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KING EIDER FORAGING EFFORT DURING THE PRE-BREEDING PERIOD IN ALASKA

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Abstract. For reproduction, many arctic-nesting migratory birds rely on nutrients obtained on the breeding grounds, so they devote sufficient time to foraging immediately prior to nesting. However, little is known about the increase in foraging effort necessary to meet the energetic requirements of reproduction. In early June 2006 and 2008, we quantified the proportion of time spent foraging before breeding by a large sea duck, the King Eider (*Somateria spectabilis*), on its breeding grounds in northern Alaska. During >235 hours of behavioral observations, both male and female King Eiders spent >50% of the day loafing (resting, sleeping, comfort behavior, or being alert). Females foraged on average 30% of the time (mean 7.2 hr day^{-1}, 95% CI 6.0–8.4 hr day^{-1}), three times as much as males (9%; 2.3 hr day^{-1}, 95% CI 1.5–2.8 hr day^{-1}). The most common prey in ponds where the eiders foraged were chironomid larvae and worms ranging in length from 1 to 30 mm. If the King Eider's daily energy expenditure on its breeding grounds is similar to values published for related species, it would need to ingest only 0.2–0.6 g dry mass of invertebrates per minute of foraging to meet its energetic requirements. Males did not lose body mass before breeding, and we assume that their foraging effort was sufficient for energy balance. Therefore, female King Eiders appear to triple their foraging effort over maintenance requirements to meet the energetic challenges of egg formation.

Key words: *behavior, chironomid, foraging, intake rate, King Eider, sea duck,* Somateria spectabilis.

Esfuerzo de Forrajeo de *Somateria spectabilis* Antes del Periodo Reproductivo en Alaska

Resumen. Muchas especies de aves migratorias que nidifican en el Ártico dependen de nutrientes presentes en las áreas de reproducción, por lo que dedican bastante tiempo al forrajeo justo antes de iniciar la anidación. Sin embargo, se sabe poco sobre el aumento del esfuerzo de forrajeo que sería necesario para alcanzar los requerimientos energéticos de la reproducción. A comienzos de junio de 2006 y 2008, cuantificamos la proporción de tiempo gastado en forrajeo por parte de un pato marino de gran tamaño, *Somateria spectabilis*, en su área reproductiva en el norte de Alaska. Durante >235 hr de observaciones de comportamiento, tanto las hembras como los machos gastaron >50% del día en comportamientos no activos (descansando, durmiendo, comportamiento de confort, o estando alerta). Las hembras forrajearon en promedio el 30% del tiempo (media 7.2 hr día^{-1}, IC de 95% 6.0–8.4 hr día^{-1}), tres veces más que los machos (9%; 2.3 hr día^{-1}, IC de 95% 1.5–2.8 hr día^{-1}). La presa más común en las lagunas en que estos patos forrajearon fueron larvas de chironomidos y gusanos que variaron en largo entre 1 y 30 mm. Si el gasto energético diario de *S. spectabilis* en sus áreas de reproducción es similar a la de los valores publicados para especies relacionadas, éstos necesitarían ingerir sólo 0.2–0.6 g de masa seca de invertebrados por minuto de forrajeo para alcanzar sus requerimientos energéticos. Los machos no perdieron masa corporal antes de la reproducción, y asumimos que su esfuerzo de forrajeo fue suficiente para lograr su balance energético. Por eso, las hembras de *S. spectabilis* parecen triplicar su esfuerzo energético por sobre sus requerimientos de mantenimiento para alcanzar las demandas energéticas de la formación de los huevos.

INTRODUCTION

Arctic-breeding birds face the challenge of a short summer for raising offspring, which requires nest initiation shortly after arrival on breeding grounds (Perrins 1996, Klaassen et al. 2006). As food resources may be limited during this time of the year, many migratory bird species breeding in the Arctic have long been assumed to rely for egg formation on stored body reserves (Ankney and MacInnes 1978, Meijer and Drent 1999). More recently, however, several arctic migrants have been found to use mostly nutrients obtained on the tundra for egg formation (Klaassen et al. 2001, Gauthier et al. 2003, Schmutz et al. 2006). This pattern implies that these birds forage extensively upon their arrival on arctic

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nesting grounds (Ganter and Cooke 1996, Morrison and Hobson 2004).

The King Eider (*Somateria spectabilis*) is a large sea duck that breeds in arctic tundra ecosystems around the world and spends 10 months of the year at sea (Suydam 2000). Outside the breeding season, it forages on marine benthic invertebrates by diving, whereas on its breeding grounds it consumes mostly small invertebrates from fresh water by dabbling (Lamothe 1973, Holcroft-Weerstra and Dickson 1997, Suydam 2000). In northern Alaska, King Eiders arrive on tundra breeding grounds approximately 2 weeks prior to clutch initiation (Phillips and Powell 2006, Oppel et al. 2008, Oppel and Powell 2010). They forage in small lakes and tundra ponds, and stable-isotope analysis of eggs has indicated that birds rely on freshwater foods for egg production (Oppel et al. 2010). However, the amount of time spent searching for and consuming prey (hereafter referred to as foraging effort) during the pre-breeding period is poorly described (Holcroft-Weerstra and Dickson 1997), and the relative increase in foraging effort required to meet the energetic demands of breeding is unknown.

During the pre-breeding period the closely related Common Eider (*S. mollissima*) increases foraging effort by about 100–250% over that in other seasons (Gorman and Milne 1971, Christensen 2000, Guillemette 2001). Such a comparison is difficult for the King Eider, because upon arrival on the breeding grounds it switches from diving for marine invertebrates in deep waters to presumably much smaller prey in much shallower fresh water (Holcroft-Weerstra and Dickson 1997). Hence, any difference in foraging effort between the breeding and nonbreeding seasons is potentially confounded by the differences in the energetic return of different prey and in the energetic cost of foraging in different environments (Butler 2000). Estimating any increase in foraging effort in preparation for breeding thus requires an estimate of the baseline foraging effort required for maintenance. Because in the eiders females bear all the costs of egg formation and incubation, the foraging effort of males and females differs on the breeding grounds (Holcroft-Weerstra and Dickson 1997). If males maintain body mass during the pre-breeding period, one can assume that their foraging effort is sufficient for maintenance (Esler and Bond 2010). This foraging rate can thus provide a baseline against which an increase in females' foraging effort can be measured (Gorman and Milne 1971, Christensen 2000, Guillemette 2001).

In this study we first captured males throughout the pre-breeding period to examine whether they maintained body mass. We then quantified the behavior of both male and female King Eiders during the time between arrival on breeding grounds and the onset of incubation in order to estimate the proportion of time each sex allocates to foraging. Furthermore, we examine the diurnal pattern of foraging on the breeding grounds under continuous daylight. We present an assessment of invertebrate prey available in ponds where we observed King Eiders foraging. We use published data on the energy content of available prey and on energy expenditure by waterfowl to estimate intake rates King Eiders require to meet their energetic demands. This study thus provides crucial information on the increase in females' foraging effort on arctic breeding grounds in preparation for breeding.

METHODS

STUDY SITE

The study was conducted near the southeast shore of Teshekpuk Lake on the arctic coastal plain of Alaska (70.46° N, 153.16° W). The area is characterized by complexes of wetlands, flat to gently rolling tundra with numerous ponds, and lakes with both soft and hard bottoms. All large and deep lakes in the study area, including Teshekpuk Lake, are covered by ice until late June. King Eiders arrive in the study area in early June (Phillips and Powell 2006, Oppel et al. 2008), and most nests are initiated around 17 June (Bentzen et al. 2008a).

CAPTURES

From 2006 to 2008, using mist net arrays and decoys, we captured 39 male King Eiders on the breeding grounds during the pre-nesting period (8–16 June). We measured the body mass of each bird with Pesola spring scales accurate to 10 g.

FIELD OBSERVATIONS

We conducted behavioral observations from 8 to 22 June 2006, 8 to 15 June 2008, and on 8 June 2009 at randomly selected lakes, ponds, and wetlands in the study area. In 2009, field operations were disrupted by a brown bear (*Ursus arctos*), and we obtained only confirmatory qualitative data on eider foraging.

In the study area, King Eiders do not occur away from water bodies, and all behavioral observations were of birds on or adjacent to water. Satellite telemetry of several females has revealed that King Eiders do not commute between tundra nesting areas and marine staging areas after arrival on their breeding grounds (Phillips and Powell 2006, Phillips et al. 2007, Oppel et al. 2008). Because large lakes were still ice-covered during the study period, the smaller lakes, ponds, and wetland complexes we observed were the only foraging areas available to King Eiders. In the study area, the sun does not set in June, and in 2008 we observed King Eiders throughout the day (00:00–24:00), with a similar number of observations made during each 2-hr period of the day (Fig. 1). Sampling effort was spread evenly throughout the pre-breeding season in both 2006 and 2008.

Following the method described by Christensen (2000), we obtained activity budgets of King Eiders by instantaneous focal-animal sampling. Briefly, we observed a focal individual

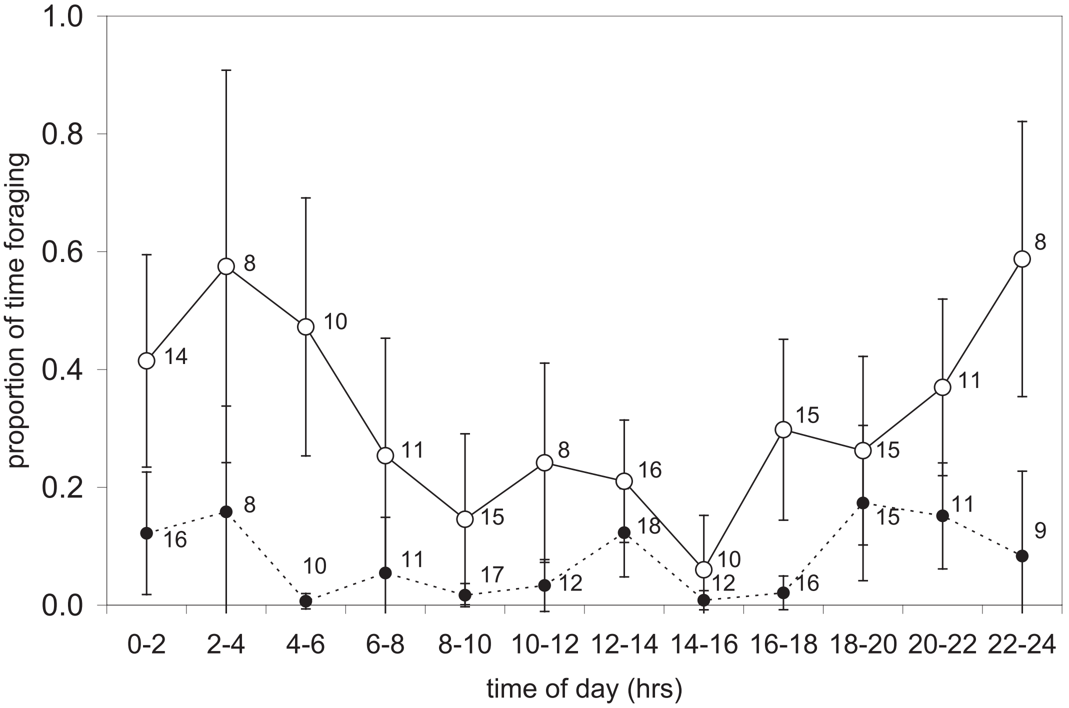

FIGURE 1. Mean (± 95% confidence intervals) proportion of time spent foraging by female (white, solid line) and male (black, dotted line) King Eiders on their breeding grounds in northern Alaska during the pre-breeding period in June 2008. Numbers next to symbols indicate sample size of 15-min observation periods.

for a given period and recorded its behavior at times separated by fixed intervals. We then calculated activity budgets by the frequency of instantaneously recorded behaviors over the period the focal individual was observed (Christensen 2000), and we use the observation period as the sample unit throughout the remainder of the paper.

In 2006, the length of observation periods was undefined, and we recorded the behavioral state of each focal individual every 5 min until it disappeared from view. In 2008, we recorded the behavior of each focal individual once a minute for a 15-min period or until the animal disappeared from view (11% of observation periods were 8–14 min). In 2009, we employed both approaches simultaneously and verified that the frequency of behaviors was equal whether recorded at intervals of 1 or 5 min. We present results from this analysis to justify our pooling of data from 2006 and 2008.

After each observation period we chose new individuals or initiated new observations in a different area to reduce the probability of repeatedly sampling the same birds. Sampling effort was spread throughout the entire study area (40 km^2), but because none of the birds was individually marked we cannot exclude the possibility that we may have sampled some individuals on more than one occasion. On the basis of the number of nests found in this area annually (48 ± 10, S. Oppel, R. Bentzen, A. N. Powell, unpubl. data) and a nest-detection rate far below 100% (Pagano and Arnold 2009), we estimate that about 200 individual King Eiders were available for sampling in the study area in mid June.

We observed birds with 30× spotting telescopes from distances >200 m in order to minimize behavioral bias due to the presence of observers. We recorded behavior in four activity classes: loafing (including resting, sleeping, preening, comfort behavior, and being alert), foraging (head-dipping, up-ending, diving), locomotion (swimming, walking, flying), and reproductive behavior (nest preparation, courtship, copulation, and aggressive interactions with conspecifics) (Goudie and Ankney 1986, Holcroft-Weerstra and Dickson 1997, Christensen 2000).

Our comparison of males' and females' time budgets assumes equal detectability of both sexes on the breeding grounds. Because King Eiders maintain a strong pair bond during the pre-breeding period, we generally observed pairs together and only a few males without female partners. Although while prospecting for nest sites females could temporarily become hard to observe, these periods of low detectability were usually very brief and characterized by males being in a state of increased alertness on a nearby pond. Hence, we are confident that any differences in foraging activity we recorded were not due to different detectability of the two sexes. All field methods had approval of the University of Alaska Fairbanks Institutional Animal Care and Use Committee under protocol 05–29.

PREY COLLECTION AND BIOMASS ESTIMATION

We sampled invertebrates in several shallow ponds and lake margins of the core study area in June 2006 and 2009. We surveyed larger invertebrates within 2 m of shorelines (water depths <50 cm) by sweeping through emergent vegetation and sieving surficial sediments with a 1.0-mm-mesh dip net in ponds and lakes of the study area where we observed King Eiders foraging. In addition to these qualitative collections, on 8 June 2009 we made a quantitative assessment of the abundance and size distribution of invertebrates near the shore (depth 40–50 cm) of a pond where we had observed two pairs of King Eiders foraging during the previous night. Because the sediment of ponds is an incoherent layer of flocculent organic material floating above frozen ground, quantitative core samples were not feasible. We therefore scooped eight randomly chosen patches of sediment (~194 cm^2 each) within an area of ~10 m^2 to a depth of 10 cm with a rectangular net, representing approximately 0.15 m^2 of pond sediment. We sieved the samples with a 0.5-mm-mesh screen, reducing the volume of the flocculent organic sediments by <50%. All benthic invertebrates >1 mm length were extracted from this quantitative sample by sucrose flotation (Butler 1982), preserved with 5% formalin, and identified to lowest practical taxonomic level (typically to genus). We photographed several individuals representative of each taxon and size class under a dissecting microscope and measured their body lengths on the digital images with the software ImageJ. We estimated the dry mass of each category of prey with appropriate length–weight regressions (Benke et al. 1999).

STATISTICAL ANALYSIS

To explore whether males' foraging effort was sufficient to maintain body mass, we analyzed the trend in body mass of males over the pre-breeding period with a linear regression.

To quantify foraging effort, we calculated the proportion of each behavior for every individual within each observation period and used those observation periods as sampling units (Christensen 2000). Observation periods were 15–160 min (mean 65 ± 30 min) in 2006 and 15 min in 2008. We averaged the frequency of each behavior across individuals for each sex and tested for significant differences between behavioral categories and sexes with nonparametric Wilcoxon tests.

To describe diurnal activity patterns in 2008, we averaged each behavior's frequency across individuals from each sex for every 2-hr period of the day starting and ending at midnight. All analyses were run in R 2.8.0, and we present results as mean and 95% confidence intervals.

ESTIMATION OF INTAKE RATES

We explored whether the foraging effort recorded in our study could explain the known pattern of nutrient allocation to eggs in the King Eider (Oppel et al. 2010) by estimating intake rates based on energetic balance. For each taxon of prey, we used energy content per dry mass from published studies (Brittain and Lillehammer 1978, Penczak et al. 1984, Custer et al. 1986) to estimate intake rates required to maintain energy balance.

TABLE 1. Energetic costs of main activities experimentally determined for several species of waterfowl.

Activity	Energetic cost (W kg^{-1})	Reference
Up-ending	9.4	Nolet et al. 2006
Head-dipping	11.8	Nolet et al. 2006
Resting	5.9	Richman and Lovvorn 2008
Swimming	17.7	Butler 2000, Prange and Schmidt-Nielsen 1970, Woakes and Butler 1983
Flying	75.0	Pelletier et al. 2008

We estimated males' daily energy expenditure on breeding grounds by multiplying activity budgets from our observations by the experimentally determined energy expenditure of White-winged Scoters (*Melanitta fusca*) resting on 9° C water (Richman and Lovvorn 2008), foraging costs of Bewick's Swans (*Cygnus columbianus bewickii*) head-dipping or up-ending in small ponds (Nolet et al. 2006), swimming costs of diving ducks (Prange and Schmidt-Nielsen 1970, Woakes and Butler 1983, Butler 2000), and flying costs of free-ranging Common Eiders in Denmark (Pelletier et al. 2008) (Table 1).

Because the energetic cost of egg formation is partly met by reducing body-maintenance costs (Nilsson and Raberg 2001, Vezina and Williams 2002, Williams 2005), we used an estimate of total daily energy expenditure during egg formation for the Common Eider (Parker and Holm 1990) as surrogate for the likely energy-intake requirements of female King Eiders. In addition, we estimated the minimum daily energy expenditure of nonbreeding females by the same approach described above for males (Table 1).

For both males and females, we estimated how much invertebrate biomass an adult eider needed to consume to ingest the required energy per day, assuming an assimilation efficiency for invertebrate prey of 85% (Reinecke and Owen 1980, Hilton et al. 2000, Richman and Lovvorn 2003, 2004). Finally, from our observations of the average daily foraging effort by each sex, we converted those estimates to intake rates (in g dry mass min^{-1}).

RESULTS

We recorded King Eider activity for a total of 9825 min over 146 observation periods in 2006 and for 4294 min over 296 observation periods in 2008. In 2009 we observed two pairs for 450 min during 8 observation periods and recorded their behaviors at both 1-min and 5-min intervals. The frequencies of the three most common behavior categories for each sex did not differ by length of observation interval, but very uncommon

TABLE 2. Relative frequency (mean ± standard deviation) of behaviors of male and female King Eiders on breeding grounds in Alaska during the pre-breeding periods in June 2006 and 2008. Observation periods in 2006 were on average four times as long as in 2008.

	Female[a]		Male[b]	
Behavior	Mean	SD	Mean	SD
2006				
Loafing (rest, alert, comfort)	0.46	0.30	0.59	0.30
Foraging	0.28	0.27	0.11	0.17
Locomotion	0.19	0.19	0.24	0.20
Reproduction (nesting, courtship, aggression)	0.06	0.17	0.04	0.12
2008				
Loafing (rest, alert, comfort)	0.56	0.35	0.74	0.26
Foraging	0.31	0.33	0.08	0.16
Locomotion	0.09	0.12	0.11	0.14
Reproduction (nesting, courtship, aggression)	0.04	0.08	0.07	0.13

[a] $n = 62$ in 2006, 141 in 2008.
[b] $n = 84$ in 2006, 155 in 2008.

behaviors (e.g., flying, aggressive interactions) were underrepresented during the 5-min intervals. As these behaviors are negligible for our purpose of analyzing foraging effort, the methods we employed in 2006 and 2008 can be considered equivalent, and we pooled data from both these years.

On average, both male and female King Eiders foraged for less than one-third of the time and spent the majority of the day loafing (Table 2). Male King Eiders weighed on average 1660 ± 130 g, and the estimated change in body mass between males captured in early June and males captured 8 days later was –3.8 ± 10.4 g day^{-1} (mass = –3.80 × time + 1710 g, $n = 39$, $P = 0.72$). We therefore assumed that males' foraging effort was sufficient for energy balance and thus useful as a baseline estimate against which increase in females' foraging effort could be measured.

Females foraged three times more than males ($P < 0.001$, $n = 442$), spending on average 7.2 hr day^{-1} (95% CI: 6.0–8.4 hr day^{-1}) foraging, while males spent only 2.3 hr day^{-1} (95% CI: 1.5–2.8 hr day^{-1}) foraging. Conversely, males spent more time loafing ($P < 0.001$, $n = 442$). Most loafing males were guarding their partner while the female was foraging. Both locomotion and reproductive behavior were relatively uncommon (Table 2), and the proportion of time males and females spent on those activities did not differ ($P = 0.08$ for locomotion, $P = 0.13$ for reproductive behavior).

In 2008 we observed a diurnal pattern in the foraging behavior of female King Eiders, with foraging more frequent during the "night" hours (20:00–06:00) and less frequent during the middle of the day (Fig. 1). For males the pattern was similar but less pronounced (Fig. 1). We were not able to explore diurnal patterns in 2006 because no data were recorded between 22:00 and 06:00.

Foraging behavior consisted mostly of birds swimming in shallow water with heads dipped under water. We also frequently observed up-ending, but we recorded diving on only four occasions. No prey handling, manipulation, or swallowing of food was observable, and the items consumed appear to have been very small. On one occasion a female was observed with a small fish in her bill, but the fish was dropped and not consumed. Some females emerged from head-dipping with aquatic vegetation attached to the bill, but it was impossible to discern whether they were foraging on vegetation or whether uptake was accidental. The birds foraged either in shallow ponds (<70 cm deep) or very near (<5 m) the shoreline of deeper ponds or lakes, and in most locations eiders were able to reach the sediment of water bodies by up-ending.

We found very few invertebrates in the water column, suggesting that King Eiders retrieve prey mostly from sediments. The most common benthic invertebrates we found were dipteran larvae of the family Chironomidae. Most chironomid larvae were <5 mm long and <0.1 mg dry mass, but late-instar larvae of larger species exceeded 10 mm length and approached 1 mg dry mass. Other large invertebrates collected included oligochaete worms, larvae of other dipterans (Muscidae, Tipulidae), caddisfly and stonefly larvae, and snails (Table 3).

The quantitative sample contained at least 13 species of potential prey but lacked some large taxa such as caddisflies, stoneflies, and snails. We estimated total prey biomass from this quantitative sample to be 350 mg dry mass m^{-2}. Oligochaete worms and larger chironomid larvae (>0.16 mg dry mass) accounted for only 17% of individuals but 88% of total invertebrate biomass.

We estimated the mean energy content of potential food items available to King Eiders in our study area as 21.8 kJ g^{-1} dry mass by averaging values in the literature for the Chironomidae, Tipulidae, Muscidae (Custer et al. 1986), Trichoptera, Plecoptera, and Oligochaeta (Brittain and Lillehammer 1978, Penczak et al. 1984). We used this mean energy content to estimate the King Eider's intake rates of invertebrate biomass on the basis of their activity budgets and published estimates of energy expenditure during those activities.

We estimated the daily energy expenditure of males to be 1372 kJ, corresponding to a required dry-mass intake of 74 g day^{-1} to maintain energy balance (Table 4). Given a foraging effort of 2.3 hr day^{-1}, males require an intake rate of 0.54 g of dry mass per minute of foraging. We estimated the daily energy expenditure of females to range from 1471 kJ day^{-1} for females not producing eggs (Table 4) to 2528 kJ day^{-1} for females producing eggs (Parker and Holm 1990). Females thus required between 80 and 137 g of dry mass to meet energetic demands. During 7.2 hr of foraging per day, a female would thus have to maintain an intake rate ranging from 0.18 to 0.32 g dry mass min^{-1}.

TABLE 3. Aquatic invertebrates found in the muddy substrate of ponds and lakes on the arctic coastal plain of Alaska where King Eiders were observed foraging during the pre-breeding period in early June 2009.

Order or class	Family	Subfamily or tribe	Genus	Size[a]
Diptera	Chironomidae	Tanypodinae	*Procladius*	large
			Conchapelopia	
		Chironomini	*Chironomus*	
			Cladopelma	small
			Cryptochironomus	large
			Dicrotendipes	large
			Stictochironomus	
		Tanytarsini	*Cladotanytarsus*	small
			Paratanytarsus	small
			Tanytarsus	small
		Orthocladiinae	*Cricotopus*	small
			Parakeifferiella	small
			Corynoneura	small
			unidentified	
	Tipulidae		*Tipula*	
	Muscidae		*Limnophora*	large
Trichoptera	Limnephilidae		*Asynarchus*	
Plecoptera	Nemouridae		*Nemoura*	
Oligochaeta	Tubificidae		unidentified	large
	Enchytraeidae		*Propappus*	large
Acari	Hydrachnidia		*Lebertia*	
Gastropoda			*Physa*	

[a] Large, some individuals in the quantitative sample exceeded 6 mm in length or 0.16 mg in estimated dry weight; small, no individual in this sample exceeded these measurements.

TABLE 4. Minimum daily energy expenditure of King Eiders during the pre-breeding period in northern Alaska, estimated from time budgets observed in this study (Table 2) and experimentally determined costs for main activities (Table 1). Foraging effort is the sum of up-ending and head-dipping activities.

Sex	Activity	Time spent (hr day^{-1})	Energetic cost (kJ hr^{-1})	Daily energy cost (kJ day^{-1})
Male	up-ending	2.0	57.5	115.0
	head-dipping	0.3	72.3	18.1
	resting	16.8	36.2	607.6
	swimming	4.8	108.5	520.8
	flying	0.2	459.0	110.2
	total			1371.7
Female	up-ending	4.8	57.5	276.0
	head-dipping	2.4	72.3	173.5
	resting	12.2	36.2	442.7
	swimming	4.3	108.5	468.8
	flying	0.2	459.0	110.2
	total[a]			1471.1

[a] For breeding females, the actual daily energy expenditure is substantially higher because of the costs of egg formation. Because egg-formation costs can be partially compensated for by reducing other metabolic costs, they could not be added to the energy budgets in this table. See text for details.

DISCUSSION

In northern Alaska, pre-breeding female King Eiders spent on average 30% of their time or 7.2 hr day^{-1} foraging in tundra lakes and ponds. Males accompanying those females foraged only for 2.3 hr day^{-1}, but our capture data indicate that males did not lose body mass during the pre-breeding period. Hence, if males' foraging reflects the minimum effort required for energy balance (Gorman and Milne 1971, Guillemette 2001), then females appear to triple their foraging effort in preparation for breeding. This increase in foraging effort may be sufficient for female King Eiders to meet the energetic demands of egg formation (Vezina and Williams 2002, Williams 2005, Nager 2006).

Foraging time alone is an insufficient measure of nutrient intake, as it does not take foraging efficiency or prey type and density into account. Most prey items available in water bodies of the study area were small relative to the King Eider's marine food resources (Merkel et al. 2007), but larger worms and insect larvae constituted the bulk of invertebrate biomass we measured in tundra ponds. Several species of waterfowl are known to forage on chironomid larvae almost exclusively (Phillips 1991, Krapu and Reinecke 1992, Green et al. 1999), and the high protein content of insect larvae renders them a food source sufficient to meet the protein requirements of egg production (Krapu and Swanson 1975, Thompson and Drobney 1997). Despite the small size of potential prey items such as chironomid larvae, they may be energetically profitable because of the low cost of foraging. While diving to capture benthic prey at sea requires considerable amounts of energy (Butler 2000, Richman and Lovvorn 2008), the modes of foraging that we observed (head dipping and up-ending) require less than half as much energy (Nolet et al. 2006).

According to our model, King Eiders must consume between 0.2 and 0.6 g of dry mass per minute of foraging, corresponding to 1.0–2.5 g of fresh invertebrate biomass (Leuven et al. 1985). These intake rates are within the range of intake rates estimated for a variety of diving ducks feeding on benthic bivalves obtained by diving: Guillemette et al. (1992) estimated wild Common Eiders to ingest 4.6 g of wet mussel mass during a 43-sec dive, de Leeuw (1999) found captive Tufted Ducks (*Aythya fuligula*) and Greater Scaup (*A. marila*) to ingest 16.2–27.6 g fresh mussel mass per minute, and Richman and Lovvorn (2003) reported that captive White-winged Scoters were able to ingest between 0.39 and 4.68 g of ash-free dry clam mass per minute. However, in all the experimental studies mentioned above, and in similar studies of dabbling ducks (Fritz et al. 2001, Arzel et al. 2007), prey densities were much higher (>10 g m^{-2}) than we recorded in our study area (0.35 g dry mass m^{-2}). We are unaware of any studies examining the sediment-filtering efficiency of eiders, but our analysis suggests that it is realistic for King Eiders to acquire a large proportion of the nutrients required for egg formation directly on breeding grounds (Lawson 2006, Oppel et al. 2010).

There is currently no information available on the prey species King Eiders actually digest on their breeding grounds. Stable-isotope analysis indicates that a wide variety of invertebrates may be consumed, but because of the isotopic variation among invertebrates the abundance of different prey items in the King Eider's diet could not be estimated reliably (Oppel et al. 2009, 2010). The guts of collected birds contained not only invertebrates but also vegetation (Lamothe 1973, Bergman et al. 1977). If part of the foraging effort is spent on ingesting vegetation, then our estimated intake rates are biased low. We speculate that intake of vegetation may be incidental and that most vegetative matter is not assimilated. More research is required to determine the exact composition of the King Eider's diet on its breeding grounds.

As daylight was not a limiting factor, foraging occurred around the clock but slightly more frequently around midnight than noon. In our study area temperatures and light intensity during June are generally lower between 22:00 and 07:00 than during the remainder of the day. The diurnal pattern of foraging may result from different prey availabilities (Holcroft-Weerstra and Dickson 1997) or from small differences in temperature making it energetically more efficient to forage during the colder part of the day (de Leeuw et al. 1998, Kaseloo and Lovvorn 2003).

In summary, our study shows that to prepare for egg formation and incubation, female King Eiders triple their foraging effort on breeding grounds between arrival and the start of incubation. As most available prey items are small and should not pose any digestive constraints (Guillemette 1994), and daylight is not limiting, a further increase of foraging effort appears possible. Thus, lower density or altered prey availability in years with unfavorable environmental conditions may not affect the ability of King Eiders to breed but may require an increase of females' foraging effort. While food from fresh water on the tundra is an important resource at all stages of the breeding season, female King Eiders still arrive with and utilize body reserves during incubation (Kellett and Alisauskas 2000, Bentzen et al. 2008b). Given the low densities of prey in tundra ponds it appears unlikely that high intake rates on the breeding grounds could compensate for birds arriving in poor body condition.

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