Intensity and Chronology of Pre-breeding and Post-breeding moult in White-faced Whistling-Ducks Dendrocygna viduata

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The intensity and chronology of moult in breeding and post-breeding White-faced Whistling-Ducks Dendrocygna viduata were studied during 1992/1993 and 1995 in a semi-arid region of Northern Province, South Africa. Adult males and females were moulting in most feather areas when they arrived on the breeding grounds in December and January and continued to do so during rapid follicular growth. Both sexes moulted at a very low intensity during reproduction, males had a higher moult intensity score than females during both laying (P=0.04) and incubation (P=0.002). Contour-feather replacement peaked during brood rearing and pre-wing moult and was followed by loss of primaries and secondaries. Most feather areas were moulting intensively during the latter stages of wing-feather growth and continued to do so after birds had regained flight capability. The ephemeral nature of breeding habitats in southern Africa may have selected for the retention of wing feathers by brood rearing adults, as well as flexibility in the timing and location of wing-moult. While White-faced Whistling-Ducks replace contour feathers during brood rearing, the low protein content of their diet and high nutrient costs associated with reproduction apparently necessitate the separation of intense feather replacement and both laying and incubation. Their single annual moult and lack of a breeding plumage permits White-faced Whistling-Ducks to initiate breeding whenever suitable habitats become available and enables them to prolong moult over a large portion of the annual cycle. Shared costs of incubation and brood rearing, perennial monogamy and lack of a breeding plumage could be the selection pressures leading to somewhat similar inter-sexual moult patterns and intensities.

Keywords: White-faced Whistling-Duck, South Africa, Moult, Reproduction

Although the pattern and process of moult has been described for several species in the anatid tribes Anatini and Aythyini, which replace contour feathers twice per annual cycle (Weller 1957, Dean 1978, Young & Boag 1981, DuBowy 1985, Wishart 1985, Austin & Fredrickson 1986, Miller 1986, Heitmeyer 1987, Lovvorn & Barzen 1988, Smith & Sheeley 1993, Hohman & Crawford 1995), the duration of the single annual moult, degree of sexual moult synchrony, and timing of wing-moult (primaries and secondaries only) in whistling ducks *Tribe*

Dendrocygnini is poorly understood (Hohman *et al.* 1992, Petrie 1998a, 1998b).

Seasonally monogamous, north-temperate duck species are sexually and seasonally dichromatic and display substantial energetic, nutrient and temporal sexual disparity in reproductive investment. This has resulted in marked sexual differences in intensity and chronology of moult throughout the annual cycle (Billard & Humphrey 1972, Miller 1986, Hohman & Crawford 1995). In contrast, White-faced Whistling-Ducks are perennially monogamous, sexually and seasonally monochromatic, and share incubation and brood rearing costs (Bolen & Rylander 1983, Rohwer & Anderson 1988). Consequently, I predicted a decreased sexual divergence in moult intensity and chronology in White-faced Whistling-Ducks relative to seasonally monogamous north-temperate species.

Waterfowl are inefficient at converting dietary protein into feathers, and their diets can be deficient in specific amino acids required for feather synthesis (cystein and methionine) (Hanson 1962, see Murphy & King 1984). Nutritional costs of moult are accordingly substantial as feathers are 93-98.5% protein (Robbins 1983). Relative to north-temperate breeding ducks, diets of White-faced Whistling-Duck *Dendrocygna viduata* are low in protein and essential amino acids, suggesting that there may be a mismatch between physiological need and environmental availability of protein (Petrie & Rogers 1996). Because protracted, low intensity moult can reduce daily nutrient requirements (Blackmore 1969, Payne 1972), the low protein content of the diet of White-faced Whistling-Duck, and the fact that they are not temporally constrained by having to acquire and subsequently relinquish a breeding plumage, may influence moult duration and degree to which it overlaps reproduction.

With exception of occasional late-nesting females, replacement of remiges on or near breeding areas is almost ubiquitous among north-temperate and arctic-breeding waterfowl (Hohman *et al.* 1992). This can be attributed to the predictable availability of suitable post-breeding habitats and foods. In contrast, large numbers of White-faced Whistling-Ducks that winter in KwaZulu-Natal, South Africa replace remiges while on wintering areas (Petrie 1998b). In semi-arid regions of South Africa, most aquatic breeding habitats are ephemeral (Tarboton & Batchelor 1981, Alexander 1985, Petrie 1998a), thereby limiting the time that waterfowl have to reproduce and complete wing-moult. However, given that semi-arid breeding waterfowl are opportunistic as well as flexible in timing and location of events in the annual cycle (*cf* Briggs 1992, Harrison *et al.* 1997, Petrie 1998a). I further predicted that at least some White-faced Whistling-Ducks would replace remiges while on breeding areas. Herein, I report on prebasic moult patterns of breeding and post breeding White-faced Whistling-Ducks in Northern Province, South Africa.

Study Area

The Nyl River floodplain is a 16,000 ha ephemeral wetland complex located in the semi-arid savanna of Northern Province, South Africa (24°39S, 28°42'E), 1,080 m above sea level. 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). Consequently, there is extreme variability in periodicity, duration, depth and timing of flooding events. During flood years a mosaic of wetland types (oxbow lakes, ephemeral pans, channel marsh, and large grass-dominated marshes) provide an array of habitat for approximately 25,000 ducks of 11 species. White-faced Whistling-Ducks are the most common anatid on the floodplain (Tarboton & Batchelor 1981) and they arrive and breed shortly after spring rains. During six out of 10 years, either no flood occurs or it is unsustained and therefore of little consequence to breeding waterfowl (Tarboton & Batchelor 1981). 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 during both wet and dry years (Personal observation).
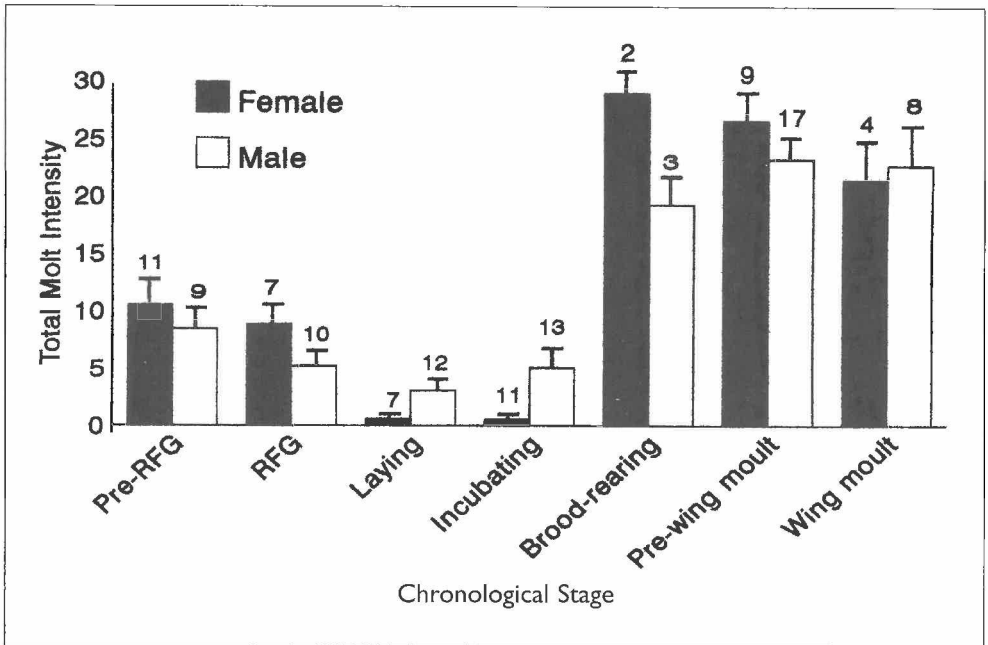
Figure 1. Moult intensity scores (mean±SE) of adult female and male White-faced Whistling-Ducks collected during 1992/93 and 1995 on the Nyl River floodplain, South Africa. Numbers above bars represent sample sizes.

Methods

Small portions of the Nyl River floodplain, the main river channel and associated stock-watering bodies contained water and were used by breeding White-faced Whistling-Ducks during 1992/1993 and 1995. As part of a larger study of bioenergetics of White-faced Whistling-Ducks, breeding and post-breeding birds were randomly collected on the floodplain and associated stock-watering ponds. Wing-moulting birds were collected only on flooded portions of the floodplain as all birds relocated to the floodplain prior to wing-moult. Collection commenced when birds arrived in December 1992 and continued until May 1993. Birds also were collected during January and February of 1995.

Female White-faced Whistling-Ducks and their mates were assigned to the following chronological stages based in part on Krapu (1974) and Hohman (1985):

1. Pre-rapid follicular growth (pre-RFG) - ovary mass < 3 g,
2. Rapid follicular growth (RFG) - pre-ovulating, ovary mass > 3 g,
3. Laying - ovulating,
4. Incubating - post-ovulating and possessing a brood patch,
5. Brood rearing - with a brood of ducklings, all brood rearing adults were collected with Class II ducklings (Gollop & Marshall 1954),
6. Pre-wing moult - females with regressed ovaries and oviduct whose brood patch showed distinct signs of decreasing vascularisation and males showing distinct signs of testicular regression, and
7. Wing-moult - birds that were in later stages of wing-feather replacement. All wing-moulting birds had regained the ability to fly when collected but none had completed wing-feather growth.

Intensity of feather replacement was determined by scoring the presence of blood quills in 20 feather regions: crown, face, chin-

Table I. Moult-intensity scores (mean + SE) of 20 feather regions for breeding and post-breeding female White-faced Whistling-Ducks collected during 1992/1993 and 1995 on the Nyl River floodplain, South Africa

Feather tract	Pre-RFG	RFG	Lay	Incubate	Brood rearing	Pre-wing Moult	Wing Moult
Crown	1.2 (0.2)	1.4 (0.2)	* 0.0	0.1 (0.1)	* 2.0 (0.0)	1.9 (0.1)	1.8 (0.3)
Face	1.1 (0.2)	1.1 (0.3)	* 0.0	0.0	* 2.0 (0.0)	1.9 (0.1)	1.5 (0.3)
Chin/throat	0.9 (0.3)	1.0 (0.4)	* 0.0	0.0	* 2.0 (0.0)	1.5 (0.2)	1.5 (0.3)
Neck	0.5 (0.2)	0.3 (0.2)	0.0	0.0	* 1.5 (0.5)	1.6 (0.2)	0.8 (0.5)
Upper back	0.5 (0.2)	0.3 (0.2)	0.0	0.1 (0.1)	* 1.5 (0.5)	1.4 (0.2)	1.0 (0.4)
Scapulars	1.3 (0.2)	1.4 (0.3)	* 0.3 (0.2)	0.0	* 2.0 (0.0)	2.0 (0.0)	2.0 (0.0)
Lower back	0.3 (0.2)	0.1 (0.1)	0.0	0.0	* 0.5 (0.5)	0.9 (0.3)	0.3 (0.3)
Rump	0.2 (0.1)	0.1 (0.1)	0.0	0.0	* 1.0 (0.5)	1.1 (0.2)	* 0.3 (0.3)
Upper tail coverts	0.4 (0.2)	0.1 (0.1)	0.0	0.0	* 1.5 (0.5)	1.3 (0.2)	0.5 (0.3)
Retrices	0.5 (0.2)	0.6 (0.4)	0.0	0.0	* 2.0 (0.0)	1.4 (0.3)	2.0 (0.0)
Lower tail covert	0.6 (0.2)	* 0.0	0.0	0.1 (0.1)	* 1.5 (0.5)	1.5 (0.2)	* 0.5 (0.5)
Belly	0.3 (0.1)	0.3 (0.2)	0.0	0.0	* 1.5 (0.5)	1.5 (0.2)	* 0.0
Centre chest	0.4 (0.2)	0.4 (0.2)	0.0	0.1 (0.1)	* 2.0 (0.0)	1.6 (0.2)	* 0.0
Side chest	0.8 (0.2)	0.6 (0.3)	* 0.0	0.1 (0.1)	* 2.0 (0.0)	1.7 (0.2)	* 0.8 (0.3)
Side	0.4 (0.2)	0.4 (0.2)	0.0	0.0	* 2.0 (0.0)	1.9 (0.1)	* 1.3 (0.3)
Flank	0.6 (0.2)	0.4 (0.2)	0.3 (0.2)	0.0	* 1.5 (0.5)	1.5 (0.2)	0.8 (0.3)
Primaries	0.0	0.0	0.0	0.0	0.0	0.0	* 2.0 (0.0)
Secondaries	0.0	0.0	0.0	0.0	0.0	0.0	* 2.0 (0.0)
Tertial	0.5 (0.2)	0.1 (0.1)	0.0	0.1 (0.1)	* 2.0 (0.0)	1.4 (0.2)	1.8 (0.0)
Wing coverts	0.3 (0.1)	0.0	0.0	0.0	* 0.5 (0.5)	1.0 (0.3)	1.8 (0.6)
n	11	7	7	11	2	9	4

Values within a row that are separated by an asterisk [*] are significantly different (P<0.05)

Table 2. Moult-intensity scores (mean + SE) of 20 feather regions for breeding and post-breeding male White-faced Whistling-Ducks collected during 1992/1993 and 1995 on the Nyl River floodplain, South Africa

Feather tract	Pre-RFG	RFG	Lay	Incubate	Brood rearing	Pre-wing Moult	Wing Moult
Crown	0.8 (0.3)	0.8 (0.3)	0.4 (0.2)	0.5 (0.2)	* 1.7 (0.3)	1.7 (0.1)	1.8 (0.2)
Face	0.3 (0.2)	0.5 (0.3)	0.4 (0.2)	0.4 (0.1)	* 1.7 (0.3)	1.5 (0.1)	1.8 (0.2)
Chin/throat	0.4 (0.2)	0.5 (0.2)	0.4 (0.2)	0.5 (0.2)	1.3 (0.3)	1.6 (0.1)	1.4 (0.2)
Neck	0.3 (0.2)	0.3 (0.2)	* 0.0	0.1 (0.1)	* 1.3 (0.3)	1.2 (0.2)	0.1 (0.3)
Upper back	0.0	0.1 (0.1)	0.0	0.1 (0.1)	* 1.0 (0.0)	1.1 (0.2)	1.0 (0.3)
Scapulars	1.2 (0.2)	0.9 (0.2)	0.7 (0.2)	0.7 (0.2)	* 2.0 (0.0)	1.9 (0.1)	1.9 (0.1)
Lower back	0.1 (0.1)	0.0	0.1 (0.1)	0.1 (0.1)	0.3 (0.3)	0.7 (0.2)	0.6 (0.3)
Rump	0.0	0.0	0.1 (0.1)	0.1 (0.1)	0.3 (0.3)	0.9 (0.2)	1.0 (0.2)
Upper tail coverts	0.3 (0.2)	0.0	0.1 (0.1)	0.1 (0.1)	* 0.7 (0.3)	1.3 (0.2)	1.0 (0.3)
Retrices	0.9 (0.3)	* 0.1 (0.1)	0.2 (0.1)	0.2 (0.1)	0.7 (0.3)	1.3 (0.2)	1.0 (0.3)
Lower tail covert	0.7 (0.2)	* 0.1 (0.1)	0.1 (0.1)	0.5 (0.2)	* 1.7 (0.3)	1.3 (0.2)	1.4 (0.3)
Belly	0.4 (0.2)	0.3 (0.2)	0.1 (0.1)	0.5 (0.2)	0.3 (0.3)	1.6 (0.1)	* 0.9 (0.3)
Centre chest	0.6 (0.2)	0.2 (0.1)	0.0	* 0.4 (0.2)	* 1.3 (0.3)	1.6 (0.1)	* 0.8 (0.3)
Side chest	1.0 (0.3)	* 0.1 (0.1)	0.1 (0.1)	0.5 (0.2)	1.0 (0.0)	1.5 (0.1)	1.0 (0.3)
Side	0.1 (0.1)	0.5 (0.2)	0.2 (0.1)	0.5 (0.2)	1.3 (0.3)	1.5 (0.2)	1.3 (0.3)
Flank	0.3 (0.2)	0.3 (0.1)	0.3 (0.1)	0.1 (0.1)	0.7 (0.3)	1.1 (0.1)	0.9 (0.2)
Primaries	0.0	0.0	0.0	0.0	0.0	0.0	* 1.0 (0.4)
Secondaries	0.0	0.0	0.0	0.0	0.0	0.0	* 1.0 (0.4)
Tertial	0.7 (0.2)	0.5 (0.2)	* 0.0	0.1 (0.1)	* 1.0 (0.6)	0.9 (0.2)	1.5 (0.3)
Wing coverts	0.2 (0.1)	0.0	0.0	0.0	0.0	0.4 (0.2)	0.6 (0.2)
n	9	10	12	13	3	17	8

Values within a row that are separated by an asterisk [*] are significantly different (P<0.05)

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 & Frederickson 1986), while plucking carcasses for subsequent body-composition analysis. Total moult intensity (MIS) was the sum of all 20 feather region scores (maximum value 40). The ovary and oviduct of females and one testis of males were excised and weighed (0.01 g) to determine breeding condition. One ninth-primary of each bird was measured to nearest 0.1 mm to determine the amount of wing-feather regrowth required before birds could regain flight capabilities.

Mann-Whitney U tests (Conover 1980) were used to detect, within chronological stage, sexual differences in MIS and differences in moult intensity of each of the twenty feather areas (Zar 1984). Between chronological stage differences in MIS and individual feather area scores were tested using Kruskal-Wallis tests (Conover 1980). Ninth primary lengths were analysed using a one-way ANOVA (Tukey HSD Multiple Comparisons tests). A Spearmans Rank Sums test was used to identify correlations between MIS and testis, ovary and oviduct mass.

Results

Male and female White-faced Whistling-Ducks had similar MIS scores ($P > 0.05$) (**Figure 1**) during pre-RFG and RFG and were moulting in most feather areas during this time (**Tables 1** and **2**). Females had higher moult intensity scores in most feather areas before ovulation, but results were only significant for the facial area during RFG ($P = 0.02$). The MIS of both sexes declined to very low levels during ovulation (**Figure 1**), probably as a consequence of increased energy and nutrient costs of egg laying in females (MIS = 0.6, $P = 0.001$) and mate defence in males (MIS = 3.1, $P = 0.11$) (see Petrie & Rogers 1997a). Although there were no sexual differences in any feather

area scores during laying ($P > 0.05$), females discontinued moult in all except scapular and flank areas while males continued to moult at low intensities in 13 of 20 feather areas (**Table 1, Table 2**). This resulted in females having a lower MIS than males during laying ($P = 0.04$). Reductions in female and male MIS during the laying period are substantiated by strong negative correlations between MIS and ovary ($r_s = -0.46$, $P < 0.01$), oviduct ($r_s = -0.49$, $P < 0.05$), and testis ($r_s = -0.64$, $P < 0.05$) mass.

Incubating females continued to moult at very low levels (MIS = 0.5, $P = 0.88$) and discontinued moult in scapular and flank ($P > 0.05$) areas and initiated low intensity moult in 6 other areas (**Figure 1**). Male MIS increased slightly during incubation (5.1, $P = 0.34$) due to moderate increases in intensity of lower tail covert, belly, center chest, side chest, and side feather replacement. Males moulted more intensely than females during incubation ($P = 0.002$), due primarily to higher intensities of moult in the face, chin/throat, scapular, belly, side, and lower tail covert areas ($P < 0.05$).

Female MIS (29.0, $P < 0.05$) and intensity of moult in 14 of 20 feather areas peaked during brood rearing (**Figure 1, Table 1**). Although MIS did not peak during brood rearing, increased moult intensity in 17 of 20 feather areas also resulted in a high male MIS (MIS = 19.3, $P = 0.01$). Brood-rearing females moulted more intensely than did males in 16 of 18 active feather areas (**Tables 1** and **2**) resulting in a higher MIS (**Figure 1**), but small sample sizes apparently precluded statistical significance ($P > 0.05$ for all comparisons).

Pre-wing moulting males and females maintained high MIS scores ($P > 0.05$). However, pre-wing moulting females moulted at higher intensities in face, side, and wing covert feather areas than did brood-rearing females ($P < 0.05$). Wing-moulting males had an MIS similar to pre-wing moulting males (22.8, $P = 0.92$) but exhibited decreased belly and centre chest moult intensity and increased primary and secondary moult intensity. The MIS of wing-moulting males and females was similar ($P = 0.61$, **Figure 1**), although moult intensity in the rump area was higher in males ($P = 0.04$).

All wing-moulting birds could fly when collected, but none had completed wing-feather growth. There were no sexual differences in ninth primary lengths during any of the stages ($P > 0.05$), so sexes were combined for further analysis. Ninth primaries of wing-moulting birds were only 89% of the length of all other moult stages combined ($P < 0.001$) and one individual was flying with growth only 77% complete. This probably does not represent minimum primary feather regrowth required to regain flight as birds were not necessarily collected on the first day they recovered flight capabilities.

Discussion

Moult Duration

White-faced Whistling-Ducks extended prebasic moult over the five months spent on breeding grounds. Prebasic moult probably also overlapped spring and autumn migration as all birds collected during peak arrival and departure from the Nyl River floodplain were moulting in most feather areas. Although long distance migrations and moult are generally mutually exclusive events (Palmer 1972), the short distance (50 to 700 km) that White-faced Whistling-Ducks travel between wintering and breeding areas (Oatley & Prys-Jones 1985, Petrie & Rogers 1997b) probably permits overlap of body moult and their nomadic movements. Prebasic moult in White-faced Whistling-Ducks also continues throughout the entire time that birds spend on wintering areas (Petrie 1998b). Being sexually and seasonally monochromatic, extension of the moult period is possible, as White-faced Whistling-Ducks are not temporally constrained by a second plumage replacement or by acquisition and relinquishment of a breeding plumage. This extended moult duration must minimise energy and protein costs on a daily basis, as it would distribute the costs of feather replacement over a longer portion of the annual cycle. This may be very important for White-faced Whistling-Ducks as they are primarily herbivorous (Petrie & Rogers 1996) and therefore, may have difficulty satisfying the

sulphur amino acid requirements of feather replacement. For instance, female Mallards complete prebasic moult in as little as six to seven weeks (Heitmeyer 1987), and incur substantial daily and total protein costs in doing so (Heitmeyer 1988).

Most anatids that have a second and third moult per cycle are omnivorous or carnivorous. Whistling ducks, geese and swans adhere to the ancestral pattern of one moult per cycle (Rohwer & Anderson 1988) and species in all three groups are either completely herbivorous or consume very small quantities of animal matter (see Krapu & Reinecke 1992, Petrie & Rogers 1996). Therefore, low dietary protein and/or deficiencies in specific amino acids may preclude the evolution of a second annual plumage replacement in these species.

Distribution of Moulting Costs

Female White-faced Whistling-Ducks virtually ceased prebasic moult during laying and incubation. Ovulation is the most energetically and nutrient costly event in the annual cycle of female waterfowl, and birds generally time moult so that it reduces overlap with egg laying and incubation (Payne 1972, Ricklefs 1974, Carey et al. 1980, Heitmeyer 1987, Alisauskas & Ankney 1992). This temporal separation of reproduction and intense feather replacement ('staggered costs') serves to mitigate energetic and nutrient constraints during breeding. Being primarily herbivorous (Petrie & Rogers 1996), it would be particularly difficult for White-faced Whistling-Ducks to satisfy the protein requirements of ovulation and feather replacement concurrently. Male White-faced Whistling-Ducks also suspended prebasic moult during laying and incubation, probably because they spend less time foraging and considerably more time alert than do females then (Petrie & Rogers 1997a). Therefore, while north-temperate duck species generally separate two distinct plumage replacement events (prebasic and prealternate) by reproduction (Wishart 1985), White-faced Whistling-Ducks interrupt one plumage replacement (prebasic) event during

reproduction. Retention of one moult per cycle permits greater flexibility in adjusting moult intensity and chronology to environmental conditions than is possible for ducks that moult twice annually (Gates et al. 1993). Availability of reproductive habitats is temporally and spatially variable in semi-arid regions (Petrie 1998a), so White-faced Whistling-Ducks simply interrupt prebasic moult whenever breeding habitats become available. A similar pattern has been reported for Gálpagos finches (Snow 1966).

In Anatinae, males generally contribute little to brood care (Kear 1970), and brood rearing reduces time that females have for maintenance (Afton & Paulus 1992). Females generally delay moult until brood rearing is complete (Wishart 1985, Austin & Fredrickson 1986), possibly to alleviate energetic constraints and provide improved brood care. In contrast, male and female White-faced Whistling-Ducks undergo intense moult of contour feathers while sharing brood-rearing costs. Co-operative brood care possibly bestows nutritional benefits to parents, as Arctic-nesting geese and swans also share brood rearing costs and they undergo wing-moult during brood rearing (Scott 1980, Ankney 1984, Earnst 1992).

Sexual Differences

Evolution of a second (or third) annual moult and substantial energetic, nutrient, and temporal sexual disparity in reproductive investment, has resulted in marked sexual differences in intensity and chronology of moult throughout the annual cycle of seasonally monogamous, north-temperate anatids (Billard & Humphrey 1972, Miller 1986, Hohman & Crawford 1995). The life-history strategies of White-faced Whistling-Ducks differ from these species in at least three respects: (1) they are not temporally or nutritionally constrained by having to moult into or out of a breeding plumage; (2) they share incubation costs; and (3) they share brood rearing costs. Thus, I suggest that absence of a breeding plumage, and relatively small sexual discrepancy in reproductive investment may have resulted in this limited sexual difference in the prebasic

moult pattern of White-faced Whistling-Ducks. However, alternating levels of moult intensity between breeding males and females are quite possibly due to sexual fluctuations in cumulative reproductive investment over time (**Figure 1**).

Typically, due to male vigilance and a compensatory reduction in foraging time (Seymour & Titman 1978, Afton 1979, Petrie & Rogers 1997a), cumulative reproductive effort in waterfowl is higher for males until females start to produce eggs (Afton & Paulus 1992). This difference in pre-ovulation effort may influence the amount of nutrients males can allocate to feather replacement as female White-faced Whistling-Ducks moulted more intensively than males before egg laying. Female cumulative reproductive effort surpasses that of their mates during ovulation and incubation (Afton & Paulus 1992) and female White-faced Whistling-Ducks almost suspended prebasic moult during this time. Although not to the extent of females, males also reduce their moult intensity to low levels during laying and incubation. White-faced Whistling-Ducks are one of only 12 anatid species that share incubation. Therefore, while a lower reproductive effort enables male White-faced Whistling-Ducks to moult at slightly higher intensities than females, the increased energetic costs of shared incubation probably preclude simultaneous high moult intensities.

Wing-Feather Loss

Arctic-nesting geese and swans have retained the ancestral pattern of one moult per cycle, they generally initiate wing-moult shortly after eggs hatch and regain flight capabilities when their young fledge (Hohman et al. 1992). Availability of food and suitable post-breeding habitats are generally predictable in the Arctic and this presumably permits simultaneous brood rearing and wing-moult. Large body size also enables geese and swans to repel some predators, even when flightless. In contrast, White-faced Whistling-Ducks moult contour feathers intensively during brood rearing and delay wing-moult until after young have fledged. There are several non-mutually exclusive

factors that may have selected for retention of wing-feathers by brood rearing adults. Aquatic habitats are ephemeral in the semi-arid regions of South Africa (Alexander 1985). Therefore, retention of flight capabilities would enable adults to explore alternate brood-rearing areas when aquatic habitats begin to desiccate, to escape predators during overland brood movements, and to desert broods during extreme drought (Klint 1982, Hohman et al. 1992), while possibly enhancing their ability to protect ducklings. White-faced Whistling-Ducks primarily consume native terrestrial seeds during breeding and post breeding on the Nyl River floodplain (Petrie & Rogers 1996, Petrie 1998a). Therefore, retention of flight would provide adults with access to terrestrial grains during brood recesses and this would also reduce competition between adults and ducklings for aquatic foods.

White-faced Whistling-Ducks leave stock-ponds and small flooded portions of the floodplain before becoming flightless (Petrie 1998a). This results in an influx of wing-moulting birds on areas of the floodplain that have become inundated, and indicates that birds make a moult migration between these two areas. However, White-faced Whistling-Ducks are unable to complete wing-feather moult on the Nyl River floodplain during years when no flood occurs or when it is unsustained. Although occurrence of wing-moult by wintering waterfowl is extremely rare for north-temperate and arctic breeding waterfowl, some White-faced Whistling Ducks do undergo wing-moult during winter in South Africa (Petrie 1998b). In contrast to the predictable availability of suitable post-breeding aquatic habitats in north-temperate and arctic regions, semi-arid wetlands are generally ephemeral (Tarboton & Batchelor 1981, Alexander 1985), resulting in considerable between-year variability in the time that waterfowl have to reproduce and complete wing-feather moult (Petrie 1998a). Therefore, timing and geographic location of wing-feather replacement is probably determined by the timing of an individuals reproductive completion and duration of suitable post-breeding aquatic habitat availability.

White-faced Whistling-Ducks are not unique in their ability to regain flight capabilities before completion of wing-feather moult (Hohman et al. 1992). However, early attainment of flight may be particularly advantageous in unpredictable environments for at least three key reasons: (1) it reduces the possibility of birds being stranded on a rapidly desiccating wetland; (2) it may substantially reduce predation pressures as there are at least four times as many species of potential predators in southern Africa as in Holarctic regions (Siegfried 1974); and (3) it reduces the time that birds are precluded from terrestrial foraging.

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