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Gary Krapu

U.S. Geological Survey, Northern Prairie Wildlife Research Center

Glen Sergeant

U.S. Geological Survey, Northern Prairie Wildlife Research Center

Alison Perkins

U.S. Geological Survey, Northern Prairie Wildlife Research Center

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DOES INCREASING DAYLENGTH CONTROL SEASONAL CHANGES IN CLUTCH SIZES OF NORTHERN PINTAILS (*ANAS ACUTA*)?

GARY L. KRAPU,^{1,3} GLEN A. SARGEANT,¹ AND ALISON E. H. PERKINS^{2,4}

¹U.S. Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, North Dakota 58401, USA; and

²California Waterfowl Association, Sacramento, California 95834, USA

ABSTRACT.—We evaluated spatiotemporal variation in clutch sizes of Northern Pintails (pintails; *Anas acuta*) nesting in California (1985 to 1996), North Dakota (1982 to 1985), Saskatchewan (1982 to 1985) and Alaska (1991 to 1993) to determine whether seasonal declines in clutch size varied in ways that were consistent with a controlling influence of increasing day length. Pintails began nesting in mid-March in California, mid-April in North Dakota and Saskatchewan, and mid-May in Alaska. Observed durations of nesting were 70 ± 2.6 days (SE) in California, 60 ± 6.3 days in North Dakota, 66 ± 1.3 days in Saskatchewan, and 42 ± 0.7 days in Alaska. Annual differences were the principal source of variation in mean clutch sizes ($\hat{\sigma}_v^2 = 0.15$, SE = 0.049), which varied little among study locations ($\hat{\sigma}_A^2 = 0.002$, SE = 0.013). Predicted rates of seasonal decline in clutch sizes increased with latitude early in the nesting season, but declined as the nesting season progressed, except in California. Rates of decline in clutch sizes thus were not directly related to rates of increase in day length. Predicted declines in numbers of eggs per clutch over the nesting season were similar for all four locations (range, 3.05–3.12) despite wide variation in durations of nesting. Evidence suggests that reduced nutrient availability during nesting contributes to a higher rate of decline in clutch sizes in Alaska than in temperate regions. Pintails that nest early lay large initial clutches, but thereafter clutch sizes decline rapidly and breeding terminates early. This reproductive strategy is adaptive because young that hatch earliest exhibit the highest survival rates; however, the conversion of grassland to cropland on the primary prairie breeding grounds has reduced hatching rates of clutches laid early in the nesting season. Under these conditions, the limited capacity to renest in late spring on their prairie breeding grounds probably has contributed to Pintail population declines. Received 28 September 2000, accepted 29 October 2001.

RESUMEN.—Evaluamos la variación espacio-temporal del tamaño de la nidada de individuos de *Anas acuta* que anidan en California (1985 a 1996), North Dakota (1982 a 1985), Saskatchewan (1982 a 1985) y Alaska (1991 a 1993) para determinar si la reducción estacional en el tamaño de la nidada varía de modo consistente con el incremento en la longitud del día. *A. acuta* comienza a nidificar a mediados de marzo en California, mediados de abril en North Dakota y Saskatchewan y mediados de mayo en Alaska. El período de nidificación observado fue de 70 ± 2.6 días (EE) en California, 60 ± 6.3 días en North Dakota, 66 ± 1.3 días en Saskatchewan y 42 ± 0.7 días en Alaska. Las diferencias anuales fueron la principal fuente de variación en el tamaño medio de la nidada ($\hat{\sigma}_v^2 = 0.15$, EE = 0.049), el cual varió poco entre los sitios de estudio ($\hat{\sigma}_A^2 = 0.002$, EE = 0.013). Las tasas predichas para la reducción estacional del tamaño de la nidada incrementaron con la latitud al comienzo de la estación de nidificación, pero declinaron a medida que la estación avanzó, excepto en California. De este modo, las tasas de reducción del tamaño de la nidada no estuvieron directamente relacionadas con las tasas de incremento en la longitud del día. Las reducciones predichas para el número de huevos por nidada durante la estación de nidificación fueron similares para los cuatro sitios (rango, 3.05–3.12), a pesar que la duración del período de nidificación varía ampliamente. La evidencia sugiere que una reducida disponibilidad de nutrientes durante la nidificación contribuye a que la tasa de reducción del tamaño de la nidada sea mayor en Alaska que en las regiones templadas. Los individuos que nidifican temprano ponen nidadas iniciales de gran tamaño, pero luego el tamaño declina rápidamente y el período reproductivo termina más temprano. Esta estrategia reproductiva es

³ E-mail: gary_krapu@usgs.gov

⁴ Present address: Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, Montana 59812, USA.

adaptativa porque los jóvenes que eclosionan más temprano exhiben las tasas de supervivencia más altas. Sin embargo, la conversión de pastizales a campos de cultivo de las principales áreas reproductivas (i.e., praderas) ha reducido las tasas de eclosión de las nidadas puestas a principio de la estación de nidificación. Bajo estas condiciones, la limitada capacidad para volver a nidificar a fines de la primavera en estas áreas reproductivas probablemente ha contribuido a que las poblaciones de *A. acuta* declinen.

CLUTCH SIZES OF many species of birds decline progressively during the nesting season (Lack 1968, Klomp 1970), including waterfowl that breed in temperate and northern regions of the northern hemisphere (Rowher 1992, Briggs 1993). Reproductive fitness is the ultimate factor controlling seasonal declines in clutch size, but proximate factors remain poorly understood. With Julian date being the best predictor of clutch size in many species of birds, day length has been identified as possibly being the primary proximate cue controlling rates of seasonal decline in clutch sizes (Murphy and Haukioja 1983, Bluhm 1988). The hypothesis that day length regulates the seasonal decline in clutch sizes of birds through an intrinsic physiological mechanism is intriguing because day length is the most reliable cue to which birds are known to be exposed during the breeding season (Farner 1964). In spring, day length increases with date and with latitude, so rate of increase in day length could potentially serve as a reliable cue for regulating rate of decline within seasons and across latitudes. Such a physiological mechanism would potentially be adaptive because survival rates of young waterfowl decline with hatch date in most species that have been studied (Rotella and Ratti 1992, Cooke et al. 1995, Grand and Flint 1996, Dzus and Clark 1998, Guyn and Clark 1999) and more rapidly in northern than temperate regions (Grand and Flint 1996, Guyn and Clark 1999). However, experiments that could corroborate or refute the hypothesis that day length is the primary proximate cue regulating rates of seasonal decline in clutch sizes have not been conducted.

To determine whether rates of increase in day length control seasonal declines in clutch sizes of temperate-breeding ducks, we studied spatiotemporal variation in clutch sizes of the Northern Pintail (*Anas acuta*; hereafter "pintail") across its latitudinal range of breeding in North America. We selected pintails for study because the species breeds across the widest range of latitudes of any species of duck (Bell-

rose 1980), exhibits low natal philopatry (Johnson and Grier 1988), and lacks significant genetic variation across its breeding range in North America (Cronin et al. 1996). We hypothesized that rates of decline in pintail clutch sizes should increase with latitude in a pattern consistent with rates of increase in day length if the seasonal decline in clutch size is controlled primarily by rate of increase in day length. Specifically, the objective of our research was to determine whether seasonal declines in clutch sizes of pintails vary with latitude, and if so, whether variation is consistent with postulated explanations for seasonal declines in clutch sizes.

METHODS

We analyzed clutch-size data collected in California (1985 to 1996), North Dakota (1982 to 1985), Saskatchewan (1982 to 1985), and Alaska (1991 to 1993). Data from California were collected by researchers affiliated with the California Waterfowl Association in four physiographic regions: the Suisun Marsh (an estuary), the Sacramento Valley, the San Joaquin Valley, and the intermountain region of northeastern California (see McLandress et al. [1996] for site descriptions). In North Dakota and Saskatchewan, data were collected in the Prairie Pothole Region by researchers affiliated with the Northern Prairie Wildlife Research Center or its cooperators. In Alaska, data were collected along the lower Kanshunuk River drainage on the outer fringe of the Yukon Delta National Wildlife Refuge by researchers affiliated with the Alaska Fish and Wildlife Research Center. Kantrud et al. (1989) described the Prairie Pothole Region in North Dakota, Greenwood et al. (1995) described study sites in Saskatchewan, and Flint and Grand (1996) described the Alaska study area.

Nest searches were conducted and clutch sizes were determined by procedures of Klett et al. (1986; California, North Dakota, Saskatchewan) or Flint and Grand (1996; Alaska). When

TABLE 1. Julian dates of first and last observed nest initiations of Northern Pintails and nesting interval (days).

Location	<i>n</i>		First initiation		Last initiation		Nesting interval
	Nests	Years	Mean (SE)	Range	Mean (SE)	Range	Mean (SE)
California	829	12	80 (2.7)	69–105	150 (2.8)	136–170	70 (2.6)
North Dakota	220	4	110 (4.1)	100–120	170 (2.4)	165–174	60 (6.3)
Saskatchewan	453	4	104 (2.3)	100–110	170 (1.9)	167–175	66 (1.3)
Alaska	339	3	136 (2.9)	133–142	178 (3.5)	174–185	42 (0.7)

each nest was discovered, the date, location, number of eggs, and stage of embryonic development (Weller 1956) were documented. At each revisit to a nest, the number of eggs and stage of development of embryos were recorded. A nest initiation date was estimated for each nest by backdating from the date of discovery to adjust for laying (assuming a laying rate of one egg per day) and stage of embryonic development. In California, nest searches began during the last week of March, except in the intermountain region, where searches started during the second week of April because nesting began later. Nest searches continued until mid-June at all California sites. In North Dakota and Saskatchewan, nest searches were begun the first week of May and continued until late June. In Alaska, nest searches were conducted from mid-May through mid-July.

Day lengths were determined by measuring the interval between sunrise and sunset and also with civil twilight included. Relative day lengths of the four study locations were affected little by the inclusion of civil twilight, so here we present results for intervals between sunrise and sunset only. Day length was determined for each date over the nesting period for each location where pintail clutch sizes were measured. Day lengths for the Central Valley of California (Sacramento; 38°34'N), the Prairie Pothole Region of North Dakota (Bismarck; 46°49'N) and Saskatchewan (Regina; 50°27'N), and the Yukon-Kuskokwim Delta in Alaska (Bethel; 60°47'N) were obtained from records maintained by the U.S. Naval Observatory, Washington, D.C.

We used random effects models to estimate annual (σ_V^2) and regional (σ_A^2) variation in mean clutch size (*c*) and bootstrapping to estimate standard errors of variance components. Our model [$c_{ijk} = \mu + a_i + y_{j(i)} + \epsilon_{k(ij)}$, $a_i \sim N(0, \sigma_A^2)$, $y_j \sim N(0, \sigma_V^2)$] included two factors: ar-

reas (a_i) and years nested within areas ($y_{j(i)}$). We used Akaike's Information Criterion (AIC; Burnham and Anderson 1998) to select multiple regression models that best described seasonal changes in clutch size. We considered three types of linear and quadratic candidate models for each location: a simple relation between clutch sizes and dates (simple linear/simple quadratic models); a parallel linear or quadratic relation for each year (parallel lines models); and a linear or quadratic relation for each year (full interaction models). After using AIC to select regression models, we used diagnostic plots to evaluate fits. To estimate annual declines in mean clutch sizes, we used differences between maximum and minimum values predicted by our models for observed dates of nest initiations. We used S-PLUS 2000 software (MathSoft 1997) for analyses.

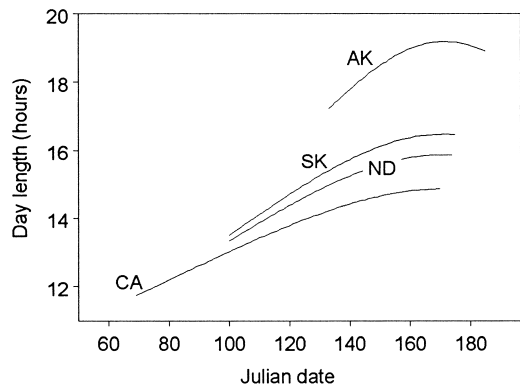


FIG. 1. Nesting intervals of Northern Pintails and associated day lengths on four study areas in temperate and Arctic North America. Day length encompasses the period from sunrise to sunset. Information is from the Central Valley in California, the Prairie Pothole Region of North Dakota and Saskatchewan, and the Yukon-Kuskokwim Delta in Alaska.

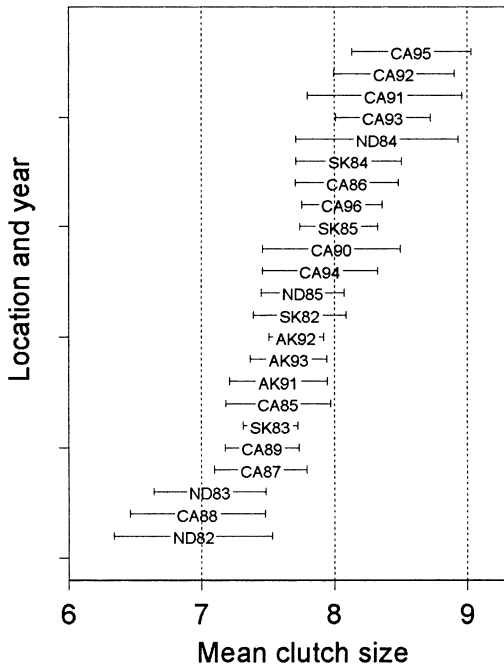


FIG. 2. Mean clutch sizes of Northern Pintails breeding at study locations in California (CA), North Dakota (ND), Saskatchewan (SK), and Alaska (AK) during 1982–1996. Bars indicate 95% confidence intervals.

length was 5.2 h longer in Alaska (17.4 h) than in California (12.2 h) (Fig. 1). During periods of nest initiation, day length varied by 2.0 h in Alaska, 2.5 h in North Dakota, 3.1 h in California, and 3.0 h in Saskatchewan (Fig. 1). Annual differences were the principal source of variation in mean clutch sizes ($\hat{\sigma}_Y^2 = 0.15$, SE = 0.049), which varied little among the four study locations ($\hat{\sigma}_A^2 = 0.002$, SE = 0.013) (Fig. 2).

Season-long relations between clutch size and initiation date were best described by a linear parallel lines model in California, a quadratic parallel lines model in North Dakota and Saskatchewan, and a quadratic model with full interaction in Alaska (Table 2). However, small differences in AIC (i.e. <2; Burnham and Anderson 1998) indicated that some models we selected were not markedly superior to all competitors (Table 2). Mean clutch sizes predicted by models are shown in Figure 3. Predicted rates of decline in clutch sizes (regression model slopes) early in the nesting season increased with latitude (Fig. 4, inset); however, changes in clutch size were not directly related to rates of change in day length (Fig. 4). Predicted declines in numbers of eggs per clutch over the nesting season were similar for all four locations (Table 3).

RESULTS

Observed dates of first nest initiation ranged from 9 March (Julian date [JD] 69) in California to 12 May (JD 133) in Alaska and dates of last nest initiation ranged from 18 June (JD 170) in California to 4 July (JD 185) in Alaska (Table 1). The observed nesting interval ranged from an average of 70 days in California to 42 days in Alaska (Table 1). At the onset of nesting, day

DISCUSSION

Several environmental factors probably contributed to annual variation in pintail clutch sizes at the four sites. Clutch sizes decline as nest initiation dates advance (Esler and Grand 1994), so any environmental factor that causes timing of nesting to vary among years contributes to annual variation in clutch sizes. In the Prairie Pothole Region, ambient temperatures

TABLE 2. Results of model selection describing changes in clutch sizes of Northern Pintails in California (1985–1996), North Dakota (1982–1985), Saskatchewan (1982–1985), and Alaska (1991–1993). For each site, the explanatory variable *d* represents the number of days elapsed from the earliest observed date of nest initiation. Δ AIC values <2 identify reasonable candidate models, with smallest values indicating best models. The subscript *i* distinguishes years.

Model	Δ AIC			
	California	North Dakota	Saskatchewan	Alaska
$y = \alpha + \beta d$	5.3	13.7	4.7	11.3
$y = \alpha_i + \beta d$	0	3.8	1.7	0.3
$y = \alpha_i + \beta_i d$	5.6	7.9	5.8	2.5
$y = \alpha + \beta d + \gamma d^2$	7	9	1.8	13.2
$y = \alpha_i + \beta d + \gamma d^2$	1.6	0	0	0.7
$y = \alpha_i + \beta_i d + \gamma_i d_i^2$	12.8	4	5.7	0

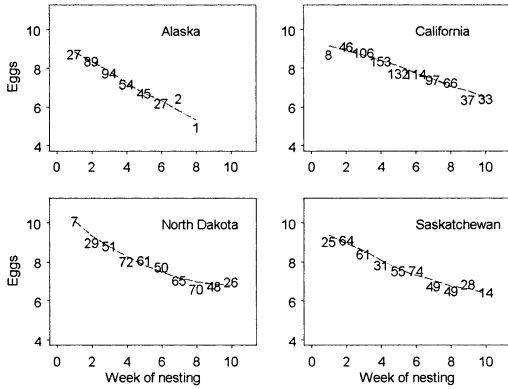


FIG. 3. Mean clutch sizes (sample sizes) and means of corresponding model predictions, by seven-day interval, for Northern Pintails nesting at locations in California (1985–1996), North Dakota (1982–1985), Saskatchewan (1982–1985), and Alaska (1991–1993).

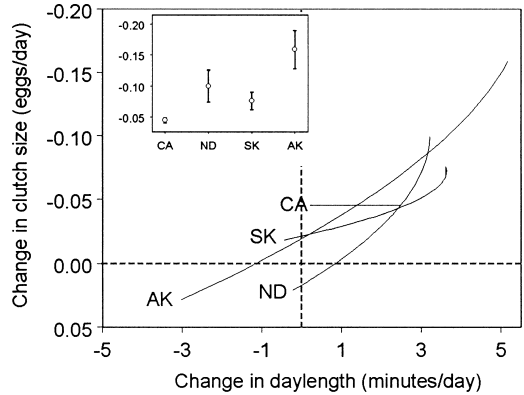


FIG. 4. Relations between rates of decline in clutch size and rates of change in day length for Northern Pintails in four regions of North America. Inset shows rate of change (\pm SE) in clutch size at the onset of nesting.

in April vary widely among years and affect the timing of arrival on breeding sites and the onset of nesting (Hammond and Johnson 1984). In cold springs, maintenance energy requirements increase (Kendeigh et al. 1977). Accordingly, when delaying nesting, birds expend a higher proportion of lipids to meet nonreproductive needs, and subsequently lay smaller initial clutches. In North Dakota, for example, clutch sizes were smallest in 1982 and 1983 (Fig. 2), years when April temperatures were below average (National Oceanic and Atmospheric Administration 1961–1990). Clutch sizes of pintails also are influenced by annual variation in water conditions on the breeding grounds (G. Krapu unpubl. data), a phenomenon that has also been documented for Gadwalls (Pietz et al. 2000). In California, pintail clutch sizes were smallest in 1988 (Fig. 2), a year when wetland habitat on all study areas

was affected by extremely dry conditions (A. E. H. Perkins et al. unpubl. data).

Day length is the primary proximate cue that brings ducks into a general state of readiness for migration and reproduction (Bluhm 1992). Pintails are among the first species of ducks to nest (Austin and Miller 1995), having evolved with a relatively short critical day length as indicated by nesting in California starting as early as 9 March (≤ 11.8 h; Fig. 1). Early nesting in northern regions is possible through extensive reliance on endogenous lipids to form early clutches (Mann and Sedinger 1993, Esler and Grand 1994). An early onset of breeding and laying of large first clutches are adaptive because young that hatch earliest survive at the highest rates (Grand and Flint 1996, Guyn and Clark 1999).

Rates of seasonal declines in clutch sizes increased with latitude, but not in patterns consistent with a controlling influence of day

TABLE 3. Predicted clutch sizes of Northern Pintails. Model coefficients are averages over n years, but R^2 values are for best-fitting models identified in Table 2. The variable d represents number of days after the earliest initiation observed at each site.

Location	Study period	n	Mean clutch size	R^2	Range of mean clutch sizes ^a
California	85–96	12	$9.545 - 0.0451d$	0.20	3.11
North Dakota	82–85	4	$9.938 - 0.0999d + 0.0008d^2$	0.22	3.12
Saskatchewan	82–85	4	$9.779 - 0.076d + 0.00038d^2$	0.34	3.11
Alaska	91–93	3	$9.8645 - 0.1589d + 0.0018d^2$	0.32	3.05

^a For nesting intervals of average duration, beginning on average dates of first initiation (see Table 1).

TABLE 4. Liver and gizzard masses of female Northern Pintails by reproductive stage in North Dakota (1969–1971) and Alaska (1987–1988).

Component	Fresh mass gram by reproductive stage ^a					
	Prelying ^b		Laying ^c		Incubation ^d	
	Mean (n)	SE	Mean (n)	SE	Mean (n)	SE
North Dakota						
Liver	23.4 (10)	1.2	20.6 (11)	1.0	16.3 (6)	1.1
Gizzard	28.5 (10)	1.1	24.3 (11)	1.0	20.5 (7)	1.1
Alaska						
Liver	12.2 (25)	0.7	12.4 (12)	0.8	11.0 (16)	0.6
Gizzard	31.5 (24)	1.1	17.7 (12)	1.0	20.8 (16)	1.9

^a Livers and gizzards were weighed to the nearest 0.1 g. All data from Alaska are derived from Mann and Sedinger (1993, table 5).

^b Prelying = no ruptured follicles and no evidence of regressing ovulated follicles or brood patches from a previous attempt. For Alaska, the prelying stage represents the combined pre-RFG and RFG categories.

^c Laying = enlarged ovary with ≥ 1 recently ovulated follicle(s) and ≥ 1 enlarged yolk-filled follicle(s) remaining to be ovulated.

^d Incubation = In North Dakota, incubating females were identified by having a well-developed and vascularized brood patch, no development of ovarian follicles preliminary to reneesting, and were feeding alone when collected. For Alaska, incubating females were collected while on nests allowing stage of embryo development to be determined following Weller (1956).

length (Fig. 4). In California, clutch sizes declined at a constant rate of 0.05 eggs per day throughout the breeding season (Table 3), even though day length increased from the onset to the end of nesting (Fig. 4). In North Dakota and Saskatchewan, rates of decline in clutch sizes initially increased as day length increased but rates slowed late in the season during periods when day length was increasing rapidly. Thus, clutch sizes of pintails were not directly related to changes in day length.

Factors potentially responsible for geographic variation in rates of decline in pintail clutch sizes include differences in food availability (and thus nutrient uptake), endogenous nutrient reserves carried to the breeding grounds by females, and metabolic costs associated with differences in ambient temperatures (Kendeigh et al. 1977, Miller and Newton 1999).

Availability of high-quality foods affects clutch size (Eldridge and Krapu 1988): geographic variation in nutrient uptake during reproduction could thus contribute to latitudinal variation in rates of decline in clutch sizes. To evaluate that possibility, we compared female pintail liver and gizzard mass changes by reproductive stage in North Dakota (Krapu 1974) and central Alaska (Minto Flats; 64°50'N, 148°50'W; Mann and Sedinger 1993) in a non-overlapping series of years. Those organs were selected for comparisons between Alaska and North Dakota because their sizes are affected by digestive activity. Liver masses averaged higher in North Dakota than in Alaska in all reproductive stages and declined from egg lay-

ing to incubation at both sites (Table 4). Lower liver masses in Alaska are consistent with patterns expected with reduced food intake (Raveling 1979, Tome 1984). Larger masses of livers in North Dakota females during reproduction probably resulted from higher metabolic activity including greater storage of protein and lipids (Ziswiler and Farner 1972). Females in North Dakota feed primarily on macro-invertebrates (Krapu 1974) that are abundant sources of most nutrients needed for egg production (Krapu and Swanson 1975), but often are deficient in the essential amino acid cysteine (Alisaukas and Ankney 1992). Glutathione pools exist in livers of birds that are adequately nourished and provide a temporary source of cysteine during molt and egg production, which may have contributed to relatively large liver masses in North Dakota (Murphy and King 1985). Female gizzard masses in central Alaska and North Dakota, on average, declined by 44 and 15%, respectively, from prelying to laying (Table 4). In Alaska, females feed primarily on seeds and other plant parts during egg production (Burriss 1991). Reduced consumption of animal matter by Alaska pintails when forming eggs has been attributed to lower availability of animal foods (Burriss 1991) and may have resulted in a greater reliance on endogenous protein from gizzards to meet part of protein requirements for egg production (see Mann and Sedinger 1993). Patterns of change in liver and gizzard masses during reproduction in North Dakota and Alaska support the hypothesis that high-quality food is less available during repro-

duction in Alaska resulting in reduced nutrient uptake and a more rapid decline in clutch size.

Geographic differences in the amount of endogenous lipids that females carry to the breeding grounds could also have contributed to variation among sites in rates of decline in clutch sizes. In Alaska, Esler and Grand (1994) found that the timing of first nests and clutch size in pintails was related to the size of female lipid reserves. Esler and Grand (1994) also found that the timing of nesting was influenced by the rate at which lipid reserves were being used to meet non-reproductive needs. Use of endogenous lipids by female pintails for non-reproductive purposes has been shown to be exceptionally high in northern regions (Mann and Sedinger 1993, Esler and Grand 1994) when compared to other species of Anatini and Aythyini breeding in temperate regions (Krapu 1981, Ankney and Afton 1988, Alisauskas et al. 1990, Afton and Ankney 1991, Ankney and Alisauskas 1991, Alisauskas and Ankney 1992, and Barzen and Serie 1990). High use of endogenous lipids by pintails for non-reproductive needs in Alaska presumably results in part from nesting starting early when temperatures are lower, but also may reflect food being less available than in temperate regions. Research is needed to determine whether the amount of lipids required to meet non-reproductive needs is higher among pintails breeding in northern than in temperate regions to further assess the hypothesis of reduced nutrient uptake in northern regions contributing to a more rapid rate of decline in clutch sizes.

Ambient temperatures potentially could have contributed to geographic variation in rates of decline in clutch sizes. However, long-term average ambient temperatures for North Dakota (Bismarck; National Oceanic and Atmospheric Administration 1961–1990), Saskatchewan (Regina; Environment Canada 1883–1990), and western Alaska (Bethel; National Oceanic and Atmospheric Administration 1961–1990) at the onset of nesting were 6.1, 4.1, and 4.4°C, respectively, indicating differences were relatively small and not consistent with a higher rate of decline in clutch size in Alaska. The long-term average ambient temperature for California (Sacramento) in March at the onset of breeding is 12.0°C (National Oceanic and Atmospheric Administration 1961–1990), 6 to 8°C higher than in North Dakota, Saskatchewan, and Alaska. Reduced

maintenance energy requirements may contribute to a slower rate of decline in clutch size in California.

Rates of decline in pintail clutch sizes slowed in North Dakota, Saskatchewan, and Alaska as the nesting season progressed (Table 3, Fig. 4) as described previously for Saskatchewan (Duncan 1987) and Alberta (Guyn and Clark 2000). The reduction in rate of decline in clutch sizes occurred during a part of the nesting interval when maintenance energy requirements presumably also were declining with rising ambient temperatures and declining body masses (Krapu 1974, Mann and Sedinger 1993, and Esler and Grand 1994). In California, rates of decline in clutch sizes were lower and did not increase as in North Dakota, Saskatchewan, and Alaska (Table 3). This difference probably reflects, in part, that females in California breed under mild conditions where maintenance energy requirements have less influence on clutch sizes than in North Dakota, Saskatchewan, and Alaska.

Pintail reproductive success on northern nesting grounds is constrained by a high rate of decline in clutch size, a short nesting interval, and a low rate of duckling survival (Grand and Flint 1996). Typically, during years of drought in the species' prairie breeding grounds (1959–1968), the proportion of the continental pintail population moving into northern areas increased and pintail production rates (indexed by the ratio of hatch-year to after-hatch-year birds in the harvest) declined (Smith 1970). Between 1969–1979 and 1980–1992, the latitudinal disparity in age ratios of pintails in the hunter harvest disappeared, suggesting production had declined on the prairie breeding grounds (Hestbeck 1995). This change was associated with the conversion of prime pintail nesting habitat in the western Canadian prairies and parklands to intensively cultivated farmland (Bethke and Nudds 1995). Nest success rates among ground-nesting ducks in the Prairie Pothole Region of Canada during 1982–1985 declined ~4% for every 10% increase in cropland and were lowest early in the nesting season (Greenwood et al. 1995). Potential compensation for the loss of early clutches through renesting is reduced in pintails because later clutches are smaller and nesting terminates exceptionally early (Krapu 2000). Thus, a human-induced decline in nest

success rate on the species' primary temperate breeding grounds in North America, along with intrinsic constraints on compensatory responses, have reduced pintail reproductive success in recent decades disproportionate to other prairie-nesting dabbling ducks. Consequently, the continental pintail population has declined and, unlike other prairie-nesting dabbling ducks, has failed to respond to improved wetland conditions recorded in the 1990s (U.S. Department of the Interior 1997).

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LITERATURE CITED

- AFTON, A. D., AND C. D. ANKNEY. 1991. Nutrient-reserve dynamics of breeding Lesser Scaup: A test of competing hypotheses. *Condor* 93:89-97.
- ALISAUSKAS, R. T., AND C. D. ANKNEY. 1992. The cost of egg laying and its relationship to nutrient reserves in waterfowl. Pages 30-61 in *Ecology and Management of Breeding Waterfowl* (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.
- ALISAUSKAS, R. T., R. T. EBERHARDT, AND C. D. ANKNEY. 1990. Nutrient reserves of breeding Ring-necked Ducks (*Aythya collaris*). *Canadian Journal of Zoology* 68:2524-2530.
- ANKNEY, C. D., AND A. D. AFTON. 1988. Bioenergetics of breeding Northern Shovelers: Diet, nutrient reserves, clutch size and incubation. *Condor* 90:459-472.
- ANKNEY, C. D., AND R. T. ALISAUSKAS. 1991. Nutrient reserve dynamics and diet of breeding female Gadwalls. *Condor* 93:799-810.
- AUSTIN, J. E., AND M. R. MILLER. 1995. Northern Pintail (*Anas acuta*). In *The Birds of North America*, no. 163 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- BARZEN, J. A., AND J. R. SERIE. 1990. Nutrient reserve dynamics of breeding Canvasbacks. *Auk* 107:75-85.
- BELLROSE, F. C. 1980. *Ducks, Geese, and Swans of North America*, 3rd ed. Stackpole Books, Harrisburg, Pennsylvania.
- BETHKE, R. W., AND T. D. NUDDS. 1995. Effect of climate change and land use on duck abundance in Canadian prairie parklands. *Ecological Applications* 5:588-600.
- BLUHM, C. K. 1988. Temporal patterns of pair formation and reproduction in annual cycles and associated endocrinology in waterfowl. *Current Ornithology* 5:123-185.
- BLUHM, C. K. 1992. Environmental and endocrine control of waterfowl production. Pages 323-364 in *Ecology and Management of Breeding Waterfowl* (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.
- BIGGS, S. V. 1993. A review of seasonal declines in clutch size of waterfowl (Anatidae) in the northern and southern hemispheres. *Ornis Fennica* 70:1-10.
- BURNHAM, K. P., AND D. R. ANDERSON. 1998. *Model Selection and Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York.
- BURRIS, F. A. 1991. Diet and behavior of sub-Arctic Northern Pintails in relation to nutritional requirements of breeding. M.S. thesis, University of Alaska, Fairbanks.
- COOKE, F., R. F. ROCKWELL, AND D. B. LANK. 1995. *The Snow Geese of La Pérouse Bay: Natural Selection in the Wild*. Oxford University Press, New York.
- CRONIN, M. A., J. B. GRAND, D. ESLER, D. V. DERKSEN, AND K. T. SCRIBNER. 1996. Breeding populations of Northern Pintails have similar mitochondrial DNA. *Canadian Journal of Zoology* 74:992-999.
- DUNCAN, D. C. 1987. Nesting of Northern Pintails in Alberta: Laying date, clutch size, and re-nesting. *Canadian Journal of Zoology* 65:234-246.
- DZUS, E. H., AND R. G. CLARK. 1998. Brood survival and recruitment of Mallards in relation to wetland density and hatching date. *Auk* 115:311-318.
- ELDRIDGE, J. L., AND G. L. KRAPU. 1988. The influence of diet quality on clutch size and laying pattern in Mallards. *Auk* 105:102-110.
- ENVIRONMENT CANADA. 1883-1990. Canadian National Climate Archive. Canadian Meteorological Centre, Downsview, Ontario.
- ESLER, D., AND J. B. GRAND. 1994. The role of nutrient reserves for clutch formation by Northern Pintails in Alaska. *Condor* 96:422-432.
- FARNER, D. S. 1964. The photoperiodic control of reproductive cycles in birds. *American Scientist* 52:137-156.

- FLINT, P. L., AND J. B. GRAND. 1996. Nesting success of Northern Pintails on the coastal Yukon-Kuskokwim Delta, Alaska. *Condor* 98:54-60.
- GRAND, J. B., AND P. L. FLINT. 1996. Survival of Northern Pintail ducklings on the Yukon-Kuskokwim Delta, Alaska. *Condor* 98:48-53.
- GREENWOOD, R. G., A. B. SARGEANT, D. H. JOHNSON, L. M. COWARDIN, AND T. L. SHAFFER. 1995. Factors associated with duck nest success in the prairie pothole region of Canada. *Wildlife Monographs*, no. 128.
- GUYN, K. L., AND R. G. CLARK. 1999. Factors affecting survival of Northern Pintail ducklings in Alberta. *Condor* 101:369-377.
- GUYN, K. L., AND R. G. CLARK. 2000. Nesting effort of Northern Pintails in Alberta. *Condor* 102:619-628.
- HAMMOND, M. C., AND D. H. JOHNSON. 1984. Effects of weather on breeding ducks in North Dakota. U.S. Department of the Interior, Fish and Wildlife Service, Fish and Wildlife Technical Report, no. 1.
- HESTBECK, J. B. 1995. Response of Northern Pintail breeding populations to drought, 1961-92. *Journal of Wildlife Management* 59:9-15.
- JOHNSON, D. H., AND J. W. GRIER. 1988. Determinants of breeding distributions of ducks. *Wildlife Monographs*, no. 100.
- KANTRUD, H. A., G. L. KRAPU, AND G. A. SWANSON. 1989. Prairie basin wetlands of the Dakotas: A community profile. U.S. Department of the Interior, Fish and Wildlife Service, Biological Report 85(7.28).
- KENDEIGH, S. C., V. R. DOL'NIK, AND V. M. GAVRILOV. 1977. Avian energetics. Pages 127-204 in *Granivorous Birds in Ecosystems* (J. Pinkowski and S. C. Kendeigh, Eds.). Cambridge University Press, Cambridge, United Kingdom.
- KLETT, A. T., H. F. DUEBBERT, C. A. FAANES, AND K. F. HIGGINS. 1986. Techniques for studying nest success of ducks in upland habitats in the prairie pothole region. U.S. Department of the Interior, Fish and Wildlife Service, Resource Publication 158.
- KLOMP, H. 1970. The determination of clutch size in birds: A review. *Ardea* 58:1-124.
- KRAPU, G. L. 1974. Feeding ecology of pintail hens during reproduction. *Auk* 91:278-290.
- KRAPU, G. L. 1981. The role of nutrient reserves in Mallard reproduction. *Auk* 98:29-38.
- KRAPU, G. L. 2000. Temporal flexibility of reproduction in temperate-breeding dabbling ducks. *Auk* 117:640-650.
- KRAPU, G. L., AND G. A. SWANSON. 1975. Some nutritional aspects of reproduction in prairie nesting pintails. *Journal of Wildlife Management* 39:156-162.
- LACK, D. 1968. *Ecological Adaptations for Breeding in Birds*. Methuen, London.
- MANN, F. E., AND J. S. SEDINGER. 1993. Nutrient-reserve dynamics and control of clutch size in Northern Pintails breeding in Alaska. *Auk* 110:264-278.
- MATHSOFT. 1997. *S-PLUS 4.5. Data Analysis Products Division*. Mathsoft, Seattle, Washington.
- MCLANDRESS, M. R., G. S. YARRIS, A. E. H. PERKINS, D. P. CONNELLY, AND D. G. RAVELING. 1996. Nesting biology of Mallards in California. *Journal of Wildlife Management* 60:94-107.
- MILLER, M. R., AND W. E. NEWTON. 1999. Population energetics of Northern Pintails wintering in the Sacramento Valley, California. *Journal of Wildlife Management* 63:1222-1238.
- MURPHY, E. C., AND E. HAUKIOJA. 1983. Clutch size in nidicolous birds. *Current Ornithology* 4:141-180.
- MURPHY, M. E., AND J. R. KING. 1985. Diurnal variation in liver and muscle glutathionine pools of molting and nonmolting White-crowned Sparrows. *Physiological Zoology* 58:646-654.
- NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION. 1960-1995. *Climatological Data: Alaska, California, and North Dakota, Monthly Summaries*. National Climatic Center, Asheville, North Carolina.
- PIETZ, P. J., G. L. KRAPU, D. A. BUHL, AND D. A. BRANDT. 2000. Effects of landscape water conditions on clutch volume, and hatchling mass of Mallards and Gadwalls in the Prairie Pothole Region. *Condor* 102:936-940.
- RAVELING, D. G. 1979. The annual cycle of body composition of Canada Geese with special reference to control of reproduction. *Auk* 96:234-252.
- ROTELLA, J. J., AND J. T. RATTI. 1992. Mallard brood survival and wetland habitat conditions in southwestern Manitoba. *Journal of Wildlife Management* 56:499-507.
- ROWHER, F. C. 1992. The evolution of reproductive patterns in waterfowl. Pages 486-539 in *Ecology and Management of Breeding Waterfowl* (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). University of Minnesota Press, Minneapolis.
- SMITH, R. I. 1970. Response of pintail breeding populations to drought. *Journal of Wildlife Management* 34:943-946.
- TOME, M. W. 1984. Changes in nutrient reserves and organ size of female Ruddy Ducks breeding in Manitoba. *Auk* 101:830-837.
- U.S. DEPARTMENT OF THE INTERIOR. 1997. *Waterfowl population status, 1997*. U. S. Department of the Interior, Fish and Wildlife Service, Washington, D.C.
- WELLER, M. W. 1956. A simple field candler for waterfowl eggs. *Journal of Wildlife Management* 20:111-113.
- ZISWILER, V., AND D. S. FARNER. 1972. Digestion and the digestive system. Pages 343-430 in *Avian Biology*, vol. 2 (D. S. Farner and J. R. King, Eds.). Academic Press, New York.

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