



## Time constraints in temperate-breeding species: influence of growing season length on reproductive strategies

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Organisms that reproduce in temperate regions have limited time to produce offspring successfully, and this constraint is expected to be more pronounced in areas with short growing seasons. Information concerning how reproductive ecology of endotherms might be influenced by growing season length (GSL) is rare, and species that breed over a broad geographic range provide an opportunity to study the effects of time constraints on reproductive strategies. We analyzed data from a temperate-breeding bird, the lesser scaup *Aythya affinis*; hereafter scaup, collected at eight sites across a broad gradient of GSL to evaluate three hypotheses related to reproductive compensation in response to varying time constraints. Clutch initiation date in scaup was unaffected by GSL and was unrelated to latitude; spring thaw dates had a marginal impact on timing of breeding. Clutch size declined during the nesting season, as is reported frequently in bird species, but was also unaffected by GSL. Scaup do not appear to compensate for shorter growing seasons by more rapidly reducing clutch size. This study demonstrates that this species is remarkably consistent in terms of timing of breeding and clutch size, regardless of growing season characteristics. Such inflexibility could make this species particularly sensitive to environmental changes that affect resource availabilities.

Spatial and seasonal variation in phenotypic traits are well-documented patterns in ecology and provide a foundation for explaining how and why organisms are affected by their environments (Blackburn and Hawkins 2004, Jetz et al. 2008, Olalla-Tarraga et al. 2009). For example, growing season length (i.e. the difference between freeze date and thaw date for soils, as per Smith et al. 2004, hereafter GSL) typically decreases with increasing latitude or elevation, subjecting seasonally-reproducing organisms to time constraints that vary along geographic gradients. Life history adaptations to increasing time constraints are observed extensively among ectotherms (Merilä et al. 2000, Berner et al. 2004, Homeny and Juliano 2007), but evidence for such adaptations in endotherms is limited (Garel et al. 2006, Ely et al. 2007). Such information is necessary to accurately predict how endotherms with wide geographic distributions

will respond to changing environmental conditions across their ranges (Visser et al. 2003, Lyon et al. 2008).

The reproductive ecology of temperate-breeding endotherms, in particular, is expected to show geographic adaptation to changes in GSL, given the strong selection for producing offspring under favourable conditions (Loison et al. 1999, Wingfield 2008). Specifically, three features of avian reproductive ecology might respond to variation in GSL, 1) clutch initiation date, 2) clutch size, and 3) seasonal patterns of clutch size decline (Briggs 1993, Fargallo 2004, Evans et al. 2009). In areas with short growing seasons, some bird species tend to initiate reproduction relatively late and also may finish laying sooner, compared to conspecifics in less time-constrained habitats (Krapu et al. 2002, Silverin et al. 2008). However, this pattern is not consistent. There is no apparent effect of time constraints on breeding phenology in

American wigeon *Anas americana*. Although little is known about arrival of resident birds, wigeon nesting on the prairies appear to wait longer between arrival and laying than is observed farther north, resulting in relatively synchronous nesting over a broad latitudinal range (Wishart 1983, Mowbray 1999). American robins *Turdus migratorius* appear to adjust clutch initiation date to increasing seasonal constraints only in eastern North America, where they delay breeding by about 3 d per degree of increasing latitude. In contrast, in their western range, American robins begin breeding at approximately the same time over 26° of latitude (Sallabanks and James 1999).

Given the strong influence of environmental variation on reproductive investment, adjustment of total clutch size is another possible response to gradients in GSL. However, investigations of the relationship between clutch size and GSL are rare. Ashmole's hypothesis states that clutch size increases with latitude as a result of increases in the seasonal flush of food resources, but this is expected to occur only when high latitude populations are both strongly resource-limited during the non-breeding season and experience reduced post-breeding survival as a direct result of increased egg production (Ashmole 1963, Ricklefs 1980, Griebler and Böhning-Gaese 2004, McNamara et al. 2008). Some recent studies suggest that decreasing GSL might not affect clutch size (Krapu et al. 2002) or might result in decreased clutch size (Yeh and Price 2004, Lu 2005).

Seasonally-declining clutch size is ubiquitous among single-brooded bird species with variable clutch size, but the effect of variation in GSL on this pattern is uncertain. Latitudinal variation in seasonal patterns of reproductive investment has been found at the intraspecific level (Dhondt et al. 2002, Gil-Delgado et al. 2005). Guyn and Clark (2000) reported a rate of seasonal clutch size decline for prairie-nesting northern pintails *Anas acuta* that was considerably lower than that observed in the arctic (Flint and Grand 1996, also see Krapu et al. 2002). In contrast, Evans et al. (2009) examined seasonal patterns in clutch size for seven single-brooded species and found that the rate of seasonal change in clutch size was constant across latitudes for all species.

Thus, although many studies have described geographic variation in timing of breeding, clutch size and seasonal changes in clutch size, observed patterns are not consistent across or within species. In addition, the proximate variables that drive these patterns remain poorly understood. Studies that evaluate simultaneously multiple hypotheses about intraspecific patterns in reproductive strategies along a known environmental gradient should offer new mechanistic insights (Robinson et al. 2010). Here, we analyze nesting data for a temperate-breeding bird, the lesser scaup *Aythya affinis*, hereafter scaup, from eight sites distributed over two unique geographic regions (Alaska and the mid-continent) to investigate three non-mutually exclusive hypotheses about how geographic variation in GSL may influence timing of breeding, clutch size and patterns of clutch size decline in migratory birds. Scaup are well suited for evaluating such hypotheses, because they nest almost continuously from northern prairie to northern boreal forest regions in central and western North America, a breeding distribution that spans about 2200 km (47°N to 68°N).

The flexible nesting date hypothesis suggests that birds adjust the timing of breeding to match local environmental conditions and maximize reproductive success (Visser et al. 1998). We tested a key prediction of this hypothesis: GSL should explain significant variation in clutch initiation dates, after accounting for other site-specific and annual effects, with birds initiating nests earlier in springs with warmer temperatures, an earlier thaw, and increased GSL.

Little is known about affiliations between wintering and breeding areas for scaup, but there could be considerable overlap (Hobson et al. 2009), such that spatially separated groups of breeding birds likely face similar resource limitations during winter. As such, Ashmole's hypothesis may not apply for this species. Alternatively, we hypothesized that birds might attempt to improve their breeding success in areas with shorter GSL by laying fewer eggs, particularly if selection favours accelerated reproduction in these habitats. Under this reduced clutch size hypothesis, we expected a positive relationship between clutch size and GSL, such that the average clutch sizes of scaup breeding at higher latitudes, or at increased elevation, would be smaller than those of scaup nesting further south or at lower elevation. Because resource availability for breeding adults or for their offspring may decline more rapidly in areas with shorter GSL, we also surmised that a more rapid decline in clutch size would occur as time constraints increase (rate of decline hypothesis). Thus, under the rate of decline hypothesis, an interaction should exist between clutch initiation date and GSL, with a stronger seasonal rate of clutch size reduction occurring in areas with shorter GSL.

## Methods

### Study areas

We analyzed nesting data collected at field sites encompassing a broad range of GSL values, located in North and South Dakota, Manitoba, Saskatchewan, Northwest Territories, Montana, and Alaska, including portions of the Missouri Coteau escarpment, the Canadian prairies, the arctic taiga shield, intermontane Alaska and the Rocky Mountains (Table 1, Fig. 1).

### Field methods

Nest searching entailed walking along wetland margins (meadow and shrubby habitat) and using hand drags and foot searches/beat-outs, or using all terrain vehicles and chain drags, to flush females from nests. When a nest was found, the number of eggs was recorded and stage of incubation was determined by egg candling (Weller 1956). Clutch initiation dates were calculated by subtracting incubation stage and full clutch size from the date of discovery and adding 1 d. Timing of nest searching occurred from late April to late July depending on the site (see references in Table 1 for details), and we assumed that nesting and clutch size data represented scaup reproductive timing and effort at each site. Although timing and methods varied to some extent among sites, we do not believe that these differences resulted in systematic biases with respect to reproductive patterns. We assumed that

Table 1. Study site names, locations, years and sources for *Aythya affinis* reproductive data.

Site	Location	Years of study	Source
Missouri Coteau	46°N, 101°W	2000–2006	Stephens et al. 2005 (includes data from 2000–2001 only)
Erickson, Manitoba	50°N, 100°W	1977–1980	Afton 1984
St Denis National Wildlife Area, Saskatchewan	52°N, 106°W	1999–2000 1980	Koons and Rotella 2003 .*
Yellowknife, Northwest Territories	62°N, 114°W	1989–2000	Fournier and Hines 2001 Brook 2002
Cardinal Lake, Northwest Territories	68°N, 134°W	2002–2007	.
Red Rock Lakes National Wildlife Refuge, Montana	44°N, 111°W	2006–2009	.
Yukon Flats National Wildlife Refuge, Alaska	66°N, 148°W	2001–2003	Corcoran et al. 2007
		2005–2008	Martin et al. 2009 (includes data from 2005–2006 only)
Minto Flats State Game Refuge, Alaska	65°N, 149°W	1989–1991	Petrula 1994
		2002–2003	Walker et al. 2005

.\*=unpublished data.

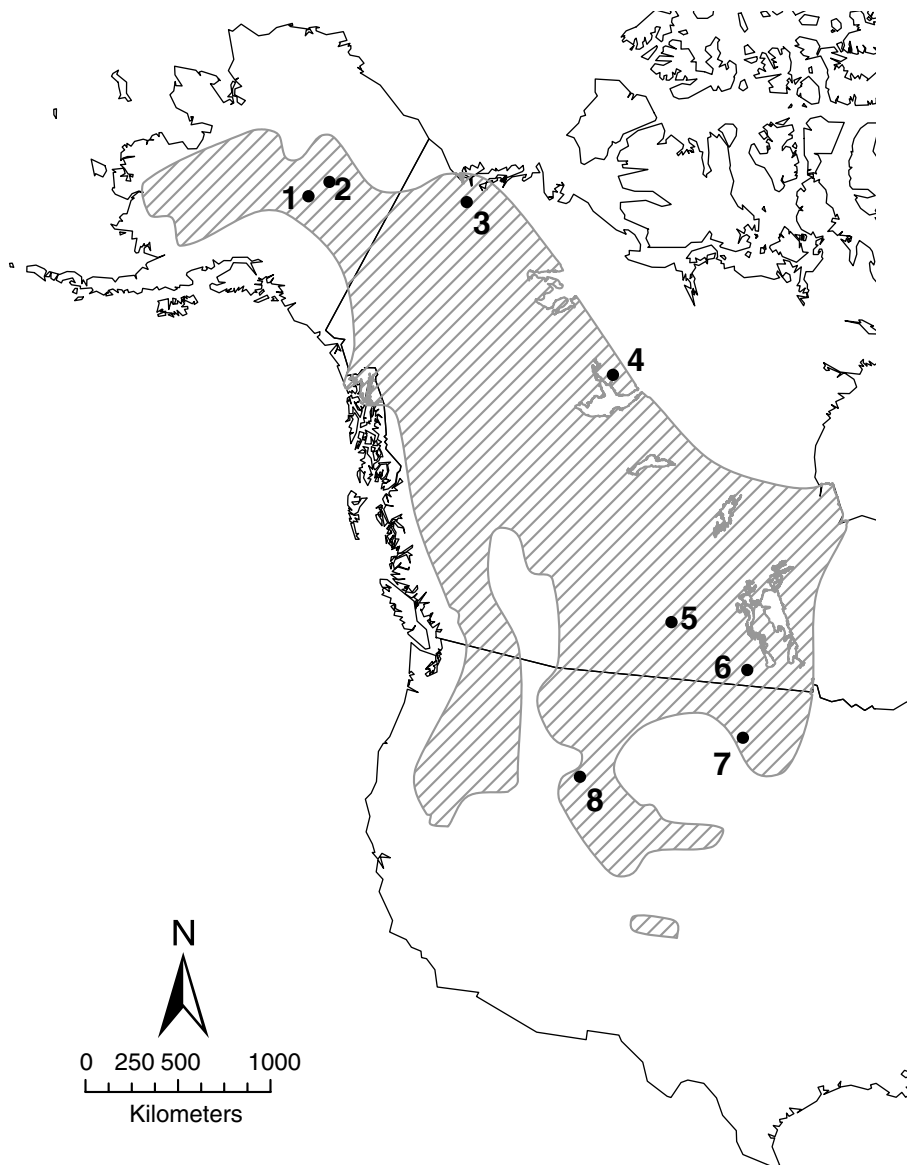


Figure 1. Map of lesser scaup breeding range (Ridgely et al. 2007). Dots denote field sites, 1 = Minto Flats State Game Refuge, 2 = Yukon Flats National Wildlife Refuge, 3 = Cardinal Lake, 4 = Yellowknife, 5 = St Denis National Wildlife Area, 6 = Erickson, 7 = Missouri Coteau, 8 = Red Rock Lakes National Wildlife Refuge.

nests with >14 eggs did not represent the effort of a single breeding female and excluded them (n = 6).

We could not distinguish replacement clutches from first breeding attempts because this study involved unmarked birds. However, this limitation likely applies to most studies of clutch size variation given that the number of nests initiated per female is underestimated even when individuals are well tracked (McPherson et al. 2003). Replacement clutches include fewer eggs and occur throughout the nesting season (i.e. after the earliest nests fail). Afton (1984) reported that re-nesting propensity in scap is generally lower than that observed in earlier-nesting waterfowl species (Arnold et al. 2010); the inability to exclude renests from our dataset likely does not cause significant bias.

### Growing season length

To calculate annual values of GSL at each site between 1988 and 2007, 1° × 1° maps produced from date of soil freeze (FREEZE) and thaw (THAW) were used (Smith et al. 2004), with  $GSL = FREEZE - THAW$ . The dates were derived from passive microwave satellite observations that correlate well with surface air temperatures and annual seasonal events such as the timing of snow cover (Smith et al. 2004). Data were not available for latitudes south of 46°N, so estimates of GSL for the Montana site were based on a location (46°N, 111°W) that closely reflects conditions at the site (Warren unpubl.). Data for the Yellowknife site (62°N, 114°W) were also unavailable, so values were estimated by averaging values obtained from 62°N, 112°W and 62°N, 116°W. Long-term means and standard deviations provide a general characterization of the GSL at each site (Table 2).

### Statistical analyses

In all analyses, we employed general linear mixed models. Such models take advantage of correlation among clusters of observations (covariance) and enable us to account for dependence among groups of birds at the region, site and year level (random effects), while examining the specific influence of GSL or other fixed effects on clutch initiation date and clutch size (Littell et al. 2006, Cheng et al. 2008).

### Clutch initiation date

To evaluate the relative support for a relationship between clutch initiation date and selected climatic variables, we used an information-theoretic approach (Burnham and Anderson 2002). We developed a set of candidate models that evaluated whether clutch initiation date was a function of an additive or multiplicative combination of fixed and random effects. The main fixed effect of interest was annual GSL, but the relative importance of each component of this composite variable, i.e. THAW and FREEZE dates, were also assessed. To compare the explanatory value of climatic attributes relative to a more commonly used geographic metric, we evaluated the effect of latitude. The same covariance structure (random effects of region, site, year, and year × site interaction) was retained for all models to ensure that model selection results were directly comparable. A Kenward–Roger correction was applied in computing denominator degrees of freedom (PROC MIXED, SAS Inst. 2002).

Because sample sizes (2283 for laying date and 1984 for clutch size) greatly exceeded the maximum number of estimable parameters in our models (8 and 6, respectively;  $n/K > 200$ ), we used first-order Akaike’s information criterion (AIC) to rank the models. In addition, because we controlled for non-independence due to region or site and year by using random effects, we did not incorporate a variance inflation term (Burnham and Anderson 2002). Semi-partial  $R^2$  statistics ( $R^2_{\beta}$ ) have limited utility in linear mixed models (Edwards et al. 2008), thus inference concerning fixed effects was based on precision (85% confidence interval) of regression coefficients ( $\beta$ ) estimated by the restricted maximum likelihood method (West et al. 2007, Arnold 2010). Inference regarding random effects in the best-approximating model was based on intraclass correlation coefficients,  $\rho$ , which describe the proportion of the total random variation in CID that is described by each random factor, based on conditional variance components,  $\tau$  (Singer 1998, McMahon and Diez 2007).

### Clutch size

To evaluate the relative support for a relationship between clutch size and key explanatory variables, we used an information-theoretic approach, as described for clutch initiation date, and all models maintained the same covariance structure, with random effects of site, year, and year × site interaction. Candidate models were specified to

Table 2. Growing season length (GSL) data for each field site, 1988–2007. Shown are mean spring thaw and fall freeze days (where 1 January = day 1), growing season lengths (i.e. freeze date – thaw date) and standard deviation (SD).

Site	Spring thaw		Fall freeze		Growing season length	
	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range
Missouri Coteau	59 (18)	27–90	316 (13)	294–336	257 (20)	223–290
Erickson, Manitoba	88 (12)	64–106	310 (14)	284–336	221 (15)	194–247
St Denis National Wildlife Area, Saskatchewan	87 (10)	68–100	305 (11)	288–325	218 (13)	194–244
Yellowknife, Northwest Territories	138 (11)	103–165	311 (5)	299–336	173 (12)	142–213
Cardinal Lake, Northwest Territories	137 (8)	121–149	273 (7)	264–285	136 (9)	121–149
Red Rock Lakes National Wildlife Refuge, Montana	142 (18)	90–174	241 (35)	122–279	100 (24)	32–143
Yukon Flats National Wildlife Refuge, Alaska	129 (6)	120–139	266 (6)	250–278	137 (10)	113–152
Minto Flats State Game Refuge, Alaska	145 (6)	136–156	261 (8)	242–271	116 (8)	102–134

represent the reduced clutch size and rate of decline hypotheses. In addition, seasonally-declining clutch size is a consistently observed pattern in single-brooded birds, so clutch initiation date (CID) was included in our biological null model (Rowe et al. 1994, Krapu et al. 2004). Models containing CID<sup>2</sup> were also evaluated to investigate a possible non-linear relationship between clutch size and CID. Main fixed effects considered were annual GSL, THAW and FREEZE dates, and latitude. Denominator degrees of freedom and procedures for making inference were as described for clutch initiation date.

## Results

### Growing season length

The sampled gradient of average GSL was ~2.5 times longer at Missouri Coteau than at Montana, with a wide range of GSL values across sites (Table 2). Annual variation in GSL was highest at Montana, where both yearly thaw and freeze dates varied considerably.

### Clutch initiation date

Across all years, mean clutch initiation dates ranged from 9 June at Minto Flats to 23 June at Cardinal Lake (Table 3). There was no support for an influence of GSL on clutch initiation date, as the deviance estimated by this model was no different than the biological null (random effects only) model (Table 4). The best-supported model suggested that clutch initiation date was positively related to spring thaw dates. Although we cannot rule out the possibility that the biological null ( $\Delta AIC = 1.2$ ) was also suitable for explaining variation in clutch initiation date, Akaike weights ( $w_i$ ) provide an evidence ratio of 37% in favour of including spring thaw date as a predictor of clutch initiation date ( $CID_{ijk} = 157.9$  (SE = 6.3) + 0.06 (SE = 0.03)  $\times$  THAW<sub>jk</sub>), and suggest that spring thaw is a better predictor of timing of nesting than either fall freeze ( $w_i = 0.20$ ) or latitude ( $w_i = 0.14$ ); 85% confidence intervals for both of these parameters included zero.

There was a positive relationship between spring thaw date and CID ( $\beta_{\alpha=0.15} = 0.009-0.112$ ), but the effect was weak (Fig. 2). Additional unexplained variation in CID, as measured by  $\rho$ , indicated that approximately 34% of variance was attributable to region, whereas site, year and

Table 4. Ranking of mixed models accounting for variation in clutch initiation dates of *Aythya affinis*. Models are ranked by differences in Akaike's information criterion,  $\Delta AIC$ . FREEZE = annual date of soil freeze, THAW = annual date of soil thaw. GSL = growing season length (FREEZE-THAW),  $-2\log L$  = Deviance,  $w_i$  = Akaike weight.

Model structure <sup>a</sup>	K <sup>b</sup>	$-2\log L$	$\Delta AIC$	$w_i$
Region+Site $\times$ Year+THAW	7	16541.7	0.0	0.37
Region+Site $\times$ Year	6	16544.9	1.2	0.20
Region+Site $\times$ Year+FREEZE	7	16542.9	1.2	0.20
Region+Site $\times$ Year+Latitude	7	16543.6	1.9	0.14
Region+Site $\times$ Year+GSL	7	16544.6	2.9	0.08
Intercept	2	17225.1	673.4	0.0

<sup>a</sup> The + between variables indicates an additive effect, the  $\times$  denotes interaction; where interactions are listed, main effects were also included.

<sup>b</sup> Number of parameters estimated.

year  $\times$  site interaction effects were relatively small (2, 4, and 6%, respectively). When comparing the conditional variance components to those in the unconditional (random effects only) model, we observed little change in  $\tau_{\text{Site}}$ ,  $\tau_{\text{Year}}$  or  $\tau_{\text{Year} \times \text{Site}}$ , which indicates that site or year  $\times$  site level variation in CID is not being accounted for by thaw dates. In summary, although timing of nesting varied between regions, it was remarkably similar among sites and years, and we obtained only weak support for predictions of the flexible nesting date hypothesis.

### Clutch size

On average, female scaup nesting at Montana laid 2 fewer eggs than did females at Manitoba (Table 3). No models containing a region effect or non-linear effects of CID received any support. Similarly, none of the climatic variables, nor latitude, had a discernable effect on clutch size (Table 5). The best-approximating model was the biological null ( $w_i = 0.97$ ), which included a fixed effect of CID (Fig. 3) and random effects of site, year and a year  $\times$  site interaction ( $\text{Clutch}_{ijk} = 23.0$  (SE = 0.7)  $- 0.084$  (SE = 0.004)  $\times$  CID<sub>jk</sub>).

Values for  $\rho$  indicated that approximately 23% of clutch size variation occurred among sites and 1% occurred among years, with an additional 4% associated with annual variation within a site. The remaining 72% (i.e. residual covariance term) of clutch size variability was unexplained by the variables we considered.

Table 3. Summary reproductive data for each field site, all years combined. For clutch initiation date, 1 January = day 1. Shown are mean values, standard deviation (SD), and sample size (n).

Site	Clutch initiation date		Clutch size	
	Mean (SD)	n	Mean (SD)	n
Missouri Coteau	166.1 (10.1)	629	9.6 (1.8)	558
Erickson, Manitoba	170.2 (9.8)	128	9.8 (1.6)	128
St Denis National Wildlife Area, Saskatchewan	166.8 (10.9)	263	9.4 (1.6)	224
Yellowknife, Northwest Territories	170.0 (9.4)	43	8.5 (1.4)	84
Cardinal Lake, Northwest Territories	173.8 (8.1)	520	8.3 (1.6)	492
Red Rock Lakes National Wildlife Refuge, Montana	171.9 (9.0)	247	7.8 (1.6)	223
Yukon Flats National Wildlife Refuge, Alaska	161.6 (9.1)	398	8.2 (1.5)	352
Minto Flats State Game Refuge, Alaska	160.3 (8.8)	341	9.6 (1.6)	259

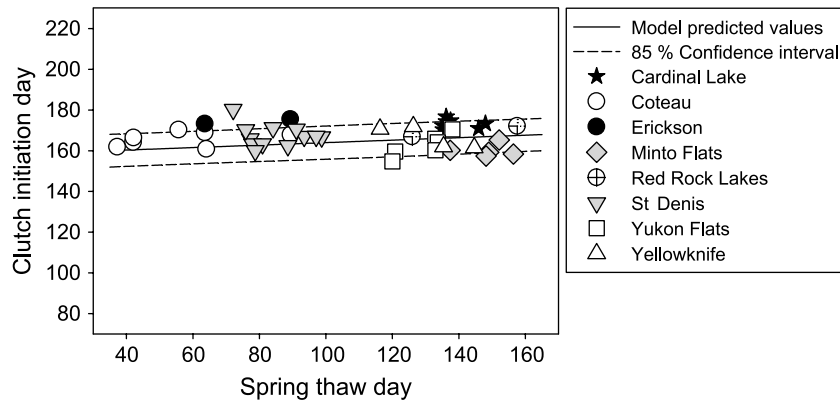


Figure 2. Model-based estimates of mean clutch initiation date (solid line) in lesser scaup *Aythya affinis*, including an 85% confidence interval (dashed lines), as a function of spring thaw day (1 January = day 1), after accounting for random effects of region, site and year, and their interaction. Annual means are plotted for each site, as described in the legend.

## Discussion

Hypothesized causes of spatial variation in reproductive ecology are infrequently examined. Here, we used a novel approach to assess specific effects of geographic variation in the length of the growing season on clutch initiation date, clutch size, and the seasonal pattern of clutch size decline in a temperate-breeding bird. By accounting explicitly for uncontrolled variation related to region, site and year in our analyses, we provide direct evidence that clutch initiation dates in scaup are only weakly correlated with growing season length or its components, suggesting that timing of breeding in these birds is not strongly responsive to climatic variation. Similarly, our results suggest that clutch size is most influenced by clutch initiation date, for the set of variables that we considered.

### Growing season length and clutch initiation dates

Breeding scaup are widely distributed and therefore experience a broad range of climatic conditions on their nesting grounds. For example, over a latitudinal range of 22°, the average timing of soil freeze varies by 43 d, average values for timing of soil thaw encompass an even greater range of

78 d (Table 2). Elevation also has a clear effect on soil freeze and thaw cycles, with the high elevation site (Montana) experiencing a very short GSL ( $100 \pm 24$  d) relative to a high latitude site such as Cardinal Lake ( $136 \pm 8$  d). In turn, these varying climatic conditions influence scaup clutch initiation dates, with scaup in Alaska tending to nest earlier than those in the mid-continent. Accounting for this regional effect, we still found that when spring thaw dates are delayed, clutch initiation dates tend to be later. However, the effect is very small, with scaup nesting approximately 1 d earlier for every 16 d reduction in thaw date.

Our finding that scaup clutch initiation date is only weakly related to climatic variables is in contrast to some other duck species that more closely track spring conditions and start nesting earlier in years with warmer springs (Hammond and Johnson 1984, Serie et al. 1992, Drever and Clark 2007). Our findings show that scaup tend to nest at a relatively fixed date and do not respond strongly to spring phenology. Timing of breeding in scaup may be based more on fixed cues (e.g. photoperiod) encountered on the breeding grounds or on timing of availability of critical resources. These hypotheses merit further investigation.

Visser et al. (1998) found that timing of reproduction in great tits *Parus major* did not respond to changes in mean spring temperature and suggested that this could lead to a

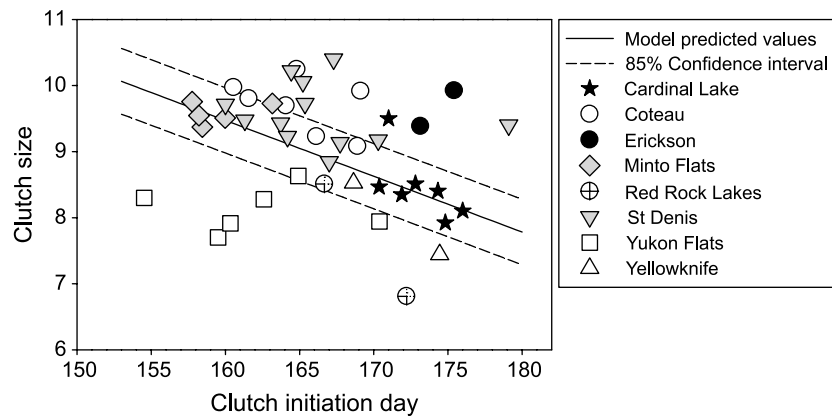


Figure 3. Model-based estimates of mean clutch size (solid line) in lesser scaup *Aythya affinis*, including an 85% confidence interval (dashed lines), as a function of clutch initiation day (1 January = day 1), after accounting for random effects of site, year, and their interaction. Annual means are presented for each site, as described in the legend.

Table 5. Ranking of mixed models accounting for variation in clutch size of *Aythya affinis*. Models are ranked by differences in Akaike's information criterion,  $\Delta AIC$ . CID =clutch initiation date, FREEZE =annual date of soil freeze, THAW =annual date of soil thaw. GSL =growing season length (FREEZE-THAW),  $-2\log L$  = Deviance,  $w_i$  =Akaike weight.

Model structure <sup>a</sup>	K <sup>b</sup>	$-2\log L$	$\Delta AIC$	$w_i$
Site $\times$ Year + CID	6	7169.7	0.0	0.93
Site $\times$ Year + CID + Latitude	7	7173.9	6.2	0.04
Site $\times$ Year + CID + Freeze	7	7175.8	8.2	0.02
Site $\times$ Year + CID + GSL	7	7177.3	9.6	0.01
Site $\times$ Year + CID + Thaw	7	7178.2	10.5	0.00
Site $\times$ Year + CID $\times$ GSL	8	7190.4	24.7	0.00
Intercept	2	7992.6	814.9	0.00

<sup>a</sup> The + between variables indicates an additive effect, the  $\times$  denotes interaction; where interactions are listed, main effects were also included.

<sup>b</sup> Number of parameters estimated.

mismatch between timing of reproduction and food abundance with potential consequences for population viability. Recently, Helm (2009) confirmed that a reliance on fixed cues for timing of breeding can limit the reproductive success of birds. When captive stonechats *Saxicola torquata* of Siberian origin were kept under temperature and day-length conditions similar to those experienced by stonechats breeding in less constrained environments, they did not adjust clutch initiation dates, and consequently suffered reduced reproductive success. If wild scaup are similarly unresponsive to variation in annual weather patterns and do not alter clutch initiation dates to contend with novel climatic conditions, as our data suggest, their reproductive success might also be reduced. Such a response is likely to be particularly important in scaup because of lower recruitment of late-hatching offspring (Dawson and Clark 2000).

We suggest that captive studies that directly examine the influence of factors such as photoperiod, ambient temperature, and abundance of food on timing of breeding in scaup might clarify the relative importance of fixed and proximate cues for this species. Such information will be needed to identify whether or not there is potential for mismatched timing of breeding. Long-term monitoring of scaup breeding biology in wild populations is also recommended; data from such studies will further increase our understanding of reproductive decisions in this species. In addition, because population growth rates in scaup may be sensitive to changes in duckling survival (Koons et al. 2006), we concur with Hobson et al. (2009) that identifying possible links between mismatched timing of breeding and survival of ducklings warrants further study.

## Clutch size

As expected, clutch size declined with advancing clutch initiation date in scaup (Fig. 3). Our findings were not consistent with the reduced clutch size or the rate of decline hypotheses; the majority of clutch size variation was unexplained by our explanatory variables. Variation in clutch size between sites was relatively high, and at sites with shortened GSL, scaup tended to lay, on average two less eggs (Table 3). The biological significance of this small reduction is unknown, but variation in proximate and

ultimate factors at this scale might be important predictors of clutch size. For example, if scaup breeding in more time-constrained areas are more nutritionally constrained during laying, are at greater risk of nest predation, or if more young birds breed in these areas, a pattern of reduced clutch size would be expected (Afton 1984, Arnold et al. 1987, Patten 2007). Research on individual-level effects and the link between clutch size and environmental covariates is necessary to obtain a more complete understanding of variation in clutch size of scaup.

Unlike what has been observed in northern pintails, we found no evidence of an increased seasonal rate of clutch size decline in scaup breeding at high latitudes. Mechanisms that lead to increasing rates of seasonal clutch size decline are not well understood but may be related, in part, to differences in nutrient availability on the breeding grounds (Krapu et al. 2002). In their multi-year study, Krapu et al. (2004) observed that intraspecific rates of clutch size decline in three waterfowl species were annually variable. They suggested that reduced rates of clutch size decline were related to variation in wetland habitat conditions that may have resulted in increasing protein and carbohydrate availability. However, these species are known to utilize primarily exogenous nutrients for egg production. Lesser scaup rely more heavily on endogenous nutrients. Therefore, nutrient reserves acquired during spring migration may have a stronger influence on seasonal clutch size patterns in this species (Afton and Ankney 1991, Esler et al. 2001).

Scaup do not seem to respond strongly to seasonally-imposed time constraints that characterize the areas in which they breed, which results in low levels of annual and between site variation in clutch initiation date and clutch size. Our results show that, although breeding scaup face varying climatic conditions across their breeding range, relatively trivial adjustments to clutch initiation dates were made in response to these cues (Fig. 2). We suggest that investigations of the mechanisms that scaup use to time the onset of breeding will help us to understand why some animals are more phenotypically plastic than others. Further, to clarify the extent to which our results represent a generalized biogeographical pattern, we recommend that these analyses be repeated in other endotherms that breed across broad environmental gradients of GSL.

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