



## Relative contribution of lipid sources to eggs of lesser scaup

Kyle A. Cutting, Keith A. Hobson, Jay J. Rotella, Jeffrey M. Warren, John Y. Takekawa, Susan E. W. De La Cruz and Michael Parker

K. A. Cutting ([kyle\\_cutting@fws.gov](mailto:kyle_cutting@fws.gov)) and J. M. Warren, US Fish and Wildlife Service, Red Rock Lakes National Wildlife Refuge, Lima, MT 59739, USA. – J. J. Rotella, Dept of Ecology, Montana State University, Bozeman, MT 59717, USA. – K. A. Hobson, Environment Canada, Saskatoon, SK S7N 0W0, Canada. – J. Y. Takekawa and S. E. Wainwright-de la Cruz, US Geological Survey, Western Ecological Research Center, Vallejo, CA 94592, USA. – M. Parker, Davis, CA 95616, USA.

Studies of how birds mobilize nutrients to eggs have traditionally considered a continuum of possible allocation strategies ranging from income breeding (rely on food sources found on the breeding grounds) to capital breeding (rely on body reserves stored prior to the breeding season). For capital breeding, stored body reserves can be acquired either on or away from the breeding grounds, but it has been difficult to quantify the relative contribution of each, precluding identification of key habitats for acquiring nutrients for clutch formation. During 2006–2009, we explored the importance of spring-staging habitats versus breeding-area habitats for egg-lipid formation in female lesser scaup *Aythya affinis* using stable carbon ( $\delta^{13}\text{C}$ ) isotope analyses. Although  $\delta^{13}\text{C}$  values for abdominal lipid reserves brought to the breeding grounds overlapped those of local amphipods, we were able to quantify the importance of local plant carbohydrates (seeds of emergent wetland plants) to the production of eggs. We compared the importance of local wetland seeds (overall  $\delta^{13}\text{C}$ :  $-29.1 \pm 0.9\text{‰}$  SD) to combined lipid stores and lipids from local amphipods (overall  $\delta^{13}\text{C}$ :  $-23.8 \pm 2.2\text{‰}$ ). Local seeds and stored body lipids contributed equally to egg lipid formation across years but we found evidence of annual variation in their relative importance. Wetland seeds contributed 39% (SE = 10%) to egg lipid production, and the importance of this source varied by year (90% CI = 47–75% in 2006, 13–42% in 2007, 29–65% in 2008, and 7–30% in 2009). In contrast to earlier studies that suggest lesser scaup predominantly employ a capital breeding strategy, our results suggest that in some years females may attain half of their energy for clutch formation from foods on the breeding grounds.

Traditionally, studies of avian nutrient dynamics have focused on a continuum to describe where nutrients were derived for clutch formation (Drent and Daan 1980). Income breeders, such as small-bodied shorebirds and songbirds, are at one end of a continuum and rely on local (i.e. exogenous) dietary sources at the breeding grounds (Klaassen et al. 2001, Langin et al. 2006). Capital breeders, such as emperor geese *Anser canagicus*, are at the other end of the continuum and rely heavily on stored (i.e. endogenous) body tissues acquired prior to arrival (Schmutz et al. 2006). Unfortunately, this concept results in limited information about where nutrient reserves are acquired. For example, a capital breeder can acquire energy both near and distant to the breeding grounds resulting in difficulty in identifying habitats most important for acquiring nutrients for clutch formation.

Populations of lesser scaup *Aythya affinis* (hereafter scaup), a diving duck, feed on amphipods (Rogers and Korschgen 1966, Anteau and Afton 2004, 2008) and seeds of emergent wetland plants (Afton and Hier 1991, Smith 2007, Strand et al. 2008) and are believed to be limited by the availability of foods high in lipid content during the prebreeding season (Afton and Ankney 1991,

Esler et al. 2001). In stochastic environments, such as those at high latitudes or high elevations, lipid-rich invertebrates (e.g. amphipods) may be scarce when migrants arrive to the breeding grounds in early spring (Woodin and Swanson 1989). Early migrants may need to select more reliable foods such as residual seeds of emergent wetland plants from the previous year's growth. Wetland seeds are high in the carbohydrates that provide substrates for lipid synthesis for rebuilding lost body reserves during spring migration (Sugden 1973, Hoffman 1983).

Scaup exhibit the most protracted spring migration of any North American duck species (Austin et al. 1998). Badzinski and Petrie (2006) showed that scaup increase lipid reserves during spring migration by an average rate of  $1.2 \text{ g d}^{-1}$  while staging on the lower Great Lakes. Afton and Ankney (1991) and Esler et al. (2001) reported that two-thirds of the nutrients for clutch formation comes from endogenous lipid reserves assumed to have been acquired on spring staging sites. However, scaup spend several weeks foraging on foods found on the breeding grounds prior to nesting in southern latitudes (Afton 1984, Cutting et al. 2011), subsequently increasing their body condition.

Following arrival on the breeding grounds, Warren et al. (2013) found that scaup increase their body condition on average  $1.29 \text{ g d}^{-1}$  during the prebreeding period until peak nest initiation. Therefore, scaup may also rely on local dietary sources for clutch lipid formation.

We explored the relative contributions of endogenous abdominal lipids obtained during spring migration versus exogenous sources consumed while on the breeding grounds. Because female scaup are one of the latest nesting ducks in North America, and spend 4–6 weeks on the breeding grounds prior to nesting (Afton 1984, Cutting et al. 2011), we hypothesized that local energy sources would provide the greatest proportion of lipid for egg formation. We also hypothesized that relative contributions of exogenous reserves would remain constant across breeding seasons, because variation in local conditions could be mediated by increased foraging opportunities during the long post-migration to pre-breeding transition.

## Methods

### Study area and field collections

Our study site was located at Red Rock Lakes National Wildlife Refuge in the Centennial Valley of southwest Montana ( $44.50^{\circ}\text{N}$ ,  $-111.83^{\circ}\text{E}$ ). Lower Red Rock Lake is a large (2332 ha), high elevation (2014 m a.m.s.l.), montane wetland. Water depths typically do not exceed 1.5 m during the nesting season, and large open water areas are interspersed with hardstem bulrush *Schoenoplectus acutus* islands. Half of the area consists of extensive stands of seasonally flooded beaked sedge *Carex utriculata* that contain small ( $\sim 2$  ha), scattered open water ponds. The high elevation wetland has a short growing season comparable to northerly breeding areas where the majority of scaup breed (i.e. the Western Boreal Forest; Gurney et al. 2011).

Stable isotopes can be used to track macronutrient allocation providing a more direct approach than older, more-conventional methods (i.e. proximate analysis, Hobson 2006). Therefore, we applied stable isotope techniques to: 1) abdominal lipids from females when they arrived on the breeding grounds, 2) local dietary items found at the breeding grounds, and 3) lipids from egg yolks. Isotopic discrimination factors were applied relating lipid sources to egg lipids (Hobson 1995), and  $\delta^{13}\text{C}$  values were compared between female lipids and foods with those from yolk lipids to estimate the relative percent contributions of abdominal lipid reserves acquired prior to arriving on the breeding grounds, and local exogenous sources. Spring migration was defined as the period between departure from the wintering grounds and arrival on the breeding areas, while pre-breeding was defined as mid-May to June, the period between a female's arrival on the breeding area and nest-initiation (Stephens et al. 2009).

From 9–12 May 2008, and 11–25 May 2009, a period during wetland ice breakup, we captured adult female scaup via night-lighting (Lindmeier and Jessen 1961). Each female was banded with a US Geological Survey aluminum leg band, and an abdominal lipid biopsy was collected for  $\delta^{13}\text{C}$  analysis. Briefly, the biopsy location was first disinfected,

the skin was lifted with forceps, a small ( $< 10$  mm) incision was made with a sterilized scalpel, and a small amount of lipid (25 mg) was removed with forceps. We determined if the sample was abdominal lipid, versus muscle connective tissue, based on color (yellowish tint), oiliness, and location on the abdomen where the sample was collected. The incision site was sealed with veterinary grade adhesive. Lipid samples were stored frozen until analyzed. Arrival dates in 2008 of six migratory female scaup that were radio-marked in 2007 were between 7–9 May (USFWS unpubl.). Thus, we made the assumption that the isotopic values of samples collected shortly thereafter were representative of distant endogenous lipid reserves exported from spring migration areas to the breeding grounds by early- and late-arriving laying birds. Capture and sampling protocols were conducted under approved federal (no. 06266), state (no. 2009-050), and animal welfare (no. 05-07) permits.

Eggs were collected from nests located during systematic nest searches of sedge-dominated habitats. Eggs were collected from nests that initiated between 21 May–7 July, 2006 ( $n = 20$ ), 9 June–11 July, 2008 ( $n = 27$ ), 25 May–4 July, 2009 ( $n = 23$ ), and by locating radio-marked females from 12–26 June, 2007 ( $n = 6$ ). For each nest found, we collected one egg at random and determined nest-initiation date by field-candling eggs (Weller 1956). Collected eggs were hard-boiled to separate yolk and albumen, and samples were stored frozen until stable isotope analysis was conducted (Gloutney and Hobson 1998).

Seeds of emergent wetland plants and amphipod samples were collected as possible scaup food items during the pre-breeding and egg-laying periods of 2007, 2008 and 2009. Amphipods (*Gammarus* spp.,  $n = 17$ ) were collected during the pre-breeding and egg-laying periods via sweep sampling using a D-shaped dip net (1200  $\mu\text{m}$  mesh, 0.072  $\text{m}^2$  opening). Samples of bulrush and sedge seeds were also collected during the pre-breeding and egg-laying periods of 2007, 2008 and 2009 for stable isotope analysis by finding intact seed heads from the previous year's growth. We also collected unidentified wetland seed samples ( $n = 2$ ) from the stomach contents of a recently deceased radio-marked female scaup during a concurrent radio-telemetry study. Scaup food samples were stored frozen until stable isotope analyses were conducted.

### Stable-isotope analysis

Amphipods were washed with deionized water, freeze-dried and powdered. An aliquot of yolk lipid was collected from each egg. Amphipod and egg yolks were lipid extracted using a 2:1 chloroform/methanol solution and dried in a fume hood (Ricca et al. 2007). Abdominal, invertebrate, egg and seed samples were weighed ( $\sim 1$  mg) into tin capsules, crushed and analyzed for stable-carbon ( $\delta^{13}\text{C}$ ) isotopes using continuous flow isotope-ratio mass spectrometry as described by Hobson et al. (2005). Samples were analyzed at the Univ. of California–Davis Stable Isotope Facility, Davis, CA, USA. Stable isotope values were reported in parts per thousand (‰) relative to the standards Vienna Pee Dee Belemnite for  $\delta^{13}\text{C}$ . Sucrose and glutamic acid were used as internal standards for mass spectrometry calibration. Both standards were calibrated against primary International

Atomic Energy Agency standards including USGS-40 and USGS-41. The  $\delta^{13}\text{C}$  values for sucrose and glutamic acid were  $-24.4\text{‰} \pm 0.2$  and  $-28.7\text{‰} \pm 0.2$ , respectively. Within run measurement precision for  $\delta^{13}\text{C}$  of both standards was 0.1‰.

Under equilibrium conditions, stable isotope values in eggs differ in a predictable manner from those in the female's diet (Hobson 1995), but such discrimination values have not been established specifically for the mobilization of endogenous reserves to eggs. Researchers instead have used isotopic discrimination factors associated with the carnivore model of Hobson (1995) as a proxy for discrimination between endogenous reserves to eggs (Gauthier et al. 2003, Schmutz et al. 2006, Bond et al. 2007). Discrimination between amphipod and abdominal lipids to yolk lipid formation was assumed to be 0.0‰ for  $\delta^{13}\text{C}$  (Hobson 1995). For discrimination associated with conversion of wetland seed carbohydrates to yolk lipid, we used a value of  $-2.6\text{‰}$  for  $\delta^{13}\text{C}$  from the income herbivore model (Hobson 1995).

## Data analysis

The relative contribution of sources to egg lipid formation was estimated using the isotope mixing model IsoError (Phillips and Gregg 2001) that accounts for both the isotopic variation in the sources and mixtures. A two-endpoint, one-isotope mixing model was used to estimate at the population level the relative contribution of the combined abdominal/amphipod lipid and wetland seeds to egg lipid formation using tissue  $\delta^{13}\text{C}$  values. We did not analyze our data at the individual level; therefore, this precluded us from testing hypotheses related to individual body condition as a function of dietary contributions to egg lipid formation. Because the confidence interval (90%) of  $\delta^{13}\text{C}$  values of female abdominal lipid and invertebrate lipid overlapped in 2008 and 2009, we could not adequately quantify the individual contribution of these two source types to yolk lipid formation in those specific years (2008 – 90% CI: abdominal lipid  $-21.7$  to  $-24.0\text{‰}$ , amphipod lipid  $-22.7$  to  $-25.7\text{‰}$ , and 2009 – 90% CI: abdominal lipid  $-23.4$  to  $-24.8\text{‰}$ , amphipod lipid  $-23.6$  to  $-26.6\text{‰}$ ). We therefore included these as a combined source, and estimated their relative contribution to that of seeds of emergent wetland plants. Lipids contain only C and H but we did not run the samples for  $\delta^2\text{H}$  because no studies have yet provided isotopic discrimination factors associated with lipid synthesis using this isotope. We therefore used only  $\delta^{13}\text{C}$  values in the isotope mixing model, and were forced to combine abdominal and invertebrate lipid in our interpretations.

For years where we had missing source isotope data, (i.e. abdominal lipids in 2006 and 2007, and amphipod lipid and wetland seeds in 2006), we combined the  $\delta^{13}\text{C}$  values for sources across all years for use in the isotope mixing model. For years where all  $\delta^{13}\text{C}$  source data were collected, we quantified year-specific contributions of the combined abdominal/invertebrate lipids and wetland seeds to egg lipid formation. Annual variation of the estimated contribution from each source to yolk lipid formation was tested by comparing confidence intervals (90%) of contribution values estimated by the mixing model.

We present both unadjusted and adjusted isotope values accounting for isotopic discrimination, but we specify if the isotope values were adjusted or not for wetland seeds.

## Results

The isotopic endpoints of the local food web were estimated from 17 amphipod lipid samples taken at 13 locations, 11 wetland seed samples at 11 locations, and 2 wetland seed samples from one recently deceased adult female scaup collected during the prebreeding season. The isotopic endpoint for female scaup abdominal lipid was estimated from 45 individuals (12 in 2008, and 33 in 2009). A total of 76 eggs from 76 nests were collected during the four-year study (20 in 2006, 6 in 2007, 27 in 2008, and 23 in 2009).

### Stable-isotopes of endogenous tissues, eggs and dietary items

The combined  $\delta^{13}\text{C}$  values for female abdominal and amphipod lipid in 2008 and 2009 was  $-23.3 \pm 0.6\text{‰}$  and  $-24.2 \pm 0.3\text{‰}$ , respectively. In contrast, the adjusted (i.e. for isotopic discrimination) mean  $\delta^{13}\text{C}$  value of wetland seeds was lower than the combined abdominal and invertebrate mean lipid values from 2008 ( $-28.8 \pm 0.7\text{‰}$ ) and 2009 ( $-28.9 \pm 0.3\text{‰}$ ). Mean  $\delta^{13}\text{C}$  values for all years combined for abdominal and amphipod lipid was  $-23.8 \pm 0.3\text{‰}$ , while the adjusted mean  $\delta^{13}\text{C}$  values for wetland seeds was  $-29.1 \pm 0.2\text{‰}$ . Egg lipid  $\delta^{13}\text{C}$  values fell between values for the abdominal and invertebrate lipids combined, and wetland seeds across all four-years of study (Table 1, 2).

### Relative contributions of endogenous and exogenous sources to egg lipid formation

In 2006, wetland seeds contributed more on average than the combined abdominal and invertebrate lipid sources to egg lipid formation (90% CI = 47 to 75%, and 25 to 53%,

Table 1. Stable-carbon isotope values (means  $\pm$  SE (n)) for aquatic amphipod lipid and wetland seed resources available to lesser scaup on the breeding grounds. None of these samples are adjusted for isotopic discrimination. All samples were collected at Red Rock Lakes National Wildlife Refuge, MT, USA.

Organism	$\delta^{13}\text{C}$ (‰)	Year of collection
Invertebrate		
Amphipods	$-22.5 \pm 0.2$ (6)	2007
Amphipods	$-24.2 \pm 0.9$ (7)	2008
Amphipods	$-25.1 \pm 0.9$ (4)	2009
All Amphipods <sup>a</sup>	$-23.8 \pm 0.5$ (17)	
Seed		
Sedge	$-26.7 \pm 0.6$ (3)	2007
Sedge	$-25.9 \pm 1.0$ (2)	2008
Bulrush	$-26.9$ (1)	2008
Sedge	$-26.0 \pm 0.2$ (5)	2009
Unidentified seeds <sup>b</sup>	$-26.9 \pm 1.0$ (2)	2009
All seed groups <sup>a</sup>	$-26.5 \pm 0.2$ (13)	

<sup>a</sup>scientific names: amphipods *Gammarus* spp., sedge *Carex* spp., bulrush *Schoenoplectus acutus*.

<sup>b</sup>unidentified seeds collected from stomach contents of a recently deceased adult female scaup during the prebreeding season.



Table 2.  $\delta^{13}\text{C}$  values for egg yolk, and abdominal lipids of arriving lesser scaup females, Red Rock Lakes National Wildlife Refuge, MT, USA, 2006–2009.

Year	Tissue	n	$\delta^{13}\text{C}$ (‰)	SE (‰)
2006	yolk lipid	20	-26.9	0.4
2007	yolk lipid	6	-25.2	0.4
2008	yolk lipid	27	-25.9	0.4
2009	yolk lipid	23	-25.1	0.2
2008	abdominal lipid	12	-22.8	0.7
2009	abdominal lipid	33	-24.1	0.4

respectively) (Table 3). In 2007 and 2009, the pattern was reversed: wetland seeds contributed less to egg lipid formation than did the combined lipid sources (90% CI = 2007: 13 to 42%, and 59 to 87%, and 2009: 7 to 30%, and 69 to 93%, respectively). In 2008, wetland seeds and the combined lipid source contributed approximately equally to egg lipid formation (90% CI = 29 to 65%, and 35 to 71%, respectively). Regardless of possible annual variation, the results indicate that carbon from both seeds of emergent wetland plants and the combined abdominal/amphipod lipids contributed to egg lipid formation, and that each source contributed at least, on average, 19% (lowest mean value for all years) to the total lipid composition of eggs in each year (Table 3).

## Discussion

Through a direct isotope tracing approach, we were able to quantify the relative importance of carbohydrates from seeds of emergent wetland plants grown on the breeding grounds to yolk lipid formation by scaup. This represents the first published finding showing inter-annual variability in nutrient allocation strategies used for clutch lipid formation in lesser scaup. These results complement our earlier study, which indicated reliance on local exogenous sources and interannual variability of protein for egg production (Cutting et al. 2011).

### Sources of lipids for eggs

Contrary to our hypothesis, the sources used for egg lipid formation varied significantly among years. Therefore, scaup might be able to adjust their breeding strategy based

Table 3. The relative contribution of combined abdominal and amphipod lipids, and seeds of emergent wetland plants to egg lipid production of lesser scaup as determined by  $\delta^{13}\text{C}$  analysis. Discrimination values were applied to  $\delta^{13}\text{C}$  values of arrival abdominal and amphipod lipids, distinguishing them from wetland seeds (Hobson 1995, Gauthier et al. 2003). Calculations were based on using a two-endpoint, one-isotope ( $\delta^{13}\text{C}$ ) linear mixing model IsoError (Phillips and Gregg 2001).

Year	Abdominal and invertebrate lipids			Local wetland seeds		
	mean (SE)	90% lcl	90% ucl	mean (SE)	90% lcl	90% ucl
2006	0.39 (0.09)	0.25	0.53	0.61 (0.09)	0.47	0.75
2007	0.73 (0.09)	0.59	0.87	0.27 (0.09)	0.13	0.42
2008	0.53 (0.11)	0.35	0.71	0.47 (0.11)	0.29	0.65
2009	0.81 (0.07)	0.69	0.93	0.19 (0.07)	0.07	0.30

on certain proximal conditions they encounter among years. For example, the percent contribution of wetland seeds was greatest during years of highest water level. In 2006 and 2008, mean water level was highest during the four-year study (Warren et al. 2013), possibly allowing scaup to easily access habitats (e.g. wetland margins) where seeds of emergent wetland plants were abundant. During years with low water level, scaup may be prevented from easily accessing the wetland margins because of dry overland habitat, forcing scaup to forage more on aquatic amphipods. Increased foraging opportunity on abundant wetland seeds during high-water years not only provides substrate for lipid synthesis for rebuilding body reserves following spring migration, but wetland seeds also provide a reliable food source regardless of wetland phenology for clutch lipid formation.

In interpreting our results, it is important to note that we could not distinguish between  $\delta^{13}\text{C}$  values of local amphipods and abdominal lipids on arrival. Therefore, it is possible that a large proportion of energy used in yolk formation was acquired from local sources. However, despite the overlap in  $\delta^{13}\text{C}$  values, we were still able to quantify the importance of local wetland seeds to the formation of egg lipids using the stable isotope approach, and this proved to be informative since its importance was previously unknown. Our findings also represent a minimum estimate of the importance of local food sources to egg lipids, and so are conservative in terms of nutrient allocation theory.

Past studies have suggested that wetland seeds are important in the diets of lesser scaup during spring migration and pre-breeding (Afton and Hier 1991, Smith 2007, Strand et al. 2008). Strand et al. (2008) found that wetland seeds were the most common diet item in terms of aggregate biomass and percent occurrence during spring migration in South Dakota. Afton and Hier (1991) showed that male and female most preferred wetland seeds during pre-rapid follicle growth and egg laying periods. Furthermore, Anteau and Afton (2006) showed that in seasonal wetland habitats the percent occurrence of wetland seeds in scaup diets increased from 40% in the 1980s to > 70% in 2000–2005. Wetland seeds are likely a reliable exogenous source of carbohydrates, since they are available during the early spring regardless of the timing of spring plant and invertebrate production. Our results corroborate these findings and have significant implications for the understanding of how scaup allocate energy to their eggs. We suggest that scaup can shift from a protein-rich invertebrate diet to a diet based on carbohydrate-rich wetland seeds during egg lipid formation.

By understanding the foraging habits of scaup during the prebreeding period, perhaps wetland managers can focus on providing habitats that ensure a diversity of invertebrate and seed resources across time and space for breeding scaup. Management strategies aimed at enhancing food sources found on spring staging and breeding area habitats may differ depending on their importance for egg formation. Research at the individual level, i.e. studies linking individual females to their eggs, will provide greater inference than will studies done at the population level, as done in this study. Thus, we encourage future multi-year and multi-area studies to further our understanding of how

flexible scaup are in their foraging and reproductive strategies.

*Acknowledgements* – We thank the staff at Red Rock Lakes National Wildlife Refuge for logistical support. We thank S. Creel and R. Garrott for constructive comments on drafts of the manuscript, and W. Cross for access to his lab. We thank our field assistants including S. Bard, E. Cutting, K. C. Cutting, W. Goldenberg, J. Karagetchevia, A. Lawson and A. Phillips. Funding for this study was provided by Delta Waterfowl Inc., Waterfowl Research Foundation Inc., US Fish and Wildlife Service, and US Geological Survey. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the US Fish and Wildlife Service and US Geological Survey.

## References

- Afton, A. D. 1984. Influence of age and time on reproductive performance of female lesser scaup. – *Auk* 101: 255–265.
- Afton, A. D. and Ankney, C. D. 1991. Nutrient-reserve dynamics of breeding lesser scaup: a test of competing hypotheses. – *Condor* 93: 89–97.
- Afton, A. D. and Hier, R. H. 1991. Diets of lesser scaup breeding in Manitoba. – *J. Field Ornithol.* 62: 325–334.
- Anteau, M. J. and Afton, A. D. 2004. Nutrient reserves of lesser scaup (*Aythya affinis*) during spring migration in the Mississippi Flyway: a test of the spring condition hypothesis. – *Auk* 121: 917–929.
- Anteau, M. J. and Afton, A. D. 2006. Diet shifts of lesser scaup are consistent with the spring condition hypothesis. – *Can. J. Zool.* 84: 779–786.
- Anteau, M. J. and Afton, A. D. 2008. Amphipod densities and indices of wetland quality across the upper-midwest, USA. – *Wetlands* 28: 184–196.
- Austin, J. E., Custer, C. M. and Afton, A. D. 1998. Lesser scaup (*Aythya affinis*). – In: *The Birds of North America*, no. 338. Am. Ornithol. Union, Washington, DC, and the Acad. Nat. Sci., PA, USA.
- Badzinski, S.S. and Petrie, S. A. 2006. Lesser scaup spring nutrient reserve dynamics on the Lower Great Lake. – *Wildl. Soc. Bull.* 34: 395–407.
- Bond, J. C., Esler, D. and Hobson, K. A. 2007. Isotopic evidence for sources of nutrients allocated to clutch formation by harlequin ducks. – *Condor* 109: 698–704.
- Cutting, K. A., Hobson, K. A., Rotella, J. J., Warren, J. M., Wainwright-de la Cruz, S. E. and Takekawa, J. Y. 2011. Endogenous contributions to egg protein formation in lesser scaup (*Aythya affinis*). – *J. Avian Biol.* 42: 505–513.
- Drent, R. H. and Daan, S. 1980. The prudent parent: energetic adjustment in avian breeding. – *Ardea* 68: 225–252.
- Esler, D., Grand, J. B. and Afton, A.D. 2001. Intraspecific variation in nutrient reserve use during clutch formation by lesser scaup. – *Condor* 103: 810–820.
- Gauthier, G., Bêty, J. and Hobson, K. A. 2003. Are greater snow geese capital breeders? New evidence from a stable-isotope model. – *Ecology* 84: 3250–3264.
- Gloutney, M. L. and Hobson, K. A. 1998. Field preservation techniques for the analysis of stable-carbon and nitrogen isotope ratios in eggs. – *J. Field Ornithol.* 69: 223–227.
- Gurney, K. E. B., Clark, R. G., Slattery, S. M., Walker, J., Stephens, S. E., Petruska, M., Corcoran, R. M., Martin, K. H., DeGroot, K. A., Brook, R. W., Afton, A. D., Cutting, K., Warren, J. M., Fournier, M. and Koons, D. N. 2011. Time constraints in temperate-breeding species: influence of growing season length on reproductive strategies. – *Ecography* 34: 628–636.
- Hobson, K. A. 1995. Reconstructing avian diets using stable-carbon and nitrogen isotope analysis of egg components: patterns of isotopic fractionation and turnover. – *Condor* 97: 752–762.
- Hobson, K. A. 2006. Using stable isotopes to quantitatively track endogenous and exogenous nutrient allocations to eggs of birds that travel to breed. – *Ardea* 94: 359–369.
- Hobson, K. A., Thompson, J. E., Evans, M. R. and Boyd, S. 2005. Tracing nutrient allocation to reproduction in Barrow's goldeneye. – *J. Wildl. Manage.* 69: 1221–1228.
- Hoffman, R. D. 1983. True metabolizable energy of seeds consumed by post-breeding ducks in Lake Eric marshes. – PhD thesis, Ohio State Univ.
- Klaassen, M., Lindström, Å., Møltofte, H. and Piersma, T. 2001. Arctic waders are not capital breeders. – *Nature* 413: 794.
- Langin, K. M., Norris, D. R., Kyser, T. K., Marra, P. P. and Ratcliffe, L. M. 2006. Capital versus income breeding in a migratory passerine bird: evidence from stable-carbon isotopes. – *Can. J. Zool.* 84: 947–953.
- Lindmeier, J. P. and Jessen, R. L. 1961. Results of capturing waterfowl in Minnesota by spotlighting. – *J. Wildl. Manage.* 25: 430–431.
- Phillips, D. L. and Gregg, J. W. 2001. Uncertainty in source partitioning using stable isotopes. – *Oecologia* 127: 171–179.
- Ricca, M. A., Miles, A. K., Anthony, R. G., Deng, X. and Hung, S. S. O. 2007. Effect of lipid extraction on analyses of stable carbon and nitrogen isotopes in coastal organisms of the Aleutian archipelago. – *Can. J. Zool.* 85: 40–48.
- Rogers, J. P. and Korschgen, L. J. 1966. Foods of lesser scaups on breeding, migration, and wintering areas. – *J. Wildl. Manage.* 30: 258–264.
- Schmutz, J. A., Hobson, K. A. and Morse, J. A. 2006. An isotopic assessment of protein from diet and endogenous stores: effects on egg production and incubation behavior of geese. – *Ardea* 94: 385–397.
- Smith, R. V. 2007. Evaluation of waterfowl habitat and spring food selection by mallard and lesser scaup on the Swan Lake, Illinois habitat rehabilitation and enhancement project. – MSc, Southern Illinois Univ.
- Stephens, P. A., Boyd, W. E. L., McNamara, J. M. and Houston, A. W. E. 2009. Capital breeding and income breeding: their meaning, measurement and worth. – *Ecology* 90: 2057–2067.
- Strand, K. A., Chipps, S. R., Kahara, S. N., Higgins, K. F. and Vaa, S. 2008. Patterns of prey use by lesser scaup *Aythya affinis* (Aves) and diet overlap with fishes during spring migration. – *Hydrobiologia* 598: 389–398.
- Sugden, L. C. 1973. Metabolizable energy of wild dock foods. – *Canadian Wildlife Service Progress Notes* 35.
- US Fish and Wildlife Service 2009. Waterfowl population status, 2009. – US Dept of the Interior, Washington, DC, USA.
- Warren, J. M., Cutting, K. A. and Koons, D. N. 2013. Body condition dynamics and the cost-of-delay hypothesis in a temperate-breeding duck. – *J. Avian Biol.* in press.
- Weller, M. W. 1956. A simple field candler for waterfowl eggs. – *J. Wildl. Manage.* 20: 111–113.
- Woodin, M. C. and Swanson, G. A. 1989. Foods and dietary strategies of prairie-nesting ruddy ducks and redheads. – *Condor* 91: 280–287.