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Molt Patterns of Nonbreeding White-faced Whistling-Ducks in South Africa

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The tribe Dendrocygnini (whistling-ducks) contains nine species that have a circumequatorial distribution (Bolen and Rylander 1983). Whistling-ducks are distinct from most other ducks in that they are perennially monogamous, share incubation and brood-rearing duties, and retain the ancestral pattern of replacing their contour feathers only once per annual cycle. The chronology of molt in whistling-ducks and the timing and location of remigial replacement are poorly understood, and whistling-ducks are one of the least-studied tribes of waterfowl in the world (Hohman et. al 1992, Hohman and Richard 1994, Petrie 1998).

The White-faced Whistling-Duck (*Dendrocygna viduata*) is widespread in the Afrotropical and Neotropical regions and in most of the semiarid regions of sub-Saharan Africa (Madge and Burn 1988). When they arrive on breeding areas in interior South Africa, White-faced Whistling-Ducks are molting in most feather tracts (Petrie 1998). Both sexes continue to molt during the period of early rapid follicle growth in females, suspend molt (or nearly so) during laying and incubation, and resume molt during the brood-rearing period. However, it is unknown if White-faced Whistling-Ducks continue this single annual molt throughout the winter and spring.

I investigated the intensity and chronology of molt in nonbreeding White-faced Whistling-Ducks in South Africa. My goal was to determine whether they replace their remiges on the wintering grounds and to evaluate their molt relative to environmental and phylogenetic constraints. Because the diet of White-faced Whistling-Ducks is relatively deficient in protein (Petrie and Rogers 1996, Petrie 1998), and prolonged low-intensity feather replacement reduces daily nutrient requirements of molt (Blackmore 1969, Payne 1972), I hypothesized that these ducks prolong the replacement of their contour feathers

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throughout winter and spring. Presumably, the temporal extension of molt is possible because whistling-ducks are not constrained by a prealternate molt.

The availability of habitat and food in north-temperate and arctic regions is determined primarily by highly regular seasonal variations in temperature. Waterfowl have responded to this predictability by synchronizing the timing and location of events in the annual cycle (Alisauskas and Ankney 1992, Krapu and Reinecke 1992, Petrie 1998). For instance, with the 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). In contrast, environmental variability (both seasonal and annual) in semiarid regions of South Africa primarily is a function of the wet/dry cycle that is regulated by convective rainfall that is highly variable in space and time (Braune 1985). Because the availability of habitat and food for waterfowl in semiarid regions ultimately is determined by these highly variable (in both timing and intensity) rainfall events (Siegfried 1970, 1974, Petrie 1998), there is extreme spatiotemporal variability in the availability of habitat for remigial replacement on and near breeding areas (Petrie 1998). This unpredictability should predispose waterfowl to be flexible in the timing of events in the annual cycle and to be opportunistic in life-history tactics. Therefore, although White-faced Whistling-Ducks have been documented to replace their remiges on breeding areas (Petrie 1998), I further hypothesized that the ephemeral nature of aquatic habitats in South Africa would cause at least some White-faced Whistling-Ducks to replace their remiges on the wintering grounds.

Study area and methods.—The study was conducted in northern KwaZulu-Natal, South Africa. The area receives approximately 60 cm of rainfall annually and is characterized by hot, wet summers and mild, dry winters (Watkeys et al. 1993). The area contains many semipermanent and permanent shallow pans (basins); two large river systems flow across the region, forming a number of floodplain and swamp systems.

These coastal plain wetlands support large concentrations of White-faced Whistling-Ducks in winter, because most natural wetlands in the semiarid interior are dry at this time (Colahan 1984). Adults and juveniles were collected by shooting at random from pans (27°38'S, 32°26'E) and the Pongolapoort Reservoir (27°30'S, 31°59'E) during early winter (8 to 16 June, $n = 40$), late winter (10 to 18 August, $n = 39$), and spring (1 to 8 October, $n = 43$) in 1995. To describe the pattern of molt in White-faced Whistling-Ducks throughout the nonbreeding period, collection periods were based on the fact that the breeding period (generally between October and April) in semiarid regions is defined more strongly by rainfall than by season (Clark 1976).

The 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, uppertail coverts, rectrices, undertail coverts, belly, center chest, side chest, side, flank, primaries, secondaries, tertials, and wing coverts. Molt intensity was scored (visual estimate) as 0, 1, or 2 for no molt, light molt (<15% of tract molting), and heavy molt (>15% of tract molting), respectively (Austin and Frederickson 1986), while plucking carcasses for subsequent analysis of body composition. The total molt-intensity score (MIS) was the sum of all 20 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. Age was determined by the presence of a bursa of Fabricius, because most juveniles had acquired the white facial feathers typical of adults.

I used Kruskal-Wallis rank-sum tests to detect differences in sex and age classes within and between collection periods in MIS and molt intensity within each of the 20 feather regions (Conover 1980). Mann-Whitney U-tests were subsequently used to determine where differences occurred. Within and between collection periods, sex- and age-related differences in number of actively molting feather areas were analyzed using one-way ANOVA and Tukey HSD multiple comparisons tests. The significance level was $P < 0.05$ for all tests and comparisons.

Results.—Females had similar ($P > 0.05$) ovary and oviduct masses during early winter (0.28 g and 0.62 g, respectively), late winter (0.22 g, 0.58 g), and spring (0.31 g, 0.53 g), whereas males had slightly heavier testes in spring (0.29 g) than during early winter (0.15 g; $P = 0.08$) and late (0.13 g; $P = 0.03$) winter. However, all males and females collected during winter and spring were in a nonreproductive state.

Adult males and females had similar MIS ($U = 121.0$, $P = 0.45$) and were molting at similar intensities in all 20 feather areas in early winter (all Ps > 0.05; Table 1, Fig. 1). All 20 feather regions had evidence of feather replacement in some ducks, and the mean number of actively molting feather regions was 15.6 and 15.5 for males and females, respectively ($P = 1.00$). Among adults collected in early winter, 11% of the females and 10% of the males were in the later stages of remigial molt. All juveniles had completed their secondary molt by early winter, and their mean MIS was not significantly different from that of adult males ($U = 63.5$, $P = 0.15$) and adult females ($U = 79.0$, $P = 0.16$; Fig. 1). With the exception of a reduced lower-back molt intensity ($U = 0.049$, $P = 0.04$), molt intensities were similar between juveniles and adults (all Ps > 0.05).

MIS in adult males and females did not change be-

TABLE 1. Number of actively molting feather areas and molt-intensity scores in 20 feather areas of White-faced Whistling Ducks collected during three periods in 1995 in northern KwaZulu-Natal, South Africa. Values are $\bar{x}$ ± SE.[a]

	Adult females			Adult males			Juveniles		
	Early winter	Late winter	Spring	Early winter	Late winter	Spring	Early winter	Late winter	Spring
No. of areas	15.5 ± 0.5	16.3 ± 0.6	15.9 ± 0.8	15.6 ± 0.7	15.3 ± 0.8	17.4 ± 0.5	13.2 ± 1.4	10.5 ± 1.6^{A}	15.5 ± 1.4^{B}
Crown	1.7 ± 0.1	1.8 ± 0.1	1.9 ± 0.1	1.7 ± 0.1^{A}	1.8 ± 0.1^{A}	2.0 ± 0.0^{B}	1.5 ± 0.2	1.4 ± 0.2	1.9 ± 0.1
Face	1.5 ± 0.1^{A}	1.9 ± 0.1^{B}	1.6 ± 0.1	1.3 ± 0.1	1.6 ± 0.1	1.7 ± 0.1	1.0 ± 0.0	1.1 ± 0.2	1.5 ± 0.2
Chin/throat	1.2 ± 0.1	1.1 ± 0.1	1.4 ± 0.1	1.4 ± 0.1	1.3 ± 0.2	1.6 ± 0.1	1.3 ± 0.3	1.1 ± 0.2	1.4 ± 0.2
Neck	1.3 ± 0.1	1.5 ± 0.1	1.4 ± 0.2	1.3 ± 0.1^{A}	1.6 ± 0.1	1.8 ± 0.1^{B}	1.3 ± 0.2	1.0 ± 0.4	1.6 ± 0.2
Upper back	0.9 ± 0.1	1.2 ± 0.1	1.0 ± 0.1	1.1 ± 0.1^{A}	1.0 ± 0.1^{A}	1.5 ± 0.1^{B}	0.7 ± 0.2	1.0 ± 0.3	1.3 ± 0.2
Scapulars	1.9 ± 0.1	1.8 ± 0.1	1.9 ± 0.1	1.7 ± 0.1	1.9 ± 0.1	2.0 ± 0.0	1.7 ± 0.2	1.6 ± 0.2	2.0 ± 0.0
Lower back	1.1 ± 0.1	0.9 ± 0.2	0.7 ± 0.1	0.9 ± 0.1	0.9 ± 0.2	1.1 ± 0.2	0.5 ± 0.2^{A}	0.4 ± 0.2^{A}	1.1 ± 0.1^{B}
Rump	1.0 ± 0.1	0.8 ± 0.2	0.9 ± 0.2	0.9 ± 0.2	0.9 ± 0.2	1.2 ± 0.2	0.5 ± 0.2^{A}	0.3 ± 0.2^{A}	1.1 ± 0.2^{B}
Uppertail coverts	1.0 ± 0.2	1.4 ± 0.2	1.5 ± 0.2	1.0 ± 0.2^{A}	1.3 ± 0.2	1.8 ± 0.1^{B}	0.8 ± 0.3	0.3 ± 0.2^{A}	1.4 ± 0.3^{B}
Rectrices	1.1 ± 0.2	1.4 ± 0.2	1.4 ± 0.2	1.1 ± 0.1^{A}	1.6 ± 0.2^{B}	1.7 ± 0.1^{B}	0.8 ± 0.3	1.3 ± 0.4	1.5 ± 0.3
Undertail coverts	1.2 ± 0.1	1.6 ± 0.2	1.5 ± 0.2	1.2 ± 0.1^{A}	1.5 ± 0.2^{A}	2.0 ± 0.0^{B}	1.3 ± 0.3^{A}	0.6 ± 0.2^{B}	1.6 ± 0.3^{C}
Belly	0.6 ± 0.1^{A}	1.3 ± 0.2^{B}	1.1 ± 0.2^{B}	0.8 ± 0.1^{A}	1.3 ± 0.2^{B}	1.6 ± 0.2^{B}	0.3 ± 0.2^{A}	0.4 ± 0.3^{A}	1.1 ± 0.2^{B}
Center chest	0.7 ± 0.2	1.2 ± 0.2	1.1 ± 0.2	0.8 ± 0.1	1.0 ± 0.2	1.2 ± 0.2	0.3 ± 0.2	0.4 ± 0.3	1.1 ± 0.3
Side chest	0.8 ± 0.2	1.1 ± 0.1	0.7 ± 0.2	0.8 ± 0.2	0.5 ± 0.1^{A}	1.0 ± 0.1^{B}	0.5 ± 0.2	1.0 ± 0.1	0.4 ± 0.2
Sides	1.6 ± 0.1	1.8 ± 0.1	1.6 ± 0.1	1.5 ± 0.2	1.5 ± 0.2	1.7 ± 0.1	1.5 ± 0.2^{A}	1.0 ± 0.3^{B}	1.8 ± 0.2^{A}
Flanks	1.7 ± 0.1	1.9 ± 0.1	1.8 ± 0.1	1.8 ± 0.1	1.9 ± 0.1	1.7 ± 0.1	1.8 ± 0.2^{A}	1.1 ± 0.2^{B}	2.0 ± 0.0^{A}
Primaries	0.2 ± 0.1	0.1 ± 0.1	0.6 ± 0.3	0.3 ± 0.1^{A}	0.0 ± 0.0^{B}	1.8 ± 0.2^{C}	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0
Secondaries	0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.0 ± 0.0^{A}	0.4 ± 0.2^{B}	0.0 ± 0.0	0.4 ± 0.2	0.0 ± 0.0
Tertials	0.9 ± 0.1^{A}	1.4 ± 0.2^{B}	1.6 ± 0.2^{B}	1.3 ± 0.1	1.2 ± 0.2^{A}	2.0 ± 0.0^{B}	1.0 ± 0.4	1.1 ± 0.3	1.8 ± 0.2
Wing coverts	0.7 ± 0.2	0.6 ± 0.2	0.9 ± 0.2	1.2 ± 0.2^{A}	0.5 ± 0.2^{B}	1.5 ± 0.2^{C}	0.8 ± 0.3^{A}	0.3 ± 0.2^{B}	1.4 ± 0.3^{C}
n	19	16	14	15	15	21	6	8	8

[a] Row values with different superscripts within age/sex categories are significantly different ($P < 0.05$).

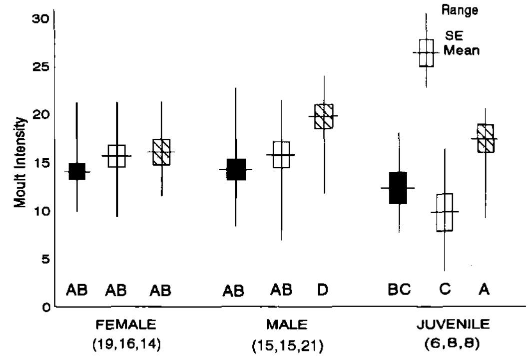

FIG. 1. Molt-intensity scores of adult and juvenile White-faced Whistling-Ducks collected in early winter (solid rectangle), late winter (open rectangle), and spring (hatched rectangle) in northern KwaZulu-Natal, South Africa, 1995. Sample sizes are in parentheses. Means not sharing the same letter are statistically different ($P < 0.05$).

tween early and late winter, and they had similar MIS scores at that time (all Ps > 0.05; Fig. 1). Molt intensity in the facial, belly, and tertial regions of females and the rectrices and belly regions of males increased from early to late winter (Table 1). Intensity of wing-covert molt in males declined between early and late winter, and no individuals collected during late winter were molting remiges (Table 1). Only one female was replacing primaries and secondaries during late winter. The only late winter sexual difference in molt was a higher intensity in the side-chest area in females ($P = 0.01$). The mean number of actively molting feather areas did not differ between early and late winter in males or females (Ps > 0.05; Table 1).

Whereas MIS in juveniles was similar in late and early winter ($U = 28.5$, $P = 0.56$; Fig. 1), molt intensity in the undertail covert, side, flank, and wing-covert areas declined between early and late winter, and primary replacement ceased during this time. Juveniles had a lower MIS than did adults during late winter ($U = 204.0$, $P = 0.005$), which can be attributed to molting in fewer feather areas during this time ($P = 0.03$; Table 1). Molt intensity in the facial and side-chest areas was lower in juveniles than in adult females ($P < 0.05$), and molt intensity in the rump, uppertail covert, undertail covert, belly, center-chest, side, and flank areas was lower in juveniles than in both adult males and adult females ($P < 0.05$).

Molt intensity in adult females was similar in all feather areas during late winter and spring ($P > 0.05$), resulting in no change in MIS between early winter, late winter, or spring (Kruskal-Wallis test, $H = 5.51$, $P = 0.06$). In contrast, MIS in males increased between late winter and spring ($U = 61.5$, $P = 0.002$) due to higher intensity in the crown, upper-back, undertail coverts, side-chest, primary, secondary, tertial, and wing-covert areas (Table 1). Males molted with greater intensity than females in the neck, upper-back, undertail, belly, tertial, and wing-covert feather areas, resulting in a higher MIS during spring ($U = 68.5$, $P = 0.008$). Males and females molted in the same number of feather areas in spring as in late winter ($P > 0.05$; Table 1). Among birds collected in spring, 29% of the females and 38% of the males were in later stages of remigial molt. Although juveniles collected in spring had completed primary and secondary growth, the mean number of actively molting feather areas was higher in spring than during late winter ($P = 0.02$), and molt intensity increased in all other feather areas (Table 1). This resulted in a higher MIS during spring ($U = 49.7$, $P = 0.007$). The MIS of juveniles was similar to that of adult females during spring ($U = 46.5$, $P = 0.52$), and molt intensity did not differ significantly among feather areas in juveniles (all Ps > 0.05). MIS was slightly lower in juveniles than in adult males ($U = 42.5$, $P = 0.04$), as was molt intensity in the primaries ($U = 52.0$, $P = 0.04$).

Discussion.—Although White-faced Whistling-Ducks have been documented to replace their remiges on breeding areas after nesting (Petrie 1998), 10% of adults collected in early winter, 3% in late winter, and 34% in spring were in later stages of remigial molt. Egyptian Geese (*Alopochen aegyptiacus*), Cape Shovelers (*Anas smithii*), Yellow-billed Ducks (*Anas undulata*), and Southern Pochards (*Netta erythrophthalma*; Dean 1978) apparently do not have distinct periods of remigial replacement in South Africa. This may be due to inherent individual variation in timing of the flightless period (Dean 1978). However, the onset of remigial replacement is strongly influenced by the timing and duration of reproduction in waterfowl (Gilmer et al. 1977, Klint 1982, Wishart 1985, Austin and Fredrickson 1986, Leafloor 1989). Therefore, the extreme variation in spatial and temporal availability of suitable breeding and molting habitat in southern Africa probably are important constraints on the timing of replacement of the remiges, ultimately causing seasonal and geographic variation in this molt. Evidence for this is provided by the facts that breeding and molt of the remiges generally are mutually exclusive events in the Anatidae, and that waterfowl that breed in xeric environments nest in more months of the year than do ducks in nonarid zones (Bellrose 1976, Briggs 1992, Harrison et al. 1997). Egg-laying White-faced Whistling-Ducks have been collected on and adjacent to the Nyl River floodplain in South Africa during every month between October and February (S.A. Petrie unpubl. data).

The prebasic molt of White-faced Whistling-Ducks extends throughout the nonbreeding season (Table 1), and with the exception of a near suspension during laying and incubation, these ducks also molt on their breeding areas (Petrie 1998). Thus, the prebasic molt of White-faced Whistling-Ducks essentially is a continuous annual-cycle event. Canada Geese (*Branta canadensis interior*) also extend their single annual molt over most of the annual cycle (Gates et al. 1993). In contrast, sexually dichromatic species, which replace their contour feathers twice during the annual cycle, complete molt in a shorter period of time. For example, female Mallards (*Anas platyrhynchos*) complete their prebasic molt in as little as six to seven weeks (Heitmeyer 1987). Being monogamous and having retained the ancestral pattern of one molt per cycle, White-faced Whistling-Ducks and Canada Geese are not constrained by the acquisition of a particular feather generation (i.e. alternate or basic) before pair-bond formation or remigial replacement, thereby permitting the temporal extension of the prebasic molt.

Rapid feather replacement can impose high protein demands (Payne 1972, Kendeigh et al. 1977, King 1980, Heitmeyer 1988) because birds have limited capabilities to store protein, and they catabolize labile protein for feather synthesis inefficiently (Blem 1990). Consequently, birds typically obtain protein and sulphur amino acids required for feather synthesis directly from their diet (e.g. Raveling 1979, Ankney 1979, 1984, Young and Boag 1982, Heitmeyer 1985, Mainguy and Thomas 1985). However, the diet of White-faced Whistling-Ducks is low in protein and in several essential amino acids (Petrie 1998, Petrie and Rogers 1996). Therefore, molt prolongation probably is a nutritional tactic to spread the demands of feather replacement throughout the annual cycle, because it would be difficult for White-faced Whistling-Ducks to satisfy the nutritional demands of rapid feather replacement given the protein content of their diet (see Heitmeyer 1988). Whereas monogamy and the retention of a single annual molt would permit the temporal extension of molt, herbivory may necessitate it.

Ducks with seasonal pair bonds and a large difference between the sexes in reproductive costs generally exhibit distinct sexual differences in molt intensity and chronology over the annual cycle (Wishart 1985, Miller 1986, Hohman et al. 1992, Smith and Sheeley 1993, Hohman and Crawford 1995). Adult male and female White-faced Whistling-Ducks have similar molt patterns throughout the winter and spring (Table 1, Fig. 1) and also exhibit parallels in molt chronology while on breeding areas (Petrie 1998). Perennial pair bonds, biparental care, and the retention of the ancestral pattern of one molt per annual cycle, apparently impose similar environmental, behavioral, and energetic constraints on male and female White-faced Whistling-Ducks (Petrie 1998). Therefore, similar intersexual molt patterns may be the result of similar selection pressures throughout the annual cycle.

Juvenile White-faced Whistling-Ducks also molted throughout winter and spring, but slightly less intensively than did adults during early and late winter (Fig. 1). Juvenile White-faced Whistling-Ducks collected on the Nyl River floodplain in South Africa also were molting less intensively than were postbreeding adults collected concurrently (Petrie 1998). Juveniles probably apportion nutrients and energy to continue body growth during winter; therefore, lower molt intensities may minimize concurrent nutritional demands. By spring, juveniles may be released from nutrient demands of growth, because molt intensity of all contour feather areas was higher (Table 1) and similar to that of adults during this period.

Research and management considerations.—Research by waterfowl biologists has focused on species that breed in north-temperate and arctic regions (Petrie 1996). This has resulted in the development of many widely held biological tenets that do not necessarily pertain to species occurring outside of these regions. Therefore, we need to develop a better understanding of the ecology of waterfowl that breed in semiarid and arid regions, particularly with respect to the extreme spatiotemporal variation in the availability of habitats and foods. For instance, the effects of spatial and temporal variation in the availability of wintering and breeding habitats on season and geographic location of remigial molt should be investigated. To better understand the influence of phylogenetic and environmental constraints on molt in semiarid waterfowl, a comparative study of species with one versus two molts per annual cycle is required. White-faced Whistling-Ducks spend large portions of the day and night foraging for native aquatic seeds throughout the winter and spring in northern KwaZulu-Natal (Petrie and Petrie 1998). Anthropogenic disturbances can decrease the carrying capacity of a habitat or region by reducing the amount of time that birds have to feed, or by preventing birds from foraging in preferred areas (Owens 1977, Bell and Owen 1989). The situation is probably particularly critical for flightless waterfowl. Consequently, the effects of human disturbance on preferred molting areas should be evaluated, and recreational access and hunting in these areas should be regulated throughout the winter.

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Metabolic Rate, Temperature Regulation, and the Energetic Implications of Roost Nests in the Bananaquit (*Coereba flaveola*)

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Many factors can influence avian metabolic rates, including ambient temperature (T_a), time of day, season, climate, and phylogenetic relationships (e.g. Lasiewski and Dawson 1967, Zar 1968, Ligon 1969, Aschoff and Pohl 1970a, b, Kendeigh and Blem 1974, Kendeigh et al. 1977, Weathers 1979, Bennett 1988). Of all the various parameters associated with basal levels of energy expenditure, perhaps the most important is body size. This relationship has been the subject of extensive research, resulting in the production of standard allometric equations that predict avian basal metabolic rate based on body mass (Brody and Proctor 1932, King and Farner 1961, Aschoff and Pohl 1970a, b, Kendeigh et al. 1977, Bennett and Harvey 1987). Most avian physiological studies, however, including those that provided the data for the allometric equations, have concentrated on birds from the temperate zone (e.g. Lasiewski and Dawson 1967,

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