

NUTRIENT RESERVE AND ORGAN DYNAMICS OF BREEDING CINNAMON TEAL¹

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Abstract. I examined nutrient and organ dynamics of breeding Cinnamon Teal (*Anas cyanoptera*) in Arizona to determine when nutrient reserves, if any, were acquired, and the relative use of endogenous and exogenous nutrient sources during clutch production. Females stored lipid and protein after arrival and through rapid follicle growth (RFG). Females expended lipid reserves during laying ($P = 0.0001$, $r^2 = 0.85$), but size of remaining lipid reserve was not related to the number of eggs laid ($P = 0.22$, $r^2 = -0.10$), nor to the estimated amount of lipid needed to complete the clutch in laying females ($P = 0.54$, $r^2 = -0.04$). Females did not use endogenous protein during laying ($P = 0.12$, $r^2 = 0.10$). Males stored protein while their mates underwent RFG. Digestive organ measures in both sexes varied in relation to feeding ecology during breeding. Small body size, the ability to exploit a diversity of foods, and time constraints on nutrient acquisition likely influence nutrient reserve dynamics of breeding Cinnamon Teal in Arizona.

Key words: *Anas cyanoptera*; body size; breeding; digestive organs; high-elevation wetlands; nutrient reserves.

INTRODUCTION

Female dabbling ducks (genus *Anas*) commonly use nutrient reserves during clutch formation, but interspecific and intraspecific differences occur in the timing of nutrient storage, the types of nutrient reserves used, and the relative contributions of endogenous reserves and dietary nutrient sources to energetic requirements (Alisauskas and Ankney 1992). Body size may influence the timing and extent of nutrient storage, because larger species can store absolutely and relatively greater reserve masses and can transport reserves with lower effects on wing-loading than smaller species (Calder 1984, Martin 1987, Blem 1990). The types of nutrient reserves used and their contribution to egg formation also can vary relative to interspecific differences in diet specialization (e.g., Ankney and Afton 1988, Ankney and Alisauskas 1991a), and among populations of a species occupying different habitats (Young 1993). Unfortunately, the timing of nutrient reserve acquisition is unknown for many dabbling duck populations. Furthermore, few studies in North America have examined nutrient dynamics in *Anas* species and populations breeding outside mid-continent prairie habitats (Alisauskas and Ankney 1992).

The Cinnamon Teal (*A. cyanoptera*) is a small-bodied dabbling duck that breeds primarily on marshes in the arid, intermountain regions of western North America (Bellrose 1980, Brown 1985). The feeding ecology of prelaying and laying female Cinnamon Teal is similar to that of closely related prairie-nesting species such as the Blue-winged Teal (*A. discors*; Gammonley 1995), but the timing of nutrient storage and use of endogenous reserves by breeding Cinnamon Teal is unknown. I predicted that female Cinnamon Teal would rely primarily on exogenous sources to meet energy and nutrient demands during clutch production, and that storage of nutrient reserves used during clutch formation would primarily occur after arrival on the breeding grounds. Because males incur lower energetic demands than females during breeding, I predicted that male Cinnamon Teal would not store or use nutrient reserves. I also predicted that the sizes of digestive organs in both sexes would vary in response to changes in feeding ecology during breeding.

METHODS

STUDY AREA

I collected Cinnamon Teal from high-elevation (1,937–2,819 m) wetlands located near the southern rim of the Colorado Plateau in Arizona in 1992 and 1993. Wetlands are scattered at low

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densities ($<0.3 \text{ km}^{-2}$) throughout the region, and include seasonally flooded and semi-permanent marshes, permanent reservoirs, and artificially-created effluent wetlands (Brown 1985, Gammonley 1995). Wetlands were ice-free each year by early March (lower elevations) to late April (highest elevations). The Cinnamon Teal is a common breeding species in the region, and breeding populations in 1992 and 1993 were approximately 1.6 and 2.3 pairs/wetland, respectively.

CARCASS AND NUTRIENT ANALYSES

I shot Cinnamon Teal 6–26 May 1992 and 24 March–3 June 1993. I assigned females to the following categories: *arrival*, migrating or arriving birds (ovary mass ≤ 0.7 g) collected before isolation of pairs occurred, and before the first early-rapid follicle growth (early-RFG) female was collected; *pre-RFG*, birds collected after first *early-RFG* female was collected, but with ovary mass ≤ 0.7 g and no developing follicles; *early-RFG*, ovary mass >0.7 g and one or two developing follicles (follicle diameter ≥ 6.0 mm and accumulating yolk); *RFG*, enlarged ovary and 3–5 rapidly developing follicles; and *laying*, ≥ 1 post-ovulatory follicles (POFs). No reneating females were collected. I collected male pair members whenever possible and assigned them to the same category as their mates. A bursa was present in six females and one male, but aging based on cloacal characteristics during spring can be unreliable for ducks (Esler and Grand 1994a); thus, I excluded age as a variable in subsequent analyses.

Following collection, I weighed each bird to the nearest 5 g on a Pesola scale and removed the esophagus and proventriculus. I measured the lengths of the culmen, tarsus, middle toe, keel (0.1 mm) and flattened wing (1.0 mm). I plucked each carcass and removed and weighed reproductive organs, right breast muscles, right leg muscles, liver, empty gizzard, empty intestine, and measured the combined length of the ceca. Following dissection, I reweighed and homogenized the eviscerated carcass (minus feathers, digestive and reproductive organs) in a meat grinder. Subsamples of ground material were oven-dried to constant mass at 85°C. Lipid content was determined using petroleum ether in a Soxhlet apparatus. Following lipid extraction, samples were placed in a muffle furnace at 600°C. Ash mass was then determined, and protein was

estimated by subtraction as ash-free lean dry mass. All carcass nutrient estimates were calculated as a proportion of eviscerated carcass mass, and are considered nutrient reserves.

The mean fresh mass of 28 Cinnamon Teal eggs was 30.8 g. I used the percentage composition of Blue-winged Teal eggs (Alisauskas and Ankney 1992) to estimate mean egg yolk lipid (4.0 g), mean egg protein (4.7 g) and mean dry egg shell (2.3 g) of Cinnamon Teal eggs. For each female, I estimated reproductive lipid as lipid in the ovary plus the product of mean egg lipid and the number of POFs; reproductive protein as the sum of ovarian protein, oviduct dry weight, and the product of mean egg protein times the number of POFs; and reproductive ash as the product of mean dry shell times the number of POFs (Alisauskas and Ankney 1985).

STATISTICAL ANALYSES

To account for the influence of body size, I performed principal component analysis (PROC PRINCOMP; SAS Institute 1985) for each sex on a correlation matrix of 5 morphological variables (culmen, tarsus, middle toe, flattened wing, and keel). The first principal component (PC₁) described positive correlation in the variables, with loadings ranging from 0.26 to 0.58 for females and 0.38 to 0.59 for males. The PC₁ eigenvalue was 2.05 and 1.98, and PC₁ accounted for 41% and 40% of the total original variance for females and males, respectively. I regressed PC₁ scores against carcass nutrients to examine variation in nutrient reserves attributable to body size (PROC GLM; SAS Institute 1985). Lipid and ash were not related to body size ($P > 0.2$), but protein was related as

$$Y = 53.3 + 2.0X$$

for females ($P < 0.001$, $r^2 = 0.22$), and as

$$Y = 54.8 + 1.2X$$

for males ($P < 0.05$, $r^2 = 0.10$). I used residuals from the regressions of PC₁ scores and carcass protein to correct for variation due to body size (Ankney and Afton 1988).

I compared body, nutrient, and organ masses between reproductive categories using *t*-tests. I used linear regression to examine the relationship between nutrient reserves and reproductive nutrients during egg formation (Alisauskas and Ankney 1985). I performed separate regressions for RFG (including early-RFG) and laying birds,

TABLE 1. Body, nutrient, muscle and organ masses (mean \pm SE) of female Cinnamon Teal in Arizona.

Component	Arrival		Pre-RFG		Early-RFG		RFG		Laying
<i>n</i>	13		12		14		13		17
Fresh mass	335 \pm 9	ns ¹	353 \pm 6	***	385 \pm 4	*	401 \pm 7	ns	404 \pm 7
Carcass mass	240 \pm 8	*	261 \pm 4	**	283 \pm 6	ns	284 \pm 5	**	267 \pm 4
Lipid	24.5 \pm 5.0	ns	23.9 \pm 7.4	*	30.0 \pm 5.1	ns	33.0 \pm 3.2	**	21.0 \pm 1.9
Protein	46.5 \pm 1.9	*	51.0 \pm 0.8	ns	53.0 \pm 1.5	**	58.3 \pm 0.9	ns	55.0 \pm 1.6
Ash	11.7 \pm 1.1	ns	13.8 \pm 1.3	ns	11.5 \pm 0.9	ns	10.5 \pm 0.7	ns	10.4 \pm 0.4
Right breast muscle	34.8 \pm 1.0	ns	36.9 \pm 0.7	ns	38.3 \pm 0.8	ns	38.7 \pm 0.7	ns	39.0 \pm 0.6
Right leg muscle	9.1 \pm 0.4	**	10.6 \pm 0.2	ns	10.8 \pm 0.3	*	11.8 \pm 0.8	ns	11.2 \pm 0.5
Liver	7.9 \pm 0.4	***	10.9 \pm 0.5	ns	11.6 \pm 0.6	ns	12.3 \pm 0.7	ns	13.0 \pm 0.3
Gizzard	9.5 \pm 0.9	ns	9.5 \pm 0.4	ns	9.0 \pm 0.5	ns	8.0 \pm 0.4	*	7.2 \pm 0.3
Intestine	15.3 \pm 0.5	*	13.6 \pm 0.5	ns	14.8 \pm 0.6	ns	15.0 \pm 0.8	**	12.6 \pm 0.5
Ceca length (mm)	195 \pm 7	***	163 \pm 5	ns	167 \pm 8	*	145 \pm 6	ns	147 \pm 6

¹ Significance level of *t*-test comparisons of adjacent columns: ns = $P > 0.05$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

as well as for both groups combined. I regressed carcass ash on reproductive ash for laying birds only. For each nutrient, I regressed male reserves on the size of their mates' reproductive nutrient commitment (Ankney and Afton 1988). I also used general linear models with Type III sums of squares (PROC GLM; SAS Institute Inc. 1985) to examine variation in nutrient reserves in relation to year, date of initiation of RFG, and reproductive nutrient.

I examined the relationship between nutrient reserves and clutch size by regressing carcass lipid and protein on the estimate of reserves required to complete the clutch in laying females with < 5 rapidly developing follicles ($n = 9$ females). I subtracted the amount of lipid or protein present in eggs that had been produced (based on the number of POFs) from the amount that would be in the completed clutch (eggs already produced + the number of developing follicles), and entered this value into the regression equation obtained for each nutrient during laying, in order to estimate nutrient reserves required to complete the clutch in these females (see Esler and Grand 1994b). I used regression to examine whether a relationship existed between reserves yet to be used and the number of eggs already laid in these females (Mann and Sedinger 1993, Esler and Grand 1994b).

RESULTS

NUTRIENT AND ORGAN DYNAMICS

Females arrived on the study area relatively lean, and gained an average of 44 g (carcass) between arrival and RFG, including 12 g of protein and 9 g of lipid (Table 1). Carcass ash content did

not change from arrival to laying. Mean leg muscle mass increased 19% from arrival to laying (Table 1). Mean liver mass increased 65% from arrival to laying, whereas mean gizzard mass decreased 24%, and intestine mass and cecal length decreased 34% and 33%, respectively (Table 1).

Mean carcass protein mass of RFG males was significantly greater than in early-RFG males (Table 2). Mean leg muscle mass increased 21% from arrival to laying (Table 2). Mean liver, gizzard, and intestine mass decreased 20%, 20%, and 26%, respectively, and cecal length decreased 25%, from arrival to laying (Table 2).

RESERVE DYNAMICS DURING EGG PRODUCTION

Year and date of initiation of RFG were not related to lipid, protein, or mineral reserves in either sex; all interactions among year, date of initiation of RFG, and reproductive nutrient were also nonsignificant ($P > 0.14$ for all comparisons). Based on simple linear regressions, females gained 3.07 g of carcass lipid per gram of reproductive lipid produced during RFG, whereas female carcass lipid declined 0.63 g per gram of reproductive lipid produced during laying (Table 3). A negative relationship between carcass and reproductive lipid also was present when RFG and laying females were combined (Table 3); using the slope value from this regression (-0.59), a female producing a typical 10 egg clutch containing 40 g of lipid (see Methods) would expend 23.7 g of carcass lipid during clutch production. Carcass protein increased 2.01 g per gram of reproductive protein produced by RFG females. Carcass and reproductive protein were

TABLE 2. Body, nutrient, muscle and organ masses (mean ± SE) of male Cinnamon Teal in Arizona.

Component	Arrival		Pre-RFG		Early-RFG		RFG		Laying	
<i>n</i>	9		10		8		9		8	
Fresh mass	383 ± 11	ns ¹	383 ± 8	ns	385 ± 11	ns	379 ± 11	ns	384 ± 13	
Carcass mass	274 ± 10	ns	280 ± 9	ns	278 ± 10	ns	284 ± 7	ns	290 ± 10	
Lipid	36.4 ± 6.3	ns	41.1 ± 5.3	ns	33.9 ± 5.6	ns	30.0 ± 4.7	ns	29.4 ± 7.0	
Protein	52.7 ± 5.0	ns	52.6 ± 3.9	ns	52.7 ± 5.7	*	57.2 ± 5.8	ns	59.9 ± 2.8	
Ash	11.0 ± 1.2	ns	10.4 ± 0.8	ns	12.6 ± 2.0	ns	12.5 ± 1.1	ns	10.3 ± 0.7	
Right breast muscle	37.2 ± 1.2	ns	38.5 ± 1.2	ns	38.2 ± 1.1	ns	39.8 ± 0.7	ns	41.2 ± 0.9	
Right leg muscle	10.4 ± 0.4	*	11.2 ± 0.3	ns	10.6 ± 0.6	**	13.0 ± 0.4	ns	13.2 ± 0.3	
Liver	9.5 ± 0.5	ns	9.8 ± 0.6	ns	9.2 ± 0.6	*	7.8 ± 0.3	ns	7.5 ± 0.3	
Gizzard	9.9 ± 0.8	ns	8.6 ± 0.4	ns	8.5 ± 0.6	ns	7.8 ± 0.6	ns	7.2 ± 0.4	
Intestine	14.9 ± 0.6	ns	14.7 ± 0.5	ns	14.7 ± 1.2	ns	13.6 ± 0.5	*	11.9 ± 0.9	
Ceca length (mm)	198 ± 13	*	167 ± 8	ns	161 ± 11	ns	147 ± 10	ns	147 ± 6	

¹ Significance level of *t*-test comparisons of adjacent columns: ns = *P* > 0.05, * = *P* < 0.05, ** = *P* < 0.01.

unrelated for laying females and for RFG and laying females combined (Table 3). Carcass and reproductive ash were unrelated (*P* = 0.15, *r*² = 0.03) in laying females.

Male carcass lipid was unrelated to female reproductive lipid during RFG, laying, and RFG and laying combined (Table 3). Male protein reserves were positively related to the reproductive protein of their mates during RFG, but there was no relationship when laying birds only and when RFG and laying birds combined were considered (Table 3). Male carcass ash was not related to female reproductive ash (*P* = 0.40, *r*² = 0.01).

Size of lipid reserves was not related to the amount of these reserves that would be used to complete the clutch (*P* = 0.54, *r*² = 0.04) in females that had already produced ≥ 5 eggs and had < 5 developing follicles (*n* = 9). Similarly,

the size of protein reserves was unrelated to the amount of carcass protein needed to complete the clutch (*P* = 0.31, *r*² = 0.01) in these females. The number of eggs laid by these females was also unrelated to lipid (*P* = 0.22, *r*² = 0.10) and protein (*P* = 0.74, *r*² = 0.01) reserves.

DISCUSSION

ROLE OF ENDOGENOUS RESERVES

As in most other anatid populations studied in North America, female Cinnamon Teal on high-elevation wetlands in Arizona use endogenous lipid reserves during clutch formation. The 23.7 g of carcass lipid expended by female Cinnamon Teal during clutch formation yields about 893 kJ of energy (Johnston 1970), equal to about 30% of the energy in a typical clutch of 10 eggs (Al-

TABLE 3. Results of linear regressions of Cinnamon Teal carcass nutrients on reproductive nutrients during RFG (27 females, 17 males), laying (17 females, 8 males), and RFG and laying combined.

Nutrient	Status	Intercept	Slope	<i>F</i>	<i>P</i>	<i>r</i> ²
Females						
Lipid	RFG	29.31 ± 2.03	3.07 ± 0.91	11.31	0.0028	0.31
	Laying	33.88 ± 1.53	-0.63 ± 0.06	92.65	0.0001	0.85
	Combined	34.23 ± 1.51	-0.59 ± 0.10	0.80	0.0001	0.48
Protein	RFG	52.16 ± 2.60	2.01 ± 0.87	5.34	0.0293	0.14
	Laying	65.90 ± 5.90	-0.40 ± 0.24	2.69	0.1216	0.10
	Combined	57.54 ± 2.01	-0.07 ± 0.13	0.29	0.5915	-0.02
Males						
Lipid	RFG	30.25 ± 4.90	0.27 ± 2.18	0.02	0.9040	-0.08
	Laying	49.73 ± 2.09	-0.78 ± 0.75	1.07	0.3412	0.01
	Combined	33.39 ± 4.30	-0.22 ± 0.25	0.80	0.3812	-0.01
Protein	RFG	45.56 ± 4.51	3.98 ± 1.39	8.20	0.0143	0.36
	Laying	64.75 ± 5.09	-0.03 ± 0.19	0.02	0.8999	-0.16
	Combined	55.01 ± 3.07	0.35 ± 0.19	3.43	0.0787	0.10

isauskas and Ankney 1992), or about 10% of the total energy required (including existence energy) during egg formation (see Arnold and Rowher 1991). These contributions by lipid reserves did not appear to proximately influence clutch size, however. Lipid reserve size was unrelated to both the number eggs already laid and the amount of lipid needed for the remaining eggs of females whose final clutch size could be determined, although the small sample size ($n = 9$) limits the statistical power of these analyses.

Despite their primary reliance on exogenous lipids for egg formation, carcass lipids in early-RFG females were greater than in pre-RFG females collected during the same period, suggesting a lipid threshold must be obtained before Cinnamon Teal initiate clutch production (Alisauskas and Ankney 1992). Such a threshold may indicate that reserves are critical during egg production and/or subsequent energy-demanding activities. I did not examine nutrient reserve dynamics beyond laying, but female Cinnamon Teal in Arizona may use lipid reserves during incubation (Gloutney and Clark 1991). Females arrived with 24.5 g of carcass lipid, slightly more than that expended during clutch production, yet acquired additional lipids on the breeding grounds. Using the regression equation for RFG and laying birds, 10.6 g of carcass lipid remained at the end of laying. This amount yields 400 kJ of energy, about 7% of the estimated energy requirements (5,362 kJ) of incubating Cinnamon Teal (Afton and Paulus 1992).

Female Cinnamon Teal are also similar to several other *Anas* species in that they appear to rely exclusively on dietary sources for egg protein requirements (Alisauskas and Ankney 1992, Krapu and Reinecke 1992). Protein reserves acquired by females after arrival and by both sexes during RFG were not used during clutch formation, and protein reserve size was not related to clutch size. Increases in carcass protein corresponded to significant increases in leg muscle mass, and may reflect an increased use of these muscles for swimming locomotion on the breeding grounds. Carcass protein may also provide a nutrient source during protein-demanding events such as post-breeding molt (Hohman et al. 1992).

TIMING OF NUTRIENT STORAGE

Female Cinnamon Teal gained carcass lipid and protein after spring arrival on Arizona wetlands. Cinnamon Teal use the study region for breeding

and as a spring stopover area, and the estimated breeding population was 83% of peak spring migration numbers counted in 1993, when I collected arrival and pre-RFG Cinnamon Teal. Thus, some birds categorized as arrival may have been migrating to more northerly breeding areas. Regardless, these results suggest that Cinnamon Teal do not transport large nutrient reserves to breeding areas.

Typically, data from both RFG and laying waterfowl are combined for regressions of carcass nutrients on reproductive nutrients (Alisauskas and Ankney 1992). However, nutrients are gained during RFG and then lost during laying in several duck species, including Wood Ducks, *Aix sponsa* (Drobney 1982), Canvasbacks, *Aythya valisineria* (Barzen and Serie 1990), Northern Pintails, *Anas acuta* (Mann and Sedinger 1993), and Cinnamon Teal (this study). Male Cinnamon Teal also gained carcass protein during RFG of their mates. These patterns can be obscured when both reproductive groups are combined in analyses (see Table 3). Separate analyses for RFG and laying categories may provide additional insights into nutrient reserve dynamics and nutrient limitation in waterfowl. Gains in carcass lipid and protein by Cinnamon Teal during RFG suggests that dietary sources of these nutrients are abundant and readily obtained during clutch production.

INFLUENCES ON NUTRIENT STORAGE AND USE

Several comparisons suggest that lipid reserves generally contribute less to egg production in Cinnamon Teal and other small-bodied dabbling ducks than in larger-bodied *Anas* species (see also Ankney and Alisauskas 1991b). First, lipid reserves of larger species are absolutely larger, and also tend to be relatively larger, than in smaller congeners. Peak carcass lipid mass was about 8% of body mass in 400 g prelaying Cinnamon Teal, 10% in 400 g Blue-winged Teal (Young 1991) and 630 g Northern Shovelers, *A. clypeata* (Ankney and Afton 1988), 14% in 876 g Northern Pintails (Mann and Sedinger 1993), and 10–16% in 1,100 g Mallards, *A. platyrhynchos* (Krapu 1981, Young 1993). Second, reserves of small species account for a smaller proportion of clutch formation costs than in larger species. Regression slopes of lipid reserve use during clutch production by female Cinnamon Teal (-0.59) and Blue-winged Teal (-0.42) (Young 1991) were not as

steep as in larger-bodied Northern Shovelers (-0.72) (Ankney and Afton 1988), Gadwalls, *A. strepera* (-0.78) (Ankney and Alisauskas 1991a), Northern Pintails (-2.4) (Mann and Sedinger 1993), and Mallards (-1.04) (Krapu 1981). Finally, contribution of reserves to total energy requirements of laying dabbling ducks ranged from 9–17% in other studies, and generally increased with body size (Arnold and Rowher 1991).

The above comparisons indicate body size constraints may account for some broad interspecific differences in contributions of lipid reserves to *Anas* clutch production. However, in Mallard populations occupying different breeding habitats, lipid slopes ranged from -0.6 to -1.5 , and reserves accounted for 8–21% of egg-forming female energy needs (Young 1993). The ranges of these values are similar to those noted in the above interspecific comparisons. Furthermore, contribution of lipid reserves to clutch production in arctic-nesting female Northern Pintails was strongly related to date of initiation of RFG (Esler and Grand 1994b). Thus, spatial and temporal variation in environmental conditions may have as much or more influence on the energetic strategies of dabbling duck populations than body-size constraints.

Body size also may influence the timing of nutrient storage by dabbling ducks. Large-bodied Mallards and Northern Pintails acquire large reserves on wintering and spring stop-over areas (Krapu 1981, Mann and Sedinger 1993), whereas Cinnamon Teal do not. Wing-loading effects on Cinnamon Teal may increase the fitness-related costs of transporting large reserves during spring migration (Blem 1990, see also Tome 1984, Alisauskas and Ankney 1994). Differences in the timing of nutrient storage also may contribute to interspecific differences in nesting chronology of dabbling ducks. In Arizona, peak nest initiation dates of Cinnamon Teal were 5–6 weeks after peak arrival of local breeding pairs, and 4–5 weeks after peak nest initiation dates of Mallards, which begin laying shortly after arrival (Gammonley, unpubl.). Gadwalls also acquire substantial nutrient reserves after arrival on breeding areas and nest later than other dabblers (Ankney and Alisauskas 1991a).

In addition to relatively late nest initiation dates, Cinnamon Teal begin fall migration earlier than many other dabbling species (Bellrose 1980; Gammonley, unpubl.). Thus, Cinnamon Teal

must complete breeding activities in a relatively short span of time. Feeding opportunities may be time-limited for brood-rearing and molting Cinnamon Teal, however, and reserves acquired before clutch production may allow these birds to complete these critical events within seasonal time constraints.

DIGESTIVE ORGAN DYNAMICS

Size variations in digestive organs reflect the dietary strategies that breeding Cinnamon Teal use to meet energetic demands. Paired females spent 56–65% of diurnal hours feeding (Gammonley 1995), and time spent foraging by females was highest during the peak period of nest initiation (Gammonley, unpubl.). Females also consumed a higher proportion of aquatic invertebrates than females at nonbreeding locations, and invertebrate consumption was highest during laying (Migoya and Baldassarre 1993, Thorn and Zwank 1993, Gammonley 1995).

Increases in liver mass of ducks have been attributed to increased food consumption and intermediary metabolism of protein and lipid (Hazelwood 1972, Drobney 1984, Ankney and Afton 1988, Heitmeyer 1988). Both of these factors may have influenced increases in liver mass of female Cinnamon Teal in Arizona. Decreases in gizzard mass can result from metabolism of gizzard protein and/or decreases in diet fiber content (Miller 1975, Krapu 1981, Drobney 1982, Kehoe et al. 1988, Mann and Sedinger 1993). Use of gizzard protein by laying female Cinnamon Teal is unlikely, because carcass protein is not used during clutch formation and is actually stored during RFG. Increased invertebrate consumption by laying females results in a lower diet fiber content (Krapu and Reinecke 1992), and probably accounts for the lower gizzard mass of laying females. Similarly, intestine mass and cecal length are typically greatest when relatively large amounts of food digestion occurs in these organs, as occurs when fiber intake is high (Miller 1975, Drobney 1984, Kehoe et al. 1988, Heitmeyer 1988). Increased consumption of relatively low-fiber invertebrate foods by breeding females compared to nonbreeding females, and by laying females compared to prelaying females, may account for decreases in intestine mass and cecal length after arrival and during clutch production.

Digestive organs of breeding male Cinnamon Teal varied less than those of their mates. Male

diets did not vary among reproductive categories, and breeding males consumed a higher proportion of hard seeds than females and spent less time feeding than their mates (Gammonley 1995). Male vigilance and mate defense are likely important factors in reproductive success, and males spend more time alert and aggressive and less time feeding as nesting proceeds (Gammonley, unpubl.). Thus, observed decreases in the size of male digestive organs were likely due to decreased food consumption from arrival to laying.

CONCLUSIONS

Breeding Cinnamon Teal in Arizona depend largely on dietary nutrient sources to meet the energetic costs of clutch formation. Lipid reserves used by laying females, and protein reserves that may be used by both sexes to meet energetic demands following clutch production, also are acquired primarily after arrival on the breeding grounds. Food abundance and its variation over time on high-elevation wetlands in Arizona is, as in most wetland systems, poorly understood. These results indicate, however, that these wetland habitats can provide adequate food sources for Cinnamon Teal to meet nutrient demands during egg production. Flexibility in diet and feeding behavior (Gammonley 1995), and in digestive organ morphology allow Cinnamon Teal to efficiently acquire these nutrients.

If food availability limits clutch size (Lack 1967) and the ability to complete other annual cycle events (e.g., incubation), factors influencing food availability after arrival on breeding areas are particularly important for Cinnamon Teal. Even when food is abundant, time may limit food availability for Cinnamon Teal, by constraining energy and nutrient acquisition in relation to optimal timing of breeding ground activities. Cinnamon Teal behavioral traits (e.g., habitat selection, homing, mate-guarding) likely reflect, in part, adaptative responses to these constraints on nutrient acquisition. Further understanding of influences on the reproductive success of Cinnamon Teal is needed, but control of factors that impede nutrient acquisition by breeding populations (e.g., human-caused disturbance) should be a management priority.

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