Complex nest decorations of a small brown bird in the Pampas

If one travels through the Pampas region in east-central South America, it is common to observe large piles of sticks on trees, shrubs, and electricity poles. These structures are the nests of a small brown bird, the aptly named firewood-gatherer (Anumbius annumbi, family Furnariidae; Figure 1a). During their life, these birds build multiple nests (Delhey et al. 2010), which accumulate throughout their territory and are often used by other species to roost and breed (Turienzo and Di Iorio 2007). The mounded nests are sturdy enclosed structures constructed from sticks and twigs, with an entrance tunnel that spirals down to the brood chamber (WebFigure 1). Their outer walls and entrance contain many curious objects that do not serve any obvious structural purposes and the presence of such "decorations" makes these oversized nests one of the more puzzling expressions of animal building behavior.

During 2005–2010, we quantified the type and quantity of decorations in 113 firewood-gatherer nests. The



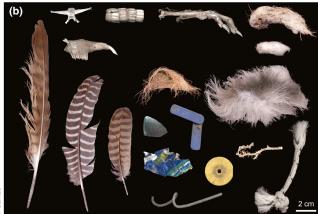


Figure 1. (a) A firewood-gatherer (Anumbius annumbi) on its oversized nest; the nest entrance and some decorations (bones, fur) are visible. (b) Detail of selected nest decorations.

decorations proved to be extraordinarily diverse (Figure 1 and WebFigures 1–3). The most common objects were clumps of fur from different species of mammals (37%), scat (35%; mainly from foxes but occasionally small pieces of cow dung), and feathers from other avian species (10%). Less common decorations included bones (7%), plants (4%; soft leaves and inflorescences), human refuse (3.6%; plastic, glass, metal, paper), and snake skin (0.3%); note that these percentages do not add up to 100% because they are averages computed over all nests. Some of the objects were very large relative to the size of the bird (Figures 1–2). Decorations accumulate throughout the nesting cycle, reaching a maximum during chick rearing.

To determine whether both members of the breeding pair decorate the nest, we observed nests both directly and by video camera where at least one individually marked member of the pair (using combinations of colored plastic bands) was of known sex (determined using genetic tests, given that males and females are otherwise indistinguishable). During 175.9 hours of observation on 43 different nests belonging to 26 pairs, firewood-gatherers carried apparent decorations to the nest on 105 occasions (in 31 out of 87 observation sessions). Female-brought objects (n = 23) were never deposited on the nest or at the entrance and therefore did not contribute to decoration of the nest. These objects were always deposited inside the structure and consisted of small (1–2 cm) fluffy items (pieces of fur, small feathers, soft plant material, and undetermined soft material), most likely to line the brood chamber. Males also brought brood chamber lining materials to the nest (n = 66), but on 16 occasions, males deposited decorations on the nest or at the nest entrance (on ten different nests by eight different males). These decorations consisted of pieces of scat (n = 5; Figure 2), fur (n = 5), feathers (n = 2), and undetermined soft material (fur or feathers; n = 4), all of which were brought to the nest during nest building (n = 2), egg laying or incubation (n = 13), and the nestling phase (n = 1). Thus, it appeared from our observations that only males decorate the outside of the nest.

Other species of birds decorate their nests for various purposes, including olfactory camouflage (scat; Schuetz 2005), repelling predators (snake skin; Medlin and Risch 2006), predator warning (pebbles; Warning and Benedict 2014), attracting prey (dung; Levey et al. 2004), repelling parasites (green leaves; Gwinner and Berger 2005), deterring rivals (plastic bags; Sergio et al. 2011), or influencing potential mates (feathers; Polo et al. 2004). Yet firewood-gatherers apparently combine nearly all known types of decorations into their nests, and such complexity has not been described for the

nests of other species. This complexity may arise if different decorations fulfill different functions. Some of the decorations could provide olfactory camouflage (scat, fur), scare off predators (snake skin), or even serve as a comfortable porch! Indeed, most (85%) of the soft decorations such as fur and feathers are found at the nest entrance where adults often rest (WebFigure 4), while hard (bones) or smelly (scat) objects are rarely found there. However, not all decorations are likely to have a utilitarian function, and these (eg large feathers, bones, human debris) may be used for signaling purposes. Given that active nests can be easily recognized because they usually have "fresh" decorations, these could be used by owners to signal territory occupancy to potential intruders (Sergio et al. 2011). Such intruders could be conspecific (firewood-gatherers form long-term pair bonds and pairs are strictly territorial) or heterospecific, since many other bird species use firewood-gatherer nests to breed (11 species at our study site), sometimes even usurping them.

Since nest decoration happens after pair formation, it might also be used to influence female fidelity or investment in reproduction (eg Polo et al. 2004) rather than attracting a potential mate. Nest decorating behavior by males is the most obvious sexually dimorphic phenotypic trait in the firewood-gatherer, a species that is otherwise monomorphic, dull colored, and unadorned (Figures 1-2). The complexity and diversity of nest decorations (Figure 1) are reminiscent of bowerbird decorations. Male bowerbirds (family Ptilonorhynchidae) build structures (bowers) that are often elaborately decorated with feathers, fruits, flowers, or human refuse, for the sole purpose of enticing females to copulate (Endler et al. 2005). In bowerbirds it has been hypothesized that the use of elaborate bower decorations enables males of some species to become less ornamented themselves and reduce their conspicuousness to predators, essentially transferring ornamentation from the plumage to the bower (Endler et al. 2005). If firewood-gatherer decorations are used in mate choice or assessment, it is tempting to speculate that non-plumage-related ornaments such as nest decorations allow males to overcome the limitations of their bodily phenotype to signal their quality to females. Could the choice of decorations be driven by aesthetic preferences such as in bowerbirds? Firewood-gatherers could constitute a suitable alternative model to investigate the evolution of preferences for object colors or shapes (Endler and Day 2006), because the type and number of decorations can be manipulated experimentally. If specific types of decorations are preferentially brought to the nest by males and favored by females, the decorating behavior of male



Figure 2. A firewood-gatherer carrying a large piece of carnivore scat for deposition on his nest. Our observations of marked individuals indicate that only males deliver such decorations to the nest.

firewood-gatherers could represent a case of convergent evolution. Our observations highlight not only the rewards inherent in studying little-known species but also the opportunities that unusual natural history insights can provide to test functional and evolutionary hypotheses.

Acknowledgements

We thank Cabaña Tres Hojas for access to the field site; C Pérez, J Pizá, L Verniere, and P Petracci for help with fieldwork; and J Pastor and B Taylor for comments on the manuscript. This work was supported by the Max Planck Society (Minerva grant to AP) and through the Australian Research Council (FT110100505 to AP and DE120102323 to KD).

Supporting Information

References and additional web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.1525/suppinfo

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