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Geographic variation in factors that influence timing of moult and breeding in waterfowl

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ABSTRACT

Waterfowl flight-feather moult is expected to occur when energy is not needed for breeding and when a suitable safe habitat is available. Flight-feather regrowth is an energetically costly stage in the annual cycle of waterfowls. In this study, we tested the hypothesis that moult will coincide with the time of year when food and aquatic habitats are most abundant. We investigated how the timing of rainfall relates to the timing of breeding and flight-feather moult in five common southern African waterfowl at two sites in South Africa with opposite rainfall regimes (one summer, one winter). We then incorporated published data to compare and contrast the relative timing of breeding and moult in southern hemisphere (southern African and Australian) waterfowl with northern hemisphere (European and North American) species. Our results showed that southern African waterfowl breed in the wet season and moult during the dry season. *Tadorna cana* was an exception, breeding in the dry season and moulting during the wet season in the summer-rainfall area. There was also a long lag period between peak breeding and peak moult in southern hemisphere waterfowl species, the longest lag being that of birds in the summer-rainfall area. By comparison, northern hemisphere waterfowl species breed and moult during the warm season, with a shorter lag period between peak breeding and peak moult compared to southern hemisphere species. We concluded that waterfowl in southern Africa (with the exception of *T. cana*), southeast Australia, Europe and North America time their breeding period to coincide with peaks in the availability of both food and breeding sites. Northern hemisphere species moult where chances of predation are low, when temperatures are warm, and before food and aquatic habitats approach their winter minima. By contrast, southern hemisphere waterfowl delay the onset of moult until the dry season, opting to moult when both food and aquatic moulting habitats are scarce.

1. Introduction

Waterfowl have evolved to survive in diverse environments with different spatio-temporal variability in climatic conditions (Owen and Black, 1990; Baldwin and Lovvorn, 1994). A significant amount of research has been dedicated to understanding how environmental factors influence the timing of reproduction and migration in north-temperate waterfowl. Moult, however, as a key component of the annual cycle, has been less well studied, especially in southern hemisphere waterfowl (Owen and Black, 1990). The risks of predation and starvation are significant for a duck during its flightless moult (Geldenhuys, 1981a; Baldassarre and Bolen, 2006). As a result, moulting ducks require habitats with sufficient food, and extent and depth of water to last for the duration of flight-feather moult. For this reason, flight-feather moult (termed 'moult' from here on) may be a potential bottleneck in the life histories of waterfowl and may be a key life-history stage around which other life-history events are scheduled.

Moult in waterfowl is expected to occur when energy is not needed for other life-history stages, particularly long-distance movements and reproduction, and when a safe moulting habitat and food are available simultaneously (Owen and Cook, 1977; Holmgren and Hedenström, 1995). The few studies that test these expectations are biased towards northern hemisphere species and show close links between the end of breeding (when young are independent) and the onset of moult (Joensen, 1973; Mathiasson, 1974; Dean, 1978; Geldenhuys, 1981a; Austin and Fredrickson,

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1986; Lovvorn and Barzen, 1988; Vrtiska et al., 1997; Kear, 2005). The availability of habitat and food in north-temperate and Arctic regions is determined primarily by large and highly predictable seasonal variations in temperature and day length. North-temperate waterfowl time their reproduction and moult stages to exploit this brief warm season (Wingfield et al., 1992; Svensson, 1995; Piersma and Drent, 2003; Bêty et al., 2004). In contrast, environmental conditions (both seasonal and annual) in the semi-arid regions of the southern hemisphere are regulated primarily by rainfall that is highly variable in space and time (Tyson and Preston-Whyte, 2000), leading to greater environmental unpredictability than birds experience at high northern latitudes. Because the availability of habitat and food for waterfowl in semi-arid regions is determined ultimately by such rainfall events, there is substantial spatio-temporal variability in the availability of suitable habitat and food resources for both reproduction and moult (Siegfried, 1974). Given this stochasticity, southern hemisphere waterfowl (especially those in semi-arid regions of South Africa and Australia) may use a variety of environmental cues to fine-tune their breeding and moult 'timetables' (Herremans, 1999; Herrmann et al., 2004).

In the southern hemisphere, rainfall influences the availability of (i) food resources prior to moult (which are essential to ensure birds commence flight-feather moult in good condition); and (ii) adequate water at wetlands that are suitable moult sites (Herrmann et al., 2004). The hypothesis that rainfall controls the timing of moult is not new (Geldenhuys, 1981a), but to date has not been tested rigorously because of a lack of data on the seasonality of moult in most species, and especially its degree of synchrony.

In the present study, we tested the hypothesis that moult will coincide with the time of year when food and water bodies are most abundant (Owen and Cook, 1977; Holmgren and Hedenström, 1995). An alternative hypothesis predicts that reproduction is more energetically costly than moult (Baldassarre and Bolen, 2006) and hence the timing of breeding coincides with peak abundance of food and aquatic habitat. Moult is then expected to follow soon after breeding (Joensen, 1973; Mathiasson, 1974; Dean, 1978; Geldenhuys, 1981a; Austin and Fredrickson, 1986; Lovvorn and Barzen, 1988; Vrtiska et al., 1997; Kear, 2005) and the two life-history stages are not expected to overlap, because flightless moult severely impairs mobility and hence the ability of the adults to care for young.

The objectives of the study were to:

(a) Determine the timing of moult in five common duck species, namely Egyptian goose (*Alopochen aegyptiaca*), spur-winged goose (*Plectropterus gambensis*), South African shelduck (*Tadorna cana*), yellow-billed duck (*Anas undulata*) and red-billed teal (*Anas erythrorhyncha*) at two sites in South Africa with contrasting rainfall regimes (one summer, one winter).
(b) Investigate how the timing of rainfall relates to the timing of breeding and moult in these five species.
(c) Compare the relative timing of breeding and moult in southern hemisphere (southern African and Australian) waterfowl with northern hemisphere (European and North American) species.

2. Materials and methods

2.1. Data collection in southern Africa

Timing of moult in southern African waterfowl was studied between February 2007 and April 2010 at Barberspan Nature Reserve (26°33′ S, 25°37′ E) in the North-West Province and Strandfontein Wastewater Treatment Works (34°05′ S, 18°32′ E) in the Western Cape Province, South Africa.

Barberspan Nature Reserve is a shallow, perennial, alkaline pan connected to the Harts River in the semi-arid, summer-rainfall region of South Africa. When full, the pan covers an area of about 1700 ha, but water levels fall substantially during late winter, at which time the pan can shrink to 1300 ha. Surrounding natural habitats are mainly gently undulating and flat, comprising short to very short grasslands interspersed with mixed acacia trees (Mucina et al., 2006). Woody species are sparse and consist mainly of *Acacia karoo*, *A. erioloba*, *Celtis africana* and *Rhus lancea*. There are also surrounding farmlands used mainly for maize and sunflower cultivation. Large numbers of waterfowl and waders use the pan for foraging, breeding, roosting and moulting (Milstein, 1975; Taylor et al., 1999). Barberspan is a Ramsar-designated site, this designation being based in part on the site's waterbird populations.

Strandfontein Wastewater Treatment Works is situated in the winter-rainfall region adjacent to the coast. The site comprises 319 ha of open permanent ponds and canals, some with sandy islands, and 58 ha of terrestrial habitats, much of which is covered with grass. Other vegetation in the area includes exotic *Acacia cyclops* thickets, and patches of *Typha*, *Phragmites* and *Scirpus* spp. (Kaletja-Summers et al., 2001). The site is hydrologically managed and some ponds have open mudflats that serve as roosting sites for waterfowl and feeding grounds for waders.

Given that our study sites were approximately 1000 km apart it was financially and logistically challenging for us to sample both sites every month. Bi-monthly counts of waterfowl were made at both study areas for the duration of the study, with each sampling session lasting 5 days (see below). 13 accessible permanent sampling points (at least 500 m apart) were selected along the shoreline at each of the study sites and marked for repeated sampling and monitoring purposes. Sampling points were approached by an observer in a vehicle. Moulters (moulting birds that ran into the water and swam away using the characteristic 'paddle fluttering' wing action of flightless anatids; Dean, 1978) and non-moulters were counted within a 150 m radius semi-circle from the sampling point using 10 × 42 binoculars. Counting at sampling sites was performed randomly over the 5-day census period. 52 counts were obtained for each study site per sampling interval, with each of the 13 sampling points being counted once a day, four times in 5 days, and at different times of the day. The total number of moulters and of non-moulters from all 52 counts was then computed to obtain a mean abundance per hectare for moulters and non-moulters of each species at each study site at each visit.

After the 5 days of counting, a further 5–8 days were dedicated to trapping. Blood samples were taken from moulting birds to determine their sex (Griffiths et al., 1998). This sampling process further validated the presence of moulting birds that were counted during the census period. However, trapping was not used to validate the ratios of moulters to non-moulters.

We recorded incidents of breeding at each site during the study period but our sample size was too small for all species other than Egyptian geese because most waterfowl rarely bred at either study site. We therefore used breeding period records for Barberspan and Strandfontein (or from areas nearby in cases where breeding data were lacking) compiled by Hockey et al. (2005) and a local bird club (Cape Bird Club) to supplement our breeding data.

We also referred to telemetry data (Cumming et al., 2012; Ndlovu et al., 2013), and the monthly bird counts of the Cape Bird Club (http://www.capebirdclub.org.za/counts-strandfontein) and Barberspan Nature Reserve to validate moult and breeding incidents for months in between our bi-monthly sampling periods.

Decadal rainfall-estimate satellite images were downloaded for the period starting 1 June 2006 until 30 April 2010 from the United States Geological Survey (USGS) Africa Data Dissemination Service website (http://earlywarning.usgs.gov/fews/ – accessed in 2010). These images were taken by NASA (National Aeronautics