NAPE COLORATION VARIES WITH SEX, NOT AGE, AMONG GREAT SHEARWATERS *ARDENNA GRAVIS*

EWAN D. WAKEFIELD[1,2], ANNA R. ROBUCK[3,4], KEVIN D. POWERS[5], ROBERT A. RONCONI[6], PETER G. RYAN[7], & DAVID N. WILEY[5]

[1]*Department of Geography, Durham University, Lower Mountjoy, South Road, Durham, DH1 3LE, UK (Ewan.Wakefield@durham.ac.uk)*
[2]*University of Glasgow, School of Biodiversity, One Health & Veterinary Medicine, Graham Kerr Building, Glasgow, G12 8QQ, UK*
[3]*University of Rhode Island Graduate School of Oceanography, Narragansett, Rhode Island, 02882, USA*
[4]*Current address: US Environmental Protection Agency, Center for Environmental Measurement and Modeling, Office of Research and Development, Narragansett, Rhode Island, 02882, USA*
[5]*Stellwagen Bank National Marine Sanctuary, National Oceanic and Atmospheric Administration, Scituate, Massachusetts, 02066, USA*
[6]*Canadian Wildlife Service, Environment and Climate Change Canada, Dartmouth, Nova Scotia, B2Y 2N6, Canada*
[7]*FitzPatrick Institute of African Ornithology, Department of Science and Technology/National Research Foundation Centre of Excellence, University of Cape Town, Rondebosch, 7701, South Africa*

Received 22 July 2024, accepted 23 September 2024

ABSTRACT

Wakefield, E. D., Robuck, A. R., Powers, K. D., Ronconi, R. A., Ryan, P. G., & Wiley, D. N. (2025). Nape coloration varies with sex, not age, among Great Shearwaters *Ardenna gravis*. *Marine Ornithology, 53*(1), 151–158. https://doi.org/10.....

Most petrels (family Procellariidae) exhibit little or no obvious variation in plumage with age or sex, either because plumage performs no sexual function or does so in a way poorly perceptible to humans. This limits the inferences that can be made from visual observations of petrels at sea. However, it has been suggested that nape coloration of Great Shearwaters *Ardenna gravis* whitens with age. Here we test this supposition using observations of known-age-class individuals. We necropsied birds bycaught around Gough Island, a major breeding colony in the South Atlantic Ocean, and in Massachusetts Bay, a wintering area off the northeastern coast of the USA, to determine sex and classify nape coloration. In addition, we classified the nape coloration of adults and fledglings photographed in colonies on Gough Island and Inaccessible Island in the South Atlantic. Across birds (n = 328), ratios of light:intermediate:dark napes did not differ significantly between age classes, and the accuracy of age classification based on putative nape variation was only 52%. Nape coloration did, however, vary systematically with sex and location: in Massachusetts Bay, light napes were more prevalent in adult females. Off Gough Island, where only adults were sampled, this disparity did not occur. We conclude that while nape coloration may vary due to feather wear, it is not a reliable indicator of age. Rather, it may perform a sexual function, possibly mediating mate choice. Further study of plumage variation and behavior at the colony would be required to test this hypothesis.

Key words: immature, juvenile, melanin, molt, petrel, plumage, Procellariidae

INTRODUCTION

The family Procellariidae (hereafter petrels) includes many of the world's most abundant pelagic seabird species as well as some of its most threatened (Brooke, 2004; Croxall et al., 2012). Petrels are long-lived compared to most other birds, with maturation taking three to twelve years (Warham, 1990). Recent interest in the early life history of petrels has been stimulated by rapid advances in bird-borne tracking technologies, which have revealed sometimes marked differences between adults and pre-breeders in both distribution and behavior (Campioni et al., 2020; Riotte-Lambert & Weimerskirch, 2013). However, because most petrels do not begin attending colonies until they are several years old, it remains challenging to track them during their first years of life (Rodríguez et al., 2019). For instance, *Ardenna* and *Puffinus* shearwaters typically first return to their colonies after a minimum of two years and an average of four to six years after fledging (Barbraud et al., 2014; Bradley et al., 1999; Fletcher et al., 2013; Perrins et al., 1973; Vanderwerf et al., 2015). Direct observational study of birds at sea could provide additional data on age-related distribution, habitat use, and behavior. For example, plumage coloration changes systematically with age in the giant petrels *Macronectes* spp. (Carlos & Voisin, 2008), and differential timing of molt and feather wear can sometimes be used to infer the age of other petrels observed at sea (Howell, 2012). In most circumstances, however, variation in plumage coloration is insufficient to readily discriminate between adults and other age classes observed at sea.

Within many avian taxa, plumage also varies with sex due to its sexual signaling function (Greene et al., 2000; Hill, 1991; Meunier et al., 2011). In contrast (with the exception of the great albatrosses *Diomedea* spp.), plumage is not known to differ between the sexes within Procellariiformes (Brooke, 2004; Onley & Scofield, 2007). Nonetheless, it is conceivable that sex differences in plumage could occur but have not hitherto been detected. It is therefore important to identify and describe systematic variation in plumage aspect with not only age but also sex.

Great Shearwaters *Ardenna gravis* are abundant (~15 million individuals; Brooke 2004) medium-sized petrels that breed in the Tristan da Cunha group of islands in the South Atlantic Ocean. Despite recent tracking and at-sea sampling (Bugoni et al., 2015; Hong et al., 2019; Powers et al., 2017; Ronconi et al., 2018), there remains some uncertainty about the movements of pre-breeding individuals (Powers et al., 2022). The ability to discriminate between adult and pre-breeding Great Shearwaters at sea would be useful (Powers et al., 2020).

In austral summer, adults forage in temperate to sub-polar waters, including the Patagonian Shelf, the Benguela Current, and intervening oceanic areas (Ronconi et al., 2018; Schoombie et al., 2018). In austral winter, adults and presumably pre-breeding birds follow a figure-of-eight migration route, initially heading northwest into the western North Atlantic. Aggregations occur in neritic waters, such as the Gulf of Maine (Powers et al., 2020), and in oceanic areas, including the Charlie-Gibbs Fracture Zone (Wakefield et al., 2021). Subsequently, they continue their migration clockwise through the North Atlantic, crossing the equator in a southerly or southwesterly direction and returning to their breeding colonies in the austral spring (Voous & Wattel, 1963). Birds that begin their southern migration later travel to waters of the Patagonian Shelf rather than to breeding colonies. It has, therefore, been suggested that these are non-breeders, including birds in their first year of life (Powers et al., 2022).

Great Shearwaters are thought to follow a complex basic molt strategy (reviewed by Flood et al., 2020; Howell, 2012; Pyle, 2008): molt of flight and body feathers overlaps. Most adults that breed successfully undergo wing molt in the western North Atlantic from late May until early August. Juveniles retain their first basic plumage until January, when they undertake their second prebasic molt. This is initiated in the South Atlantic and completed either there by around April–May or following migration into the North Atlantic by around June–August. Adults that skip or fail breeding and pre-breeding birds are thought to follow a similar schedule.

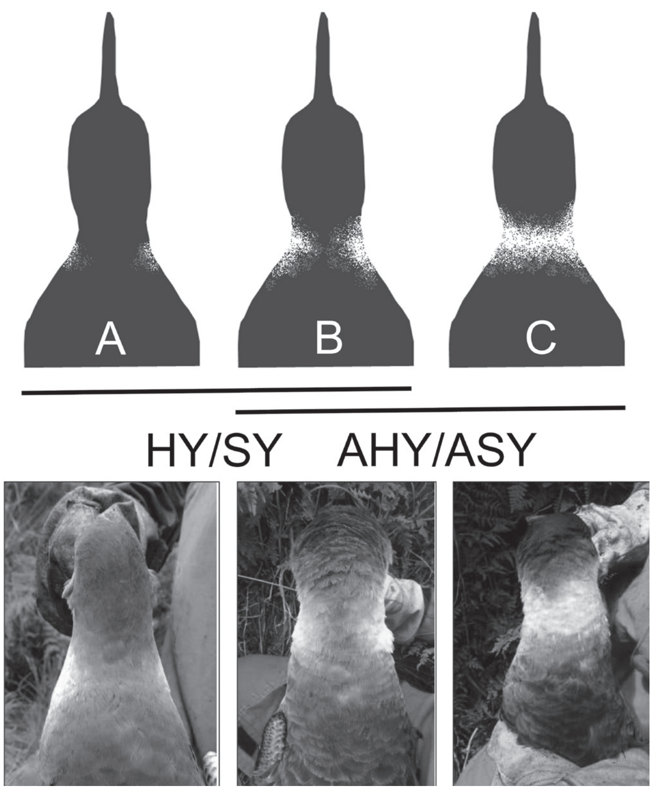

Fig. 1. Putative relationship between the coloration of the napes of Great Shearwaters *Ardenna gravis* and age (top row, redrawn from Pyle 2008), plus examples of each nape type from this study (bottom row). HY/SY = hatch/second year; AHY/ASY = after hatch/second year.

Great Shearwaters have a dark-brown cap and mantle that is separated by a partial or complete collar of light, white to cream-colored feathers[1] (Fig. 1). Pyle (2008) tentatively suggested that juvenile (hatch year/second year, HY/SY) Great Shearwaters have a "Nape with [an] indistinct to incomplete white collar," while older (after hatch year/after second year, AHY/ASY) birds, including breeding individuals, have a "Nape with [an] indistinct to distinct white collar." Pyle's Figure 201 illustrates three nape types (A, B, C) that form a spectrum from dark to partial to light coloration (Fig. 1). The caption adds that "it is possible that AHY/ASYs resembling C can reliably be aged to ASY/ATY [after second year/after third year] or older", but it notes that more study is required to confirm these patterns. Some field guides also indicate that juvenile Great Shearwaters have darker nape plumage than adults (Harrison et al., 2021; Howell, 2012; Howell & Zufelt, 2019). Here we assess nape plumage of known-age-class Great Shearwaters sampled both in their colonies and bycaught in the South and North Atlantic to test whether nape coloration is a reliable marker of age. In addition, we test for variation in nape coloration by sex, region, and season.

METHODS

The National Oceanic and Atmospheric Administration's Northeast Fisheries Observer Program (Falmouth, USA) supplied us with 153 dead Great Shearwaters bycaught in fisheries in Massachusetts Bay, USA (42°22′N, 070°48′W). These birds were caught between 14 May and 15 December of 2010–2017, with the majority caught in August (Table 1). Tristan da Cunha Conservation Department supplied an additional 25 Great Shearwaters bycaught adjacent to the breeding colony at Gough Island (40°19′S, 009°56′W) in the South Atlantic in March 2018 during the chick-rearing period. We partially thawed and necropsied each bird following van Franeker (2004), recording the following: plumage characteristics, external

TABLE 1
Monthly distribution of Great Shearwaters *Ardenna gravis* bycaught in fisheries in Massachusetts Bay, USA, between 14 May and 15 December of 2010–2017

Month	*n*
May	1
June	2
July	8
August	102
September	18
October	7
November	11
December	4

1 For the purposes of our analysis, we simply distinguish between "light" and "dark" nape colouration and use these terms when referring to our results. In the literature, the functional significance of "black and white" plumage is often discussed, even though in reality the respective colors are often dark brown/dark gray and cream/off-white, due, for example, to feather wear. We therefore use the term "white" when discussing plumage in a more general sense and when quoting Pyle (2008).

morphometrics, organ weights, body condition, sex, and stomach contents. In addition to assigning the ages of birds to the two classes referred to by Pyle (2008) apropos of nape coloration (HY/SY vs. AHY/ASY), we classified each bird as HY, pre-breeding (PB), or breeding (B) age. We determined age principally from internal anatomy based on Powers et al. (2020) and Broughton (1994) (Table 2). In brief, if the bursa of Fabricius was present, we assumed birds to be HY. If the bursa was absent and the gonad class (sensu Powers et al., 2020) was 1 or 2, birds were assumed to be AHY/PB. If the gonad class was 3 or 4, birds were assumed to be of breeding age. We also checked that primary molt score (Ginn & Melville, 1983) was consistent with the date of collection and putative age (Pyle, 2008). In potentially ambiguous cases of HY versus AHY/PB birds, age was also confirmed by examining feather and claw wear. For example, the bursa was present but deflated in one bird that was bycaught in July. Sharp claws and all fresh plumage confirmed age to be HY (Pyle, 2008). ARR and/or KDP classified napes blind (i.e., prior to necropsy) following Pyle (2008; Fig. 1) as type A, B, or C.

The napes of known-age Great Shearwaters were photographed at breeding colonies. During the 2009/10 breeding season, we photographed the napes of 15 adults on Gough Island and Inaccessible Island (37°18′S, 012°41′W) during a tagging study (Ronconi et al., 2018). On Gough Island, the napes of birds were photographed during the initial colony arrival and courtship period (22 September to 02 October). All were attending nests, and some were observed copulating. On Inaccessible Island, birds were removed by hand from burrows or caught opportunistically at burrow entrances and photographed during early incubation (10 November to 01 December). The age at first breeding of Great Shearwaters is unknown but among other *Ardenna* spp., it is at least four to five years, and on average seven or eight years (Bradley et al., 1999; Fletcher et al., 2013), so we assumed that these birds were at least two years old. During the 2017/18 breeding season, 83 adults were photographed by staff from the Royal Society for the Protection of Birds on Gough Island between colony arrival and early chick-rearing (22 September to 06 January), and 31 fledglings (i.e., HY individuals) were photographed just prior to leaving the colony (03–08 May). All birds were removed by hand from burrows during the daytime, photographed, then returned to their burrows. Adults were either known breeders, previously marked as part of long-term demographic and tracking studies, or unmarked non-breeders. Photographed fledglings had attained their juvenile plumage, but some retained traces of down.

TABLE 2
Criteria used to assign Great Shearwater *Ardenna gravis* age class based on Pyle (2008) and Powers et al. (2020)

Classification scheme	Age class[a]	Bursa present	Gonad class 1 or 2	Gonad class 3 or 4
Pyle	HY/SY	X	X	
	AHY/ASY		X	X
Powers et al.	HY	X	X	
	AHY/PB		X	
	B			X

[a] HY/SY = hatch/second year; AHY/ASY = after hatch/second year; PB = pre-breeder; B = breeder.

Napes of birds caught in colonies were independently scored as A (dark), B (intermediate), or C (light) by ARR and KDP. To ensure that this was done double-blind, EDW supplied ARR and KDP a portable document format (pdf) file of the photographs that they had not previously seen. A custom R script generated the pdf with the anonymized images arranged in a random order. A separate file, not disclosed to ARR and KDP, detailed the true ages for subsequent reference. Classification was highly consistent between observers; birds where disagreement occurred ($n = 7$) were not included in the analysis.

We used chi-square tests of independence or Fisher's exact tests to compare ratios of nape types between age groups, sexes, locations, and sampling years. We used confusion matrices (Kolo, 2010) to assess the accuracy, sensitivity (true positive rate), and specificity (true negative rate) of the classification of known-age birds (HY or breeding age), based on Pyle's suggested approach. We omitted any necropsied birds that were classified as AHY/PB from this part of the analysis, as this category could include both Pyle's HY/SY and AHY/ASY classes. We carried out all analyses in R statistical software (R Core Team, 2024).

RESULTS

We classified the nape plumage of 328 Great Shearwaters (129 photographed in colonies and 199 necropsied). Across all birds, prevalence of type A (dark) napes decreased with age class (Fig. 2), but this effect was small and the ratio of nape types A:B:C

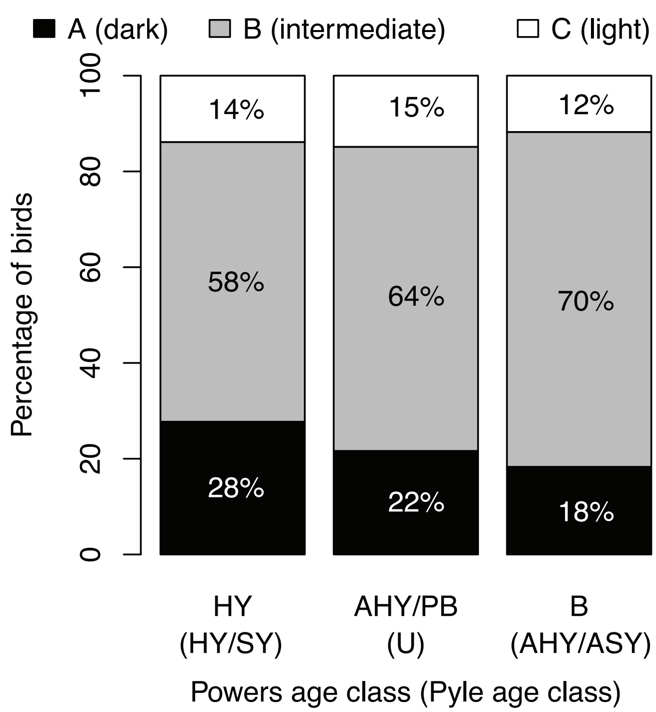

Fig. 2. Variation in nape coloration with age class of Great Shearwaters *Ardenna gravis* ($n = 328$) across all sampling locations. Age was defined following Powers et al. (2020), with the equivalent age classes defined following Pyle (2008) in parentheses. AHY = after hatch year, ASY = after second year, HY = hatch year, PB = pre-breeder, B = breeder, SY = second year, U = unknown (not clearly meeting all criteria for HY/SY or AHY/ASY in the Pyle classification scheme).

did not differ significantly between age classes ($\chi^2_{4,328}$ = 4.17, *p* = 0.384).

We determined the age class of 254 birds photographed in colonies or necropsied. Most (65%) had type B nape coloration, meaning their ages were ambiguous in Pyle's (2008) scheme. Of the remaining 88 birds, 67% of known HY birds had type A napes and would, therefore, have been correctly classified as HY/SY under Pyle's scheme. Only 39% of known mature birds had type C (light) napes and would have been correctly classified as AHY/ASY. The overall accuracy of Pyle's proposed scheme, excluding type B napes, was therefore 52%. Its sensitivity was 39% and its specificity 67% (Table 3).

At all locations, some mature birds had type A napes and some HY birds had type C napes (Fig. 3). Considering only birds bycaught in Massachusetts Bay (2010–2017), the ratio of nape types A:B:C did not differ significantly among sampling years (Fisher's exact test, two-sided, *p* = 0.230). The prevalence of type C napes was higher among mature birds, but this difference was not significant ($\chi^2_{4,174}$ = 4.54, *p* = 0.338). Similarly, among birds photographed in colonies or bycaught during the breeding season off Gough Island, the ratio of nape types A:B:C did not differ significantly between age groups ($\chi^2_{2,154}$ = 2.34, *p* = 0.310). Considering only mature birds, the A:B:C ratio differed significantly between birds sampled in or near breeding colonies compared to Massachusetts Bay, with a greater prevalence of type C napes among the latter ($\chi^2_{2,154}$ = 11.99, *p* = 0.002). This trend was also evident but not significant among HY birds ($\chi^2_{2,154}$ = 2.17, *p* = 0.338).

TABLE 3
Confusion matrix comparing the age-classification of Great Shearwaters *Ardenna gravis* from nape plumage following the method proposed by Pyle (2008) against their true ages established via necropsy or observation at the colony[a]

	Predicted AHY/ASY	Predicted HY/SY
True AHY/ASY	18	28
True HY/SY	14	28

[a] HY/SY = hatching/second year, AHY/ASY = after hatching/second year. Note: 107 HY/SY and 59 HY/SY birds had intermediate nape coloration and could not be assigned unambiguously to an age class using the method of Pyle (2008).

Molt scores indicated that most birds necropsied from Massachusetts Bay were bycaught nearly at the end of or after completion of wing molt (mean [range] wing molt score: HY = 50 [41–50], AHY/PB = 47 [0–50], and B = 47 [31–50]). The greater prevalence of type C napes among these birds was apparently driven by a sex imbalance in nape coloration (Fig. 4), with a higher proportion of females than males having type C napes ($\chi^2_{2,174}$ = 9.92, *p* = 0.007). Although this difference was evident in all age classes, it was only significant when the data were aggregated across age classes (sex difference within ages classes: HY birds $\chi^2_{2,70}$ = 2.22, *p* = 0.330; AHY/PB birds $\chi^2_{2,74}$ = 3.36, *p* = 0.187; breeding-age birds Fisher's exact test, two-sided *p* = 0.168). This is presumably because the effect was small among sub-adults, and although the effect was larger among mature birds, the sample size for this group was small. Among mature birds bycaught off Gough Island, ratios of nape types did not differ between the sexes ($\chi^2_{2,25}$ = 0.74, *p* = 0.691). We could not ascertain if this also applied to birds photographed in the breeding colonies, because the sexes of most of these were unknown.

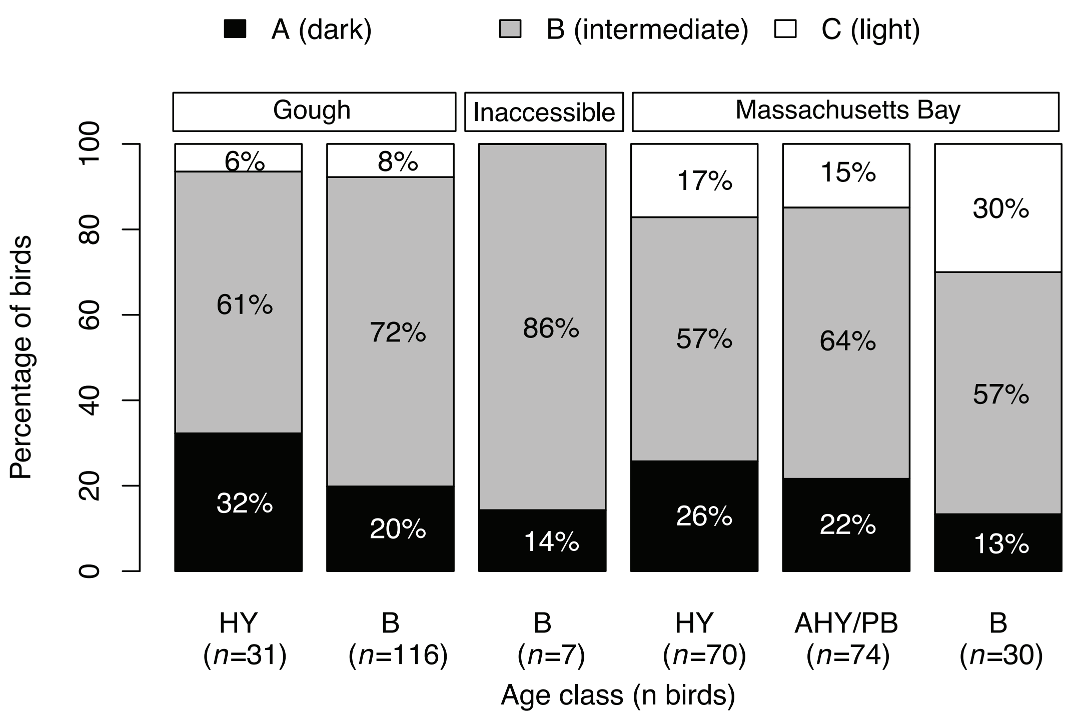

Fig. 3. Variation with age class in the nape coloration of Great Shearwaters *Ardenna gravis*. Birds were either photographed in colonies (Inaccessible Island or Gough Island) during the breeding season, bycaught off Gough Island during the breeding season, or bycaught in Massachusetts Bay, USA, during the non-breeding period. Age classes follow Powers et al. (2020): AHY = after hatch year, HY = hatch year, PB = pre-breeder, B = breeder.

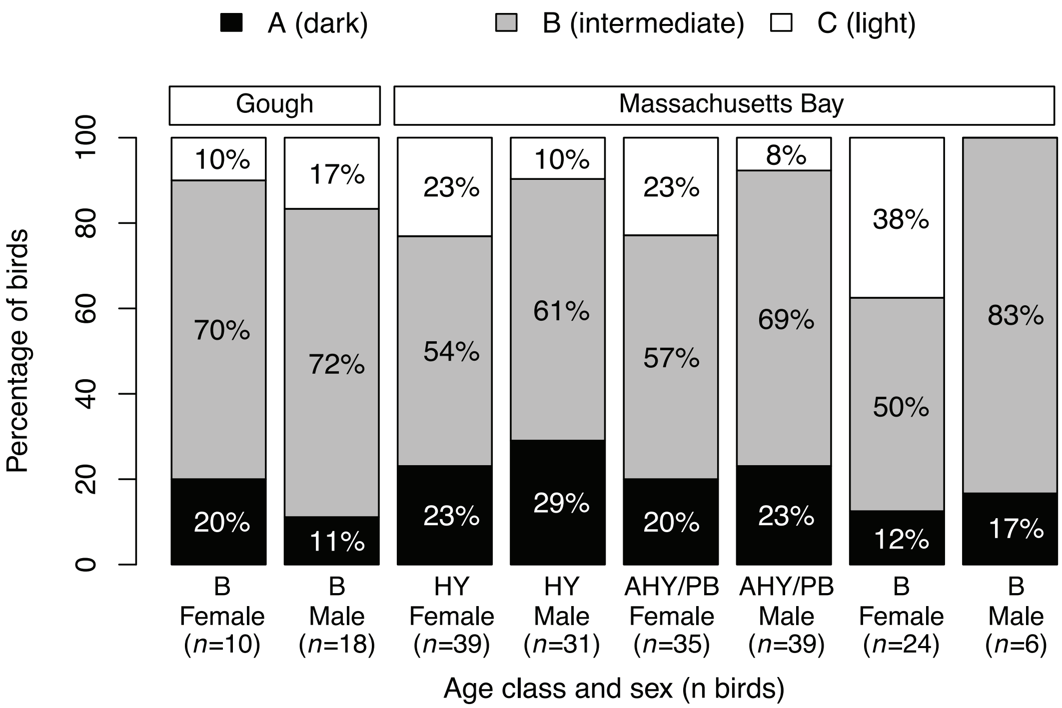

Fig. 4. Variation with age class and sex in the nape coloration of Great Shearwaters *Ardenna gravis*. Birds were photographed on Gough Island during the breeding season, bycaught near Gough Island during the breeding season, or bycaught in Massachusetts Bay, USA, during the non-breeding period. Age classes follow Powers et al. (2020): AHY = after hatch year, HY = hatch year, PB = pre-breeder, B = breeder.

DISCUSSION

Our results show that while a slightly higher proportion of fledgling and first-year Great Shearwaters have all-dark napes compared to adults, this effect is small and not a reliable way of discriminating between HY/SY and AHY/ASY or older birds. Moreover, most Great Shearwaters, regardless of age, were intermediate between having a dark or light nape, making nape coloration a poor indicator of age. In short, contrary to the tentative suggestion by Pyle (2008), we found no evidence of a marked lifetime progression from dark to light napes.

We did note a small (but not significant) reduction in the prevalence of all-dark napes between juvenile birds sampled during the breeding season and first-year birds in their winter quarters. It is conceivable that this was due to feather wear, rather than changes in feather pigmentation per se. The body feathers of Great Shearwaters are white with brown tips, so wear could result in the sides of the neck becoming paler as feathers wear between molts. Potentially, this could also explain why some authors have reported that juveniles have darker napes than adults (Harrison et al., 2021; Howell, 2012; Howell & Zufelt, 2019; Pyle, 2008). For example, it is plausible that these inferences were based primarily on observations of Great Shearwaters wintering in the western North Atlantic. Juveniles would be most distinguishable from adults during the early boreal summer, due to their plumage being relatively fresh in comparison to adults, most of which do not complete their prebasic molt until late August (Howell, 2012). If nape coloration was particularly susceptible to feather wear, there could be a relatively high prevalence of lighter napes among adults during this period. By late boreal summer, after adults had molted, the situation could be reversed. However, it would then be less feasible to discriminate adults from juveniles based on plumage aspect because both would have relatively fresh plumage, so such an inversion might not be noticed. Unfortunately, we could not test these suppositions because most of the birds from Massachusetts Bay that we necropsied were bycaught after they had completed or nearly completed molt. Future studies may refine understanding of these points, for example, by examining high-resolution digital photographs of Great Shearwaters taken throughout the year and at a variety of locations.

We also found that nape plumage varies subtly but systematically with sex and location: occurrence of light napes (type C) was disproportionately high among females bycaught in Massachusetts Bay. Conceivably, this could also arise due to feather wear combined with a difference in the timing of molt, in a manner similar to that postulated above for wintering juveniles versus adults. This would require that females molt later than males, as is the case among Wandering Albatross *Diomedea exulans* (Weimerskirch, 1991). As far as we are aware, there is no evidence of such a difference among Great Shearwaters, nor among other petrels (Allard et al., 2008; Alonso et al., 2009; Bourgeois & Dromzée, 2014; Bugoni et al., 2015; Carvalho et al., 2022).

Alternatively, the sex-specific shift in the prevalence of light napes between locations, especially among mature females, could be due to nape plumage having a sexual display function. In many bird taxa, plumage coloration and brightness signal mate quality (Mason & Bowie, 2020). Although this is often mediated via carotenoid pigmentation (Hill, 1991), black or dark-brown coloration produced via melanin can play a similar role (Galván & Solano, 2016; Meunier et al., 2011). White plumage results from a lack of pigmentation (Tickell, 2003), but its brightness can nonetheless act as an honest signal of quality because it is dependent on feather microstructure, which in turn is dependent on diet during molt plus subsequent feather wear (Soravia et al., 2020). Maintenance of strong contrast between white and dark plumage patches can also reflect mate quality (Galván & Sanz, 2008). Nape coloration could also enhance visual courtship displays. For example, among Pelecaniformes with predominantly black and white plumage, complexity of courtship displays is negatively correlated with the relative size of white plumage patches, which are assumed to accentuate conspicuousness (Galván, 2008). Like many birds, allopreening, especially of the head and neck, is important in the pair formation/maintenance behavior of Great Shearwaters (Brooke, 2004). Their predominantly brown and white plumage is more patterned than that of most other shearwaters (Brooke, 2004), and their vocalizations have less pronounced sexual differences (Brooke, 1988). Plumage may, therefore, provide important visual cues during courtship, especially as this tends to occur in the evening (Brooke, 2004), when white plumage patches are thought to be conspicuous (Penteriani & Delgado, 2017).

Consistent with the hypothesis that light nape plumage plays a role in courtship, the prevalence of type C napes in females bycaught in their winter quarters was higher among mature birds than among either HY or PB birds, although this effect was not significant. These birds were bycaught between August and November and would probably have already replaced their neck plumage (Bugoni et al., 2015) prior to the breeding period, which starts around mid-September (Cuthbert, 2005). Unfortunately, this does not explain why mature females and males bycaught around Gough Island towards the end of the breeding season had a similar and relatively low proportion of type C napes. In that regard, our dataset is insufficient to quantify lifetime ontogeny of nape plumage or any variation over the breeding cycle. Instead, this hypothesis could be tested by observing variations in nape plumage at the colony, including those perceptible to birds but not necessarily humans (Soravia et al., 2020), and testing for systematic variations with this and reproductive and agonistic behaviors.

In summary, our findings show that contrary to previous suggestion, nape color is not a reliable signal of age in Great Shearwaters. However, the incidence of sex-specific nape coloration and sexual variation in other plumage characteristics warrants further study in this species. Although ultraviolet sensitivity is apparently low among petrels (Machovsky Capuska et al., 2011), such studies should also consider whether plumage varies systematically with sex or age in ways imperceptible to the human eye (Finger & Burkhardt, 1994; Soravia et al., 2020).

ACKNOWLEDGEMENTS

We are very grateful to Peter Pyle and Robert Flood for constructive comments on an initial version of this paper; Michael J. Moore for necropsy facility use; Vonica A. Perold and Maëlle Connan for necropsy assistance in South Africa; Johanna Pedersen for necropsy and data entry assistance in the US; Fabrice le Bouard, Jaimie Cleeland, and Kate Lawrence for collecting data on Gough Island; the Royal Society for the Protection of Birds for facilitating fieldwork on Gough Island; and the Tristan da Cunha Government for permitting our study. Funding was provided by the UK Natural Environmental Research Council (grant NE/M017990/1, awarded to EDW). ARR acknowledges support from the National Oceanic and Atmospheric Administration's Dr. Nancy Foster Scholarship program, the Robert and Patricia Switzer Foundation, the STEEP Superfund Research Program (NIEHS Award Number P42ES027706), and the Oak Ridge Institute for Science and Education (ORISE) program. During the 2009 work on Gough and Inaccessible islands, RAR was supported by a scholarship from the Natural Sciences and Engineering Research Council of Canada (NSERC) and the Killam Trusts via Dalhousie University. Funding for work at Massachusetts Bay was provided by the Volgenau Foundation and the Stellwagen Bank National Marine Sanctuary.

AUTHOR CONTRIBUTIONS

Conceptualization: EDW, ARR, KDP, DNW. Formal Analysis: EDW, ARR. Funding acquisition: EDW, ARR, RAR, PGR, DNW. Investigation: EDW, ARR, KDP, RAR, DNW. Methodology: EDW, ARR, KDP. Project administration: DNW. Resources: DNW. Software: EDW, ARR. Supervision: DNW. Writing – original draft: EDW, ARR. Writing - review and editing: all coauthors.

ETHICS STATEMENT

Data collection at Gough Island in 2017/18 was undertaken with the approval of the University of Glasgow's School of Veterinary Medicine Ethics Committee (ref. 39a/16) and under permit from the Tristan da Cunha Government. Permits to capture, handle, and tag birds in the Gulf of Maine were obtained from the US Department of the Interior (permit #21963). Permits to capture, handle, and tag birds off the coast of Massachusetts were obtained from the Massachusetts Division of Fisheries and Wildlife (permit #202-17SCB). This work is not a product of the United States Government or the United States Environmental Protection Agency (US EPA), and ARR did not do this work in any governmental capacity. The views expressed are those of the authors only and do not necessarily represent those of the United States or the US EPA.

REFERENCES

Allard, K. A., Mallory, M. L., Wilcox, K. L., & Forbes, M. R. (2008). Prebasic molt initiation and progress in Northern Fulmars of the High Arctic: Do molt and breeding overlap? *Polar Biology, 31*(2), 181–188. https://doi.org/10.1007/s00300-007-0345-4

Alonso, H., Matias, R., Granadeiro, J. P., & Catry, P. (2009). Moult strategies of Cory's Shearwaters *Calonectris diomedea borealis*: The influence of colony location, sex and individual breeding status. *Journal of Ornithology, 150*(2), 329–337. https://doi.org/10.1007/s10336-008-0354-2

Barbraud, C., Booth, A., Taylor, G. A., & Waugh, S. M. (2014). Survivorship in Flesh-footed Shearwater *Puffinus carneipes* at two sites in northern New Zealand. *Marine Ornithology, 42*(2), 91–97. http://doi.org/10.5038/2074-1235.42.2.1074

Bourgeois, K., & Dromzée, S. (2014). Moulting strategies of the Yelkouan Shearwater *Puffinus yelkouan* during the breeding season. *Journal of Ornithology, 155*(1), 265–271. https://doi.org/10.1007/s10336-013-1011-y

Bradley, J. S., Gunn, B. M., Skira, I. J., Meathrel, C. E., & Wooller, R. D. (1999). Age-dependent prospecting and recruitment to a breeding colony of Short-tailed Shearwaters *Puffinus tenuirostris*. *Ibis, 141*(2), 277–285. https://doi.org/10.1111/j.1474-919X.1999.tb07550.x

Brooke, M. (2004). *Albatrosses and Petrels Across the World*. Oxford University Press.

Brooke, M. de L. (1988). Sexual dimorphism in the voice of the Greater Shearwater. T*he Wilson Bulletin, 100*(2), 319–323. http://www.jstor.org/stable/4162578

Broughton, J. M. (1994). Size of the bursa of Fabricius in relation to gonad size and age in Laysan and Black-Footed albatrosses. *The Condor, 96*(1), 203–207. https://doi.org/10.2307/1369079

Bugoni, L., Naves, L. C., & Furness, R. W. (2015). Moult of three Tristan da Cunha seabird species sampled at sea. *Antarctic Science, 27*(3), 240–251. https://doi.org/10.1017/s0954102014000583

Campioni, L., Dias, M. P., Granadeiro, J. P., & Catry, P. (2020). An ontogenetic perspective on migratory strategy of a long-lived pelagic seabird: Timings and destinations change progressively during maturation. *Journal of Animal Ecology, 89*(1), 29–43. https://doi.org/10.1111/1365-2656.13044

Carlos, C. J., & Voisin, J.-F. (2008). Identifying giant petrels, *Macronectes giganteus* and *M. halli*, in the field and in the hand. *Seabird, 21*, 1–15. https://www.seabirdgroup.org.uk/seabird-21

Carvalho, P. C., Ronconi, R. A., Bugoni, L., & Davoren, G. K. (2022). Moult chronology and strategies of sympatric Great (Ardenna gravis) and Sooty (A. grisea) Shearwaters based on stable isotope analysis. *Ibis, 164*(4), 998–1012. https://doi.org/10.1111/ibi.13060

Croxall, J. P., Butchart, S. H. M., Lascelles, B., Stattersfield, A. J., Sullivan, B. J., Symes, A., & Taylor, P. (2012). Seabird conservation status, threats and priority actions: A global assessment. *Bird Conservation International, 22*(1), 1–34. https://doi.org/10.1017/S0959270912000020

Cuthbert, R. J. (2005). Breeding biology, chick growth and provisioning of Great Shearwaters (*Puffinus gravis*) at Gough Island, South Atlantic Ocean. *Emu - Austral Ornithology, 105*(4), 305–310. https://doi.org/10.1071/MU05036

Finger, E., & Burkhardt, D. (1994). Biological aspects of bird colouration and avian colour vision including ultraviolet range. *Vision Research, 34*(11), 1509–1514. https://doi.org/10.1016/0042-6989(94)90152-X

Fletcher, D., Moller, H., Clucas, R., Bragg, C., Scott, D., Scofield, P., Hunter, C. M., Win, I., Newman, J., McKechnie, S., De Cruz, J., & Lyver, P. (2013). Age at first return to the breeding colony and juvenile survival of Sooty Shearwaters. *The Condor, 115*(3), 465–476. https://doi.org/10.1525/cond.2013.110151

Flood, B., Fisher, A., & Gale, J. (2020). *Multimedia identification guide to North Atlantic seabirds: Shearwaters: Jouanin's & White-Chinned Petrels.* Scilly Pelagics.

Galván, I. (2008). The importance of white on black: Unmelanized plumage proportion predicts display complexity in birds. *Behavioral Ecology and Sociobiology, 63*(2), 303–311. https://doi.org/10.1007/s00265-008-0662-9

Galván, I., & Sanz, J. J. (2008). The cheek plumage patch is an amplifier of dominance in Great Tits. *Biology Letters, 4*(1), 12–15. https://doi.org/10.1098/rsbl.2007.0504

Galván, I., & Solano, F. (2016). Bird integumentary melanins: Biosynthesis, forms, function and evolution. *International Journal of Molecular Sciences, 17*(4), Article 520. https://doi.org/10.3390/ijms17040520

Ginn, H. B., & Melville, D. S. (1983). *Moult in birds*. British Trust for Ornithology.

Greene, E., Lyon, B. E., Muehter, V. R., Ratcliffe, L., Oliver, S. J., & Boag, P. T. (2000). Disruptive sexual selection for plumage coloration in a passerine bird. *Nature, 407*(6807), 1000–1003. https://doi.org/10.1038/35039500

Harrison, P., Perrow, M., & Larsson, H. (2021). *Seabirds: The new identification guide*. Lynx Edicions.

Hill, G. E. (1991). Plumage coloration is a sexually selected indicator of male quality. *Nature, 350*(6316), 337–339. https://doi.org/10.1038/350337a0

Hong, P., Wiley, D. N., Powers, K. D., Michener, R. H., Kaufman, L., & Hatch, K. A. (2019). Stable isotope analyses of multiple tissues of Great Shearwaters (*Ardenna gravis*) reveals long-term dietary stability, short-term changes in diet, and can be used as a tool to monitor food webs. *Diversity, 11*(9), Article 163. https://doi.org/10.3390/d11090163

Howell, S. N. G. (2012). *Petrels, albatrosses, and storm-petrels of North America: A photographic guide.* Princeton University Press.

Howell, S. N. G., & Zufelt, K. (2019). *Oceanic birds of the world: A photo guide*. Princeton University Press.

Kolo, B. A. (2010). *Binary and multiclass classification*. Weatherford Press.

Machovsky Capuska, G. E., Huynen, L., Lambert, D., & Raubenheimer, D. (2011). UVS is rare in seabirds. *Vision Research, 51*(12), 1333–1337. https://doi.org/10.1016/j.visres.2011.04.008

Mason, N. A., & Bowie, R. C. K. (2020). Plumage patterns: Ecological functions, evolutionary origins, and advances in quantification. *Auk, 137*(4), Article ukaa060. https://doi.org/10.1093/auk/ukaa060

Meunier, J., Figueiredo Pinto, S., Burri, R., & Roulin, A. (2011). Eumelanin-based coloration and fitness parameters in birds: A meta-analysis. *Behavioral Ecology and Sociobiology, 65*(4), 559–567. https://doi.org/10.1007/s00265-010-1092-z

Onley, D., & Scofield, P. (2007). *Albatrosses, petrels and shearwaters of the world*. Christopher Helm Publishers Ltd.

Penteriani, V., & Delgado, M. del M. (2017). Living in the dark does not mean a blind life: Bird and mammal visual communication in dim light. *Philosophical Transactions of the Royal Society B, 372*(1717), Article 20160064. https://doi.org/10.1098/rstb.2016.0064

Perrins, C. M., Harris, M. P., & Britton, C. K. (1973). Survival of Manx Shearwaters *Puffinus puffinus. Ibis, 115*(4), 535–548. https://doi.org/10.1111/j.1474-919X.1973.tb01991.x

Powers, K. D., Wiley, D. N., Robuck, A. R., Olson, Z. H., Welch, L. J., Thompson, M. A., & Kaufman, L. (2020). Spatiotemporal characterization of non-breeding Great Shearwaters *Ardenna gravis* within their wintering range. *Marine Ornithology, 48*(2), 215–229. http://doi.org/10.5038/2074-1235.48.2.1376

Powers, K. D., Pratte, I., Ronconi, R. A., Wong, S. N. P., Ryan, P. G., Welch, L. J., Silva, T. L., Hatch, K. A., Westgate, A. J., & Wiley, D. N. (2022). Age-related interactions with wind during migration support the hypothesis of developmental learning in a migrating long-lived seabird. *Frontiers in Marine Science, 9*, Article 938033. https://doi.org/10.3389/fmars.2022.938033

Powers, K. D., Wiley, D. N., Allyn, A. J., Welch, L. J., & Ronconi, R. A. (2017). Movements and foraging habitats of Great Shearwaters *Puffinus gravis* in the Gulf of Maine. *Marine Ecology Progress Series, 574*, 211–226. http://www.int-res.com/abstracts/meps/v574/p211-226/

Pyle, P. (2008). *Identification guide to North American birds, Part 2: Anatidae to Alcidae*. Slate Creek Press.

R Core Team. (2024). *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Riotte-Lambert, L., & Weimerskirch, H. (2013). Do naive juvenile seabirds forage differently from adults? *Proceedings of the Royal Society B, 280*(1768), Article 20131434. https://doi.org/10.1098/rspb.2013.1434

Rodríguez, A., Arcos, J. M., Bretagnolle, V., Dias, M. P., Holmes, N. D., Louzao, M., Provencher, J., Raine, A. F., Ramírez, F., Rodríguez, B., Ronconi, R. A., Taylor, R. S., Bonnaud, E., Borrelle, S. B., Cortés, V., Descamps, S., Friesen, V. L., Genovart, M., Hedd, A.,…Chiaradia, A. (2019). Future directions in conservation research on petrels and shearwaters. *Frontiers in Marine Science, 6*, Article 94. https://doi.org/10.3389/fmars.2019.00094

Ronconi, R. A., Schoombie, S., Westgate, A. J., Wong, S. N. P., Koopman, H. N., & Ryan, P. G. (2018). Effects of age, sex, colony and breeding phase on marine space use by Great Shearwaters *Ardenna gravis* in the South Atlantic. *Marine Biology, 165*(3), 58, Article 58. https://doi.org/10.1007/s00227-018-3299-x

Schoombie, S., Dilley, B. J., Davies, D., & Ryan, P. G. (2018). The foraging range of Great Shearwaters (*Ardenna gravis*) breeding on Gough Island. *Polar Biology, 41*(12), 2451–2458. https://doi.org/10.1007/s00300-018-2381-7

Soravia, C., Aguado-Giménez, F., & Avilés, J. M. (2020). The reliability of achromatic displays is island-dependent in nocturnal storm petrels. *Ibis, 162*(3), 655–672. https://doi.org/10.1111/ibi.12772

Tickell, W. L. N. (2003). White plumage. *Waterbirds, 26*(1), 1–12. https://doi.org/10.1675/1524-4695(2003)026[0001:wp]2.0.co;2

van Franeker, J. A. (2004). *Save the North Sea Fulmar-Litter-EcoQO manual - Part 1: Collection and dissection procedures.* Alterra. https://edepot.wur.nl/40451

Vanderwerf, E. A., Smith, D. G., Vanderlip, C., Marie, A., Saunter, M., Parrish, J., & Worcester, N. (2015). Status and demographic rates of the Christmas Shearwater *Puffinus nativitatis* on Kure Atoll. *Marine Ornithology, 43*(2), 199–205. http://doi.org/10.5038/2074-1235.43.2.1131

Voous, K. H., & Wattel, J. (1963). Distribution and migration of the Greater Shearwater. *Ardea, 51*, 143–157.

Wakefield, E. D., Miller, D. L., Bond, S. L., le Bouard, F., Carvalho, P. C., Catry, P., Dilley, B. J., Fifield, D. A., Gjerdrum, C., González-Solís, J., Hogan, H., Laptikhovsky, V., Merkel, B., Miller, J. A. O., Miller, P. I., Pinder, S. J., Pipa, T., Ryan, P. M., Thompson, L. A.,…Matthiopoulos, J. (2021). The summer distribution, habitat associations and abundance of seabirds in the sub-polar frontal zone of the Northwest Atlantic. *Progress in Oceanography, 198*(November), Article 102657. https://doi.org/10.1016/j.pocean.2021.102657

Warham, J. (1990). *The petrels: Their ecology and breeding systems*. Academic Press.

Weimerskirch, H. (1991). Sex-specific differences in molt strategy in relation to breeding in the Wandering Albatross. *The Condor, 93*(3), 731–737. https://doi.org/10.2307/1368205