Nutrient-reserve dynamics of semiarid-breeding White-faced Whistling Ducks: a north-temperate contrast

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Abstract: Little is known about the nutrient-reserve dynamics of waterfowl that breed in semiarid environments. Breeding White-faced Whistling Ducks, *Dendrocygna viduata* (L., 1766), were collected on the Nyl River floodplain, South Africa, during 1992–1993 and 1995. Mass of major lipid (wet skin + visceral fat + abdominal fat) and protein (breast muscle + leg muscle + gizzard) deposits and organs of males and females were evaluated in relation to sex and reproductive stage. Both sexes arrived at breeding areas with large lipid reserves and did not store additional lipid after arrival. Stored reserves enabled females to begin laying shortly after arrival, an important adaptation to ephemeral wetlands in semiarid environments. Females catabolized at least 37 g of lipid and 27 g of body protein during rapid follicular growth and ovulation. This accounted for 87% of their total lipid and 60% of their protein requirements during egg laying. Males catabolized at least 19 g of lipid between arrival and the end of laying. Although diets of breeding White-faced Whistling Ducks are high in fat, females satisfied most of their lipid requirements for clutch formation from endogenous reserves. Female White-faced Whistling Ducks can reproduce despite their reliance on a relatively low protein diet, and this suggests that they efficiently assimilate amino acids from plant matter. Biparental care apparently decreases the reliance of female White-faced Whistling Ducks on stored nutrients after ovulation, thereby allowing greater allocation of stored nutrients to egg production.

Résumé : On connaît mal la dynamique des réserves alimentaires de la sauvagine qui se reproduit dans les environnements semi-arides. Nous avons récolté des dendrocygnes veufs, *Dendrocygna viduata* (L., 1766), qui se reproduisaient sur la plaine de débordement de la Nyl, en Afrique du Sud, en 1992–1993 et en 1995. Nous avons évalué la masse des principaux dépôts de graisses (peau humide + graisse viscérale + graisse abdominale) et de protéines (muscles pectoraux + muscles des pattes + gésier) et celle des organes en fonction du sexe et de l'état reproductif. Les oiseaux des deux sexes arrivent aux sites de reproduction avec d'importantes réserves lipidiques et n'accumulent plus de graisse additionnelle après leur arrivée. Ces réserves accumulées permettent aux femelles de commencer la ponte peu après leur arrivée, une adaptation importante dans les milieux humides temporaires des environnements semi-arides. Les femelles catabolisent au moins 37 g de graisses et 27 g de protéines corporelles durant la croissance rapide des follicules et l'ovulation, ce qui représente respectivement 87 % et 60 % de leurs besoins en graisses totales et en protéines durant la ponte. Les mâles catabolisent au moins 19 g de lipides entre leur arrivée et la fin de la période de ponte. Bien que le régime alimentaire des dendrocygnes veufs en période de reproduction soit riche en lipides, les femelles assurent la majorité de leurs besoins en lipides durant la formation de la couvée à partir de leurs réserves endogènes. Les dendrocygnes femelles peuvent se reproduire malgré un régime alimentaire pauvre en protéines, ce qui indique qu'elles peuvent assimiler efficacement les acides aminés à partir de la matière végétale. Après l'ovulation, les soins donnés par les deux parents réduit la dépendance des dendrocygnes femelles de leurs réserves nutritives, ce qui leur permet d'allouer plus des nutriments en réserve à la production d'oeufs.

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Introduction

The relative importance of endogenous and exogenous lipid and protein has been extensively studied in north-temperate-breeding ducks (Alisauskas and Ankney 1992). For most species, females satisfy the majority of protein costs of egg formation by consuming protein-rich aquatic macroinvertebrates, whereas most of their lipid requirements are met by catabolizing endogenous fat reserves (Drobney 1980; Krapu 1981; Hohman 1986a). Two competing hypotheses have been proposed to explain the substantial use of endogenous lipid for egg formation in north-temperate ducks: (1) the

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protein limitation hypothesis and (2) the lipid limitation hypothesis. The protein limitation hypothesis states that heavy reliance on stored lipid reserves enables females to forage intensively for protein-rich yet relatively scarce aquatic invertebrates during egg formation (see Drobney 1980; Krapu 1981; Hohman 1986a; Ankney and Alisauskas 1991). In contrast, the lipid limitation hypothesis states that protein is easier to obtain than lipid in productive north-temperate wetlands, and consequently, lipid is stored prior to ovulation because it is more likely to limit clutch size than protein (Afton and Ankney 1991). Regardless of which nutrient ultimately is limiting, all species of north-temperate-breeding ducks increase their consumption of aquatic macroinvertebrates during reproductive periods (Krapu and Reinecke 1992) and appear highly dependant on the high protein content of these foods to reproduce successfully (Krapu 1979; Eldridge and Krapu 1988; Krapu and Reinecke 1992 and references therein).

Unlike north-temperate-breeding ducks, White-faced Whistling Ducks, *Dendrocygna viduata* (L., 1766), primarily consume native terrestrial seeds during reproduction (Petrie and Rogers 1996); it also has been suggested that aquatic macroinvertebrates are less readily available to semiarid than to north-temperate-breeding waterfowl (Petrie 1996). Because eggs contain nearly equal amounts of protein and lipid, and because the diets of White-faced Whistling Ducks during breeding have high lipid and low protein contents, we predict that unless they are very efficient at assimilating amino acids from plant matter that they would have to catabolize large amounts of endogenous protein during egg formation.

The ability of waterfowl to store nutrients on breeding areas depends on the quality and quantity of food and the time required to obtain those foods. The spatiotemporal predictability of suitable aquatic habitats and foods enable many north-temperate ducks to arrive on breeding areas with endogenous reserves (lipid and protein) smaller than those required for reproduction and to subsequently store nutrients after arrival (Tome 1984; Hohman 1986a; Alisauskas and Ankney 1992). Because many aquatic habitats are ephemeral in semiarid regions of South Africa and seasonal rains are annually variable in timing and intensity, temporal and spatial availabilities of suitable aquatic habitats and foods are unpredictable (Siegfried 1970, 1974; Petrie 1998a). Thus, we predicted that White-faced Whistling Ducks would acquire reproductive reserves before their arrival on breeding areas, because this would ensure that females were able to initiate egg laying as soon as suitable habitats become available, thereby increasing the likelihood of successful reproduction.

Use of stored nutrient reserves during incubation is common among waterfowl in which only females incubate (as reviewed by Afton and Paulus 1992). However, in 12 of 144 extant waterfowl species, males and females adjust to high reproductive demands by sharing incubation and brood-rearing costs; these include Magpie Geese (*Anseranas semipalmata* (Latham, 1798)), 8 species of whistling ducks (*Dendrocygna* spp.), White-backed Ducks (*Thalassornis leuconotus* Eyton, 1838), Cape Barren Geese (*Cereopsis*

Fig. 1. Geographic location of the Nyl River floodplain study area, South Africa.

novaehollandiae Lathan, 1802), and Black Swans (*Cygnus atratus* (Lathan, 1790)) (Rohwer and Anderson 1988; Afton and Paulus 1992). Therefore, we tested the final prediction that shared incubation and brood rearing would liberate females from a postovulatory dependance on stored reserves, as biparental care would presumably provide females with enough time to satisfy the energy requirements of incubation directly through dietary intake.

Study area and methods

The Nyl River floodplain is a 160-km^2 ephemeral wetland complex located in the semiarid savanna of Northern Province, South Africa (24°39′S, 28°42′E; 1080 m above sea level) (Fig. 1). Semiarid conditions are caused by high summer temperatures (mean daily = 29 °C), low and often erratic rainfall (Huntley and Morris 1978), and an annual evaporation rate that is almost twice the mean annual precipitation (Frost 1987). These climate conditions create extreme variability in periodicity, duration, depth, and timing of flooding events. During wet years, a mosaic of wetland types (oxbow lakes, ephemeral pans, channel marsh, and large grass-dominated marshes) provide habitat for approximately 25 000 ducks of 11 species, the White-faced Whistling Duck being most common (Tarboton and Batchelor 1981).[3] White-faced Whistling Ducks arrive and breed immediately after spring rains, and subsequently, complete wing-feather molt on the floodplain if water availability permits (Petrie 1998a, 1998b). During an average of 6 out of 10 years, either no flooding occurs or it is unsustained and therefore of little consequence to breeding and molting waterfowl (Tarboton and Batchelor 1981).[3] Over 200 stock-watering ponds and small dams have been constructed on and in close proximity to the Nyl River floodplain. White-faced Whistling Ducks commonly use these ponds for breeding and sporadically for wing-feather molting during dry years (Petrie 1998b).

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[3] W.R. Tarboton and G.R. Batchelor. 1981. The Nyl River floodplain: a unique South African ecosystem threatened. Unpublished report of the Transvaal Provincial Administration, Pretoria.

Collection

Small portions of the Nyl River floodplain, main river channel, and associated stock-watering bodies contained water and were used by breeding White-faced Whistling Ducks during 1992–1993 and 1995. Breeding birds (pairs when possible) were collected on the floodplain and associated stock ponds using a shotgun or a 22-calibre rifle. Collection began as soon as birds arrived on 21 December 1992 and continued until 11 May 1993. Birds also were collected from 10 January until 17 February 1995. Birds were tagged for identification, placed in a cooler with ice, and then taken to a laboratory for dissection.

Dissection

Birds were towel-dried, weighed, and structural measurements were taken, including: (*i*) culmen length (±0.1 mm) from the commissural point to the tip of the upper mandible; (*ii*) tarsus bone length (±0.1 mm); (*iii*) flattened wing length (±0.5 mm) taken from the wrist to the tip of the ninth primary with wing flattened and flexed at the wrist; and (*iv*) body length (±0.5 mm) from the tip of bill to the base of middle rectrix with the bird held unstretched on its back. Birds were then plucked and the following tissues were dissected out and weighed to within 0.01 g: (*i*) plucked skin including all subcutaneous fat; (*ii*) right breast muscle (i.e., pectoralis and supracaracoideus); (*iii*) leg muscle (i.e., all muscle associated with the femur and tibiotarsus); (*iv*) gizzard, less contents; (*v*) small intestine, less contents; (*vi*) abdominal (omental) fat; (*vii*) visceral fat, including all fat attached to the viscera; (*viii*) testes; (*ix*) ova and ovary; and (*x*) oviduct. Number of developing and postovulatory follicles were counted and oviductal eggs were weighed. Gastrointestinal tract contents were weighed and subtracted from body mass to calculate ingesta-free body mass.

Reproductive classification

Female White-faced Whistling Ducks and their mates were assigned to the following six chronological stages: (1) arrival — prerapid follicular growth, ovary mass <3 g; (2) rapid follicular growth (RFG) — preovulating, ovary mass >3 g; (3) laying — ovulating with between 1 and 6 postovulatory follicles; (4) end of laying — at least 8 postovulatory follicles, an ovum in the oviduct and no developing follicles remaining, or postovulating birds with which the ovary and oviduct were in early stages of regression; (5) mid- or late incubation — postovulating, possessing a brood patch (vascularization of breast region), with regressed ovary and oviduct; and (6) brood rearing — with a brood of ducklings, all brood-rearing adults were collected with class-II ducklings (Gollop and Marshall 1954).

When unsuccessful in collecting females of a pair, males were assigned to reproductive categories when possible by comparing these "unknown" birds against the reproductive state (i.e., testicular development or regression) of others collected at known stages. Collection date and (or) presence/absence of a brood were also used to assign reproductive state to these birds. Preovulating females and their mates were placed into Arrival and RFG categories to determine if birds arrived on the Nyl River floodplain with endogenous protein and lipid reserves for reproduction or if they supplemented these reserves after arrival on the floodplain. There were no resident White-faced Whistling Ducks on the Nyl River floodplain during the winters of 1992–1993 or 1994–1995. Therefore, several stock-watering ponds and dams were monitored daily until birds arrived, at which time collection began. All females with ovaries <3 g and their mates (Arrival) were collected between 14 December and 14 January when birds were arriving on the Nyl River floodplain.

Proximate analysis

To verify the suitability of using specific lipid and protein deposits to assess nutritional condition of breeding White-faced Whistling Ducks, all 23 birds (Arrival = 3, RFG = 4, Laying = 11, Incubate = 5) collected in 1995 were dissected (as above) and, subsequently, double bagged and frozen for further analysis. Frozen carcasses (i.e., less ingesta, feathers, bill, feet, ovaries, testes) were thawed, cut into small pieces, ground twice in a meat grinder, and weighed. The homogenate was dried to constant mass at 70 °C and reweighed to determine water content. Dried carcass homogenate was passed twice through a Fritsch Pulverizette 14 laboratory rotor mill and mixed thoroughly by hand after each grind. A subsample (approximately 20 g) of homogenate was frozen for future analysis. Moisture accumulated during freezing was subsequently removed by drying samples to constant mass at 50 °C. Fat was extracted from a 3-g subsample from each bird using petroleum ether in a modified Soxhlet apparatus. Resulting fat-free residue was dried in a vacuum oven and reweighed to obtain estimates of their lipid content. Fat-free residues were then ashed at 600 °C in a muffle furnace for 6 h. Ash-free lean dry mass (an index of protein content) was calculated by subtracting ash mass from lean dry mass. Resulting lipid, protein, and ash estimates from each bird were used to calculate the nutrient composition of the entire carcass.

Statistical analysis

Pearson's rank correlations (Conover 1980) were used to determine if lipid and protein deposits were reliable indices of carcass fat and carcass protein content in breeding White-faced Whistling Ducks. A correlation matrix including carcass fat, abdominal fat, visceral fat, skin (including subcutaneous fat), and LDEP (i.e., mass of abdominal fat + visceral fat + subcutaneous fat) was used to assess the veritability of using particular fat deposits, while a matrix including carcass protein, breast muscle, leg muscle, gizzard, and PDEP (i.e., mass of breast muscle + leg muscle + gizzard) was used for protein. LDEP ($r^2 = 0.89$, df = 1,23, $P < 0.001$) and PDEP ($r^2 = 0.83$, df = 1,23, $P < 0.001$) were more strongly correlated with the mass of carcass fat and carcass protein than was the mass of each individual deposit. As such, LDEP and PDEP were used to assess the condition of all birds collected during 1992–1993 and 1995. These two indices include the largest and most labile protein and lipid deposits, so they should provide a good approximation of overall changes in carcass nutrients (i.e., reserves).

Structural size is an important source of variation in the size of a birds' nutrient reserves (Alisauskas and Ankney 1987) and digestive organs (Thomas 1984; Kehoe and Ankney 1985). To correct for differences in structural size, the correlation matrix of four structural measurements (body, wing, culmen, and tarsus length) of each bird was subjected

Table 1. Changes in organ mass (g; mean ± SE) of female and male White-faced Whistling Ducks, *Dendrocygna viduata*, collected throughout reproduction on the Nyl River floodplain, South Africa, during 1992–1993 and 1995.

Variable	Sex	Arrival	Rapid follicular growth (RFG)	Laying	End of laying	Mid- or late incubation	Brood rearing
			Reproductive stage				
Gizzard	Female	27.0±2.3a	28.8±3.7a	**26.6±1.7ab**	**26.4±2.4ab**	19.9±1.0b	25.3±2.2ab
	Male	22.9±1.9a	27.4±2.8a	**22.2±1.3ab**	**21.7±2.6ab**	19.7±1.5a	32.5±8.9a
Small intestine	Female	**6.7±0.6ab**	**7.0±0.3ab**	*6.6±0.4ab*	*8.3±1.0a*	5.0±0.3b	6.0±0.6ab
	Male	**5.2±0.3a**	**4.9±0.2a**	*4.5±0.3a*	*4.2±0.2a*	4.5±0.2a	4.9±0.6a
Oviduct	Female	4.3±0.6a	*15.4±2.9b*	17.5±4.9b	10.7±4.8b	1.5±0.2a	0.6±0.2a
Ova and ovary	Female	1.9±0.2a	*15.6±4.8b*	11.0±5.5b	11.1±9.6b	0.7±0.1a	0.2±0.04a
Testes	Male	5.0±0.4a	*4.8±0.6a*	4.6±0.6a	5.1±0.5a	3.0±0.7ab	0.2±0.03b
n	Female	11	7	5	4	10	2
	Male	9	10	11	4	10	3

Note: Values within a row not sharing the same letter are different (Tukey's honestly significantly different (HSD) multiple comparisons test, $P < 0.05$) and groups of values within a column set in boldfaced and italic types are different (Tukey's HSD multiple comparisons test, $P < 0.05$).

to principal component analysis (PCA). The first principal component (PC1) described a positive correlation among all measures with loadings ranging from 0.63 to 0.86. The first principle component accounted for 57% of the variance in the original measures and had a corresponding eigenvalue of 2.31. Following Ankney and Alisauskas (1991), we interpreted this covariation as variation in structural size. Therefore, we used PC1 scores for each bird as a measure of the overall structural size in regressions of PDEP, LDEP, carcass (less reproductive tissue, feathers, bill, and ingesta), gizzard, and small intestine mass on PC1. LDEP ($P = 0.348$), gizzard ($P = 0.415$), and small intestine ($P = 0.300$) mass were unrelated to body size, but PDEP (PDEP = $249.08 + 34.43$PC1, $r^2 = 0.23$, df = 1,84, $P < 0.0001$) and carcass mass (Carcass = $607.39 + 72.45$PC1, $r^2 = 0.19$, df = 1,84, $P < 0.0001$) were related. Regression residuals were used to calculate a size-adjusted value (y_i) for PDEP (AdjPDEP) and carcass (ADJcarcass) mass using the following equation: $y_i = y_{obs} - (a + b$PC1$) + $ mean y_{obs} where a is the y intercept and b is the slope between PC1 and the raw reserve value (Ankney and Alisauskas 1991).

Differences in body mass, AdjPDEP, ADJcarcass, LDEP, gizzard, small intestine, oviduct, ova and ovary, and testis mass related to sexual and reproductive stage were compared using a one-way analysis of variance (Tukey's honestly significantly different (HSD) multiple comparisons tests; Wilkinson 1988). We also used regression analysis to determine if the amount of nutrients committed to clutch lipid and clutch protein were correlated with LDEP and PDEP, respectively. We were unable to acquire a fresh clutch of White-faced Whistling Duck eggs for analysis. Therefore, using the mean White-faced Whistling Duck egg mass of 36 g (Johnsgaard 1978) and the equation egg constituent = $a + b$(egg mass) where b is 0.149 for egg lipid and 0.145 for egg protein (Alisauskas and Ankney 1992), the lipid and protein compositions of a White-faced Whistling Duck egg were estimated (5.36 g of lipid, 5.58 g of protein). These values were multiplied by the number of burst follicles to estimate the amount of lipid and protein that females had committed to clutch formation. Nutrients contained in developing follicles and the ovary were also considered to be committed to clutch formation.

Results

Results are based on 39 female and 47 male White-faced Whistling Ducks collected throughout reproduction (Table 1). Ten of 11 females collected during peak arrival on the Nyl River floodplain had not initiated RFG (ovary <3 g), but males had already attained maximum testis mass at this time (Table 1). Both males and females arrived with large fat reserves (LDEP) and neither sex anabolized additional lipid after arrival (Table 2). Neither ADJcarcass ($r^2 = 0.02$, $F_{[1,18]} = 0.38$, $P = 0.54$) nor LDEP ($r^2 = 0.14$, $F_{[1,18]} = 3.04$, $P = 0.1$) was different among sexes during the arrival period, but females, on average, had 23% heavier LDEP than males, which may be attributed to increased foraging by females since they had heavier small intestines ($r^2 = 0.25$, $F_{[1,18]} = 6.1$, $P = 0.02$) than males during this time (Table 1). Female ADJcarcass mass (not including reproductive tissue) did not change appreciably ($r^2 = 0.25$, $F_{[1,16]} = 1.6$, $P = 0.22$) between Arrival and RFG, even though they anabolized $24.8 ± 4.1$ g of reproductive tissue (ovary and oviduct) during this time ($r^2 = 0.51$, $F_{[1,16]} = 16.73$, $P = 0.001$). Therefore, females apparently were able to satisfy most of the protein and lipid costs of reproductive tissue development directly through dietary intake. No male carcass components changed between Arrival and RFG, but RFG males had smaller ADJcarcass, LDEP, AdjPDEP, and small intestine mass than did RFG females ($P < 0.05$ for all comparisons; Tables 1 and 2).

Females catabolized, on average, 37.4 g of their LDEP between Arrival and End of lay ($r^2 = 0.39$, $F_{[1,13]} = 8.32$, $P = 0.013$) and 26.6 g of their PDEP between RFG and End of lay ($r^2 = 0.45$, $F_{[1,9]} = 7.3$, $P = 0.02$) (Table 2). Because we used lipid and protein deposits rather than overall composition, these values may not reflect the total endogenous nutrient commitment to clutch formation. However, because the largest and most labile lipid and protein deposits were analyzed, and birds in the End-of-laying category had finished committing nutrients to egg laying, these values should closely represent the total endogenous nutrient commitment to clutch formation. Males catabolized significant amounts of their LDEP ($r^2 = 0.22$, $F_{[1,18]} = 5.0$, $P = 0.04$) between Arrival and Laying (Table 2). Males had lighter gizzards

Table 2. Changes in mass (g; mean ± SE) of body, carcass, and nutrient reserve deposits of female and male White-faced Whistling Ducks collected throughout reproduction on the Nyl River floodplain, South Africa, during 1992–1993 and 1995.

Variable	Sex	Reproductive stage					
		Arrival	RFG	Laying	End of laying	Mid- or late incubation	Brood-rearing
Body*	Female	686±24ab	**734±22a**	**699±23ab**	651±20b	**637±17b**	635±20ab
	Male	698±14ab	**661±14ab**	**625±20ab**	635±17b	**679±10a**	703±14ab
Carcass[†]	Female	637±18.5ab	*652±18.4b*	643±13.3ab	608±12.8a	602±11.8ab	590±20.0ab
	Male	625±16.4a	*589±13.8a*	577±14.6a	592±12.4a	617±9.2a	642±28.8a
LDEP[‡]	Female	75.3±7.6a	***62.0±4.1ab***	47.3±4.8b	37.9±1.6b	41.7±2.3ab	41.6±4.9ab
	Male	58.2±5.6a	***49.0±3.9ab***	43.7±3.6b	39.2±2.1ab	44.6±2.2ab	49.1±9.3ab
PDEP[§]	Female	253±7.8a	<u>263±6.8a</u>	240±8.5a	236±5.1a	254±5.1a	255±13.3a
	Male	251±5.7ab	<u>241±6.4a</u>	232±6.4a	242±4.7ab	263±3.2b	266±10.5b
n	Female	11	7	5	4	10	2
	Male	9	10	11	4	10	3

Note: Values within a row not sharing the same letter are different (Tukey's HSD multiple comparisons test, $P < 0.05$) and groups of values within a column set in boldfaced, italic, and boldfaced–italic types and underlined are different (Tukey's HSD multiple comparisons test, $P < 0.05$).

*Body mass excludes the mass of the esphageal contents.

[†]Carcass mass excludes the mass of the reproductive tissue, feathers, bill, and esophageal contents, and has been adjusted according to structural size; see Methods.

[‡]Lipid deposit (LDEP) mass is the combined mass of the skin, viseral fat, and abdominal fat.

[§]Body protein deposit (PDEP) mass includes the combined mass of the breast muscle, leg muscle, and gizzard, which has been adjusted according to structural size; see Methods.

($r^2 = 0.30$, $F_{[1,15]} = 6.3$, $P = 0.02$) and small intestines ($r^2 = 0.47$, $F_{[1,14]} = 12.2$, $P = 0.004$) compared with females during Laying, which could be indicative of differences in foraging effort at that time (Table 1). Although sample sizes were small, evidence tended to suggest that both males and females were able to satisfy incubation and brood-rearing costs exogenously (i.e., they did not catabolize appreciable amounts of protein or lipid reserves during incubation or brood rearing; Tables 1 and 2).

Using the estimated nutrient composition of White-faced Whistling Ducks eggs (see Methods), and the number of burst follicles in birds in the End-of-lay category, we estimated (assuming a 100% conversion efficiency) that female White-faced Whistling Ducks satisfied 87% of the lipid requirements and 60% of protein requirements of egg laying through catabolization of LDEP and AdjPDEP. Regressions of body lipid against clutch lipid ($r^2 = 0.31$, $F_{[1,25]} = 11.32$, $P = 0.002$) and size-adjusted body protein against clutch protein ($r^2 = 0.11$, $F_{[1,25]} = 3.24$, $P = 0.084$) indicated that female White-faced Whistling Ducks relied more heavily on endogenous lipid than protein during egg laying (Figs. 2 and 3).

Discussion

Nutrient acquisition

White-faced Whistling Ducks apparently acquire most, if not all, of the endogenous nutrient reserves needed for reproduction prior to arrival on breeding areas, because birds arriving on the Nyl River floodplain had large stores of lipid and did not store additional lipid after arrival.

Environmental variability (both seasonal and annual) in semiarid systems of South Africa is primarily a function of the wet/dry phase that is regulated by convective rainfall producing mechanisms which are highly variable in space and time (Braune 1985). In contrast, the cyclical annual en-

vironmental pattern of north-temperate regions is ultimately driven by the cold/warm cycle, the regularity or seasonality of which is a direct function of the precise and predictable elliptical orbit of the earth around the sun (Mitchell and Rogers 1985). While the availability of waterfowl habitat and food in north-temperate regions is determined primarily by these highly regular (timing and intensity) seasonal variations in temperature, basic waterfowl requirements in semiarid regions are ultimately determined by rainfall, which is extremely variable in its timing and intensity (Siegfried 1970, 1974). Consequently, the spatiotemporal availability of habitat and food is relatively more predictable and less variable in north-temperate than in semiarid systems. This is supported by the fact that waterfowl species which breed in xeric environments lay eggs in more months of the year than non-arid-zone ducks (Briggs 1992; Harrison et al. 1997). Therefore, the predictable availability of foods to north-temperate-breeding waterfowl enables those ducks to be more flexible in acquiring additional endogenous nutrients after arrival on breeding areas (Drobney 1982; Tome 1984; Hohman 1986*a*; Alisauskas et al. 1990; Barzen and Serie 1990; Afton and Ankney 1991; Ankney and Alisauskas 1991), but the lack of such conditions in semiarid regions forces White-faced Whistling Ducks to arrive on breeding areas with large endogenous nutrient stores for reproduction.

The relatively short distances (<700 km) between wintering and breeding areas (Oatley and Prys Jones 1985; Petrie and Rogers 1997*b*) and the associated low costs of transporting reproductive fat reserves enables White-faced Whistling Ducks to transport stored nutrients from wintering areas. Furthermore, the time lag between spring rains and peak native-seed availability (S.A. Petrie, personal observation) and the stochastic availability of breeding habitat likely has selected for birds that acquire large fat reserves on wintering areas (S.A. Petrie, unpublished data). Acquisition of endoge-

Fig. 2. Relation between body protein (PDEP) mass and estimated protein commitment to eggs and oviduct by prelaying (●) and laying (■) female White-faced Whistling Ducks.
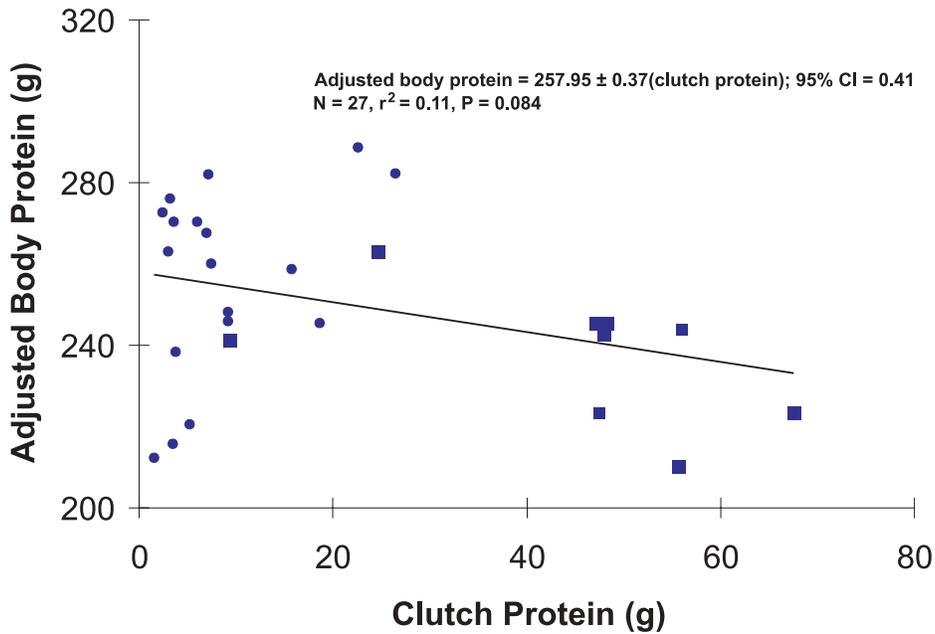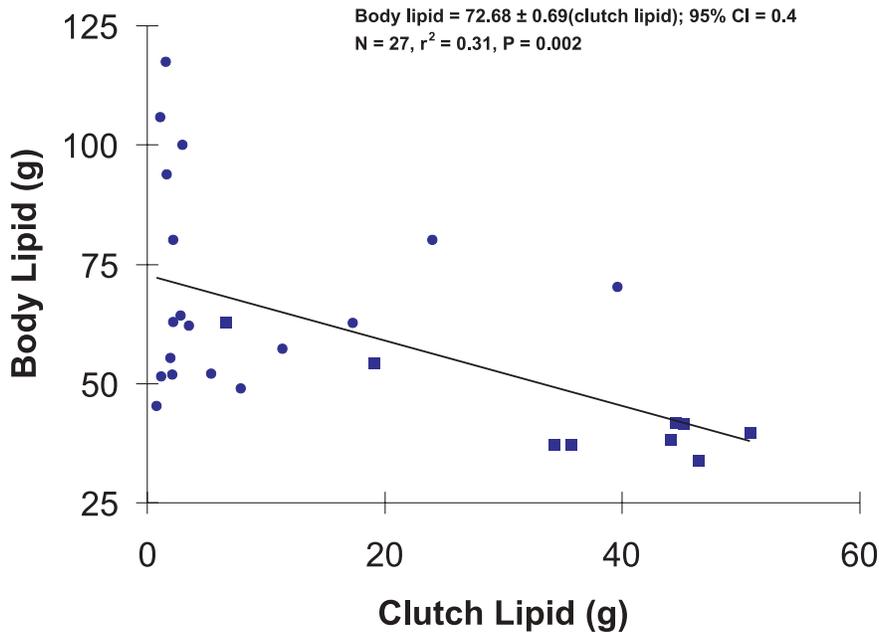

Fig. 3. Relation between body lipid (LDEP) mass and estimated lipid commitment to ovulation by prelaying (●) and laying (■) female White-faced Whistling Ducks.

nous lipid reserves prior to arrival on breeding grounds ensures that birds are in breeding condition as soon as suitable habitat becomes available, which is an important adaptation given the seasonal variations in timing and intensity of spring rains and the fact that many aquatic habitats in the semiarid regions of South Africa are ephemeral. Therefore, the storage of fat prior to arrival on breeding areas can be ascribed to, and termed, the reproductive uncertainty hypothesis. Arctic-nesting geese also arrive on breeding areas with most of the nutrients necessary for egg production and this has been attributed to the lack of food availability upon arrival

and the need to initiate laying early as a result of the short duration of Arctic summers (Raveling 1978, 1979).

Preincubation nutrient-reserve dynamics

North-temperate-breeding waterfowl primarily consume aquatic macroinvertebrates during egg laying (mean = 80.7%, range = 41%–100% for 18 species; see review in Krapu and Reinecke 1992). In contrast, White-faced Whistling Ducks (99.8%) and Red-billed Teal (*Anas erythrorhyncha* Gmelin, 1789) (86.8%, RFG and laying combined) primarily consume native terrestrial seeds while breeding on the Nyl River

floodplain (Petrie 1996; Petrie and Rogers 1996). It has been suggested that protein is more difficult to obtain than lipid when waterfowl are undergoing RFG and ovulation on periodically flooded semiarid wetlands (Petrie 1996; Petrie and Rogers 1996). Despite the fact that native seeds have low crude protein content and are deficient in several amino acids required for egg formation (Petrie and Rogers 1996), we calculated that female White-faced Whistling Ducks satisfied 40% of the protein requirements of clutch formation directly through dietary sources. These calculations support our hypothesis that White-faced Whistling Ducks are efficient at assimilating amino acids from plant matter (Petrie and Rogers 1996). White-faced Whistling Ducks are apparently intermediate in their use of reserve protein, as temperate-breeding ducks exhibit minor changes in carcass protein (Krapu 1981; Drobney 1982; Reinecke et al. 1982; Ankney and Afton 1988), but Arctic-nesting geese catabolize substantial amounts of protein during reproduction (Ankney and MacInnes 1978; Raveling 1979). This can be attributed to the fact that White-faced Whistling Ducks, unlike temperate-breeding ducks, are almost totally herbivorous throughout reproduction, and unlike Arctic-nesting geese, continue to forage during egg laying and incubation (Petrie and Rogers 1996).

The protein limitation hypothesis states that north-temperate-breeding ducks catabolize large amounts of endogenous lipid as a result of the high foraging costs associated with obtaining macroinvertebrates, whereas the lipid limitation hypothesis attributes high dependence on stored fat to protein being more easily obtained on north-temperate wetlands than lipid (see Ankney and Afton 1988; Ankney and Alisauskas 1991). Therefore, because breeding White-faced Whistling Ducks spend considerably less time foraging for macroinvertebrates than do north-temperate species (Petrie and Rogers 1997a) and because their diet has a high fat and low protein content (Petrie and Rogers 1996), clutch formation should theoretically be virtually independent of endogenous lipid, regardless of which of the aforementioned hypotheses is more tenable. However, females catabolized lipid stores throughout egg laying, which satisfies at least 87% of clutch-formation requirements in this manner. Therefore, we suggest that lipid may be the most limiting nutrient to breeding White-faced Whistling Ducks. However, although it has been suggested that nutrients which are limiting during reproduction will be stored by females of the species and subsequently used when required (Ankney and Afton 1988), lipid is a more efficient energy and nutrient store than protein and is more efficiently metabolized (Robbins 1983). Therefore, storage and conversion efficiencies alone might explain why White-faced Whistling Ducks, as well as most other waterfowl species, rely more heavily on endogenous lipid than protein during ovulation. Male White-faced Whistling Ducks, on average, catabolized 19 g of reserve lipid while their mates were undergoing RFG and ovulation. This can be attributed to the fact that males spent more time alert and less time foraging than did their mates at this time (Petrie and Rogers 1997a).

Postovulation nutrient-reserve dynamics

Afton and Paulus (1992) reviewed body-mass loss in 24 species of waterfowl in which only females incubate. Body-mass loss ranged from 3% to 33% and averaged 17.5%,

which suggested that reserve catabolism during incubation is ubiquitous among these species. It has been suggested that nest attentiveness reduces time spent foraging and results in catabolism of endogenous reserves (Krapu 1981; Hohman 1986b; Afton and Paulus 1992; Alisauskas and Ankney 1992). Whereas most waterfowl species experience minimum annual body masses at the end of incubation (Afton and Paulus 1992), biparental care apparently releases White-faced Whistling Ducks from a postovulatory dependence on stored reserves. This may enable females to use a larger portion of their reserves during egg laying. A similar situation has been reported for American Coots, *Fulica americana* J. F. Gmelin, 1789 (Alisauskas and Ankney 1985; also see Afton and Paulus 1992).

The ability of White-faced Whistling Ducks to metabolize large amounts of stored reserves during ovulation may be particularly important for successful reproduction, given the low protein, high fiber content of their diet. While Arctic-nesting geese are structurally capable of storing and maintaining large nutrient stores for use during ovulation, as well as incubation, the small size of White-faced Whistling Ducks probably precludes this as a viable tactic, making biparental care a particularly important life-history strategy. Male White-faced Whistling Ducks lost body mass during RFG and ovulation, but they gained mass during incubation. Therefore, shared incubation by males and females may be less energetically costly to male White-faced Whistling Ducks than is mate attentiveness during RFG and ovulation. Alternatively, males may simply be able to spend more time foraging during incubation than during RFG (see Petrie and Rogers 1997a).

Relative to north-temperate-breeding species, most arid- and Arctic-breeding waterfowl have extended pair bonds or long-term monogamy (Siegfried 1974; Rohwer and Anderson 1988; Briggs 1992). This suggests that selective advantages obtained from extended mate attendance may be more important in variable and harsh environments. This is further supported by the fact that only 12 of 144 extant waterfowl species share incubation (Rohwer and Anderson 1988; Afton and Paulus 1992), all of which occur in arid, semiarid, and subtropical environments.

Research and management implications

In semiarid regions, there is substantial spatiotemporal variation in the availability of aquatic habitats and particular food items. Annual and seasonal variability and the ephemeral nature of aquatic systems apparently have selected for semiarid-breeding waterfowl that are opportunistic as well as flexible in the timing and location of events in the annual cycle (Petrie 1998a, 1998c). Waterfowl species that breed in xeric environments lay eggs in more months of the year than nonarid-zone ducks (Briggs 1992; Harrison et al. 1997) and they generally do not have a specific season or location in which they replace wing feathers (Dean 1978; Petrie 1998b). Therefore, since years of comparable resource availability (spatial, temporal, quantity, and quality) are replicated at unpredictable intervals, if at all, long-term studies over several years are required to determine the extent and nature of intraspecific and inter-year variation in the timing and location of annual cycle events and the tactics employed to satisfy those events.

The nesting success and brood survival of all of southern Africa's waterfowl species remain enigmatic. This is problematic, as these are key determinants of annual recruitment and population sizes. This situation is intensified by the fact that in southern Africa, (*i*) there are at least four times as many species of potential predators as in Holarctic regions (Siegfried 1974); (*ii*) increased cultivation and overgrazing reduces the availability of suitable nesting sites, which has probably increased predation pressures; (*iii*) the ephemeral nature of aquatic habitats may compromise brood survival; and (*iv*) widespread wetland drainage and development compromises availability of suitable breeding habitats. Therefore, the reproductive ecology of waterfowl in semiarid southern Africa requires further study so that constraints on nest success, brood survival, and juvenile recruitment can be identified.

Acknowledgements

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