USING BODY SIZE TO ESTIMATE GOSLING AGE

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Abstract.—Growth rates of young geese are among the fastest of any bird with precocial young. Gosling growth also varies significantly in response to even small variations in the quantity and quality of food. As such, it is important to be able to assess gosling age precisely to separate age-dependent growth from other factors. In some studies, where goslings are individually marked at hatching, gosling age can be assigned precisely (age = encounter date − marking date). However, this process is time-consuming and expensive, and the encounter rate of marked goslings can be low. In such cases, some researchers have made use of one or more body size measures as a surrogate for true age. We examined the utility of using body size to estimate gosling age, using a large data set for which true age is known. We show that some characters, most notably feather length, are highly correlated with true age, but using these characters to predict gosling age may introduce significant biases into typical analyses, which may reduce statistical power to an unacceptable degree.

UTILIZACIÓN DEL TAMAÑO CORPORAL PARA ESTIMAR LA EDAD DE GANSOS JUVENILES

Sinopsis.—La tasa de crecimiento de gansos juveniles es una de las más altas entre las aves precoces. El crecimiento de éstas aves varía significativamente en respuesta, inclusive, a pequeñas variaciones en la cantidad y calidad del alimento. Como tal, es importante poder determinar con precisión la edad de éstos para separar, unos de otros, los factores de los cuales depende el crecimiento. En algunos estudios, en donde los gansos juveniles son marcadas al nacer, la edad de estos puede ser determinada con precisión (edad = la fecha en que se encuentra − la fecha en que fue marcado). Sin embargo, este proceso consume mucho tiempo y dinero, y la tasa de recaptura de las aves marcadas puede ser bien baja. En estos casos, algunos investigadores han hecho uso de una o más medidas del tamaño corporal para tratar de determinar la edad de las aves. Examinamos la utilidad de medidas corporales para estimar la edad de estas aves, utilizando un conjunto ámplio de datos para los cuales se sabía la verdadera edad. Mostramos que algunos caracteres, principalmente la longitud de plumas, se correlacionan con la verdadera edad. Pero la utilización de estos parámetros para predecir la edad de los gansos juveniles puede introducir un sesgo significativo dentro de una análisis típico. Esto podría reducir estadísticamente el poder de la prueba a un grado inaceptable.

The ability to age young birds accurately is important to many studies, but it is often difficult and time consuming to obtain a large sample of known-aged young birds. In such cases, predictive models for age may be the only recourse. Generally, these approaches involve deriving a predic-

tive equation for age based on the available sample of young where age is known. Most often these equations relate one or more body size characters to age.

For studies of birds with nidicolous young, where it may be possible to measure the birds at regular intervals through the period of early growth, a variety of mathematical models have been used to characterize growth. Most of these models (e.g., logistic, Gompertz, von Bertalanffy) are non-linear functions, which accommodate the fact that growth is not linear over all ages (although it may be effectively linear over a certain age range) (Starck and Ricklefs 1998 and references therein). For species with precocial, nidifigous young, logistical constraints may prohibit more than two measurements being made on a given individual in the wild. The total sample generally consists of several birds all measured at hatching (age = 0 days), and another group of birds (not always those measured at hatch) of a range of ages measured at fledging. In such cases, it is difficult to fit a non-linear growth function in any meaningful way, since in general the best fit between what is in effect a pair of points is a straight line.

In this paper we consider the problem of estimating the age of young of a species with precocial young, the Lesser Snow Goose (*Anser c. caerulescens*), using data from a long-term study of a population breeding at La Pérouse Bay, Manitoba, Canada. As an adaptation to the short arctic breeding season, goslings of arctic-breeding geese (including the Lesser Snow Goose) exhibit rapid growth for species with precocial young (Sedinger 1986, Whitehead et al. 1990, Starck and Ricklefs 1998, and references therein). As a result, growth and development of many species of geese is sensitive to variation in the quality and quantity of food (Cooch et al. 1991a,b; Sedinger and Flint 1991; Larsson and Forslund 1991; Loonen et al. 1997). Slower growing goslings become smaller adults (Cooch et al. 1991b, Larsson and Forslund 1991, Sedinger et al. 1995, Loonen et al. 1997), and there is evidence for some species that smaller adult body size may significantly reduce lifetime fitness (Sedinger et al. 1995, but see Cooke et al. 1995). Because of the potential significance of even small differences in early growth in geese, the ability to age precisely goslings measured at fledging is important. Many researchers investigating variation in gosling growth in one or more goose species have increasingly relied on using size at fledging as a predictor of true gosling age. In some cases, gosling age is predicted using equations derived from a smaller sample where age is known (e.g., Lindholm et al. 1994), while in other studies, where no sample of known-age goslings are available, the size of one or more characters is substituted for age in all analyses (e.g., Aubin et al. 1993). We examine the utility of body size (using both univariate and multivariate measures of size) to predict gosling age, and discuss the factors contributing to variation in bias and precision using such approaches. We show that reliance upon predictors of gosling age leads to systematically biased estimates of gosling age, which in practice increases the chances of Type II error in some typical analyses.

METHODS

Data on the breeding biology of the snow goose have been collected annually from the colony at La Pérouse Bay (LPB; 58°4'N, 94°4'W) from 1968 to the present. General field methods are described elsewhere (Cooke et al. 1995). Those particular procedures relevant to this study are described briefly here.

The colony, presently numbering 45,000–50,000 breeding pairs is in the southern portion of the species' breeding range. Each year, approximately 2000 nests are monitored at hatching, and each hatchling is weighed and marked with an individually numbered web-tag. Approximately 5 wk after hatching, before the goslings are fully fledged, the adults molt their primary flight feathers and are temporarily flightless. While the adults are flightless, approximately 1500 families (4000–5500 adults and goslings) were rounded up, aged, sexed, and banded. A proportion of the goslings caught in these banding drives had web-tags. All web-tagged goslings in the banding drives and a sample of the adults were weighed and measured. Web-tagged goslings could be aged precisely (age = days since hatching). Since 1976, approximately 7000 web-tagged goslings have been captured and measured at banding.

Data set restrictions.—Because there is sexual dimorphism in the pattern of growth in this species (Cooch et al. 1996, Cooch et al. 1997), we restricted most of our analyses to female goslings only. Because of long-term deterioration in habitat conditions at La Pérouse Bay (Cooke et al. 1995), there has been a significant long-term decline in gosling survival from hatching to banding (Williams et al. 1993) and a systematic decline in the number of web-tagged goslings encountered during banding. We restricted our analyses to years when at least 25 web-tagged female goslings were encountered. We also restricted our data to years in which all standard size measurements were made (see below). In the early years of the study, only gosling mass and a measure of bill length were recorded.

Body size measurements.—We examined the relationship between gosling size and age using eight different individual characters (following Dzubin and Cooch 1992: *culmen 1*—the chord of the upper mandible length, measured medially from the point where the integument meets the horny portion of the mandible to the distal tip of the bill nail; *culmen 2*—the diagonal length of the upper mandible from the bill nail to the proximal tip of the posterior lateral extension of the upper mandible; *head length*—the length of the skull from the external occipital ridge to the distal tip of the bill nail; *total tarsus*—the diagonal distance from the posterior junction of the tibiotarsus and tarsometatarsus to the distal junction of the tarsometatarsus at the base of the middle toe; *tarsus bone*—the diagonal length of the tarsometatarsus bone only; *mid-toe*—the length of the middle phalanx along its dorsal surface from the proximal articular surface at the tarsometatarsal juncture to the distal end of the toe at the base of the claw; *ninth primary*—the total length of the feather from the insertion of the remige calamus to the distal end of the feather; *mid-tail*—

the length of one of the two center rectrices from the point of insertion
to the tip of the feather, and 2 multivariate indices of size (PC^H–derived
from culmen 1 & 2, head length, total tarsus and tarsus bone—the 'hard'
characters, and PC^A––derived from all eight individual characters). All
linear measurements were in mm.

Analysis methods.—SAS (SAS 1989) was used for all analyses. Simple
Pearson correlations were used to assess the strength of the relationship
between gosling age and body size separately for each year. Spearman
rank correlations and concordance analysis were used to assess covariation
in the ranked-order of annual measures of association between age and
size and other factors.

To measure precision and bias in predicted age, we performed a series
of cross-validation analyses using approximately equal partitions of the
available data in a given year; half of the data was used to derive the
predictive equation, which was then used to derive predicted ages using
the remaining half of the data set. For multivariate measures, PC scores
were calculated for the test sample by multiplying the transposed eigen-
vector from the principal component analyses by each bird's vector of
normalized z-scores. We repeated the cross-validation analysis 100 times,
on each occasion using a different random partition of the data. The
mean error (i.e., true age − predicted age) is reported.

Gosling size is significantly influenced by hatch date in snow geese and
related species; late-hatching goslings of a given age are significantly
smaller than goslings of the same age but hatching earlier in the season
(Cooch et al. 1991a, Sedinger and Flint 1991, Larsson and Forslund 1991,
Sedinger et al. 1997). Because most older goslings encountered and mea-
sured during banding are early hatching goslings, and (conversely) since
most younger goslings encountered at banding are late-hatching goslings,
there is a systematic bias in size of goslings encountered during banding
(Sedinger and Flint 1991). Unless hatch date is controlled for explicitly,
the estimated age of younger (late-hatching) goslings will be biased low,
whereas the estimated age of older (early-hatching) goslings will be biased
high. Therefore, we also examined for systematic bias in predicted ages
as a function of hatch date, using a sample of the data for which hatch
date was known precisely.

<div align="center">RESULTS</div>

At La Pérouse Bay, data were available for 1261 known-aged female
goslings, from 1981–1989. For nearly all years and all characters, there
was a highly significant positive correlation between gosling size and gos-
ling age (Table 1). In 8 of 9 years, the length of the ninth primary showed
the highest correlation with gosling age. Mid-tail length and PC^A showed
the second and third highest correlations, respectively (Table 1).

For all univariate measures and both multivariate indices, there was
significant heterogeneity among years in the slope of the size-age regres-
sion. However, despite significant annual variation in mean gosling age
over years ($F_{8,1229} = 180.4$, $P < 0.001$), there was significant concordance

TABLE 1. Annual variation in correlation between univariate and multivariate measures of size and true age (in days) of goslings measured at La Pérouse Bay. Utility (measured as the intra-year rank-order of the absolute magnitude of the correlation) is shown in parentheses. Ranks are formed in descending order (i.e., strongest correlation has the lowest ranking), and average utility (rank) is calculated as the integer average of the annual ranks.

| | | | | | | | Measurement[a] | | | | | |
Year	n	Age[b]	C1	C2	HD	TT	TB	TOE	NIN	TAIL	PC[H]	PC[A]
81	345	29.6	0.661 (7)	0.670 (6)	0.780 (4)	0.550 (8)	0.531 (9)	0.455 (10)	0.901 (1)	0.862 (2)	0.693 (5)	0.782 (3)
82	285	37.9	0.373 (7)	0.433 (6)	0.561 (4)	0.206 (10)	0.238 (8)	0.209 (9)	0.872 (1)	0.819 (2)	0.452 (5)	0.610 (3)
83	166	32.6	0.413 (8)	0.529 (6)	0.597 (4)	0.351 (9)	0.484 (7)	0.302 (10)	0.867 (1)	0.793 (2)	0.564 (5)	0.651 (3)
84	102	33.1	0.623 (7)	0.668 (6)	0.776 (5)	0.431 (9)	0.413 (7)	0.373 (10)	0.932 (1)	0.899 (2)	0.670 (4)	0.778 (3)
85	120	32.2	0.646 (7)	0.646 (6)	0.768 (4)	0.543 (10)	0.560 (9)	0.568 (8)	0.875 (2)	0.889 (1)	0.702 (5)	0.791 (3)
86	45	33.8	0.662 (6)	0.655 (7)	0.791 (3)	0.576 (9)	0.395 (10)	0.619 (8)	0.806 (1)	0.791 (2)	0.699 (5)	0.743 (4)
87	101	31.9	0.402 (7)	0.443 (6)	0.544 (4)	0.317 (10)	0.381 (9)	0.382 (8)	0.735 (1)	0.559 (3)	0.486 (5)	0.575 (2)
88	67	37.4	0.501 (7)	0.561 (4)	0.527 (6)	0.420 (9)	0.434 (8)	0.382[c] (10)	0.735 (1)	0.559 (2)	0.486 (5)	0.575 (3)
89	30	35.3	0.812 (6)	0.805 (7)	0.858 (4)	0.663 (8)	0.636 (9)	0.485[c] (10)	0.885 (1)	0.862 (3)	0.828 (5)	0.875 (2)
Pooled[b]	1261	33.2	0.498 (7)	0.561 (4)	0.648 (4)	0.343 (9)	0.283 (8)	0.292 (10)	0.848 (1)	0.648 (2)	– (5)	– (3)

[a] C1 = culmen 1; C2 = culmen 2; HD = head length; TT = total tarsus; TB = tarsus bone; TOE = midtoe; NIN = ninth primary; TAIL = midtail; PC[H] = PC1 of {C1, C2, HD, TT and TB}; PC[A] = PC1 of all characters.
[b] Mean age of goslings in sample (in days).
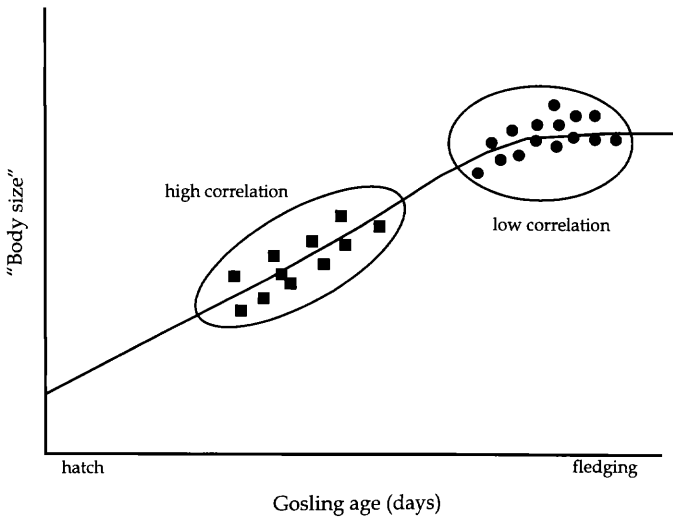[c] Not significant at α = 0.10 level.

FIGURE 1. Hypothetical relationship between gosling age and the correlation between age and size. When goslings are in their linear growth phase, the expected correlation between age and size is greater than when goslings are measured near the growth asymptote.

in the annual ranking among characters over all years (Table 1; Friedman $\chi_r^2 = 85.2$, $P < 0.001$). While the utility (i.e., the strength of the correlation with gosling age) of some characters improved in years where the average age of goslings was younger, the relative utility among characters did not change significantly. Ninth primary length, mid-tail length and the multivariate index PC^A were consistently the best predictors of gosling age. Notably, the ninth primary and mid-tail lengths were both consistently better than PC^A, despite the fact that PC^A was derived from a set of measurement including both these characters.

Despite the consistency in rank-ordering of the size-age correlation among years, the magnitude of the correlation for a given character with age varied considerably among years. Because there are significant differences in age at which growth of individual characters is asymptotic (Sedinger 1986, Leafloor et al. 1998), we expected the annual correlation (and slope) of a given character with gosling age to vary as a function of annual mean gosling age of the sample (Fig. 1). Thus, we compared the magnitude of the annual size-age correlation with the annual mean age of the goslings in the sample for that year. A negative correlation in this analysis indicates that as the mean age of the sample increases (i.e., as the birds approach the growth asymptote for one or more characters), the correlation between size and age decreases (Fig. 1). The correlation between the annual size-age correlations and annual mean gosling age varied from −0.12 for mid-tail length (NS at $\alpha = 0.10$) to −0.82 for tarsus bone ($P < 0.001$) (Table 2). Thus, a significant proportion of the annual

TABLE 2. Correlation between the value of the annual correlation between size and true gosling age in days and the annual mean age (in days) of the goslings in the sample.

Character	Correlation	Rank	Utility[b]
Culmen 1	−0.651	5	7
Culmen 2	−0.670	6	6
Head	−0.586	3	4
Total tarsus	−0.755	9	9
Tarsus bone	−0.812	10	8
Mid-toe	−0.742	8	10
Ninth primary	−0.185[a]	2	1
Mid-tail	−0.118[a]	1	2
PC[H]	−0.717	7	5
PC[A]	−0.640	4	3

PC[H] = PC1 of {culmen 1, culmen 2, head, total tarsus and tarsus bone}; PC[A] = PC1 of all characters.

[a] Not significant at $\alpha = 0.10$.

[b] Rank-order of absolute magnitude of correlation between character and gosling age (Table 1).

variation in the size-age correlations (Table 1) reflected annual differences in the mean age of the goslings measured during banding. In addition, there was a significant positive correlation overall between the rank of the correlation between annual mean gosling age and the annual age-size correlation, and the average utility of a given character over years ($r_s = 0.88$, $P < 0.001$); those characters that were consistently good at predicting gosling age over years (Table 1) were also those characters that were furthest from their respective growth asymptotes. For example, ninth primary and mid-tail length, which had the highest and second-highest size-age correlation over all years respectively, had the lowest correlations between the annual size-age correlation and annual mean gosling age. The opposite was true for the two tarsus measurements (total tarsus and tarsus bone) and mid-toe length, which had the lowest annual size-age correlations. For the tarsus and toe measurements, gosling age was only well-predicted when the mean age of the goslings in the sample was relatively young, and when growth of these characters was still approximately linear.

Precision and bias of predicted age.—We used cross-validation analysis to assess the utility of using the magnitude of certain characters to predict gosling age. We restricted these analyses to ninth primary, which had the highest annual size-age correlation among univariate characters, and PC[A], which was the better of the two multivariate measures.

There was significant variation in the average error (true age − predicted age) among years using either ninth primary length ($F_{8,612} = 3.52$, $P < 0.005$) or PC[A] ($F_{8,519} = 4.12$, $P < 0.001$). In most years, the predicted age was within ±1 day of true age for 60–85% of all individuals (with a greater proportion with 1 day using ninth primary than PC[A], Table 3). The correlation between predicted and true age using ninth primary var-

TABLE 3.   Estimation of the annual variation in the magnitude of error in estimating gosling age using size (ninth primary length (NIN) and PC^A). Values represent the mean proportion of all individuals in the sample for which predicted age deviated from true age by *n* days, calculated over 100 random partitions of the data set (see text).

	Year	n^a	(Predicted age − true age)							r^b
			−3	−2	−1	0	1	2	3	
a. NIN	81	175	1.13	10.65	27.88	25.78	22.97	7.35	4.39	0.901
	82	138	4.78	11.01	20.62	31.54	17.19	10.21	4.68	0.871
	83	86	2.77	12.60	22.82	23.92	24.87	11.63	2.35	0.866
	84	44	2.60	5.38	23.85	40.22	19.18	8.40	2.74	0.931
	85	63	5.04	11.04	23.18	26.90	20.78	8.81	4.67	0.875
	86	22	8.03	12.73	22.28	22.45	20.88	13.73	6.72	0.795
	87	41	3.24	5.63	25.44	36.15	24.16	4.27	3.96	0.733
	88	27	3.46	9.85	21.21	26.33	18.46	9.39	5.95	0.769
	89	17	9.09	17.96	24.11	17.79	19.47	18.23	11.69	0.878
	pooled	613	2.78	10.27	24.44	28.59	21.03	8.97	3.92	0.943
b. PC^A	81	137	9.94	13.18	21.37	19.92	12.31	10.53	12.77	0.777
	82	137	15.41	14.21	14.48	16.37	12.95	10.77	15.80	0.612
	83	100	11.00	18.41	15.81	13.63	14.62	13.46	13.81	0.665
	84	48	10.60	12.75	19.65	18.10	12.16	13.56	13.81	0.771
	85	57	12.56	12.20	18.70	17.13	14.29	10.67	14.59	0.781
	86	22	8.98	17.12	22.53	22.62	17.35	10.80	9.78	0.753
	87	45	3.57	9.75	23.69	27.71	26.25	5.78	5.16	0.580
	88	37	9.43	13.04	18.70	28.18	15.50	9.92	9.67	0.632
	89	14	19.43	15.86	21.74	22.38	20.01	15.97	16.63	0.860
	pooled	597	10.92	13.78	18.51	18.83	14.42	10.69	12.86	0.866

[a] Mean size of cross-validation sample used to test predictive equation (ca. 50% of total sample in each year). Sample size marginally lower for PC^A due to some individuals where not all measurements were made.

[b] Correlation between true and predicted age in test sample. Pooled values estimated from partial correlation analysis controlling for year as a classification variable.

ied from 0.73 to 0.93. The mean correlation, controlling for annual differences, was 0.94. Using PC^A, the correlation varied from 0.61 to 0.86. The mean correlation, controlling for year, was 0.87. Although the correlations for both measures were significant, the correlation for ninth primary was significantly greater than that for PC^A ($Z = 7.76$, $P < 0.001$). The mean annual error ranged from −0.082 to 0.035 days for ninth primary (negative in 6 of 9 years), and 0.072 to 0.029 days for PC^A (negative in 6 of 9 years). Mean error rates pooled over years were −0.026 (SE = 0.005) and −0.044 (SE = 0.012) days for ninth primary and PC^A, respectively. Both values were significantly different from 0 ($P < 0.001$), indicating a significant bias; a negative mean error indicates that on average, for our data, predicted gosling age will be significantly younger than true age.

Sources of bias.—Since hatch date contributes significantly to variation in gosling growth rates, we tested for covariation of hatching date with the error between predicted and true gosling age, for both ninth primary and PC^A. We used the subset of our data for which hatching date was

TABLE 4. Variation in average error (difference between predicted and observed gosling age) with hatching date.

Character	Hatching period[a]	Mean error[b-]	SE	P^c
Ninth primary	early	0.57	0.20	0.011
	middle	0.12	0.07	
	late	−0.34	0.14	
PC^A	early	0.84	0.22	0.003
	middle	0.23	0.10	
	late	−1.17	0.20	

[a] Early hatching nests <(−2) days before annual mean hatch date. Late hatching nests >(+2) days after annual mean hatch date. Hatch periods used in table to simplify presentation.

[b] Average error (predicted age − true age), in days, adjusted for annual variation (least-square means).

[c] Probability of a significant trend over hatch date.

known precisely. Hatching date was expressed as $\pm n$ days from the annual mean hatch date. Averaged over 100 random partitions of the data, the bias decreased from significantly positive for early-hatching goslings (predicted age of early hatching goslings biased high), to significantly negative for late-hatching goslings (predicted age of late-hatching goslings biased low), in virtually all years for both ninth primary and PC^A. Pooled over years, bias decreased from +0.56 to −0.34 and +0.84 to −1.17 for ninth primary and PC^A, respectively (Table 4).

Is the error bias in predicted age important?—Although the error bias in predicted gosling age, using either ninth primary or PC^A as the predictor, is statistically significant, we attempted to characterize the 'biological' significance of the error bias by redoing two analyses from previously published work, using either ninth primary alone (reflecting what might happen in those cases where there are no web-tagged goslings available to derive an annual predictive equation), or using gosling age predicted from ninth primary. We used ninth primary because it was clearly the single best predictor overall—any significant consequences of using ninth primary would be even larger if other characters were used. The analyses selected are representative of recent research on variation in gosling growth rates.

(Example 1: *does gosling growth rate decline with hatch date?*).—In several species of geese, average gosling growth rates decline with later hatch date (Cooch et al. 1991a, Sedinger and Flint 1991, Larsson and Forslund 1991, Lindholm et al. 1994). We examined a subset of years (1978–1985) previously analyzed in Cooch et al. (1991a). These years were chosen because they had relatively large sample size, maximizing our power to resolve the potential effects of the error bias in predicted gosling age. We subdivided hatching dates into early (<−2 days before mean hatch) and late (>+2 days after mean hatch) periods. Only significant terms were

TABLE 5. Influence of using (i) ninth primary or (ii) gosling age predicted from ninth primary on analyses of seasonal variation in gosling growth rates. Data from 1978–1985.

	Character	Source	df	F	P
a. using true gosling age[a]	body mass	year	7	21.37	<0.001
		age	1	243.93	<0.001
		hatch period[c]	2	60.32	<0.001
	culmen 1	year	7	28.99	<0.001
		age	1	294.06	<0.001
		hatch period	2	12.89	<0.001
b. using ninth primary length	body mass	year	7	14.04	<0.001
		ninth	1	657.18	<0.001
		hatch period	2	19.45	<0.001
	culmen 1	year	7	16.75	<0.001
		ninth	1	536.90	<0.001
		hatch period	2	1.96	0.162
c. using predicted gosling age[b]	body mass	year	7	30.53	<0.001
		predicted age	1	524.42	<0.001
		hatch period	2	31.33	<0.001
	culmen 1	year	7	41.76	<0.001
		predicted age	1	483.72	<0.001
		hatch period	2	4.40	0.036

[a] Days since hatching.
[b] Gosling age predicted from ninth primary length, using annual regressions of ninth primary length against true gosling age from known-aged samples.
[c] Early–<2 days before mean hatch date; late–>2 days after mean hatch date.

included in the final model. We examined variation in body mass (g) and culmen length (using culmen 1; mm) among hatch periods.

Using true gosling age in the analysis, there was significant variation between hatch periods in both gosling mass and culmen length (Table 5); early-hatching goslings were significantly heavier and had bigger culmens than did later-hatching goslings. This is consistent with results from Cooch et al. (1991a) using a larger data set. Using ninth primary alone, there was still a significant decrease in mass between early- and late-hatching goslings, but there was no significant difference in culmen length between hatching periods (Table 5). Using gosling age predicted from ninth primary for a sample of birds for which true age was known, body mass again differed significantly between the early and late hatching periods (Table 5). Culmen length also differed significantly, but the magnitude of the significance was reduced compared to the analysis using true gosling age directly. Although the difference in mass between hatch periods was still significant when age predicted from ninth primary was used, there was a systematic reduction in the magnitude of the difference for both mass and culmen (Fig. 2).

(Example 2: *does gosling growth vary among different brood-rearing areas?*).—Cooch et al. (1993) demonstrated that there was significant spatial variation in the growth of goslings, dependent upon brood-rearing location. Goslings reared on the traditional salt-marsh at La Pérouse Bay were
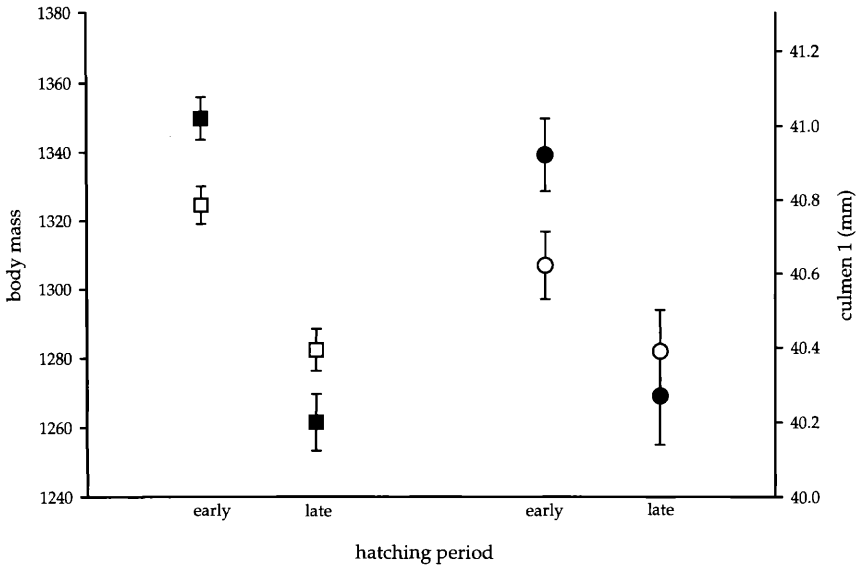
FIGURE 2.   Effect of using gosling age predicted from ninth primary length on analysis
    seasonal variation in gosling growth. Goslings categorized as early-hatching ($<(-2)$) days
    before mean hatch) or late-hatching ($>(+2)$) days after mean hatch). Values represent
    least-square means (and associated SE) from a model correcting for either (a) true age,
    or (b) age predicted from ninth primary length. Variation in both body mass (g) and
    culmen length (culmen 1; mm) is presented. Closed symbols indicate least-square means
    estimated using true age. Open symbols indicate least-square means estimated using
    predicted gosling age instead of true age.

significantly lighter and smaller than goslings reared in non-traditional
foraging habitats. Similar significant spatial variation for snow geese at a
different colony has also been suggested by Aubin et al. (1993), who used
a single character (culmen length) as an indirect index of age (they did
not have a web-tagged sample to derive a predictive equation). For our
purposes, we simply separated goslings into those measured at La Pérouse
Bay (LPB) and those measured elsewhere (non-LPB). As with the pre-
ceding example, we examined variation in body mass (g) and culmen
length (mm) length among the 2 rearing sites. Data from 1990 and 1991
were used. Because of the small sample sizes of known-aged goslings in
these years, we used both female and male goslings in our analysis, in-
cluding 'sex' (and associated interaction terms, as needed) as a fixed
factor in the analysis.

    Using true gosling age, gosling mass and culmen length at the non-
LPB site were significantly greater than goslings measured at the LPB site
(Table 6), consistent with results from Cooch et al. (1993). Using ninth
primary alone, there was no significant difference in body mass between
sites, and only a marginally significant difference in culmen length (Table
6). When age predicted using ninth primary length of known-aged gos-

TABLE 6. Influence of using (i) ninth primary or (ii) gosling age predicted from ninth primary on analyses of variation in gosling growth rates as a function of brood-rearing site. Data from 1990–1991. Male and female goslings included in the analysis. Non-significant interaction terms excluded from final model.

	Character	Source	df	F	P
a. using true gosling age[a]	body mass	year	1	1.37	0.245
		age	1	16.74	<0.001
		sex	1	2.02	0.159
		site[c]	1	7.71	0.007
	culmen 1	year	1	1.36	0.247
		age	1	0.55	0.459
		sex	1	1.32	0.254
		site	1	15.59	<0.001
b. using ninth primary length	body mass	year	1	1.01	0.318
		ninth	1	64.06	<0.001
		sex	1	5.46	0.022
		site	1	3.27	0.074
	culmen 1	year	1	0.01	0.986
		ninth	1	19.76	<0.001
		sex	1	2.74	0.101
		site	1	4.43	0.038
c. using predicted gosling age[b]	body mass	year	1	17.67	<0.001
		predicted age	1	52.58	<0.001
		sex	1	5.42	0.022
		site	1	3.49	0.065
	culmen 1	year	1	4.14	<0.001
		predicted age	1	16.61	<0.001
		sex		2.96	0.089
		site	1	4.78	0.031

[a] Days since hatching.
[b] Gosling age predicted from ninth primary length, using annual regressions of ninth primary length against true gosling age from known-aged samples.
[c] Site: LPB and non-LPB (see text).

lings was used, the results were equivalent—no significant difference in body mass and a marginally significant difference in culmen length (Table 6). In this example, using ninth primary instead of true gosling age eliminated our ability to detect differences among sites (Fig. 3). Again, use of ninth primary lead to a systematic reduction in the difference between the two sites. In this example, the reduction was sufficient to lead to the conclusion of no significant difference.

DISCUSSION

Ninth primary is clearly the best single predictor of true gosling age of the measurements normally made from goslings captured during annual banding drives. It had greater precision and less bias as a predictor than any other univariate character. Ninth primary length alone was also a better predictor (both in terms of precision and bias) than either of two different multivariate indices of size. This contrasts with Gilliland and
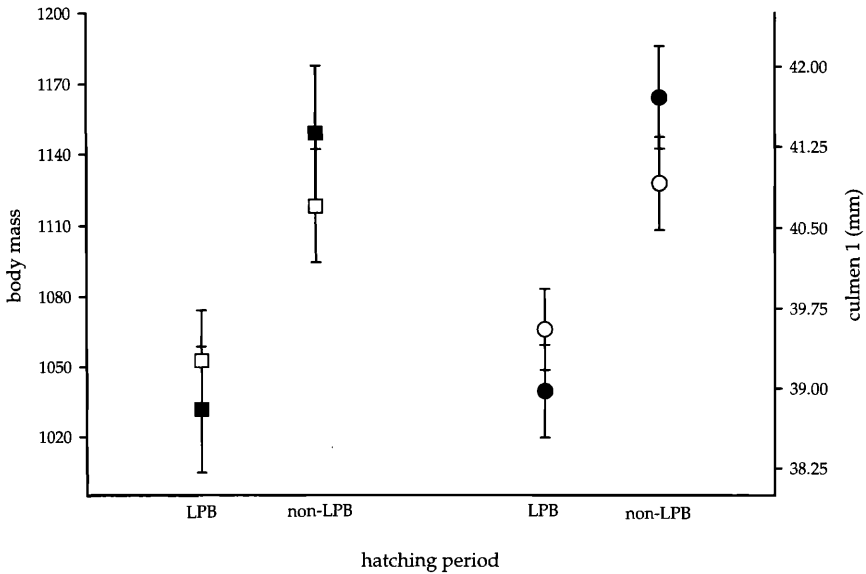
FIGURE 3.   Effect of using gosling age predicted from ninth primary length on analysis of
spatial variation in gosling growth. Goslings categorized as LPB (reared and measured
at LPB) or non-LPB (reared and measured outside of LPB). Values represent least-square
means (and associated SE) from a model correcting for either (a) true age, or (b) age
predicted from ninth primary length. Variation in both body mass (g) and culmen
length (culmen 1; mm) is presented. Closed symbols indicate least-square means esti-
mated using true age. Open symbols indicate least-square means estimated using pre-
dicted gosling age instead of true age.

Ankney (1992) who showed that multivariate indices of size were signifi-
cantly better predictors of age of Great Black-backed Gulls (*Larus mari-
nus*) than were any univariate measure. However, because they were able
to measure birds in their sample on a near-continuous basis, they were
able to use robust non-linear growth curves to fit their data. In our ana-
lyses, the multivariate indices of size worked significantly better than all
but the two measures of feather growth (ninth primary and mid-tail).
Feather growth is effectively linear over the range of gosling ages typically
encountered during banding, and will typically be more robust at pre-
dicting age than non-linear curve fits.

Our finding that ninth primary length was the best predictor of true
gosling age is consistent with, and provides quantitative support for, sev-
eral earlier studies of waterfowl which relied heavily on use of patterns of
feather tract development (Southwick 1953, Yocum and Harris 1965, Pir-
kola and Högmander 1974, Bellrose 1980, Owen 1980, Bowler 1992, Se-
dinger 1992).

However, while ninth primary is the best single predictor of gosling
age, using ninth primary length, either directly (*sensu* Aubin et al. 1993)
or indirectly as a means for predicting age (*sensu* Lindholm et al. 1994),

can introduce significant bias in analyses that need to adjust for gosling age. This bias reflects, primarily, two things: (1) where on the growth curve goslings are measured, and (2) whether or not the sample of gos-lings measured at banding is unbiased with respect to other variables that may contribute to variation in size, such as hatching date. If the ninth primary (and indeed, any character) is measured during the period of early rapid growth, the relationship between size and gosling age is effec-tively linear (Fig. 1), and bias is minimized. In our study, and for virtually all geese studied to date, early-hatching goslings are generally larger for a given age than late-hatching goslings. This introduces a systematic bias when using size to estimate age; estimated age for early-hatching goslings will be biased high, whereas estimated age for late-hatching goslings will be biased low (Table 4).

The effects of both sources of bias, but in particular the hatching-date bias, are notable in typical analyses of gosling growth rate variation. Con-sider the analysis of gosling size variation as a function of brood-rearing location (Example 2; Table 6). On average, goslings at the non-LPB site hatched from earlier-hatching nests (Cooch et al. 1993), while goslings at the LPB site came primarily from later-hatching nests. Because predicted age for early-hatching goslings is biased high, and biased low for late-hatching goslings (Table 4), scaling for predicted age will bias the ad-justed body size lower for early-hatching goslings, and higher for late-hatching goslings. This is precisely what was observed in our reanalysis of these data (Fig. 3). Bias in predicted age induced by the seasonal decline in gosling growth rates will systematically bias any analysis where gosling size is adjusted for predicted age. In effect this reduces differences and increases the chances of making a Type II error. Because statistical power is defined as $1 - \beta$, using age predicted from body size may significantly reduce statistical power in some analyses. It is worth noting that in both our example analyses, the bias lead to a reduction in the estimated dif-ference in size between the two respective groups. However, in other study situations, the particular pattern of age-bias among locations could in theory inflate the observed size differences. The more critical consider-ation is the reduced precision that this bias will cause.

Researchers who use body size to estimate age may fall victim to a statistical tautology, wherein they use size to estimate age in order to analyze size. Failure to control for other factors which may contribute to size variation (independent of age), may make it difficult to resolve dif-ferences in size with any satisfactory power. The increased probability of making a Type II error increases investigator confidence if in fact a sta-tistically significant result is found, but we submit that acceptance of meaningful null hypotheses is as interesting from a biological perspective as are rejections. We urge investigators who use size to estimate age to consider carefully whether or not they may unwittingly be minimizing the chances of fully utilizing their data. We grant that the methods required to obtain a known-aged sample are often laborious and expensive, but when compared to the systematic reduction in statistical power caused by

using size a surrogate for age, the apparent cost may in fact be worth it in the end. One important factor which should be also be considered is that our analyses were predicated on the observation that growth in geese is significantly influenced by environmental conditions during brood rearing (primarily differences in food quality and quantity). However, some characters are less susceptible to environmental variation than others. For example, in our study, ninth primary is consistently the best predictor of gosling age in all years (Table 1), despite a significant long-term deterioration in the environment during the course of the study (Williams et al. 1993, Cooke et al. 1995). Clearly, the potential bias in using body size as a surrogate for age will be minimized if the character(s) used are those most strongly buffered against environmental variation. Because flight in a precocial bird breeding in the short Arctic summer is strongly selected, it is perhaps less likely to vary due to differences in growth conditions. However, this is arguably an *a posteriori* conclusion. Unfortunately, many shorter-term studies may not have sufficient data in hand to identify these metrics.

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