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Contributions of feather microstructure to eider down insulation properties

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Insulation is an essential component of nest structure that helps provide incubation requirements for birds. Many species of waterfowl breed in high latitudes where rapid heat loss can necessitate a high energetic input from parents and use down feathers to line their nests. Common eider *Somateria mollissima* nest down has exceptional insulating properties but the microstructural mechanisms behind the feather properties have not been thoroughly examined.

Here, we hypothesized that insulating properties of nest down are correlated to down feather (plumule) microstructure. We tested the thermal efficiency (fill power) and cohesion of plumules from nests of two Icelandic colonies of wild common eiders and compared them to properties of plumules of wild greylag goose *Anser anser*. We then used electron microscopy to examine the morphological basis of feather insulating properties. We found that greylag goose down has higher fill power (i.e. traps more air) but much lower cohesion (i.e. less prone to stick together) compared to common eider down. These differences were related to interspecific variation in feather microstructure. Down cohesion increased with the number of barbule microstructures (prongs) that create strong points of contact among feathers. Eider down feathers also had longer barbules than greylag goose down feathers, likely increasing their air-trapping capacity. Feather properties of these two species might reflect the demands of their contrasting evolutionary history. In greylag goose, a temperate, terrestrial species, plumule microstructure may optimize heat trapping. In common eiders, a diving duck that nests in arctic and subarctic waters, plumule structure may have evolved to maximize cohesion over thermal insulation, which would both reduce buoyancy during their foraging dives and enable nest down to withstand strong arctic winds.

Avian nest structure is an elaborate trait that has evolved to meet some of the needs arising during incubation, including protection from the physical environment and from predators (Hansell and Deeming 2002) and constructing a well-insulated nest can help meet these demands more effectively. Nest insulation is an important component of nest structure, particularly for species breeding in cold and/or exposed environments. In these habitats bird can lose heat rapidly both, from the parent's body and from the nest and its contents (Collias and Collias 1984, Hansell 2000) and thus, their incubation requires a high energetic input (Piersma et al. 2003).

Amongst the nest materials commonly used by birds, plumules have particularly strong insulation properties (Hilton et al. 2004). When lining the nest, they improve the efficiency of incubation (White and Kinney 1974, Drent 1975) and offspring survival (Winkler 1993). Many species of waterfowl breeding in cold environments line their nests with down feathers that come off their breast and belly areas (Caldwell and Cornwell 1975, McCracken et al. 1997, Carey 2002). Females often replace nest down after wind blows older down from the nests (Cooper 1978, Jónsson et al. 2006).

Common eiders *Somateria mollissima* are sea ducks that live in temperate and arctic zones (Ogilvie 2005) where the climate is often harsh and characterized by strong winds (Murray 1998). Female common eiders line their nests (a natural hollow on the ground; Carboneras et al. 2016a) with a cohesive mass of nest down that contain mostly plumules. Plumules, or true down (Lucas and Stettenheim 1972) are soft small feathers with a short calamus, usually entirely imbedded in the skin (epidermis and dermis), the shaft is poorly developed and branches radially into barbs giving a characteristic fan or semi spherical shape (Chandler 1916; Fig. 1). These downy feather types are distributed in a variety of ways on the bird's body and may differ in location between species. Plumules are usually completely covered by contour feathers on adult birds. Plumulaceous barbs branch into barbules, and are found in true down, at the base of contour feathers and in afterfeathers (the lower barbs of a feather). The texture is recognized as being soft and fluffy, filamentous, long, and lack interlocking hooklets (Lucas and Stettenheim 1972). According to Dove (2000) plumulaceous downy barbules (pennulum) branch off the rachilla (midrib) of downy barbs and have a flattened cell base consisting of segments of long filiform cells that can

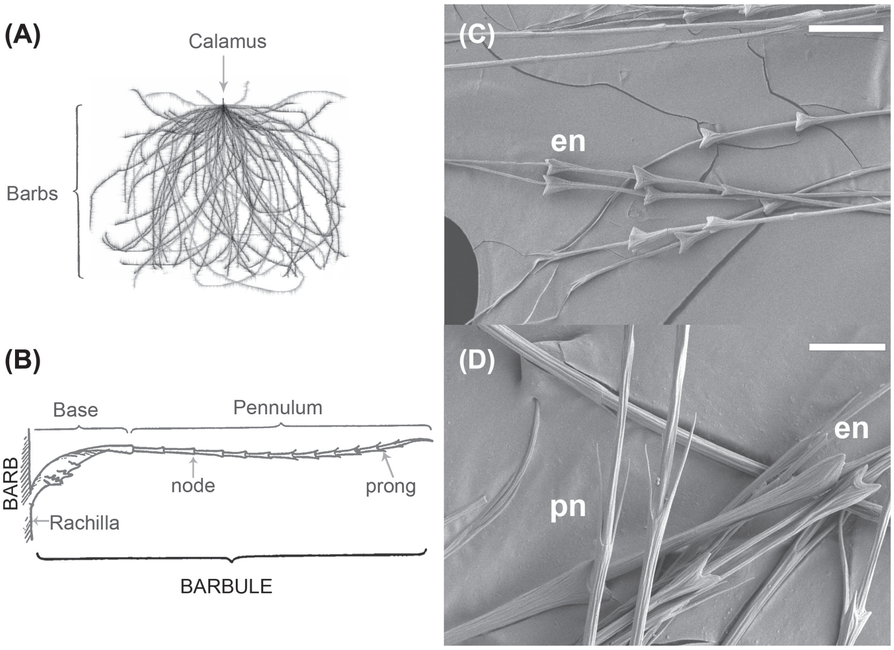

Figure 1. Structure of plumules comprising eider down samples. (A) Schematic representation of a single plumule showing a characteristic fan shape, fine barbs radiate from the central, reduced calamus. (B) Diagram of a single barbule indicating the location of nodal structures. (C) Typical expanded nodes (en) found in greylag goose barbules, scale bar 50 μm. (D) Long prongs (pn) at distal nodes representative of common eider plumule barbules, scale bar 20 μm.

vary and be evenly thick or have expanded or swollen nodes located at cell junctions; distal nodes can sometimes have structures at the cell junctions of varying lengths and morphologies (spined and pronged, Fig. 1; Dove and Agreda 2007).

Wind intensity at the breeding sites has a strong effect on nest microclimate and incubation effort of female common eiders (D'Alba et al. 2009, Høyvik Hilde et al. 2016). Because their nests consists of a simple, shallow hollow on the ground, maintaining a suitable microclimate largely depends on the degree of natural shelter surrounding the nest and the quality of the nest lining (Fast et al. 2007, D'Alba et al. 2009, but see Kristjánsson and Jónsson 2011). Preventing the continuous loss of feathers from the nest and thus maintaining the structural integrity of the nest lining during the entire incubation period should be important for eiders to preserve the insulating and or protective functionality of their nests.

Interest in the insulating properties of down feathers extends beyond behavioral and ecological studies of birds. In the down industry, domestic goose *Anser anser domesticus* down is a common material used for clothing and bedding. It is regarded as superior to duck down (IDFL 2010) and because it is sourced in large volumes from domestic birds it is considered an ideal commercial insulating material. Instead, common eider down feathers are collected from nests in the wild, after females themselves pluck their belly feathers and use them to line the nests. The exceptional thermal properties of eider down have been recognized for centuries and they rank first among natural insulating materials (Jónsson 2001, Bédard et al. 2008). The insulating properties, lightness, cohesion and elasticity of eider-down make it a highly prized product in cold-weather clothing and bedding. Decades ago Loconti (1955) hypothesized that the distinctive morphology of plumules confers its exceptional thermal properties but, remarkably, this has not been investigated further. Down thermal efficiency is rated by its fill power, which is defined as 'the volumetric measurement of a specific amount of down and feathers subject to a standard compression weight' (IDFL 2010); in other words, the higher the fill power the more air the down can trap. Eider down exhibits an exceptional average fill power of 813 inches^3 30 g^{-1} (IDFL 2009), and superb grade down used in high quality products has a fill power of 800 inches^3 30 g^{-1} (PHDesigns 2016). Cohesion is another property of natural materials that allow individual fibers to be held together in bundles (Zhang 2014), i.e. plumules stick together as a mass (Carlsen 2013); in natural polymer fibers it is determined by the presence of surface scales (e.g. wool) or the crimp of cotton fibers (Alexander et al. 1962). Despite the logical relevance of cohesion to the functionality of the down mass, to our knowledge this property has not been previously investigated within the context of feathers. Information about the mechanisms behind the exceptional properties of eider down could inform the biomimetic design of better insulating materials.

The aims of this study are to investigate the morphological basis of the thermal efficiency and cohesion of common eider down (a specialized arctic species) and to compare these properties to greylag goose down (a common temperate species). Plumules of eider and geese were collected from natural nests in Iceland. We test the hypothesis that plumule microstructure is associated with two down properties (fill power and cohesion). We also investigate individual variation in down feather properties among eider nests of two Icelandic common eider colonies.

Methods and material

Sample collection and preparation

The study was conducted in Iceland in the summer of 2014. We collected down samples from a total of twenty different nests from two colonies, Vigur (66°3′20.2″N, 22°49′42.6″W) and Kaldaðarnes (63°55′37.2″N, 21°9′28.1″W). The complete nest down mass was collected from each nest in the second half of the incubation period and replaced with a similar mass of dry hay.

We processed all nest down samples in the facilities of the King Eider Co. (<http://kingeider.is>) in Stykkishólmur, Iceland. To dry the down samples after collection we used a custom made oven at a temperature of 110°C for 16 h. Samples were then cleaned in a custom-made down rinsing machine (King Eider Co., Iceland, Supplementary material Appendix 1 Fig. A1) using a combination of two cycles, first 36 s/45 Hz and then 36 s/52 Hz. In the final stage of cleaning, any contour feathers were handpicked and excluded from each down mass to ensure that only plumules were used in the tests. Samples were weighed (1 ± 0.01 g) before and after cleaning using a digital balance.

Because goose down is considered an optimal standard for insulating materials, we compared plumule microstructure of common eiders to plumules of greylag goose *Anser anser* also breeding in Iceland. A sample of 16.52 g of greylag goose down was obtained from six nests in one location (Landey, Iceland) and processed in the same manner as common eider down samples.

Fill power and cohesion

We used a custom-made, piston-cylinder device to measure fill power (Skipavík, Stykkishólmur, Iceland, Supplementary material Appendix 1 Fig. A2) following specifications from the Japan Down Products Corporative Association. Before measuring fill power, all samples were acclimatized for 24 h in 20°C and 28% relative humidity (the testing room conditions). The amount of down used for one fill-power test was on average 16 g (± 0.8 g). We placed the down sample at the bottom of the cylinder (29 cm in diameter) of the device procuring a homogeneous spread by the sample and avoiding any air pockets. We then very slowly lowered the aluminum disc (120.0 g) until it rested on top of the down sample. After one minute we read the values (± 0.1 cm) indicated by the three sensors attached to the disc and obtained an average volume filled by each sample. Fill power is expressed in cubic centimeters/g and calculated from the formula for the volume of a cylinder: $V = \pi r^2 h$, where V is volume or fill power, r is the radius of the plexitube and h is the measured height of the down sample in the cylinder. We measured fill power on three replicates (1 ounce each) per down sample.

We developed a simple technique to measure cohesion (force that maintains plumules together) of eider down. We randomly selected dots of 10 g from each down sample, manually compressed each dot and then let it recover for 1 min. We then clipped each dot to a spring scale ($100 \text{ g} \pm 0.3$ g Pesola, Switzerland) and measured the maximum weight (g) before the sample broke apart (Supplementary material Appendix 1 Fig. A2). We estimated the maximum force (N) before sample failure following the equation:

$$Fw = m \times g$$

Where Fw represents force in Newtons, m is mass (kg) and g is gravity (9.8 m s^{-2}).

Cohesion was measured by the same person (THC) on five trials to obtain an average for each down sample.

Barbule microstructure

We examined and compared microstructure of plumule barbules from the greylag goose sample and from ten different individual nests from two common eider colonies (10 nests from each colony). We used scanning electron microscopy (SEM) to compare microstructure of down feather barbules. We randomly selected ten single feathers from the down mass of each nest, we took a photograph of each feather under a dissecting microscope (Leica M60, Leica Microsystems, Wetzlar, Germany) and mounted them on separate stubs with carbon tape, sputter-coated them with silver and viewed them on a scanning electron microscope (JSM7401F; JEOL, Japan). For each downy feather we selected four to six barbs, measured their length and the length of ten barbules located at the mid-section of the barb. We measured from the basal cell division (where barbule meets the rachilla) to the tip of the barbule (Fig. 1A). We also recorded the number of total, expanded and pronged nodes at the cell junctions on each barbule (Fig. 1B).

Statistical analyses

Our data did not depart from normality (determined by visual inspection of P-P plots and results of Shapiro–Wilk tests where all p-values > 0.05); thus, we used parametric tests in all cases.

We used Student's t-tests to compare the number of nodes in barbules and barbule length between species or between the two common eider colonies. To analyze the relationship between cohesion and fill power in the 20 common eider individual nest samples we used a linear regression model.

We tested whether the microstructure of eider down feathers is associated with fill power or cohesion using general linear mixed models with either fill power or cohesion as dependent variables, colony as a random effect and barbule length, number of prongs, number of expanded nodes or total number of prongs as fixed effect variables.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.pg1p2> (D'Alba et al. 2017).

Results

Feather microstructure

Plumules of these two species of waterfowl show a semi-spherical shape (Fig. 1A). Barbules branch off rachilla at near orthogonal angles in relation to the barb's axis (common eiders mean angle = 101.01 ± 2.96 degrees; greylag goose mean angle = 69.33 ± 4.42 degrees). Common eider barbules were on average 684 (± 11) nm long, represented on average 5.43% (± 0.13%) of the barb's length and had internode distances of 68 (± 2) nm. In comparison, barbules of greylag goose were significantly shorter in absolute length (539 ± 13.28 nm; $t_{173} = 4.29$, $p < 0.01$) and relative to the barb length (4.81 ± 0.16%). The nodes present two distinctive morphologies: 1) a trifurcated, pronged node and, 2) an expanded node (Fig. 1C). On common eider barbules these two types of nodal morphologies were sometimes found interspersed along the same barbule but often one type was exclusively found on a single feather. Greylag goose barbules showed almost exclusively expanded nodes but some pronged nodes at the very distal portion of the barbule were sometimes observed.

The number of nodes on each barbule differed between goose and eider feathers, as goose plumules had one more nodal structure per barbule than eider barbules ($t_{98} = 3.36$, $p = 0.001$). Pronged nodes were significantly more common in eider plumules than in goose barbules ($t_{98} = 19.47$, $p < 0.001$; Fig. 2).

The number of nodal structures per barbule and barbule length were similar between the Vigur and Kaldaðarnes colonies (all variables $p > 0.05$).

Cohesion and fill power

Common eider down showed strong cohesion (0.75 ± 0.03 N) but lower fill power (263.97 ± 3.96 cm^3 g^{-1}) compared to greylag goose down (cohesion mean = 0.29 ± 0.03 N; fill power = 282.02 ± 8.6 cm^3 g^{-1}).

Cohesion and fill power were not significantly correlated in down samples from Vigur and Kaldaðarnes ($r = 0.29$, $p = 0.21$). Down samples from Kaldaðarnes showed significantly higher cohesion than samples from Vigur ($t_{18} = 2.38$, $p = 0.028$) but down samples did not differ significantly in fill power between locations ($t_{18} = 0.88$, $p = 0.38$; Fig. 3).

Barbule microstructure and down mass properties

We found a significant association between feather microstructure and cohesion of the down mass: cohesion increased as the total number of nodes, the number of pronged nodes and barbule length increased (Table 1, Fig. 4A–C). Cohesion was not associated with the number of expanded nodes (Table 1). Colony was a significant random effect ($p = 0.004$; Table 1)

In contrast, fill power was negatively associated with the total number of nodes ($F_{1,16} = 5.25$, $p = 0.03$) and the number of pronged nodes ($F_{1,16} = 8.25$, $p = 0.01$) in barbules (Fig 4D; Table 1), only marginally affected by barbule length and not associated with the number of expanded nodes (Table 1). There was significant variation in fill power within colony ($p = 0.006$; Table 1).

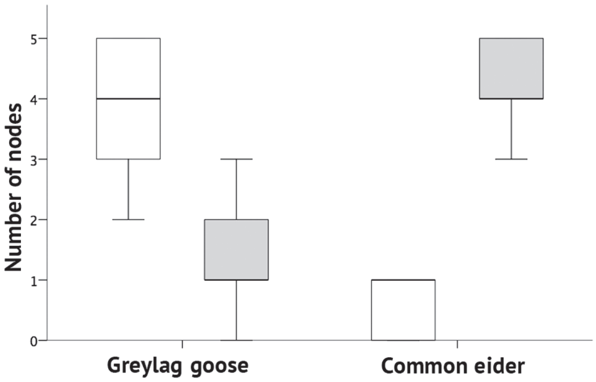

Figure 2. Comparison of the number and type of nodes (white bars = expanded nodes, black bars = pronged nodes) found in greylag goose (n = 10) and common eider plumule barbules.

Discussion

We showed that greylag goose and common eider plumules differ in insulating properties and that those differences are related to differences in feather microstructure. Feather properties of these two species might reflect the demands of their contrasting evolutionary histories and their respective climate regions (temperate vs arctic). For example, greylag geese are grazing birds found in north and central Europe that build their nests among reed beds, often surrounded by thick vegetation or even on trees (Carboneras et al. 2016b) where their nests are rarely exposed to strong winds. Conversely, common eiders are diving ducks that breed in circumpolar, coastal regions and tundra pools where their nests are often exposed to harsher climate (Martin and Wiebe 2004) and stronger feather cohesion would be advantageous. These results support previous evidence indicating that feather structure can correlate with specific habitats and behaviors; for example, independent of phylogeny, the level of resistance to water penetration of contour, pennaceous feathers is higher in diving birds compared to aquatic surface feeders and terrestrial birds and it is determined by the inter-barb spacing and diameter (Rijke and Jesser 2011).

Distinctive, three-dimensional plumule geometry was evident in all our samples. This shape is established by the arrangement of barbules, showing a fractal geometry (Gao and Pan 2009) and is essential in determining down's insulating capacity (Gao et al. 2009). Compared to contour feathers that have a flat geometry, plumules insulate equally along all axes, blocking heat flow in all directions. The high degree of hierarchical organization of down feathers suggests that they have evolved to optimize heat trapping (Burtt and Ichida 2006). We also observed a distinctive morphology in common eider plumules dominated by the presence of long barbules and pronged nodes at the distal end of barbules. In comparison, greylag goose plumules were shorter and characterized by predominantly expanded nodes. Similar barbule structures with numerous distal pronged nodes have been observed in plumules of other diving birds including loons, alcids, penguins, grebes and some suliformes (Dove 2000).

This convergence of plumule microstructure, first noted by Dove (2000), suggests that pronged nodes could provide a more compressed and insulative barrier to the skin when diving, thereby helping diving birds decrease buoyancy by reducing the amount of air trapped next to the skin (Dove

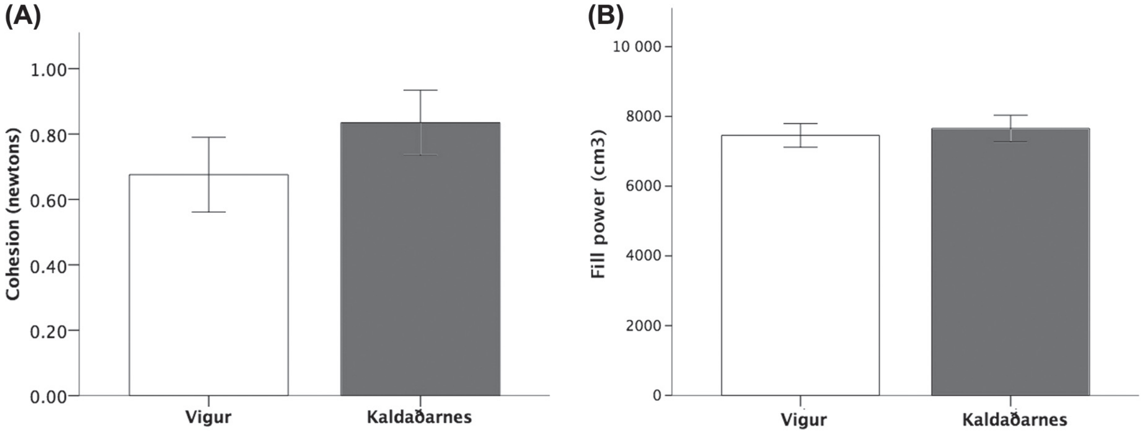

Figure 3. Comparison of cohesion and fill power of samples from two common eider colonies studied in Vigur and Kaldaðarnes, Iceland. Values presented are means ± 95% CI.

2000). Arctic climate has alternated between cooling and warming periods during eider evolutionary history, and as the glaciation (Ice age) periods alternated with deglaciation periods, common eider plumules could have evolved as a trade-off between the need to reduce buoyancy during their foraging dives, and the need of nest down to withstand strong arctic winds during incubation periods.

Compared to goose down, fill power of eider down was lower while cohesion was higher and these differences were associated with the presence of a larger number of pronged nodes on common eider barbules. Similarly, the more cohesive eider down samples were composed of plumules with a larger number of prongs and shorter barbules; in contrast, fill power decreased with increased numbers of pronged nodes. Variation in barbule microstructure among eider females could be explained by differences in feather maturity and/or individual age, where younger individuals have reduced barbules or undeveloped nodal structures (Robertson et al. 1984) that could result in decreased cohesion.

Our findings on common eider down properties suggest that barbule nodes (particularly the pronged type) increase cohesion of the down mass but at the same time could prevent eider plumules from trapping air, and potentially maintaining temperature inside the nest, to their maximum capacity, which would explain the negative association between number of prongs and fill power. This notion is supported by previous studies, which demonstrated that 1) in domestic duck and goose down feathers, prongs interact with barbules to create strong points of contact (Supplementary material Appendix 1 Fig. A3) that prevent slippage of barbules and increase resistance to compression (Wilde 2004) and strength (Pan et al. 2001), and 2) expanded nodes, which are flat on their distal end might be less effective at trapping other barbs (Supplementary material Appendix 1 Fig. A4) compared to pronged nodes (Fuller 2015).

Table 1. General linear models showing the association between properties and barbule microstructure of eider down (n = 20 nests). Parameter estimate (slope), F-tests are provided for each variable tested.

Term	β (SEM)	F	p
Cohesion			
Expanded nodes	–0.067 (0.065)	1.056	0.31
Pronged nodes	0.11 (0.022)	24.38	< 0.01
Total number	0.165 (0.025)	44.69	< 0.01
Barbule length	–0.001 (0.00)	24.13	< 0.01
Random factor: colony	Z = 2.915		0.004
Fill power			
Expanded nodes	13.80 (7.18)	3.60	0.08
Pronged nodes	–9.57 (3.43)	8.25	0.01
Total number	–9.391 (4.74)	5.25	0.03
Barbule length	0.054 (0.026)	4.19	0.056
Random factor: colony	Z = 2.739		0.006

If indeed the pronged nodes increase cohesion among plumules this would suggest that in eiders these structures have evolved to maximize cohesion over thermal insulation. Alternatively, the pronged nodes could have evolved to further improve the thermal efficiency of eider plumules. Common eider plumules also have significantly longer barbules than greylag goose plumules in true down. Long fibers increase the air-trapping capacity by creating a highly space-filling shape, particularly when aided by the presence of strong attachment points at the tips (Fuller 2015).

The need for optimized down cohesion is particularly relevant for common eiders. Since females nest in a simple, shallow natural hollow on the ground (Carboneras et al. 2016a), eggs could be completely exposed to the elements when females leave the clutch unattended without a tight mass of nest down and sometimes, a natural shelter (rocks or vegetation) surrounding the nest. Intense wind has a particularly strong effect on egg temperature (D'Alba et al. 2009) and incubation effort of female eiders (Høyvik Hilde et al. 2016) and can easily blow feathers off nests (Cooper 1978). The nest down does not seem to have a particularly strong effect on temperature of incubation or cooling rates of eggs compared to dry hay, at least in Icelandic locations with relatively milder climate than more arctic locations (Kristjánsson and Jónsson 2011, but see Hilton et al. 2004 and D'Alba 2007) suggesting that insulation might not be its primary function, that insulation is important predominantly during harsh weather or that insulation would only be effective if the down mass is strongly cohesive. Other

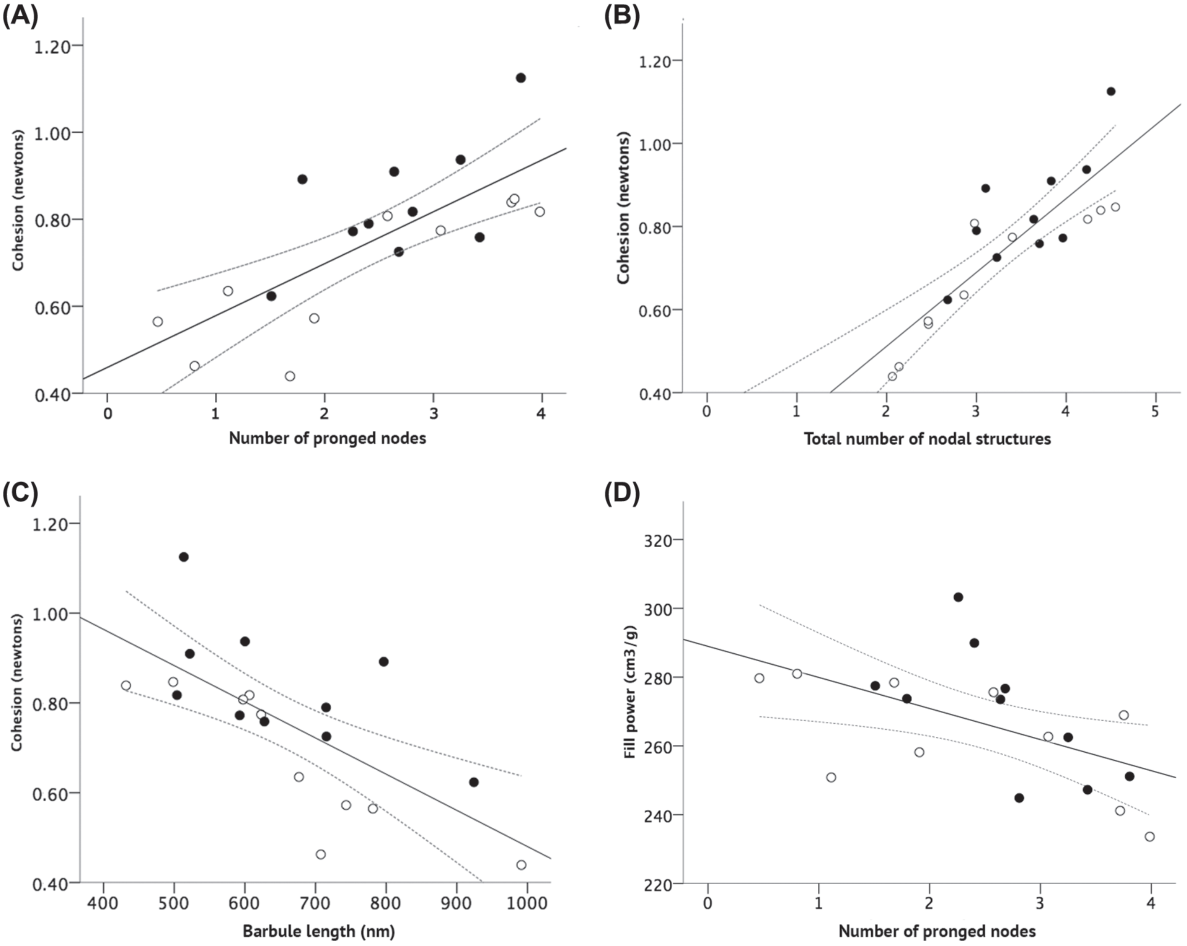

Figure 4. Relationship between common eider down cohesion and the number of pronged nodes (A), barbule length (B) and total number of nodal structures (C) of down samples from Vigur (open circles) and Kaldaðarnes (filled circles). The association between fill power and the number of pronged nodes on common eider barbules is shown in (D). For all panels the estimated regression lines and 95% CI envelopes are shown.

functions of nest down are to provide concealment against predators (Kreisinger and Albrecht 2008), mechanical protection to prevent eggs from moving around and/or cracking against the hard substrate or against each other (Healy et al. 2015) or nest sanitation (Dawson et al. 2011). These functions of nest down could be enhanced by a strong down mass cohesion.

Finally, plumules are not found inside nests in isolation (individually), so we need to understand the properties of down mass as a bulk material. For example, we need to study how individual barbules and feathers interact with each other to form a down mass and whether activity of incubating hens affects cohesion within the down mass. In addition, future studies should focus on experimentally testing the effects of down properties on egg temperature and cooling rates. This information along with the new (to our knowledge) insight into the morphological bases of insulation properties presented here, could provide fundamental sources of inspiration for the development of artificial insulating materials.

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Author contributions – We have no competing or financial interests. LDA, THC and JEJ conceived the study; THC, AA, and LDA, collected the data and performed experiments; LDA analysed the data; MDS provided logistic support. All authors contributed to drafting and revising the article.

Permit – No live animals were used in the study.

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Supplementary material (Appendix JAV-01294 at <www.avianbiology.org/appendix/jav-01294>). Appendix 1.