

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

2 **1. Introduction**

3 From the honeybee waggle dance to the dazzling mating display of cuttlefish, all live animals
4 possess the capacity to convey to others information that is crucial in various biological
5 contexts (Bradbury and Vehrencamp, 2011). While numerous species use bodily traits or
6 behavioural displays to communicate, signals can also be expressed externally by animals as
7 an extension of their phenotype (Dawkins, 2016). These ‘extended phenotype signals’
8 originate from the manipulative action or construction behaviour of the signaller and have the
9 ability to provide information efficiently even in the signaller’s absence (Schaedelin and
10 Taborsky, 2009). Recently, extended phenotype signals have received considerable attention
11 in evolutionary and behavioural research as they represent excellent opportunities to study
12 animal communication, and, contrary to bodily traits, are particularly well suited to
13 experimental manipulations (Coleman et al., 2004; Jordan et al., 2016; Madden 2002;
14 Magalhaes et al., 2013; Schaedelin and Taborsky, 2009). For instance, a wide range of animal
15 taxa use purely ornamental extended phenotype signals, resulting in the collection of
16 decorative materials (reviewed in Schaedelin and Taborsky, 2009). Those materials can be
17 easily experimentally manipulated and thus offer elegant, relevant models for elucidating how
18 they have evolved, what signalling function they serve, and how flexible individuals are in
19 their deployment (Hansell, 2000; Keagy et al., 2009; Sergio et al., 2011).

20 This latter behaviour i.e., the gathering of objects as decorations, has been particularly well
21 described in birds, probably due to high observation effort (Amundsen, 2003), ease of
22 observation (Shumaker et al., 2011), and intricate nest-building abilities (Hansell, 2000;
23 Moreno, 2012). In most cases, objects are associated with the building of nests or with the
24 manipulative actions involved in nest construction (Borgia, 1986). Such decorations can
25 originate from various types of inorganic (e.g. glass, small stones: Borgia, 1995), vegetal (e.g.
26 berries: Gilliard, 1969; Forshaw and Cooper, 1977; flowers: Borgia, 1986), animal (e.g.
27 animal fur: Pruett-Jones and Pruett-Jones, 1988; feathers: Veiga and Polo, 2005), or human
28 artefact materials (e.g. toothbrush: Velenga, 1970; foil: Jagiello et al., 2018). The diversity of
29 these decorations and their taxonomically widespread use throughout the class Aves has
30 fuelled the debate over their function for decades (Schuetz, 2005).

31 Probably the most famous examples of avian extended phenotype signals are found in the
32 *Ptilonorynchidae* family (Passeriformes), where males of 15 species build structures – *bowers*
33 – that are often elaborately adorned to attract females during the breeding season (Borgia
34 1986; Doerr and Endler, 2015; Endler, 2012; Endler et al., 2006; Endler et al., 2010; Endler et

al., 2014; Hansell 2000; Haruyama et al., 2013; Kelley and Endler, 2012). In some bowerbirds, decorations coupled with structure building capacity may be associated with a larger brain compared to other 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 been particularly flourishing and has revealed nonmutually exclusive functions (e.g. indicators of viability, territory quality, and conflict dominance of the signaller: Canal et al., 2016; Sergio et al., 2011) and factors affecting its expression (e.g. social environment, Rubalcaba et al., 2017).

So far, only a few bird species – mainly Passeriformes – have been the object of experimental investigations (Schuetz, 2005; Sergio et al., 2011; see **Figure S1** in Supplementary Materials). For a better 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., 2011; Sanz and García-Navas, 2011). García-Navas et al. (2015) working on rock sparrows (*Petronia petronia*) have suggested two major signalling functions of nest decorations in birds: signalling individual and parental quality or advertising social status to other conspecifics. The fact that birds as distantly related as raptors (Sergio et al., 2011) and starlings (Veiga and Polo, 2005) use nest decorations as signals lead us to assume that these elaborated displays are 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 of this behaviour.

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 *minor*, closely related to *Pluvianellidae*, Charadriiformes; Winkler et al., 2020), a small terrestrial shorebird, which inhabits coastal regions of the sub-Antarctic Kerguelen Islands (Bried and Jouventin, 1998; Burger and Kirwan, 2020). In these rigorous environments characterized by inclement weather and high predation levels, sheathbills are the only common land-based birds. To survive in these islands, they adapt their foraging to any form of animal or vegetal matter and are highly opportunistic (Burger, 1979; Blankley, 1981; Winkler et al., 2020). They are scavengers, predators, and kleptoparasites, and their diet includes a large variety of food types e.g., algae (*Ulva lactuca*, *Porphyra* sp.), carrion, chicks and eggs, feather-shafts, marine and terrestrial invertebrates, or seabirds' faeces (Burger, 1981). On *Ile Verte*, an island situated in the Morbihan Gulf within the Kerguelen archipelago, sheathbills breed on shores free of penguin colonies and forage mainly on algae,

crustaceans, marine mussels (*Aulacomya ater*, *Mytilus edulis desolationis*), and limpets (*Nacella kerguelensis*) (Jouventin et al., 1996). Large amounts of these food types are provided in the intertidal zones, which allow sheathbills to stay on their territory year-round (Burger and Kirwan, 2020; Jouventin et al., 1996). At one of the neighbouring islands (Mayes), this species spends 12% of its foraging time feeding on invertebrates (including molluscs i.e., marine mussels and limpets), with variations in prey capture between seasons (Jouventin et al., 1996). Black-faced sheathbills are monogamous and both sexes defend one specific site – which serves as a feeding and breeding territory – against intruders through ritualized display calls (i.e., the common ‘bob-call’) and threat postures (Bried and Jouventin, 1996; Burger, 1979; Burger, 1980; Burger and Millar, 1980; Jouventin et al., 1996; Verheyden, 1988). The nest consists of a simple cup (made up of algae, feathers, and grass) hidden from view within a natural cavity such as a crevice, small cave, or more occasionally a petrel burrow (Winkler et al., 2020). We noted that many nests open onto areas covered with colourful and pearly mussel shells. Through systematic observations, we documented this previously undescribed behaviour and investigated the possibility that these objects located in and around the nest were not incidental accumulations of debris and/or prey remains, but rather served as decorative materials. If so, we expected the birds to engage in the collection of materials and in specific manipulative behaviours targeted at them at the nest area. As incubation is undertaken by both sexes in this species (Burger and Kirwan, 2020), we also examined whether only one or both individuals of the breeding pair engaged in these behaviours.

2. Material and Methods

2.1. Study site and subjects

Observations took place at *Ile Verte* (148 ha; 49°30’23’’S; 70°02’40’’E), Kerguelen archipelago (48°25’–50°00’S; 68°27’–70°35’E), during the December 2019 – January 2020 breeding season. At this location, black-faced sheathbills defend and remain in one territory all year (Burger and Kirwan, 2020; Jouventin et al., 1996), thus facilitating observations. The collection of decorations starts approximately in December (SD, personal observation). Three nest cavities were identified (6 nests in total according to ongoing follow up work, all but one with an exhibition area): Nest 1 belonged to breeding pair A1/A2, and Nest 2 & Nest 3 to breeding pair B1/B2. Areas that contained objects consisted of two terrace areas: one below (terrace area 1) and one above (terrace area 2) the nest cavity for Nest 1 and Nest 3 (see example of Nest 1 in **Figure 1**), and one circular area in front of the nest cavity for Nest 2 (**Figure 2**).

< Insert Figure 1 and Figure 2 about here >

Daily observations confirmed that Nest 2 was still maintained but, probably due to its location (well above the shore) and ease of access by nearby avian predators (e.g., brown skuas, *Catharacta antarctica* ssp *lonnbergi*; Burger, 1979, 1982), the pair selected another cavity to incubate the eggs, i.e. Nest 3, which was located about 6 meters away from Nest 2.

2.2. Set up and materials

Data collection consisted of daily observations supplemented by photographs and video recordings (camera traps). Direct observations, which did not exceed 15 min each, were conducted every two days between 8 a.m. and 11 a.m. through December 2020 - January 2021. This 15 min duration and photographs were used to minimise disturbance to the birds during the breeding period (Jouventin et al., 1996). During January 12-14 2020, one camera trap with motion detection recording (RECONYX® HL2X HyperFire 2) was set up within each territory in order to collect data on the type, manipulation time, origin, and dropping zone of objects. Through January 27-29 2020, one camera trap was also used to determine whether both mates contributed simultaneously to collection.

2.3. Scoring and analysis

2.3.1. Photographs and observations. For each photograph, we quantified (i) the type of objects (from complete and fragment materials), (ii) their position (observe: topside up vs reverse: topside upside down), and (iii) their number and location in their respective areas (circular: Nest 2, and terrace areas: Nest 1 & 3). On four different shore locations, each positioned at a cardinal point, we counted the number of marine shells present on a zone composed of a minimum of 100 empty shells (*North* location: 5m²; *West* location: 10m²; *South* location: 15 m²; *East* location: 5m²).

2.3.2. 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), where it was dropped off (inside/outside the nest cavity, high/low terrace area), and (v) the duration of sheathbills' nest attendance (i.e. incubation) and objects' manipulation (inside/outside the nest). We also noted whether both mates contributed simultaneously to collection, and if the bird that manipulated objects subsequently entered within the nest cavity to incubate the eggs. Lastly, we counted the number of times the partner was/wasn't manipulating objects while its mate was in the nest incubating.

3. Results

3.1. Nest-decoration behaviours.

3.1.1. Photographs and observations.

(i) *Type*. Marine mussels (ribbed mussel *Aulacomya ater* and blue mussel *Mytilus edulis desolationis*) and limpets (*Nacella kerguelensis*) were reported at each of the studied nests (**Figure 3**). For all four shore locations taken together, the mean number \pm SD of counted mussels was 83 ± 8 ribbed mussels, 15 ± 9 blue mussels, and 1 ± 2 limpets.

(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.

(iii) *Number and location*. The objects at Nest 1, terrace area 1 (below the nest cavity entrance), were 96% ribbed mussels, 3% blue mussels, and 1% limpets. The materials at terrace area 2 (above the entrance) were 92% ribbed mussels, 6% blue mussels, and 2% limpets (**Table 1**). Across the two terrace areas, Nest 1 thus had 95% ribbed mussels, 4% blue mussels, and 1% limpets. At Nest 2 the main circular area contained 98% ribbed mussels, 1.80% blue mussels, and 0.20% limpets. The objects at Nest 3, terrace area 1, were 96% ribbed mussels, 2% blue mussels, and 2% of limpets, while the materials at terrace area 2 were 95% ribbed mussels and 5% limpets. Across the two terrace areas, Nest 3 thus had 96% ribbed mussels, 1% blue mussels, and 3% limpets.

< Insert Figure 3 and Table 1 about here >

3.1.2. Video recordings (January 12-14 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 *Senecio vulgaris* plants.

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

(vi) *Origin and dropping zones*. We never observed birds carrying objects inside the nest cavity, although 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.

(v) *Nest attendance and manipulation of objects.* Sheathbills spent 26% of the time manipulating objects at the nest and 74% of the time incubating.

3.2. Contribution to collection.

3.2.1. Video-recordings (January 27-29 2020)

At the time of the observational pilot study, we were unauthorized to catch and manipulate the breeding pair to identify the sex of each individual. However, we were able to determine that both partners contributed to nest decoration. When an individual contributed to collection and, after some time, took over incubation from its mate, the previously incubating bird also moved and placed objects within the filming zone after leaving the nest (object manipulations that occurred during pre- and post-switching event: twice on January 27, once on January 28, and once on January 29). We also observed both individuals engaging in object manipulation before and after switching incubation four times on January 13. In no case did members of the same pair manipulate and place objects simultaneously. When a bird entered the nest cavity to incubate the eggs, it had previously manipulated objects 80% of the time (within 0 – 2 min interval). When one sheathbill was incubating within the nest cavity, its mate was manipulating the objects 67% of its time inside the nest and 28% of its time outside the nest on the display areas.

4. Discussion

We document for the first time aspects of object transportation, handling, and arranging in the vicinity of the nest, in Charadriiformes. Similar nest-decoration behaviour has been reported in relatively distantly related species with different ecological backgrounds, such as kites and starlings (e.g. Sergio et al., 2011; Veiga and Polo, 2005, 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. Although marine mussels are abundant in the Kerguelen archipelago (Caza et al., 2015, 2016), pearly and purple ribbed mussels largely dominated the mussel beds investigated on *Ile Verte* (**Figure 3**, see also **Figure S2** in Supplementary Materials). Video recordings confirmed birds' direct handling of the shells seen in the

photographs and revealed another type of object scavenged from the environment: dry *Senecio vulgaris* plants, also commonly collected. The ephemeral property of light plant material (i.e. leaves and twigs) within the windy Kerguelen archipelago might explain why they were missing from the photographs. Although birds' preference for shells has been ascribed to a need for calcium-rich food items for successful breeding in some bird species (e.g. small passerines: Bureš and Weidinger, 2001), the sheer quantity of empty mussels within and outside the nest cavity makes this explanation unlikely. Importantly, all mussels and limpets were predominantly placed with their topsides uppermost on specific platforms, and their origin and displacements within the nest area 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 reproductive requirements (e.g. insulation) or strict survival (e.g. feeding). For instance, the nest cup was deprived of shells and we never observed a sheathbill entering the cavity with a full mussel, which, as a shore feeder, it usually eats on the intertidal zone (Burger, 1982). One may argue that the shells covering the exhibition areas may function as antipredatory acoustic cues (Leader and Yomtov, 1998; Warning and Benedict, 2015, 2016), alerting sheathbills when a predator (e.g. the brown skua) approaches the nest cavity. However, although the skua might represent a potential predator of sheathbill eggs/chicks, such predation cases are rare on *Ile Verte* (FB, SD, personal observations). Only sheathbills were seen landing on exhibition areas, causing only a slight noise when empty shells covered the platforms in a sufficient number (i.e. mussel beds made up of at least 20 shells, e.g. Nest 1, Nest 2, Nest 3). Furthermore, for each reported nest, exhibition areas were very close to the nest cavity entrance, which would prevent the sheathbills from escaping efficiently upon hearing the cue. Therefore, we believe exhibition areas do not serve an anti-predatory function in sheathbills. Moreover, this species uses different types of materials for decorating or building its nest. Marine shells and dry plants are placed *outside* the nest cup, while algae and feathers (on *Ile Verte*: feathers of e.g. blue petrel *Halobaena caerulea*, Antarctic prion *Pachyptila desolata*) *compose* the nest cup. This precludes the possibility that decorations may represent a byproduct of nest-building behaviour through an excess of discarded nest materials. The possibility that decorations serve a utilitarian function can be excluded, and lead us to suggest that they may have a signalling function in this species (Avilés et al., 2010; Canal et al., 2016; Veiga and Polo, 2005).

Similarly to sheathbills, a number of species carry materials to their nests without any apparent purpose in incubation or nestling rearing (e.g. mated pairs of spotless starlings *Sturnus unicolor*: Polo et al., 2004; Polo and Veiga, 2006; male blue tits *Cyanistes caeruleus*: Sanz and García-Navas, 2011; and mated pairs of black wheatears *Oenanthe leucura*: Moreno et al., 1994). Three non-mutually exclusive explanations may be suggested in regard to *what* information sheathbills convey with these objects: mate attraction before pair formation (e.g. Endler et al., 2005), post-mating sexual selection (e.g. mate fidelity and investment in reproduction, Polo et al., 2004), and intraspecific interaction (e.g. Sergio et al., 2011; Veiga and Polo, 2005).

The number of objects displayed at nesting sites, i.e. the quantity of empty mussels sheathbills are able to collect, may represent reproductive traits indicative of genetic quality ('good genes' of males, Iwasa et al., 1991; Zahavi, 1975). In starlings, the number of nest decorations reinforces the attractiveness of the provider prior to pairing (Eens et al., 1993; Gwinner, 1997; Veiga et al., 2005). For instance, in the spotless starling, where most males do not incubate eggs and supply poorly in nestlings' feedings (Moreno et al., 1999; Veiga et al. 2002), males that mated with more females provided more ornaments than males which mated with few or inexperienced females (Veiga et al., 2005). In sheathbills, however, both partners contribute to breeding (Burger and Kirwan, 2020). Although we cannot rule out the possibility that some form of mate attraction occurs during the pre-mating period, nest-decoration behaviour may share other nonmutually exclusive functions.

Signalling through nest decoration after pairing may be driven by post-mating forms of sexual selection, for instance through partners' differential allocation of investment of mates in the clutch or feeding effort (Moreno et al., 1994; Sheldon, 2000). Sheathbills' nest decorations may represent honest signals of quality that partners can exploit to adjust their reproductive efforts. The fact that most birds which took over incubation were manipulating the objects previously and that manipulation occurred before the incubating individual (75% of the time inside the nest) supports this hypothesis. Differential allocation after pair bond formation has been shown in several avian species where both sexes contribute to nest decoration and/or nest construction (e.g. black wheatears: Moreno et al., 1994; blue tits *Cyanistes caeruleus*: Sanz and García-Navas, 2011; but see Tomás et al., 2006; Lambrechts et al., 2012; magpies *Pica pica*: Soler et al., 2001; buff-breasted wrens *Cantorchilus leucotis*: Gill and Stutchbury, 2005). Longer incubation shifts have been observed in some male sheathbills (mean incubation shift length for males and females = 172 minutes and 90 minutes, respectively; Burger and Kirwan, 2020). Females may benefit from increased efforts

expanded by males in incubation duration. In turn, male sheathbills that contribute more to nest decoration may prompt a heavier investment in offspring by females. However, although this differential allocation hypothesis (Burley, 1988) represents a plausible evolutionary scenario for other species, this assumption remains speculative and needs to be adequately tested in sheathbills.

Another non-mutually exclusive explanation to a sexual component is the use of nest decorations in the context of intraspecific interaction. For instance, on return from its migration, the black kite (*Milvus migrans*) occupies a breeding territory that is defended by both individuals within the pair (Bustamante and Hiraldo, 1993). Beyond contributing together to nest building, the partners also decorate the nest with various materials that they arrange in a conspicuous fashion (Mazumdar et al., 2017). This latter feature, i.e. conspicuousness, represents a reliable signal indicating viability, territory quality, and conflict dominance of the signaller (Sergio et al., 2011), but also enhances nest visibility to aerial receivers (Canal et al., 2016). Less fierce birds such as starlings also use nest decorations (i.e. feathers) to deter potential nest visitors (Veiga and Polo, 2005). The non-randomly positioned feathers, which are exhibited on their more reflective sides, enhance nest visibility which suggests a signalling function (Avilés et al., 2010; Veiga and Polo, 2005). The accumulation of objects around the nest is conspicuous and positioned non-randomly by sheathbills on *Ile Verte*, which actively advertise and defend their territories all year (Jouventin et al., 1996). Decorations or nest-decoration activity do not seem to attract the attention of potential predators such as skuas (SD, personal observation). In this species, both territorial partners advertise their presence, evict intruding non-territorial conspecifics, and maintain boundaries between neighbouring territories by exhibiting the visual and auditory ‘bob-call’ display (Burger, 1980; Burger and Millar, 1980). This latter behaviour also plays an important role in maintaining the social bond and tolerance within the breeding pair (Burger, 1980). It is therefore a possibility that nest decorations serve to reinforce the visual and auditory advertisement of the territorial pair in sheathbills.

Overall, our findings provide subjective evidence of nest-decoration behaviour in black-faced sheathbills, which may act as an extended phenotype signal. It is worth noting that nest decoration with marine mussels and dry plants has not been reported in individuals of the same species that breed and feed within seabird colonies at Kerguelen (e.g. crested penguins or Kerguelen cormorants *Phalacrocorax atriceps verrucosus*, Weimerskirch et al., 1989), which paves the way to future intraspecific comparative studies in order to understand the ecological circumstances favouring - or preventing (if the behaviour is hindered in some way

by the presence of other species e.g., nearby predators such as the giant petrel) - the emergence of nest decoration in this peculiar species. We hypothesize that differences attributable to contrasting ecologies and population dynamics (e.g. foraging for mussels in the intertidal zone, predictable and more competitive environment for sheathbills living in localities free of penguins; Jouventin et al., 1996) may play a role in the emergence of nest-decoration behaviour.

Further manipulative experiments, inspired by well-established studies in other species, will be necessary to address more nuanced questions about the behaviour. These should assess whether the signal is *reliable* in the context of sexual competition and intraspecific interaction (e.g. Madden, 2002; Sergio et al., 2011), seek correlations between the quantity (or quality) of nest decoration and reproductive success/offspring fitness, and learn more about the decoration process itself (e.g. Borgia, 1985; Borgia et al., 1987; Maxwell, 1999; Vellenga, 1986).

5. Conclusions

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 studied in a small range of avian orders, and more particularly in passerine species where decorations can be 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.

Declarations

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Conflict of interest – The authors do not have any conflict of interest to declare.

Ethics – The research conforms to the 'Guidelines for the use of animals in research' as published in Animal Behaviour (1991, 41, 183-186) and the ARRIVE guidelines, and has been carried out in accordance with the U.K. Animals (Scientific Procedures) Act, 1986 and associated guidelines, EU Directive 2010/63/EU for animal experiments, and the National

Institutes of Health guide for the care and use of Laboratory animals (NIH Publications No. 8023, revised 1978).

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532 **Tables**

533 Table 1. Type and number of decorative objects at each of the studied nests and reported from
 534 the photographs. Decorations consist of ribbed mussels, blue mussels, and limpets (dry plants
 535 were not visible on the photographs). TO = number of shells turned over (reverse side).

	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

Figure captions.

Figure 1. Configuration of the nest and accumulated objects at Nest 1. Terrace areas 1 & 2 contain a large number of objects, mainly *Aulacomya ater* mussel shells. The inset magnifying the inside of the nest cavity shows an incubating bird (**a**) and accumulated objects (**b**) [Photo credit: S. Danel].

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

Figure 3. Three main types of nest-decoration objects documented at black-faced sheathbill nests. **a** and **c** are marine mussel shells: ribbed mussel *Aulacomya ater* (**a**) and blue mussel *Mytilus edulis desolationis* (**c**); **b** is the limpet *Nacella kerguelensis*. Birds were also observed collecting and manipulating dry plants (not pictured). [Photo credit: S. Danel].

Figure 1.

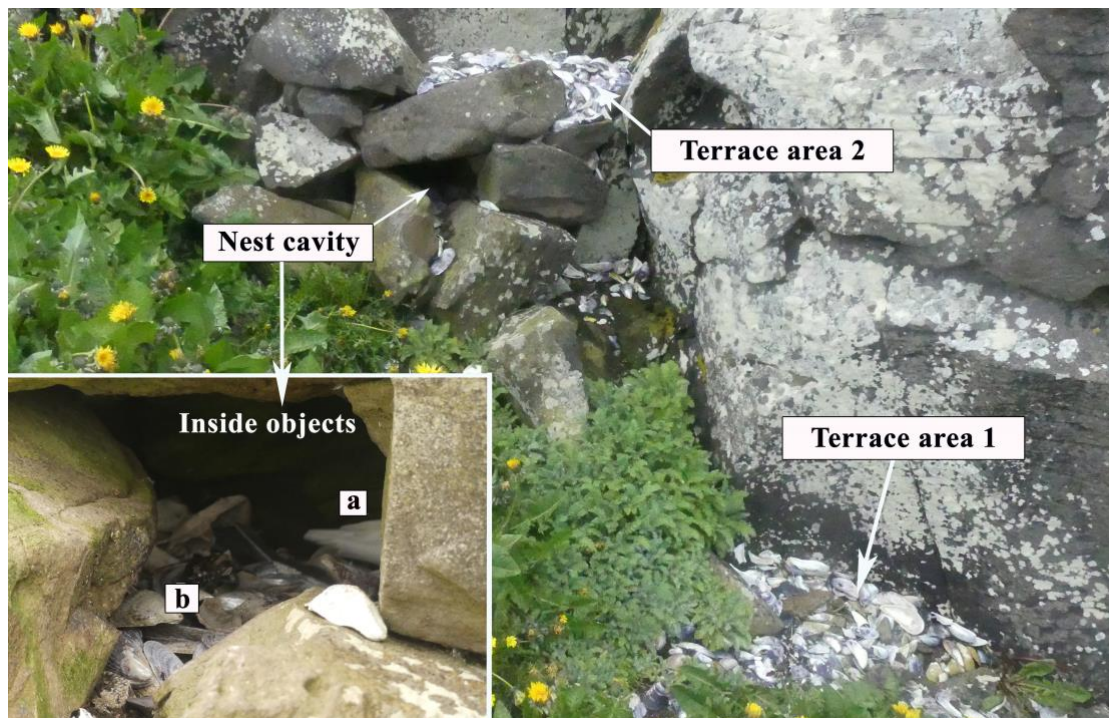


Figure 2.

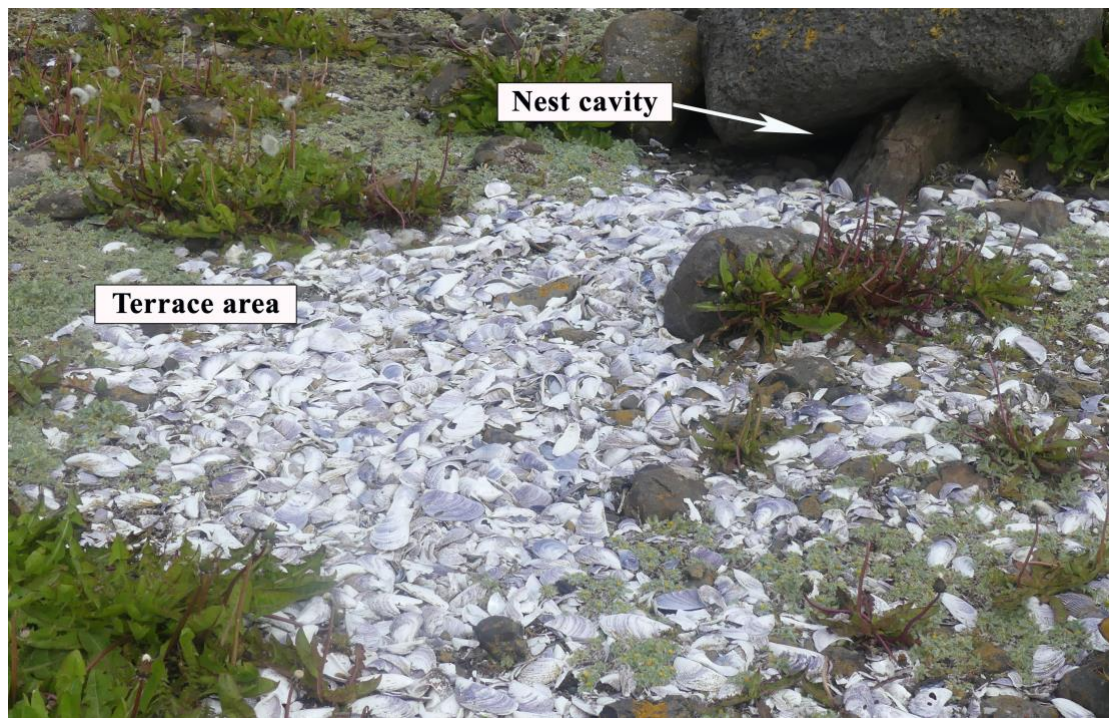
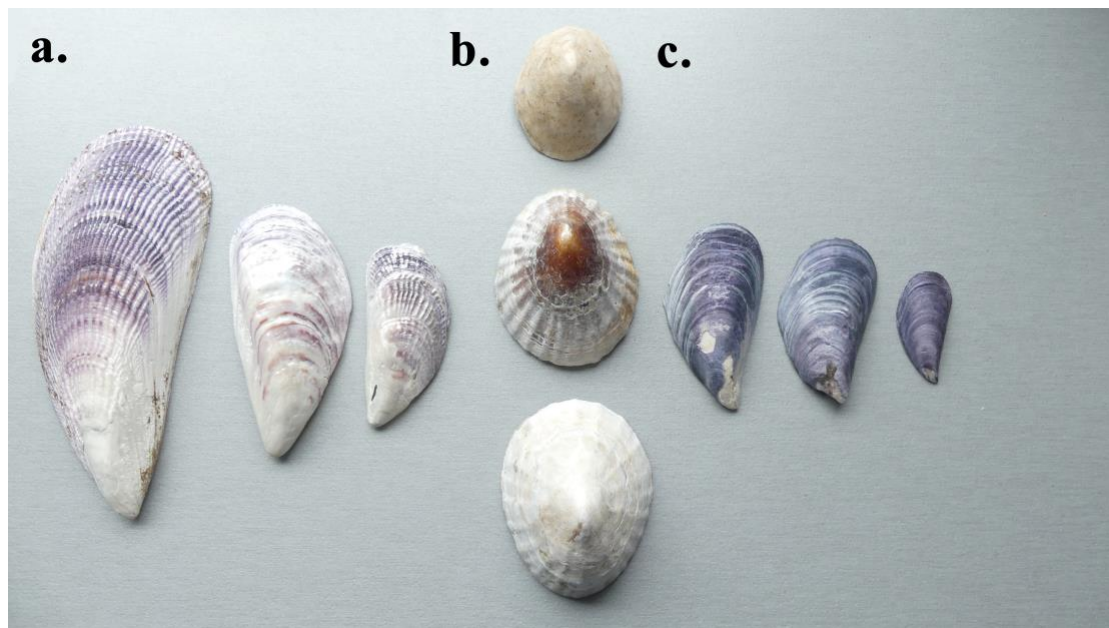


Figure 3.



Supplementary Materials

Figure S1. Phylogenetic and geographic distribution of avian nest-decoration behaviours for communication purposes between conspecifics. **a** Phylogeny of birds with illustrations of selected species displaying this behaviour (based on the updated phylogeny of Prum et al., 2015) **b** Worldwide distribution of avian species exhibiting nest-decoration behaviour as a signal (examined experimentally in: *Cyanistes caeruleus*: Sanz and García-Navas, 2011; *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). *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., 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 al., 2001). Areas indicated with the coloured circles represent the species' year-round distribution.

Figure S2. Reverse side of the three main types of nest-decoration objects documented at black-faced sheathbill nests. **a** and **c** are marine mussel shells: ribbed mussel *Aulacomya ater* (**a**) and blue mussel *Mytilus edulis desolationis* (**c**); **b** is the limpet *Nacella kerguelensis*. [Photo credit: S. Danel].

Video S3. Manipulations of nest materials (shells) *outside* Nest 1.

Video S4. Manipulations of nest materials (dry plants) *outside* Nest 1.

Video S5. Manipulations of nest materials (both shells and dry plants) *inside* Nest 1.

Figure S1.

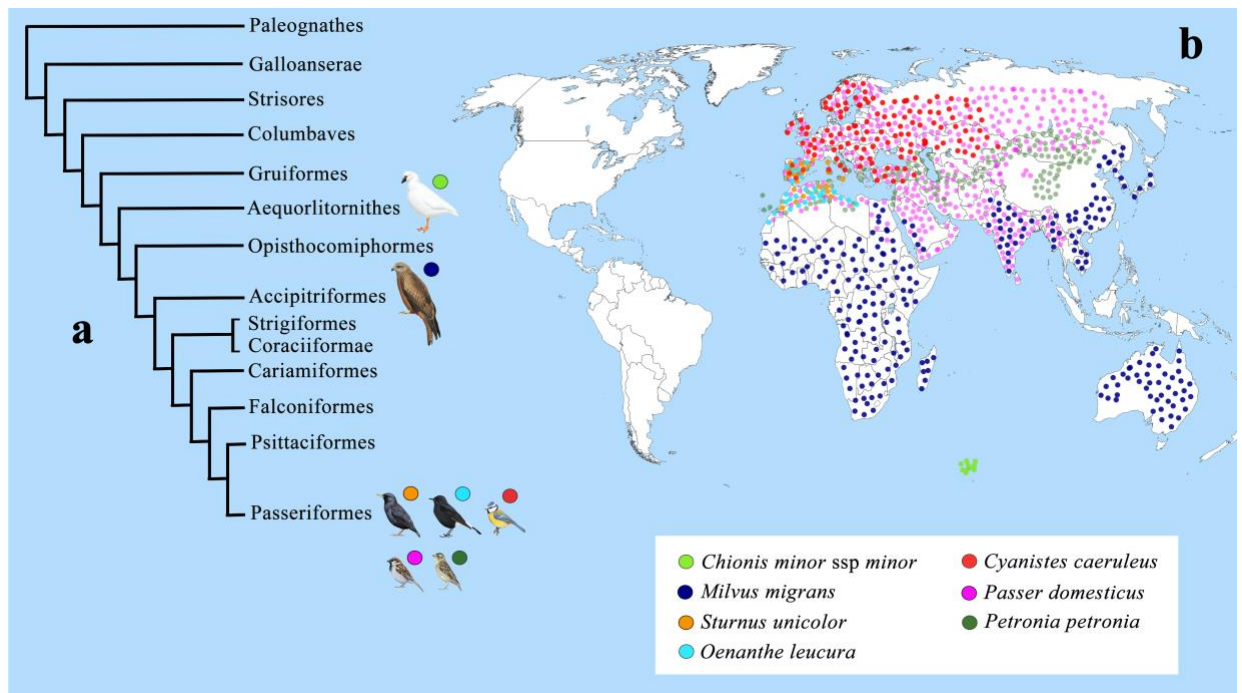


Figure S2.

