Exploring determinants of breeding success in the Greenland Barnacle Goose *Branta leucopsis*

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Abstract

In many bird species across a variety of taxa, larger individuals with greater body stores are more likely to breed successfully. The migratory Barnacle Goose *Branta leucopsis* breeds in arctic regions including Greenland, Svalbard, Russia, and the North and Baltic Seas. Larger body size and metabolic body stores (weight relative to body size) have been linked to increased fitness through larger clutch size, social dominance, better overall health and more efficient feeding for the Svalbard and Baltic subpopulations, but this has not yet been shown for the Greenland subpopulation. In Greenland, the geese breed in remote areas inaccessible for study, but observations made on the wintering grounds in northwest Scotland and Ireland can provide important insight into factors affecting trends in abundance. To determine the influence of larger body stores or physical size on breeding success in the Greenland Barnacle Goose subpopulation, a dataset with 60 years of morphometric measurements and field observations at one of the principal wintering grounds in Ireland was analysed. Both males and females with larger body stores were more likely to breed successfully, and this relationship was significant. Males with larger body size were also more likely to breed successfully, although this relationship was not significant. Similar relationships were not seen with pairing success, suggesting that body stores and size may have more direct influence on the ability to raise offspring than on securing a mate. While all of the Barnacle Goose subpopulations showed a dramatic increase in the past 60 years, they are susceptible to pressures on both breeding and wintering grounds (*e.g.* human–wildlife conflicts and avian influenza), necessitating an understanding of the factors that contribute to their population dynamics.

Key words: arctic migrants, body size, body stores, fitness, population dynamics.

The Barnacle Goose *Branta leucopsis* is an arctic migratory species with subpopulations breeding in Greenland, Svalbard and Russia. Over the past 60 years, all three subpopulations have shown a significant growth in numbers (Phillips *et al.* 2003; van der Jeugd *et al.* 2009; Jensen *et al.* 2018; Doyle *et al.* 2018; Mitchell & Hall, 2020). As this increase has continued, Barnacle Geese have begun to breed in the Baltic and North Seas, and birds from the Greenland subpopulation have also started to breed in Iceland (van der Jeugd *et al.* 2003; Jensen *et al.* 2018; Mitchell & Hall 2020).

Despite only a relatively small proportion of Barnacle Goose individuals successfully breeding each year, with paired geese often foregoing nesting in some years, the Greenland subpopulation has increased rapidly (Cabot & West 1983; Choudhury *et al.* 1996; Mitchell & Hall 2020). Within the subpopulation, the first-winter birds generally constitute < 14% of flocks (Owen and Black, 1989; Mitchell & Hall 2020). From 1963–2022, the Greenland Barnacle Goose subpopulation had an average of *c.* 6.6% first-winter birds as monitored on the Inishkea Islands, Co. Mayo, Ireland (Doyle *et al.* 2020a; Fig. 1). As this growth is driven by a small number of successful breeders, understanding the factors that contribute to breeding success, and how they may influence productivity at an

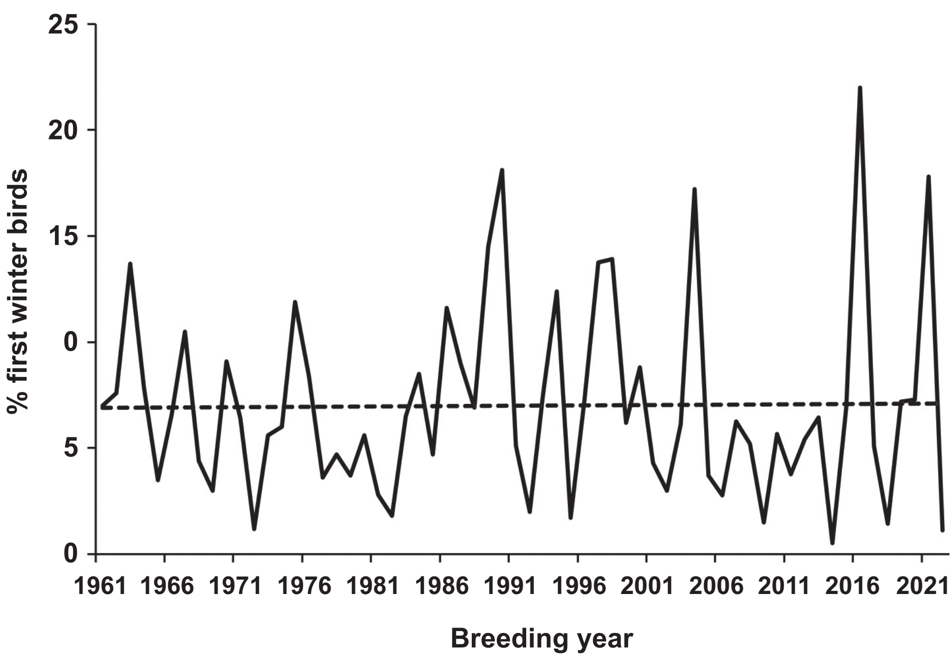

Figure 1. Percentage of first-winter birds within the Greenland Barnacle Goose population wintering on the Inishkea Islands, Co. Mayo, Ireland from 1961–2022. The percentage of first-winter birds has shown a stable trend (trendline shown by dashed line).

individual level, is essential to understanding current population dynamics.

It has been shown across a variety of taxa that individual fitness may be influenced by variations in internal factors such as body condition or size. Metabolic body stores (weight relative to body size), hereafter referred to as "body stores", can also influence fitness, as body stores constitute stored energy or other nutrients (Johnson *et al.* 1985; Milenkaya *et al.* 2015). For example, in the Crimson Finch *Neochmia phaeton*, the birds with larger body weight relative to size (and hence greater body stores) produced more young, and thus had increased fitness, compared with birds with less weight relative to body size (Milenkaya *et al.* 2015). In long-distance migrants such as Brent Geese *Branta bernicla*, the departure weight of adult birds correlated with breeding success, suggesting those birds with higher body stores were able to produce more offspring (Dokter *et al.* 2018). In the Svalbard Barnacle Goose *Branta leucopsis* subpopulation, larger structural body size (skull and tarsus length) has been linked to increased fitness through elevated breeding success (Choudhury *et al.* 1996). Heavier females produce larger clutch sizes and spend less time away from incubation for feeding (Tombre *et al.* 2012). Larger individuals with greater size and weight are more socially dominant, occupying better feeding patches (Stahl *et al.* 2001). Another advantage of larger body size is that large-sized individuals have a disproportionately bigger bite size than smaller individuals, allowing the larger geese to feed more efficiently (Cope *et al.* 2005). A generally larger body size and greater body stores have been suggested as indicative of a healthier bird with fewer parasites, higher immunity, better digestion and overall better internal vitality (Choudhury *et al.* 1996; Dokter *et al.* 2018). Barnacle Geese breeding in the Baltic Sea similarly showed a link between size and fitness, with larger males more likely to win in contests with conspecifics, allowing them to secure better territory to hatch young (van der Jeugd 2001). Larger-sized females were more successful in breeding as they produced larger clutches of larger eggs which hatched earlier in the season and produced more fledged young (Larsson *et al.* 1998). Migratory geese can carry body stores from their wintering grounds to their breeding grounds, enabling an earlier start to breeding with reduced dependence on food availability at the breeding site (Drent *et al.* 2007; Hahn *et al.* 2011). In the Svalbard Barnacle Goose subpopulation, females use an average of 41–54% of resources acquired on their southern grounds for egg formation (Hahn *et al.* 2011).

The Greenland subpopulation of Barnacle Geese breeds in northeast Greenland and winters in northwestern Ireland and Scotland (Cabot 1973; Mitchell & Hall 2013; Doyle *et al.* 2018). The geese wintering in Ireland represented *c.* 23% of the flyway subpopulation of Greenland Barnacle Geese in 2018 (Doyle *et al.* 2018). Unlike the Svalbard and Baltic subpopulations, no study to our knowledge has examined the link between body stores or size and breeding fitness in the Greenland subpopulation. Thus, the aims of this study are to determine, through statistical analysis of a long-term database of morphological measurements and field observations, if body stores or size similarly influence breeding fitness for the Greenland Barnacle Goose subpopulation. Given that the Barnacle Geese wintering in Ireland migrate to Greenland to breed, and that accessing their breeding grounds for study is challenging (Mitchell & Hall 2013), characterising individual fitness parameters on the wintering grounds provides important insights into the reproductive capacity of this arctic migrant.

Methods

Over the years 1969–2018, Barnacle Geese were captured on their wintering grounds on the Inishkea Islands, Co. Mayo, Ireland (54.117°N, 10.208°W) using cannon and mist netting (Figs. 2 & 3; Cabot 1973; Doyle *et al.* 2021a, 2023). Each bird was aged based on its plumage (juvenile up to one year or adult; juveniles were excluded from the remainder of the study), and sex was determined by cloacal examination (male or female). Two morphological measurements associated with breeding success were taken from each captured bird: weight (measured with scales to the nearest 10 g); and tarsus length (measured in mm using calipers). All measurements were taken by the same researcher (DC), thus ensuring consistency of measurement methods. These data were used to create an index of (i) body stores and (ii) body size. Body stores, represented by body weight relative to size, were calculated as weight divided by tarsus

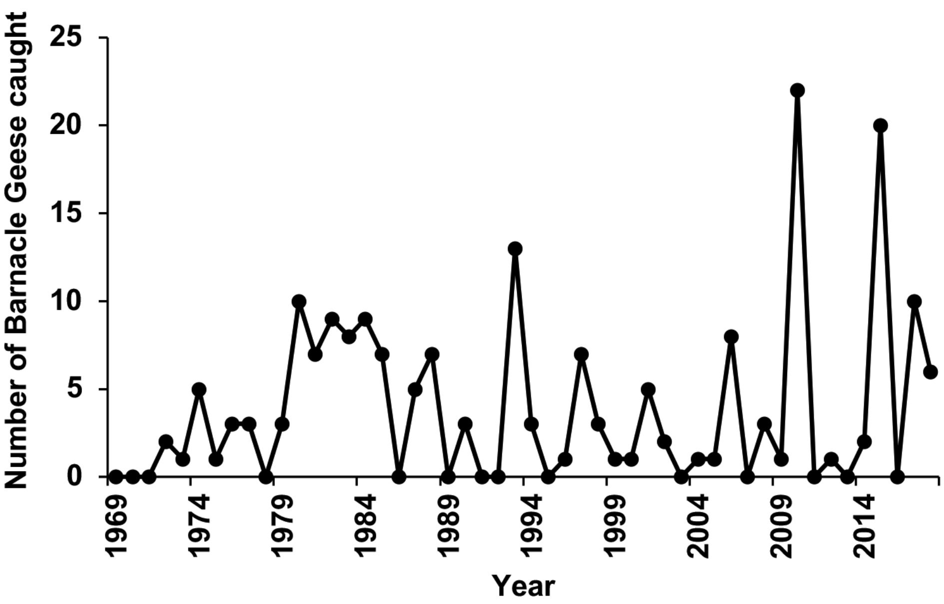

Figure 2. Number of Barnacle Geese captured on their wintering grounds on the Inishkea Islands, Co. Mayo, Ireland per year, 1969–2018. The catches included making morphometric measurements of the birds' weight and tarsus length, with subsequent observations determining their pairing or breeding success upon return to the wintering grounds post-breeding season.

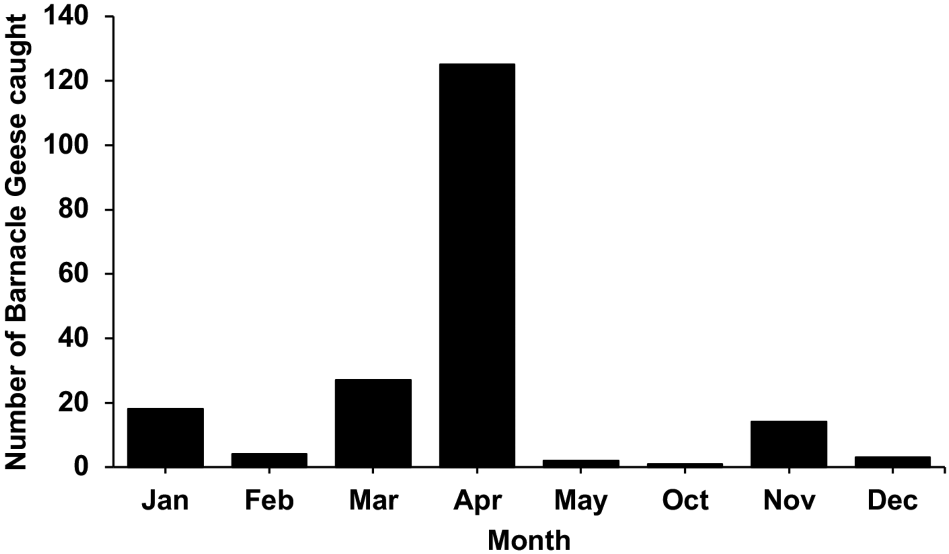

Figure 3. Total number of Barnacle Geese captured per month on the wintering grounds on the Inishkea Islands, Co. Mayo, Ireland, 1969–2018. The majority of the catches (125 out of 194; 64%) occurred in April, when the geese were preparing to return to their Greenland breeding site. No catches occurred during the months of June–September.

length. This provides a more informative measure than weight alone as it also accounts for the size of the individual goose (Johnson *et al.* 1985). Body size was represented by tarsus length. Tarsus length does not change after one year of age, providing an informative measure of lifetime structural size (Larsson & Forslund 1991). Individual three-digit alpha-numeric leg rings were applied prior to release to identify individual birds in the field. All birds were released near the area where they were captured.

Subsequently, the Barnacle Geese migrated to their breeding grounds in Greenland for the summer season, before returning to their wintering grounds in Ireland. There, the individuals marked with leg rings were observed by telescope over the course of the following winter season (October–April inclusive) to record whether they were paired with a mate or had produced offspring the preceding summer. As these geese demonstrate fidelity to their wintering grounds, a high number of follow-up observations of the individually marked geese were recorded, and it was possible to record the presence or absence of a mate or offspring, as family groups tend to associate throughout the young birds' first winter. If the individual was seen once with a mate, it was considered to be paired. Similarly, if the individual was seen once with a family group including first-winter birds, it was considered to have bred. An individual had to be seen at least three times without a mate to be considered unpaired, or at least three times without a family group to be considered non-breeding. Birds that were not seen, or which were seen < 3 times without a mate or offspring, were excluded from the analysis.

The associations between body stores or size and pairing or breeding success were assessed using the R statistical language and environment 4.2.2 (R Core Team 2022). A total of four separate models were used to examine each combination of variables. The proportion deviance explained by the model was calculated using adjusted R^2 in R package MuMIn (Guisan & Zimmermann 2000; Bartoń 2009).

The relationship between breeding success (breeding or non-breeding) and body stores was analysed using a Bayesian generalized mixed-effect linear model with a binomial distribution and logit link function in R package blme (Chung *et al.* 2013; Bolker *et al.* 2009; Dobson & Barnett 2018). The random effects terms consisted of breeding year (because breeding success can be strongly influenced by external effects such as weather in a given year, *e.g.* Doyle *et al.* 2020a) and month of measurement (because body weight fluctuates during the winter season; Owen 1981). A Bayesian prior with a Wishart distribution was applied over the covariance matrix of the random effects to estimate among-month and among-year group variance because of the small sample size compared to the number of groups in our data. The fixed effect terms consisted of the interaction between body stores and sex, to account for possible variation in effects between males and females.

All combinations of fixed effect terms were modelled and the best supported model (consisting of the term body stores only) was selected as the model with the lowest AICc (R package MuMIn: Bartoń 2009; Burnham & Anderson 2004), which is corrected for small sample size to account for potential bias from a data/parameter ratio lower than 40.

The relationship between breeding success and body size was analysed using a generalized linear mixed-effect model with a binomial distribution and logit link function (R package lme4: Bates *et al.* 2015; Bolker *et al.* 2009; Dobson & Barnett 2018). The random effects terms consisted of breeding year only, as tarsus length does not vary between months. The fixed effect terms consisted of the interaction between scaled body size and sex. All combinations of fixed effects terms were modelled and the best supported model was again selected as the model with the lowest AICc (R package MuMIn: Bartoń 2009; Burnham & Anderson 2004).

The relationship between pairing success and body stores was analysed using a Bayesian generalized linear mixed-effect model with a binomial distribution, logit link function and Wishart Bayesian prior. The random effects term consisted of month of measurement only, as pairing success is less likely to be influenced by population-level external factors given that the geese form lifetime monogamous pair bonds (Black 2001). The fixed effect terms consisted of the interaction between body stores and sex. All combinations of fixed effects terms were modelled and the best supported model, selected as the model with the lowest AICc, was the null model.

The relationship between pairing success and body size was analysed using a generalized linear model with a binomial distribution and logit link function. The covariate terms consisted of the interaction between scaled body size and sex. All combinations of covariates were modelled and the best supported model, selected as the model with the lowest AICc, was the null model.

Results

A total of 193 adult Barnacle Geese was included in the analysis (86 males and 107 females) (Figs. 2 & 3). Only one individual was recaptured and included in the data set twice, a male recorded in 1985 and again in 1994 as paired but without offspring in both years, providing 194 records in total (Table 1). The mean weight was 1,980 g (s.d. ± 218 g, range = 1,300–2,460 g) and the mean tarsus measurement was 70 mm (± 5 mm, 59–89). Using weight divided by tarsus, body stores were calculated with a mean of 28.3 g/mm (± 3.2 g/mm, 17.6–35.5). A summary of morphometric measurements is provided in Table 1.

Of the 194 records, 182 were recorded as geese as being paired with a mate, with 12 being unpaired. Additionally, 21 were recorded as breeding successfully the following year, whereas 173 appeared to have been unsuccessful. These Barnacle Geese therefore had an observed pairing success rate of 93.8% and breeding success rate of 10.8%.

The best supported model of the relationship between breeding success and body stores included the random effects of capture month and breeding year (Table 2). The model outputs show a significant positive relationship between breeding success and body stores, after accounting for variation in breeding success between different years and variation in body stores between different months (Table 2, Table 3A). The probability of breeding success increases as body stores increases (odds ratio = 1.21, 95% CI = 1.01–1.46, $P = 0.04$; Table 3A); therefore, Barnacle Geese with greater body stores were more likely to be successful breeders. The model explained 33% of variation in breeding success; 8% of which was attributed to body stores (Table 3A).

The best supported model of the relationship between breeding success and body size included the interaction term between body size and sex and the random effect of breeding year (Table 2). The effect of body size on breeding success was modulated by sex ($P = 0.01$; Table 2, Table 3B). The probability of breeding success increases as body size decreases in females (odds ratio = 0.14, 95% CI = 0.03–0.60), whereas the probability of breeding success increases as body size increases in males (increase of 8.46 in the odds ratio for males, thus the odds of breeding success increase to 1.20, 95% CI = 0.60–2.42 for a unit increase in body size). While male Barnacle Geese with larger body size tended to be more likely to be successful breeders, this relationship is not significant as the confidence intervals include the null value. The influence of both body stores and body size on pairing success was best represented by the null model, suggesting that these factors do not have a significant relationship with pairing success (Table 2). No relationships were observed between body stores or body size and success in procuring a mate.

Table 1. Summary of morphometric measurements taken from adult Barnacle Geese captured on their wintering grounds on the Inishkea Islands, Co. Mayo, Ireland from 1969–2018. Values show means ± s.d. with ranges in parentheses. Body stores index was calculated as weight (g) divided by tarsus length (mm).

TOTAL	**Count**	**Weight (g)**	**Tarsus length (mm)**	**Body stores index (g/mm)**
Successful breeders	21	2,050 ± 225 (1,650–2,400)	69 ± 6 (60–77)	29.7 ± 2.9 (24.7–35.5)
Unsuccessful breeders	173	1,970 ± 217 (1,300–2,460)	70 ± 5 (59–89)	28.1 ± 3.2 (17.6–33.6)
All	194	1,980 ± 218 (1,300–2,460)	70 ± 5 (59–89)	28.3 ± 3.2 (17.6–35.5)
MALES	**Count**	**Weight (g)**	**Tarsus length (mm)**	**Body stores index (g/mm)**
Successful breeders	11	2,160 ± 178 (1,900–2,400)	73 ± 4 (62–77)	29.7 ± 3.3 (24.7–35.5)
Unsuccessful breeders	76	2,080 ± 202 (1,300–2,400)	72 ± 4 (59–89)	28.8 ± 3.0 (17.6–33.3)
All	87	2,090 ± 200 (1,300–2,400)	72 ± 4 (59–89)	28.9 ± 3.0 (17.6–35.5)
FEMALES	**Count**	**Weight (g)**	**Tarsus length (mm)**	**Body stores index (g/mm)**
Successful breeders	10	1,920 ± 206 (1,650–2,250)	65 ± 3 (60–70)	29.6 ± 2.7 (26.2–34.6)
Unsuccessful breeders	97	1,890 ± 192 (1,300–2,460)	69 ± 4 (61–85)	27.6 ± 3.4 (18.6–33.6)
All	107	1,900 ± 193 (1,300–2,460)	69 ± 4 (60–85)	27.8 ± 3.3 (18.6–34.6)

Table 2. Intercept, degrees of freedom (d.f.), log likelihood (LogLik), Akaike information criterion (AICc), change in AICc from top performing model (delta AICc), and model weight for pairing success and breeding success of Barnacle Geese captured on their wintering grounds on the Inishkea Islands, Co. Mayo, Ireland from 1969–2018. Best models as selected by lowest AICc are shown in bold typeface.

Response variable	Explanatory variable	Model	Intercept	d.f.	LogLik	AICc	Delta AICc	Model weight
Pairing success	Body stores	stores * sex	2.719	4	–43.144	94.5	2.45	0.166
		stores + sex	2.128	3	–43.691	93.5	1.45	0.272
		1 (null model)	**2.719**	**1**	**–45.016**	**92.1**	**0.00**	**0.563**
	Structural size	tarsus * sex	3.462	4	–43.552	95.3	3.26	0.096
		tarsus + sex	3.285	3	–43.744	93.6	1.56	0.225
		tarsus	2.724	2	–44.947	94.0	1.90	0.189
		1 (null model)	**2.719**	**1**	**–45.016**	**92.1**	**0.00**	**0.490**
Breeding success	Body stores	stores * sex + (1|month) + (1|breeding_year)	–9.476	6	–63.986	140.5	3.61	0.090
		stores + sex + (1|month) + (1|breeding_year)	–7.409	5	–64.215	138.8	1.93	0.209
		stores + (1|month) + (1|breeding_year)	**–7.506**	**5**	**–64.308**	**136.8**	**0.00**	**0.549**
		1 + (1|month) + (1|breeding_year) (null model)	–2.080	3	–66.646	139.4	2.59	0.151
	Structural size	**tarsus * sex + (1|breeding_year)**	**–3.717**	**5**	**–58.397**	**127.1**	**0.00**	**0.978**
		tarsus + sex + (1|breeding_year)	–2.448	4	–63.266	134.8	7.62	0.022
		1 + (1|breeding_year) (null model)	–2.037	2	–65.088	134.2	9.20	0.007

Table 3. The relationship between morphometrics and breeding success in Greenland Barnacle Geese wintering on the Inishkea Islands, Co. Mayo, Ireland. Model outputs of best models for the influence of: A) body stores on breeding success, and B) structural body size on breeding success.

A) Model output of the best supported model on the influence of body stores on breeding success.

	Relationship between body stores and breeding success		
Predictors	**Odds ratios**	**95% CI**	***P***
(Intercept)	0	0.00–0.13	
Body stores	1.21	1.01–1.46	**0.042**
Random Effects			
σ^2		3.29	
$\tau_{00\ \text{breeding\_year}}$		0.43	
$\tau_{00\ \text{month}}$		0.82	
ICC		0.28	
Marginal R^2/Conditional R^2		0.076 / 0.331	

B) Model output of the best supported model for the influence of structural body size on breeding success.

	Relationship between structural body size and breeding success		
Predictors	**Odds ratios**	**95% CI**	***P***
(Intercept)	0.02	0.00–0.13	
Tarsus (scaled)	0.14	0.03–0.60	**0.008**
Sex male	5.95	1.09–32.49	**0.039**
Tarsus (scaled):Sex (male)	8.46	1.65–43.29	**0.010**
Random Effects			
σ^2		3.29	
$\tau_{00\ \text{breeding\_year}}$		0.07	
ICC		0.02	
Marginal R^2/Conditional R^2		0.394 / 0.407	

Discussion

This study showed relationships between body stores and body size and breeding success (although not pairing success) in the Greenland Barnacle Goose based on long-term data gathered annually on a major Irish wintering site. The relationship between larger birds and breeding success has been suggested in many bird species, including the Svalbard and Baltic subpopulations of Barnacle Geese.

The study focused only on short-term breeding success – the presence of offspring in the following breeding year. Further analysis would be required to determine the effects of body size or body stores on lifetime breeding success. However, there are several reasons why geese with greater body stores may be more likely to breed successfully in a given year. Geese with greater stores may arrive earlier to nesting grounds as they have sufficient body stores to migrate with a shorter stopover (Butler *et al.* 1998), allowing them to secure better nesting and foraging resources than their conspecifics. Body stores carried from the wintering grounds can also allow for earlier egg production at the breeding grounds, with less reliance on local resources (Hahn *et al.* 2011). Female geese with larger body stores can spend less time away from the nest foraging, which increases the probability of successful nesting (Prop *et al.* 1984; Tombre *et al.* 2012). Similarly, males with greater body stores can spend less time foraging and devote more time to vigilance and protection behaviour (Choudhury *et al.* 1996).

Structural body size showed a positive relationship with increased probability of breeding success in male geese, although this relationship was not significant, suggesting that body stores may have a greater influence on breeding success than body size. As structural body size is determined at one year of age and influenced by environmental factors, males with larger body size may have experienced favourable conditions during early growth (Larsson & Forslund 1991; Black *et al.* 2014). Larger-sized males are more dominant and display more vigilance behaviour (Stahl *et al.* 2001). On the wintering grounds, dominant geese have access to the leading edge of the flock's feeding area, where vegetation has not yet been picked over (Black *et al.* 2014). In the pre-breeding areas, larger, more dominant males can ensure access to resources for their mates, thereby improving the pair's body stores and breeding success rate (Hübner 2006). Larger males have a competitive advantage when establishing territory, allowing these larger birds to procure breeding areas with the best resources (van der Jeugd 2001). During the nesting period, larger males displaying increased vigilance behaviour allow their mates to take breaks from incubation (Black *et al.* 2014).

No relationship was observed between body stores or size and pairing success. Barnacle Geese pair selectively with partners of similar size (large males with large females, small males with small females), and this compatibility has been shown to increase breeding success (Choudhury *et al.* 1996; Boyd 2000). In the Svalbard subpopulation, body stores were not correlated prior to pairing; as geese in established pairs experienced similar conditions and gained higher rank over single birds, body stores became similar over time (Choudhury *et al.* 1992). However, larger females with greater body stores were chosen as mates at an earlier age, suggesting that they are chosen preferentially (Choudhury *et al.* 1996). Other traits that have been suggested as influences on mate choice include familiarity due to prior association, increased vigilance behaviour and darker facial markings (Black *et al.* 2014). Our study examined ultimate pairing success, rather than the preferences and timing of mate choice in Greenland Barnacle Geese. Approximately 94% of the geese wintering on the Inishkea Islands in Ireland were successful in pairing with a mate, suggesting that geese with a wide range of morphological traits are able to procure a mate.

While the percentage of first-winter birds within the group wintering in Ireland varies from year to year, the long-term trend 1963–2022 has been stable at an average of 6.6% (Fig. 1; Doyle *et al.* 2020a). This aligns with the low frequency of breeding success, 10.8%, seen in our data set.

Our results for the effect of body stores on breeding success included the lower confidence interval approaching the null value of one, suggesting that other factors also play a strong role in individual breeding success. For instance, elsewhere, high plant biomass and therefore food availability has been suggested as contributing to the breeding success of Barnacle Geese in the Russian subpopulation (Rozenfeld *et al.* 2021). Nesting density also plays an important role in success for Barnacle Geese breeding in the Baltic (van der Jeugd 2001). This subpopulation is further affected by such factors as predation, a late breeding period and the environmental characteristics of the area (Kouzov *et al.* 2019). The breeding success of the Svalbard subpopulation is affected by factors such as parental age (Black & Owen 1995), parasites such as fleas (de Jong *et al.* 2019), mate familiarity and pair-bond duration (Choudhury & Black 1994; Black 2001). The Greenland-breeding subpopulation may be similarly affected by some or all these factors.

While the Greenland Barnacle Goose subpopulation increased rapidly from 1969–2013, more recently the numbers wintering in Ireland have decreased slightly (Doyle *et al.* 2018). Wintering ground provisioning is important as nesting usually starts when local food resources at the breeding site are still scarce, thus females must rely on body stores for egg production and incubation (Eichhorn *et al.* 2010). This also highlights the importance of management implications for the areas used as feeding and staging grounds in spring, as maintaining higher body stores and therefore good condition is vital for geese prior to embarking on their long-distance migration routes.

Conclusion

From the data analysed, a positive relationship was seen between winter body stores (weight relative to size) and fitness in Greenland Barnacle Geese. Additionally, structural body size was found to positively influence breeding success in males, although to a lower degree than body stores.

Barnacle Geese wintering on the Inishkea Islands summer in remote inaccessible arctic breeding areas, which make it difficult to collect such long-term data outside of the winter period. For this reason, it is vital to continue to collect winter data on factors potentially influencing the breeding fitness of such arctic migrants, as they are susceptible to pressures on both their breeding and wintering grounds, including anthropogenic effects and conflict (Doyle *et al.* 2020b; Mitchell & Hall 2020), climate change (Doyle *et al.* 2021b), and more recently, outbreaks of avian influenza (Madslien *et al.* 2021; EFSA 2022). The results from such research can be used to inform actions in such applied ornithological issues as species management, protected areas, human–wildlife and interspecies conflict, and transmission of zoonotic disease.

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Photograph: Barnacle Goose, by Susan Doyle.