ORIGINAL ARTICLE

CrossMark

Has winter body condition varied with population size in a long-distance migrant, the Bewick's Swan (*Cygnus columbianus bewickii*)?

Kevin A. Wood [1] · Julia L. Newth [1] · Geoff M. Hilton [1] · Eileen C. Rees [1]

Abstract

Assessments of body condition can provide useful information on changes in the state of individuals within a population, which may in turn help to inform conservation efforts. For example, decreases in body condition over time can indicate reduced food resources. Mass and skull length measures recorded for 195 adult and 467 first winter (cygnets) Bewick's Swans (*Cygnus columbianus bewickii*) at wintering sites in the UK between winters 1966/1967 and 2017/2018 therefore were analysed to determine whether a ca. 40% decline in numbers in the Northwest European Bewick's Swan population between 1995 and 2010 corresponded with poorer body condition from the mid-1990s onwards. Parents and siblings were known for all individuals, allowing us to account for shared genetic factors and rearing environment in our analysis. We used linear mixed-effects models and an information-theoretic approach to test different models of temporal variation in scaled body mass index (SBMI). Within our study population, although SBMI values varied both within and between years, we found no evidence of any directional trends in body condition. Of our competing time models of swan SBMI, a model in which age-specific body condition was constant over time received the greatest support in the data. Body condition was greater for adults than cygnets, but did not vary between sexes or wintering sites. Our findings suggest no connection between the recent declines in population size and body condition. Population decline is therefore unlikely to be caused by inadequate food supplies.

Keywords Animal biometrics · Energy reserves · Food resources · Long-term ecological studies · Species conservation · Waterbirds · Waterfowl demography

Introduction

Globally, around 19% of bird species are migratory, undertaking seasonal movements between breeding and non-breeding areas (Kirby et al. 2008). Such migratory species are valuable sentinels of environmental change over time, as their productivity and survival rates integrate information on the ecological status of multiple habitats across their migratory range (Piersma and Lindström 2004; Stillman et al. 2015). Undertaking long-distance movements as part of migration requires a considerable investment of energy and nutrients (McWilliams et al. 2004; Newton 2006). Migrants must

therefore attempt to regulate their energy reserves to gain and maintain body condition to allow them to complete movements between feeding sites. Hence, body condition in one part of a species' range will reflect, at least in part, conditions experienced during migration from another part of the range (Bearhop et al. 2004). Temporal declines in body condition at a site over successive years can highlight reductions in the ability of individuals to acquire food, for example because food supplies have been lost or disturbance has reduced available feeding time (Mainguy et al. 2002; Brown and Sherry 2006). During years in which available food supplies are reduced, individuals may not be able to gain sufficient body condition to complete migration successfully, which can lead to increased mortality risk and hence reduced population size (Burton et al. 2006; Newton 2006; Morrison et al. 2007). Repeated assessments of body condition at key sites can provide valuable insight into changes in the state of individuals within a population that can help inform species conservation (Armstrong and Perrott 2000; Stevenson and Woods 2006).

✉ Kevin A. Wood
kevin.wood@wwt.org.uk

[1] Wildfowl & Wetlands Trust, Slimbridge, Gloucestershire GL2 7BT, UK

Temporal declines in body condition can indicate the need for conservation actions (e.g. supplementary feeding) to ensure that adequate food resources are available throughout a species' range (Armstrong and Ewen 2001; Newton 2013).

One migratory population of conservation concern is the northwest European population of the Bewick's Swan (*Cygnus columbianus bewickii*). Population size has fluctuated markedly over recent decades; the total counts on the wintering grounds increased from approximately 16,500 in 1984 to 29,000 individuals in 1995, before undergoing a sustained decline to 18,000 individuals in 2010 for reasons that remain unclear (Rees and Beekman 2010). Due to this substantial unexplained decline in winter numbers, an international species action plan (the Bewick's Swan single Species Action Plan, BSSAP) was developed for the population and was adopted by the African–Eurasian Waterbird Agreement (AEWA) in 2012 (Nagy et al. 2012). The population was also classified as endangered on the European Red List of Birds (BirdLife International 2015). A recent study found no evidence that Bewick's Swan breeding success had fallen since the onset of the decline in population size, although a number of years of very low productivity have been observed since 1995 (Wood et al. 2016). An assessment of Bewick's Swan survival rates between 1970 and 2014 found that apparent survival of all age classes had fluctuated over time broadly in line with changes in population size (Wood et al. 2018). Suboptimal feeding conditions at stopover and wintering sites was highlighted as a potential causal factor in the observed population decline that required investigation (Nagy et al. 2012). Any impact of suboptimal feeding conditions is likely to be reflected in reduced body condition. Yet, to date, no study has tested whether the body condition of Bewick's Swans has varied over time with the trends in population size.

In this study, we used a unique 51-year individual-based data set to examine temporal changes in body condition of Bewick's Swans during winter. Our key prediction was that body condition values would be lower in years in which population size was declining. Individual body condition on the wintering grounds will reflect conditions experienced not only at winter feeding sites but also at migratory stopover sites and on the breeding grounds. Individual biometric data have been collected at key sites on the wintering grounds since the 1960s (Evans and Kear 1978; Rees 2006). We used scaled body mass index (SBMI) as our measure of individual body condition, as SBMI represents total energy reserves corrected for structural size (Peig and Green 2009). Cygnets migrate from the breeding grounds to wintering sites with their parents and remain together as a family group throughout their first winter (Scott 1980; Nolet et al. 2014). Such prolonged parental care facilitates the assessment of body condition at wintering sites whilst accounting for parent and brood identity, which are two potential sources of pseudoreplication (sensu Hurlbert 1984) in studies of body condition.

Methods

Study system

Bewick's Swans are large-bodied herbivorous wildfowl easily distinguished through their all-white plumage and characteristic yellow and black bill markings (Rees 2006). The northwest European population breeds on the open maritime tundra of European Arctic Russia between 66–70°N and 44–66°E (Rees 2006). Following the breeding season (May–September), the birds migrate southwest to spend the winter in northwest Europe, predominantly in the UK, the Netherlands and Germany (Rees 2006). Over the course of the winter period, the birds feed primarily on pasture grasses (e.g. ryegrass *Lolium perenne*) and agricultural crops such as sugar beet (*Beta vulgaris*), potatoes (*Solanum tuberosum*), wheat (*Triticum aestivum*) and oilseed rape (*Brassica napus*), with aquatic plants such as pondweeds (*Potamogeton* spp.) also consumed where available, particularly in the eastern parts of the winter range (Rees 1990; Dirksen et al. 1991; Rees 2006; Meier-Peithmann 2011). During the autumn migration, the swans spend several weeks feeding at coastal and agricultural sites across Estonia, which makes this small country a key stopover area for the birds (Luigujõe et al. 1996).

Cygnet capture and biometric measurements

Between the winters of 1966/1967 and 2017/2018, Bewick's Swans were caught for ringing at or near four wintering sites: Slimbridge (southwest England; 51°N, 02°W), Martin Mere/Ribble Estuary (northwest England; 54°N, 03°W), Caerlaverock (southwest Scotland; 55°N, 04°W) and the Ouse Washes (east-central England; 53°N, 00°E). The principal methods of capture were to attract the swans into decoy-type 'swan-pipes' (as described in Evans 1982) and cannon-netting of swans feeding on agricultural fields on the Ouse Washes (Dill and Thornsberry 1950; O'Brien et al. 2016). Sex was determined for each individual by cloacal examination on capture. Plumage characteristics were used to determine age class, as cygnets had a high proportion of grey feathers, whilst adults had all-white plumage (Rees 2006). Body mass was determined in situ (± 0.1 kg) using a spring balance, as described by Evans and Kear (1978). We also measured individual skull length with a sliding calliper (± 1.0 mm).

To estimate body condition as body mass corrected for skeletal size, we calculated the SBMI proposed by Peig and Green (2009) for each individual, a method used recently for Whooper Swans (*Cygnus cygnus*) by Newth et al. (2016). Whilst energy reserves are well known to increase under favourable environmental conditions (e.g. Stillman et al. 2015), previous research has shown that the growth in structural size (e.g. skull length) in herbivorous waterfowl during early life can also reflect the environmental conditions

experienced (e.g. Larsson et al. 1998). Previous research on Bewick's Swans has found that cygnet body mass and skull length continue to increase during their first winter (Evans and Kear 1978). Therefore, whilst we expected swan body condition (as the most labile biometric measurement) to show the strongest responses to changes in foraging conditions, structural size (e.g. skull length) could also have shown more limited responses too, and so we selected a measure of body condition that represented total energy reserves as body mass corrected for structural size (Peig and Green 2009). Ln-transformed skull length was regressed against ln-transformed body mass to obtain and compare the slope estimates of this relationship within and between age classes and sexes, using standardised major axis regression implemented via the smatr package in R (Warton et al. 2012, R Development Core Team 2016). Slope estimates differed significantly between age classes ($\Lambda_1 = 8.526$, $P = 0.004$), but not between sexes ($\Lambda_1 = 0.005$, $P = 0.945$), and thus different mean slope estimates (b_{SMA}) were used for adults (mean = 3.20, 95% CI = 2.82–3.63) and cygnets (mean = 4.00, 95% CI = 3.70–4.33). Finally, the SBMI value (kg) for each individual was calculated as:

$$SBMI = M_i \cdot (L_o/L_i)^{bSMA},$$

where M_i and L_i are the body mass (kg) and skull length (mm) of individuals, respectively, and L_o is the arithmetic mean skull length (adults = 160.8 mm, cygnets = 158.8 mm) for the whole sample. Where the same individual was captured multiple times, we included only the biometric values from the first capture in our analysis.

Each captured individual was assigned (1) a 'parent ID' unique to all individuals hatched by a particular adult pair, and (2) a 'brood ID' unique to all individuals hatched to a particular adult pair in a single year, as the responses of individual quality to environmental change will be influenced by the shared environmental conditions experienced by siblings within the same brood as well as genetic factors (Monaghan 2008), which needed to be accounted for in our models. The parents of each individual were identified on the basis of close proximity and social interactions in its first winter, recorded during the detailed near-daily observations made of swans wintering in the study areas (Rees 2006). Based on field evidence, brood amalgamation is considered to be rare among swans (Eadie et al. 1988). Indeed, despite the extensive study of Bewick's Swan breeding biology (Rees 2006), we are aware of only one single record of brood amalgamation (Brazil 2002), and therefore we consider it unlikely that brood amalgamation affected our assessments of parent and brood identity. Thus, all the individuals of a pair had the same parent ID, but only those hatched to those parents in a given year shared the same brood ID. Individuals caught for whom one or more of their parents were unknown were not included in any part of our analyses.

As swan biometric values, predominantly body mass and hence body condition, will increase over winter (Evans and Kear 1978), we estimated the number of days after the year-specific date of the arrival of the first Bewick's Swan on the winter grounds that the individual was captured (hereafter termed 'capture date'). The year-specific first arrival date of Bewick's Swans was determined at the key winter site at Slimbridge, based on daily monitoring (Evans 1979; Rees 2006).

Statistical analyses

We used linear mixed-effects models with Gaussian error structures to test 19 candidate models of temporal variation in Bewick's Swan winter body condition. These candidate models allowed us to test the following mutually exclusive temporal patterns in body condition: the null model of no temporal pattern (i.e. constant body condition), a linear temporal trend, a quadratic trend, constant condition within each decade, constant condition within each half-decade (i.e. 5-year periods), different condition depending on whether the population was increasing, stable or decreasing in that year (modelled as a three-level categorical variable, based on count data for the subsequent January) and annual variation in body condition (i.e. body condition is modelled as a categorical main effect to allow a different value in each year). We sequentially tested each of these temporal models with swan age class (1) not included, (2) included as a main effects term only and (3) included as a two-way interaction with the temporal effect term. For the population trends model, estimates of the northwest European Bewick's Swan population for each year between 1966 and 2017 were derived from co-ordinated international censuses of the wintering grounds conducted in 1958, 1972, 1976, 1978, 1983, 1986, 1990, 1995, 2000, 2005, 2010 and 2015 (Rees and Beekman 2010; Wetlands International/IUCN-SSC Swan Specialist Group unpublished data), with linear interpolation used to impute counts in years between these surveys. In all candidate models, we included parent ID and brood ID as random categorical factors, as well as capture date as a random covariate. SBMI values were $\log_{10}$-transformed to ensure that model residuals met the assumptions of our mixed-effects modelling approach (Bolker et al. 2009; Zuur et al. 2010).

Our mixed-effects models were carried out in R version 3.3.0 (R Development Core Team 2016), using the MuMIn and lme4 packages (Barton 2012; Bates et al. 2015). For each candidate model, we calculated the value of second-order Akaike's Information Criteria (AIC_c). The model with the lowest AIC_c value was judged to be our best-supported model, whilst any model with an AIC_c value of within 2.0 of the lowest AIC_c was also judged to have received substantial support in the data (Burnham and Anderson 2004). To facilitate more detailed comparisons among our candidate models, we also calculated the Akaike weight (hereafter 'w_i', defined as

the ratio of ΔAIC_c values for each model relative to the whole set of candidate models) and the evidence ratio (termed '*ER*', defined as how many more times less likely to be the best-fitting model compared with the best-supported model shown by AIC_c) associated with each model as indicators of the relative strength of model support in the data (Burnham et al. 2011). To assess the proportion of the variance in swan body condition explained by each model, we calculated two values of R^2 proposed by Nakagawa and Schielzeth (2013) for each model: the marginal R^2 ($R^2_{GLMM(m)}$), which indicates the proportion of variance explained by the fixed factors alone, and the conditional R^2 ($R^2_{GLMM(c)}$), which indicates the proportion of variance explained by both the fixed and random factors.

We ran four additional models to determine whether individual sex or winter capture site influenced any temporal pattern in body condition. These four models were the best-supported time model with sex (S_x; 'male' or 'female') included as a categorical fixed factor ((1) main effects only and (2) two-way interaction with age class), and the best-supported time model with capture site ('Caerlaverock', 'Martin Mere', 'Ouse Washes' and 'Slimbridge') included as a categorical fixed factor ((3) main effects only and (4) two-way interaction with age class). We assessed the AIC_c values associated with these four models to see whether they received greater support in the data than the best-supported time model.

Results

Across all 662 individuals (467 cygnets + 195 adults) measured during our 1966/1967–2017/2018 study period, the mean (± standard deviation) cygnet body mass and skull length values were 5.36 ± 0.79 kg (range = 2.90–7.80) and 158.80 ± 6.01 mm (range = 141.00–175.00), respectively, whilst the mean adult body mass and skull length values were 6.31 ± 0.77 kg (range = 4.60–8.50) and 160.80 ± 6.19 mm (range = 144.00–180.90), respectively. The first winter SBMI values ranged between 3.17 and 9.00 kg, with a mean value of 5.37 ± 0.83 kg, whilst the adult SBMI values ranged between 4.02 and 9.13 kg, with a mean value of 6.33 ± 0.83 kg (Fig. 1).

A comparison of our candidate models of body condition indicated that temporal variation in SBMI was best explained by a model in which body condition was constant over time within each age class (Tables 1 and 2). Adults had higher body condition than cygnets (Table 2; Fig. 1). There was strong support for this best-supported model in the data, as it accounted for 97% of the total w_i of our candidate models (Table 1). As the fixed effect in our best-supported model, age class explained 20% of the variance in Bewick's Swan SBMI, whilst the full model including random effects terms accounted for 63% of the variance in swan SBMI values (Table 1). Of the three random effects terms included in our best-supported model, the date of capture accounted for the
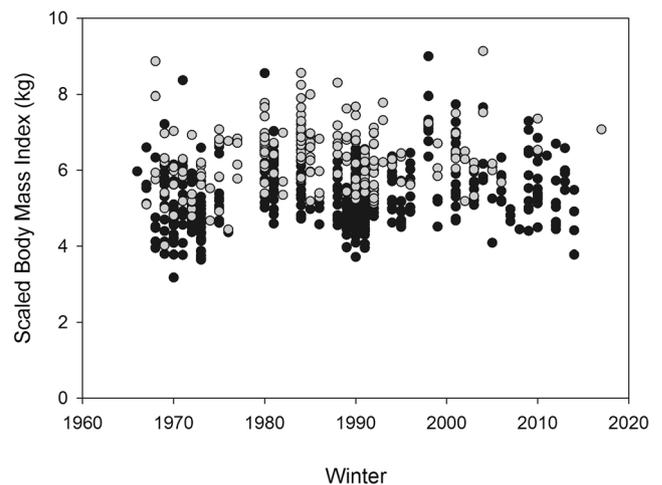

Fig. 1 Individual scaled body mass index (SBMI) values for Bewick's Swan adults (grey circles) and cygnets (black circles) captured on the winter grounds in the UK between winters 1966/1967 and 2017/2018

greatest variance in SBMI values, whilst parent identity accounted for more than brood identity; however, the variance associated with each of these three random effects was lower than the residual variance (Table 2).

No other candidate model had an associated ΔAIC_c value within 2.0 of our best-supported model. The next best-supported model was one in which adult and cygnet SBMI values were allowed to vary between years of increasing, stable or decreasing population size. However, this population trend model had an associated ΔAIC_c value of 7.1, w_i of 0.03 and an *ER* of 34.2 (Table 1); therefore, this model was considered to have limited support in the data. All ten of the candidate models that received more support in the data than the null model included the age class effect (Table 1).

The best-supported time model was not improved by the addition of either sex or capture site as explanatory variables, as neither the addition of sex or site as main effects or as interactions with age class resulted in models that were ≤ 2.0 of the ΔAIC_c value of the best-supported model. The addition of individual sex to the best-supported model resulted in ΔAIC_c values of 6.4 and 13.1 for the main effect and two-way interaction with age class, respectively. Similarly, the addition of individual capture site to the best-supported model resulted in ΔAIC_c values of 19.7 and 37.7 for the main effect and two-way interaction with age class, respectively. Furthermore, the mean (± SD) SBMI values were similar between males and females, and also between the four capture sites, for each age class (Table 3).

Discussion

In this study, we used a unique dataset that spanned over half a century to show that there were no consistent temporal patterns in the body condition of Bewick's Swan adults or

Table 1   A comparison of the support and explanatory power of the ten best-supported (plus null model) candidate models of $\log_{10}$-transformed swan SBMI values

Time model	k	AIC_c	ΔAIC_c	Akaike weight (w_i)	Evidence ratio (ER)	$R^2_{GLMM(m)}$	$R^2_{GLMM(c)}$
$\boldsymbol{log_{10}\,SBMI = i + A + RE}$	**2**	**−1906.9**	**0.0**	**0.97**	**1.0**	**0.20**	**0.63**
$log_{10}\,SBMI = i + A + P + RE$	5	−1899.8	7.1	0.03	34.2	0.24	0.63
$log_{10}\,SBMI = i + A + L + RE$	3	−1895.3	11.6	0.00	331.8	0.22	0.62
$log_{10}\,SBMI = i + A + D + RE$	8	−1894.0	12.9	0.00	649.7	0.28	0.65
$log_{10}\,SBMI = i + A \cdot P + RE$	8	−1885.3	21.6	0.00	$4.8 \cdot 10^4$	0.25	0.63
$log_{10}\,SBMI = i + A \cdot L + RE$	4	−1880.0	26.9	0.00	$6.9 \cdot 10^5$	0.22	0.62
$log_{10}\,SBMI = i + A + Q + RE$	4	−1873.7	33.2	0.00	$1.6 \cdot 10^7$	0.22	0.62
$log_{10}\,SBMI = i + A + H + RE$	12	−1873.0	33.9	0.00	$2.3 \cdot 10^7$	0.32	0.67
$log_{10}\,SBMI = i + A \cdot D + RE$	14	−1858.1	48.8	0.00	$4.0 \cdot 10^{10}$	0.29	0.65
$log_{10}\,SBMI = i + A \cdot H + RE$	24	−1810.4	96.5	0.00	$9.2 \cdot 10^{20}$	0.33	0.67
$log_{10}\,SBMI = i + RE$	1	−1803.4	103.5	0.00	$3.0 \cdot 10^{22}$	0.00	0.64

The best-supported model is indicated in bold. k refers to the number of fitted fixed-effect parameters in each candidate model. $R^2_{GLMM(m)}$ indicates the proportion of variance explained by the fixed effects alone, while $R^2_{GLMM(c)}$ indicates the proportion of variance explained by both the fixed and random effects (Nakagawa and Schielzeth 2013). Parameters: i = intercept, A = age class (0 = cygnet, 1 = adult), P = population size trend ('increasing', 'decreasing', 'stable'), L = year as a linear predictor, Q = year as a quadratic predictor, D = decade, H = half-decade, RE = random effects terms (parent ID, brood ID, capture date)

cygnets. Whilst SBMI values showed some variation both within and between years, the temporal variation showed neither a consistent trend over time or localised periods of decline or elevation. Whilst many studies have examined trends in avian body condition (Brown 1996), our analysis accounted for shared genetic factors and rearing environment between individuals born to the same parents and raised in the same brood, which few studies have been able to do previously. The long-term, detailed studies of swans visiting key winter sites within the UK (e.g. Scott 1966; Evans 1979; Rees and Bowler 1996) allowed such relationships to be identified and accounted for in our analysis.

Repeated assessments of body condition can provide valuable information on the energetic state of individuals within a population (Armstrong and Ewen 2001; Hoare et al. 2006). In contrast to our prediction, we found no evidence that swan body condition was lower during periods of population decline compared with periods of population stability or growth. Our measure of body condition reflects the conditions experienced by each individual not only at winter feeding sites but also at migratory stopover sites and on the breeding grounds. The relative stability of body condition over time suggests that

there has been no apparent decline in the ability of swans to find and exploit food supplies between the breeding and wintering areas. However, the link between changes in food resources, individual body condition and population size could be examined in greater detail in future studies. Further research could also extend our examination of Bewick's Swan body condition to include additional sites across the flyway, including at migratory stopover and breeding sites. Such a flyway-scale approach would allow a more comprehensive understanding of the regulation of body condition throughout the annual cycle. If it proved impractical to capture birds at key sites in order to measure their biometrics, indirect methods for the estimation of body condition based on abdominal profiles could be used (e.g. Bowler 1994). Furthermore, field investigations could be complemented with mechanistic models of foraging animals, such as individual-based models, which allow the effects of past and future changes in food biomass, extent and nutritional quality on individual foraging behaviour and physiological state (including energy reserves) to be assessed (Wood et al. 2015).

The site within the UK at which the swans were captured had no influence on body condition, with similar SBMI values

Table 2   A summary of the parameter estimates associated with our best-supported model of $\log_{10}$-transformed SBMI values

Effects	Variable	Mean estimate	SE	Variance	SD
Fixed effects	Intercept	0.7199	0.0057	–	–
	Age class	0.0717	0.0060		
Random effects	Brood ID	–	–	0.0004	0.0207
	Parent ID	–	–	0.0007	0.0258
	Capture date	–	–	0.0012	0.0340
	Residual	–	–	0.0019	0.0442

Table 3 A summary of the age-specific mean (± SD) SBMI values (kg) for both sexes and all four capture sites (the number of individuals measured (n) is also given for each group)

Age class	Grouping	Mean	SD	n
Adult	Sex: male	6.3	0.9	101
	Sex: female	6.4	0.8	94
	Site: Caerlaverock	6.4	–	1
	Site: Martin Mere	6.1	0.9	14
	Site: Ouse Washes	6.5	0.7	22
	Site: Slimbridge	6.3	0.8	158
Cygnet	Sex: male	5.2	0.8	201
	Sex: female	5.5	0.9	266
	Site: Caerlaverock	6.2	0.6	14
	Site: Martin Mere	5.4	0.7	66
	Site: Ouse Washes	5.4	0.8	35
	Site: Slimbridge	5.3	0.9	352

found across all four sites, despite some differences in the food resources available at each site. Swans feed predominantly on pasture grasses at Slimbridge and Caerlaverock, and on early-growth cereals and unharvested remains of root crops in agricultural fields around Martin Mere and the Ouse Washes (Rees 2006). Although a small quantity of grain has been distributed throughout each winter to encourage the swans and other waterbirds to frequent areas in front of the hides at all four catch sites, it should be noted that the swans feed almost exclusively on agricultural land in the surrounding area during the day, returning to the reserves mainly to roost (Rees 2006). The main purpose of this supplementary food was to provide a viewing opportunity for the public, not to provide part of the swan's diet (Rees and Bowler 1996). Furthermore, Bewick's Swans' use of supplementary grain declined between the mid-1980s and mid-1990s, ceasing thereafter, at the Ouse Washes site, and the Bewick's Swans largely stopped wintering at Martin Mere and Caerlaverock in the mid- to late-1990s due to a combination of short-stopping with the warmer winters and competition with larger Whooper Swans (*Cygnus cygnus*) at these sites (Black and Rees 1984; Rees 2006; Worden et al. 2006); yet, despite the differing temporal patterns of visitation and provisioning at each site, we found no evidence that site was important in determining body condition. Furthermore, we controlled for winter site use by including capture date in all models, which accounted for variation between individuals in the time spent at wintering sites before biometric measurements were taken.

All swan species show some degree of sexual dimorphism, with males typically larger in body mass and structural size (e.g. biometrics such as bill length) compared with females (e.g. Evans and Kear 1978; Limpert et al. 1987; Albertsen et al. 2002; Ciach et al. 2018). However, in our study we found no evidence that male and female swans differed in body condition, a measure which corrects body mass for the structural size of the individual. Reduced early winter body condition over time in just one sex could have indicated a sex-dependent issue in foraging performance within the flyway, for example if one sex was more prone to disturbance. Similarly, we found the same lack of temporal trend in body condition for both adults and cygnets, despite the smaller energy reserves and lower foraging efficiency of cygnets relative to adults (Nolet et al. 2014; this study). The parity in body condition between sexes suggests that all swans probably experienced similar foraging conditions across the flyway, or that any differences were sufficiently minor that they could be compensated for prior to the early winter period. Indeed, neither migratory route nor diet are thought to vary between male and female Bewick's Swans (Rees 2006). Similarly, Wood et al. (2018) found little difference in the annual survival rates of male and female Bewick's Swans from 1970 to 2014.

Across all individuals, SBMI varied from 3.2 to 9.0 kg in cygnets and from 4.0 to 9.1 kg in adults, which demonstrated considerable variation between individuals within any given year. Our best-supported model accounted for 63% of the variation between individuals, which was associated with age class, shared parents, shared brood identity and the number of days since the year-specific arrival date that the individual was captured. Information on social status, which was difficult to obtain given the capture methods used, could have accounted for some of the unexplained variance in body condition; in common with most other waterbird species (Rees 2006; Wood et al. 2017), male Bewick's Swans undertake the primary role in the defence of feeding areas, and so paired adult Bewick's Swan males with young exhibit progressively poorer body condition compared with paired females during winter (Bowler 1994). Future work which measured natal habitat quality could examine the relative importance of the effects of shared rearing environment and shared genetic factors between siblings on body condition. Furthermore, future research on individuals' migratory routes and phenology, together with the conditions encountered at each site, for example through telemetry, could allow a more detailed examination of the causes of variation in body condition between individuals. In particular, measurements of food resources could prove insightful because waterfowl body condition is known to reflect the food supplies available at feeding sites (Norambuena and Bozinovic 2009). For example, Owen and Cook (1977) reported a positive relationship between the body condition of Northern Mallard (*Anas platyrhynchos*) and the amount of food available on their feeding grounds. As previous studies have found considerable heterogeneity among individuals in Bewick's Swan migration routes and use of stopover sites (e.g. Nowak et al. 1990; Rees and Bacon 1996; Nuijten et al. 2014; Griffin et al. 2016), differences in SBMI might therefore reflect differences in foraging conditions encountered at migratory stopover sites.

Conclusions

Since the 1960s, the northwest European population of Bewick's Swans has shown marked variations in the numbers recorded on the wintering grounds (Rees and Beekman 2010). The observed decline in population size of almost 40% between 1995 and 2010 has represented a particular concern for conservationists. However, our results suggested that winter body condition is unlikely to have played a role in influencing changes in population size. Crucially, we found no evidence that adult or cygnet body condition varied between years in which population size was increasing, stable or decreasing. Our findings suggest that the Bewick's Swan population decline is therefore unlikely to have been caused by inadequate food supplies on the breeding grounds or at sites used during autumn and early winter. The lack of information on feeding conditions at such sites was highlighted in the Bewick's Swan Single Species Action Plan (Nagy et al. 2012). Therefore, we argue that our findings will be useful to swan conservation, by helping to shift the focus of researchers and practitioners away from factors unlikely to have contributed to the population decline.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Albertsen JO, Abe Y, Kashikawa S, Ookawara A, Tamada K (2002) Age and sex differences in biometrics data recorded for whooper swans wintering in Japan. Waterbirds 25:334–339

Armstrong DP, Ewen JG (2001) Testing for food limitation in reintroduced Hihi populations: contrasting results for two islands. Pac Conserv Biol 7:87–92

Armstrong DP, Perrott JK (2000) An experiment testing whether condition and survival are limited by food supply in a reintroduced Hihi population. Conserv Biol 14:1171–1181

Barton K (2012) MuMIn: model selection and model averaging based on information criteria. R package version 1.13.4

Bates D, Mächler M, Bolker BM, Walker SC (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48

Bearhop S, Hilton GM, Votier SC, Waldron S (2004) Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. Proc R Soc B 271(Suppl 4):S215–S218

BirdLife International (2015) European red list of birds. Office for Official Publications of the European Communities, Luxembourg

Black JM, Rees EC (1984) The structure and behaviour of the whooper swan population wintering at Caerlaverock, Dumfries and Galloway, Scotland: an introductory study. Wildfowl 35:21–36

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24:127–135

Bowler JM (1994) The condition of Bewick's swans Cygnus columbianus bewickii in winter as assessed by their abdominal profiles. Ardea 82:241–241

Brazil M (2002) Brood amalgamation in Bewick's swan Cygnus columbianus bewickii: a record from Japan. J Yamashina Inst Ornithol 33:204–209

Brown ME (1996) Assessing body condition in birds. In: Nolan V Jr, Ketterson ED (eds) Current ornithology. Springer, New York, pp 67–135

Brown DR, Sherry TW (2006) Food supply controls the body condition of a migrant bird wintering in the tropics. Oecologia 149:22–32

Burnham KP, Anderson DR (2004) Multimodel inference: understanding AIC and BIC in model selection. Sociol Methods Res 33:261–304

Burnham KP, Anderson DR, Huyvaert KP (2011) AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behav Ecol Sociobiol 65:23–35

Burton NH, Rehfisch MM, Clark NA, Dodd SG (2006) Impacts of sudden winter habitat loss on the body condition and survival of redshank Tringa totanus. J Appl Ecol 43:464–473

Ciach M, Czyż S, Wieloch M (2018) Bill colour pattern in Bewick's swan: information on sex and body size displayed on face? Ethol Ecol Evol 30:39–50

Dill HH, Thornsberry WH (1950) A cannon-projected net trap for capturing waterfowl. J Wildl Manag 14:132–137

Dirksen S, Beekman JH, Slagboom TH (1991) Bewick's swans Cygnus columbianus bewickii in the Netherlands: numbers, distribution and food choice during the wintering season. Wildfowl (Supplement No. 1):228–237

Eadie JM, Kehoe FP, Nudds TD (1988) Pre-hatch and post-hatch brood amalgamation in north American Anatidae: a review of hypotheses. Can J Zool 66:1709–1721

Evans ME (1979) Aspects of the life cycle of the Bewick's swan, based on recognition of individuals at a wintering site. Bird Study 26:149–162

Evans ME (1982) Movements of Bewick's swans, Cygnus columbianus bewickii marked at Slimbridge, England from 1960 to 1979. Ardea 70:59–75

Evans ME, Kear J (1978) Weights and measurements of Bewick's swans during winter. Wildfowl 29:118–122

Griffin LR, Rees EC, Hughes B (2016) Satellite-tracking of Bewick's swan migration in relation to offshore and onshore wind farm sites: final report to the Department of Energy and Climate Change. Wildfowl & Wetlands Trust, Slimbridge

Hoare JM, Pledger S, Keall SN, Nelson NJ, Mitchell NJ, Daugherty CH (2006) Conservation implications of a long-term decline in body condition of the Brothers Island tuatara (Sphenodon guntheri). Anim Conserv 9:456–462

Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. Ecol Monogr 54:187–211

Kirby JS, Stattersfield AJ, Butchart SH, Evans MI, Grimmett RF, Jones VR, O'Sullivan J, Tucker GM, Newton I (2008) Key conservation issues for migratory land- and waterbird species on the world's major flyways. Bird Conserv Int 18:S49–S73

Larsson K, Van der Jeugd HP, Van der Veen IT, Forslund P (1998) Body size declines despite positive directional selection on heritable size traits in a barnacle goose population. Evolution 52:1169–1184

Limpert RJ, Allan HA Jr, Sladen WJ (1987) Weights and measurements of wintering tundra swans. Wildfowl 38:108–113

Luigujõe L, Kuresoo A, Keskpaik J, Ader A, Leito A (1996) Migration and staging of the Bewick's swan (Cygnus columbianus) in Estonia. Gibier Faune Sauvage 13:451–461

Mainguy J, Bêty J, Gauthier G, Giroux JF (2002) Are body condition and reproductive effort of laying greater snow geese affected by the spring hunt? Condor 104:156–161

McWilliams SR, Guglielmo C, Pierce B, Klaassen M (2004) Flying, fasting, and feeding in birds during migration: a nutritional and physiological ecology perspective. J Avian Biol 35:377–393

Meier-Peithmann W (2011) Dokumentation des nahrungsokologischen Wandels bei Sing-, Zwerg- und Hockerschwan Cygnus cygnus, C. bewickii, C. olor von 1965 bis 2010 in den Dannenberger Elbbogen. Vogelwelt 132:57–79 [In German with English summary]

Monaghan P (2008) Early growth conditions, phenotypic development and environmental change. Philos Trans R Soc B 363:1635–1645

Morrison RIG, Davidson NC, Wilson JR (2007) Survival of the fattest: body stores on migration and survival in red knots Calidris canutus islandica. J Avian Biol 38:479–487

Nagy S, Petkov N, Rees EC, Solokha A, Hilton G, Beekman J, Nolet B (2012) International Single Species Action Plan for the Northwest European Population of Bewick's Swan (Cygnus columbianus bewickii). AEWA Technical Series No 44, Bonn

Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods Ecol Evol 4:133–142

Newth JL, Rees EC, Cromie RL, McDonald RA, Bearhop S, Pain DJ, Norton GJ, Deacon C, Hilton GM (2016) Widespread exposure to lead affects the body condition of free-living whooper swans Cygnus cygnus wintering in Britain. Environ Pollut 209:60–67

Newton I (2006) Can conditions experienced during migration limit the population levels of birds? J Ornithol 147:146–166

Newton I (2013) Bird populations. Harper Collins, London

Nolet BA, Gyimesi A, Lith B (2014) Lower foraging efficiency of offspring constrains use of optimal habitat in birds with extended parental care. Ibis 156:387–394

Norambuena MC, Bozinovic F (2009) Health and nutritional status of a perturbed black-necked swan (Cygnus melanocoryphus) population: diet quality. J Zoo Wildl Med 40:607–616

Nowak E, Berthold P, Querner U (1990) Satellite tracking of migrating Bewick's swans. Naturwissenschaften 77:549–550

Nuijten RJ, Kölzsch A, van Gils JA, Hoye BJ, Oosterbeek K, de Vries PP, Klaassen M, Nolet BA (2014) The exception to the rule: retreating ice front makes Bewick's swans Cygnus columbianus bewickii migrate slower in spring than in autumn. J Avian Biol 45:113–122

O'Brien MF, Lee R, Cromie R, Brown MJ (2016) Assessment of the rates of injury and mortality in waterfowl captured with five methods of capture and techniques for minimizing risks. J Wildl Dis 52:S86–S95

Owen M, Cook WA (1977) Variations in body weight, wing length and condition of mallard Anas platyrhynchos platyrhynchos and their relationship to environmental changes. J Zool 183:377–395

Peig J, Green AJ (2009) New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. Oikos 118:1863–1891

Piersma T, Lindström Å (2004) Migratory shorebirds as integrative sentinels of global environmental change. Ibis 146:s61–s69

R Development Core Team (2016) R: a language and environment for statistical computing [3.3.0]. R Foundation for Statistical Computing, Vienna http://www.R-project.org/

Rees EC (1990) Bewick's swans: their feeding ecology and coexistence with other grazing Anatidae. J Appl Ecol 27:939–951

Rees EC (2006) Bewick's swan. T&AD Poyser, London

Rees EC, Bacon PJ (1996) Migratory tradition in Bewick's swans (Cygnus columbianus bewickii). Gibier Faune Sauvage 13:407–420

Rees EC, Beekman JH (2010) Northwest European Bewick's swans: a population in decline. Br Birds 103:640–650

Rees EC, Bowler J (1996) Fifty years of swan research and conservation by the Wildfowl & Wetlands Trust. Wildfowl 47:248–263

Scott P (1966) The Bewick's swans at Slimbridge. Wildfowl 17:20–26

Scott DK (1980) Functional aspects of prolonged parental care in Bewick's swans. Anim Behav 28:938–952

Stevenson RD, Woods WA (2006) Condition indices for conservation: new uses for evolving tools. Integr Comp Biol 46:1169–1190

Stillman RA, Wood KA, Gilkerson W, Elkinton E, Black JM, Ward DH, Petrie M (2015) Predicting effects of environmental change on a migratory herbivore. Ecosphere 7:114

Warton DI, Duursma RA, Falster DS, Taskinen S (2012) Smatr 3—an R package for estimation and inference about allometric lines. Methods Ecol Evol 3:257–259 Accessible at https://CRAN.R-project.org/package=smatr

Wood KA, Stillman RA, Goss-Custard JD (2015) Co-creation of individual-based models by practitioners and modellers to inform environmental decision-making. J Appl Ecol 52:810–815

Wood KA, Newth JL, Hilton GM, Nolet BA, Rees EC (2016) Interannual variability and long-term trends in breeding success in a declining population of migratory swans. J Avian Biol 47:597–609

Wood KA, Ponting J, D'Costa N, Newth JL, Rose PE, Glazov P, Rees EC (2017) Understanding intrinsic and extrinsic drivers of aggressive behaviour in waterbird assemblages: a meta-analysis. Anim Behav 126:209–216

Wood KA, Nuijten RJM, Newth JL, Haitjema T, Vangeluwe D, Ioannidis P, Harrison AL, MacKenzie C, Hilton GM, Nolet BA, Rees EC (2018) Apparent survival of an Arctic-breeding migratory bird over 44 years of fluctuating population size. Ibis 160:413–430

Worden J, Cranswick PA, Crowe O, McElwaine G, Rees EC (2006) Numbers and distribution of Bewick's swan Cygnus columbianus bewickii wintering in Britain and Ireland: results of international censuses, January 1995, 2000 and 2005. Wildfowl 56:3–22

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1:3–14