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RESEARCH ARTICLE

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ABSTRACT

In addition to estimating survival probability of adult birds, estimating recruitment of new individuals into avian breeding populations is fundamental to understanding rates of population change. Notions about mean recruitment age can lead to erroneous conclusions about population projections if the probability of capture is ignored. We calculated the mean recruitment age of King Eiders (*Somateria spectabilis*) using two methods: (1) a naive estimate based strictly on observed age at first recapture of marked ducklings as nesting females; and (2) reversed capture histories, which incorporate probability of capture into estimates. From 1996 to 2009, we marked 2,390 King Eider ducklings, 53 of which were recaptured from 2007 to 2010 as females nesting at Karrak Lake, Nunavut, in Canada's Central Arctic region. The naive approach estimated mean ($\pm$ 95% CL) recruitment age as 4.58 $\pm$ 0.42 yr, whereas reversed capture histories estimated mean recruitment age as 4.08 $\pm$ 0.34 yr. We illustrate the influence of recruitment age (range: 3–9 yr) on the predicted annual rate of population change. We fit numerous ecological covariates to test for cohort effects, phenology of vernal thaw, absolute and relative nesting phenology of mothers, maternal body size, density dependence, and relative clutch size on age-specific recruitment probability. There was good support for a negative effect of relative initiation date of nests that produced ducklings, and equivocal support for an additive negative influence of vernal thaw at the age that ducklings were recruited as breeders. We discuss the implications of variation in female recruitment age for King Eider population biology and fitness. More broadly, we reiterate previous advice (e.g., Pradel et al. 1997, Schwarz and Arnason 2000), against calculation of mean recruitment age from age at first capture, regardless of study species, particularly when detection probability of recruits is low.

Keywords: age of first nesting, Arctic, breeding ecology, Karrak Lake, King Eider, population biology, population modeling, recruitment, *Somateria spectabilis*

Recrutement in situ en fonction de l'âge des femelles de *Somateria spectabilis* estimé par marquage–recapture

RÉSUMÉ

En plus d'estimer la probabilité de survie des oiseaux adultes, l'estimation du recrutement de nouveaux individus dans les populations reproductrices est fondamentale pour comprendre les taux de variation démographique. Les notions sur l'âge de recrutement moyen peuvent mener à des conclusions erronées à propos des projections démographiques si la probabilité de capture est ignorée. Nous avons calculé l'âge de recrutement moyen de *Somateria spectabilis* à l'aide de deux méthodes: (1) un estimateur naïf strictement basé sur l'âge observé lors de la première recapture de canetons devenus des femelles nicheuses, et (2) les histoires de capture inversées, qui incorporent la probabilité de capture dans les estimations. De 1996 à 2009, nous avons marqué 2 390 canetons de *S. spectabilis*, desquels 53 ont été recapturés entre 2007 et 2010 en tant que femelles reproductrices au lac Karrak, au Nunavut, dans l'Arctique central canadien. L'approche naïve a estimé que l'âge de recrutement était de 4,58 $\pm$ 0,42 ans (niveau de confiance à 95 %), alors que l'approche des histoires de capture inversées a estimé que l'âge de recrutement moyen était de 4,08 $\pm$ 0,34 ans. Nous illustrons l'influence de l'âge de recrutement, allant de 3 à 9 ans, sur le taux de variation démographique annuel prédit. Nous appliquons de nombreuses covariables écologiques pour évaluer les effets de la cohorte, de la phénologie du dégel printanier, de la phénologie de nidification maternelle absolue et relative, de la taille corporelle maternelle, de la dépendance de la densité et de la taille relative des couvées sur la probabilité de recrutement en fonction de l'âge. Les résultats supportaient l'hypothèse d'un effet négatif de la date relative d'initiation des nids qui ont produit les canetons, et avaient un support équivoque pour une influence négative cumulative du dégel printanier sur l'âge auquel les canetons ont été recruté comme des reproducteurs. Nous discutons des implications de la variation de l'âge de recrutement des femelles dans la biologie des populations et la condition physique de *S. spectabilis*. De façon plus générale, nous réitérons le conseil préalablement énoncé, par exemple par Pradel et al. (1997)

et Schwarz et Arnason (2000), contre le calcul d'un âge moyen de recrutement à partir de l'âge à la première capture, indépendamment de l'espèce étudiée, particulièrement lorsque la probabilité de détection des recrues est faible.

Mots-clés: âge à la première nidification, Arctique, écologie de reproduction, lac Karrak, Eider à tête grise, biologie des populations, modélisation des populations, recrutement, *Somateria spectabilis*

INTRODUCTION

Fundamental to an understanding of annual rates of change in avian populations is knowledge of (1) the relative contributions of per capita recruitment of breeders as new additions to the nesting population and (2) survival probability of previous breeders (Nichols et al. 2000). There is also immediate relevance to life history theory, because fitness is a function of both of these vital rates. Compared with annual probability of adult survival, the recruitment process is considerably more complex ecologically, because it is the product of fecundity and a number of transition probabilities between life states prior to sexual maturity. Although recruitment can be estimated directly from recaptures of individually marked animals (Pradel 1996), decomposition of the recruitment process may provide further insight on the relative contributions of each component, their sensitivities to environmental covariates, and, thus, the ecological mechanisms that guide recruitment. One component of recruitment, essential to the formulation of reasonable population models such as those based on Leslie matrices, is an estimate of the age of first breeding, or *primiparity*. Age of maturation affects generation time, which is a key determinant of growth potential for populations (Caswell 2001), and individual variation in primiparity has implications for individual fitness (Cole 1954). From an applied standpoint, prescriptions for conservation and management also should originate from empirically based estimates of additions to, and removals from, populations of interest. Unbiased estimates of the relative contributions of recruitment and mortality toward rates of population change ideally should guide inferences and decisions about the life history components upon which conservation attention might focus. We were motivated to begin studying the population biology of King Eiders (*Somateria spectabilis*) in 1995 by the absence of information about basic life history and by conservation concern for this widespread and Holarctic-nesting species (Dickson 1997, Gratto-Trevor et al. 1998, Suydam et al. 2000). Scant information about breeding biology had been documented, and the few studies were generally descriptive (e.g., Dement'ev and Gladkov 1952, Parmelee et al. 1967, Lamothe 1973). A search of banding data from the Bird Banding Laboratory revealed that only 77 King Eiders had been marked in North America from 1941 to 1994. The virtual absence of marked birds prevented the use of modern methods (e.g., Brownie et al. 1985, Pollock et al.

1990, Lebreton et al. 1992, Pradel 1996) for proper estimation of various probabilities and rates relevant to informed conservation prescriptions.

In the present study, we estimated the age at which female King Eiders marked as ducklings from 1996 to 2009 were recaptured, between 1997 and 2010, as recruited breeders near Karrak Lake (67°14′N, 100°15′W). We compared naive estimates of age of first nesting based on observations of returning birds (i.e. without accounting for probabilities of breeding detection) with those based on mark–recapture methods using simultaneous estimation of recruitment and detection probabilities, and examined the influence of estimates obtained by these methods on the annual rate of population change.

METHODS

Field Methods

Following methods of Kellett et al. (2003), we systematically searched all 107 islands (encompassing 2.7 km^2) of Karrak Lake and adjacent Adventure Lake for King Eider nests, beginning in mid-June of each year. We also monitored the very few nests that were encountered on the adjacent mainland. We marked nests with small stakes placed 1 m from nest bowls and revisited nests weekly during incubation. We calculated nest initiation dates by backdating from known egg-laying dates or hatch dates, or from incubation stages estimated by candling eggs (Weller 1956). We assumed a laying interval of 1 egg day^{-1} (Lamothe 1973) and incubation length of 23 days (Parmelee et al. 1967). We attempted to capture all nesting females on nests with mist nets, usually after ~13 days of incubation. Females were weighed (±10 g), measured for structural size (specific measurements are described below), and marked with federal leg bands. We visited nests more frequently as predicted hatch dates approached, so that all or nearly all ducklings in each nest could be individually marked. Web tags and plasticine-filled leg bands were applied to newly hatched ducklings in nests, or at the pipped egg stage (Blums et al. 1994, 1999). Web tags were used exclusively during 1996 and 1997, in combination with plasticine bands during 1998–2000 and 2002, and only plasticine bands were used during 2001 and 2003–2009. We observed no foot deformities. Sex of ducklings was not determined.

Thus, captured adults were all nesting females on nests, and we had no information about whether prebreeding individuals were present on the study area. Unlike in

TABLE 1. Age of first recapture of 53 nesting female King Eiders initially marked as ducklings near Karrak Lake, Nunavut, Canada, 1996–2010.

Year marked	Number of ducklings marked[b]	Age (yr) first detected nesting[a]										
		1	2	3	4	5	6	7	8	9	10	11
1996	23	0	0	0	0	0	0	0	0	0	0	0
1997	180	0	0	2	6	1	1	0	0	0	0	0
1998	162	0	0	3	4	1	1	0	0	0	0	0
1999	227	0	0	1	4	1	1	1	0	1	0	0
2000	168	0	0	2	1	2	1	2	1	0	0	
2001	178	0	0	0	0	1	0	0	0	0		
2002	182	0	0	0	2	2	2	0	2			
2003	121	0	0	0	0	0	0	0				
2004	215	0	0	5	0	0	0					
2005	181	0	0	1	0	0						
2006	166	0	0	0	0							
2007	200	0	0	1								
2008	267	0	0									
2009	120	0										
Totals	2,390	0	0	15	17	8	6	3	3	1	0	0

[a] Females only.
[b] Sex not determined, so includes males and females in an assumed ratio of 1:1.

sympatric Long-tailed Ducks (*Clangula hyemalis*), we did not observe apparently unpaired groups of females early in the nesting season. Failure to recapture marked birds on nests could have been an outcome of death since marking, absence from the study area (as a nester or non-nester), presence on the study area as a non-nester, or presence on the study area as an uncaptured nester.

We estimated age-specific probabilities of first-time nesting following reasoning provided by Pradel et al. (1997). Essentially, they illustrated how probability of first reproduction, b (they denoted this β, which we use to denote estimates of slope parameters herein), or the probability that a member of the population has not bred previously, can be estimated from captures of marked animals, as formalized by Pradel (1996). The complement to b is the probability that an animal has bred previously, which can be referred to as seniority probability, γ, hence $b = 1 - \gamma$. Pradel et al. (1997) noted that logistic linear models of γ are equivalent to logistic linear models of b except that the sign is reversed, such that $\text{logit}(\gamma) = -\text{logit}(b)$. For estimation of $\hat{\gamma}$, capture histories of birds were considered by Pradel et al. (1997) in reverse time, with initial capture near hatch, and all subsequent encounters as breeding or nesting adults. Thus, no assumptions are required about survival or the age at which breeding propensity stabilizes to a maximum value (Pradel et al. 1997). We used the "Pradel data type" within Program MARK (White and Burnham 1999) to estimate seniority probability ($\hat{\gamma}$) and capture probability ($\hat{p}$) of known-age hens initially marked as ducklings and recruited as breeders.

An important distinction between our approach to manipulation of capture histories and that of Pradel et al.

(1997) is based on our unavoidably small sample size of 53 known-age female King Eiders returning to the study area as nesters, despite having marked 2,390 ducklings over 14 nesting seasons (Table 1). We were most interested in a global estimate of age-specific probability of entry into the breeding cohort by female King Eiders near Karrak Lake. Following Pradel et al. (1997), we manipulated capture histories to condition on year since first capture as a duckling, so that all capture histories began with the year following marking as occasion 1 (see Appendix). Hence, cohort information—a combination of age and temporal information—was conflated simply into age information, by conditioning on time since first capture as a duckling. However, duckling cohort effects were modeled by inclusion of the year of hatch as a covariate (see below). Reversal of capture histories was done automatically by Program MARK when selecting the "Pradel seniority only" data type.

We tested goodness of fit with Program RELEASE (Burnham et al. 1987) and found that models were appropriate for our reversed capture histories ($\chi^2 = 6.41$, $df = 16$, $P = 0.99$). As a check, we also estimated a variance inflation factor $\hat{c} = 1.006$, with the median $\hat{c}$-test available in Program MARK, applied to the global Cormack-Jolly-Seber model $\{\varphi(\text{age})p(\text{age})\}$ on the 53 capture histories of recruited ducklings. Both results suggested goodness of fit, given our data, so we subsequently used Akaike's Information Criterion adjusted for small sample size (AIC_c), instead of QAIC_c, for model selection (Burnham and Anderson 2002).

Our first step in model selection was to determine the best model from the set that included age-related

TABLE 2. Quality ranking of Pradel's (1996) models for estimation of probabilities of seniority ($\hat{\gamma}$), and capture ($\hat{p}$), by age (yr) of 53 female King Eiders nesting near Karrak Lake, Nunavut, Canada. Seniority and capture probabilities were structured by age class (a) or by linear age trend (A, logit scale) or were unstructured by age (.). The best model without fixture of γ to 0, {γ(A) p(.)}, was further constrained so that γ were fixed to zero for each increasing age class from γ_1 cumulatively with each model to γ_5.

Model		ΔAIC_c	AIC_c weights	Number of parameters	Deviance
γ(A) | $\gamma_1, \gamma_2, \gamma_3 = 0$	p(.)	0.00	0.70	3	245.50
γ(A) | $\gamma_1, \gamma_2 = 0$	p(.)	4.38	0.08	3	249.88
γ(A)	p(.)	4.42	0.08	3	249.92
γ(A) | $\gamma_1 = 0$	p(.)	4.42	0.08	3	249.92
γ(A)	p(A)	4.76	0.06	4	248.13
γ(a)	p(.)	24.60	0.00	14	244.48
γ(.)	p(a)	25.76	0.00	14	245.64
γ(.)	p(A)	31.99	0.00	3	277.49
γ(a)	p(a)	56.44	0.00	26	241.82
γ(.)	p(.)	62.08	0.00	2	309.68
γ(A) | $\gamma_1, \gamma_2, \gamma_3, \gamma_4 = 0$	p(.)	12,665.40	0.00	3	12,910.91
γ(A) | $\gamma_1, \gamma_2, \gamma_3, \gamma_4, \gamma_5 = 0$	p(.)	26,746.87	0.00	3	26,992.38

constraints on latent parameters γ and p, using the logit link. This first candidate set included seven models for γ and p structured by age class {γ(a)p(a)}, structured by age trend {γ(A)p(A)}, or unstructured by age {γ(.)p(.)} (Table 2).

Although detections of duckling recruitment never occurred before their fourth summer on the study area (i.e. 3 yr old), it was possible that a fraction nested for the first time before this age but were not detected. Using the best model from the initial set, in which γ was allowed to vary as a linear function of age, {γ(A)p(.)}, we further considered models in which γ_1 was fixed with zero probability, and added this fixture cumulatively to each age in sequence, until AIC_c increased. We found that fixing γ_1, γ_2, and $\gamma_3 = 0$ produced the best-supported model, compared with having fewer or greater age-specific seniorities so constrained (Table 2). Fixing more than the first three age-related seniorities resulted in very high deviances, indicating very poor model structure, inappropriate for modeling increasing age trends in seniority.

In addition to our goal of estimating age-specific entry of recruits into the breeding cohort, $\hat{b}_a$, where a is age (in years), we tested specific hypotheses about potential ecological covariates individually associated with recruited females, either as ducklings or as breeders. We used the base model {γ(A)p(.) \| γ_1, γ_2, $\gamma_3 = 0$} as a template for assessing whether individual duckling covariates explained additional variation in age-specific recruitment. We had only 53 capture histories and so initially considered only models with one additional covariate. We also fit models with multiple covariates, including covariates from single-covariate models that reduced AIC_c below the base model.

We tested for trend effects of variation in $\hat{b}_a$ by coding the year that ducklings hatched from 1997 to 2007 as individual covariates. We did not have specific a priori notions about the direction of this effect but included it to detect an unknown source of variation for trend in $\hat{b}_a$ associated with duration of study.

The abundance of breeding females at Karrak Lake increased markedly from the beginning of our study in 1995 ($\hat{N}_{1995} = 54$) to 2010 ($\hat{N}_{2010} = 314$) (R. T. Alisauskas and D. K. Kellett personal observation; based on methods of Arnold et al. [2007] to account for nests failed prior to discovery). We predicted that $\hat{b}_a$ might decline in a density-dependent fashion with increasing density of nesting females. Specifically, we tested the prediction that $\hat{b}_a$ declines at higher nesting densities, perhaps at the time that ducklings hatched, $\hat{N}_{hatch}$, or in the year corresponding to the age at which individuals recruited as breeders, $\hat{N}_{age}$.

The timing of ice melt at Karrak Lake is a general metric of spring phenology that may affect several breeding parameters of King Eiders there, such as nest success and clutch size (Alisauskas and Kellett personal observation). King Eiders arrive on the study area when Karrak Lake is still frozen, which prevents them from feeding on local foods, most likely benthic invertebrates, until the benthos of surrounding water bodies become accessible after ice begins to break up. However, some feeding on neighboring small ponds that thaw earlier than Karrak Lake or Adventure Lake was evident from the presence of invertebrates found in esophagi and gizzards of dissected birds (Alisauskas and Kellett personal observation). We predicted that $\hat{b}_a$ might decline in years with persistent ice cover, measured as the date in June that ice on Karrak Lake broke apart, ICE, either when ducklings hatch, ICE_{hatch}, or in the year corresponding to the age at which individuals recruited as breeders, ICE_{age}.

We also tested whether age-specific recruitment was influenced by the median date of nesting by the local population both in years when ducklings hatched, NID_{hatch}, and in the year corresponding to the age at

which individuals recruited as breeders, NID_{age}. Furthermore, we derived a metric of relative phenology for nests that produced individual ducklings, devNID, in relation to the population median, $\text{NID}_{\text{hatch}}$ above, and similarly, a metric of relative fecundity for ducklings' mothers by subtracting clutch size from the population mean in the year that ducklings were produced, devCS.

Finally, we tested whether age-specific recruitment was influenced by variation in the asymptotic body size of mothers that recruited ducklings. Body size of nesting hens is known to affect duckling survival (Mehl and Alisauskas 2007) and may also influence the age at which surviving ducklings recruit. We used principal component analysis (Proc PRINCOMP in SAS version 9.1; SAS Institute, Cary, NC, USA) of six morphological measures from 528 adult females captured from 1995 to 2010 to calculate the first principal component as a univariate metric of body size, PRIN1 (Alisauskas and Ankney 1987). Measurements were from the tip of the bill mediodorsally to the most anterior feather (culmen1), tip of bill to posteriormost edge of the fleshy bill (culmen2), head length, head width, tarsal bone length (all ±0.1 mm), and wing chord (±1 mm). The first principal component accounted for 41% of variation in cumulative variance in the six original measurements with loadings of culmen1 (0.41), culmen2 (0.53), head length (0.55), head width (0.25), tarsus length (0.34), and wing chord (0.27).

Estimates of slopes for covariate effects were used to estimate covariate-specific and age-specific estimates of $\hat{\gamma}$ or its complement, $\hat{b}$, using the back-transformation

$$\hat{b}_{x_1, i} = \frac{e^{(\hat{\beta}_0 + \hat{\beta}_1 x_1 + \hat{\beta}_i i)}}{1 + e^{(\hat{\beta}_0 + \hat{\beta}_1 x_1 + \hat{\beta}_i i)}}$$

where x_1 is the individual covariate, and i is an integer value of age (yr).

Estimation of Mean Breeding Age

Given that no female King Eiders were detected breeding before 3 yr of age, and that the best model in Table 2 suggested that γ_1 to γ_3 were zero, the probability that 4-yr-olds bred previously, γ_4, pertained to 3-yr-old recruits. Because the age series in γ is a representation of cumulative additions to the breeding cohort, differences between sequential seniorities represent age-specific probabilities of recruitment, α_i, for age i: $\alpha_i = \gamma_{i+1} - \gamma_i$, where

$$\sum_{i=1}^{max} \alpha_i = 1$$

Thus, mean age of recruitment was estimated ad hoc as the sum of age-specific recruitment probabilities weighted by age,
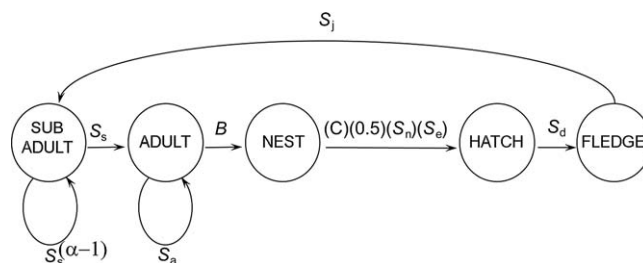

FIGURE 1. Life-cycle graphs for King Eiders, showing all major life stages and transition probabilities. Transition probabilities between stages shown are breeding propensity (B), clutch size (C), nest success (S_n), egg survival in successful nests (S_e), duckling survival (S_d), subadult survival (S_s; i.e. >1 yr old, but prebreeding), and adult survival (S_a). Mean age of first breeding is denoted α.

$$\hat{\bar{\alpha}} = \sum_{i=1}^{max} \hat{\alpha}_i \cdot i$$

We applied this method to two sets of proportions or probabilities. First, we used this estimator to infer mean breeding age from our 125 encounters of 53 known-age females recruited as breeders (i.e. naive inference without accounting for detection probability through mark–recapture methods). We then applied age-specific probabilities of recruitment (as estimated above using mark–recapture methods) to the observed sample size of 53.

We assessed the response in the annual rate of population change, λ, to variation in $\hat{\bar{\alpha}}$. The life-cycle graph in Figure 1 shows the appropriate life stages and transition probabilities for King Eiders and is relevant to most species of waterfowl. For this assessment, we assumed a stable age distribution and thus used $\lambda = S_a + f$ to predict lambda, where S_a is true annual adult survival probability equal to 0.94 (Oppel and Powell 2010), and f is the number of recruits per adult female in the population. We used $f = B \cdot C \cdot x \cdot S_n \cdot S_e \cdot S_d \cdot S_s^{\bar{a}}$, with respective terms in the right side of the equation representing breeding probability (B), clutch size (C), proportion of ducklings produced that were female (x), composite nest survival during laying and incubation (S_n), egg survival (S_e), duckling survival until fledging (S_d), and subadult survival (S_s), exponentiated to mean recruitment age ($\bar{a}$). "Breeding propensity" applies to adult (i.e. sexually mature) females and is defined as the probability that an animal that has already nested will nest again on the study area (Cooke et al. 1995). For this exercise, we used Coulson's (1984) estimate of breeding propensity = 0.78 for recruited female Common Eiders, in the absence of current estimates for King Eiders. Kellett and Alisauskas (1997) estimated that C = 5.4, and S_n = 0.459, and we assumed that S_e = 1 in successful nests. We also assumed that the primary sex ratio was balanced, so that x = 0.5. Mehl and Alisauskas

(2007) estimated that $S_d = 0.10$, but we also considered $S_d = 0.15$ and $S_d = 0.20$, in combination with different mean age of recruitment estimated using mark–recapture versus mean age of first capture as a nester. Assuming survival probability of 0.67 for juvenile females (i.e. <1 yr old; Oppel and Powell 2010) and that S_s was equal to that of adult females (i.e. breeders), we used $S_s = \hat{S}_a = 0.94$ (Oppel and Powell 2010).

RESULTS

Mean age of first capture as a nester. Among 2,390 ducklings of both sexes marked from 1996 to 2009, only 53 (2.2%) had been subsequently captured as females nesting on the study area from 1997 to 2010 (Table 1). Thus, assuming equal sex ratio at hatching, the raw return rate of females was 4.4%. No ducklings from any cohort were detected as nesting before 3 yr of age. Also, none was observed to have nested for the first time after 9 yr of age, although only cohorts of ducklings marked before 2002 were ≥9 yr old by 2010. The 95% confidence limit (CL) of mean age at which females were first detected as nesters (i.e. based strictly on observations of returning birds) was 4.58 ± 0.42 ($n = 53$). For this subset of birds, modal age of first nesting was 4 yr (32%), with 28% first nesting at 3 yr, 15% at 5 yr, 11% at 6 yr, 6% at 7 yr, 6% at 8 yr, and 2% at 9 yr of age.

Accounting for incomplete detection of breeding females. We compared the quality of 12 a priori models following analysis of mark–recapture information, whereby both seniority and capture probabilities were estimated (Table 2). The best model $\{\gamma(A)\ p(.)|\gamma_1, \gamma_2, \gamma_3 = 0\}$ structured seniority probability as fixed at zero until age 3 yr, but an increasing function of age on the logit scale thereafter, until all 53 ducklings had recruited, with no age dependence in capture probability. We were reasonably certain that this model was superior to the others because its model weight was 0.70; also, the next-best model $\{\gamma(A)\ p(A)|\gamma_1, \gamma_2 = 0\}$ had $\Delta AIC_c = 4.38$ and model weight of only 0.08. Detection probability estimated from the best model was $\hat{p} = 0.50 \pm 0.11$ (95% CL). Age-specific seniority probabilities (Figure 2) were used to calculate age-specific recruitment probabilities (Figure 3). In general, the probability distribution of encounters strictly from observations of returning birds was skewed right compared with that estimated from mark–recapture methods (Figure 3). The mean age of recruitment as estimated using mark–recapture was lower by a half year than the naive estimate (Figure 3). Most of the discrepancy was related to an underestimate of the proportion of females recruiting at 3 yr of age and an overestimate of the proportions recruiting from 4 to 9 yr of age, when using the naive approach.
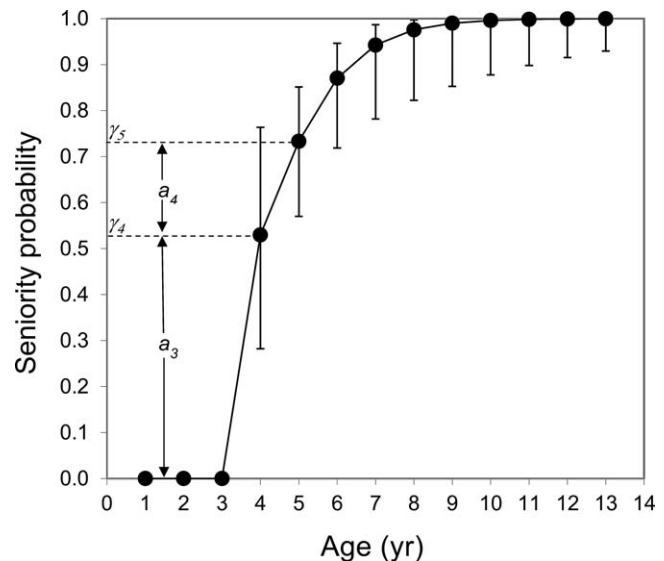

FIGURE 2. Estimates of age-specific probability of seniority as a breeder, 95% confidence limit ($\hat{\gamma}$), from recaptures of 53 King Eider ducklings recruited as breeding females nesting near Karrak Lake, Nunavut, Canada. Also shown are age-specific probabilities of recruitment, $\hat{a}_i = \hat{\gamma}_{i+1} - \hat{\gamma}_i$, for 3-yr-olds and 4-yr-olds, as examples.

Influence of inferred breeding age on predicted rate of population growth. Assuming the vital rates outlined above, we calculated the annual rate of population change in the absence of immigration of new recruits for duckling survival probabilities of 0.10, 0.15, and 0.20 (Figure 4). Differences in mean recruitment age, whether calculated solely from observations of returning birds or estimated using mark–recapture methods, had a smaller influence on predicted lambda than the range in duckling survival (Figure 4). However, there was considerable variation in predicted lambda over the potential range in recruitment age, even for constant duckling survival. Note that inference from this exercise was restricted to contributions solely from in situ recruitment and thus did not consider recruited immigrants.

Covariates of age-specific recruitment probability. Of the 10 covariates considered, the best models included relative nest initiation date (devNID; Table 3 and Figure 5). Ducklings had higher recruitment probabilities in each age class if their mothers nested early in relation to the annual mean NID (Figure 6). In addition, there was some support for a negative relationship between recruitment probability and timing of vernal thaw at the age that ducklings recruited as breeders (ICE_{age}). Although confidence limits of the slope between duckling cohort and recruitment probability did not include zero, that model was of poor quality, probably because of some covariation between duckling cohort and age. All other slope estimates
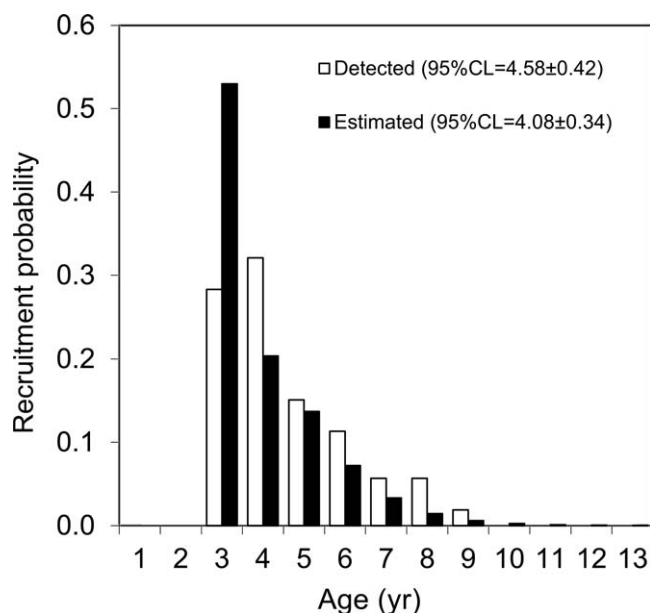
FIGURE 3. Probability distribution for age-specific recruitment into the breeding cohort by 53 King Eiders nesting at Karrak Lake, Nunavut, Canada, based solely on mean age of first capture as a nester (clear) compared with inferred probabilities based on mark–recapture estimation (filled). Shown are 95% confidence limits for estimates recruitment age from each distribution.

overlapped zero, except for devNID when modeled additively with ICE$_{age}$ in the best model.

DISCUSSION

Palmer (1976) wrote explicitly that there was "no information, from banded known-age individuals, on age when King Eiders first breed." Other than anecdotal evidence, apparently from unmarked birds, little information could be found about the age at which female King Eiders recruited into breeding cohorts. A translation of Dement'ev and Gladkov (1952) stated that "Judging from the succession of age plumages, puberty apparently sets in during third year of life," although Portenko (in Palmer 1976) reported that some 2-yr-olds could breed. Recently, King Eiders marked with satellite transmitters in northern Alaska were not found to breed before 3 yr of age (Oppel and Powell 2010), despite most returning to the study area at age 2, probably as prebreeders prospecting for future breeding sites (Reed et al. 1999). We also did not detect any breeding before 3 yr of age at Karrak Lake, where 53% of female King Eiders recruited at age 3 yr. Our estimates of variance for age-specific proportions were high, partially because we recaptured only 53 marked ducklings as breeding adults. Nevertheless, this was a sufficiently large sample from which to estimate entry into the breeding cohort, producing our ad hoc estimate of 95% CL ($\hat{\bar{\alpha}}$) =
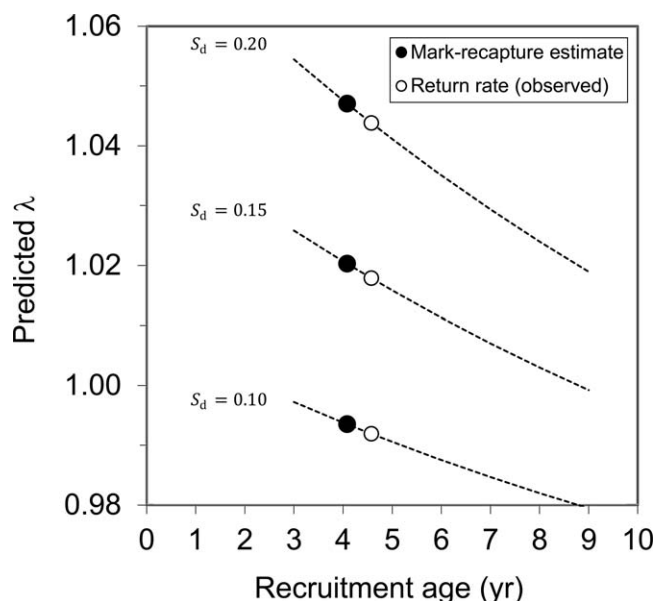

FIGURE 4. Annual rate of population change (λ) predicted from variation in mean recruitment age of King Eiders nesting near Karrak Lake, Nunavut, Canada, as estimated using mark–recapture methods compared with mean age of first capture as a nester. Relationship of λ to recruitment age is shown for duckling survival probabilities of 0.10, 0.15, and 0.20 with other vital rates held constant.

4.08 $\pm$ 0.34 yr. We suspect that 3 yr is an evolved lower limit to recruitment age in female King Eiders, perhaps constrained largely by ontogeny and physiology of sexual maturation, and that earlier recruitment, if possible, is probably rare.

Although we estimated that 53% of females recruited at 3 yr of age, individual variation in recruitment age spanned 3 yr to 9 yr. Our inferred age of recruitment is the product of probabilities of breeding and philopatry to the natal colony (Pradel et al. 1997), and so it is plausible that later-recruiting females may have first nested outside our study area before we captured them. However, natal site fidelity appears to be high in King Eiders (Mehl 2004, Oppel and Powell 2010), and females may be particularly inclined to return to productive breeding sites such as Karrak Lake (Kellett et al. 2003). Recruitment age can vary between breeding sites (Hénaux et al. 2007), and so our estimates of recruitment age were specific to Karrak Lake and the associated ecological conditions responsible for the growing population there. As such, our estimated mean age of recruitment may differ from those for other sites, particularly if recruitment of immigrants is different from that of returning birds.

In the absence of tradeoffs with other life history traits, earlier recruitment to the breeding cohort leads to a higher annual rate of growth for a population (Figure 4), or to increases in individual fitness (Stearns 1992). In Blue-

TABLE 3. Quality ranking of Pradel's (1996) models for estimation of probabilities of seniority (γ), and capture (p), by age (yr) for 53 female King Eiders nesting near Karrak Lake, Nunavut, Canada. Shown are models with individual covariate effects additive to a linear relationship of seniority with age on the logit scale; capture probability is constant. The sixth (BASE MODEL), in which γ_1 to γ_3 were fixed to zero, is the best from Table 2, against which effects of individual covariates were tested.

Model		ΔAIC_c	AIC_c weight	Number of parameters	Deviance
$\gamma(A+devNID+ICE_{age})$	$p(.)$	0.00	0.22	5	238.37
$\gamma(A+devNID)$	$p(.)$	0.71	0.15	4	241.26
$\gamma(A+devNID+N_{age})$	$p(.)$	1.28	0.11	5	239.65
$\gamma(A+devNID+ICE_{age}+N_{age})$	$p(.)$	2.07	0.08	6	238.23
$\gamma(A+N_{age})$	$p(.)$	2.27	0.07	4	242.82
$\gamma(A+ICE_{age})$	$p(.)$	2.31	0.07	4	242.85
$\gamma(A)$ BASE MODEL	$p(.)$	2.83	0.05	3	245.50
$\gamma(A+devCS)$	$p(.)$	3.50	0.04	4	244.05
$\gamma(A+NID_{hatch}+NID_{age})$	$p(.)$	3.80	0.03	5	242.17
$\gamma(A+ICE_{hatch}+ICE_{age})$	$p(.)$	3.99	0.03	5	242.37
$\gamma(A+N_{hatch}+N_{age})$	$p(.)$	4.14	0.03	5	242.51
$\gamma(A+Cohort)$	$p(.)$	4.29	0.03	4	244.83
$\gamma(A+PRIN1)$	$p(.)$	4.39	0.02	4	244.94
$\gamma(A+NID_{hatch})$	$p(.)$	4.61	0.02	4	245.15
$\gamma(A+N_{hatch})$	$p(.)$	4.85	0.02	4	245.39
$\gamma(A+NID_{age})$	$p(.)$	4.94	0.02	4	245.48
$\gamma(A+ICE_{hatch})$	$p(.)$	4.96	0.02	4	245.50

footed Boobies (*Sulo nebouxii*), for example, females that recruited earlier showed higher lifetime reproductive success (Kim et al. 2011). Although tradeoffs between investment in reproduction and survival are expected to lead to selection for an adaptive age of recruitment, observed variation in recruitment age within a species may result from changing environmental conditions (Kim et al. 2011) or from variation in quality among individuals. Although our best estimates of mean age of in situ female recruitment was $\hat{\bar{\alpha}} = 4.08$ yr, with most recruitment at 3 yr of age, there was considerable individual variation in recruitment age, with greater implications for relative fitness among females.

Ducklings tended to show higher recruitment probability in each age class if their mothers nested early in relation to the median nest initiation date specific to each year of the study (Figure 6). Nest initiation date of King Eiders is correlated with spring phenology at Karrak Lake (Alisauskas personal observation). However, spring phenology or cohort (a metric of annual variation) in the year that ducklings were produced did not contribute to age of recruitment, which suggests that nest initiation date may correlate with female quality, which, in turn, may be a consistent trait among individuals, as in Common Terns (*Sterna hirundo*; Ezard et al. 2007). In King Eiders, such earlier-nesting females tended to have higher body mass, corrected for structural size, and showed relatively high repeatability of 0.62 for this trait (Kellett and Alisauskas 2000), which suggests individual variation in quality. Of the 53 recruited ducklings used in these analyses, the mothers of 47 were known; these 47 ducklings were produced by

only 37 of 375 hens (10%) captured from 1996 to 2007. Seven of these hens each produced two or three recruited ducklings, often over >1 yr. This repeatability of successful recruitment by the same females again suggests their high quality. Older or larger females may nest earlier, but missing data precluded including these covariates in our analyses. Mehl and Alisauskas (2007) reported that surviving ducklings were produced by larger females and that survival of ducklings from relatively small females was low, regardless of nesting phenology. Such complexities of interacting effects found to influence duckling survival may also be pertinent to recruitment age, but despite marking a large number of female ducklings (assuming an equal sex ratio of hatchlings), only 4.4% survived, returned, and were captured as recruited females in our study. This low sample size prevented analysis of cohort effects independently of recruitment age, and also precluded more complex models of variation in recruitment. With continued long-term study, it is hoped that increased sample size will permit such analyses to elucidate more complex interactions among predicted ecological influences on recruitment age.

In turn, high-quality females may produce and care for higher-quality ducklings. Anderson and Alisauskas (2001) reported a positive correlation between egg size and duckling size in King Eiders, and larger ducklings showed better locomotor performance than smaller conspecifics and, presumably, higher survival potential. Such high-quality ducklings may recruit earlier as nesters and, thus, experience higher inclusive or lifetime fitness if there are no tradeoffs between early recruitment and survival
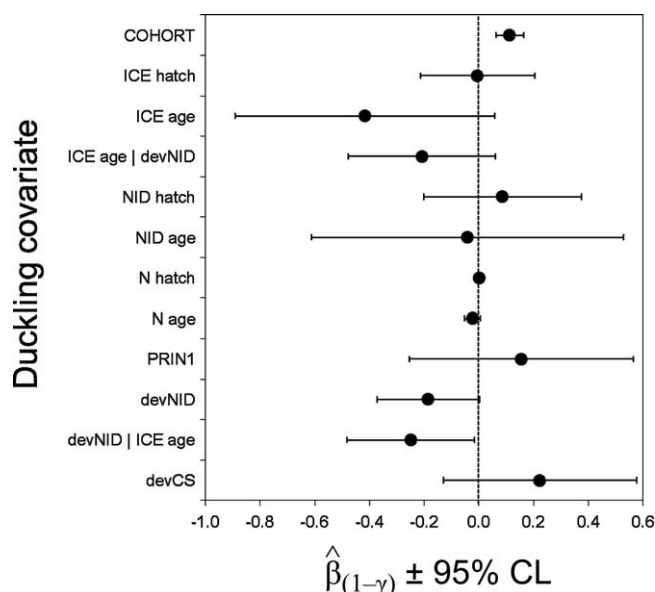
FIGURE 5. Estimated slopes between probability of recruitment as a breeder, $1 - \hat{\gamma}$, and 10 covariates measured from King Eider ducklings recruited as breeders: the year that ducklings hatched from 1997 to 2007 (Cohort), date in June when ice broke up on Karrak Lake in the year that ducklings hatched (ICE_{hatch}) or their adult age (ICE_{age}, in years), median nest initiation date in the year that ducklings hatched (NID_{hatch}) or at their adult age (NID_{age}), size of nesting population on the study area in the year that ducklings hatched (N_{hatch}) or at adult age (N_{age}), body size of duckling mothers (PRIN1), nest initation date of nests that produced ducklings in relation to the annual median (devNID), and clutch size of nests from which ducklings hatched in relation to the annual median (devCS). Also shown are slope estimates for additive effects of devNID and ICE_{age} from the best model in Table 3.

probability. Such a tradeoff seems unlikely, given that the true survival probability of adult King Eiders captured in northern Alaska was estimated to be very high (0.94; Oppel and Powell 2010), similar to the apparent survival probability estimated at Karrak Lake (0.87; Mehl 2004), and little year-to-year variation in survival is expected in long-lived species (Sæther et al. 2004; but see Tavecchia et al. 2001). However, tradeoffs among individual females between age of recruitment and annual survival or successful breeding remain equivocal (Tavecchia et al. 2001, Kim et al. 2011, Gauthier et al. 2012), and costs associated with early reproduction may have contributed to the evolution of deferred breeding in this species.

Although vernal thaw in the year that ducklings were produced did not affect recruitment, there was some evidence that vernal thaw influenced recruitment probability after ducklings reached >3 yr of age. Thus, the quality of ducklings' mothers (expressed as relative nesting phenology) and the phenology of ice melt when ducklings returned as adults additively affected recruitment in the same manner: Earlier is better. Such climatic variation may

be pertinent to future population growth of King Eiders if recent warming of the Arctic continues.

Intraspecific variation in recruitment age has also been linked to breeding densities in other avian species, most often inversely (Bendell et al. 1972, Coulson et al. 1982, Porter and Coulson 1987, Kress and Nettleship 1988, Pyle 2001), but also directly (Wyllie and Newton 1991). All these studies that found increasing age-specific recruitment with declining population density were based on observations of returning birds, without consideration of imperfect detection and the associated potential for bias (i.e. because detection probabilities are likely higher at lower densities of birds). However, several studies that have accounted for imperfect detection have also reported an inverse relationship between breeding density and age of recruitment (Pradel et al. 1997, Crespin et al. 2006, Gauthier et al. 2012). Such relationships are often associated with the hypothesis that declines in population density and older recruitment age both result from constraints associated with reduced food availability, in turn constraining younger birds from attaining breeding condition (Pyle 2001). We found no strong evidence for density dependence either in the year that ducklings hatched or at the age when they recruited. Part of the reason for an apparent absence of density-dependent effects on recruitment age may be related to conditions on our study area. Karrak Lake is found within a large breeding colony of Lesser Snow and Ross's Geese (*Chen caerulescens* and *C. rossii*: collectively "light geese") that has been growing in size and abundance since it was discovered in 1965 (Ryder 1969); it was estimated in 2010 to contain ~1.14 million nesting geese in a contiguous nesting area of ~277 km^2 (Alisauskas et al. 2012). Indeed, most known relatively high concentrations of King Eiders nesting south of Queen Maud Gulf are associated with colonially nesting light geese, which suggests a positive association (Kellett et al. 2003); of six archipelagos in freshwater lakes searched for nesting King Eiders, the three archipelagos with the highest numbers of King Eider nests found were associated with sympatric nesting by light geese. Such high concentrations of geese result in high nutrient inputs from the geese themselves (R. T. Alisauskas personal observation), as well as local devegetation (Alisauskas et al. 2006) contributing to enhanced runoff during spring snow melt. All these factors may increase eutrophication of Karrak Lake and surrounding water bodies, resulting in a hyperabundance of food for nesting King Eiders and their ducklings. Such inputs likely increase the carrying capacity of nesting King Eiders and their young, thereby relaxing the potential for density dependence at Karrak Lake. Additionally, high densities of colonially nesting light geese that surround archipelagos with nesting King Eiders probably reduce probability of
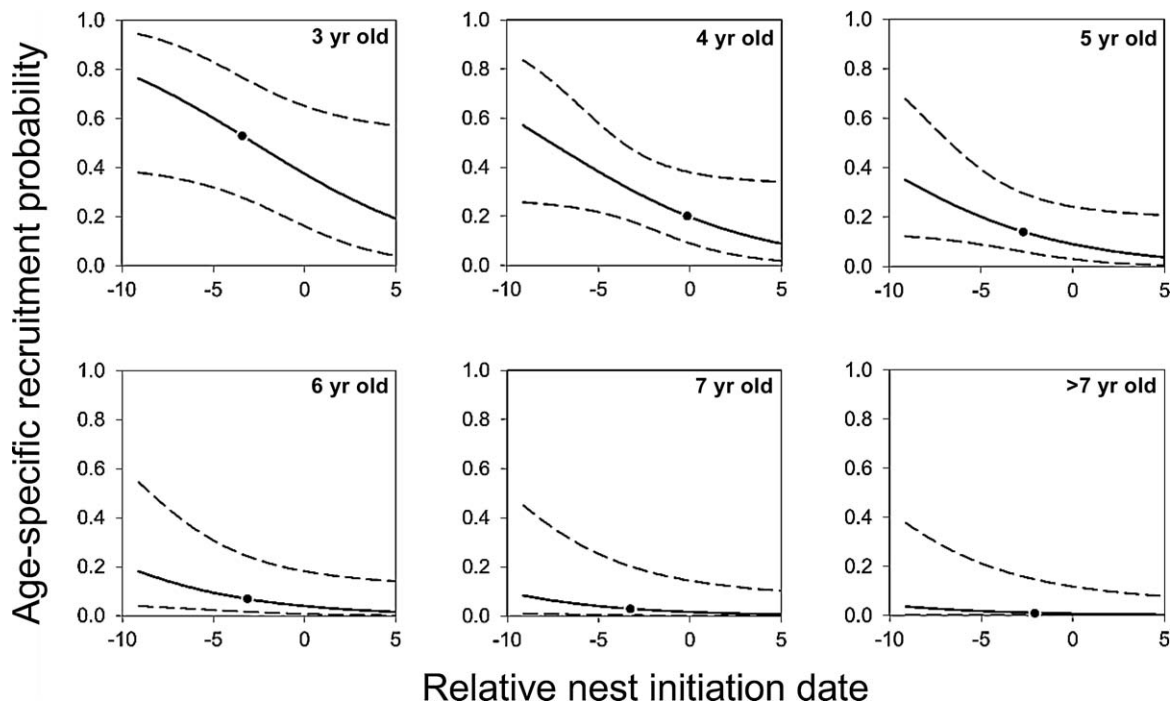
FIGURE 6. Age-specific probabilities of recruitment to the breeding cohort, 95% CL, for female King Eiders nesting near Karrak Lake, Nunavut, Canada, in relation to the initiation date of nests from which recruited ducklings hatched in relation to the population median (devNID). Round symbols on lines predicted for each age class represent the median nest initiation date of recruited ducklings; corresponding probabilities of recruitment sum to 1 across all ages; note that in most cases, deviations of nest initiation dates are negative, regardless of recruitment age, which suggests that recruits hatched earlier than nonrecruits.

nesting failure by both geese and sympatric ducks by swamping local predators.

As noted by Pradel et al. (1997) and Schwarz and Arnason (2000), failure to account for incomplete detection of new recruits can lead to biased estimates of mean age of first nesting. We found that failure to estimate and incorporate incomplete detection of recruited King Eiders resulted in overestimation of mean age of first breeding. Although population trajectories of long-lived species are expected to be more sensitive to changes in adult survival than to changes in recruitment, use of biased estimates of mean age of recruitment in population models, in turn, can lead to erroneous conclusions from projected population trajectories. Such incorrect inference about population health could easily lead to misguided prescriptions for rescue of a healthy population and, perhaps worse, divert resources from genuine conservation problems. For these reasons, we urge researchers to use modern methods of estimation for drawing inferences about recruitment in avian populations.

ACKNOWLEDGMENTS

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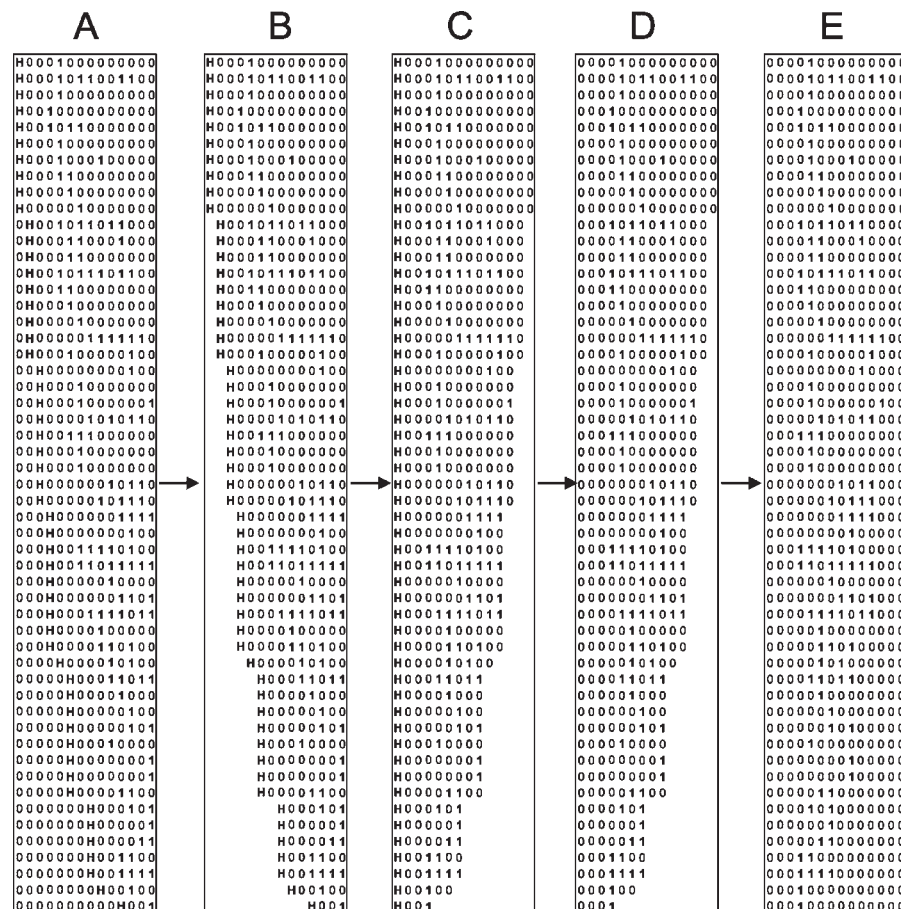
APPENDIX

See Figure 7.

FIGURE 7. Manipulation of (**A**) 53 encounter histories of female King Eiders initially captured as ducklings, denoted by 'H', and recaptured as nesting adults, denoted by '1', from 1997 to 2010 at Karrak Lake, Nunavut, Canada. Years when nesting females were not captured are denoted by '0'. Following Pradel et al. (1997), we first removed zeros before years that King Eiders were marked as ducklings (**B**), and aligned year of marking to be the first column (**C**), thereby rendering the histories to condition on age, rather than year of study; the third step was to replace first captures of ducklings (denoted 'H') with '0' (**D**), and finally to right-fill histories with zeros (**E**), which was used as input data for Program MARK