from over 500 genera were examined and their details recorded on a standardized check sheet. For those nests with an outer lichen covering and still attached to a length of supporting branch equal to at least 2·5 × the nest width, the presence or absence of lichen on the branch was recorded. Nests of 26 species fulfilled these conditions.

The function of materials other than lichens applied to the nest exterior

The examination of nests of such a large number of species allowed me to record data on the application to the other nest surface of materials other than lichen including man-made materials.

Branch diameter

The external diameter of the nest and the diameter of the branch just below its site of attachment were measured. For nests attached to several branches, the diameter of the largest branch close to the nest was recorded.

Results

The presence of lichen on branches bearing lichen-covered nests

(*a*) Long-tailed Tit (*Aegithalos caudatus*): only 7/45 (16%) Long-tailed Tit nests were on branches bearing lichen, however, all the nests bore lichen on their surface. The proportion of nests and branches bearing lichen was highly significantly different in a χ^2 test using a 2×2 contingency table ($\chi^2 = 65{\cdot}8$, 1 df, $P \leqslant 0{\cdot}01$) indicating a strong tendency for nests not to be on lichen-bearing branches.

(*b*) Blue-grey Gnatcatcher (*Polyoptila caerulea*): the relationship between lichen application to the nest and its occurrence on the branch in this species is shown in Table 1. There was no evidence for an association between lichen on the nest and on the branch to which it was attached. (Kruskal Wallis one-way ANOVA $H = 4{\cdot}79$, 3df, $P = 0{\cdot}189$ for a two-tailed test).

Table 1. Blue-grey Gnatcatcher (*Polyoptila caerulea*): association between the amount of lichen on the nest and on the branch to which the nest was attached, where presence of lichen is on four-point scale (0 = no lichen and 3 = a virtually complete covering).

		Lichen score for nest				
		0	1	2	3	Totals
Lichen score for branch	0	1	11	11	9	32
	1	1	1	5	6	13
	2		1	5	7	13
	3		3		3	6
Totals		2	16	21	25	64

Table 2. Number of 26 species of birds (excluding the Long-tailed Tit and Blue-grey Gnatcatcher) making lichen-covered nests, belonging to different families shown according to two different taxonomic authorities, Sibley and Monroe (1990) and Howard and Moore (1991).

Sibley and Monroe (1990)		Howard and Moore (1991)	
Trochilidae	15	Trochilidae	15
Tyrannidae	2	Tyrannidfae	2
Vireonidae	2	Vireonidae	2
		{Platysteiridae	1
Corvidae	4	{Dichruridae	1
		{Monarchidae	2
Bombycillidae	1	Bombycillidae	1
Aegithalidae	1	Aegithalidae	1
Fringillidae	1	Fringillidae	1

(*c*) Other species: in only two of the other 26 lichen-bearing species (i.e. *Batis molitor* Küster [Corvidae] Chinspot Batis, and *Eugenes fulgens* Swainson the Magnificent Humming Bird) was lichen also present on the branch (Table 2). No null hypothesis is possible here as nests were selected for the presence of lichen on them, however, these data again fail to provide support for the substratum matching hypothesis.

In the two species referred to above and the majority of Blue-grey Gnat-catcher nests where lichen was present on both nest and branch, the lichen was of similar appearance on both. However, on two specimens of Blue-grey Gnatcatcher nests it was observed that, whereas the branch was covered almost completely with a creamy-coloured lichen with scattered spots of a virtually white kind (possibly another species), the nests were covered in the white form alone (consistent with the light reflection hypothesis).

Materials other than lichens applied to the nest exterior

(a) Natural materials: white or pale materials other than lichen are applied to the exterior surface of the nests of several species where dislodging or disturbing them with fine forceps suggests that they have no significant structural role.

Table 3. Number of species of bird belonging to different families which include white silk patches on the exterior nest surface.

Sibley and Monroe (1990)		Howard and Moore (1991)	
Tyrannidae	3	Tyrannidae	3
Meliphagidae	1	Meliphagidae	1
Eopsatriidae	2	Eopsatriidae	2
Vireonidae	3	Vireonidae	3
Corvidae	4	Monarchidae	4
Aegithalidae	2	Aegithalidae	2
Nectriniidae	1	Nectriniidae	1
Fringillidae	3	{Parulidae	1
		{Emberizidae	2

The most frequent of these materials is densely spun white spider egg case cocoon silk or spider retreat silk. This material may occur as a complete external covering (e.g. nests of the Crimson-backed Sunbird *Nectarinia minima* Sykes), interspersed among flakes of lichen (e.g. *Aegithalos caudatus* nests), or as scattered white spots contrasting with the darker underlying structural layer of the nest (e.g. African Paradise-flycatcher *Terpsiphone viridis* Müller).

Silk is often an important structural material for nest construction in many small bird species so, in deciding whether white silk was being used as an exterior 'decoration', I applied a conservative rule. If by dislodging pieces of the silk concerned, there was any evidence that it served a structural role, it was discarded from the analysis. This left 19 species belonging to the families listed in Table 3. Of these, three species had white cocoons associated with lichen on the nest (two Aegithalidae and one Eopsaltriidae), but the rest had an outer application of white silk alone.

Only two other natural materials with no other obvious property than their pale appearance were found to be applied to the external surface of the nest. The nest of a Plain-throated Sunbird (*Anthreptes malacensis* Scopoli, Nectariniidae) had an almost complete covering of loosely applied pieces of skeletonized leaf with a pale silvery-grey cuticle, and the nest of the African Paradise-flycatcher (*Terpsiphone viridis*, Corvidae) was coated in feathers together with some white spider egg cocoons.

On the other hand the nests of two species were found to have materials applied to their external surfaces which were not obviously pale. The nest of the Broad-billed Hummingbird *Cynanthus latirostris* Swainson had brownish oval leaves scattered over its surface, and two specimens of the nest of the Grey-breasted Wood-wren *Henicorhina leucophrys* Tschudi (Certhiidae) had small, greyish, downy feathers scattered over the outer surface, with no feathers in the nest cup. In neither species did these materials contrast with those of the nest wall but nor did they obviously match the appearance of the nest attachment site, although it is possible that the leaves on the hummingbird nest were applied when they were green and matched the neighbouring foliage. A nest of the Jacky-winter *Microeca fascinans* Latham (Eopsaltriidae) on the other hand had silver-grey flakes of bark applied to it which closely matched the shade and texture of the forked branch to which the nest was attached and the branch at this point was of similar diameter to the nest; features supporting a branch matching explanation for the covering of bark.

In a few other species the structural wall of the nest was itself very pale yet had materials applied to it which partially or largely obscured it. The domed nest of the

Northern Jery (*Neomixis tenella* Hartlaub, Sylviidae) was constructed largely of white plant down, yet strands and patches of moss were applied to this to give a more dappled appearance apparently disruptive coloration achieved through the addition of darker decorative materials. In another member of the Sylviidae, the Buff-bellied Warbler (*Phyllolais pulchella* Cretzschmar) and five species of hummingbirds (Trochilidae) lichen flakes were applied to a nest cup composed of pale or virtually white plant down.

(b) Man-made materials: examination of the external surfaces of 40 Long-tailed Tit (*Aegithalos caudatus*) nests revealed that man-made materials were present on 45% of them among the lichens and white spider cocoons. Yet only on one of these nests was there a material (of greyish synthetic fibre) which blended inconspicuously with the structural wall. On this and all the other nests the artificial material were white paper and newsprint, and white expanded polystyrene (paper = 4, polystyrene = 13, both = 1). The number of pieces varied from single figures to, in one nest, 1568 polystyrene foam spheres.

Examination of 32 nests of the Bushtit *Psaltiparus minimus* Townsend (Aegithalidae), a close relative of the Long-tailed Tit and with a nest of similar construction, revealed pieces of near-white paper among the lichen flakes on the surface of six (19%) of them. The oldest of these was collected in 1892 indicating that the use of such materials for nest building is not a new phenomenon.

Three species from the family Vireonidae also used white paper fragments on the nest exterior. A nest of the Rufus-browed Peppershrike *Cyclarhis gujanensis* Gmelin included thin strips of white paper among the creamy lichen flakes; the Plumbeous Vireo *Vireo solitarius plumbeus* had pieces of white and yellow tissues among white cocoons and the Western Warbling Vireo *Vireo gilvus swainsonii* Baird had white tissue fragments alone among the white cocoons.

Finally two specimens of nests of Anna's Hummingbird (*Calypte anna* Lesson) from California had an external layer composed of flakes of paint instead of the usual lichen but still contrasting strongly with the brown colouring of the underlying nest cup wall. In one specimen the paint was all white while the other included some sky blue pieces among the white.

Branch diameter

Figure 1 plots the nest diameter against the diameter of the thickest supporting branch for the nests of 25 species bearing lichen on their outer surface. Nests were $>2\times$ the diameter of the branch in 21 (84%) out of the 25 species and $>10\times$ the diameter of the branch in 12 (48%) of them.

Lichen only occurred on the measured attachment branch in four of these species. These include the Blue-grey Gnatcatcher where lichen was only found on the branch at the attachment site of 50% of the nests (Table 1). but exclude the Long-tailed Tit where lichen on the branch was atypical.

This result again fails to support the hypothesis that nests are constructed so as to resemble part of the branch or branches to which they are attached.

Discussion

In this bird nest study direct evidence of crypsis from field observation is largely absent; nevertheless it is shown that the branch matching hypothesis does generate predictions readily testable by the methods reported here and that these predictions receive only weak support.

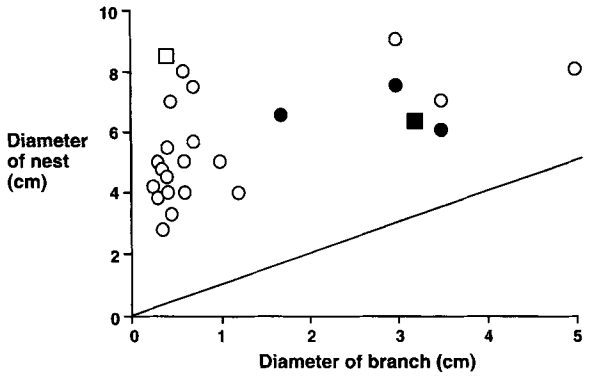

FIG. 1. Diameter of nests of 25 species plotted against diameter of the largest branch supporting each nest measured just below the attachment site. All the nests bore an exterior covering of lichen. All points with open symbols were nests attached to branches which bore no lichen. The open square represents a single but typical specimen of Long-tailed Tit nest. All solid symbols represent nests attached to branches also bearing lichen. The solid square is a point based on mean values from 44 Blue-grey Gnatcatcher nests; solid symbol is used for this species although only half the nests in the sample were attached to a lichen-bearing branch. A 'line of equality' is included to show where points should fall if nest diameters matched those of the branches to which they were attached.

The Long-tailed Tit always applied lichen to the nest and only a small proportion of nests were attached to sites where lichens occurred. This pattern also held for other species. Half of the nests of the blue-grey Gnatcatcher were on branches which bore lichen, but there was no significant association between lichen applied to the nest and that present on the branch. On two branches bearing predominantly cream-coloured lichen, the lichen used by the birds to cover the nest was virtually white, thus supporting the notion that light reflection rather than resemblance to the attachment site is the protective mechanism.

It could be argued that the nests may resemble the tree or bush in which they are sited in a more general way because, for example, matching lichen was distributed widely on the trees. In the Long-tailed Tit this is sometimes the case. However, on bramble, gorse or broom which together formed the majority of sites in this study, lichen is generally completely absent. Also, if protection is indeed being achieved by a more general matching of the nest to a sample of the background (crypsis), then how is it brought about? This paper presents data which suggest that reflection of light from the nest surface to help it merge into a paler background beyond the tree is at least a contributory mechanism for the majority of species that apply lichen and whiter spider cocoons to the nest exterior. Nevertheless, most of the data reported here come from the examination of museum specimens, which, it may be argued, are a biased sample being those nests which were discovered. This criticism would be hard to dismiss where a species is represented by a very small number of nests, however with more than 50 species studied including statistical samples of the nests of Blue-grey Gnatcatcher and Long-tailed Tit, this problem should not be serious enough to threaten the conclusions. Another possible criticism is that since many of the nests are 50–100 years old, some of the lichen colours may have faded with age. The Long-tailed Tit nests, however, were examined within a few months of collection and the lichen covering was clearly more pale than the underlying moss. Applying water to the lichen did make it appear more green but still paler than the moss. In addition, 11 colour photographs of nests *in situ*

show that the nests look pale rather than match the appearance of the branches to which they are attached. Almost white spots, apparently of lichen, can also be seen attached to a darker nest surface in published photographs of some species, for example the Rufous-collared Monarch *Arses (telescopthalmus) insularis* Meyer (Corvidae: Sibley and Monroe) and the Obscure Berrypecker, *Melanocharis arfakiana* Finsch (Melanocharitidae) (Coates, 1990). These examples do not exclude the possibility of lichen fading in museum collections but at least suggest that the observer is not being seriously misled about its colour.

The interpretation of the original colour of spider cocoons seems to pose no problems. Arthropod silks come in a variety of natural colours including brown, orange, yellow and green as well as white. Museum specimens which have been stored in the dark for several decades still appear to retain the original colour and texture of the silk. So it can reasonably be concluded that pieces of white silk applied to the nest exterior and with no discernible mechanical role, have the function of reflecting light. This interpretation is also supported by the inclusion of pale man-made materials.

The consequence of the application of these pale materials seems to be that the nest, instead of being revealed as a dark shape in a tree or bush, blends into a background which, depending upon the position of the nest, might either be the sky or foliage and ground with light reflected from it. This mechanism of concealment is *crypsis* or resembling a random sample of the background (Endler, 1981).

On the other hand the *masquerade* or tree matching hypothesis fails to find significant support. In particular most examples of nests covered in lichen did not match the surface of the branches to which they were attached. These supporting branches were also generally much smaller in diameter than the nest; consequently, even if the surface of nest and branch were identical, the nest would still appear to be an unusual structure in the tree.

The instances where nests made of a pale structural material receive further decorative layer does, however, warn that explanations may be more complex than considered here. It may be that the white nest of *Neomixis tenella* when dappled by added patterns of moss matches a random sample of the background more closely. The application of lichen flakes to the already pale nest cups of some hummingbirds raises the possibility that lichen layers serve other functions than those concerned with nest concealment; preventing water penetration for example or even conserving humidity. These deserve experimental investigation but are not incompatible with the crypsis through light reflection hypothesis.

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