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Nest decorations: an 'extended' female badge of status?

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Extended phenotypes as signals are widely distributed among animal taxa. For example, many bird species build eye-catching nests or structures, which can potentially mirror the quality or ability of the builder. Rock sparrow, *Petronia petronia*, nests are usually overly decorated with feathers belonging to different species. Feather carrying in this and other species seems to play a role beyond their supposed thermoregulatory function, that is, to provide insulation to eggs and developing chicks. In this study, we documented for the first time this intriguing pattern of behaviour in the rock sparrow and experimentally tested its potential role as a sexually selected or status signal by means of a feather supplementation experiment carried out in two distinct populations from Italy and Spain. We found that females were responsible for feather carrying, laid larger clutches and provisioned their young at a lower rate in those nests with experimentally added feathers. Decorated nests sustained fewer intrusions by floater individuals and were defended with greater intensity by both parents than control nests, which supports the role of nest ornamentation as a status signal to conspecifics. Presence of experimental feathers did not significantly increase the frequency with which males provisioned their young but males tended to desert their brood less often and spent more time guarding the brood in experimental nests, indicating that feather presence may also play a role in an intersexual context. Overall, our results allow us to exclude the thermoregulation hypothesis as a likely explanation for the occurrence of these decorations and provide partial evidence for the idea that feather carrying conveys information to the partner and potential competitors. Our study thus supports the notion that nonbodily traits serving a direct (naturally selected) function can also evolve a signalling component.

Many animals transfer information to conspecifics through morphological or behavioural traits such as gaudy plumages, extravagant body ornaments (antlers, horns) or courtship displays (Maynard Smith & Harper, 2003). From these conspicuous signals, receivers can assess the quality of the bearer (e.g. the fighting ability of a rival or the quality of a potential mate). Some species go further, collecting different materials to build complex structures or decorate their nests, which are used as an extension of their phenotype ('extended phenotype' sensu Dawkins, 1982). The extended phenotype concept refers to the potential effects of genes on the environment beyond the individual's body (reviewed in Schaedelin & Taborsky, 2009). For example, certain orb web spiders add extra silk structures to their capture webs whose function may be to deter predators or provide a warning signal for organisms that might destroy the web (Herbestein, Craig, Coddington, & Elgar, 2000; Théry & Casas, 2009; Walter & Elgar, 2012). Thus, the contemporary signal effect of such decorations is different from their original function (i.e. entangle unsuspecting prey). In some cases, a novel trait can acquire a signalling effect and may explain, for example, the occurrence of odd items such as flowers, stones, snake skins, scats or human-derived material (foil, plastics) in the breeding structures of many species (e.g. Östlund-Nilsson & Holmlund, 2003; Schuetz, 2005; Trnka & Prokop, 2011). The presence of this unusual nest-building material may indicate the builder's vigour, technical or harvesting ability and capacity to deter rivals (Mainwaring et al., 2014; Moreno, 2012). Thus, nests not only provide a protective environment for developing eggs and offspring but may also constitute an important signalling device to reveal information for members of the opposite sex (Barber, Nairn, & Huntingford, 2001; Brouwer & Komdeur, 2004; Hoi, Schleicher, &Valera, 1996; Schaedelin & Taborsky, 2006) or potential competitors (Penteriani & Delgado, 2008). In this sense, on the basis of the existing literature, we can discern two main functions of nest (or similar structures) decorations as visual cues: (1) to act as a pre- or postmating sexual signal (intersexual context) and (2) to advertise social status to potential intruders (intrasexual context).

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Regarding the former (male–female communication), a well-understood example is the case of birds of the family Ptilonorhynchidae (bowerbirds). Males of most of these species build and decorate stick structures (called bowers) to attract the females with which they mate (Borgia, 1985; Endler, Endler, & Doerr, 2010; Madden, 2003). The use of nest-building activity as a sexual signal has been observed in other taxa as well. For example, in many species of African cichlids, males build sand craters to attract females for spawning (Barber, 2013; Schaedelin & Taborsky, 2010). Pebble heaps of wheatears, *Oenanthe leucura*, or multiple nests of Australian reed warblers, *Acrocephalus australis*, and Eurasian wrens, *Troglodytes troglodytes*, seem to play a similar role as a source of information to current or potential partners (Berg, Beintema, Welbergen, & Komdeur, 2006; Garson, 1980; Soler, Soler, Møller, Moreno, & Lindén, 1996). Such information can be used by females to ascertain male condition and obtain cues about future paternal investment in their brood (Soler, Møller, & Soler, 1998; Soler, de Neve, Martínez, & Soler, 2001). Evidence for social status signalling has been provided by two recent studies on territorial raptors (eagle owl, *Bubo bubo*: Penteriani & Delgado, 2008; black kite, *Milvus migrans*: Sergio et al., 2011). Penteriani and Delgado (2008) reported that owls use their own faeces and prey feathers, deposited on posts and plucking sites in proximity to the nest, to mark their territory and signal current reproductive status to potential trespassers. Sergio et al. (2011) found that nest decorations (mainly human rubbish such as plastic bags) observed in most (80%) black kite nests can serve as a signal of the builder's physical prowess and thus as a threat against conspecifics. However, these two alternatives are not mutually exclusive and nest ornamentation may have multiple functions.

Next to plant matter and fur, feathers are one of most common nest-building materials (Hansell, 1995, 2000). Many passeriformes use downy feathers from other species for lining their nests. Feathers are generally deposited within the nest cup, in contact with the eggs, and therefore it has been traditionally considered that these possess a thermoregulatory function (Dawson, O'Brien, & Mlynowski, 2011; Lombardo, Bosman, Faro, Houtteman, & Kluisza, 1995; McGowan, Sharp, & Hatchwell, 2004). Some species carry flight or contour feathers to their nests with a merely ornamental purpose, not to provide insulation, placed outside the nest cup in very visible locations (Veiga & Polo, 2005). Feathers constitute a limiting resource because they usually come from dead or killed birds (Hansell, 1995) and thus feather gathering may be indicative of good physical condition or high predisposition to devote time and energy to reproduction. Observational and experimental evidence for this comes from a study by Sanz and García-Navas (2011), which showed that female blue tits, *Cyanistes caeruleus*, use nest decoration as a source of information about male quality, and, accordingly, modulate their level of parental investment. However, feather carrying is not a male-exclusive behaviour as it has also been described in females of the spotless starling, *Sturnus unicolor* (Polo & Veiga, 2006; Veiga & Polo, 2011).

Rock sparrows, *Petronia petronia*, like other Old World sparrows (Spanish sparrow, *Passer hispaniolensis*: Alonso, 1982; tree sparrow, *Passer montanus*: Pinowski et al., 2006; house sparrow, *Passer domesticus*: García-López de Hierro, Moleón, & Ryan, 2013), usually carry feathers from other species (hoopoe, *Upupa epops*, wood pigeon, *Columba palumbus*, azure winged-magpie, *Cyanopica cyanus*, Eurasian jay *Garrulus glandarius* and raptors) to their nests. Feathers are placed on the nest rim, stacked in the straw like 'hunting trophies' in a conspicuous manner (Fig. 1, see also Fig. S1 in the Supplementary Material). In the present study, we documented this previously undescribed behaviour and tested the possible function of feather delivery by means of a feather addition experiment carried out in two separate Mediterranean populations. Specifically, we predicted that (1) if feather carrying is primarily for

Figure 1. Examples of rock sparrow nests exaggeratedly decorated with feathers belonging to different species including Eurasian black vulture, *Aegypius monachus*, common buzzard, *Buteo buteo*, Eurasian jay, *Garrulus glandarius*, azure-winged magpie, *Cyanopica cyanus*, red-legged partridge, *Alectoris rufa*, and golden oriole, *Oriolus oriolus*. Note that feathers are not embedded within the nest matrix but they are arranged to maximize its visibility. Photos: Vicente García-Navas.