Spring body condition, moult status, diet and behaviour of white-faced whistling ducks (*Dendrocygna viduata*) in northern South Africa

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Many white-faced whistling ducks (*Dendrocygna viduata*) have responded to European colonization by overwintering on irrigation and stock-watering ponds in the semi-arid interior of South Africa. I studied the body condition, diet, behaviour and moult intensity of white-faced whistling ducks prior to departure for breeding areas during spring 1995. Other than higher protein levels in immature males than immature females, there were no sexual differences in body mass or levels of lipid, protein, or ash in adults or immatures. Adults were heavier than immatures and had higher levels of ash. There were no sex- or age-related differences in the proportion of individual food items consumed, 96.6% of which was maize. By foraging on neighbouring agricultural fields, birds were able to spend large portions (80%) of the day/night in comfort-related activities (preen, loaf, sleep) and little time foraging (8.8%) while on ponds. There were no sex- or age-related differences in overall moult intensity score or intensity of moult in 20 feather areas. With exception of primaries and secondaries, birds were moulting moderately to heavily in all feather regions. Agricultural ponds permit white-faced whistling ducks to overwinter close to breeding areas, while the high availability and energy content of maize enables them to attain higher spring fat levels than birds that overwinter on traditional sites closer to the coast. Intensive agriculture has probably contributed to the population increase and range expansion of white-faced whistling ducks in South Africa.

Key words: agriculture, *Dendrocygna viduata,* semi-arid, South Africa, white-faced whistling ducks.

INTRODUCTION

Owing to semi-arid conditions, few natural wetlands in the northern interior of South Africa retain water throughout the winter dry season. However, post-European settlement, provision of permanent and semi-permanent irrigation and stock-watering ponds has enabled small populations of white-faced whistling ducks (*Dendrocygna viduata*) to overwinter close (<100 km) to breeding areas (Petrie & Rogers 1997). Birds generally try to overwinter as near to their breeding grounds as is habitable (Gauthreaux 1982; Alonso *et al.* 1994) and this can be beneficial in several ways: 1) they do not incur the high energetic costs and mortality of long migrations (Odum *et al.* 1961; Bairlein & Gwinner 1994); 2) they are able to arrive on breeding grounds earlier, and possibly with larger lipid reserves, than those that overwinter further away (Sayler & Afton 1981); and 3) density-dependent mortality factors may be reduced (Fretwell 1972; Alexander 1987; Dubovsky & Kaminski 1994). The major trade-off for waterfowl overwintering close to breeding areas in north-temperate regions is that increased thermoregulatory costs can have deleterious physiological effects, ultimately influencing overwinter survival and future reproductive output (Smith & Prince 1973; Krapu 1981; Whyte & Bolen 1984; Morton *et al.* 1990; Suter & van Eerden 1992; Pawlina *et al.* 1993). Relatively high winter temperatures in northern South Africa (Limpopo Province mean monthly minimum = –0.2 to 3.5°C, maximum = 13 to 20°C, Coetzee *et al.* 1976) would however, ensure that periods of temperature-induced physiological stress are relatively infrequent and of shorter duration than in north-temperate regions.

Providing that the availability of food is not limited, the low thermoregulatory costs associated with overwintering on irrigation ponds close to breeding areas should enable white-faced whistling ducks to acquire large fat stores prior to departure for breeding areas. To test this prediction, the spring body condition and diet of white-faced whistling ducks using irrigation ponds

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in Limpopo Province, South Africa, were analysed prior to departure for breeding areas. To further our understanding of the importance of man-made aquatic habitats to non-breeding white-faced whistling ducks, I also report on the activity patterns and moult status of birds using irrigation ponds during spring.

White-faced whistling ducks that overwinter in northern KwaZulu-Natal, South Africa spend large portions of the day and night searching for native seeds and are in poorer condition in spring than in early winter (Petrie 1998a; Petrie 2000). Therefore, to determine if 'short-stopping' (remaining near breeding areas) conveys ecological advantages, the results of this study were compared to those for white-faced whistling ducks overwintering in more traditional wintering areas in northern KwaZulu-Natal (Petrie & Petrie 1998; Petrie 2000).

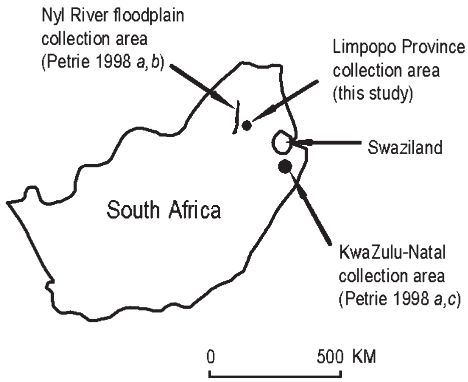

Fig. 1. Geographic location of Limpopo Province (this study), northern KwaZulu-Natal (Petrie 1998a) and Nyl River floodplain (Petrie 1998a) white-faced whistling duck collection sites.

STUDY AREA

The study was conducted throughout the northern portion of the Springbok Flats (24°30′S–25°00′S, 28°55′E–29°15′E) (Fig. 1), a semi-arid plain in Limpopo Province, South Africa. Since European settlement, extensive areas of the plain have been converted to agriculture, the main crops being cotton, maize, sunflowers, wheat, millet and groundnuts, while cattle ranching is also common. Semi-arid conditions are the result of high summer temperatures (mean daily = 29°C), low and often erratic rainfall (Huntley & Morris 1978), and an evaporation rate that is almost twice the mean annual precipitation (Frost 1987). Therefore, successful agricultural expansion has been dependent on the construction of irrigation and stock watering ponds throughout the region, many of which are utilized by small populations (10–200) of overwintering white-faced whistling ducks (Petrie & Rogers 1997; Petrie *et al.* 1998).

METHODS

Collection and structural measurements

Adult and immature white-faced whistling ducks were collected from 23 August to 14 October 1995 on irrigation ponds in the Nutfield, Roedtan, and Marble Hall regions of Limpopo Province (Fig. 1). Birds were collected throughout the day using a shotgun. To prevent *post-mortem* digestion approximately 20 ml of 80% ethanol was injected down the throat of all specimens immediately upon collection. Birds were subsequently tagged for identification, placed in a cool bag with ice and returned to the laboratory. Birds were towel-dried, weighed and the following structural characteristics were measured: (1) culmen (±0.1 mm) from commissural point to tip of the upper mandible, (2) bill width, widest point of ramphotheca, (3) bill height, widest dorsoventral point of ramphotheca, (4) tarsus bone length, (5) flattened wing length (±0.5 mm), (6) total body length, taken after retrices removal, and (7) keel length, after feather removal.

Moult intensity and chronology

Intensity of feather replacement was determined by scoring the presence of blood quills in 20 feather regions: crown, face, chin-throat, neck, upper back, scapulars, lower back, rump, upper tail coverts, retrices, lower tail coverts, belly, centre chest, side chest, side, flank, primaries, secondaries, tertials, and wing coverts. Moult intensity was scored (visual estimate) as 0, 1, or 2 for no moult, light moult (<15% of tract moulting), and heavy moult (>15% of tract moulting), respectively (Austin & Fredrickson 1986; Petrie 1998b,c), while plucking carcasses for subsequent body composition analysis. Total moult intensity score (MIS) was the sum of all 20 feather regions and had a maximum value of 40. Kruskal-Wallis rank sums multiple comparisons tests were used to detect sex- and age-related differences in MIS as well as the moult intensity of each of 20 feather regions (Conover 1980).

Dietary intake

Oesophageal contents were removed and stored in 80% ethanol within six hours of collection. Food samples were subsequently sorted, dried at 60°C for 24 hours and then weighed. Those individuals which possessed an insignificant diet sample (<5 items or <0.01 g) were excluded from the dietary analysis. Seeds were identified to genus or species level by Department of Agriculture personnel in Pretoria. Plant and invertebrate dietary data are expressed as mean aggregate percentage dry mass and frequency of occurrence (Swanson *et al.* 1974). Kruskal-Wallis rank sums multiple comparison tests were used to compare proportions of each food item in the diet of adult males, adult females, and immatures.

Dissection

The following tissues were dissected and weighed to within 0.01 g: (1) small intestine, less contents, (2) testis, (3) ovary, (4) oviduct, and (5) lipid deposit (LDEP), combined plucked skin mass, visceral fat, abdominal fat. LDEP was quantified to allow condition comparisons with pre-breeding adult white-faced whistling ducks collected upon arrival at the Nyl River floodplain, South Africa (Petrie & Rogers 2004). Gastrointestinal tract contents were weighed and subtracted from body mass to calculate ingesta-free body mass. Ovaries and testes were weighed to confirm that birds were not in a reproductive state. Immature and adult birds were distinguished by plumage characteristics and presence or absence of a bursa. Birds were subsequently double bagged and frozen.

Carcass analysis

Birds were thawed, cut into small pieces (all portions except feet, bills, feathers, ingesta) ground twice in a meat grinder and weighed. Ovaries and testes were retained with the carcass as only one bird was in reproductive condition and it was excluded from the analysis. The homogenate was dried to constant mass at 70°C and re-weighed to determine moisture content. The dried carcass homogenate was passed twice through a Fritsch Pulverisette 14, laboratory rotor mill and was mixed thoroughly by hand after each grind. A subsample of homogenate (approx. 20 g) was subsequently frozen for future analysis. Moisture accumulated during freezing was 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 (to remove petroleum-ether) in a vacuum oven and reweighed to obtain estimates of lipid content. Fat-free residues were ashed at 600°C in a muffle furnace for 6 h. Ash-free lean dry mass (an index of protein) was calculated by subtracting ash mass from lean dry mass. Lipid, protein and ash estimates for each bird were used to extrapolate the nutrient composition of the entire carcass.

Corrections for structural size

Structural size can provide an important source of variation in the size of a bird's nutrient reserves (Alisauskas & Ankney 1987) and digestive organs (Thomas 1984; Kehoe & Ankney 1985). Therefore, I used principal components analysis (PCA) to generate a single measure of structural size which was subsequently used to correct for variation in nutrient reserves related to body size. Use of all seven morphological measurements in the PCA resulted in a substantial reduction in sample size, as collection resulted in damage to morphological structures of some specimens. Therefore, I constructed a correlation matrix of four structural measurements of each bird (body length, culmen length, bill width, tarsus length) and subjected it to PCA. For this analysis only, I included 122 white-faced whistling ducks collected in northern KwaZulu-Natal, South Africa, June–October 1995 (Petrie 1998a). The first principal component (PC_1) described positive correlation among all measures with loadings ranging from 0.58 to 0.80. The first principal component accounted for 48% of the variance in the original measures and had a corresponding eigenvalue of 1.9. Following Ankney & Alisauskas (1991), I interpreted this covariation as variation in structural size and used PC_1 scores for each bird as a measure of body size in regressions of protein, fat, ash and small intestine mass on PC_1. Body fat and small intestine mass were unrelated to PC_1 ($P > 0.05$) but protein and ash were as follows:

$$\text{Protein} = 134.27 + 1.45(PC_1),$$
$$\text{d.f.} = 155,\ r^2 = 0.294,\ P < 0.001,$$

$$\text{Ash} = 29.296 + 5.363(PC_1),$$
$$\text{d.f.} = 155,\ r^2 = 0.946,\ P < 0.001.$$

Regression residuals were used to calculate a size-adjusted value (y_i) for protein (ADJprotein) and ash (ADJash) (Ankney & Alisauskas 1991):

$$y_i = y_{obs} - [a + b(PC_1)] + \text{mean } y_{obs}.$$

Sexual and age-related differences in body mass, ADJprotein, ADJash, lipid, and small intestine values were analysed using one-way analysis of variance (Tukey HSD multiple comparisons tests).

Activity budgets

Activities of birds using irrigation ponds were monitored from 19 August to 23 September 1995 using focal sampling techniques. Diurnal observations were made using a 15–60 power, 60 mm spotting scope and nocturnal observations were made with an NB 20 Second Generation 75 mm night vision scope (Eloptera, Division of Denel, Johannesburg). Observations were made from permanent blinds, portable blinds and from a vehicle. To test for differences in activities throughout the day and night, each day was divided into seven time blocks; 1) Dawn (0.5 hour before sunrise until 0.5 hour after sunrise), 2) Morning (0.5 hour after sunrise until 10:30), 3) Midday (10:30–14:30), 4) Afternoon (14:30 until –0.5 hour before sunset), 5) Dusk (0.5 hour before sunset until 0.5 hour after sunset), 6) <Midnight (0.5 hour after sunset until 12:00), and 7) >Midnight (12:00 until 0.5 hours before sunrise).

Activity budgets were performed during at least one time block each day. Owing to limitations of using night vision equipment, nocturnal observations had to be performed when the moon was at least 3/4 full and cloud cover minimal. Birds were observed while in groups of between two and 200 individuals. Focal individuals were selected by pointing the spotting scope towards a flock and selecting the bird closest to the center of vision. Activities of each bird were recorded every 15 seconds for up to 10 minutes at a time and categorized as 1) aggression (chasing, biting, threatening), 2) alert (standing or sitting with head and neck protracted), 3) sleeping (bill tucked under wing), 4) loafing (standing or sitting with head and neck contracted), 5) preening (preening, bathing, stretching), 6) locomotion (flying, swimming, walking), and 7) feeding. Feeding was further divided into 7a) diving, 7b) subsurface and surface dabbling, 7c) upending and 7d) bottom (feeding with head submersed but not upending or diving). Males, females, and immatures were indistinguishable so were grouped and a composite activity budget generated.

White-faced whistling ducks were observed for a total of 76 h consisting of 18 240 instantaneous recordings. The number of instantaneous recordings of each activity for each bird was divided by the total number of recordings (e.g. 40 for a 10-minute period) to obtain a percentage of time spent per activity. Arcsine transformations were applied to all percentage data in order to satisfy normality assumptions (Zar 1974). Between time block activity differences were analysed using analysis of variance (Tukey HSD multiple comparison tests). The seven time blocks were subsequently weighted according to proportion of the day that they represented, and combined in order to generate a composite 24-hour time budget.

RESULTS

Dietary intake

Food samples were obtained from 11 adult female, 15 adult male, two immature female and five immature male white-faced whistling ducks. As there were no sex- or age-related differences in the proportion of individual food items consumed ($P > 0.05$ for all comparisons), the diet of all birds was combined and a composite diet generated (Table 1). The seeds of two species of agricultural plants, six native terrestrial plants, five aquatic/semi-aquatic plants, as well as one species of diptera were consumed. Maize made up over 96 % of the aggregate percentage dry mass of the diet.

Moult intensity and chronology

Males, females and immatures had similar overall moult intensity scores and moulted at similar intensities in all 20 feather areas ($P > 0.05$ for all comparisons) (Table 2). With exception of primaries and secondaries, birds were moulting moderately to heavily in all feather areas. One female was in the late stages of primary replacement and had regained flight capabilities.

Nutrient reserves

Adult males were structurally (PC_1) larger than adult females ($r^2 = 0.14$, $F = 5.3$, d.f. = 1,32, $P = 0.028$); however, there were no sex-related differences in body ($r^2 = 0.05$, $F = 1.6$, d.f. = 1,32, $P = 0.22$), ADJprotein ($r^2 = 0.00$, $F = 0.002$, d.f. = 1,32, $P = 0.97$), lipid ($r^2 = 0.003$, $F = 0.105$, d.f. = 1,32, $P = 0.75$), ADJash ($r^2 = 0.07$, $F = 2.4$, d.f. = 1,32, $P = 0.13$), or small intestine mass ($r^2 = 0.003$, $F = 0.094$, d.f. = 1,32, $P = 0.76$) (Table 3). While small sample sizes may have obscured significance, immature males and females did not differ structurally ($r^2 = 0.023$, $F = 0.119$, d.f. = 1,5, $P = 0.745$), and had similar body ($r^2 = 0.300$, $F = 2.14$, d.f. = 1,5, $P = 0.203$), lipid ($r^2 = 0.03$, $F = 0.144$, d.f. = 1,5, $P = 0.72$), ADJash ($r^2 = 0.185$, $F = 1.13$, d.f. = 1,5, $P = 0.336$), and small intestine mass ($r^2 = 0.0.08$, $F = 0.425$, d.f. = 1,5, $P = 0.543$); immature males had heavier ADJprotein than immature females ($r^2 = 0.66$, $F = 9.5$, d.f. = 1,5, $P = 0.027$) (Table 3).

Table 1. Aggregate percentage dry mass and percentage occurrence of foods in the upper digestive tract of combined adult male, adult female, and immature (*n* = 15, 16, 7, respectively) white-faced whistling ducks collected during spring on irrigation ponds in Limpopo Province, South Africa, 1995.

Food Item	Aggregate percentage dry mass	Percentage occurrence
Plant matter		
Agricultural grains		
Zea mays (maize)	96.6	44.7
Sorghum halepense (sorghum)	Tr[a]	5.3
Native terrestrial seeds		
Echinochloa crus-galli	0.7	23.7
Chenopodium sp.	0.3	13.2
Salvia sp.	0.1	2.6
Urochloa sp.	Tr	5.3
Panicum coloratum	Tr	5.3
Sesamum triphyllum	Tr	2.6
Aquatic and semi-aquatic seeds		
Scirpus sp.	0.8	55.3
Polygonum lapathifolium	0.4	36.8
Nymphaea sp.	Tr	5.3
Cyperus difformis	1.0	2.6
Cyperus sp.	0.1	5.3
Animal matter		
Diptera sp.	Tr	2.6

[a]Tr = <0.05 aggregate percentage dry mass.

Overall, adult body mass was higher than that of immatures ($r^2 = 0.163$, $F = 7.6$, d.f. = 1,39, $P = 0.009$), and they also had higher levels of ADJash ($r^2 = 0.200$, $F = 9.7$, d.f. = 1,39, $P = 0.004$), while there was evidence that they were structurally larger ($r^2 = 0.071$, $F = 2.97$, d.f. = 1,39, $P = 0.093$), and had higher levels of ADJprot ($r^2 = 0.068$, $F = 2.9$, d.f. = 1,39, $P = 0.099$), and lipid ($r^2 = 0.055$, $F = 2.29$, d.f. = 1,39, $P = 0.138$). There was some evidence that immatures had heavier small intestines than adults ($r^2 = 0.078$, $F = 3.30$, d.f. = 1,39, $P = 0.077$).

Activity budgets

Since white-faced whistling ducks acquired most of their nutrition by feeding terrestrially on maize, only 8.8% of combined diurnal and nocturnal time was spent foraging on irrigation ponds (Fig. 2). Birds foraged more intensively on ponds during Dawn, Dusk, <Midnight and >Midnight time blocks than they did during Morning, Midday and afternoon time blocks ($P < 0.05$ for all comparisons) (Fig. 2). Bottom feeding (head or head and neck submerged, 77.4% of feeding time) and upending (22.2%) were the most common foraging modes, while surface/subsurface feeding (0.1%) and diving (0.3%) were less frequently observed.

Table 2. Moult intensity scores (mean ± S.E.) for twenty feather areas and overall MIS of adult female (*n* = 16), adult male (*n* = 19) and immature (*n* = 7) white-faced whistling ducks collected during spring on irrigation ponds in Limpopo Province, South Africa, 1995.

Feather tract	Adult female	Adult male	Immature
Crown	1.9 (0.1)[a]	1.8 (0.3)	1.6 (0.2)
Face	1.4 (0.1)	1.6 (0.1)	1.4 (0.2)
Chin/throat	1.3 (0.2)	1.5 (0.2)	1.3 (0.3)
Neck	1.7 (0.2)	1.5 (0.2)	1.9 (0.1)
Upper back	0.9 (0.1)	1.0 (0.2)	0.9 (0.1)
Scapulars	1.6 (0.2)	1.8 (0.2)	2.0 (0.0)
Lower back	0.9 (0.2)	0.8 (0.1)	0.9 (0.3)
Rump	0.9 (0.2)	0.8 (0.1)	0.7 (0.3)
Upper tail coverts	1.6 (0.2)	1.7 (0.1)	1.4 (0.2)
Retrices	1.7 (0.2)	1.8 (0.1)	1.9 (0.1)
Lower tail coverts	1.6 (0.2)	1.6 (0.1)	1.1 (0.3)
Belly	1.4 (0.2)	1.1 (0.2)	1.3 (0.3)
Centre chest	1.4 (0.2)	1.1 (0.2)	1.3 (0.2)
Side chest	0.9 (0.2)	1.0 (0.2)	0.7 (0.2)
Side	1.6 (0.2)	1.7 (0.1)	1.9 (0.1)
Flank	1.8 (0.2)	1.9 (0.1)	2.0 (0.0)
Primaries	0.1 (0.1)	0.0 (0.0)	0.0 (0.0)
Secondaries	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Tertial	1.1 (0.2)	1.6 (0.2)	1.3 (0.3)
Wing coverts	1.1 (0.2)	1.0 (0.2)	1.1 (0.3)
MIS	25.4 (2.1)	24.1 (2.3)	24.6 (2.3)

[a]Moult scores: 0 = no moult; 1 = <15% moult; 2 = >15% moult.

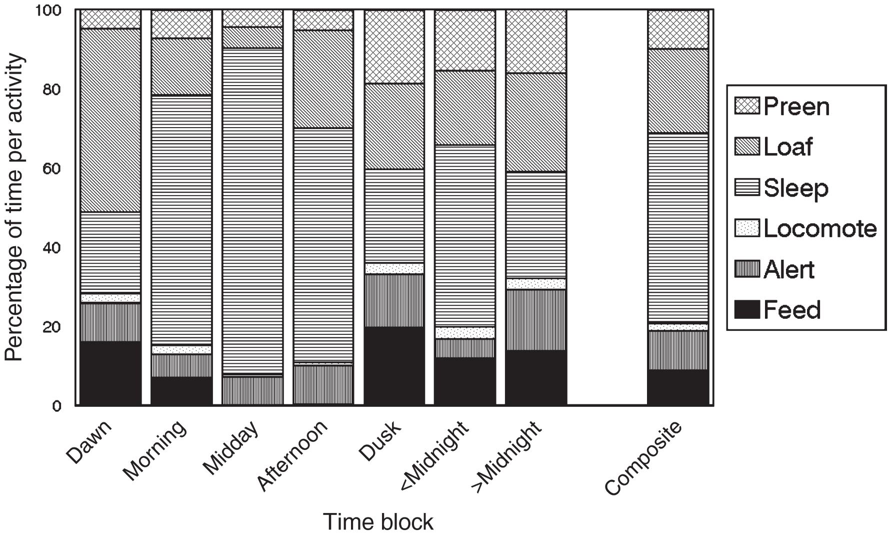

Fig. 2. Activity budget of white-faced whistling ducks using irrigation ponds in Limpopo Province, South Africa, during spring 1995. See Methods for a temporal breakdown of time blocks.

Table 3. Body mass (mean ± S.E.), body composition and small intestine mass of adult and immature white-faced whistling ducks collected during spring on irrigation ponds in Limpopo Province, South Africa, 1995.

Sex	Age	*n*	Body mass[a]	Carcass[b] protein	Carcass lipid	Carcass[b] ash	Small intestine	PCA_1[c]
Female	Adult	15	694 (17)	149 (4.8)	70.0 (8.0)	31.9 (0.8)	6.3 (0.4)	–0.21 (0.1)
	Juvenile	2	601 (7)	127 (2.4)	54.0 (3.5)	25.2 (4.8)	8.6 (1.9)	–0.25 (0.7)
Male	Adult	19	719 (12)	149 (3.6)	66.5 (7.2)	30.5 (0.6)	6.2 (0.4)	0.11 (0.1)
	Juvenile	5	658 (23)	142 (2.8)	48.0 (9.5)	28.3 (0.9)	7.1 (1.1)	0.02 (0.6)

[a]Excludes injesta contents.
[b]Adjusted to body size – see Methods.
[c]Scores along the first principal component – see Methods.

White-faced whistling ducks spent most of the day and night in comfort-related (preen, loaf, sleep) activities while on irrigation ponds (Fig. 2). Birds slept more during Morning, Midday and Afternoon than during other time blocks ($P < 0.05$) and spent more time preening and loafing during crepuscular and nocturnal time blocks ($P < 0.05$). Aggression only represented 0.1% of the composite diurnal and nocturnal budgets and was therefore combined with alert behaviours in Fig. 2. Birds were most alert during Dusk and >Midnight time blocks ($P < 0.05$). While birds locomoted least during Midday ($P < 0.05$), this activity accounted for <3% of the activities during all seven time blocks. No courtship was observed.

DISCUSSION

The diet of white-faced whistling ducks that breed on the Nyl River floodplain consists almost entirely of native terrestrial seeds (Petrie & Rogers 1996). As native seed and water availability decline in autumn and early winter, birds depart from the floodplain and at least a portion of that population overwinters on irrigation and stock-watering ponds in Limpopo Province (Petrie & Rogers 1997; Petrie *et al.* 1998). The provision of permanent waterbodies and agricultural grain following European settlement permits white-faced whistling ducks to overwinter in close association (<100 km) with breeding areas, and birds consume over 96% maize while overwintering on irrigation ponds. Waterfowl of north-temperate regions have also responded to the provision of agricultural grains; however, these food items generally do not represent such a high proportion of the diet (McLandress & Raveling 1981; Jorde *et al.* 1983; Delnicki & Reinecke 1986; Miller 1987; Alisauskas & Ankney 1992). The almost sole consumption of maize by white-faced whistling ducks may be indicative of the extremely low availability of native terrestrial and aquatic seeds in Limpopo Province during winter. For instance, irrigation ponds often undergo substantial changes in water levels (pers. obs.), and many of them are too deep for optimum aquatic macrophyte growth (*cf.* Spence 1982; Chambers & Kalff 1985). By contrast, white-faced whistling ducks that overwinter in northern KwaZulu-Natal, South Africa, did not consume agricultural grains during winter or spring, apparently due to low cereal grain availability and a high availability of natural pans, thereby increasing the relative availability of aquatic and 'moist-soil' seeds (Petrie 2000).

During late winter and spring waterfowl generally spend large portions of the day foraging, and this has been attributed to the need to acquire large fat reserves for reproduction (Hickey & Titman 1983; Hohman 1984; Bergan *et al.* 1989). However, white-faced whistling ducks only spent approximately 1.8 h aquatic foraging (Fig. 2) and 2–3 h field-feeding (pers. obs. – assuming they foraged the entire time they were on fields), which constitutes between 17 and 23% of diel activities. Low foraging effort can be attributed to the almost sole consumption of maize during crepuscular foraging flights, the seeds of which are extremely large relative to native seeds (Petrie & Rogers 1996), are highly nutritious, highly digestible and probably readily available. By contrast, white-faced whistling ducks in northern KwaZulu-Natal spend a much greater portion of the day and night foraging (>40%) during late winter and spring (August–October) (Petrie & Petrie 1998). This can be attributed to the fact that they consume relatively small aquatic seeds that are much higher in crude fibre, have a lower fat content, and probably require high search and handling times (Petrie 2000; Petrie & Petrie 1998). Therefore, the anthropogenic provision of cereal grains enables white-faced whistling ducks in Limpopo Province to satisfy their nutritional requirements more rapidly than birds that consume indigenous aquatic seeds in northern KwaZulu-Natal.

The high nutritional content of maize, and reduced foraging effort associated with its consumption, convey nutritional advantages to birds that overwinter on irrigation ponds. White-faced whistling ducks that consume maize in Limpopo Province had higher lipid levels during spring (adult female 70 ± 8.0 g (S.E.), adult male 67 ± 7.2, juveniles 50 ± 6.6), than birds that consume native aquatic seeds in northern KwaZulu-Natal (43 ± 4.1, 49 ± 4.4, 32 ± 4.0) (Petrie 1998a). The most likely consequences of having large fat stores during spring and overwintering in close proximity to breeding areas are that birds would arrive on breeding areas with large endogenous reserves and possibly initiate egg laying earlier, a distinct advantage given the ephemeral nature of aquatic habitats in Limpopo Province.

The lipid deposit (LDEP) of adult males and females using Limpopo Province irrigation ponds during spring were 26 g (45%) and 32 g (42%) heavier than pre-breeding birds collected upon arrival on the Nyl River floodplain (Petrie & Rogers 2004). As there is a time lag between spring rains and peak availability of native seeds in semi-arid regions, white-faced whistling ducks probably experience a reduction in food availability and quality after leaving agricultural regions. Therefore, acquisition of large lipid stores may provide birds with an energy source while seeking a suitable breeding area when native seed availability is limited. The LDEP of spring-collected white-faced whistling ducks were also considerably heavier than birds collected during peak departure from breeding areas (Petrie 1998a). Therefore, irrigation ponds and agricultural grains are probably also important for post-reproductive recovery of endogenous reserves.

Ten per cent of white-faced whistling ducks collected during late winter in northern KwaZulu-Natal and 34% collected during spring were in the later stages of flight-feather replacement (Petrie 1998c), and wing moulting birds have also been collected during late summer on the Nyl River floodplain (Petrie 1998b). Of 34 adults collected in Limpopo Province, only one female was in the late stages of wing-feather replacement and had regained flight capabilities. She was close to starvation as her body, lipid, and protein mass were 551, 5 and 113 g, respectively. This suggests that replacement of flight feathers on irrigation ponds isolates birds from their primary food source and is apparently nutritionally stressful. Owing to resource limitations, most birds that overwinter on irrigation ponds probably replace flight feathers while on breeding areas. However, the incidence of wing-feather replacement on irrigation ponds and their suitability for satisfying the nutritional requirements of flightless waterfowl requires further study.

White-faced whistling ducks extend their single annual plumage replacement over the entire annual cycle, the intensity of which depends on concurrent nutritional costs (i.e. egg laying) (Petrie 1998b,c). Adult and immature white-faced whistling ducks in Limpopo Province had similar overall moult intensity scores to birds in northern KwaZulu-Natal collected at the same time (Petrie 1998c); however their MIS was considerably higher (female = 25, male = 24) than birds arriving on the Nyl River floodplain prior to reproduction (female = 8, male = 11) (Petrie 1998b). This reduction in moult intensity prior to arrival on breeding areas may be a consequence of the increased nutrient demands of seeking breeding areas and strengthening pair bonds, combined with the time lag between spring rains and peak availability of native seeds on breeding areas.

The possible ecological advantages of overwintering close to breeding areas and attaining high levels of body fat during spring are: 1) reduced mortality risks associated with a relatively short migration, 2) higher winter survival due to a reduction in density-dependent mortality factors, 3) early arrival on breeding areas and earlier breeding attempts, 4) more endogenous nutrients to contribute to ovulation, resulting in increased clutch sizes and more nesting attempts following predation, and 5) heightened reproductive success and juvenile recruitment. Any or all of these factors may have contributed to the range expansion and population increase of white-faced whistling ducks in southern Africa (*cf.* Maclean 1997). Interestingly, rapidly expanding goose populations in North America have been attributed largely to the use of agricultural habitats during winter and migration, thereby increasing survival and nutrient reserve accumulation prior to reproduction (Alisauskas & Ankney 1992; Gauthier *et al.* 1992; Ankney 1996). I suggest that, while the anthropogenic provision of permanent waterbodies has enabled white-faced whistling ducks to expand their overwintering range, agricultural grain availability has simultaneously increased survival and reproductive output, thereby influencing population expansion.

Use of man-made waterbodies by waterfowl increases with pond size, age, presence of loafing sites, emergent vegetation, shoreline irregularity index and proximity to other ponds (Lokemoen 1973; Evrard 1975; Hudson 1983; Belanger & Couture 1988). Therefore, farmers should be encouraged to construct and manage ponds in such a way as to encourage aquatic bird use. This practice will increase the suitability of man-made waterbodies for breeding as well as overwintering waterfowl and will partially offset the effects of extensive wetland drainage and destruction in South Africa.

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