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2 First description of nest-decoration behaviour in a wild sub-Antarctic

3 shorebird

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5 A wide range of animal species accumulate objects in, on, and/or around structures they build. 6 Sometimes, these accumulations are purely incidental, while in other cases the materials are 7 deliberately displayed to serve signalling purposes (extended phenotype signals). In this pilot 8 study, we employed systematic in situ observations and camera trapping to describe for the 9 first time that both sexes of a territorial shorebird, the black-faced sheathbill (Chionis minor 10 ssp minor) collect, carry, and arrange colourful marine shells and dried twigs within and 11 around their nest cavity. Our observations expand the taxonomic breadth of avian extended 12 phenotype signals, by showing that at least one species within a largely understudied group 13 i.e., Aequorlitornithes, exhibits nest-decoration behaviour. Multiple manipulative 14 experiments are needed to explore further the signalling function of these 15 decorations, which opens new exciting avenues for animal communication and 16 cognition research.

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18 Keywords: animal communication · *Charadrius* · extended phenotype · nest decoration ·
19 non-bodily ornament · signal

24 Introduction

25 From the honeybee waggle dance to the dazzling mating display of cuttlefish, all live animals 26 possess the capacity to convey to others information that is crucial in various biological 27 contexts (Bradbury and Vehrencamp 2011). While numerous species use bodily traits or 28 behavioural displays to communicate, signals can also be expressed externally by animals as 29 an extension of their phenotype (Dawkins, 2016). These 'extended phenotype signals' 30 originate from the manipulative action or construction behaviour of the signaller and have the 31 ability to provide information efficiently even in the signaller's absence (Schaedelin and 32 Taborsky 2009). Recently, extended phenotype signals have received considerable attention 33 in evolutionary and behavioural research as they represent excellent opportunities to study animal communication, and, contrary to bodily traits, are particularly well suited to 34 35 experimental manipulations (Coleman et al. 2004, Jordan et al. 2016, Madden 2002, 36 Magalhaes et al. 2013, Schaedelin and Taborsky 2009). For instance, a wide range of animal 37 taxa use purely ornamental extended phenotype signals, resulting in the collection of 38 decorative materials (reviewed in Schaedelin and Taborsky 2009). Those materials can be 39 easily experimentally manipulated and thus offer elegant, relevant models for elucidating how 40 they have evolved, what signalling function they serve, and how flexible individuals are in their deployment (Hansell 2000, Keagy et al. 2009, Sergio et al. 2011). 41

This latter behaviour i.e., the gathering of objects as decorations, has been particularly well described in birds, probably due to high observation effort (Amundsen 2003), ease of observation (Shumaker et al. 2011), and intricate nest-building abilities (Hansell 2000). In most cases, objects are associated with the building of nests or with the manipulative actions involved in nest construction (Borgia, 1986). Such decorations can originate from various types of inorganic (e.g. glass, small stones: Borgia 1995), vegetal (e.g. berries: Gilliard 1969, Forshaw and Cooper 1977, flowers: Borgia 1986), animal (e.g. animal fur: Pruett-Jones and

49 Pruett-Jones 1988, feathers: Veiga and Polo 2005), or human artefact materials (e.g.
50 toothbrush: Velenga 1970, foil: Jagiello et al. 2018). The diversity of these decorations and
51 their taxonomically widespread use throughout the class Aves has fuelled the debate over
52 their function for decades (Schuetz 2005).

53 Probably the most famous examples of avian extended phenotype signals are found in the 54 *Ptilonorynchidae* family (Passeriformes), where males of 15 species build structures – *bowers* 55 - that are often elaborately adorned to attract females during the breeding season (Borgia 56 1986, Hansell 2000, Doerr and Endler 2015, Endler et al. 2006, Endler et al. 2010, Endler 2012, Kelley and Endler 2012, Endler et al. 2014). In some bowerbirds, decorations coupled 57 58 with structure building capacity may be associated with a larger brain compared to other 59 related and unrelated non-bower building bird species (Madden 2001), and are hypothesized to be subject to cultural transmission (Madden 2008). Lately, the study of nest decorations has 60 61 been particularly flourishing and has revealed other nonmutually exclusive functions (e.g. 62 indicators of viability, territory quality, and conflict dominance of the signaller, Sergio et al. 63 2011, Canal et al. 2016) and factors affecting its expression (e.g. breeding density, Rubalcaba 64 et al. 2017).

So far, only a few bird species - mainly Passeriformes - have been the object of 65 experimental investigations (Schuetz 2005, Sergio et al. 2011, Figure 1). For a better 66 67 understanding of the factors that drove the evolution of this behaviour, more effort is necessary in exploring nest-decoration activity in a larger range of species (Delhey et al. 68 69 2011, Sanz and García-Navas 2011). García-Navas et al. (2015) working on rock sparrows 70 (Petronia petronia) have suggested two major signalling functions of nest decorations in 71 birds: signalling individual and parental quality or advertising social status to other 72 conspecifics. The fact that birds as distantly related as chinstrap penguins (Fargallo et al. 73 2001) and blue tits (Sanz and García-Navas 2011) might use decorations as a post-mating sexual display, or that objects deployed by raptors (Sergio et al. 2011) and owls (Penteriani and Delgado 2008) act as reliable threats to conspecifics, lead us to assume that nest decoration is the result of convergent evolution (Delhey et al. 2017). As such, reports on nest decoration in taxonomically distinct species can bring immense opportunities to assess, through comparative evaluation, *what* socioecological features may have driven the emergence this behaviour.

80

< Insert Figure 1 about here >

81 The purpose of the present paper is to contribute to such a broad comparative endeavour, by describing nest-decoration behaviour in the black-faced sheathbill (Chionis minor ssp 82 83 minor, closely related to Pluvianellidae, Charadriiformes, Winkler et al. 2020), a small 84 terrestrial shorebird, which inhabits coastal regions of the Subantarctic Kerguelen Islands 85 (Bried and Jouventin 1998, Burger and Kirwan 2020). In these rigorous environments 86 characterized by inclement weathers and high predation levels, sheathbills are the only 87 common land-based birds. To survive in these islands, they adapt their foraging to any form 88 of animal matter and are highly opportunistic (Burger 1979, Blankley 1981, Winkler et al. 89 2020). They are scavengers, predators, and kleptoparasites, and their diet includes a large 90 variety of food types e.g., algae, invertebrates, carrion, seabirds' faeces, feather-shafts, eggs, 91 and chicks (Burger 1981). Black-faced sheathbills are monogamous and both sexes 92 vigorously defend their feeding and breeding territories against intruders through ritualized 93 display calls (i.e. the common 'Bob-call') and threat postures (Burger 1979, Burger 1980, 94 Verheyden 1988, Bried and Jouventin 1996, Jouventin et al. 1996). The nest consists of a 95 simple cup hidden from view within a natural cavity such as a crevice, small cave, or more 96 occasionally a petrel burrow (Winkler et al. 2020). In the Kerguelen archipelago, we noted 97 that many nests open onto areas covered with conspicuous purple mussel shells. Through 98 systematic observations, we documented this previously undescribed behaviour and 99 investigated the possibility that these objects located in and around the nest were not 100 incidental accumulations of debris and/or prey remains, but rather served as decorative 101 materials. If so, we expected the birds to engage in the collection of materials and in specific 102 manipulative behaviours targeted at them at the nest area. As incubation is undertaken by both 103 sexes in this species (Burger and Kirwan 2020), we also examined whether only one or both 104 individuals of the breeding pair engaged in these behaviours.

105 Material and Methods

106 Study site and subjects

107 Observations took place at *Ile Verte* (49°30'23''S, 70°02'40''E - 1.5 km²), an island situated 108 within the Morbihan Gulf, Kerguelen archipelago (48°28'–50°S, 68°28'–70°35'E), during the 109 Dec 2019 – Jan 2020 breeding season. At this location, black-faced sheathbills defend and 110 remain in one territory all year (Burger and Kirwan 2020), thus facilitating observations. 111 Three nest-cavities were identified: Nest 1 belonged to breeding pair A1/A2, and Nest 2 & 112 Nest 3 to breeding pair B1/B2. Areas that contained objects consisted of two terrace areas: 113 one below (terrace area 1) and one above (terrace area 2) the nest cavity for Nest 1 and Nest 3 114 (see example of Nest 1 in Figure 2), and one circular area in front of the nest cavity for Nest 115 2 (Figure 3).

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< Insert Figure 2 and Figure 3 about here >

117 Daily observations confirmed that Nest 2 was still maintained but, probably due to the high 118 nest cavity visibility and ease of access that attracted nearby avian predators (e.g., brown 119 skuas *Catharacta antarctica* ssp *lonnbergi*), the pair selected another cavity to incubate the 120 eggs, i.e. Nest 3, which was located about 6 meters away from Nest 2.

121 Set up and materials

122 Data collection consisted of daily observations supplemented by photographs and video123 recordings (camera traps). Direct observations, which did not exceed 15 min each, were

124 conducted every two days between 8 a.m. and 11 a.m. through Dec-Jan 2020. From 12th Jan 125 to 14th Jan 2020, one camera trap with motion detection recording (RECONYX® HL2X 126 HyperFire 2) was set up within each territory in order to collect data on the type, manipulation 127 time, origin, and dropping zone of objects. From 27th Jan to 29th Jan 2020, one camera trap 128 was also used to determine whether both mates contributed simultaneously to collection. We 129 used daily observations and photographs to minimise disturbance to the birds during the 130 breeding period (Jouventin et al. 1996).

131 Scoring and analysis

Photographs. For each photograph, we quantified (i) the type of objects (from complete and
fragment materials), (ii) their position (coloured topside up/down), and (iii) their number and
location in their respective areas (circular: Nest 2, and terrace areas: Nest 1 & 3).

Video-recordings. We examined: (iv) which object the bird was manipulating (objects newly collected or already present in the display areas), (v) the total manipulation time (from the time the bird first picks up the object, or first appears in view carrying it, until it drops it on the terrace areas or outside the field of the camera), (vi) the origin of the object (inside the nest, terrace areas, outside the filming zone), and where it was dropped off (inside/outside the nest cavity, high/low terrace area). We also noted whether both mates contributed simultaneously to collection.

142 **Results**

143 Nest-decoration behaviours.

144 *Photographs.*

(i) Type. Marine mussels (ribbed mussel Aulacomya ater and blue mussel Mytilus
desolationis) and limpets (Nacella kerguelenensis) composed the pattern of objects (Figure
4).

(*ii*) *Position*. Most shells, irrespective of the species, were placed with their shiny coloured
topsides uppermost: 98% across the two terrace areas at Nest 1, 98% in the circular area at
Nest 2, and 92% across the two terrace areas in Nest 3.

151 (iii) Number and location. At Nest 1, terrace area 1 (below the nest cavity entrance) was 152 composed of 96% ribbed mussels, 3% blue mussels, and 1% limpets. Terrace area 2 (above 153 the entrance) contained 92% ribbed mussels, 6% blue mussels, and 2% limpets (**Table 1**). 154 Across the two terrace areas, Nest 1 thus had 95% ribbed mussels, 4% blue mussels, and 1% 155 limpets. At Nest 2 the main circular area contained 98% ribbed mussels, 1.80% blue mussels, 156 and 0.20% limpets. At Nest 3, terrace area 1 was composed of 96% ribbed mussels, 2% blue 157 mussels, and 2% of limpets, while terrace area 2 contained 95% ribbed mussels and 5% 158 limpets. Across the two terrace areas, Nest 3 thus had 96% ribbed mussels, 1% blue mussels, 159 and 3% limpets.

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< Insert Figure 4 and Table 1 about here >

161 *Video recordings (12th - 14th Jan 2020)*

(*iv*) *Type*. In a total of 299 video recordings (recording time for each video: 30 s), 42% of
the objects manipulated were shells (ribbed mussels: 16%, unidentified mussels: 11%, and
limpets: 15%), 5% were unknown objects, and 53% were dry *Scenecio vulgaris* twigs.

165 (v) Manipulation time. Mean \pm SD manipulation time was 5 ± 5 s (n = 2, range 1-20 s) for 166 ribbed mussels, 6 ± 5 (n = 2, range 1-12 s) for unidentified mussels, 7 ± 5 (n = 2, range 2-20 167 s) for limpets, 7 ± 9 (n = 2, range 1-30 s) for twigs, and 2 ± 2 (n = 2, range 1-6 s) for unknown 168 objects.

(vi) Origin and dropping zones. We never observed birds carrying objects inside the nest cavity, however sheathbills manipulated objects already within the nest cavity in 12% of observations. When objects were moved between areas, the direction of movement most often included bringing objects from beyond the nest area (from outside the filming zone) to terrace areas (the camera trap was only able to cover terrace area 2, 19% of observations), but we also observed carrying from the nest cavity to terrace area 2 (1%), and from the terrace area to outside the nest area (3%). The manipulation and displacement of objects within the same area (terrace area 2) were noted in 33% of observations. Finally, in 32% of observations, birds arrived with an object from outside the nest area but did not deposit it; i.e. they eventually left the nest area holding the same object.

179 *Contribution to collection.*

180 Video-recordings (27th Jan - 29th Jan 2020)

181 Neither breeding pair ever manipulated and placed objects simultaneously. However, when 182 an individual contributed to collection and, after some time, took over incubation from the 183 partner, the previously incubating bird also moved and placed objects within the filming zone 184 during its off-duty (object manipulations that occurred during pre- and post-switching event: 185 twice on Jan 27th, once on Jan 28th, and once on Jan 29th). We also observed both partners 186 engaging in object manipulation before and after switching incubation 4 times on Jan 13th.

187 **Discussion**

We document for the first time aspects of object transportation, handling, and arranging in the vicinity of the nest, in Aequorlitornithes. Similar nest-decoration behaviour has been reported in relatively distantly related species with different ecological backgrounds, such as kites and bowerbirds (e.g. Sergio et al. 2011, Borgia 1986; respectively). We suggest that sheathbills offer an interesting comparison to investigate which factors drove the evolution of this behaviour among birds.

Most of the material collected was composed of ribbed mussels, followed by, to a lesser extent, blue mussels and limpets. All these materials are highly abundant in the sheathbills' environment. Video recordings confirmed birds' direct handling of the shells seen in the photographs and revealed another type of object scavenged from the environment: dry

198 Scenecio vulgaris dried twigs, also commonly collected. The volatile property of twigs within 199 the windy Kerguelen archipelago might explain why they were missing from the photographs. 200 Although birds' preference for shells has been ascribed to a need for calcium-rich food items 201 for successful breeding in some bird species (e.g. small passerines Bureš and Weidinger 202 2001), the sheer quantity of empty mussels within and outside the nest cavity makes this 203 explanation unlikely. Importantly, all objects were predominantly placed with their topsides 204 uppermost on specific platforms, and their origin and displacements within the nest area 205 seemed to indicate a selection of the objects arranged on the terrace areas.

The fact that sheathbills select, carry, and arrange empty shells on nest areas align well with our hypothesis that the configuration of objects is not purely incidental. Materials placed by sheathbills seem rather to be decorations independent of strict survival or reproductive requirements (i.e. not collected in the context of feeding or to serve as insulation, for example). We therefore suggest, for the first time, that the decorations may have a signalling function in sheathbills (Veiga and Polo 2005, Canal et al. 2016).

212 Similarly to sheathbills, a number of species use materials that they place outside the nest 213 without any apparent purpose in incubation or nestling rearing (e.g. male yellow-breasted 214 bowerbirds Chlamydera lauterbachi, Gilliard 1969, Dunning 1993, female spotless starlings 215 Sturnus unicolor, Polo et al. 2004, Polo and Veiga 2006, male blue tits Cyanistes caeruleus, 216 Sanz and García-Navas 2011, and mated pairs of black wheatears Oenanthe leucura, Moreno 217 et al. 1994). Three non-mutually exclusive explanations may be suggested in regard to what 218 information sheathbills convey with these objects: mate attraction before pair formation (e.g. 219 Endler et al. 2005), post-mating sexual selection (e.g. mate fidelity and investment in 220 reproduction, Polo et al. 2004), and territory occupancy (e.g. Sergio et al. 2011).

On Verte Island, sheathbills breed on shores free of penguin colonies and forage mainly on
algae, crustaceans, and molluscs (Jouventin et al. 1996). The number of objects displayed at

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223 nesting sites, i.e. the quantity of empty mussels sheathbills are able to collect, may represent 224 reproductive traits indicative of genetic or parental quality, such as feeding effort and foraging 225 ability (Sanz and García-Navas 2011). In polygynous species such as bowerbirds, the number 226 and quality of nest decorations (i.e. blue feathers) reinforce the attractiveness of the males 227 (Haruyama et al. 2013). For instance, Borgia (1985) observed fewer copulations of satin 228 bowerbirds (*Ptilonorhynchus violaceus*) when ornaments were removed (experimental group) 229 than when no manipulation occurred (control group). Yet, selection occurs solely prior to 230 pairing in bowerbirds, and only one sex - the male - invests in nest construction and 231 associated ornamental addition. In sheathbills, however, both partners contribute to breeding 232 and we found that they start to engage in decoration collection approximately two months 233 after they first occupy their territory in October (i.e. laying period, Burger and Kirwan 2020). 234 Although we cannot rule out the possibility that some form of mate attraction occurs before 235 pairing, nest-decoration behaviour may share other nonmutually exclusive functions.

236 Signalling through nest decoration after pairing may be driven by post-mating forms of 237 sexual selection, for instance through partners' differential allocation of investment of mates 238 in the clutch (Moreno et al. 1994). Differential allocation after pair bond formation has been 239 shown in several avian species where both sexes contribute to nest decoration and/or nest 240 construction (e.g. black wheatears, Moreno et al. 1994, blue tits Cyanistes caeruleus, Sanz 241 and García-Navas 2011, but see Tomás et al. 2006, Lambrechts et al. 2012, magpies Pica 242 pica, Soler et al. 2001, buff-breasted wrens Cantorchilus leucotis, Gill and Stutchbury 2005). 243 Longer incubation shifts have been observed in some male sheathbills (mean incubation shift 244 length for males and females = 172 minutes and 90 minutes, respectively; Burger and Kirwan 245 2020). Females may benefit from increased efforts expanded by males in incubation duration. 246 In turn, male sheathbills that contribute more to nest decoration may prompt a heavier 247 investment in offspring by females. For instance, as hatching is asynchronous in this species

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(i.e. eggs in a single clutch hatch sequentially, Burger and Kirwan 2020), females may decide
to incubate earlier by allowing greater intervals between egg-laying, thus facilitating brood
reduction (Soler et al. 2001).

251 Another non-mutually exclusive explanation to a sexual component is the use of nest 252 decorations in the context of resource defence (Sergio et al. 2001). Similarly to the sheathbill, 253 on return from its migration, the black kite (*Milvus migrans*) occupies a breeding territory that 254 is highly defended by both individuals within the pair (Bustamante and Hiraldo 1993). 255 Beyond contributing together to nest building, the partners also decorate the nest with various 256 materials that they arrange in a conspicuous fashion (Mazumdar et al. 2017). This latter 257 feature, i.e. conspicuousness, represents a reliable threat indicating viability, territory quality, 258 and conflict dominance of the signaller (Sergio et al. 2011), but also enhances nest visibility 259 to aerial receivers (Canal et al. 2016). Raptors such as black kites are fierce birds (Orta et al. 260 2020), so natural selection (in the form of, for example, nest predation) is unlikely to have 261 significantly constrained signalling through nest decoration and construction (Moreno et al. 262 2012). Although the accumulation of objects around the nest is conspicuous in sheathbills, 263 nest-decoration activity and high visibility may attract the attention of predators such as skuas 264 and other sheathbills (Burger and Bonan 2020). If this resource-defence hypothesis is true, a 265 trade-off may therefore exist between elaborate nest decoration to warn off competitors and 266 the need for concealment of the nest from predators (the latter may be modulated by choosing 267 less conspicuous locations during nest-site selection). Best quality mates exhibiting numerous 268 decorations may be more able to cope with (the potential cost of) facing potential predators 269 and conspecific intruders, echoing the handicap principle (Zahavi 1975).

Overall, our findings lead us to suggest that sheathbills' nest decoration acts as an extended phenotype signal that has evolved due to sexual selection, potentially through differential allocation of investment by partners. Our results also support the nonmutually exclusive

273 hypothesis of territory defence, potentially traded off against natural selection in the form of 274 predation risk. It is worth noting that nest decoration has not been reported in sheathbills that 275 breed and feed within seabird colonies (e.g. crested penguins or Kerguelen cormorants 276 Phalucrocorux atriceps verrucosus, Weimerskirch et al. 1989), which paves the way to future 277 intraspecific comparative studies in order to understand the ecological circumstances 278 favouring the emergence of nest decoration in this peculiar species. We hypothesize that 279 differences attributable to contrasting ecologies and population dynamics (e.g. foraging for 280 mussels in the intertidal zone, predictable and more competitive environment for sheathbills 281 living in localities free of penguins) may play a role in the emergence of nest-decoration 282 behaviour.

283 While our study provides clear evidence of nest-decoration behaviour in black-faced 284 sheathbills, further manipulative experiments, inspired by well-established studies in other 285 species, will be necessary to address more nuanced questions about the behaviour. These 286 should assess whether the signal is *reliable* in the context of territory defence and sexual 287 competition (e.g. Madden 2002, Sergio et al. 2011), seek correlations between the quantity (or 288 quality) of nest decoration and reproductive success/offspring fitness, and learn more about 289 the decoration process itself (e.g. Borgia, 1985, Borgia et al., 1987, Vellenga, 1986, Maxwell, 290 1999).

In conclusion, in this observational study we suggest that the materials placed by sheathbills in and around the nest cavity serve a signalling function. This discovery extends the known phylogenetic and geographic spread of this rare behaviour among birds, and supports the hypothesis that nest decoration in sheathbills may represent a case of convergent evolution. Manipulative experiments, with marked individuals of known age, sex, and body condition, need to be conducted before firm conclusions can be drawn about the precise function of these decorations. Despite its broader appeal, so far nest decoration has been

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studied in a small range of avian orders, and more particularly in passerine species where decorations are deployed by one sex solely for mate attraction and courtship (Sergio et al., 2011). The black-faced sheathbill may represent a new model species for investigating the function and evolution of ornamental extended phenotype signals – as well as the cognition underpinning it – thus opening up new promising avenues for future research.

303 Declarations

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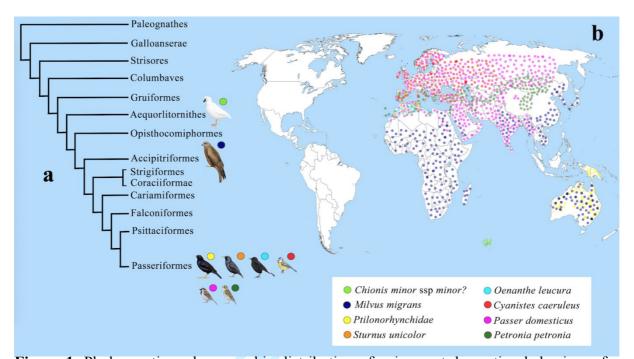
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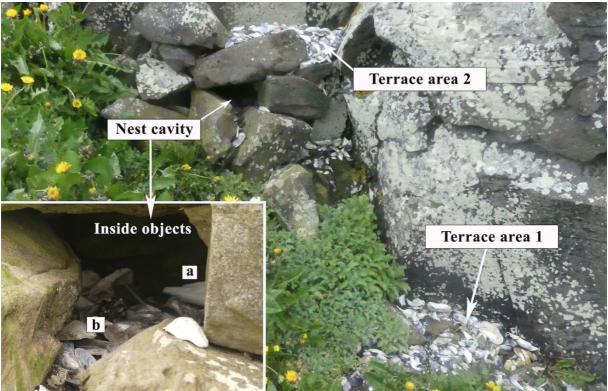
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460 Figures and Tables with captions



461 Figure 1. Phylogenetic and geographic distribution of avian nest-decoration behaviours for 462 communication purposes between conspecifics. a Phylogeny of birds with illustrations of 463 selected species displaying this behaviour (based on the updated phylogeny of Prum et al. 464 2015) **b** Worldwide distribution of avian species exhibiting nest-decoration behaviour as a 465 signal (examined experimentally in: Cvanistes caeruleus, Sanz and García-Navas, 2011; 466 Milvus migrans, Sergio et al., 2011; Oenanthe leucura, Soler et al. 1996; Passer domesticus, García-Lopez de Hierro et al., 2013; Petronia petronia, García-Navas et al., 2015; 467 468 Ptilonorhynchidae, Borgia, 1985; Sturnus unicolor, Polo et al., 2004, Polo and Veiga, 2006). 469 Suspected nest-decoration behaviours serving a signalling function are not shown in **a** and **b** (e.g. Acrocephalus arundinaceus, Trnka and Prokop, 2011; Anumbius annumbi, Delhey et al. 470 471 2017; Athene cunicularia, Smith and Conway, 2007; Bubo bubo, Penteriani and Delgado, 2008; Parotia lawesii, Pruett-Jones and Pruett-Jones, 1988; Pygoscelis antarctica, Fargallo et 472 473 al., 2001). Areas indicated with the coloured circles represent the species' year-round 474 distribution.

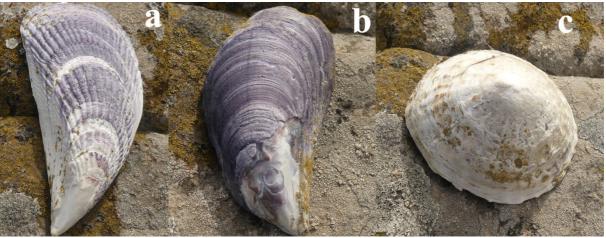


475 **Figure 2.** Configuration of the nest and accumulated objects at Nest 1. Terrace areas 1

- 476 & 2 contain a large number of objects, mainly *Aulacomya ater* mussel shells. The inset
- 477 magnifying the inside of the nest cavity shows an incubating bird (a) and accumulated objects
- 478 (**b**) [Photo credit: S. Danel].



- est . Figure 3. Circular terrace area at Nest 2, composed of mussel shells and limpets 479
- [Photo credit: S. Danel]. 480



- 481 Figure 4. Three main types of nest-decoration objects documented at black-faced
- 482 sheathbill nests. **a** and **b** are marine mussel shells: ribbed mussel *Aulacomya ater* (**a**) and
- 483 blue mussel *Mytilus desolationis* (**b**); **c** is the limpet *Nacella kerguelenensis*. Birds were also
- 484 observed collecting and manipulating twigs (not pictured). [Photo credit: S. Danel].

Table 1. Type and number of decorative objects at each of the studied nests and reported
from the photographs. Decorations consist of ribbed mussels, blue mussels, and limpets
(twigs were not visible on the photographs). TO = number of shells turned over (top upside
down).

	Ribbed	Blue	Limpets	Total shells	Total TO
Nest 1					
Terrace 1	159	5	2	166	3
Terrace 2	56	4	1	61	1
Total	215	9	3	227	4
Nest 2					
Circular	434	8	1	443	8
Nest 3					
Terrace 1	54	1	1	56	-
Terrace 2	18	-	1	19	6
Total	72	1	2	75	6

22

Supplemental material

- Video 1. Manipulations of nest materials (shells) *outside* Nest 1.
- Video 2. Manipulations of nest materials (twigs) outside Nest 1.
- Video 3. Manipulations of nest materials (both shells and twigs) inside Nest 1.

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