Moult as a dynamic link in the annual cycle of birds: insights from seabirds and a long-distance migratory raptor

Oluwadunsin E. Adekola

Thesis Presented for the degree of
DOCTOR OF PHILOSOPHY
FitzPatrick Institute of African Ornithology, DSI-NRF Centre of Excellence,
Department of Biological Sciences, Faculty of Science,
UNIVERSITY OF CAPE TOWN

May 2022

Supervisor: Prof. Peter G. Ryan

May 2022

DECLARATIONS

This thesis reports original research that I conducted while enrolled as a PhD student at the FitzPatrick Institute of African Ornithology, Department of Biological Sciences, Faculty of Science, University of Cape Town, South Africa. All assistance received has been fully acknowledged. This work has not been submitted in any form for a degree at another university.

I know the meaning of plagiarism and hereby declare that all the work in this thesis except for those properly acknowledged are authentic research work carried out by me. I have followed all the guidelines for preparing a thesis and now presenting it for examination for the award of Doctor of Philosophy.

Signed by candidate

……………………………

Oluwadunsin E. Adekola

May 2022

CONFERENCE PRESENTATIONS

- **Oluwadunsin E. Adekola**, David G. Allan, Zephne Bernitz, Wiseman Dlungwana and Peter G. Ryan. *Extent and symmetry of tail moult in Amur Falcons.* 12th Asian Raptor Research and Conservation Network Symposium, Malaysia (presented remotely). January 2022
- **Oluwadunsin E. Adekola**, Robert J. M. Crawford, Bruce M. Dyer, Azwianewi B. Makhado, Leshia Uphold and Peter G. Ryan. *Timing, duration and symmetry of moult in Cape Gannets.* 3rd World Seabird Conference, Hobart (presented remotely). October 2021
- **Oluwadunsin E. Adekola**, David G. Allan, Zephne Bernitz, Wiseman Dlungwana and Peter G. Ryan. *Extent and symmetry of tail moult in Amur Falcons.* African Bird Fair, South Africa. July 2021
- **Oluwadunsin E. Adekola**, Robert J. M. Crawford, Bruce M. Dyer, Azwianewi B. Makhado, Leshia Uphold and Peter G. Ryan. *Timing, duration and symmetry of moult in Cape Gannets.* LAB (Learn About Birds) Conference, co-hosted by BirdLife South Africa and the FitzPatrick Institute of African Ornithology, South Africa. May 2021
- **Oluwadunsin E. Adekola**, Robert J. M. Crawford, Bruce M. Dyer, Azwianewi B. Makhado, Leshia Uphold and Peter G. Ryan. *Patterns of moulting in the Cape Gannet.* World Seabird Twitter Conference. April 2019

PUBLICATIONS ARISING FROM THE THESIS

Two chapters in this thesis have already been published (Chapters 3 and 6). The two have been edited from the published version to ensure consistency with the rest of the thesis. The two are multi-author papers; here I explain the contributions of the various authors.

- **Oluwadunsin E. Adekola**, Robert J. M. Crawford, Bruce M. Dyer, Azwianewi B. Makhado, Leshia Uphold and Peter G. Ryan (2021a). Timing, duration and symmetry of moult in Cape Gannets. *Ostrich: African Journal of Ornithology* 92: 1-12 https://doi.org/10.2989/00306525.2021.1988745.

  The data published in this paper are presented in Chapter 3. I collected all data in 2018-2019, analysed all the data, drafted the manuscript, and responded to the reviewers' comments. BMD and LU were involved in data collection (from 2002-2004), under the direction of RJMC. RJMC and ABM reviewed the manuscript. PGR supervised the project and helped to revise the manuscript.
- **Oluwadunsin E. Adekola**, David G. Allan, Zephne Bernitz, Wiseman Dlungwana and Peter G. Ryan (2021b). Extent and symmetry of tail moult in Amur Falcons. *Journal of Ornithology* 162: 655-667 https://doi.org/10.1007/s10336-021-01874-0.

  The data published in this paper are presented in Chapter 6. I led the team collecting the moult data, together with DGA, ZB and PGR; WD made all measurements of the falcons to ensure consistency. I analysed all the data, drafted the manuscript, and responded to the reviewers' comments. DGA, BZ and WD were involved in data collection. PGR was involved in conceptualization, data collection, data analysis, manuscript writing and supervision. DGA and BZ also reviewed the draft manuscript.

My supervisor has attested that I was principal in design and data analyses of the research toward publishing the articles and that I independently wrote the manuscripts with his support in form of comments and suggestions (see Supplemental Material 8).

DEDICATION

This thesis is dedicated to:

the Almighty God, for always been my source of wisdom and strength.
my late Dad, Jacob Adekola who gave all for me and my siblings.
my mum, Grace Adekola, who is the best mum on earth.
my siblings, Esther, Toluwalope, Samuel and Mary.
Temitope Adekola, I will never forget you.
my wife, Oluwakemi Adekola.

ACKNOWLEDGEMENTS

Foremost, I wish to express my profound and sincere appreciation to my wonderful and intelligent supervisor, Prof. Peter Ryan, for his support, guidance and encouragement throughout this PhD journey. Despite your extremely busy schedule, you always found the time to provide constructive and meaningful feedback on my “many” drafts. When I felt overwhelmed and confused about my work, you provided solace and assurance that I needed. I have learnt so much from you. Thank you so much for your patience in guiding me to become a better researcher.

To my awesome family: my amazing mum, Grace Adekola and my caring siblings (Esther, Tolulope, Samuel and Mary Adekola), I honestly could not have done this without your support and prayers. I left Nigeria for South Africa when you needed me most. Thank you for allowing me to pursue my dream despite the challenges we had as a family. Thank you for your understanding, patience and unrelenting support throughout this PhD journey (despite the fact that I could not visit Nigeria throughout this phase).

To my loving wife, Oluwakemi (Ifemi), you have sacrificed immensely and at the same time you have been a pillar of support and strength to me. You stood with me throughout this journey as we talk literally every day and you never got fed-up listening to my jokes. Thank you for your understanding. I look forward to spending the rest of my life with you.

Thanks to Prof. Rob Crawford, Dr Azwianewi Makhado and Leshia Uphold from South Africa’s Department of Forestry, Fisheries and Environment for providing some of the gannet moult data presented in Chapter 3. I especially thank Bruce Dyer for times spent together at Malgas Island and teaching me how the island works (most importantly, how to catch a gannet).

I also thank David Allan from Durban Natural Science Museum and the staff of FreeMe KwaZulu-Natal Wildlife Rehabilitation Centre for making the Amur Falcon carcasses available (Chapters 2 and 6). Thanks also to Zephne Bernitz and Wiseman Dlungwana for help with scoring moult and taking morphometrics from falcons.

Thanks to the fishery observers and BirdLife’s Albatross Task Force who kindly supplied carcasses of gannets, petrels and albatrosses killed by fishing operations. I also thank John Graham who provided images of White-chinned Petrels in flight.

To Wilmari Uys and Adeyemi Daniel Adetimehin, thanks for helping with feather microstructural measurements.

I am grateful to the staff and colleagues at the FitzPatrick Institute of African Ornithology for their support and encouragement. The Fitz is really a home away from home!

To Dr Marc Burman and Dr Birgit Erni for help with statistics, and especially on how to use the moult package in R, at the initial stage of my research, I say thank you.

Pastor Taiwo and Dr (Mrs) Omoyemi Ola-Omole, Pastor (Dr) Temitope and Bukola Egbebiyi, Pastor (Dr) Gbenga Ajayi, Daddy and mummy Oke, thank you for your prayers and encouragements.

Prof. Ulf Ottosson, Dr Temidayo Osinubi, Dr Chima Nwaogu, Joshua and Dr (Mrs) Bukola Azaki: thank you for your advice.

Staff of Ecotourism and Wildlife Management Department, Federal University of Technology, Akure, Nigeria: thank you for your support.

To my friends, both near and far: Adeyemi Daniel Adetimehin, Victor Rotimi Oladugba, Abidemi Raji, Eniola Olarewaju, Adeola Ayoola, Ebenezer Ofuya, Olufemi Olubodun, Timothy Aikins, Glory Oden and Desiree Moodley: thank you for always being there.

This project would not have been possible without the financial and logistical support of the South African National Research Foundation (NRF), FitzPatrick Institute of African Ornithology, UCT International Scholarships for Postgraduate Students, South Africa’s Department of Forestry, Fisheries and Environment, Idea Wild and AGNES-Bayer Foundation and with the support of the Alexander von Humboldt Foundation (AvH).

In writing this thesis, I have used the word ‘I’ liberally to describe ‘my’ undertakings and findings. In truth, this work could not have been completed without the active involvement of numerous people and institutions. Every time I use the word ‘I’ in the pages of this thesis, it is used in the most global of senses and should be understood as acknowledging the fundamental contribution of the people listed above.

TABLE OF CONTENTS

SUMMARY

Moult is one of three major and costly events in the annual cycle of birds, alongside breeding and migration. Unlike breeding and migration, moult is indispensable, and its patterns vary considerably among species. Despite the importance of moult, it has been relatively less studied than breeding or migration. Moult can evolve rapidly in response to environmental changes and may make substantial demands on endogenous metabolism. Moult represents perhaps the single highest cost of maintenance for birds and requires a major allocation of resources. The study of moult has important consequences for understanding bird biology and conservation. Knowledge of moult is central to understanding life-history trade-offs in birds and to predict the consequences of global change. To date, most moult studies mainly focus on primaries, but it is important to understand other feather tracts, such as the secondaries, which can exceed primaries in number, total length and mass in long-winged birds.

Feather replacement is more challenging for large birds than small birds, due to the time required to grow their long wing feathers. In this thesis, I explore how different birds balance moult with other aspects of their annual cycles. In particular, I assess how large, long-winged birds manage to replace their large number of secondaries. I also explore whether nestlings grow flight feathers of equal quality as adults in a long-distance migratory raptor. The study of feather quality in birds is still in its infancy, but the few studies to date indicate that chicks compromise feather quality to minimise their nestling period. In addition, few studies have explored how moult strategies are influenced by differences in food availability or habitat quality. To explore these questions, I describe moult strategies in three seabird species (Cape Gannet *Morus capensis,* White-chinned Petrel *Procellaria aequinoctialis* and White-capped/Shy Albatrosses *Thalassarche steadi/cauta*) and a long-distant migratory raptor (Amur Falcon *Falco amurensis*). My choice of study species was driven principally by the

large data sets available for them. I also explore structural variations of flight feathers and primary coverts in 100 non-moulting Amur Falcons.

There are seven chapters including an introductory first chapter. In Chapter 1, I introduce the importance of feathers and why maintaining their quality is key to birds' survival. Feathers are dead structures once formed, and have to be replaced regularly. However, this replacement is costly. Using relevant literature, I summarize moult in seabirds and raptors. I also give the rationale, knowledge contribution and outline of the thesis.

In Chapter 2, I compare the structure of flight feathers and primary coverts of non-moulting Amur Falcons of known age and sex. Adults had longer and relatively heavier feathers than juveniles, but other microstructural measurements did not differ between ages or sexes. Adults and juveniles had similar calamus length across primaries, secondaries, rectrices and primary coverts. However, juvenile primaries, secondaries and rectrices had a shorter rachis than adults. There were no age-related differences among primary coverts. There were no age-related differences among primary coverts. Body condition was higher in females than males in both adults and juveniles. In general, adults and juveniles with better body condition tended to have longer and heavier feathers, with limited variations across feather tracts, suggesting that feather traits could be used as reliable indicators of a bird's health. Contrary to previous studies that growing feathers fast reduces their quality, my results suggest that juvenile Amur Falcons manage to grow quality flight feathers in terms of microstructure even though they fledge in about one month, and they do not appear to wear faster than adult flight feathers.

In Chapter 3, I show that moult duration and symmetry, but not timing, differ between two breeding colonies of Cape Gannets in South Africa. My results suggest that moult may be used as an index of condition. Primary moult is protracted, with multiple active centres and up to five primaries growing at the same time. Secondary moult commences after primary moult has started and proceeds from two nodal points, growing more feathers simultaneously than primaries. Tail moult also overlaps with that of the primaries, with multiple active centres and up to eight rectrices growing at once. I suggest that differences in moult duration and perhaps asymmetry between breeding colonies may be linked to foraging conditions, given that gannets breeding at Lambert's Bay are under greater food stress than those breeding on Malgas Island.

In Chapter 4, I describe patterns of wing and tail moult in White-chinned Petrels and assess whether flight activity is reduced during the period of most intense wing moult. White-chinned Petrels exhibit a simple descendent primary moult, with age- and sex-related differences in the timing of moult. Secondary moult is extensive and commenced after 3–4 primaries had been dropped, typically progressing from three nodal sites. Photographs of non-moulting birds at sea confirm that some White-chinned Petrels do not replace all secondaries each year. Tail moult usually commences with the start of secondary moult and is highly variable, with 1–12 rectrices growing at once. Unlike many smaller petrels, there is little evidence that adults reduce the time spent flying while moulting, despite the intense nature of wing and tail moult.

In Chapter 5, I show that despite being on their non-breeding grounds, there was low proportion of moulting White-capped/Shy Albatrosses. Although a few birds exhibited intense moult, replacing up to six primaries and 14 secondaries at once, the norm was for replacing only 1-2 primaries (mean ± SD, 1.9 ± 1.2), and 2-6 secondaries (3.9 ± 3.0) at once, which is surprising given the expectation that large, long-winged birds should be under time pressure to complete their moults. This occurs as adults typically take a year off between successful breeding attempts, seemingly allowing time for a more protracted moult. Secondary moult overlaps with primary moult and progresses from three nodal sites: first dropping the innermost five to eight secondaries, followed by the outermost four secondaries and almost simultaneously with S16–S22 and S4–S7, ending with the middle secondaries (although not all moulted each year). Tail moult commences at the start of primary moult, with multiple active centres (2.7 ± 1.6; 1–6) and 3.8 ± 2.9 feathers growing at the same time (range 1–11). Most birds replaced their rectrices in pairs, starting from the central feathers, but some birds replaced alternate feathers, or replaced almost all rectrices at once. Age and sex differences in moult intensity may be due to time constraints. The low proportion of moulting birds on their non-breeding grounds might suggests that moult in White-capped Albatrosses is more constrained during the non-breeding period in southern African waters.

In Chapter 6, I present the results of extent and symmetry of moult in a long-distance migratory raptor, the Amur Falcon, killed by hailstorms at its roosts in South Africa during March. By this time of year, most adults have completed replacing their remiges, with only a few still growing 1–3 feathers (mainly secondaries), but most are still growing their tail feathers. Moult typically is distal from the central rectrices, but 25% of adults and 1% of juveniles replace the outer tail first, and a few individuals exhibit other moult patterns (simultaneous moult across the tail, or among the inner and outer feathers). These different moult strategies are independent of sex. Adults that replace the outer tail first typically have replaced a greater proportion of the rectrices than adults starting from the central tail. The extent of tail moult is correlated with body condition in adults and juveniles, suggesting that moult pattern might be used as an indicator of fitness in falcons.

Finally, in the thesis synthesis (Chapter 7), I summarise the main results from the previous chapters. I also explore the relative impact of secondary moult in terms of loss of wing area in 102 bird species, ranging from small passerines to seabirds, raptors, waterfowl and other large birds. I measure the proportion of total wing area accounted for by the secondaries projecting beyond the greater secondary coverts across the different bird species to show that seabirds (apart from cormorants, Phalacrocoracidae) have less secondary area than most other groups of birds. I also show that secondary wing area is less in long-winged birds. The

significant positive correlation between proportion of secondary area and body mass indicates that secondary area scales allometrically. I propose that the relatively small secondary area not covered by greater coverts in long-winged seabirds allows these species to replace large numbers of secondaries at once. At least in petrels and some gulls, this adaptation is facilitated by the near-simultaneous replacement of most greater secondary coverts at the start of primary moult, so the secondary coverts are already replaced once secondary moult starts.

CHAPTER 1

General introduction: moult as a dynamic link in the annual cycle of birds

Plumage structure, function and quality

Feathers are a unique characteristic of birds (Chen et al. 2015) and their ancestors, the two-legged theropods dinosaurs (Norell and Xu 2005), although they also have been reported in pterosaurs (Cincotta et al. 2022). Feathers cover almost the entire surface of the body and allow birds to exploit many niches through their varied functions (Ginn and Melville 2007; Bodde et al. 2011). Birds use feathers for flight, insulation, display, camouflage, protection and waterproofing. There are three main feather types: flight feathers (remiges and rectrices), body contour feathers (wing coverts, external layer of body feathers) and down feathers (proximal layer of body feathers). The first two classes of feathers have at least some pennaceous feather parts (planar feather vanes with barbs interlocked), whereas down feathers are fully plumulaceous (Prum 1999). Flight feathers function in propulsion, lift and manoeuvring; body contour feathers in streamlining, protection, camouflage, communication and insulation; and down feathers in insulation (Ginn and Melville 2007). To achieve their complex functions, feathers have evolved a variety of shapes, sizes and structures (Stettenheim 2000). Feathers are light, flexible and strong to withstanding the aerodynamic force to which they are exposed (Videler 2005; Pennycuick 2008).

Despite their many useful properties, feathers are dead structures once formed, and start to degrade through the combined impact of ultraviolet radiation, parasites and mechanical abrasion (Moreno-Rueda 2017). Old, worn feathers might not adequately insulate, fly, or signal, etc. (Achache et al. 2018). Body feather loss (Clayton 1990) could impair heat conservation capacity and consequently increase energy expenditure (Booth et al. 1993) and raise predation risk (Carr and Lima 2012). Cost of loss or altered feather structure might also result in less colourful sexual ornaments (Shawkey and Hill 2005; Griggio et al. 2009; Galván 2011). As a result of all this, feathers have to be replaced regularly. But this is costly.

Moult is an inevitable consequence of wear (Raikow et al. 1974; Szép et al. 2019). This process of feather replacement is essential for the renewal of feather functionality (Williams and Swaddle 2003; Pap et al. 2007) and has impacts on future fitness (Vágási et al. 2012). Moult has crucial importance in life-history evolution (Nilsson and Svensson 1996; Dawson et al. 2000), as timing and duration of moult may affect subsequent processes ('carry-over' effects) (Nilsson and Svensson 1996; Dawson et al. 2000; Harrison et al. 2011). Recording moult progression is key to understanding the carry-over effects of phenological interruptions (Marra et al. 2015). Moult interacts dynamically with other life-history components (Monaghan et al. 2009; Selman et al. 2012), making it a prominent life-history trait (Vágási et al. 2012).

Birds want to minimise the frequency of replacement. This can be assisted by slowing the rate of wear through feather care and growing good quality feathers. The cost of moult is usually linked to quality in original growth (microstructure) and rate of wear (frequency of replacement) (Macleod et al. 2005). Birds must juggle these factors to ensure survival and hopefully reproduction. The rate of feather growth tends to impact significantly on feather quality, as rapid growth is thought to result in lower quality plumage (Nilsson and Svensson 1996; Dawson et al. 2000; de La Hera et al. 2009; Weber et al. 2010; Broggi et al. 2011). Dawson et al. (2020) showed evidence of reduced quality (i.e., feather wear and less functionality) of feathers grown in a rush.

Moult as an energy-demanding activity in birds

The annual cycle of birds depends on an endogenous rhythm organizing annual events like moulting, breeding and migration (Gwinner 1996). However, not all birds follow an annual cycle (e.g., some tropical seabirds, Reynolds et al. 2014), and timing of key events may be linked to factors such as rainfall and temperature (e.g., in desert birds) rather than annual cycles (Barrientos et al. 2007; Mares et al. 2017). Moult is an essential and indispensable part of avian life (Payne 1972; Murphy 1996). Moult strategies might be subject to evolution, with timing and intensity of moult evolving rapidly in response to environmental changes. Moult has a profound disturbance of endogenous metabolism (Thompson and Powers 1924), and alters body protein metabolism (Murphy and King 1991). Moult is a costly process both in terms of energy and reduced flight ability (Murphy 1996; Bridge 2006) but necessary for the maintenance and adjustment of plumage functionality throughout the annual cycle of birds (Saino et al. 2013). Moult represents perhaps the single highest cost of maintenance for birds and requires a major allocation of resources.

The study of moult is important to understand bird biology and conservation. The timing of moult plays an important part in the annual cycle of a bird to reduce conflict with other demanding activities (Murphy and King 1992; Wikelski et al. 2008), and understanding moult strategies provides insights into the plasticity and phylogenetic conservation of feather replacement, which can influence species distributions (Wolfe et al. 2009). Moult not only results in physiological and behavioural stress, but also can be seen as a component of broader patterns of phenotypic plasticity (Price 2006). The duration of moult is a function of the rate of feather growth and intensity of feather replacement. Feather growth influences feather structure and functionality (Hemborg 1999). Knowledge of moult is crucial to understanding life-history trade-offs in birds (Rohwer 1999; Filardi and Rohwer 2001; Leu and Thompson 2002). Moult can be used to determine a bird’s age, which is essential for understanding their population dynamics (Pyle 2009). Moult study has been used to assess territory quality and as a tool to study population ecology (Espie et al. 1996). Moult extent and symmetry have also been proposed as predictors of fitness in birds (Minias and Iciek 2013).

Every bird must moult, and when and where it moults reflects resource availability in space and time balanced with other aspects of its life cycle. Most birds have a complete (or near-complete) moult once a cycle, usually after breeding. Birds also may alter their behaviour during moult, frequently reducing their level of activity (Cherel et al. 2016; Grissot et al. 2020;

Jones et al. 2020); some species even become flightless (Bluethroat *Luscinia svecica* and the Redwing *Turdus iliacus*; Haukioja 1971). Feather size is an important determinant of the duration of moult, as large feathers take longer, and more energy, to be replaced (Rohwer 1999; Edwards and Rohwer 2005). Timing, location, extent and intensity of feather replacement tends to be plastic in many bird species (Rohwer et al. 2009), more so than moult sequence. Due to the paucity of information on the often complex moult strategies in seabirds (Bridge 2006), I focus on how large-winged seabirds fit replacement of flight feathers into their annual cycles and if this replacement is fixed or variable across remiges and rectrices.

Moult in seabirds

Seabirds are a taxonomically varied group of some 400 species (about 3.5% of all birds) that depend on the marine environment for at least part of their life cycle (Harrison et al. 2021). They tend to be larger than most terrestrial species, and vary greatly in structure in relation to foraging mode, with wings in particular adapted to diving (Wilson et al. 1992). As a result of their large size, they are challenged to replace all primaries in a year without becoming flightless, as time required to replace all remiges is determined primarily by the intensity of moult (Rohwer 1999). A few species can afford to become flightless while moulting (or year-round). However, many large, long-winged species have to retain the ability to fly year-round. In this thesis I explore how these species manage their moult schedules.

Understanding moult patterns in seabirds is critical for studies on population dynamics (Ainley and Boekelheide 1991). However, moult is poorly understood in many seabirds because most replace their feathers at sea during the non-breeding season (Ramos et al. 2009). In addition, complex moult patterns are more likely to occur in large birds (Prevost 1983; Langston and Rohwer 1996; Edwards and Rohwer 2005).

Some large seabirds undergo “serial” or “stepwise” wave moult (also known as *Staffelmauser*; Stresemann and Stresemann 1966). This strategy means that most or all primaries can be replaced in a shorter period, because two or more small gaps in the wing at one time have less of an impact on flight performance than a large gap (Stresemann and Stresemann 1966). In some cases, two or more primaries are replaced at the same time at different positions along the wing (Stresemann and Stresemann 1966; Rohwer et al. 2011). Whereas *Staffelmauser* among primaries has been studied in many large species, patterns of replacement among secondaries and rectrices are poorly studied. Generally, smaller seabirds present a simple descendent primary moult (Brown 1988; Marchant and Higgins 1990; Cooper et al. 1991; Bridge 2006), but their secondary and rectrix moult can be more complex (Ramos et al. 2009). As a result, seabirds exhibit a great range in the duration of a full moult cycle (the time taken to replace a full set of remiges and rectrices). The replacement of all flight feathers can take up to three years in some albatrosses (Prince et al. 1993; Langston and Rohwer 1995), eight to nine months in storm-petrels (Ainley et al. 1976), and one to two months in alcids (Bridge 2004).

Bridge (2006) reported a significant positive relationship between moult duration and wingspan, which means that in addition to moult intensity, wing size is also a factor responsible for the time required for all primaries (and secondaries) to be replaced (Rohwer 1999). The evolution of complex patterns of feather replacement is linked to the size of flight feathers, as long-winged birds need more time to replace their remiges (Bridge 2006).

Moult in raptors

Like seabirds, most raptors are larger birds that often have complex moult strategies. They reveal different patterns of moult linked to evolutionary histories (Pyle 2013) and always maintain flight during moult (Rohwer et al. 2011; Zuberogoitia et al. 2013; 2016). The growth of juvenile flight feather varies (Wolfe et al. 2014; Howell and Pyle 2015; Zuberogoitia et al. 2018), taking up to three weeks in smaller species (e.g., Lesser Kestrel *Falco naumanni*), to four months in the large ones (Ontiveros 1995; Zuberogoitia et al. 2018). Adults, on the other hand, replace their feathers gradually and per moult cycle (Pyle 2008). Moult cycles range from complete single moult cycles (Zuberogoitia et al. 2018), to multiple moult cycles (Clark 2004; Forsman 2016; Zuberogoitia et al. 2016).

The frequency of moult varies among feather tracts, whereby different bird species prioritize the replacement of some feathers than others (Brommer et al. 2003; Rohwer et al. 2011; Zuberogoitia et al. 2013; Ellis et al. 2016). This variation in the frequency of feather replacement could be linked to allocation of position-specific energetic costs in large birds (Brommer et al. 2003). The pattern of flight feather moult depends on array of factors including age, sex, location, breeding status, etc. (Korpimäki and Hakkarainen 2012). Some raptors finish replacing their feathers before the post-breeding migration or before winter (for resident species). However, for most migratory species, replacement of flight feathers is usually completed in their winter quarters (Edelstam 1984; Arroyo and King 1996; Olle and Estrada 2017), although some continue moulting during migration (Forsman 2016).

Falcons (Falconidae) usually replace their wing feathers in an unusual sequence, proceeding bidirectionally in two moult series among both the primaries and secondaries (Cramp and Simmons 1980; Pyle 2005; 2008). Patterns of feather replacement can be used to age falcons through their second or third year (Clark 2004). Female breeding falcons begin flight feather moulting during incubation and suspend it during chick rearing to resume after breeding (Stresemann and Stresemann 1966).

Understanding moult patterns in falcons has wide conservation implications: moult study has been used to assess territory quality and as a tool to study population ecology (e.g., Merlins *Falco columbarius*, Espie et al. 1996). Moult can also serve as an indicator of other life-history stages that cannot be quantified directly. This reveals the importance of moult to test biological, physiological and ecological variables (Karell et al. 2011).

Thesis rationale

This thesis explores how different birds fit moult into their annual cycles and assesses how large, long-winged birds manage to replace their flight feathers, with a focus on secondaries given their large number and total length and paucity of data on secondary moult. The thesis also explores the intensity and speed of moult vis-à-vis variations in structural parameters (as a proxy for feather quality) in a long-distance migratory raptor. The study of feather quality in birds is still also poorly understood. In addition, only few studies have explored how moult strategies are influenced by differences in food availability or habitat quality (Borras et al. 2004; Helm and Gwinner 2006).

I explore the extent, timing, duration, sequence and symmetry of moult in three seabirds, Cape Gannets *Morus capensis*, White-chinned Petrels *Procellaria aequinoctialis* and White-capped/Shy Albatrosses *Thalassarche steadi/cauta*, and one long-distance migratory raptor, Amur Falcons *Falco amurensis*. I further explore variations in structural parameters (as a proxy for feather quality) between juvenile and adult Amur Falcons and the relationship of these structural parameters with body condition. In Cape Gannets, I compare moult in birds from two breeding colonies that experience different levels of food stress to investigate if they differ in their timing, duration and symmetry of moult. In White-chinned Petrels, I explore the extent of moult among secondaries, given a simple complete replacement of primaries. I also assess whether this species reduces its activity while moulting, given the intense nature of wing and tail moult in this species. In White-capped/Shy Albatrosses, I extend the moult analysis reported by Flood and Ryan (2018), adding more birds and describing the timing of secondary and rectrix moult, the intensity of flight feather moult and assessing symmetry of rectrix moult. In Amur Falcons, I compare timing and extent of moult in relation to body condition and variations in structural parameters (feather length, calamus length, mass, ratio of mass and length, calamus width, rachis width, barb length, barb density and barbule density) between juveniles and adults.

I was fortunate to have access to a large data set for over 1300 Cape Gannets from two South Africa breeding colonies (Lambert’s Bay and Malgas Islands). I contributed two years of moult data at Malgas Island (2018 to 2019). I used a 23-year moult dataset (1997 to 2020) for over 2400 White-chinned Petrels and 22-year moult dataset (1999 to 2020) for over 600 White-capped/Shy Albatrosses from fishing bycatch off southern Africa. I scored moult from almost 2000 Amur Falcons killed in two hailstorms in Kwazulu-Natal, South Africa in March 2019 and explored relationship between extent of moult and body condition vis-à-vis exploring feather quality between juvenile and adult Amur Falcons and the relationship of these structural parameters with body condition.

Contributions to knowledge

In this thesis, I address the question of how birds fit moult into their life-history activities and to what extent, and with what intensity, they replace their feathers. I mostly focus on flight feathers and explore how large-winged birds schedule replacement of their remiges and rectrices. I further explore extent of moult and feather quality in a long-distance migratory raptor.

To do this, I have brought array of questions together into a multi-faceted study. Understanding the conservation implications of moult in life history modulation requires addressing different questions: first, how large-winged birds fit replacement of flight feathers into their annual cycles and if this replacement is fixed or variable across remiges and rectrices (Chapters 3–5); second, how extent and intensity of moult correlates with body condition (Chapter 6); third, using moult pattern as an index of condition linking to conservation by investigating how moult duration and asymmetry differs between populations of birds (Chapter 3); fourth, to test if reduced flight activity is linked to moult period (Chapter 4), as reported in some seabirds (Cherel et al. 2016; Grissot et al. 2020; Jones et al. 2020); and finally, how feather quality varies between juveniles and adults in a long-distance migratory raptor (Chapter 2), bearing in mind the trade-off between growth rate and feather quality that chicks face when growing their first set of feathers (Dawson et al. 2000; de La Hera et al. 2009; Weber et al. 2010; Broggi et al. 2011; Saino et al. 2014). This project makes novel contribution in support of much-needed study related to how birds fit moult into their life-history activities.

Thesis outline

The objective of this research is to contribute new insights into how long-winged birds negotiate life history trade-offs relating to the scheduling and intensity of flight feather moult. The research focuses on three seabird species and one long-distance migratory raptor and brings new observations on the timing of moult, variation among individuals, and age-related differences in feather quality. My choice of study species was driven principally by the large data sets available for them. I address this research objective in five chapters, structured as follows:

Chapter 2 addresses the apparent trade-off between feather growth rate and quality for among flight feathers in juvenile and adult Amur Falcons.

Chapter 3 presents differences in moult duration and perhaps asymmetry in Cape Gannets between two breeding colonies linked to foraging conditions. This chapter draws on an existing moult dataset collected from 2002 – 2004, which I augmented with data collected in 2018 – 2019. This chapter has been published in the *Ostrich: African Journal of Ornithology* (Adekola et al. 2021a).

Chapter 4 presents moult data on the timing, duration and symmetry of flight feather moult in White-chinned Petrels. I also test evidence of reduced flight activity during moult period from adult White-chinned Petrels.

Chapter 5 presents moult data on the timing, intensity and symmetry of moult in White-capped Albatrosses.

Chapter 6 presents data on the extent and symmetry of tail moult in Amur Falcons. I also explore the relationship between extent of tail moult and body condition. This chapter has been published in the *Journal of Ornithology* (Adekola et al. 2021b).

The final chapter summarises the main lessons of the thesis, while also presenting data on how long-winged birds might manage to replace their large number of secondaries without unduly impacting their flight ability.

Each chapter has been written in the form of a stand-alone paper, to facilitate their publication. As such, a degree of repetition with regards to framing the introductions and methods is unavoidable. However, to avoid needless repetition, all literature cited is compiled in a single list towards the end of the thesis. Supplemental materials for each of the main chapters (Chapters 2-6) follow each chapter.

CHAPTER 2

Are juvenile Amur Falcon flight feathers of lesser quality than adults?

Abstract

Feather quality is critically important, especially for long-distance migratory birds. However, studies on age-related variation in feather morphology and wear rates are limited. At least among passerines, juvenile contour feathers tend to be simpler and faster wearing than adult feathers. I test whether there are age-related differences in flight feather quality in a migratory raptor. Amur Falcons are long-distance migratory raptors that breed in Asia and spend their non-breeding season in southern Africa. Juvenile Amur Falcons undertake up to three migrations on their first set of flight feathers, whereas adults only make two. I compare the microstructure of flight feathers and primary coverts of 100 non-moulting Amur Falcons of known age and sex killed at their roosts during two exceptional hailstorms in KwaZulu-Natal, South Africa in March 2019. Adults had longer and relatively heavier feathers than juveniles but microstructural measurements did not differ between ages or sexes. Adults and juveniles had similar calamus length across primaries, secondaries, rectrices and primary coverts. However, juvenile primaries, secondaries and rectrices had a shorter rachis than adults. There were no age-related differences among primary coverts. Body condition was higher in females than males in both adults and juveniles. In general, adults and juveniles with better body condition tended to have longer and heavier feathers, with limited variations across feather tracts, suggesting that feather traits could be used as reliable indicators of a bird’s health. Contrary to previous studies that growing feathers fast reduces their quality, my results suggest that juvenile Amur Falcons manage to grow quality flight feathers in terms of microstructure even though they fledge in about one month, and they do not appear to wear faster than adult flight feathers.

Introduction

Feathers are one of the most important and unique avian features (Xu and Guo 2009; Pan et al. 2019). Fully grown feathers are dead structures that have to be replaced periodically (Raikow et al. 1974; Szép et al. 2019). Feather condition is crucial for flight, as well as insulation, protection, camouflage, social signalling, etc. (Møller et al. 2006; Hagelin 2007; Clark et al. 2011). Feather characteristics can be useful tools for investigating evolutionary and ecologically relevant parameters (Saino et al. 2013; Tellería et al. 2013). Also, some feather characteristics have been used as indicators of body condition in birds (Carbonell and Tellerfa 1999) and related to flight efficiency in migrants (Pap et al. 2015; de la Hera et al. 2020).

Bird plumage consists of three main types of feathers: flight feathers (primaries, secondaries and rectrices), body contour feathers (wing coverts and external layer of body feathers), and down feathers (proximal layer of body feathers) (Vágási et al. 2016; Osváth et al. 2018). Flight feathers are chiefly responsible for propulsion, lift and manoeuvring (Norberg 1990; Wang et al. 2012; Pap et al. 2015); body feathers contribute to insulation, streamlining, protection, camouflage and communication, whereas down feathers help in insulation (Ginn and Melville 1983). Flight and contour feathers have a complex structure, with a main support (calamus, rachis), and interlocking barbs and barbules, that together form the feather vane. The relative size and weight of these structures determine feather length, area, mass, strength and flexural stiffness, which link to most feather functions (Pap et al. 2015; 2019).

Feather quality and rate of feather wear determine feather condition, such that a bird with good quality feathers might have poorer feather condition if its feathers are older and hence more worn than a bird with poorer quality feathers. In other words, poor quality feathers wear more quickly than feathers of better quality. Birds with poor quality feathers need to replace their feathers more frequently or suffer periods with very poor feather condition because they wear more quickly (Dawson et al. 2000; Echeverry-Galvis and Hau 2013).

Feather quality can be measured via structural (mass, length, area, rachis width, branch spacing, barb and barbule density, mass relative to feather length) and mechanical properties (flexural stiffness, bending stiffness and Young's modulus) (Bonser 1996; Dawson et al. 2000; Bachmann et al. 2012; Pap et al. 2015, 2019; Vágási et al. 2016; Hernández-Téllez et al. 2021), or other proxies of feather quality, such as wear rate, level of melanisation, and occurrence of abnormalities such as feather holes and fault bars (Dawson et al. 2000; Weber et al. 2005; Pap et al. 2007; Vágási et al. 2012; Kiat and Sapir 2018). The structure and complexity of barbs and barbules, and weight of feathers are often used as an indicator of quality (Podlaszczuk et al. 2016). Denser feathers (defined as mass per unit length) have more barbs and barbules, which indicates a higher allocation of resources to feather growth, and are assumed to wear more slowly and are less likely to break (Patanella 2018). Several studies have used feather weight and microstructure to explore variations among bird populations (Broggi et al. 2011; Hope et al. 2016). For example, northern European Great Tits *Parus major* differed from southern European populations in having shorter and denser feathers (Broggi et al. 2011; Gamero et al. 2015).

Feather quality varies among ages, sexes and populations (Pap et al. 2015; Szép et al. 2019; Hernández-Téllez et al. 2021). When time available for moult is limited, feather quality can be impaired (Dawson et al. 2000; Hall and Thord 2000; Vágási et al. 2012). Many juvenile birds face a challenging trade-off in this regard: they need to leave the nest to reduce the risk of predation, but rushing feather growth results in poor quality feathers. Many passerines accept this cost, producing a flimsy initial set of body coverts, which are replaced within a few weeks or months of fledging (Butler et al. 2008). Females may also have more abraded feathers due to greater investment in breeding than males (Merilä and Hemborg 2000; Moreno-Rueda 2011; Sild et al. 2011). Male Jungle Crows *Corvus macrorhynchos* had higher barbule densities and shorter inter-barbule distances than females, probably because of their colour, which may be sexually selected (Lee et al. 2009).

Feather quality is related to the nutritional state of a bird during moult and the speed of feather growth (Carbonell and Tellerfa 1999; Vágási 2001; Broggi et al. 2011; Marzal et al. 2013; Hernández-Téllez et al. 2021). For example, Dawson et al. (2000) showed that birds forced to rush moult had lower survival over winter (Takaki et al. 2001; Podlaszczuk et al. 2016). Also, lower quality feathers may break more readily, creating gaps in the plumage and potentially affecting a bird's flight ability (Strochlic and Romero 2008; DesRochers et al. 2009). Better quality feathers wear more slowly, and this is important because worn feathers are less able to perform their functions (Swaddle and Witter 1997; Berggren et al. 2004; Echeverry-Galvis and Hau 2013; Zuberogoitia et al. 2018; Szép et al. 2019).

To date, most studies of flight feather allometry have focused on the primaries (Butler et al. 2008; Dawson et al. 2000; Pap et al. 2015) and rectrices (De La Hera et al. 2010). Migrants tend to grow their feathers faster than resident birds (Kiat et al. 2019), which might lead to lower quality. Migration also can result in additional wear compared to resident species, and this effect is most marked in long-distance migrants (Kiat et al. 2019). On the other hand, evidence that feather quality is related to growth rate comes from contour feathers and insulation, and no test of this for flight feathers. Juvenile Amur Falcons undertake up to three migrations on their first set of flight feathers, compared to adults that only make two. The nestling period, which determines how fast the juvenile feathers are grown, lasts approximately 1 month (del Hoyo and Collar 2016). Juveniles probably are still growing outer primaries when they fledge, but the flight feathers do not start growing immediately after hatching, so they probably grow the flight feathers in about 30 days, and for the longest primary (195 mm), means that they have to grow it at around 6.5 mm per day, which is towards the upper end of the growth rate of feathers (Rohwer and Rohwer 2013). I test whether juvenile flight feathers are of lesser quality due to rapid growth than adult Amur Falcons and investigate the relationship between feather morphology and body condition.

Methods

Study species

Amur Falcons are long-distance migratory raptors that breed in Asia and spend their non-breeding season in southern Africa (Alexander and Symes 2016; Adekola et al. 2021b). Juvenile Amur Falcons only replace rectrices (some or all) during their first winter (Adekola et al. 2021b). Initiation of primary moult varies between P4 and P5 in falcons (Pyle 2013). Adults usually start replacing their remiges on their breeding grounds before suspending moult for autumn migration and resuming moult in the winter quarters (Cramp and Simmons 1977; Adekola et al. 2021b), which means that early-moulted primaries (P4 and P5) are about the same age as juvenile feathers, whereas those replaced in southern Africa are a few months younger.

Data collection

I sampled wing and tail feathers from adult and juvenile Amur Falcons killed at two roosts during exceptional hailstorms in KwaZulu-Natal, South Africa, in March 2019 (Allan 2019; Adekola et al. 2021b). Of the more than 2000 dead birds, I selected 100 birds that showed little evidence of storm damage and were not growing any flight feathers. The birds were categorized into age-classes and sexed by plumage characters (Cramp and Simmons 1977; Adekola et al. 2021b): 52 adults (30 females and 22 males) and 48 juveniles (21 females and 27 males). Juveniles were distinguished by their buffy-edged upperpart feathers and pale buff cheeks and throat. The following measurements were taken from all birds: mass (to the nearest 0.1 g), bill length (from nostril to the bill tip) and depth (of both mandibles in line with the nostril), head length and tarsus length, all to the nearest 0.1 mm (using digital Vernier callipers), and wing (flattened chord) and tail length (both to the nearest 1 mm). To ensure consistency, all measurements were taken by one observer (Adekola et al. 2021b). I removed one entire wing (usually the right wing, unless that wing was damaged) from each bird. This was kept refrigerated until the feathers were sampled; all primaries (P1–P10), secondaries (S1–S11), rectrices (R1–R6) and greater primary coverts (PC1–PC10) were carefully plucked, dried and stored in envelopes until they were measured. I tried to measure rate of feather growth directly from growth bars, but not reliably visible in the Amur Falcon.

Feather measurements

For each feather, I measured (Supplemental Figure 2.1) total length to the nearest 1 mm as the flattened and straightened distance from the calamus base to the feather tip. Calamus length (from the calamus base to the start of the vane) was measured to the nearest 1 mm, and rachis length was estimated as the total length minus the calamus length. Feather mass was recorded to the nearest 0.1 mg on an analytical balance. I used mass per unit length (mg/mm) as a proxy for feather quality. In addition, I measured microstructure from selected feathers: the longest primary (P9), the innermost primary (P1), the outermost secondary (S1) and central rectrix (R6; cf. Dawson et al. 2000). I chose P9 because it is feather most exposed to aerodynamic forces as the longest flight feather in the Amur Falcon. All measurements were taken using a Zeiss Discovery V20 stereo microscope (axiocam 503 colour) with objective PlanApo S 1.0x FWD 60 mm, with the aid of ZEN 2.3 pro software. Parameters measured were calamus and rachis width, barb length, and barb and barbule density. Rachis width was measured at the middle of the feather while the calamus width was measured at the base of the vane. Barb (number/cm) and barbule density (number/mm) were measured on the inner feather vane, at the middle part along the rachis. Barb density was estimated by counting the number of barbs per 10 mm section along the rachis. Barbule density was estimated by measuring the length of barb supporting ten barbules (i.e. higher distance values indicate a lower density; cf. Pap et al. 2015; Supplemental Figure 2.1).

Statistical analyses

All statistical analyses were performed within the R statistical environment (R Core Team 2019). Body condition was expressed as Scaled Mass Index (SMI; Peig and Green 2009), which is a size-corrected body condition index using ‘lmodel2’ package in R (see Adekola et al. 2021b for more details). I used general linear models to test for differences in feather morphological variables in relation to age, sex, body condition and the interactions between these variables (if statistically significant; $\alpha = 0.05$). The effect of body condition on juveniles and adults was also analysed. All models met the assumptions of parametric tests except for barb density, which was log-transformed (log base 10) to ensure normality. Akaike’s Information Criterion (AIC) was used to select the best-fitting model. All statistical estimates are reported as means ± standard deviations (SD). Graphical representation of t-tests is based on predicted marginal means, obtained from the ‘emmeans’ package in R (Lenth 2020).

Results

Feather length and mass

Adult Amur Falcons had longer and heavier primaries (Figure 2.1, Supplemental Table 2.1), secondaries (Figure 2.2, Supplemental Table 2.2) and rectrices (Figure 2.3, Supplemental Table 2.3) than juveniles (Figures 2.1-2.3, Supplemental Table 2.1-2.3). However, the length and mass of primary coverts did not differ between adults and juveniles (Figure 2.4, Supplemental Table 2.4). On average, adult primaries were 3% longer and 12% heavier (Supplemental Table 2.1), adult secondaries were 3% longer and 13% heavier (Supplemental Table 2.2) and adult rectrices were 4% longer and 7% heavier (Supplemental Table 2.3) than juveniles (Supplemental Tables 2.1-2.3). On average, females tended to have longer and heavier primaries (Supplemental Table 2.1) and secondaries (Supplemental Table 2.2) than males (Supplemental Tables 2.1-2.2). Although rectrices had similar length in both sexes (Supplemental Table 2.3), males had heavier rectrices than females (Supplemental Table 2.3). There were no sex-related differences in the primary coverts.

Calamus length was similar between ages and sexes across primaries (Supplemental Table 2.1), secondaries (Supplemental Table 2.2), rectrices (Supplemental Table 2.3) and primary coverts (Supplemental Table 2.4). On average, adult Amur Falcons had longer rachises than juveniles for primaries (Supplemental Table 2.1), secondaries (Supplemental Table 2.2) and rectrices (Supplemental Table 2.3) but not for primary coverts (Supplemental Table 2.4). Females had longer rachises than males for primaries (Supplemental Table 2.1) and secondaries (Supplemental Table 2.2), but similar for rectrices and primary coverts (Supplemental Tables 2.3-2.4).

The ratio of primary, secondary, rectrix and primary covert mass to length were significantly greater in adult than juvenile Amur Falcons (Figures 2.5-2.6, Supplemental Table 2.5, Supplemental Figures 2.2-2.5). Females had greater mass to length ratio for primaries and secondaries (Supplemental Table 2.5) than males, but not for rectrices and primary coverts (Supplemental Table 2.5). However, age and sex had no significant effect on feather microstructure (calamus width, rachis width, barb length, barb density and barbule density; Table 2.1). Among the primaries, P9 generally had a longer calamus width and barb length and higher barb density than the inner primary (P1), but there was no significance difference in rachis width and barbule density (Table 2.1).

Correlations with body condition

Body condition was higher in females than males in both adult and juvenile Amur Falcons (Supplemental Figure 2.6). Juveniles were physically smaller than adults (adults: 141.77 ±

11.11 g vs juveniles: 134.78 ± 13.55 g; t = 2.81, df = 91.09, p = 0.01). In general, adults and juveniles with better body condition tended to have longer (Figure 2.7) and heavier feathers (Figure 2.8), with some variation among feather tracts (Supplemental Figures 2.7-2.14).

Discussion

The need to explore feather characteristics between adult and juvenile birds, especially among long-distant migrants, is key to understanding feather morphology. To the best of my knowledge, this is the first study to explore differences in feather quality across remiges, rectrices and primary coverts in a long-distant migrant and compare these differences between juveniles and adults. Juvenile Amur Falcons are capable of three migrations on their first set of flight feathers, unlike adults that only make two migrations per feather set.

I found no sex-related differences in structural measurements among the Amur Falcons. However, females tended to have longer and heavier feathers than males. Siefferman and Hill (2003) reported no sex differences in feather microstructures of Eastern Bluebirds *Sialia sialis*, even though males have longer, heavier feathers, and longer wings than females probably due to sexual selection for males to indicate quality as an honest signal (Meillère et al. 2017). Longer and more pointed wings are linked to flight efficiency in migratory birds (Leisler and Winkler 2003; Sheard et al. 2020).

Age and sometimes sex are significant factors in determining the quality of feathers in birds (Pap et al. 2007). Adult Amur Falcons generally had longer and heavier feathers than juveniles, and this was the case for all feathers, irrespective of whether they were moulted early or late in the adult moult sequence. The mass per unit length results indicated that juvenile feathers are lighter for a given length, even for the first-replaced primaries, which are moulted on the breeding grounds, and thus are of a similar age and wear status (1 migration old) as juvenile feathers. Juvenile birds are usually thought to have feathers of lower quality because of the short time they have to invest in feather growth, and the many conflicting demands for resources during rapid nestling growth (Pap et al. 2007; Butler et al. 2008).

Microstructural measurements (calamus width, rachis width, barb length, barb density and barbule density) did not differ with age or sex in Amur Falcons, suggesting that juveniles are able to grow equally complex structures as adults, but with less mass. At time of sampling, most adults had completed primary, secondary and tail moult (Adekola et al. 2021b). The juvenile feathers sampled are all the same age, roughly 6-7 months old, as the chicks fledge in August-September (del Hoyo and Collar 2016). Adult feathers are newer (1-3 months old) as they are moulted in the austral summer. Despite the greater wear in juveniles, I found few significant differences among adult and juvenile birds. Within species variation, Pap et al. (2015) reported that larger feathers have thicker shafts with corresponding longer barbs and denser barbules. By comparison, Butler et al. (2008) showed greatly reduced feather complexity (microstructure) in juveniles. Rachis width is positively associated with migratory distance in European Robins *Erithacus rubecula* (de la Hera et al. 2020), but not in Eurasian Blackcaps *Sylvia atricapilla* where migrants had a narrower rachis than resident birds (Hernández-Téllez et al. 2021). Narrower rachises in rectrices could be useful to reduce drag in migratory birds (Hernández-Téllez et al. 2021), despite the better mechanical properties linked to wider rachis in long-distant migrants (de la Hera et al. 2010). It is still unclear quite how rachis width affects flight mechanics and if it can be considered as an adaptive trait related to migration (Lees et al. 2017).

Among the primaries, P9 generally had a broader calamus width and barb length and higher barb density than the inner primary (P1), but there was no difference in barbule density. Pap et al. (2015) reported microstructural differences between proximal and distal primary feathers related to flight style in different bird species. They suggested that flight style, habitat and moult strategy affect the functional morphology of flight feathers, with more significant effects on inner than outer primaries. They found P1 had a higher barb density than P8, suggesting that barb density may be under selection for aerodynamic performance (Ennos et al. 1995; Dial et al. 2012). In this study, I found P1 had a higher barbule density than P9 among adult and male Amur Falcons (but not in juveniles and females).

Another interesting aspect of this study is the relationship between body condition and feather parameters. Body condition was higher in females than males in both adult and juvenile Amur Falcons (Adekola et al. 2021b). Length and mass of feathers generally increased with body condition. Pap et al. (2008) showed that feather deformities is linked to low body condition, showing that birds in poor condition during moult grow lower quality remiges which became more rapidly damaged. Vágási et al. (2012) also reported that body condition was positively associated with feather traits (primary, secondary and tail lengths). Patanella (2018) also reported relationship between feather quality and body condition of Eastern Bluebirds from two urban and two rural sites, showing that the ratio of rectrix mass to length and barbule density increased with body measurements. Therefore, feather traits may be reliable indicators of bird health. Contrary to previous studies that growing feathers fast reduces their quality, my results suggest that juvenile Amur Falcons manage to grow quality flight feathers in terms of microstructure even though they fledge in about one month. There are mass differences, but microstructure is similar, and they do not appear to wear faster than adult flight feathers of comparable age. The study adds to the limited knowledge about age-related variability in feather quality.

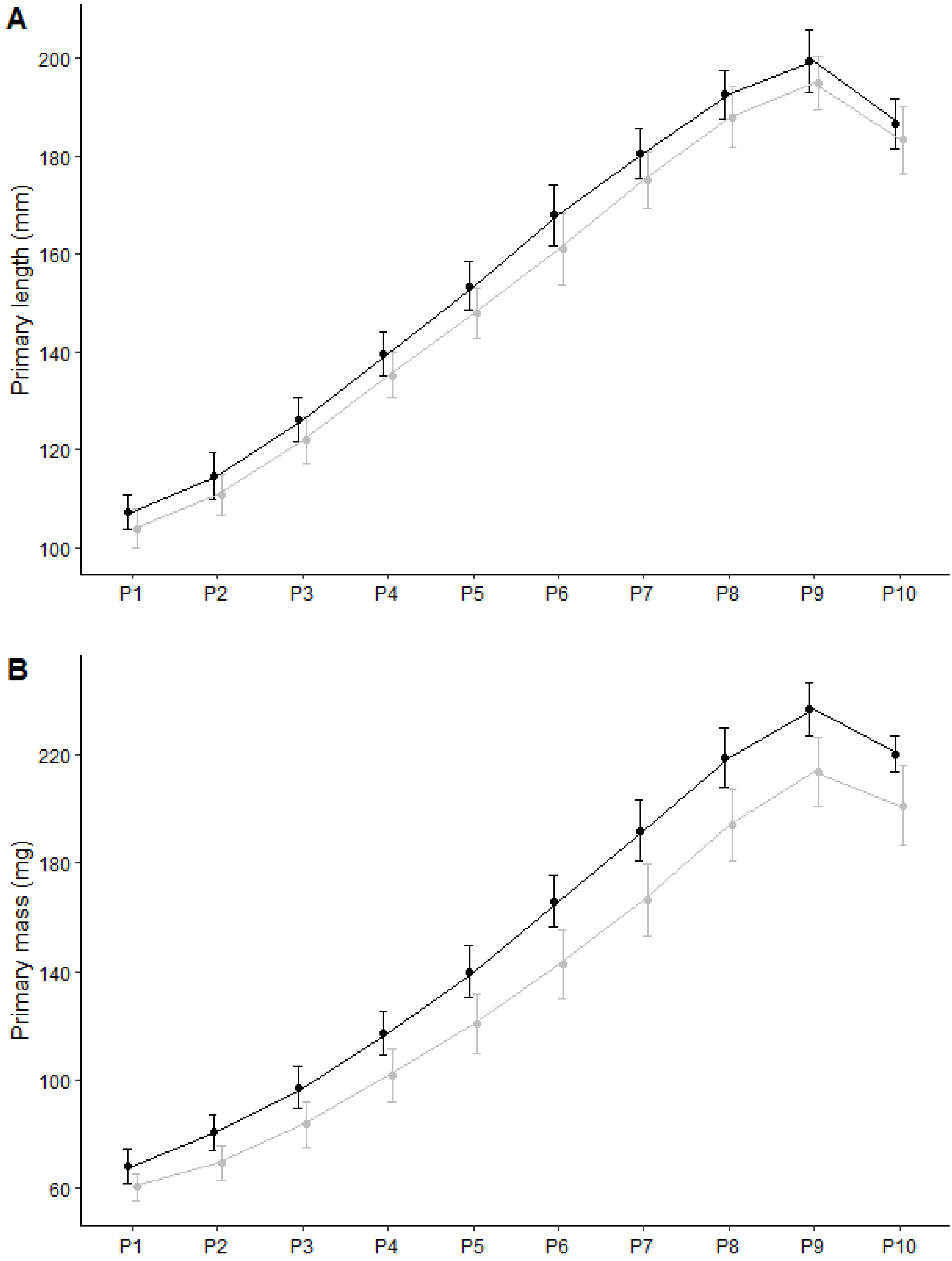


Figure 2.1: Average ± 1SD primary length (A) and mass (B) in adult (black) and juvenile (grey) Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa in March 2019.

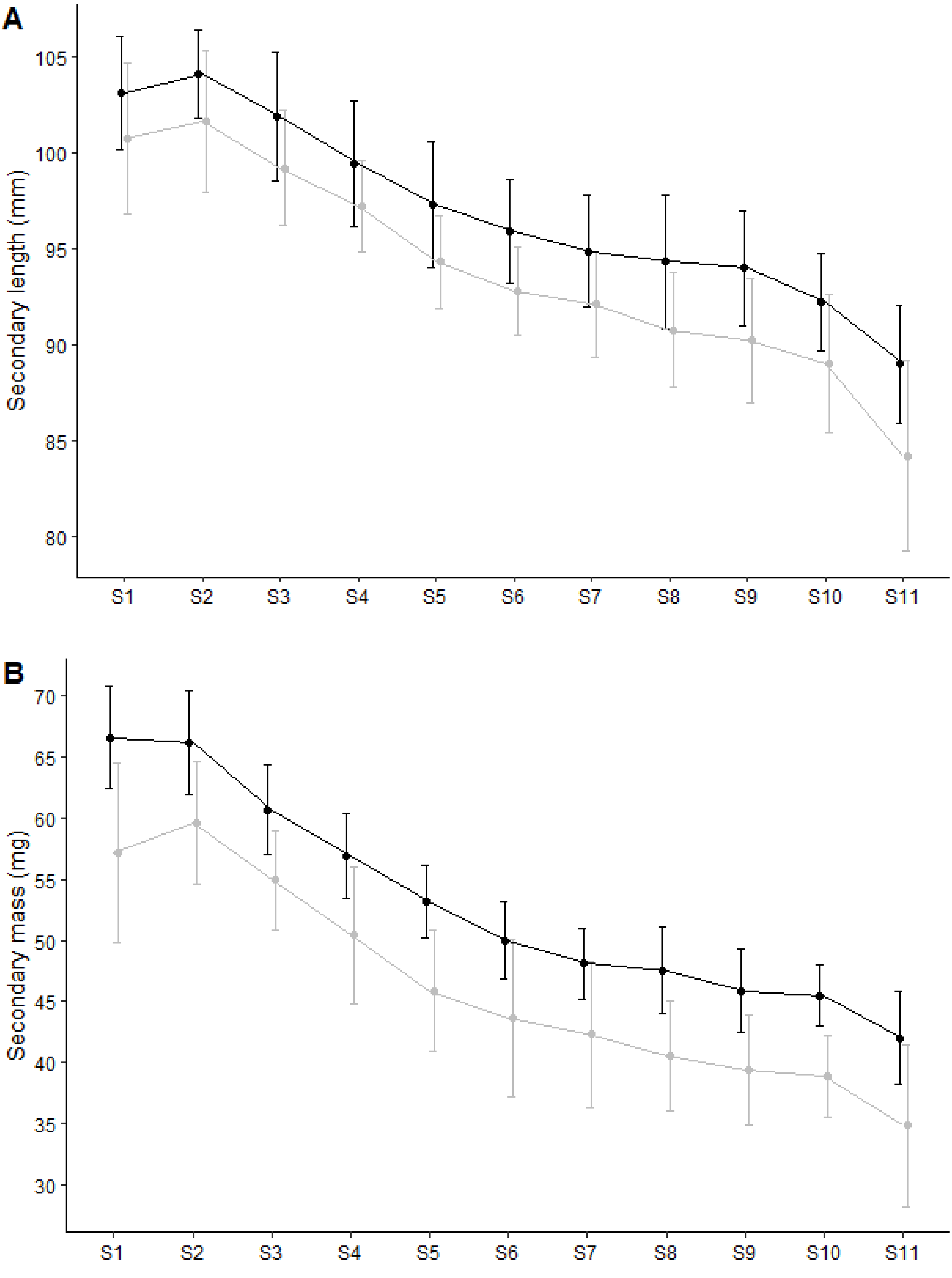


Figure 2.2: Average ± 1SD secondary length (A) and mass (B) in adult (black) and juvenile (grey) Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa in March 2019.

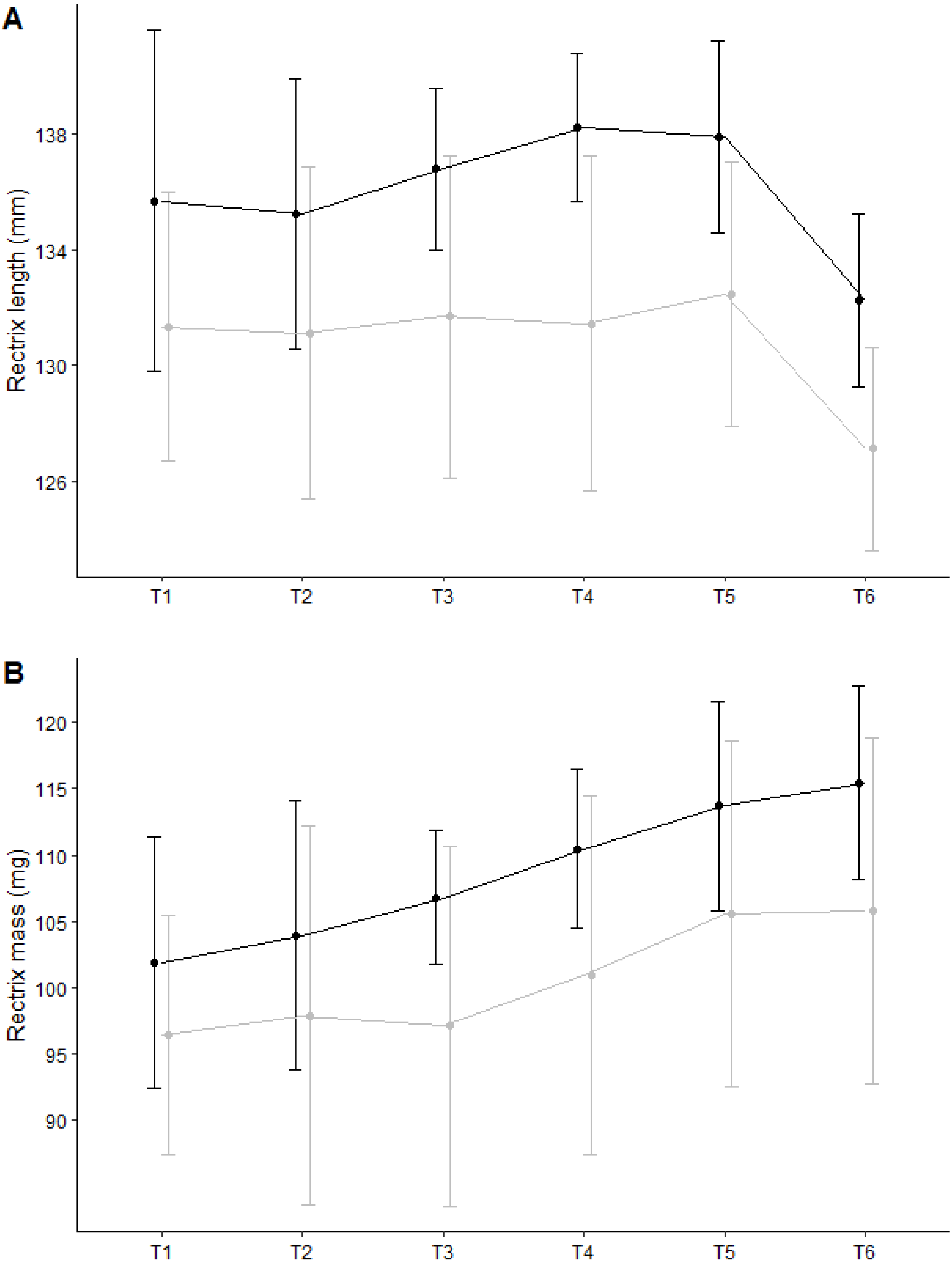


Figure 2.3: Average ± 1SD rectrix length (A) and mass (B) in adult (black) and juvenile (grey) Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa in March 2019.

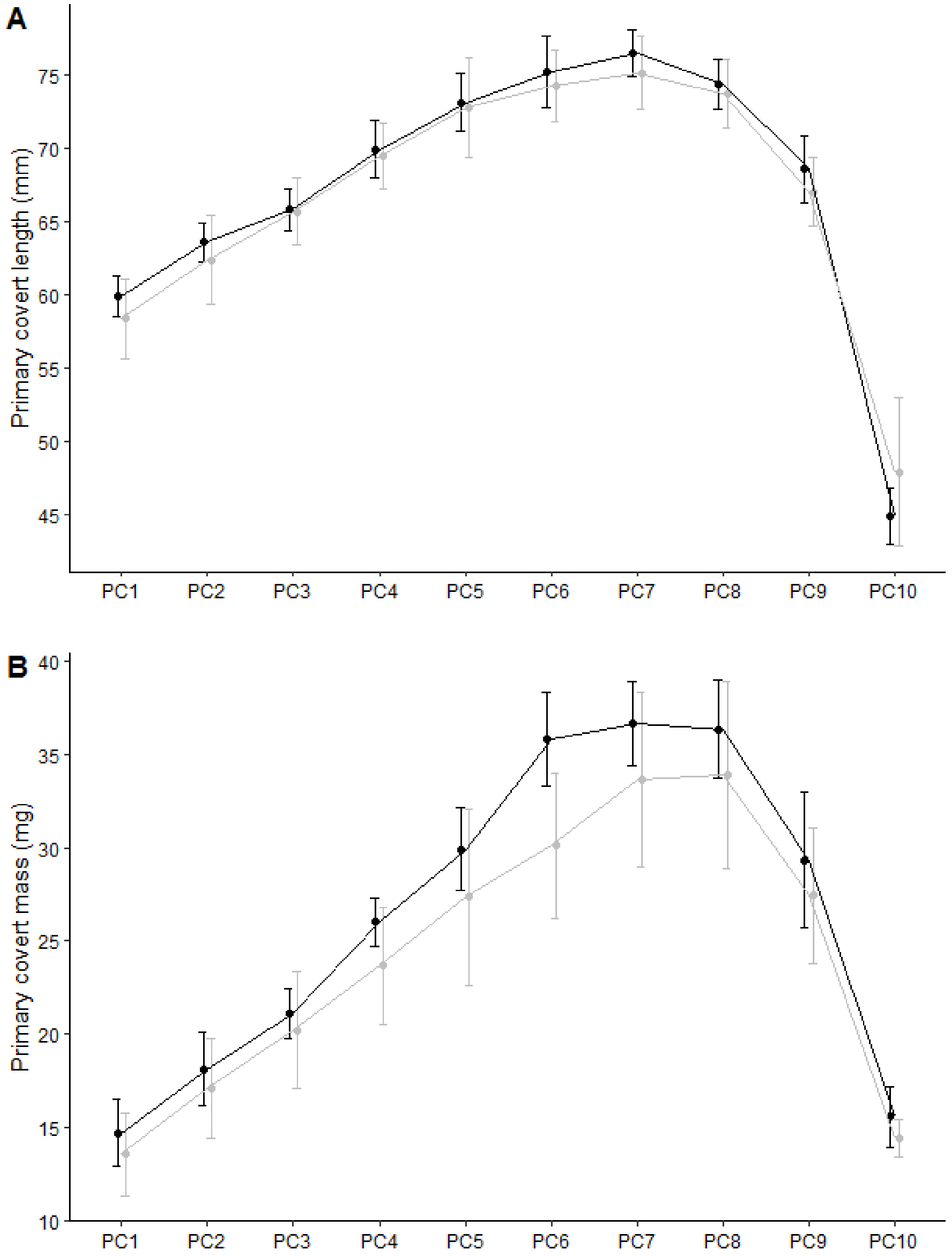


Figure 2.4: Average ± 1SD primary covert length (A) and mass (B) in adult (black) and juvenile (grey) Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa in March 2019.

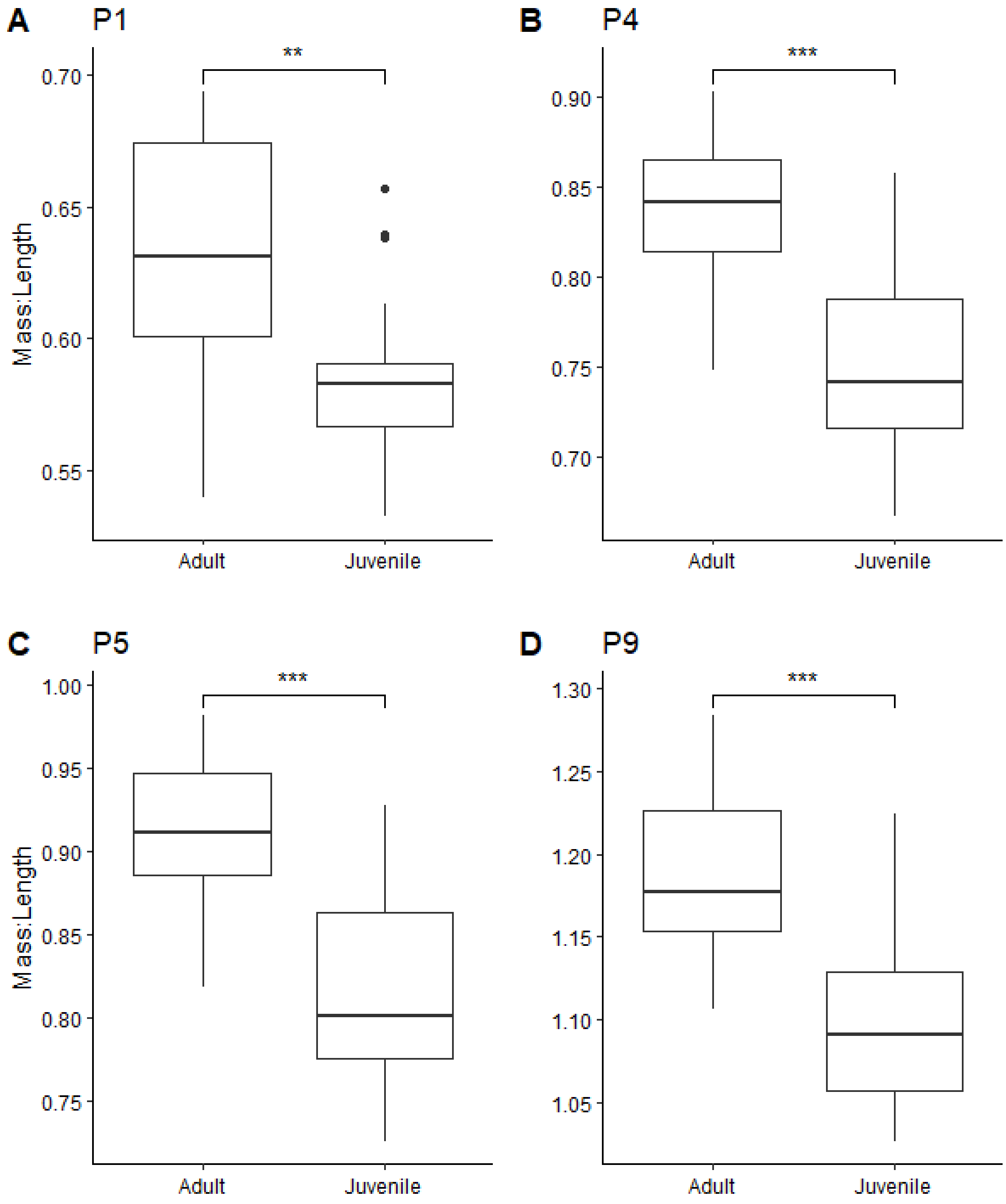


Figure 2.5: Differences between ratio of mass (mg) to length (mm) in (A) P1, (B) P4, (C) P5 and (D) P9 between 52 adult and 48 juvenile Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa in March 2019. (Bold line: median ratio of mass and length; boxes: 25th–75th percentile; whiskers: 10th/90th percentile; points: outliers; ***: comparison between groups as it relates to significance level).

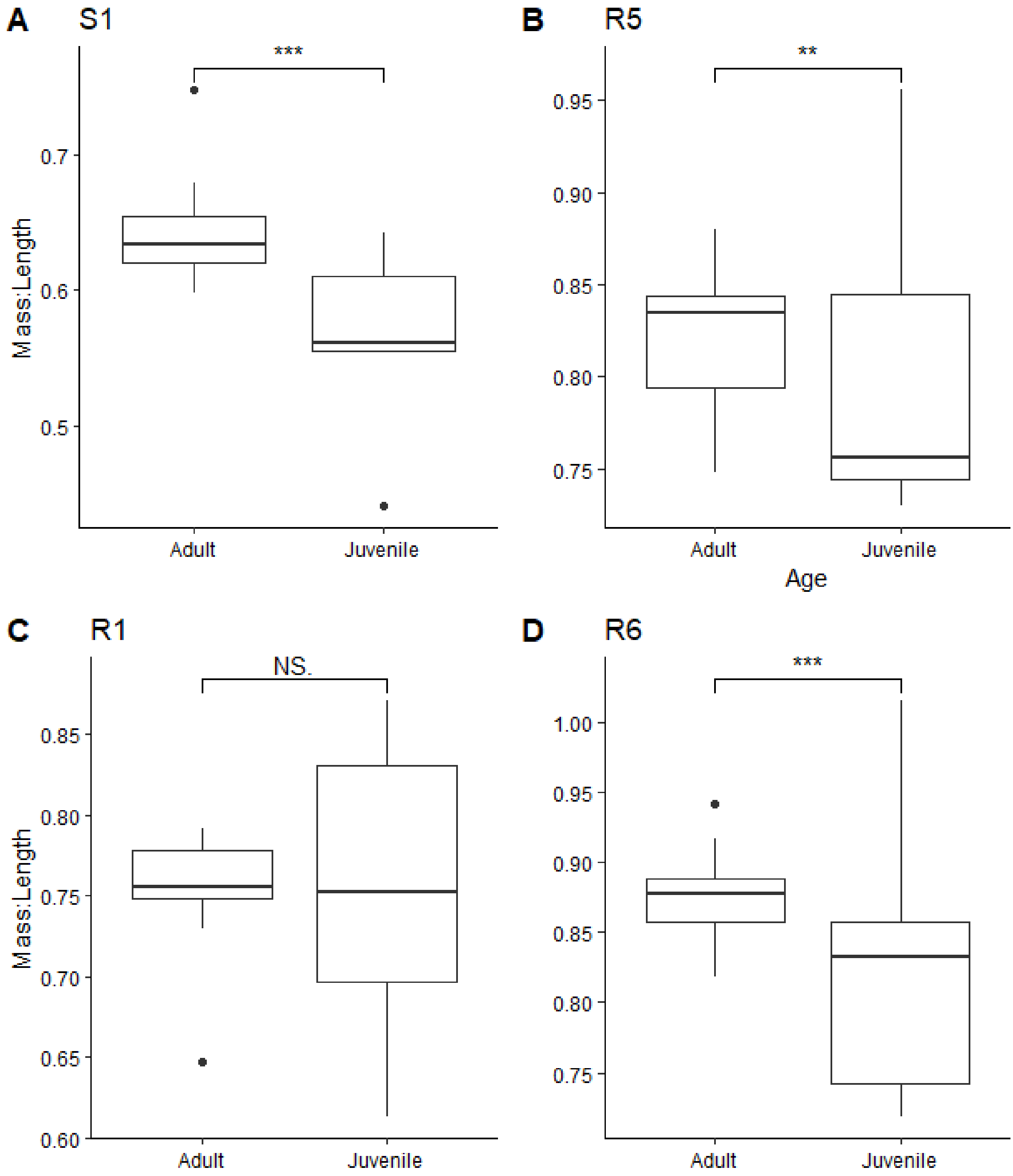


Figure 2.6: Differences between ratio of mass (mg) to length (mm) in (A) S1, (B) S5, (C) R1 and (D) R6 between 52 adult and 48 juvenile Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa in March 2019. (Bold line: median ratio of mass and length; boxes: 25th–75th percentile; whiskers: 10th/90th percentile; points: outliers; ***: comparison between groups as it relates to significance level; NS: Not significance level between groups comparison).

Table 2.1: Microstructural measurements (calamus width, rachis width, barb length, barb density and barbule density) between proximal (P1) and distal (P9) primaries, innermost secondary (S1) and central rectrix (R6) between adult, juvenile, female and male Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa in March 2019.

Parameters	Age		Sex		F	*P*
	Adult	Juvenile	Female	Male		
Calamus width (mm)						
P1	2.22 ± 0.38	2.48 ± 0.30	2.68 ± 0.30	2.02 ± 0.38	0.97	0.43
P9	2.36 ± 0.31	2.82 ± 0.24	2.79 ± 0.24	2.38 ± 0.31	1.01	0.41
S1	2.04 ± 0.43	2.62 ± 0.34	2.64 ± 0.34	2.02 ± 0.43	0.96	0.43
R6	2.08 ± 0.42	2.77 ± 0.36	2.63 ± 0.36	2.22 ± 0.42	0.79	0.49
Rachis width (mm)						
P1	1.68 ± 0.46	1.49 ± 0.36	1.66 ± 0.36	1.51 ± 0.46	0.11	0.90
P9	1.66 ± 0.51	1.80 ± 0.39	1.89 ± 0.39	1.57 ± 0.51	0.13	0.88
S1	1.20 ± 0.37	1.46 ± 0.28	1.40 ± 0.28	1.26 ± 0.37	0.17	0.85
R6	1.24 ± 0.42	1.69 ± 0.36	1.48 ± 0.36	1.45 ± 0.42	0.34	0.30
Barb length (mm)						
P1	10.40 ± 1.58	11.20 ± 1.22	11.61 ± 1.22	9.96 ± 1.58	0.37	0.71
P9	11.30 ± 2.43	11.90 ± 1.88	11.40 ± 1.88	11.80 ± 2.43	0.04	0.96
S1	12.30 ± 1.21	12.40 ± 0.94	12.70 ± 0.94	12.00 ± 1.21	0.09	0.92
R6	9.51 ± 1.06	7.25 ± 0.90	8.41 ± 0.90	8.35 ± 1.06	1.47	0.49
Barb density (n/cm)						
P1	27.23 ± 6.40	28.11 ± 6.08	28.32 ± 6.08	27.03 ± 6.40	0.32	0.74
P9	30.58 ± 7.51	28.38 ± 6.94	28.94 ± 6.94	30.02 ± 7.51	0.26	0.78
S1	26.64 ± 6.45	28.10 ± 6.12	28.27 ± 6.12	26.47 ± 6.45	0.65	0.55
R6	30.36 ± 5.97	30.63 ± 6.68	28.23 ± 6.68	30.76 ± 6.97	0.04	0.96
Barbule density (n/mm)						
P1	33.33 ± 8.38	33.26 ± 8.30	32.98 ± 8.30	33.61 ± 8.38	0.88	0.46
P9	33.02 ± 8.40	33.26 ± 8.31	33.03 ± 8.31	33.24 ± 8.40	0.25	0.78
S1	32.89 ± 8.25	33.15 ± 8.20	33.15 ± 8.20	32.90 ± 8.25	0.51	0.62
R6	33.43 ± 8.31	32.98 ± 8.27	32.94 ± 8.27	33.47 ± 8.31	1.01	0.42

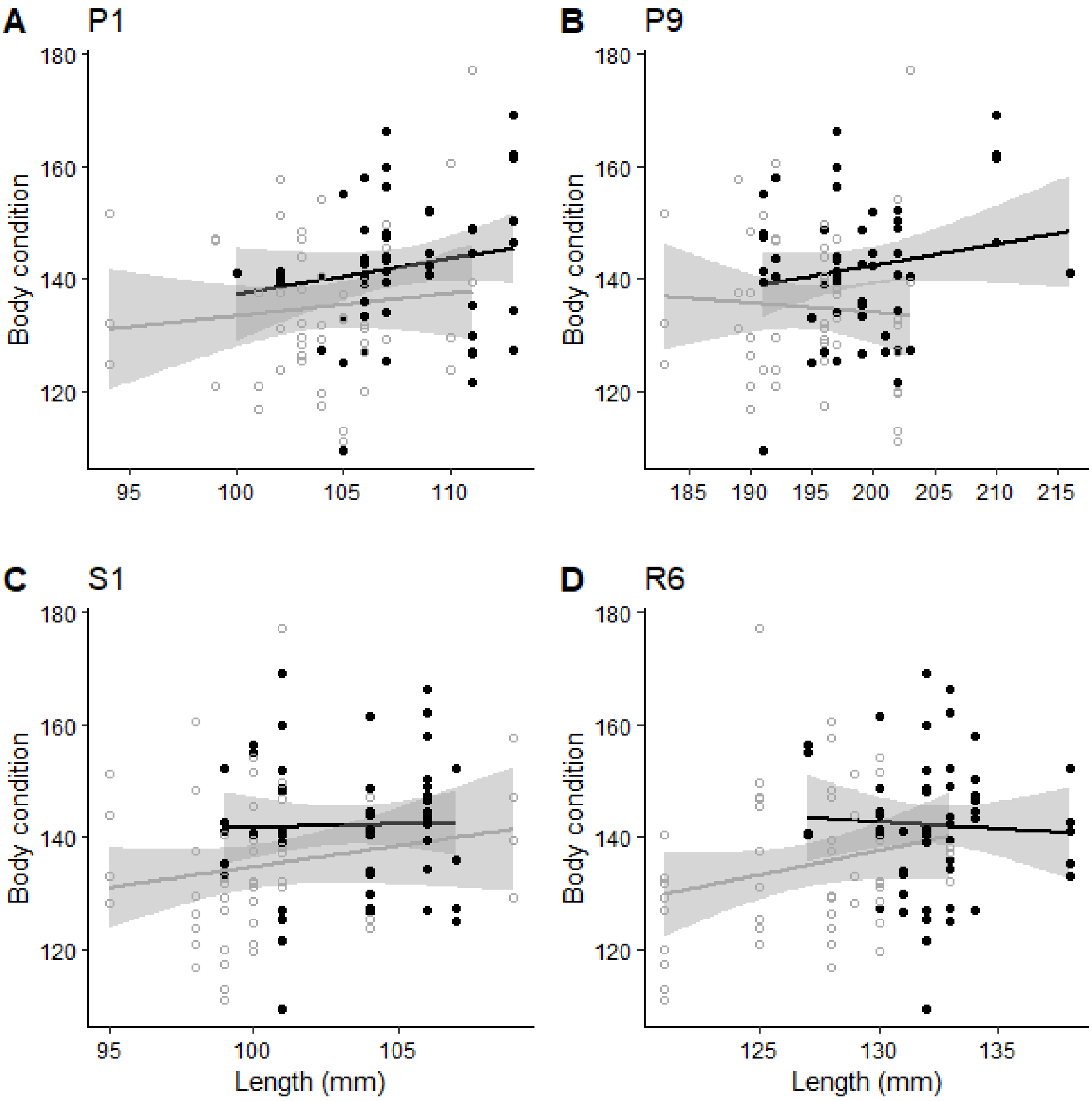


Figure 2.7: Relationships between body condition and length of (A) P1, (B) P9, (C) S1 and (D) R6 of adult (black) and juvenile (grey) Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa in March 2019.

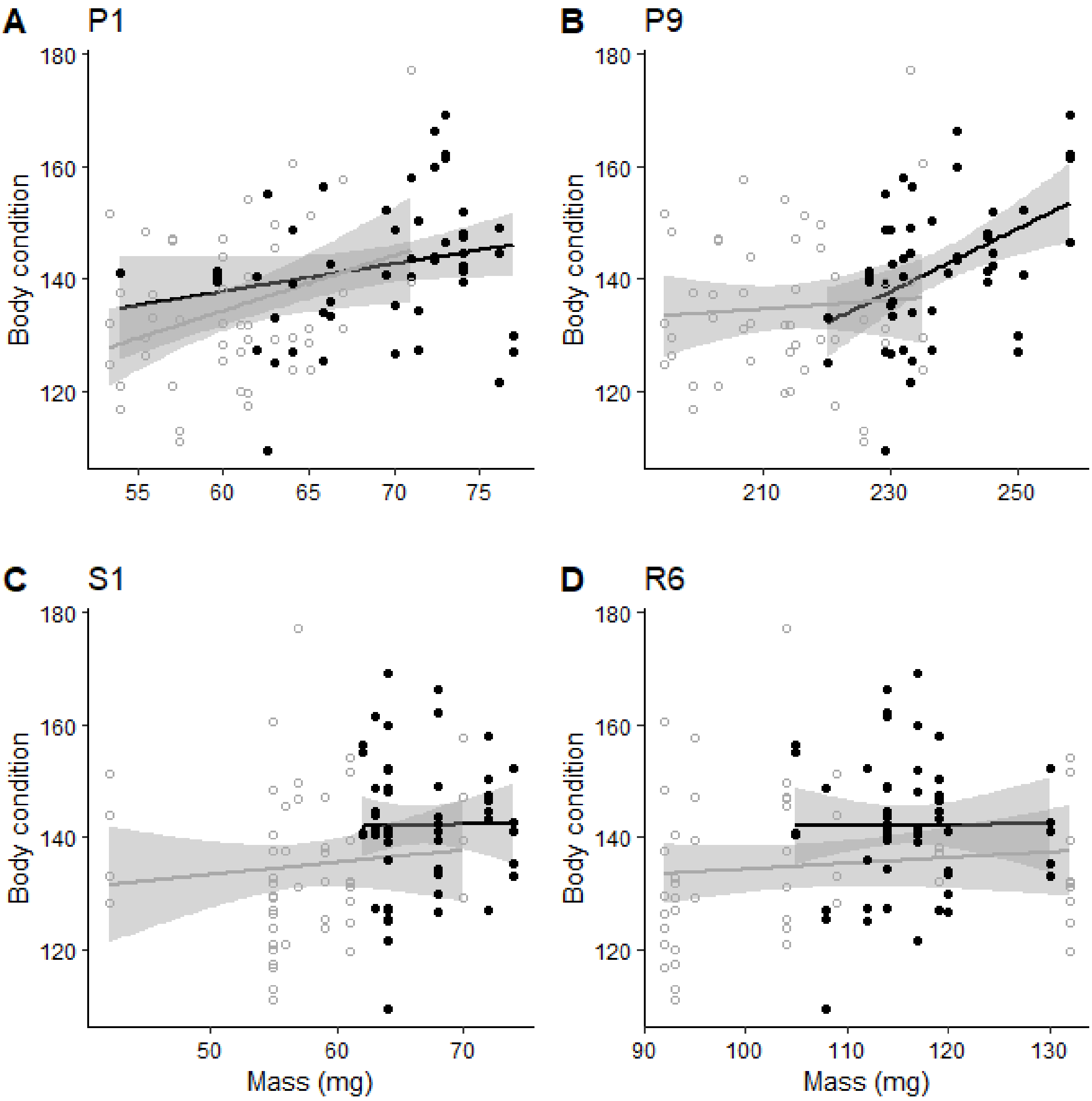


Figure 2.8: Relationships between body condition and mass of (A) P1, (B) P9, (C) S1 and (D) R6 of adult (black) and juvenile (grey) Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa in March 2019.

Supplemental material

Supplemental Table 2.1: Differences in primary length, calamus length, mass and rachis length between adult, juvenile, and female and male Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa in March 2019.

Parameters	Age		Sex		F	*P*
	Adult	Juvenile	Female	Male		
Total length (mm)						
P1	107.33 ± 1.60	103.82 ± 3.94	106.24 ± 4.15	105.06 ± 2.12	4.11	0.03
P2	114.67 ± 4.73	110.76 ± 2.05	114.29 ± 5.11	111.33 ± 2.07	5.70	0.01
P3	126.17 ± 4.60	121.94 ± 2.74	124.76 ± 5.47	123.50 ± 1.74	3.79	0.03
P4	139.61 ± 4.46	135.24 ± 1.56	138.71 ± 5.00	136.33 ± 1.79	5.39	0.01
P5	153.44 ± 4.96	147.94 ± 7.03	151.82 ± 5.58	149.78 ± 2.70	5.97	0.01
P6	167.94 ± 3.34	161.12 ± 7.34	165.18 ± 8.09	164.11 ± 4.26	4.31	0.02
P7	180.61 ± 2.19	175.18 ± 5.81	179.24 ± 2.67	176.78 ± 6.37	5.11	0.01
P8	192.56 ± 3.82	188.00 ± 6.30	191.24 ± 5.79	189.50 ± 3.18	3.24	0.05
P9	199.44 ± 2.27	194.94 ± 5.52	196.94 ± 3.32	197.56 ± 7.18	2.53	0.10
P10	186.61 ± 4.99	183.29 ± 5.91	184.00 ± 5.43	185.94 ± 6.77	1.84	0.17
Calamus length (mm)						
P1	21.33 ± 2.06	21.88 ± 2.29	21.29 ± 2.02	21.89 ± 2.30	0.58	0.56
P2	24.05 ± 1.62	24.76 ± 2.41	24.12 ± 2.06	24.67 ± 2.06	0.81	0.46
P3	26.33 ± 2.52	26.18 ± 1.91	26.18 ± 1.59	26.33 ± 2.72	0.04	0.96
P4	27.78 ± 1.86	26.94 ± 3.19	27.35 ± 3.24	27.39 ± 1.88	0.44	0.65
P5	29.61 ± 2.03	29.29 ± 2.02	29.88 ± 2.15	29.06 ± 1.83	0.83	0.45
P6	30.39 ± 1.72	29.64 ± 3.24	30.76 ± 1.92	29.33 ± 2.93	1.77	0.19
P7	30.06 ± 2.73	29.88 ± 2.42	30.00 ± 3.18	29.94 ± 1.86	0.02	0.98
P8	30.89 ± 2.25	30.29 ± 2.64	30.47 ± 2.50	30.72 ± 2.42	0.30	0.74
P9	27.72 ± 2.51	27.35 ± 3.08	27.06 ± 3.36	28.00 ± 2.06	0.58	0.57
P10	22.67 ± 2.99	22.76 ± 1.75	22.88 ± 3.10	22.56 ± 1.65	0.08	0.92
Mass (mg)						

P1	68.09 ± 6.27	60.70 ± 4.86	66.73 ± 6.61	62.39 ± 3.23	11.15	< 0.001
P2	80.82 ± 3.57	69.21 ± 6.32	77.71 ± 9.32	72.80 ± 7.48	18.29	< 0.001
P3	97.32 ± 5.94	83.58 ± 8.47	93.14 ± 11.25	88.29 ± 9.82	14.25	< 0.001
P4	117.18 ± 5.19	101.62 ± 9.66	112.37 ± 12.13	107.03 ± 10.23	15.64	< 0.001
P5	140.08 ± 9.25	120.61 ± 11.04	133.43 ± 11.95	127.97 ± 14.04	17.13	< 0.001
P6	165.99 ± 9.50	142.71 ± 12.66	157.90 ± 12.95	151.64 ± 16.14	20.95	< 0.001
P7	191.97 ± 11.34	166.28 ± 13.39	184.02 ± 10.87	175.21 ± 17.20	22.60	< 0.001
P8	218.67 ± 10.88	194.03 ± 13.18	208.82 ± 17.08	204.87 ± 10.51	18.10	< 0.001
P9	236.73 ± 9.86	213.64 ± 12.56	226.51 ± 16.32	224.58 ± 12.32	17.97	< 0.001
P10	220.02 ± 6.66	201.05 ± 14.64	210.02 ± 13.34	211.54 ± 16.20	12.29	< 0.001
Rachis length (mm)						
P1	86.00 ± 3.25	81.94 ± 5.45	84.94 ± 4.28	83.17 ± 2.38	7.75	0.00
P2	90.61 ± 6.72	86.00 ± 3.50	90.18 ± 7.79	86.67 ± 4.10	9.62	0.00
P3	99.83 ± 6.60	95.76 ± 4.10	98.59 ± 5.16	97.17 ± 8.44	3.25	0.05
P4	111.83 ± 3.99	101.62 ± 5.79	111.35 ± 4.96	108.94 ± 8.22	4.22	0.02
P5	123.83 ± 4.38	118.65 ± 7.72	121.94 ± 3.93	120.72 ± 5.51	5.83	0.01
P6	137.56 ± 5.90	131.47 ± 7.53	134.41 ± 9.57	134.78 ± 7.30	3.49	0.04
P7	150.56 ± 5.44	145.29 ± 8.39	149.24 ± 5.51	146.83 ± 8.30	4.96	0.01
P8	161.67 ± 7.67	157.71 ± 5.77	160.76 ± 5.89	158.78 ± 8.07	2.56	0.09
P9	171.72 ± 6.96	167.59 ± 3.88	169.88 ± 5.45	169.56 ± 7.86	1.74	0.19
P10	163.94 ± 6.14	160.53 ± 8.56	161.12 ± 5.54	163.39 ± 7.25	1.89	0.17

Supplemental Table 2.2: Differences in secondary total length, calamus length, mass and rachis length between adult, juvenile, and female and male Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa in March 2019.

Parameters	Age		Sex		F	*P*
	Adult	Juvenile	Female	Male		
Total length (mm)						
S1	103.11 ± 2.93	100.78 ± 3.93	102.70 ± 3.95	101.00 ± 3.02	2.11	0.16
S2	104.11 ± 2.26	101.67 ± 4.71	104.20 ± 5.66	101.25 ± 3.28	6.75	0.01
S3	101.89 ± 3.37	99.22 ± 2.99	101.20 ± 3.43	99.75 ± 3.37	2.71	0.10
S4	99.44 ± 3.28	97.22 ± 2.39	99.10 ± 2.88	97.38 ± 3.07	2.70	0.12
S5	97.33 ± 3.28	94.33 ± 2.40	96.40 ± 4.13	95.13 ± 3.31	3.13	0.07
S6	95.89 ± 2.71	92.78 ± 3.28	94.80 ± 4.12	93.75 ± 2.71	3.83	0.05
S7	94.89 ± 5.93	92.11 ± 2.71	94.10 ± 6.18	92.75 ± 3.01	5.04	0.02
S8	94.33 ± 5.46	90.78 ± 2.99	93.30 ± 5.77	91.63 ± 3.46	4.62	0.03
S9	94.00 ± 6.00	90.22 ± 3.27	92.70 ± 5.92	91.38 ± 3.29	4.78	0.02
S10	92.22 ± 5.54	89.00 ± 3.61	91.60 ± 4.75	89.90 ± 2.77	5.71	0.01
S11	89.00 ± 3.08	84.22 ± 4.94	86.90 ± 5.86	86.25 ± 3.01	3.40	0.06
Calamus length (mm)						
S1	16.33 ± 2.29	17.33 ± 2.24	16.80 ± 1.87	16.88 ± 2.80	0.45	0.64
S2	16.33 ± 1.41	17.78 ± 1.92	17.70 ± 1.77	16.25 ± 1.58	2.90	0.09
S3	17.00 ± 1.66	17.22 ± 1.48	17.10 ± 1.20	17.13 ± 1.96	0.05	0.95
S4	17.11 ± 1.62	16.22 ± 1.30	16.60 ± 1.35	17.00 ± 1.69	0.96	0.41
S5	15.67 ± 1.12	15.44 ± 0.73	15.80 ± 0.79	15.25 ± 1.04	1.14	0.35
S6	15.56 ± 1.01	15.44 ± 1.33	15.60 ± 1.26	15.38 ± 0.92	0.12	0.89
S7	15.33 ± 0.87	15.44 ± 1.59	15.40 ± 1.51	15.38 ± 0.92	0.02	0.98
S8	15.67 ± 1.87	15.00 ± 1.50	15.20 ± 1.40	15.50 ± 2.07	0.34	0.71
S9	15.22 ± 0.83	15.33 ± 1.87	15.80 ± 1.62	14.63 ± 0.74	1.71	0.21
S10	14.00 ± 0.71	14.67 ± 1.50	14.70 ± 1.49	13.88 ± 0.35	1.56	0.24
S11	13.33 ± 1.12	13.67 ± 2.29	13.20 ± 1.62	13.88 ± 1.96	0.48	0.63
Mass (mg)						

S1	66.56 ± 4.22	57.11 ± 7.30	61.00 ± 8.65	62.88 ± 6.33	5.30	0.02
S2	66.14 ± 4.20	59.56 ± 6.98	63.33 ± 4.35	62.25 ± 7.17	5.49	0.02
S3	60.67 ± 3.71	54.89 ± 6.04	58.10 ± 4.75	57.38 ± 6.15	5.73	0.01
S4	56.93 ± 3.47	50.44 ± 5.59	54.64 ± 8.59	52.50 ± 5.78	6.56	0.01
S5	53.11 ± 2.98	45.89 ± 4.99	50.10 ± 6.08	48.75 ± 4.83	9.07	0.00
S6	50.00 ± 3.16	43.67 ± 6.46	47.30 ± 7.01	46.25 ± 4.59	4.07	0.04
S7	48.12 ± 2.90	42.33 ± 5.96	45.81 ± 6.30	44.50 ± 4.44	4.29	0.03
S8	47.56 ± 6.57	40.56 ± 4.45	44.90 ± 5.93	43.00 ± 4.60	10.19	0.00
S9	45.89 ± 6.37	39.44 ± 4.50	43.10 ± 5.59	42.13 ± 4.70	7.13	0.01
S10	45.44 ± 2.51	38.89 ± 5.37	42.40 ± 6.99	41.88 ± 3.94	13.00	0.00
S11	42.02 ± 3.76	34.89 ± 6.60	37.82 ± 7.52	39.25 ± 4.98	3.72	0.05
Rachis length (mm)						
S1	86.78 ± 2.05	83.44 ± 4.03	85.90 ± 6.48	84.13 ± 3.60	4.47	0.03
S2	87.78 ± 1.92	83.89 ± 3.06	86.50 ± 2.80	85.00 ± 4.63	9.08	0.00
S3	84.89 ± 4.62	82.00 ± 2.60	84.10 ± 5.18	82.63 ± 2.56	5.02	0.02
S4	82.33 ± 3.35	81.00 ± 1.94	82.70 ± 5.16	80.38 ± 2.97	3.44	0.06
S5	81.67 ± 3.00	78.89 ± 1.90	80.60 ± 1.72	79.88 ± 3.09	3.51	0.06
S6	80.33 ± 2.24	77.33 ± 1.73	79.20 ± 2.35	78.38 ± 5.72	7.16	0.01
S7	79.56 ± 5.51	76.67 ± 2.18	78.70 ± 6.58	77.38 ± 2.88	5.98	0.01
S8	78.67 ± 3.20	75.78 ± 2.54	78.10 ± 4.51	76.13 ± 2.47	5.17	0.02
S9	78.78 ± 2.54	74.89 ± 3.62	76.90 ± 4.31	76.75 ± 2.87	3.61	0.05
S10	78.22 ± 4.49	74.33 ± 2.92	76.90 ± 5.70	75.50 ± 2.78	7.41	0.01
S11	75.67 ± 2.83	70.56 ± 4.71	73.70 ± 6.79	72.38 ± 3.34	7.53	0.01

Supplemental Table 2.3: Differences in rectrix total length, calamus length, mass and rachis length between adult, juvenile, and female and male Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa in March 2019.

Parameters	Age		Sex		F	*P*
	Adult	Juvenile	Female	Male		
Total length (mm)						
R1	135.67 ± 5.89	131.33 ± 4.64	133.80 ± 5.63	133.13 ± 5.94	1.67	0.22
R2	135.22 ± 4.68	131.11 ± 5.73	132.50 ± 5.82	134.00 ± 5.35	1.33	0.29
R3	136.78 ± 2.82	131.67 ± 5.55	133.90 ± 5.02	134.63 ± 5.32	2.88	0.09
R4	138.22 ± 2.54	131.44 ± 5.77	135.00 ± 5.64	134.63 ± 5.83	5.57	0.02
R5	137.89 ± 3.33	132.44 ± 4.56	135.60 ± 3.75	134.63 ± 6.07	5.03	0.02
R6	132.22 ± 2.99	127.11 ± 3.52	129.40 ± 3.57	130.00 ± 4.96	5.28	0.02
Calamus length (mm)						
R1	16.78 ± 1.30	17.33 ± 2.60	17.30 ± 2.06	16.75 ± 2.05	0.25	0.78
R2	16.22 ± 1.09	16.78 ± 2.22	16.60 ± 1.96	16.38 ± 1.51	0.22	0.81
R3	15.22 ± 1.09	16.44 ± 1.81	16.00 ± 1.76	15.63 ± 1.41	1.42	0.27
R4	15.56 ± 2.01	16.11 ± 1.36	15.80 ± 1.62	15.88 ± 1.89	0.25	0.78
R5	15.22 ± 0.44	16.44 ± 1.59	16.00 ± 1.49	15.63 ± 1.06	2.34	0.13
R6	14.11 ± 0.60	14.89 ± 0.93	14.60 ± 0.70	14.38 ± 1.06	2.10	0.16
Mass (mg)						
R1	101.89 ± 9.44	96.44 ± 9.00	95.20 ± 9.47	104.13 ± 6.90	2.84	0.09
R2	103.92 ± 10.12	97.89 ± 14.29	97.33 ± 12.96	105.38 ± 10.80	1.25	0.32
R3	106.79 ± 5.06	97.11 ± 13.55	100.41 ± 11.60	103.88 ± 10.89	1.93	0.18
R4	110.44 ± 5.96	100.89 ± 13.50	105.20 ± 11.11	106.25 ± 12.17	1.80	0.20
R5	113.69 ± 7.91	105.56 ± 13.02	108.92 ± 9.23	110.50 ± 14.02	1.20	0.33
R6	115.44 ± 7.32	105.78 ± 12.99	109.90 ± 8.01	111.50 ± 15.18	1.78	0.20
Rachis length (mm)						
R1	118.89 ± 5.35	114.00 ± 4.06	116.50 ± 5.95	116.38 ± 4.63	2.43	0.12
R2	119.00 ± 4.44	114.33 ± 4.56	115.90 ± 5.45	117.63 ± 4.50	2.33	0.13
R3	121.56 ± 2.60	115.22 ± 4.49	117.90 ±4.72	119.00 ± 5.21	6.31	0.01

R4	122.67 ± 2.24	115.33 ± 4.97	119.20 ± 5.71	118.75 ± 5.15	9.06	0.00
R5	122.67 ± 3.16	116.00 ± 4.15	119.60 ± 4.17	119.00 ± 6.09	8.38	0.00
R6	118.11 ± 2.85	112.22 ± 2.99	114. 80 ± 3.46	115.63 ± 5.10	8.72	0.00

Supplemental Table 2.4: Differences in primary covert total length, calamus length, mass and rachis length between adult, juvenile, and female and male Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa in March 2019.

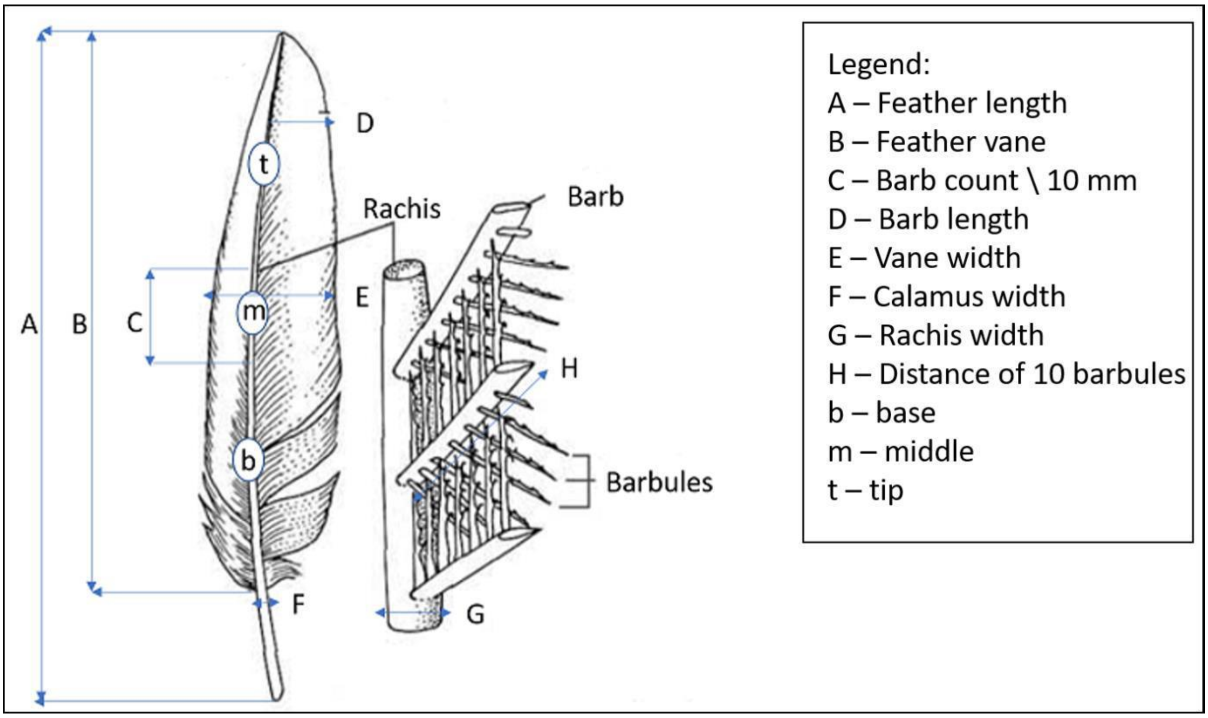
Parameters	Age		Sex		F	*P*
	Adult	Juvenile	Female	Male		
Total length (mm)						
PC1	59.89 ± 1.36	58.33 ± 2.69	59.30 ± 2.45	58.88 ± 2.03	1.47	0.26
PC2	63.56 ± 1.33	62.33 ± 3.04	63.40 ± 2.27	62.38 ± 2.50	1.37	0.29
PC3	65.78 ± 1.48	65.67 ± 2.29	66.20 ± 1.69	65.13 ± 2.03	0.80	0.47
PC4	69.89 ± 1.96	69.44 ± 2.24	69.80 ± 1.93	69.50 ± 2.33	0.20	0.66
PC5	73.11 ± 1.96	72.78 ± 3.38	73.60 ± 3.06	72.13 ± 2.03	0.17	0.84
PC6	75.22 ± 2.44	74.22 ± 2.44	75.10 ± 2.92	74.25 ± 1.67	0.79	0.47
PC7	76.44 ± 1.59	75.11 ± 2.53	76.10 ± 2.33	75.38 ± 2.00	1.46	0.26
PC8	74.33 ± 1.73	73.67 ± 2.35	74.30 ± 2.00	73.63 ± 2.13	0.60	0.56
PC9	68.56 ± 2.30	67.00 ± 2.35	67.90 ± 2.92	67.63 ± 1.69	1.13	0.35
PC10	44.89 ± 1.90	47.89 ± 5.06	45.80 ± 2.78	47.13 ± 5.30	2.07	0.16
Calamus length (mm)						
PC1	14.33 ± 0.50	14.00 ± 1.41	14.00 ± 1.15	14.38 ± 0.92	0.39	0.68
PC2	15.89 ± 1.05	16.22 ± 2.40	16.00 ± 1.05	16.25 ± 2.55	0.20	0.82
PC3	16.33 ± 1.22	16.89 ± 1.05	16.90 ± 1.10	16.25 ± 1.16	1.03	0.38
PC4	18.78 ± 0.83	18.00 ± 1.00	18.30 ± 0.95	18.50 ± 1.07	1.51	0.25
PC5	20.00 ± 0.71	20.22 ± 3.46	20.50 ± 3.17	19.63 ± 0.92	0.27	0.77
PC6	20.67 ± 0.87	20.11 ± 0.78	20.40 ±0.97	20.38 ± 0.74	1.04	0.38
PC7	20.22 ± 0.97	20.22 ± 0.44	20.20 ± 0.79	20.50 ± 0.71	0.01	0.90
PC8	19.78 ± 1.09	19.56 ± 0.88	19.60 ± 0.97	19.75 ± 1.04	0.23	0.64
PC9	17.67 ± 1.00	16.44 ± 1.01	16.80 ± 1.48	17.38 ± 0.52	3.63	0.06
PC10	9.44 ± 0.53	9.78 ± 0.44	9.50 ± 0.53	9.75 ± 0.46	2.27	0.14
Mass (mg)						
PC1	14.70 ± 1.81	13.56 ± 2.19	14.83 ± 2.05	13.25 ± 1.75	3.34	0.06
PC2	18.11 ± 1.96	17.11 ± 2.67	18.40 ± 2.27	16.63 ± 2.13	2.52	0.11

PC3	21.11 ± 1.36	20.22 ± 3.15	21.10 ± 2.56	20.13 ± 2.23	0.85	0.45
PC4	26.00 ± 1.32	23.67 ± 3.12	25.10 ± 2.47	24.50 ± 2.93	2.65	0.10
PC5	29.91 ± 2.23	27.33 ± 4.69	29.02 ± 4.36	28.13 ± 3.18	2.22	0.16
PC6	35.80 ± 2.49	30.11 ± 3.89	32.42 ± 4.81	33.63 ± 3.81	6.41	0.01
PC7	36.67 ± 2.24	33.67 ± 4.69	35.80 ± 4.29	34.38 ± 3.42	3.00	0.10
PC8	36.34 ± 2.65	33.89 ± 5.01	35.51 ±4.75	34.63 ± 3.33	1.69	0.21
PC9	29.33 ± 3.64	27.44 ± 3.64	29.30 ± 3.92	27.25 ± 3.20	1.21	0.19
PC10	15.56 ± 1.67	14.44 ± 1.01	14.90 ± 1.52	15.13 ± 1.46	2.92	0.11
Rachis length (mm)						
PC1	45.56 ± 1.51	44.33 ± 1.87	45.30 ± 1.83	44.50 ± 1.69	2.33	0.15
PC2	47.67 ± 1.50	46.00 ± 2.74	47.40 ± 1.78	46.13 ± 2.80	2.56	0.09
PC3	49.44 ± 1.01	48.78 ± 1.56	49.30 ± 1.16	48.88 ± 1.55	1.15	0.30
PC4	51.11 ± 2.03	51.44 ± 1.51	51.50 ± 1.58	51.00 ± 2.00	0.16	0.70
PC5	53.11 ± 1.69	52.56 ± 1.42	53.10 ± 1.66	52.50 ± 1.41	0.57	0.46
PC6	54.56 ± 2.24	54.11 ± 1.90	54.70 ± 2.45	53.88 ± 1.36	0.21	0.66
PC7	56.22 ± 2.04	54.89 ± 2.26	55.90 ± 2.42	55.13 ± 1.96	1.72	0.21
PC8	54.56 ± 1.81	54.11 ± 2.15	54.70 ± 2.06	53.88 ± 1.81	0.23	0.64
PC9	50.89 ± 2.15	50.56 ± 2.60	51.10 ± 2.81	50.25 ± 1.58	0.38	0.67
PC10	35.44 ± 1.81	38.11 ± 5.01	36.30 ± 2.63	37.38 ± 5.24	2.25	0.15

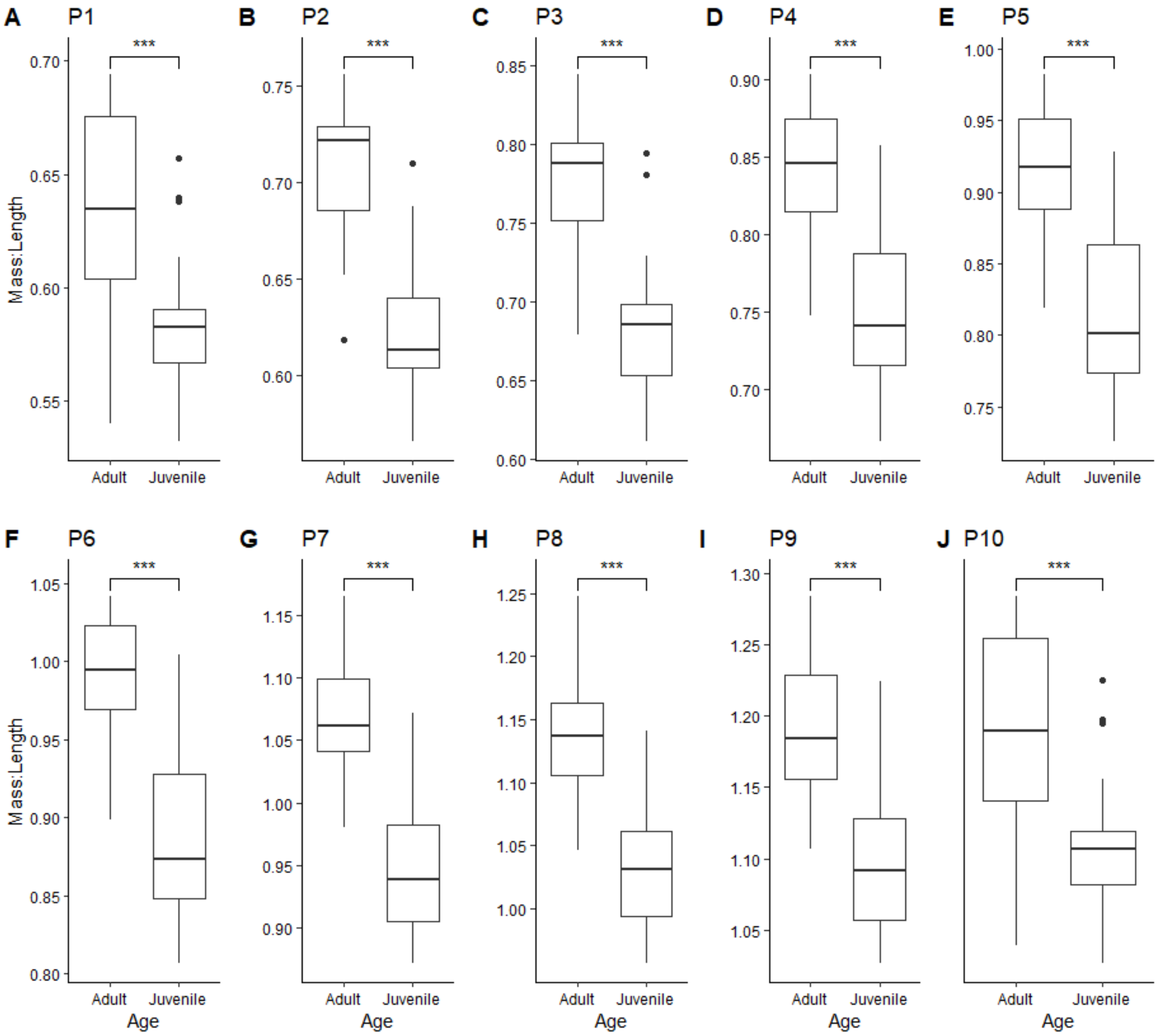
Supplemental Table 2.5: Ratio of mass to length across primaries, secondaries, rectrices and primary coverts between covert total length, calamus length, mass and rachis length between adult, juvenile, and female and male Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa in March 2019.

Parameters	Age		Sex		F	*P*
	Adult	Juvenile	Female	Male		
Primaries						
P1	0.63 ± 0.14	0.59 ± 0.03	0.63 ± 0.15	0.59 ± 0.04	11.31	0.00
P2	0.70 ± 0.14	0.63 ± 0.04	0.68 ± 0.16	0.65 ± 0.05	21.32	< 0.001
P3	0.77 ± 0.14	0.69 ± 0.04	0.74 ± 0.17	0.71 ± 0.06	19.35	< 0.001
P4	0.84 ± 0.14	0.75 ± 0.05	0.81 ± 0.17	0.78 ± 0.06	16.41	< 0.001
P5	0.91 ± 0.14	0.82 ± 0.05	0.87 ± 0.17	0.85 ± 0.07	18.50	< 0.001
P6	0.99 ± 0.14	0.89 ± 0.05	0.95 ± 0.27	0.92 ± 0.07	24.77	< 0.001
P7	1.06 ± 0.15	0.95 ± 0.05	1.02 ± 0.18	0.99 ± 0.07	26.04	< 0.001
P8	1.14 ± 0.15	1.03 ± 0.05	1.09 ± 0.18	1.08 ± 0.07	17.02	< 0.001
P9	1.19 ± 0.15	1.10 ± 0.05	1.15 ± 0.17	1.14 ± 0.07	14.46	< 0.001
P10	1.18 ± 0.14	1.10 ± 0.04	1.14 ± 0.17	1.14 ± 0.07	11.18	< 0.001
Secondaries						
S1	0.65 ± 0.14	0.58 ± 0.05	0.60 ± 0.17	0.61 ± 0.06	5.74	0.01
S2	0.64 ± 0.13	0.58 ± 0.03	0.61 ± 0.13	0.61 ± 0.05	4.97	0.02
S3	0.60 ± 0.12	0.55 ± 0.03	0.58 ± 0.13	0.57 ± 0.04	6.20	0.01
S4	0.57 ± 0.12	0.51 ± 0.04	0.56 ± 0.14	0.53 ± 0.05	7.01	0.01
S5	0.55 ± 0.12	0.48 ± 0.03	0.53 ± 0.15	0.50 ± 0.04	7.58	0.01
S6	0.52 ± 0.12	0.47 ± 0.04	0.50 ± 0.16	0.49 ± 0.04	3.30	0.06
S7	0.51 ± 0.12	0.46 ± 0.04	0.49 ± 0.16	0.47 ± 0.03	3.83	0.04
S8	0.51 ± 0.12	0.44 ± 0.03	0.49 ± 0.15	0.46 ± 0.03	12.49	0.00
S9	0.49 ± 0.12	0.43 ± 0.03	0.47 ± 0.14	0.45 ± 0.04	7.59	0.01
S10	0.49 ± 0.12	0.44 ± 0.02	0.47 ± 0.14	0.46 ± 0.03	17.05	< 0.001
S11	0.47 ± 0.13	0.41 ± 0.05	0.44 ± 0.16	0.45 ± 0.04	4.05	0.04
Rectrices						

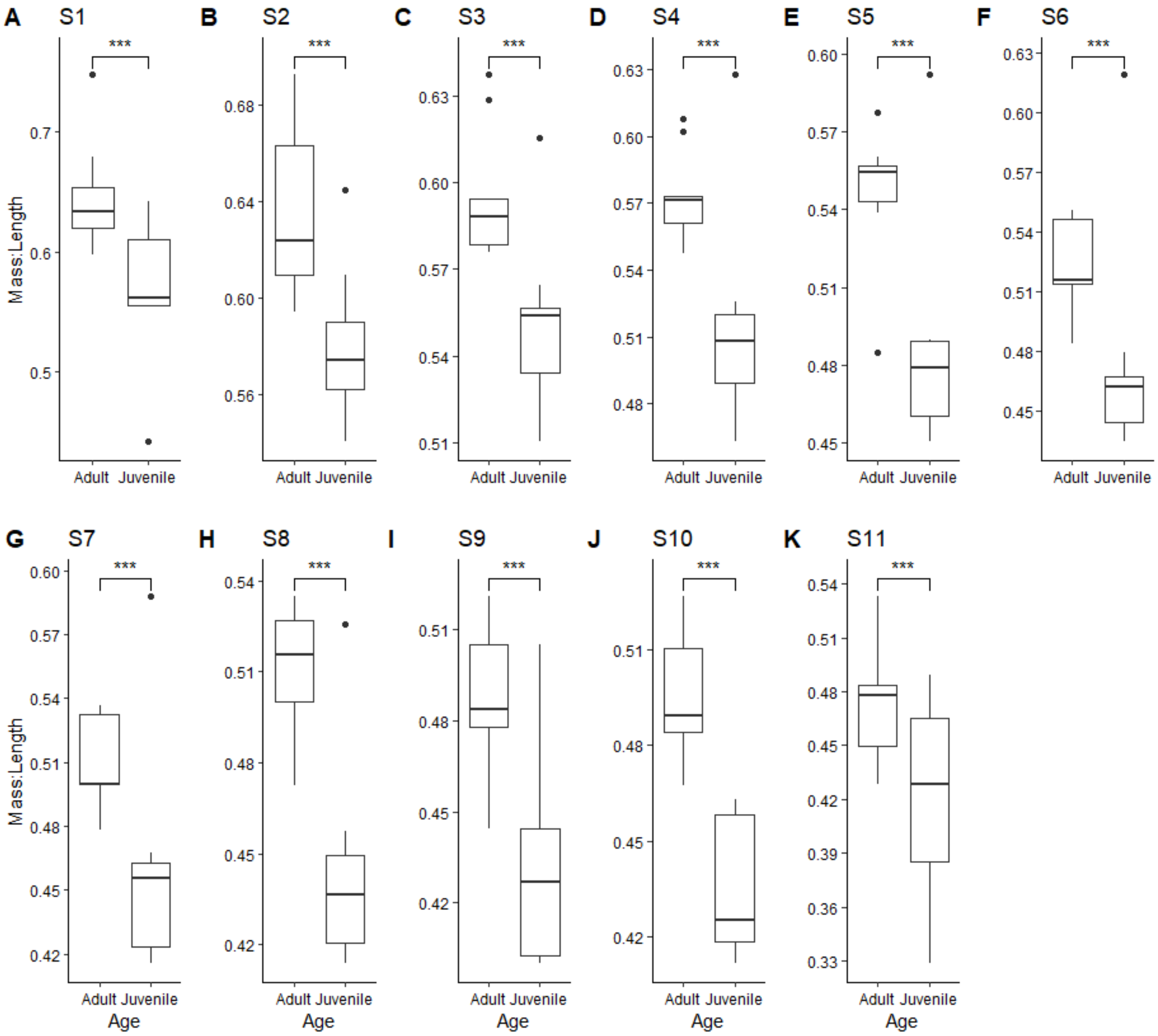
R1	0.75 ± 0.04	0.75 ± 0.08	0.71 ± 0.05	0.78 ± 0.25	4.33	0.03
R2	0.76 ± 0.05	0.75 ± 0.07	0.73 ± 0.07	0.78 ± 0.06	1.54	0.25
R3	0.78 ± 0.03	0.74 ± 0.07	0.75 ± 0.06	0.77 ± 0.06	1.43	0.27
R4	0.80 ± 0.03	0.77 ± 0.07	0.78 ± 0.06	0.78 ± 0.06	0.77	0.48
R5	0.82 ± 0.04	0.80 ± 0.08	0.81 ± 0.05	0.82 ± 0.08	0.31	0.74
R6	0.87 ± 0.03	0.83 ± 0.10	0.85 ± 0.05	0.85 ± 0.10	0.59	0.57
Primary coverts						
PC1	0.25 ± 0.03	0.23 ± 0.03	0.25 ± 0.13	0.22 ± 0.03	3.86	0.04
PC2	0.29 ± 0.03	0.27 ± 0.03	0.29 ± 0.03	0.26 ± 0.03	2.11	0.16
PC3	0.32 ± 0.02	0.31 ± 0.04	0.32 ± 0.04	0.31 ± 0.03	0.71	0.51
PC4	0.37 ± 0.12	0.34 ± 0.03	0.36 ± 0.03	0.35 ± 0.04	3.35	0.06
PC5	0.41 ± 0.02	0.37 ± 0.04	0.40 ± 0.04	0.39 ± 0.04	2.13	0.15
PC6	0.48 ± 0.13	0.41 ± 0.04	0.44 ± 0.06	0.44 ± 0.05	7.72	0.00
PC7	0.48 ± 0.02	0.44 ± 0.05	0.47 ± 0.05	0.45 ± 0.04	2.05	0.16
PC8	0.49 ± 0.03	0.46 ± 0.05	0.48 ± 0.06	0.47 ± 0.04	1.03	0.38
PC9	0.43 ± 0.04	0.40 ± 0.04	0.43 ± 0.04	0.40 ± 0.04	1.85	0.19
PC10	0.35 ± 0.13	0.30 ± 0.02	0.33 ± 0.03	0.32 ± 0.04	5.53	0.02



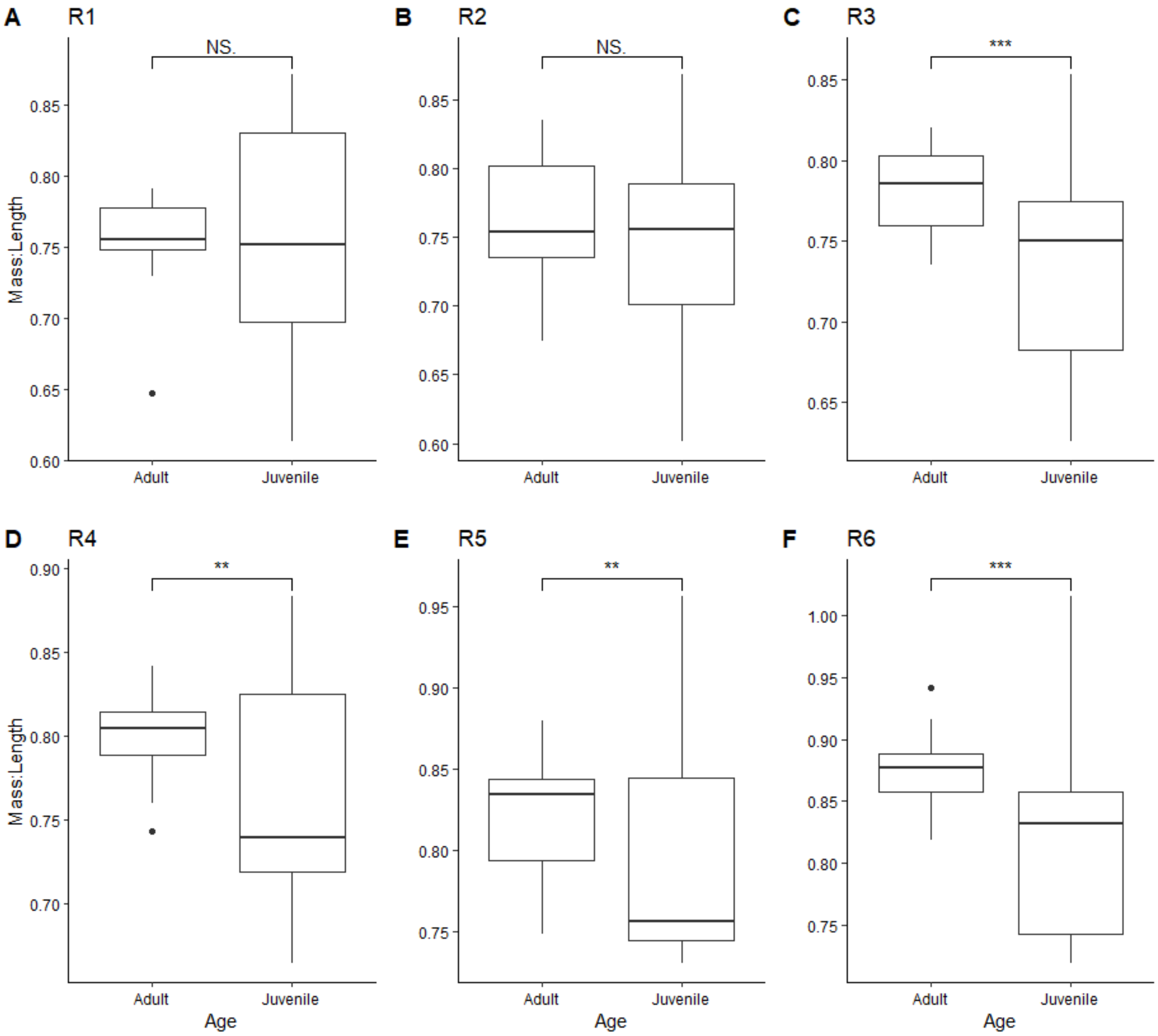
Supplemental Figure 2.1: The structure of a pennaceous feather (adapted from Cecile Duray-Bito, courtesy of Google images; from Moloto 2019)



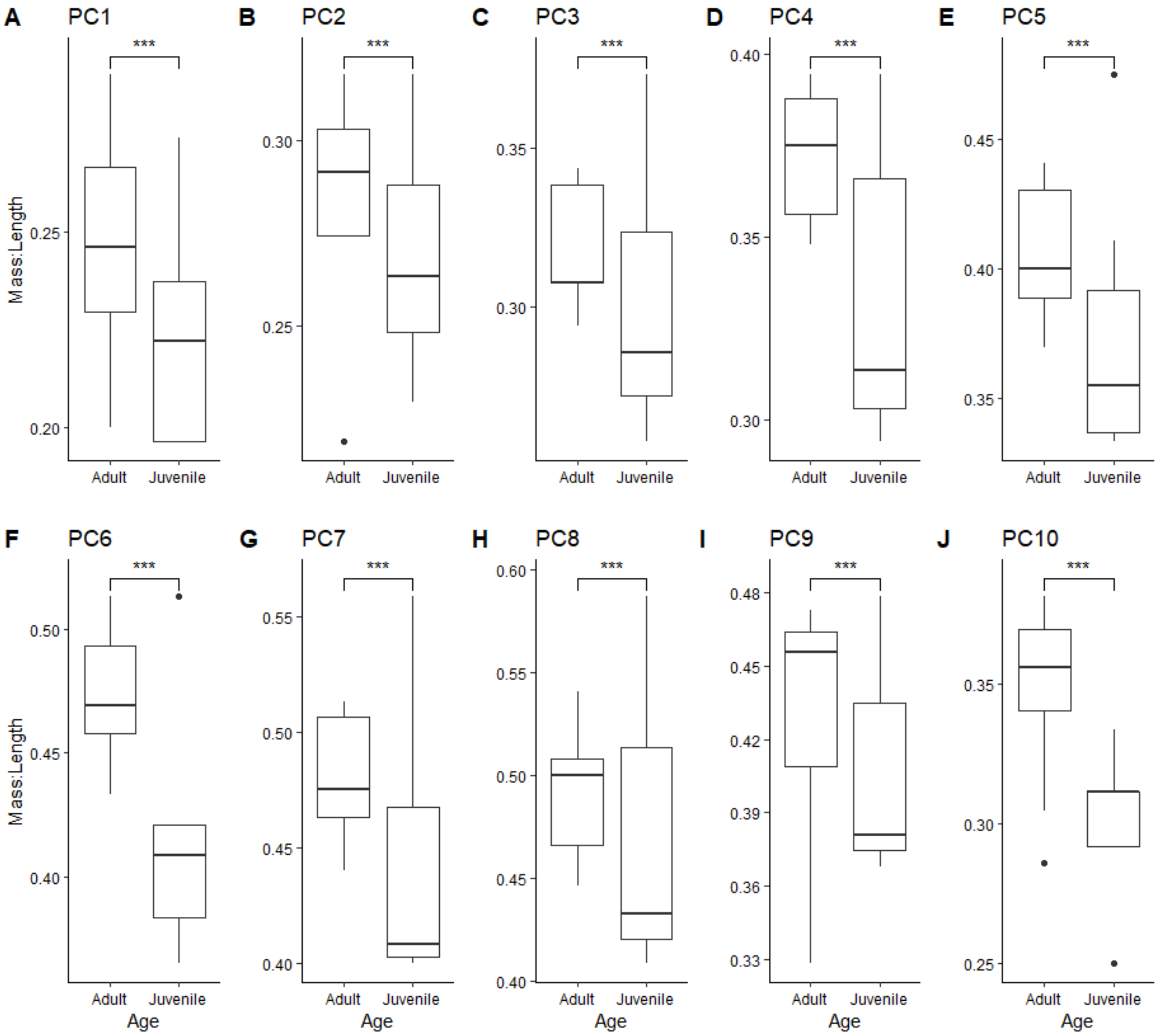
Supplemental Figure 2.2: Differences between ratio of mass and length in (A) P1, (B) P2, (C) P3, (D) P4, (E) P5, (F) P6, (G) P7, (H) P8, (I) P9 and (J) P10 between adult and juvenile Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa in March 2019. (Bold line: Median ratio of mass and length for primaries; Boxes: 25th–75th percentile; Whiskers: 10th/90th percentile; ***: comparison between groups as it relates to significance level).



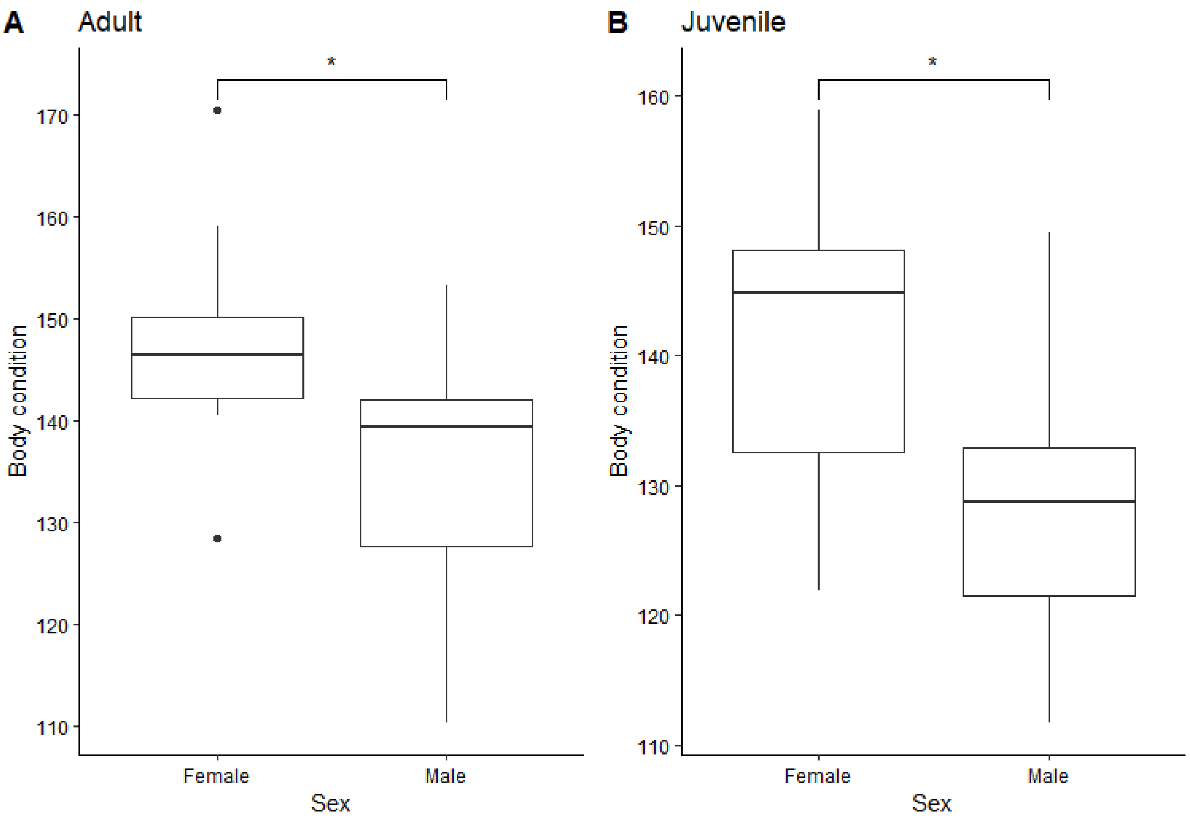
Supplemental Figure 2.3: Differences between ratio of mass and length in (A) S1, (B) S2, (C) S3, (D) S4, (E) S5, (F) S6, (G) S7, (H) S8, (I) S9 (J) S10 and (K) S11 between adult and juvenile Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa in March 2019. Conventions as Suppl. Fig. 1.



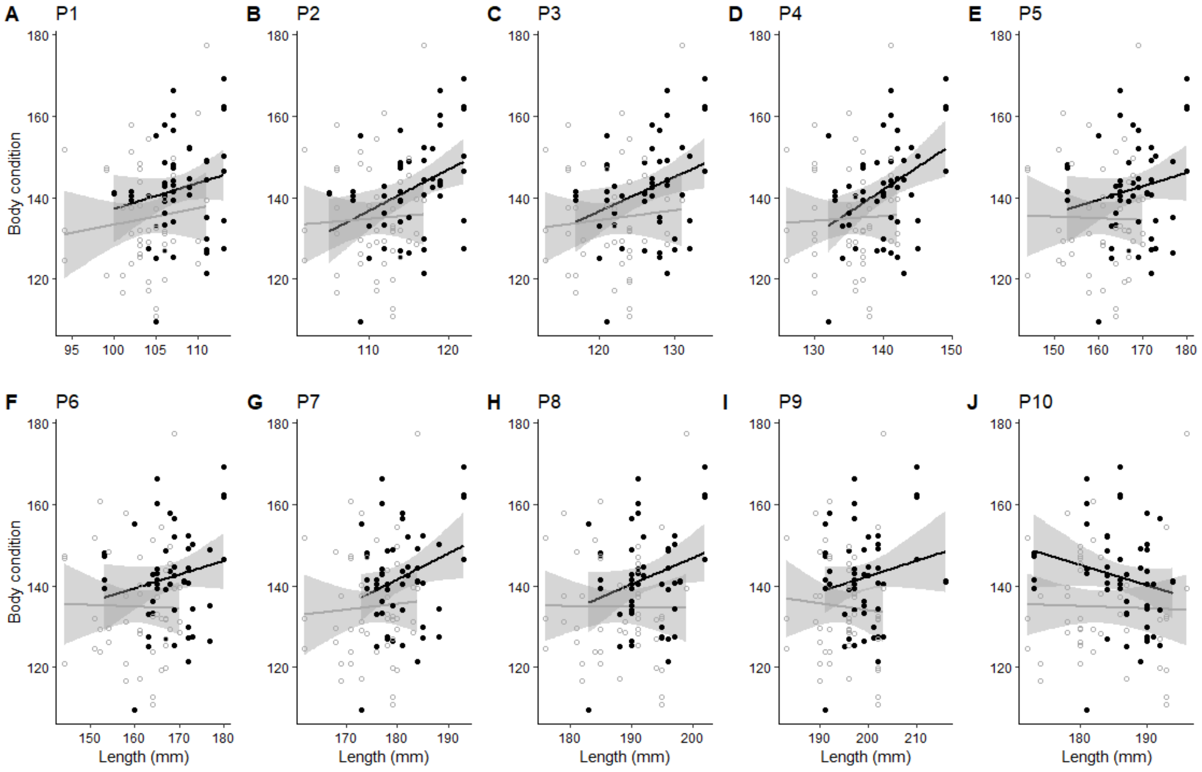
Supplemental Figure 2.4: Differences between ratio of mass and length in (A) R1, (B) R2, (C) R3, (D) R4, (E) R5, and (F) R6 between adult and juvenile Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa in March 2019. Conventions as Suppl. Fig. 1.



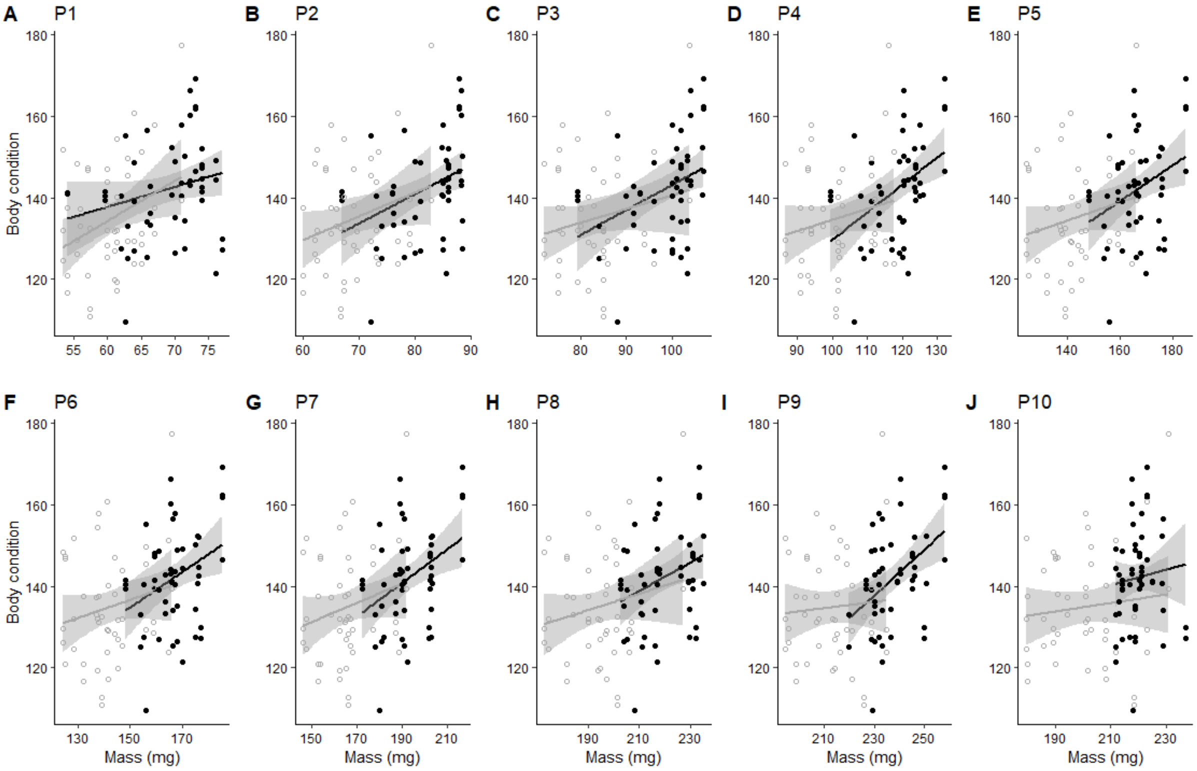
Supplemental Figure 2.5: Differences between ratio of mass and length in (A) PC1, (B) PC2, (C) PC3, (D) PC4, (E) PC5, (F) PC6, (G) PC7, (H) PC8, (I) PC9 and (J) PC10 between adult and juvenile Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa in March 2019. Conventions as Suppl. Fig. 1.



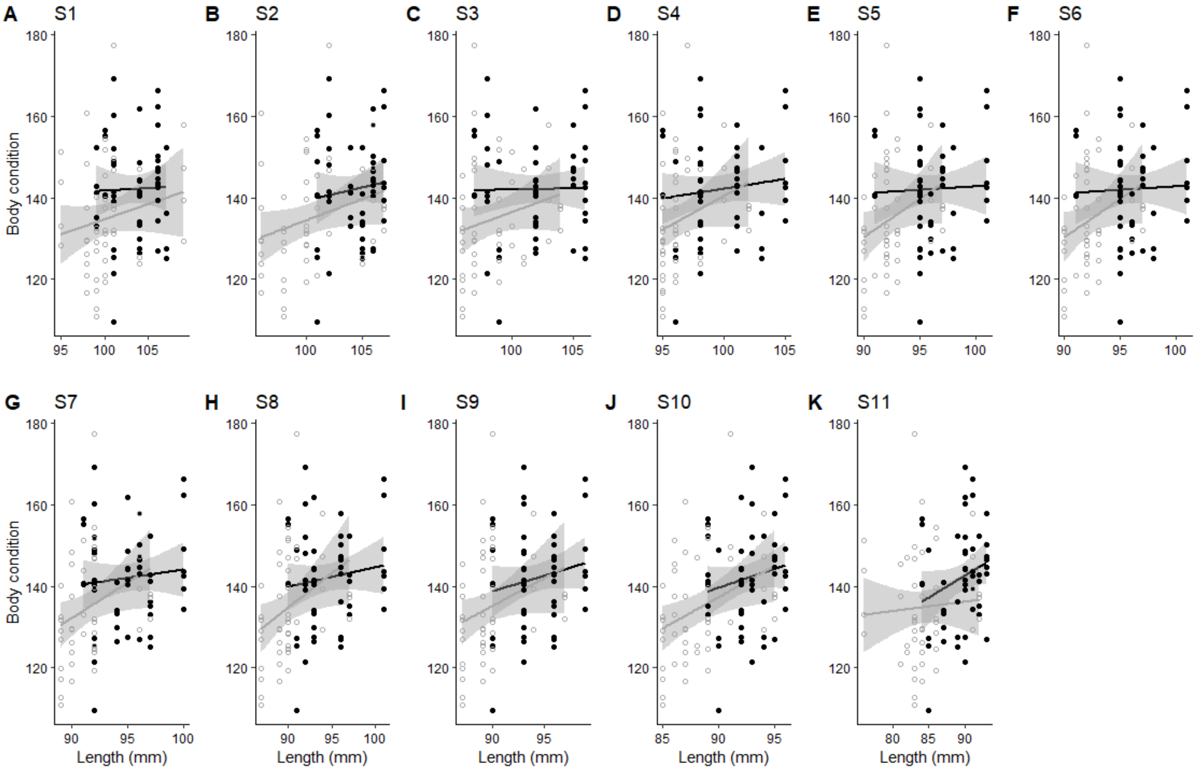
Supplemental Figure 2.6: Sex-related differences in body condition (g) between (A) adult and (B) juvenile Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa, in March 2019 (bold line: median body condition; boxes: 25th–75th percentile; whiskers: 10th/90th percentile; points: outliers; *: comparison between groups as it relates to significance level).



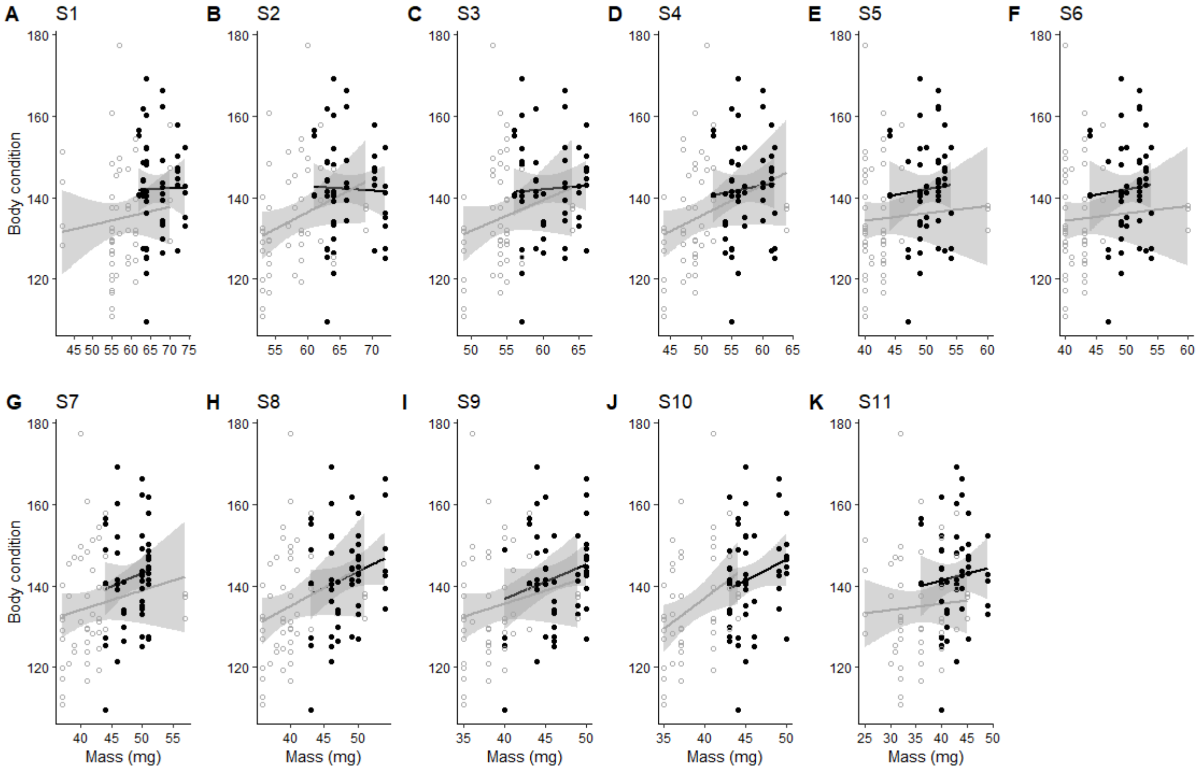
Supplemental Figure 2.7: Relationships between body condition and length of (A) P1, (B) P2, (C) P3, (D) P4, (E) P5, (F) P6, (G) P7, (H) P8, (I) P9 and (J) P10 of adult (black) and juvenile (grey) Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa in March 2019.



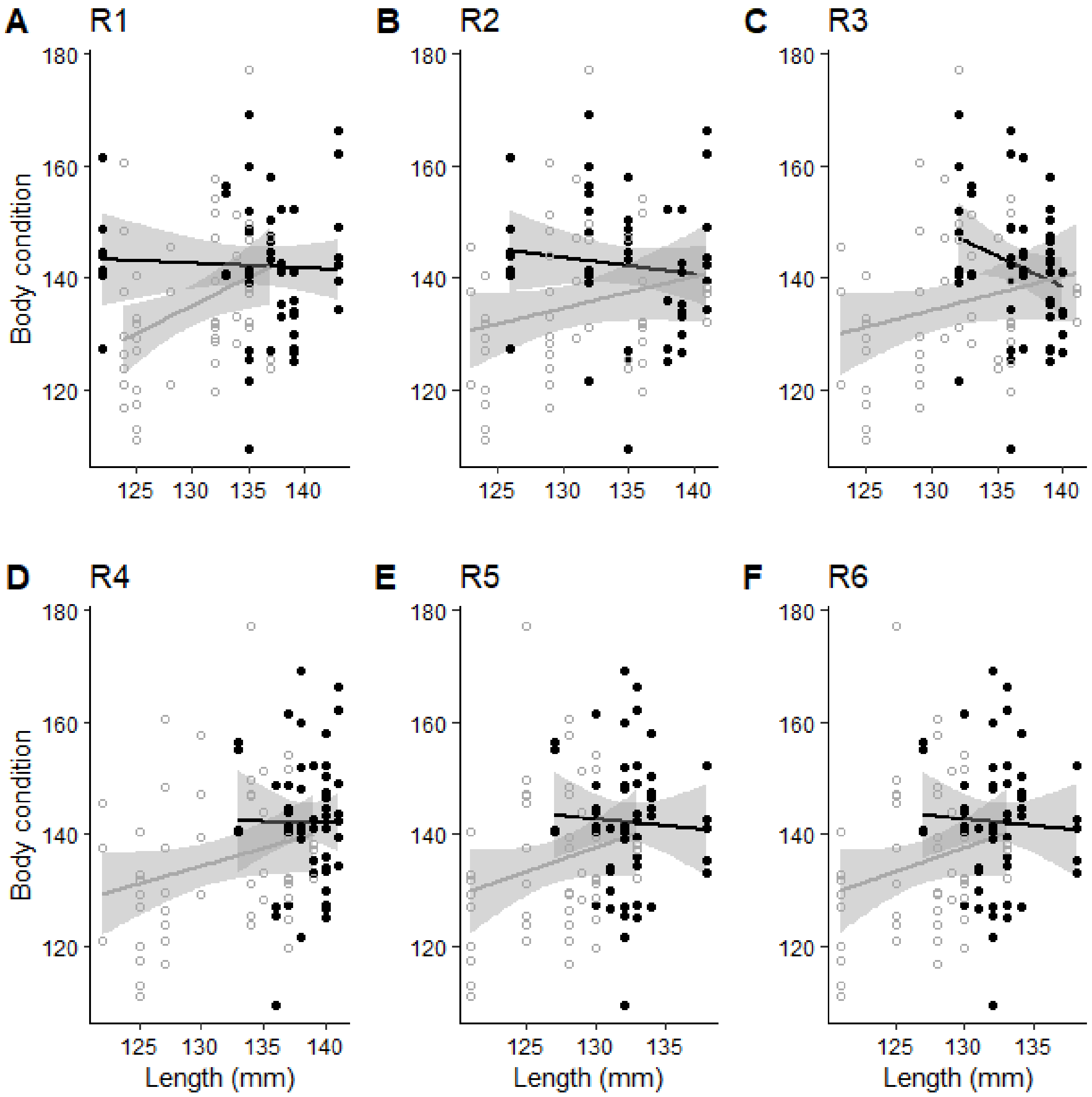
Supplemental Figure 2.8: Relationships between body condition and mass of (A) P1, (B) P2, (C) P3, (D) P4, (E) P5, (F) P6, (G) P7, (H) P8, (I) P9 and (J) P10 of adult (black) and juvenile (grey) Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa in March 2019.



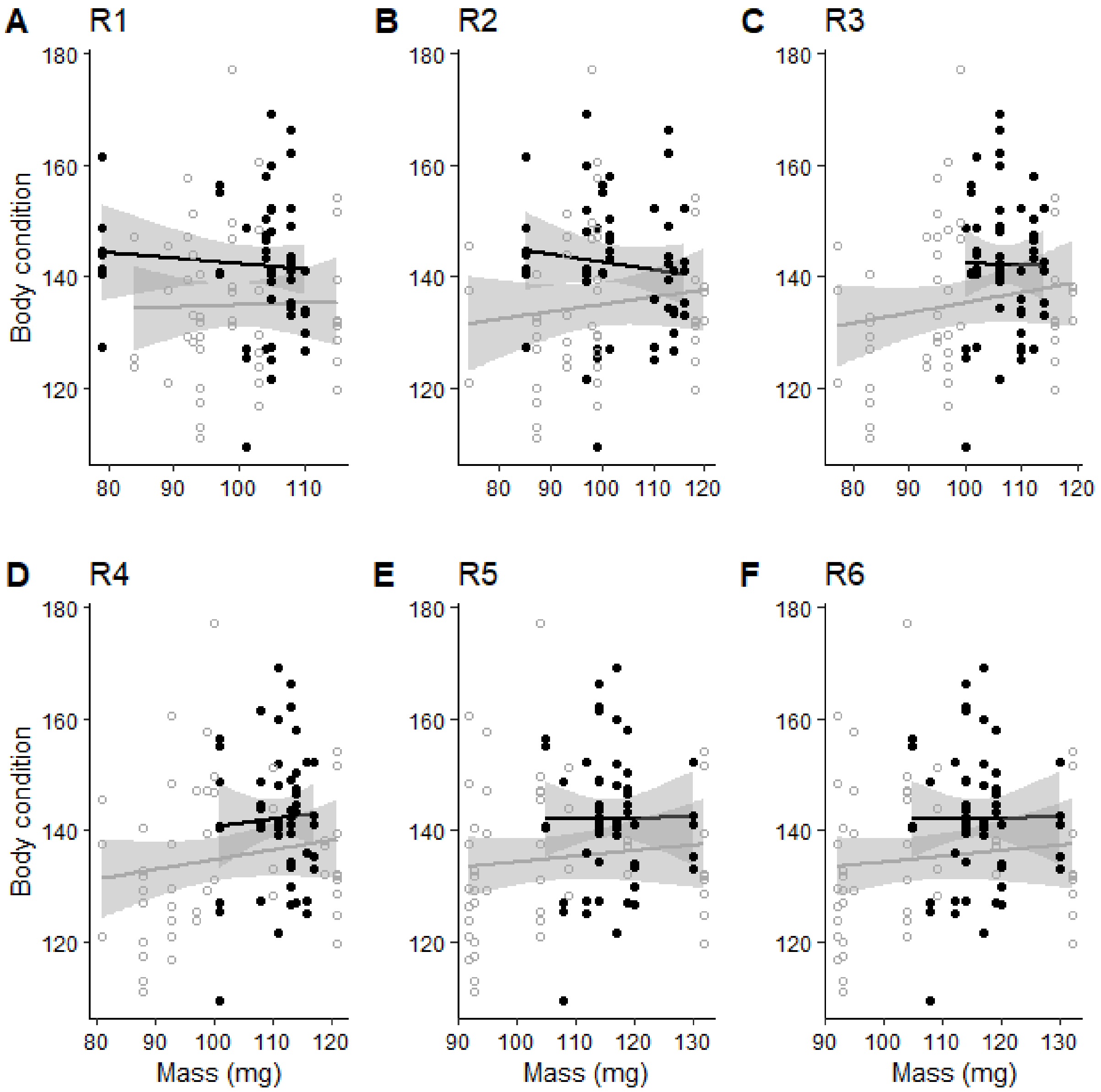
Supplemental Figure 2.9: Relationships between body condition and length of (A) S1, (B) S2, (C) S3, (D) S4, (E) S5, (F) S6, (G) S7, (H) S8, (I) S9, (J) S10 and (K) S11 of adult (black) and juvenile (grey) Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa in March 2019.



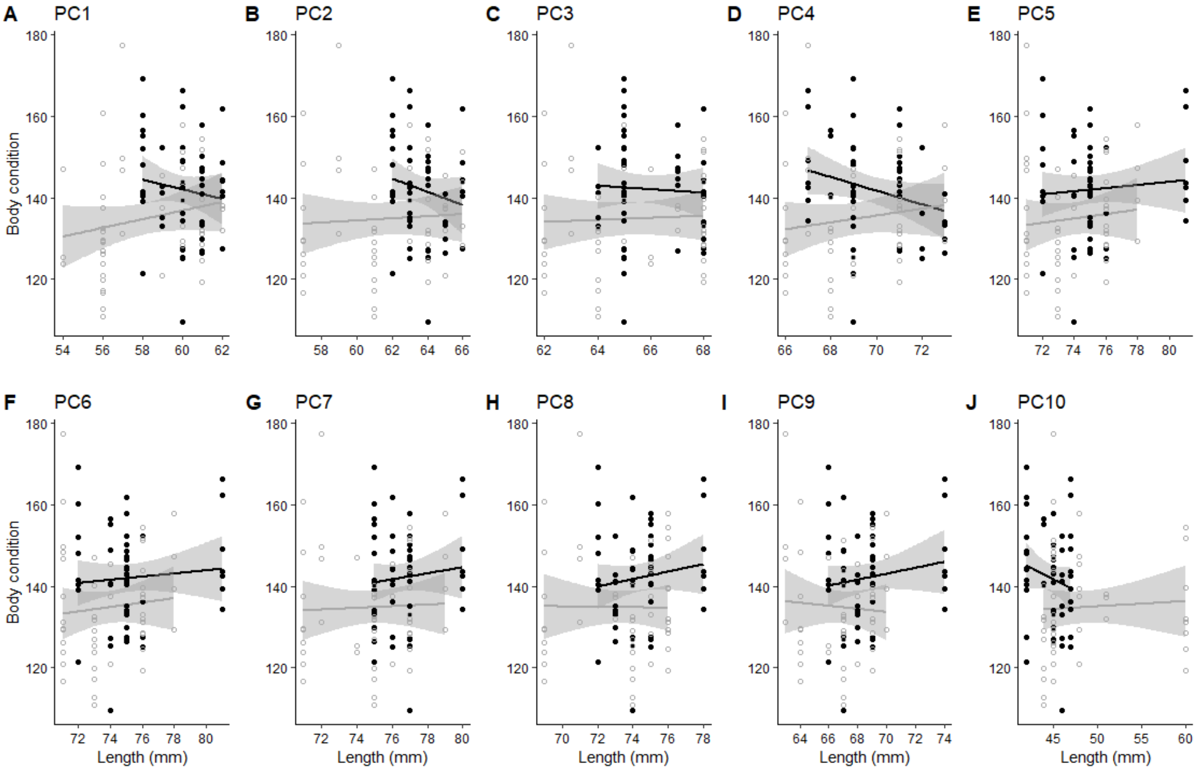
Supplemental Figure 2.10: Relationships between body condition and mass of (A) S1, (B) S2, (C) S3, (D) S4, (E) S5, (F) S6, (G) S7, (H) S8, (I) S9, (J) S10 and (K) S11 of adult (black) and juvenile (grey) Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa in March 2019.



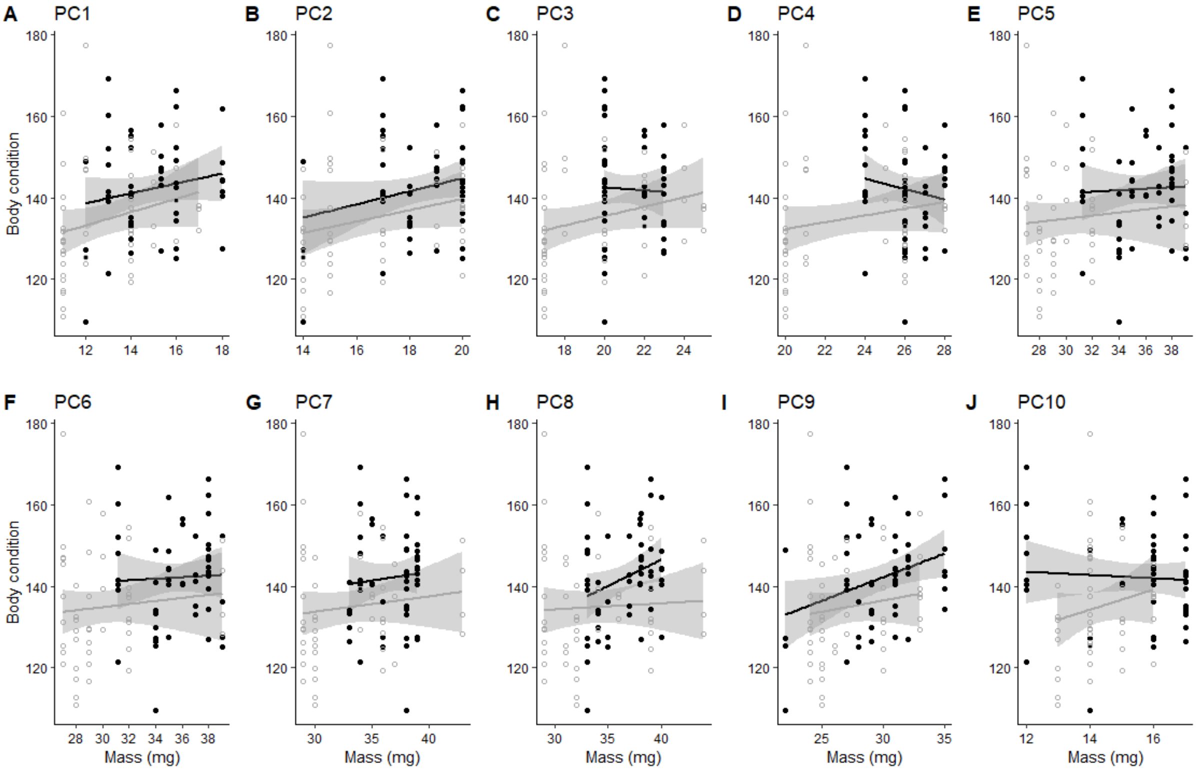
Supplemental Figure 2.11: Relationships between body condition and length of (A) R1, (B) R2, (C) R3, (D) R4, (E) R5 and (F) R6 of adult (black) and juvenile (grey) Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa in March 2019.



Supplemental Figure 2.12: Relationships between body condition and mass of (A) R1, (B) R2, (C) R3, (D) R4, (E) R5 and (F) R6 of adult (black) and juvenile (grey) Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa in March 2019.



Supplemental Figure 2.13: Relationships between body condition and length of (A) PC1, (B) PC2, (C) PC3, (D) PC4, (E) PC5, (F) PC6, (G) PC7, (H) PC8, (I) PC9 and (J) PC10 of adult (black) and juvenile (grey) Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa in March 2019.



Supplemental Figure 2.14: Relationships between body condition and mass of (A) PC1, (B) PC2, (C) PC3, (D) PC4, (E) PC5, (F) PC6, (G) PC7, (H) PC8, (I) PC9 and (J) PC10 of adult (black) and juvenile (grey) Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa in March 2019.

CHAPTER 3

Timing, duration and symmetry of moult in Cape Gannets

Abstract

Little has been reported on moult in sulids, including gannets. The Cape Gannet is an endangered seabird endemic to southern Africa. I describe the timing, duration, symmetry and sequence of flight feather moult in Cape Gannets from two breeding colonies and assess whether moult can be used as an index of condition. Using the Underhill-Zucchini model, I estimate moult parameters based on the proportion of feather mass grown. Adult Cape Gannets began primary moult at the beginning of January (2–3 January ± 28 days SD) at both colonies. Primary moult is protracted, with multiple active centres (mean ± SD 1.8 ± 0.8, range 1–4) and 2.0 ± 0.9 feathers growing at the same time (range 1–5). Primary moult is suspended by early June at Malgas Island (estimated duration of moult ± SE, 153.9 ± 4.1 days) and late June at Lambert's Bay (176.5 ± 5.5 days). Secondary moult commenced in late January and proceeded from two nodal points. Despite more secondaries (3.3 ± 1.9, range 1–8) being grown simultaneously than primaries, 8% of birds were still moulting secondaries at the start of the breeding season. However, it was not certain that these individuals were breeding. Tail moult also overlapped with that of the primaries, with multiple active centres (2.7 ± 1.2, 1–6) and 2.9 ± 1.3 feathers growing at the same time (range 1–8). Almost all primary (98%) and secondary moult (97%) was symmetrical, but there was little symmetry in tail moult (54%). Rectrix symmetry tended to be greater among gannets at Malgas Island (T1: 58%; T2–T6: 67–73%) than at Lambert's Bay (T1: 50%; T2–T6: 55–66%). Differences in moult duration and perhaps asymmetry between locations may be linked to foraging conditions, given that Lambert's Bay gannets are thought to be under greater food stress than Malgas birds.

Introduction

The study of moult, a key event in the annual cycle of birds, is important for understanding avian seasonality. Moult strategies are a combination of three variables: pattern, timing and duration (Bridge 2006). Moult pattern is the sequence in which feathers are replaced, timing is the occurrence of moult relative to breeding activity or seasonal cues, and duration is determined by the rapidity or synchrony with which feathers are replaced (Bridge 2006). Simple or complex moult patterns are often used to describe patterns of feather replacement in terms of moult series (e.g. Langston and Rohwer 1995; Shugart and Rohwer 1996; Bridge 2006; Rohwer 2008; Rohwer and Rohwer 2018). Moult pattern is said to be simple when it is descendent (only one moult series) or synchronous (nearly simultaneous loss) among the primaries (Rohwer and Rohwer 2018), and complex when patterns involve multiple concurrent moult series, such as stepwise moult (Rohwer et al. 2011).

Seabirds are unique for their morphologies, conservative life histories and often large size, which create significant challenges for replacing their flight feathers (Bridge 2006). In many adult seabirds, moult is thought to be one of the most significant activities outside the breeding season (Langston and Rohwer 1996; Prince et al. 1997), as it requires a high energetic and nutritional investment (Murphy 1996), and because the temporary loss of flight feathers may compromise flight efficiency (Bridge 2003; Williams and Swaddle 2003). Many seabirds have evolved complex moulting patterns (Bridge 2006; Ramos et al. 2009), linked to their relatively large size, and the resultant increased time and energy demands associated with replacing long flight feathers (Langston and Rohwer 1996; Edwards and Rohwer 2005). Yet because most species undergo moult at sea during the non-breeding season (Ramos et al. 2009), the understanding of seabird moult remains relatively poor (Furness et al. 1995; Bridge 2006).

Moult timing and pattern in seabirds is influenced by age, breeding and migratory status, food availability and local adaptation (Alonso et al. 2009). For example, some species overlap moulting with breeding (e.g., Cory's Shearwaters *Calonectris [diomedea] borealis*; Alonso et al. 2009; Ramos et al. 2009), but most seabirds undergo a post-breeding moult at sea (Warham 1996; Bridge 2006). Studies of seabirds in active moult tend to rely on birds found dead, although some studies have caught non-breeding birds at sea (Bugoni et al. 2014) or used photographs of birds at sea (Keijl 2011; Ryan et al. 2020). Smaller seabirds generally exhibit a simple descendent primary moult, from the innermost primary outwards (Marchant and Higgins 1990; Cooper et al. 1991; Bridge 2006). Giant petrels *Macronectes* spp. are among the largest birds that undergo a complete primary moult annually without losing the ability to fly. They do this partially by overlapping moulting with breeding, and by moulting several primaries at once (Hunter 1984; Rohwer et al. 2009). Common Terns *Sterna hirundo* even replace some primaries more than once per year, with the number of inner primaries replaced following the initial complete moult serving as a signal of individual quality (Bridge and Nisbet 2004).

In most birds, moult of secondaries and rectrices tends to start once primary moult is well-advanced, but there are numerous exceptions to this pattern (Edelstam 1984; Zuberogoitia et al. 2018). Tail moult starts with the central pair of feathers and moves outwards, and often exhibits more asymmetrical feather replacement than the remiges (Ainley et al. 1976). The number of tail feathers grown at once also varies greatly, even among closely related species. For example, most Cory's Shearwaters replace their tails slowly, growing only one pair of feathers at a time (Monteiro and Furness 1996), whereas many White-chinned Petrels replace all their tail feathers at once (Chastel 1995). There can also be considerable variation in tail moult among individuals within the same species (Adekola et al. 2021b).

The gannets and boobies (Sulidae) are medium- to large-sized seabirds with long, slender wings. Surprisingly little is known about moult in sulids (Nelson 1978; Marchant and Higgins 1990). In the Masked Booby *Sula dactylatra*, primary moult is arrested before egg laying and resumes during incubation from the points where it stopped (Dorward 1962). In North Atlantic Gannets *Morus bassanus*, the first post-juvenile moult wave begins with the innermost primary and progresses outwards. However, second and third moult waves begin at the innermost primary before all the distal feathers have been replaced, resulting in multiple active moult centres (*Staffelmauser* or wave moult) (Nelson 1966; Ginn and Melville 1983). Like most seabirds, adult gannets usually start moulting after breeding (Nelson 1978).

Little has been reported on moult patterns in Cape Gannets (Hockey et al. 2005). One of three gannet species, the Cape Gannet is an Endangered seabird endemic to southern Africa that only breeds at six islands off the coasts of Namibia and South Africa (Crawford et al. 1983; BirdLife International 2021). Egg-laying starts in August/September and continues to November (Staverees et al. 2008), but some adults visit colonies all year, allowing year-round access to adult birds at colonies (Crawford et al. 2007). Understanding moult patterns in seabirds is important for studies of their population dynamics (Ainley and Boekelheide 1991). Understanding moult in the Cape Gannet is key to improving knowledge of its life history, annual cycle and perhaps can be used as an index of stress, especially between populations from different colonies (Moseley et al. 2012). In this study, I describe moult strategies in Cape Gannets at two South African breeding colonies. I test inter-colony differences linked to regional patterns of threat due to changed food resources (Cohen et al. 2014).

Methods

The study took place at two Cape Gannet breeding colonies on islands off the west coast of South Africa: Bird Island, Lambert’s Bay (32°09' S, 18°32' E) and Malgas Island (33°05' S, 17°92' E). Gannets returning to the colony were caught at random, primarily for diet studies

(Berruti et al. 1993; Grémillet et al. 2008; Cohen et al. 2014), using a crook on a long pole. Moult data were collected from gannets monthly at both islands from June 2002 to July 2004. Additional gannets were sampled monthly at Malgas Island between August 2018 and March 2019, and in October and November 2019. In the breeding months (which differs among colonies, but similar at Lambert's Bay and Malgas Islands), I tried to avoid catching birds or partners that were incubating or brooding, although I scored the moult of breeding birds caught for a tracking study in November 2019. Most birds were in adult plumage, but a few caught in January, February and November retained some immature feathers and were treated separately during the analyses.

Moult data

Gannets have 10 functional primaries, 26–28 secondaries and 12 tail feathers. I scored moult according to Ginn and Melville (1983), where old feathers = 0, growing feathers = 1 to 4 for increasing stages of development, and fully-grown new feathers = 5. Primaries were numbered from P1 (innermost) out to P10; secondaries from S1 (outermost) in to S28 (but ranges between 26–28); and rectrices from T1 (central pair) out to T6 on each side of the tail. The Primary Moult Score (PMS) was calculated for each bird as the sum of the moult scores of the ten primaries on the left wing (range 0–50). Similarly, I calculated Secondary Moult Score (SMS, range 0–140 for a bird with 28 secondaries) but given variations in the number of secondaries, I standardised SMS scores from 0–1 by dividing by the maximum total score; and a Tail Moult Score (TMS) for the entire tail (range 0–60). The left primaries and all rectrices were scored in 2002–2004 but in 2018–2019, all primaries, secondaries and rectrices were scored from both sides of the bird to assess moult symmetry. Moult scoring in 2018–2019 was conducted from photographs of the spread wing and tail, which allows more feathers to be examined with less disturbance to the birds due to reduced handling time (Osborne and Ryan 2021).

PMS, SMS and TMS were converted into Percentage Feather Mass Grown (PFMG) using the relative masses of primaries, secondaries and rectrices respectively (Underhill and Joubert 1995). Feather masses were obtained by collecting flight feathers from 12 adult Cape Gannets killed incidentally during fishing operations. After plucking, the feathers were air dried for several days then measured (flattened total length to the nearest 1 mm) and weighed (to the nearest 1 mg). The average masses for each primary, secondary and rectrix (Supplemental Table 3.1) was used to calculate relative feather mass for each tract (Underhill and Joubert 1995).

The wave moult system, which sees successive waves of moult proceed across the primaries, suspended during breeding, which prevented an estimate of the proportion of primaries replaced each year. However, the resultant age contrasts between adjacent moult waves were generally minor and may have resulted from within-season age differences rather than across season differences, so it was not feasible to assess the proportion of feathers replaced in each moult (Zuberogoitia et al. 2016). I was able to recognize nodal points in the secondaries where there was a new feather older than adjacent new feathers (cf. Rohwer and Rohwer 2018). I observed three tail moult ‘strategies’: (i) Outward, where moult starts at the centre (usually T1 but occasionally T2) and proceeds outwards; (ii) Inward, where moult starts from the outer rectrices (usually T6 but occasionally T5) and proceeds inwards; and (iii) Mixed, where moult occurs at multiple positions with no clear pattern or order (Adekola et al. 2021b).

Symmetry of moult was assessed by comparing the moult scores of each feather pair on either side of the bird. A simple index of asymmetry was calculated as the standardised moult score asymmetry (i.e. asymmetry score/50 for primaries, asymmetry score/130 or 140 for secondaries and asymmetry score/30 for rectrices, expressed as %), given that the maximum possible asymmetry would have a summed moult score difference of 50 for primaries (all primaries on one wing old, and those on the other wing new), 130 or 140 for secondaries and 30 for rectrices. Differences in moult score of 1 between a pair of feathers were regarded as ‘minor’ asymmetries (i.e. 0–1, 1–2, 2–3, 3–4 and 4–5); differences of 2 – 3 as ‘intermediate’ (i.e. 0–2, 0–3, 1–3, 1–4, 2–4, 2–5, 3–5) and of 4 – 5 as ‘major’ asymmetries (i.e. 0–4, 0–5, 1–5). To test whether asymmetry at a feather position is random, I used Pearson’s chi-squared goodness-of-fit tests with Yates’ correction for continuity to compare the observed frequency of asymmetry with that expected by chance (assuming random replacement) for a given level of feather replacement (cf. Adekola et al. 2021b). The degree of partial-moult asymmetry depends on the number of feathers moulted, because if no feather, or all feathers are moulted, the moult pattern will be symmetrical. The potential for moult asymmetry peaks when half the feathers are moulted (in the most extreme case, one side is replaced and the other is not, giving an asymmetry score of 1), with a range of possible maximum asymmetry values between these extremes. As a result, differences in the proportion of feathers moulted must be controlled for when comparing asymmetry across feathers.

Data analyses

Annual estimates of flight feather moult start date and duration (± standard deviation) were obtained using the combined PFMG of all flight feathers in the ‘moult’ package in R (Erni et al. 2013). Mean start date and duration of primary moult were estimated by modelling PFMG values against Julian day from 1 September (at the start of the breeding season that falls outside the primary moult period in adult Cape Gannets). Because the number of feathers moulted in a season differed between individuals, it was not possible to calculate the proportion of feather mass grown (the moult index used in the Underhill–Zucchini models) in the current season, notably for birds with incomplete or stepwise moults. I modelled the moult of Cape Gannets using the data type 1, requiring only data on whether a bird has not yet started moult, is in moult, or has completed moult, using only the current year's moulting feathers for analyses (cf. Zuberogoitia et al. 2013; 2016; 2018). I fitted the model using the maximum likelihood method (Underhill and Zucchini 1988; Newton 2009) and calculated 95% confidence limits for moult parameters following Erni et al. (2013). These models give estimates of moult duration, average start and end dates, and their standard errors. Models were compared using Akaike Information Criteria (AIC), and significant differences between models were tested using log-likelihood ratio tests (Burnham and Anderson 2002). General linear model was used to explain the differences in moult strategies observed in the rectrices. To test whether moult tends to be symmetrical across flight feathers, I compared observed values of asymmetry to those expected assuming moult is random with respect to location (Brommer et al. 2003; Adekola et al. 2021b). All statistical analyses were performed in the R statistical environment (R Core Team 2019).

Results

I scored moult from 1326 adult and 33 immature Cape Gannets: 1064 sampled in 2002–2004 (487 at Bird Island, Lambert's Bay, and 577 at Malgas Island) and 295 at Malgas Island in 2018–2019.

Primary moult

Of the 1326 adults scored for primary moult, 503 (38%) were moulting primaries. Of the 33 immatures, 9 (27%) were moulting primaries (with 8 moulting primaries in January and February). Most adults were in active primary moult between January and June at Lambert's Bay (Figure 3.1A), and January and May at Malgas Island (Figure 3.1B). The Underhill-Zucchini moult model estimated that adult Cape Gannets began primary moult on 2–3 January (± 28 days SD) at both colonies (Figure 3.2). At Malgas Island, primary moult was suspended by 7 June (estimated duration of moult ± SE, 153.9 ± 4.1 days), but lasted more than three weeks longer at Lambert's Bay (176.5 ± 5.5 days), finishing on 27 June (Figure 3.2). Primaries were growing at 1.8 ± 0.8 moult centres; most birds (42%, n = 503) had one active centre, 37% had two, 19% had three, and 3% had four active centres. These proportions differed among colonies, with Malgas Island birds having more active centres ($\chi^2 = 8.75$, df = 1, p = 0.01). Most moult centres had only one growing feather; the average number of growing primaries was 2.0 ± 0.9. Amongst birds in primary moult, the proportion moulting each primary varied from 7% (P2) to 13% (P9) (Figure 3.3). Most birds (40%, n = 503) were growing one primary, 33% were growing two, 19% were growing three, 7% were growing four, 5 (1%) were growing five primaries, and 1 bird (0.2%) was growing six primaries (three in stage 4, almost fully grown). No gannets (all ages) captured in November and December 2018–2019 (n = 66) were moulting primaries, but 8% of 196 adults sampled in November and December 2002–2003 were moulting primaries. As expected, wave moult in the primaries was largely distal; however, in 27% of cases of adjacent growing feathers, the outer feather was more advanced than the inner. These cases were spread across the primaries (not confined to the inner or outer primaries) (Supplemental Table 3.2).

Secondary moult

Of the 262 adults scored for secondary moult at Malgas Island in 2018–2019, 158 (60%) were moulting secondaries, greater than the proportion replacing primaries (48%; $\chi^2 = 3.38$, df = 1 p = 0.04). Of the 33 immatures, 7 (21%) were moulting secondaries (all moulting in January and February). All adults checked from January to March were in active secondary moult, compared to only 8% of adults from August to October (with the proportion relatively constant over these three months; no birds were checked in April–July). None of the 33 birds with small chicks in November and December was moulting secondaries. Most adults (64%) had 28 secondaries, 27% had 26 and 9% had 27. The mean starting day estimated for replacing secondaries was 22 January (± 27 days SD; data only for Malgas Island). Secondary moult overlapped with primary moult, starting once 2–3 primaries had been replaced (Figure 3.4).

Secondary moult mainly progressed from nodal points at S4 and in the inner secondaries (S25–S27) (Table 3.1). The average number of moult centres was 3.3 ± 1.9 (range 1–8); 24% of birds ($n = 158$) had one active centre, 16% had two, 14% had three, 19% had four, 14% had five, 9% had six, 3% had seven, and 1% had eight active centres. Like the primaries, most moult centres had only one growing feather. Moulting birds were replacing 3.4 ± 1.9 (range 1–8) secondaries; 22% were growing one secondary, 17% were growing two, 13% were growing three, 20% were growing four, 13% were growing five, 9% were growing six, 4% were growing seven, and 2 (1%) were growing eight secondaries ($n = 158$). Because most active moult centres involved a single feather, there was little evidence to show the direction of secondary moult (Table 3.1).

Tail moult

Tail moult was more frequent among adults (68% of 1326 birds) than either primary (38%, $\chi^2 = 111.77$, $df = 1$, $p < 0.001$) or secondary moult (48%; $\chi^2 = 2.43$, $df = 1$, $p = 0.08$ for secondaries). Tail moult was even more prevalent among immatures (88% of 33 birds), where it was also more common than primary (27%, $\chi^2 = 9.50$, $df = 1$, $p < 0.01$) and secondary moult (7%, $\chi^2 = 12.25$, $df = 1$; $p < 0.001$). Although tail moult largely overlapped with primary moult (Figure 3.5), some birds with active tail moult were observed year-round. Tail moult was least often recorded during the early breeding season, from August to October at both Lambert's Bay (Figure 3.6A, Supplemental Figure 3.1) and Malgas Island (Figure 3.6B, Supplemental Figure 3.2). Peak replacement of rectrices (up to 8 feathers) occurred in July (Figure 3.7). Tail moult was variable and often intense, growing 1–8 feathers at once (2.9 ± 1.3; Figure 2.6), from 2.7 ± 1.2 multiple moult centres (range 1–6); 16% of birds ($n = 1326$) were growing one rectrix, 28% were growing two, 24% were growing three, 20% were growing four, 10% were growing five, 2% were growing six, and 1 bird (0.08%) was growing eight rectrices. Most birds (31%) had two active moult centres, 25% had three, 20% had four, 17% had one, 6%

had five, and 1% had six active centres (n = 1326). Rectrix moult was mostly inward (Table 3.2), with a marked difference in tail moult scores between strategies: birds with inward moult typically had more advanced moult (0.67 ± 0.29) than birds with outward (0.29 ± 0.33) or 'mixed' replacement patterns (0.25 ± 0.21; $F_{2,889} = 184.50$, $p < 0.001$). Of the 'mixed' strategy, 37% showed active moult in the inner and outer rectrices, with the remainder moulting at multiple positions with no clear pattern.

Moult intensity of flight feathers

Birds replacing 5–6 primaries at the same time reduced the total length of all their primaries by 40–51% and the total mass by 29–40% (Supplemental Table 3.1). Expressed as a proportion of totals for all flight feathers, birds growing 5–6 primaries were simultaneously replacing 10–13% of their overall length and 11–16% of their overall mass. Replacing 7–8 secondaries at the same time amounted to 27–30% of their total length and 32–36% of their total mass, and to 14–16% of the overall length and 10–11% of the overall mass of all flight feathers (Supplemental Table 3.1). Replacing 5–6 rectrices at the same time equated to 86–100% of their total length and 89–100% of their total mass, or 12–14% of the overall length and 14–16% of the overall mass of all flight feathers (Supplemental Table 3.1).

Symmetry of moult

Almost all moult in the primaries (98%) and secondaries (97%) was symmetrical, with only minor asymmetries observed among the remiges. There was no evidence of asymmetric cessation of moult in the remiges during breeding. No birds had entirely asymmetrical tails (all old one side and all new on the other), but active moult was confined to one side of the tail in 24% of birds. Among birds in active moult on both sides of the tail, the same basic pattern (inward/outward/mixed) was found on both sides of the tail in 86% of birds, but all possible combinations were present in at least some birds (Table 3.2). Asymmetry among the rectrices (46%) was substantially greater than among the remiges, although only 25% was major asymmetry. However, despite the relatively high level of asymmetry, there was strong selection for moult symmetry across the rectrices ($p < 0.05$, except for T1 and T2 at Lambert's Bay; Table 3.3). Rectrix asymmetry tended to be greater among gannets at Lambert's Bay (T1: 50%; T2–T6: 34–45%) than at Malgas Island (T1: 42%; T2–T6: 27–33%), even though the probability of feather replacement was similar at both colonies (Table 3.3).

Discussion

Birds can decrease the time required to renew feathers by increasing the rate at which individual feathers grow and by growing more feathers simultaneously (Rohwer and Rohwer 2013). The rate of feather growth only increases slightly with body mass and feather size (Rohwer et al. 2009; de La Hera et al. 2012), presumably because faster growth rates compromise feather quality (e.g., Dawson et al. 2000). This means that large birds take longer to replace their flight feathers, unless they increase the number of feathers replaced at the same time, i.e. increase the intensity of moult (Bridge 2006; Rohwer and Rohwer 2013; Ryan et al. 2020). The time required to replace all primaries is probably mainly determined by the intensity of moult and the lengths of the primaries that must be replaced (Rohwer 1999). However, increasing moult intensity creates large gaps in the wing when a single wave moult pattern is maintained (e.g., giant petrels; Hunter 1984). *Staffelmauser* is a way to moult more feathers without forming large gaps in the wing (Stresemann and Stresemann 1966). Gannets reduce such gaps by typically moulting only one feather at once in each active moult site.

Stepwise replacement of the primaries occurs in many large birds, including most Suliformes (Stresemann and Stresemann 1966; Bridge 2006). Like Northern Gannets, adult Cape Gannets have a protracted moult after the breeding season, from mid- to late-summer to mid-winter (Nelson 1978), with multiple active centres. Primary moult is mostly distal, as is typical of most birds that replace primaries in a sequential pattern (Stresemann and

Stresemann 1966). Endocrinological and neurological processes have been suggested to determine the location of moult inititaion and sequences within remiges (Bridge 2011). However, rectrix moult was mostly inward, although with considerable variation among and within individuals. This variation in moult sequence suggests moult plasticity (Adekola et al. 2021a). Further study is needed to investigate the causes and consequences of the various tail moult strategies found in Cape Gannets.

Most birds start to moult after breeding when their body reserves of lipid and protein may be depleted (Austin and Fredrickson 1987). Although gannets from Lambert's Bay and Malgas Island started moult at the same time (with similar breeding seasons at both colonies), birds from Malgas Island moulted for a shorter period. This may be because Malgas Island birds have a more reliable source of food scavenging from fishing boats in autumn and winter (Grémillet et al. 2008; Mullers et al. 2009; Crawford et al. 2019; Grémillet et al. 2019), while Lambert's Bay birds are more likely to be under greater food stress, because the availability of natural prey tends to decrease farther north up the west coast, and there is less opportunity to scavenge from trawlers in this area (Okes et al. 2009; Sherley et al. 2019). However, the colony at Malgas Island at the time of the core study was almost three times larger (31 000 pairs) than that at Lambert's Bay (11 000 pairs, Crawford et al. 2007), so there might be greater intra-specific competition for food, forcing birds to moult fewer feathers so they have more time after moult to prepare for breeding. The relationships between moulting periods, and the adjustment of their duration, and the annual life cycle of a species forms a most fascinating part of moult studies (Freed and Cann 2012). Different populations of a species can have different moult strategies (e.g., Dunlin *Calidris alpina*; Greenwood 1983). During peak of flight feather moult, some albatrosses and petrels significantly reduce their time in flight (Cherel et al. 2006; Gutowsky et al. 2014); other species, such as diving petrels, even becoming flightless (Bridge 2004). Some adult Cape Gannets migrate when not breeding, but some do not (Grémillet et al. 2008), and the birds sampled clearly remained around the colonies. Quite why they don’t migrate, particularly if food is scarce around the colony, is unclear.

Several loci of secondary moult were observed in the Cape Gannet. This is a common pattern in birds with long wings (e.g. Edelstam 1984), and like *staffelmauser* in the primaries, presumably minimises large gaps in the secondaries. However, intensive moult of secondaries has been observed in many seabirds (Ryan et al. 2020). Secondary moult was observed starting rapidly from S4 and innermost secondaries. This finding is related to these feathers being subjected to more exposure and faster wear rates than the mid-secondaries (Zuberogoitia et al. 2013; Osborne and Ryan 2021).

Annual rectrix replacement mostly overlapped with primary moult, suggesting that metabolic costs of primary moult may not be overly restrictive (Bugoni et al. 2014), with highest asymmetry at the central rectrices. Many studies have reported tail moult being stereotyped (Prince et al. 1993; Bugoni et al. 2014). However, I found considerable individual plasticity (on either side of the tail) in Cape Gannets (Adekola et al. 2021b). Barta et al. (2006) also found that individual variation in moult sequence can be an adaptive response to environmental conditions in non-migratory birds. The tips of the rectrices tend to wear rapidly due to abrasion on land and therefore birds replace them regularly to keep the tail functional (Adekola et al. 2021b).

The consistent pattern of feather replacement and strong moult symmetry observed in the primaries and secondaries suggests the importance of these flight feathers (Brooke 1981). The higher level of symmetrical moult in the primaries and secondaries compared to tail feathers supports the prediction that birds try to minimise asymmetry where the functional importance of the feather is greatest (Swaddle and Witter 1997). Strong flyers in particular face strong stabilizing selection for moult symmetry. Although asymmetrical wing moult is seldom described, it has been reported in some species (e.g. Yellow-nosed Albatross *Thalassarche chlororhynchos*, Furness 1988; and Wandering Albatross *Diomedea exulans*, Weimerskirch 1991). Arroyo et al. (2004) also mentioned asymmetry in wing and tail moult in the European Storm Petrel *Hydrobates pelagicus* and Shugart and Rohwer (1996) reported that the last primaries in a moult wave are replaced out of sequence in the post juvenile moult of the Black-crowned Night Heron *Nycticorax nycticorax*, a species with a serial annual moult. Asymmetry in flight feathers has associated aerodynamic costs, and reduces manoeuvrability (Thomas 1993). Additionally, costs of asymmetry, particularly in tracts associated to locomotion, should be increasingly greater when occurring away from the centre of gravity (Swaddle and Witter 1997). The inter-colony differences in moult duration and perhaps asymmetry may be linked to foraging conditions, given that Lambert's Bay gannets are thought to be under greater food stress than Malgas Island birds. Cape Gannets in Malgas Island moulted in shorter period than those from Lambert's Bay, suggesting that moult pattern might be used as an index of condition linking to conservation (Adekola et al. 2021b).

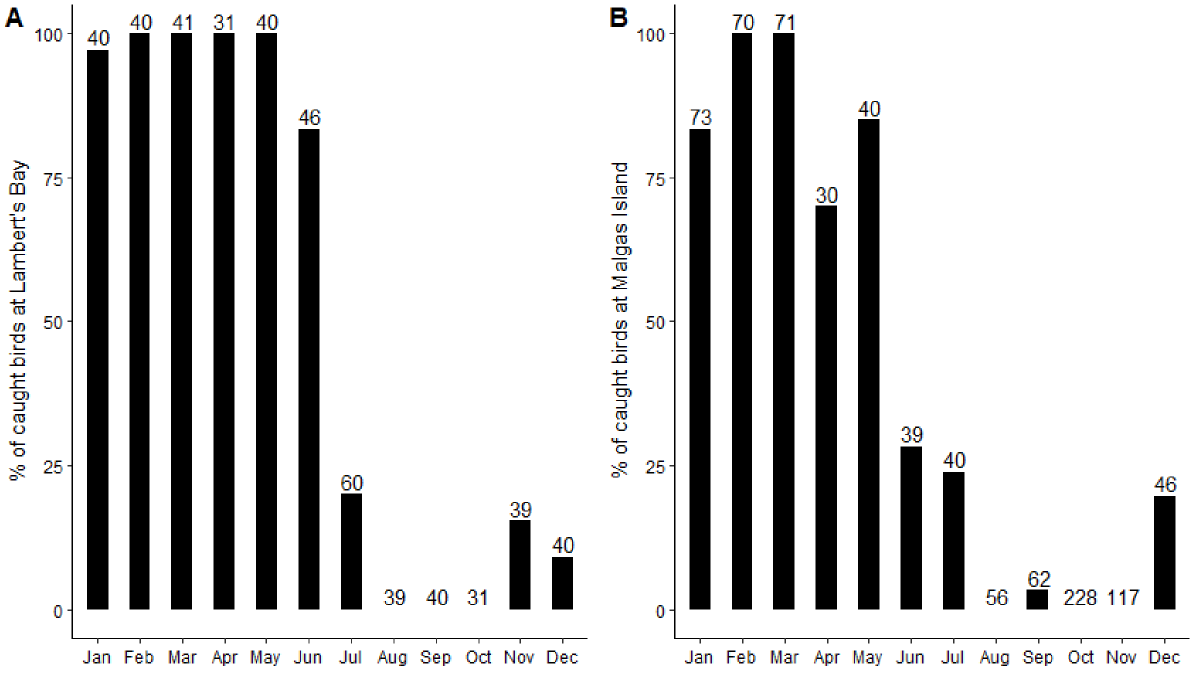


Figure 3.1: Monthly proportions of adult Cape Gannets in active primary moult at (A) Lambert's Bay and (B) Malgas Island. The numbers above the bars are the sample sizes.

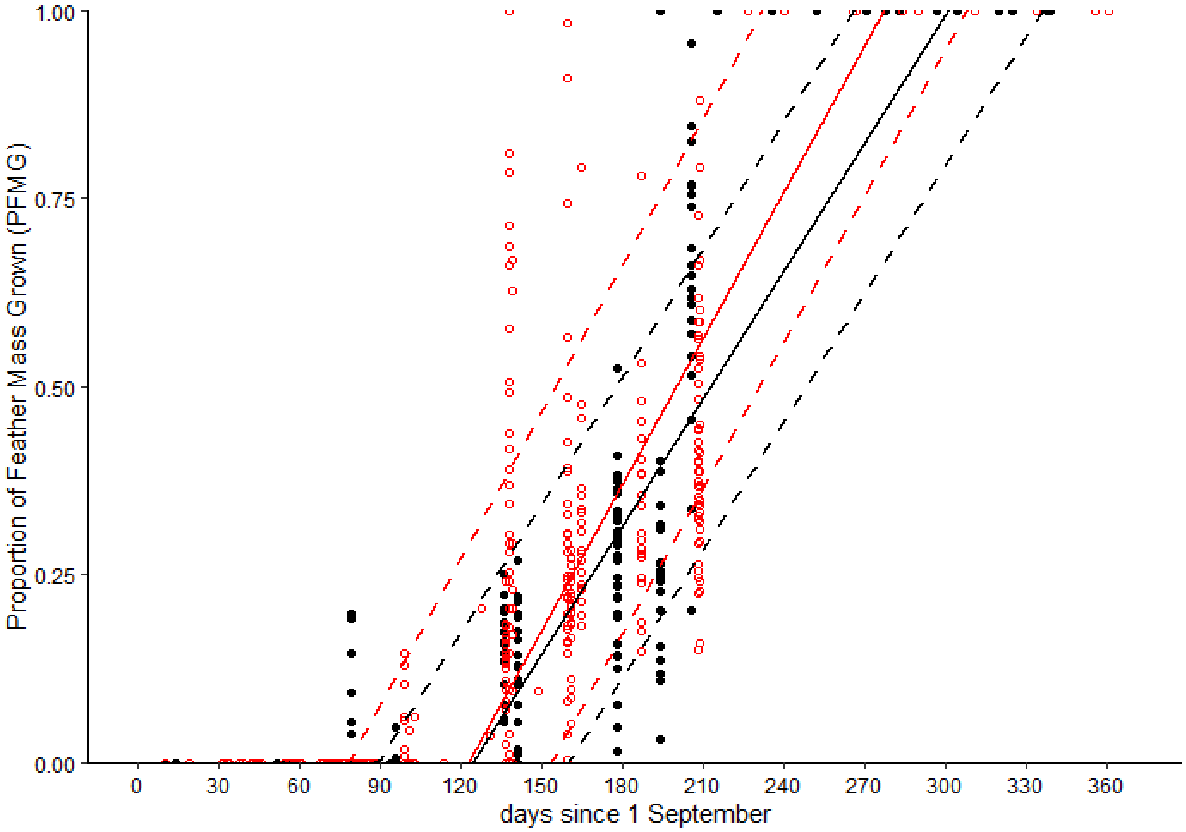


Figure 3.2: Temporal distribution of the proportion of feather mass grown (PFMG) of adult Cape Gannets at Lambert's Bay (black) and Malgas Island (red), South Africa. The continuous line shows the average moult trajectory, dashed lines show 95% confidence intervals.

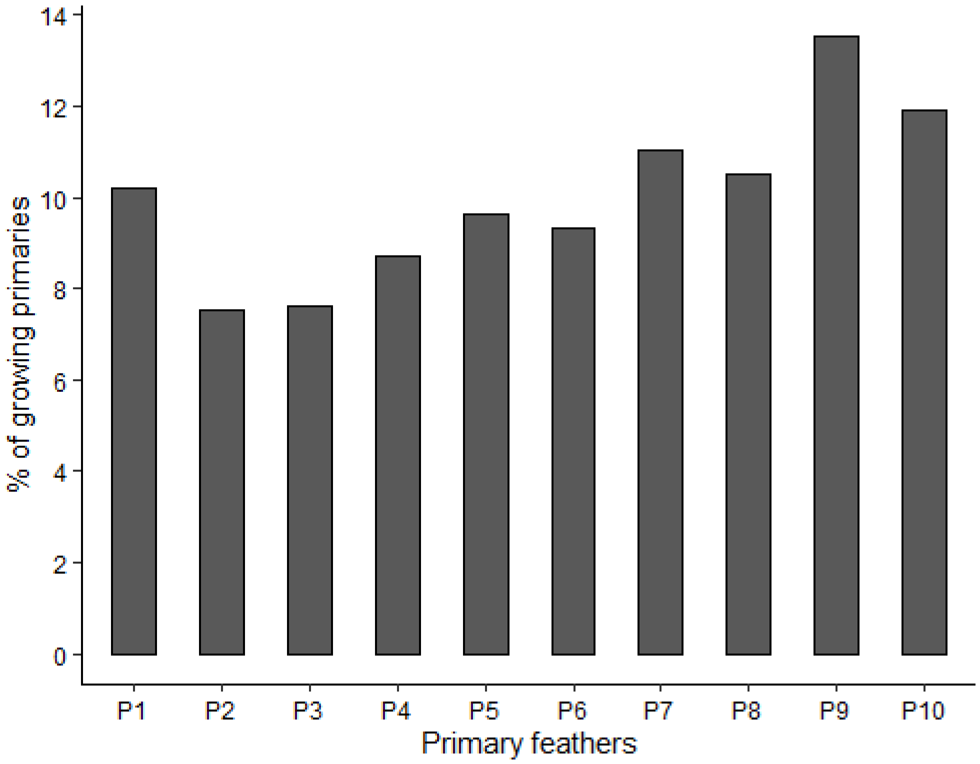


Figure 3.3: Percentage of growing primaries in 582 adult Cape Gannets moulting primaries.

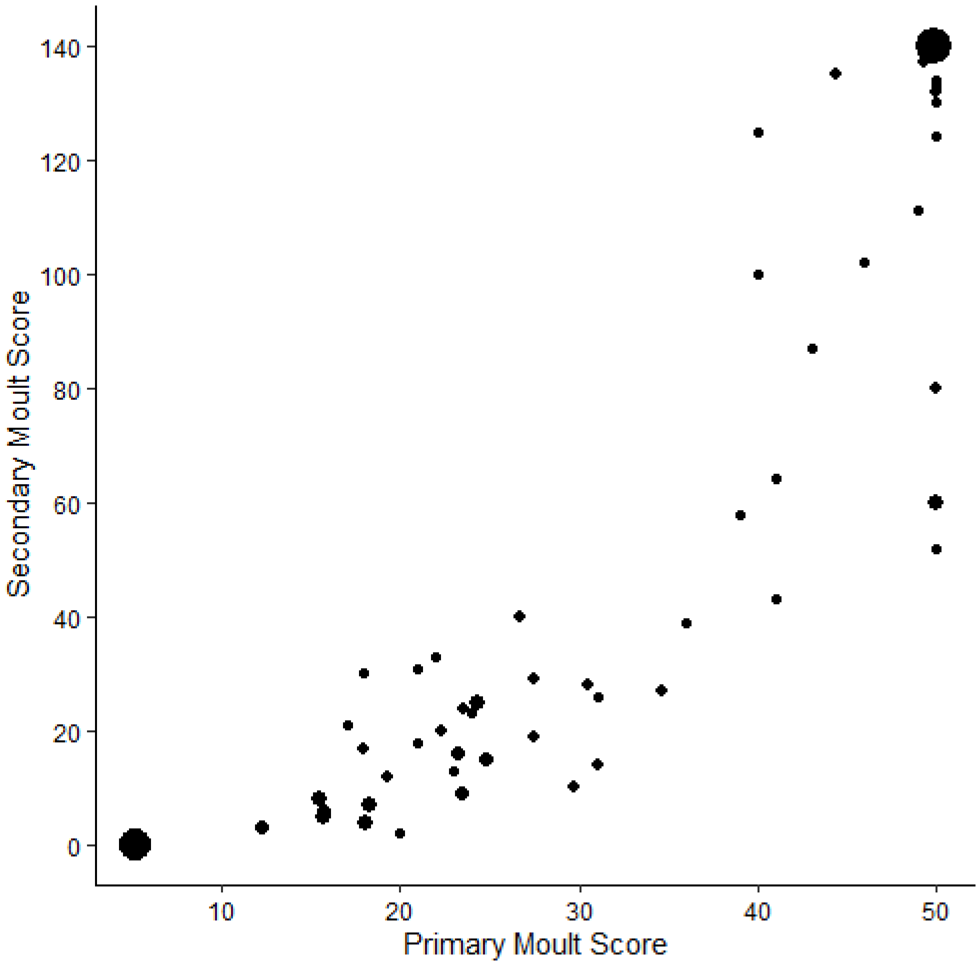


Figure 3.4: Secondary moult scores in relation to primary moult scores of 262 adult Cape Gannets captured at Malgas Island, South Africa. Note: sample size for the largest sample points = 86.

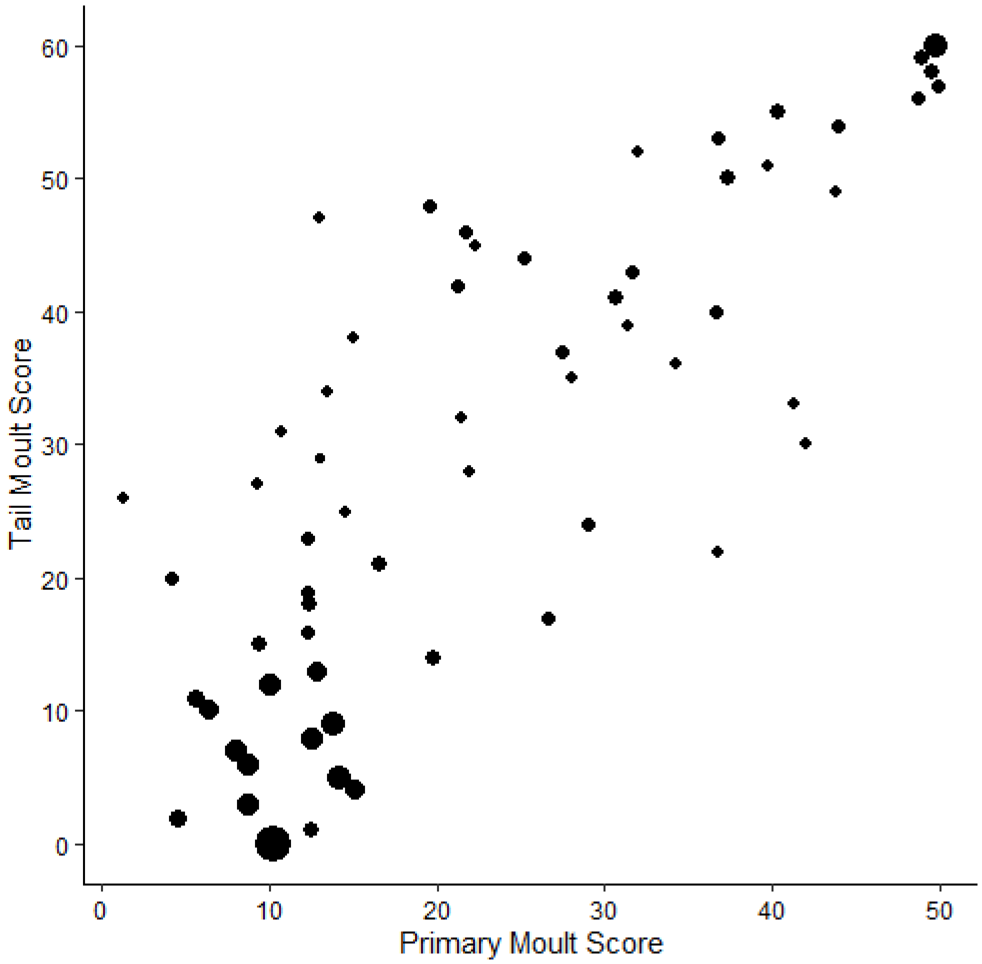


Figure 3.5: Moult scores of rectrices in relation to primary moult scores of 1326 Cape Gannets captured at Lambert’s Bay and Malgas Islands, South Africa. Note: sample size for the largest sample points = 128.

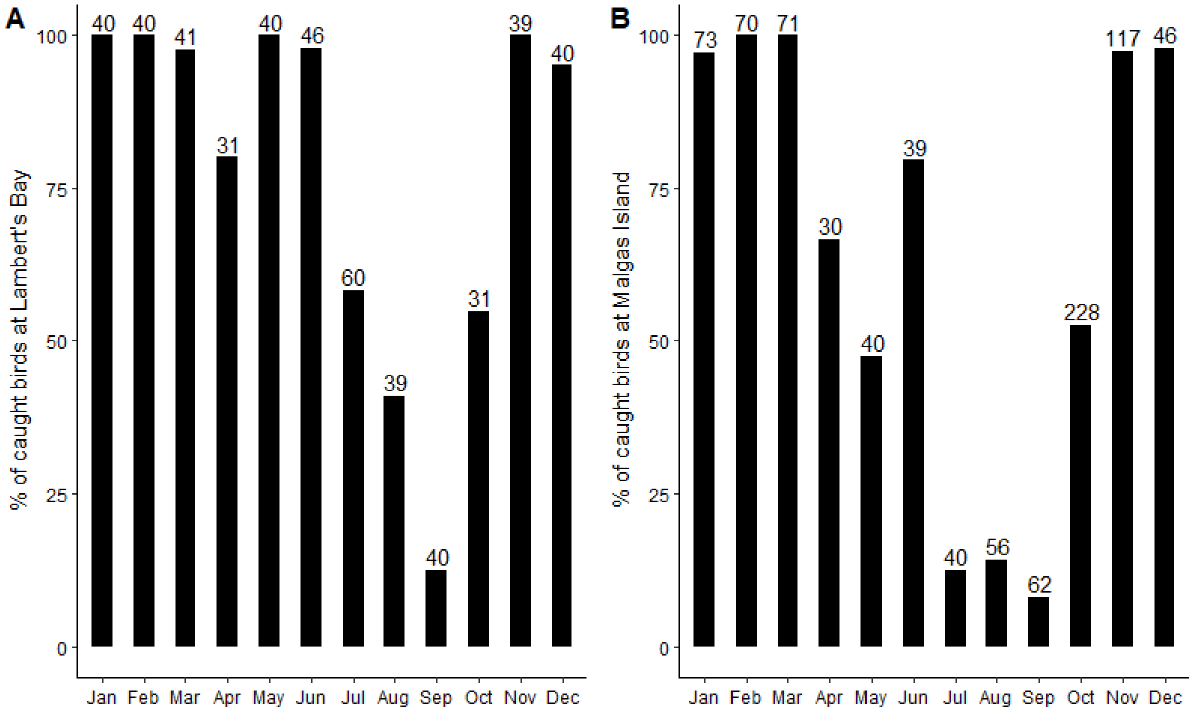


Figure 3.6: Monthly proportions of Cape Gannets in active rectrix moult at (A) Lambert's Bay and (B) Malgas Island. The numbers above the bars are the sample sizes.

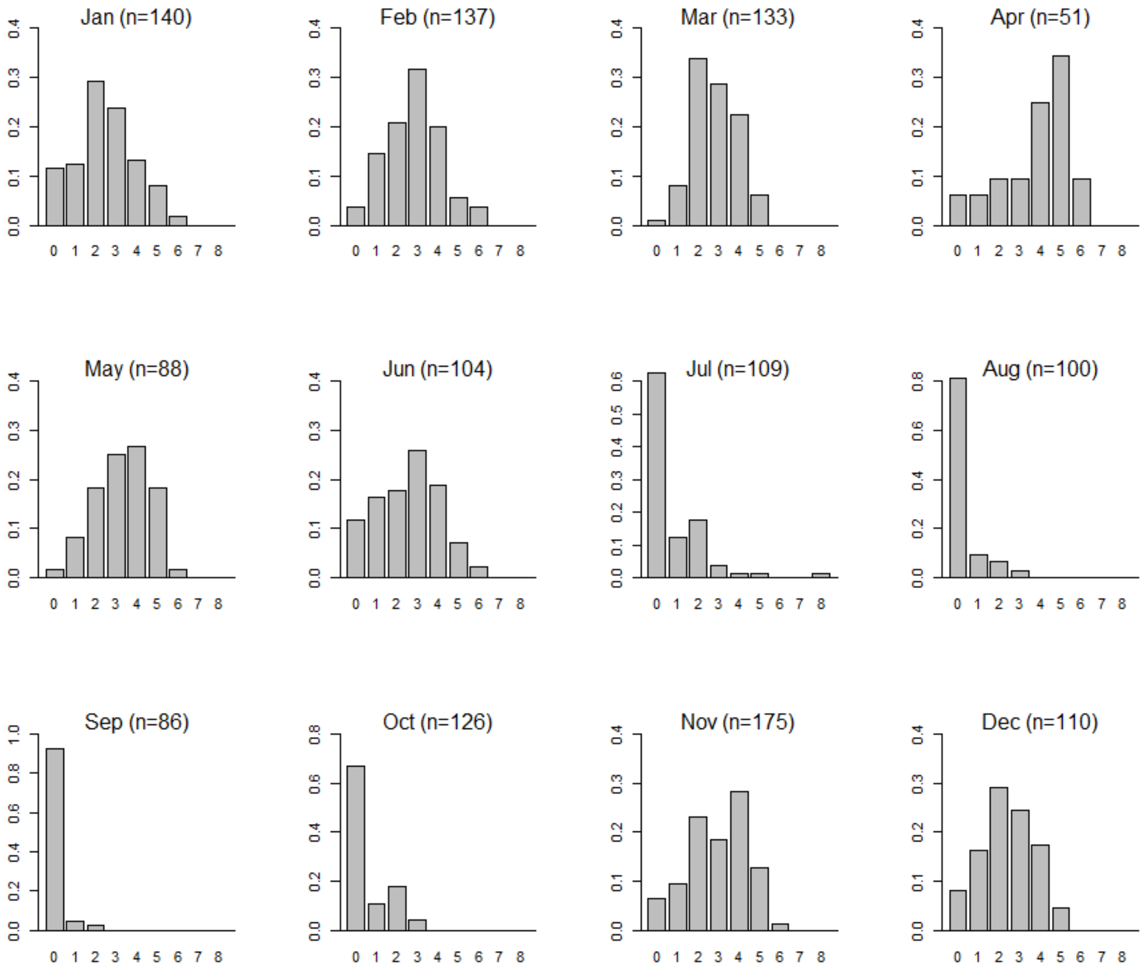


Figure 3.7: Proportions of Cape Gannets (n = 1359) moulting different numbers of tail feathers (0–8) at both Lambert's Bay and Malgas Island from January to December.

Table 3.1: Secondary moult summary table (showing nodal and terminal sites) for 165 Cape Gannets growing secondaries captured at Malgas Islands, South Africa. It was difficult to deduce the directional pattern (i.e. distal or proximal) of moult. However, two birds were growing secondaries distally at S3 and S25, while one was growing secondaries proximally at S27.

	S1	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**	**S8**	**S9**	**S10**	**S11**	**S12**	**S13**	**S14**	**S15**	**S16**	**S17**	**S18**	**S19**	**S20**	**S21**	**S22**	**S23**	**S24**	**S25**	**S26**	**S27**	**S28**
Nodal	3	3	3	12			3	6	3		3			6									6	6	15	10	8	6
Terminal		3		3	3							9	3			3		3		3					3		6	3
Growing	14	18	18	25	20	14	18	18	17	22	15	24	25	22	24	22	29	31	18	15	28	26	18	28	21	9	13	1

Table 3.2: Rectrix moult summary table for 1326 adult Cape Gannets captured at Lambert’s Bay and Malgas Islands, South Africa.

		Right side				
		Outward	Inward	Mixed	All new	All old
Left side	Outward	84	10	12	4	21
	Inward	8	329	18	22	10
	Mixed	9	21	47	15	32
	All new	8	26		226	
	All old	22	12	15		375

Table 3.3: Probabilities of rectrix replacement among 1326 adult Cape Gannets (487 from Lambert's Bay and 839 from Malgas Island) and comparison between observed and expected asymmetry (see Methods for details).

Parameters	**T1**	**T2**	**T3**	**T4**	**T5**	**T6**
Lambert's Bay						
Probability of replacement	0.36	0.35	0.33	0.36	0.36	0.36
Symmetry (%)	50.5	54.9	64.0	60.3	62.7	66.2
Asymmetry: major (%)	18.9	12.5	11.3	14.0	10.6	11.8
intermediate (%)	16.7	15.2	13.0	12.0	15.5	11.5
minor (%)	13.9	17.4	11.8	13.7	11.3	10.5
Total asymmetry (%)	49.5	45.1	36.0	39.7	37.3	33.8
Expected (null model) (%)	52.3	48.7	43.7	53.7	53.0	51.5
χ^2 values	1.93	0.70	10.27	6.73	12.48	23.16
p-value	0.11	0.30	0.00*	0.01*	0.00*	0.00*
Malgas Island						
Probability of replacement	0.38	0.38	0.36	0.37	0.37	0.34
Symmetry (%)	58.3	66.6	68.9	71.0	67.4	73.3
Asymmetry: major (%)	17.1	13.2	9.6	7.8	10.1	9.6
intermediate (%)	15.3	9.1	10.4	9.3	10.3	9.9
minor (%)	9.3	11.1	11.1	11.9	12.2	7.3
Total asymmetry (%)	41.7	33.4	31.1	29.0	32.6	26.7
Expected (null model) (%)	54.9	54.9	50.8	53.7	52.2	45.5
χ^2 values	4.08	27.92	35.00	25.65	29.28	52.06
p-value	0.03*	0.00*	0.00*	0.00*	0.00*	0.00*

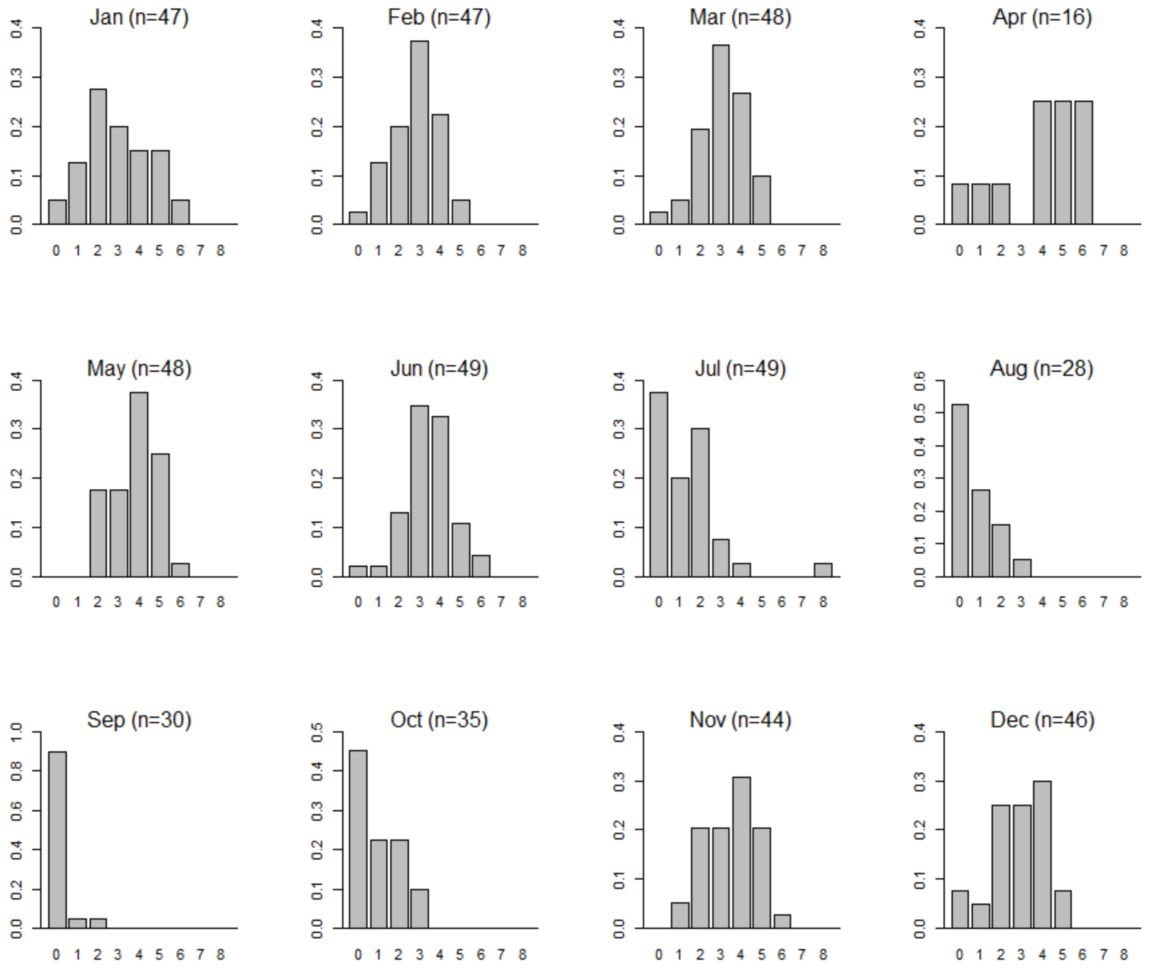
Supplemental material

Supplemental Table 3.1: The average (± SD) mass (mg) and length (mm) of primaries, secondaries and rectrices of Cape Gannets (n =12) killed by fishing operations.

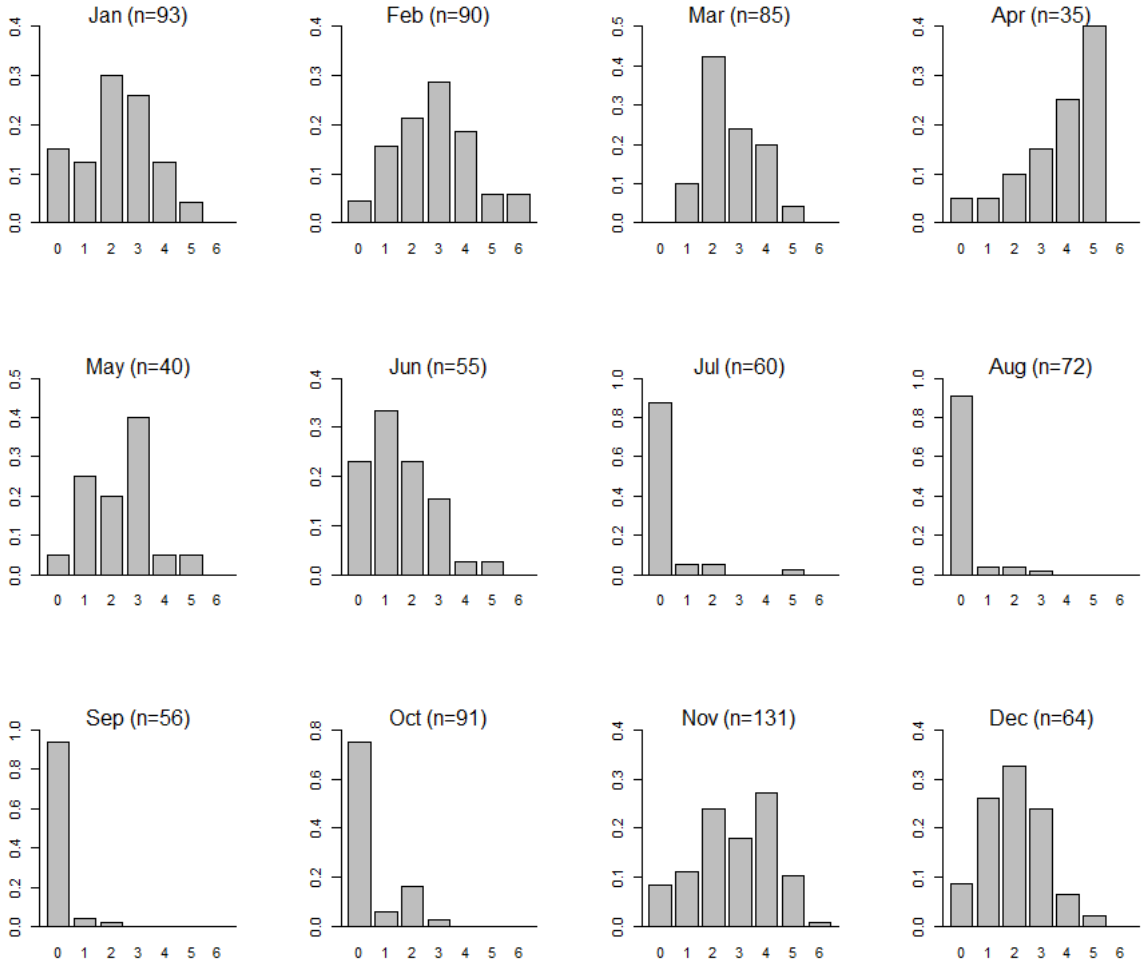
Feathers	Mass (mg)	Length (mm)
	Primaries (n = 12)	
P10	1350 ± 21.7	316 ± 7.7
P9	1531 ± 24.4	333 ± 8.2
P8	1676 ± 27.2	345 ± 8.4
P7	1451 ± 25.5	325 ± 7.5
P6	1137 ± 20.4	288 ± 7.1
P5	881 ± 18.7	258 ± 7.2
P4	687 ± 18.2	230 ± 6.7
P3	545 ± 17.6	202 ± 6.5
P2	447 ± 17.0	189 ± 5.4
P1	380 ± 14.7	179 ± 5.1
Total	**10085 ± 205.4**	**2665 ± 69.8**
	Secondaries (n =12)	
S1	329 ± 12.4	168 ± 5.1
S2	294 ± 12.1	165 ± 5.2
S3	268 ± 12.2	163 ± 5.2
S4	251 ± 11.8	160 ± 5.2
S5	241 ± 11.4	159 ± 4.9
S6	220 ± 11.4	155 ± 5.1
S7	211 ± 11.2	156 ± 5.1
S8	206 ± 11.3	155 ± 5.3
S9	203 ± 12.1	154 ± 4.9
S10	204 ± 12.4	156 ± 4.9
S11	194 ± 10.7	152 ± 5.2
S12	194 ± 11.5	154 ± 5.2
	Secondaries	
S13	193 ± 11.2	152 ± 5.1
S14	183 ± 10.4	151 ± 5.1
S15	188 ± 10.6	152 ± 5.2
S16	188 ± 10.1	151 ± 5.3
S17	183 ± 11.4	152 ± 5.1
S18	190 ± 11.4	152 ± 4.9
S19	189 ± 12.2	151 ± 5.2
S20	192 ± 11.1	152 ± 5.1
S21	196 ± 9.2	152 ± 5.2
S22	195 ± 8.7	150 ± 4.8
S23	195 ± 10.2	152 ± 5.0
S24	187 ± 10.8	150 ± 4.8
S25	182 ± 9.7	148 ± 4.5
S26	155 ± 9.8	144 ± 4.4
S27	113 ± 9.2	129 ± 4.4
S28	65 ± 8.5	102 ± 4.1
Total	**5607 ± 305.0**	**4237 ± 139.2**
	Rectrices (n = 12)	
T1	654 ± 18.4	220 ± 7.1
T2	621 ± 16.8	212 ± 7.2
T3	550 ± 16.1	196 ± 6.7
T4	453 ± 15.2	183 ± 6.5
T5	408 ± 14.8	173 ± 6.4
T6	333 ± 14.2	157 ± 6.2
Total	**3018 ± 95.5**	**1141 ± 40.1**

Supplemental Table 3.2: Primary moult summary table (showing proximal and distal sites) for 582 adult Cape Gannets growing primaries captured at Lambert’s Bay and Malgas Islands, South Africa.

	P1	**P2**	**P3**	**P4**	**P5**	**P6**	**P7**	**P8**	**P9**	**P10**
Proximal	3	0	0	2	1	2	1	1	3	
Distal	6	2	6	5	1	7	2	3	4	



Supplemental Figure 3.1: Proportions of Cape Gannets (n = 487) moulting different numbers of tail feathers (0–8) at Lambert's Bay from January to December.



Supplemental Figure 3.2: Proportions of Cape Gannets (n = 872) moulting different numbers of tail feathers (0–6) at Malgas Island from January to December.

CHAPTER 4

Timing, duration and symmetry of flight feather moult in White-chinned Petrels

Abstract

The cost of moult is substantial, especially in seabirds where moult schedule of flight feathers is critical. More than 2400 White-chinned Petrels killed in fisheries off southern Africa were scored for moult from 1996 to 2020. The petrels showed a simple descendent primary moult and one active moult centre, although moult of P2-3 sometimes started before P1. Among adults, the Underhill-Zucchini model estimated that primary moult started on 7 May (± 8 days SD) and lasted 103 days (mean end date 20 August ± 10 days). Most adults visiting colonies at the end of the breeding season were yet to start moulting, with the first adult seen in primary moult on 25 April. Adult males started and finished primary moult 10 days before females. Moult was particularly intense in the inner primaries, growing up to six feathers at once, slowing to at most 3–4 outer primaries. Overall, the average number of primaries moulted at once was greater in adults (2.3 ± 1.1) than immatures (1.9 ± 1.2), independent of sex, presumably because moult started earlier in immatures than adults. Secondary moult started two weeks later than primary moult, after 3–4 primaries had been dropped. Secondary moult typically progressed from three nodal sites: starting with the innermost secondaries, and inward waves from S1 and S5. The secondaries were replaced from 2.7 ± 1.3 active moult centres (range 1–6), replacing 4.6 ± 2.7 (1–13) secondaries at once. Adults had more intense secondary moult (4.7 ± 2.8 growing feathers) than immatures (3.6 ± 2.3), again with no difference between the sexes. However, photographs of non-moulting birds at sea show that 27% of birds do not replace all secondaries each year. Tail moult usually commenced with the start of secondary moult and was highly variable, with 1–12 rectrices growing at once. Adults typically had more active centres (3.0 ± 1.4) than immatures (2.3 ± 1.0). Moult symmetry was greater among the primaries (84%) than either the secondaries (46%) or rectrices (68%). Although adult wing moult was intense, there was no clear evidence of reduced flight activity from breeding adults fitted with leg-mounted activity loggers during the moult period.

Introduction

In general, birds tend to avoid overlap of moulting with other energy-demanding activities, such as breeding and migration (Ginn and Melville 1983; Bridge 2006; Newton 2009; Ausems et al. 2019). Moult is costly, especially for large birds because large feathers take longer to grow (Rohwer et al. 2009). Consequently, large birds either simultaneously shed all flight feathers and thus become temporarily flightless (e.g. most ducks and grebes; Newton 2009) or have complex moult strategies, not replacing all feathers in a year (Langston and Rohwer 1995; Rohwer et al. 2009). Detailed knowledge of moult patterns is needed to better understand life history traits, distribution, energy budget strategies and consequences of human activities on bird populations (Cooper et al. 1991; Bridge 2006; Allard et al. 2008; Bugoni et al. 2014).

The Procellariidae, which includes the fulmars, petrels, prions, shearwaters and diving petrels, all (except some diving petrels) undergo a complete, sequential annual primary moult, with variations in timing and extent of secondary, tail and body moult (Marchant and Higgins 1990). In most cases, secondary moult begins half-way through primary moult, and in some larger species not all secondaries are moulted annually (Marchant and Higgins 1990). Moult studies mainly focus on primary replacement, with less attention on secondaries and rectrices (Bugoni et al. 2014). Greater attention is needed on secondary moult, because large gaps among this feather tract greatly impact aerodynamic performance given their importance in generating lift (Hedenström and Sunada 1999; Ramos et al. 2009). Intense moult affects flight ability (e.g. shearwaters; Brown 1988) and recent studies have shown that during wing moult, fulmars, prions and other small petrels greatly reduce the proportion of each day spent in flight (Cherel et al. 2016; Grissot et al. 2020; Jones et al. 2020).

Flight feather moult among adult petrels is usually fairly rapid and intense (e.g. Great Shearwater *Ardenna gravis*, Brown 1988; Sooty Shearwater *A. griseus*, Brown 1988; Northern Fulmar *Fulmarus glacialis*, Brown 1988; Blue Petrel *Halobaena caerulea*, Ryan et al. 2020) but is more protracted in Cory's Shearwater (Ramos et al. 2009). The inner primaries are usually shed almost simultaneously, and the outer primaries shed one or two at a time (Bugoni et al. 2014). Moult and breeding are typically segregated (Brown 1988; Warham 1996; Bridge 2006), but moult overlaps with breeding in a few species (e.g. giant petrels *Macronectes* spp., Hunter 1984; Cory's Shearwater, Alonso et al. 2009). Interestingly, timing of moult also differs between closely-related species. For example, Southern Fulmars *F. glacialoides* start primary moult during incubation (Barbraud and Chastel 1998), while Atlantic Fulmars only start after their chicks fledge (Allard et al. 2008). Failed breeders generally start to moult earlier than successful breeders (Conroy 1972; Hunter 1984; Marchant and Higgins 1990) and immatures start earlier than adults (Marchant and Higgins 1990), with sex-related differences in some species (Marchant and Higgins 1990; Weimerskirch 1991). The sex with the lesser investment in parental care during chick-rearing can allocate more time, resources and energy to feather replacement (Svensson and Nilsson 1997; Alonso et al. 2009). For example, males of both species of giant petrels start primary moult earlier than females (Hunter 1984).

The variations in moult strategies among petrels make it difficult to assume the same patterns across species (Bridge 2011; Bugoni et al. 2014). Understanding moult strategies in seabirds is often hindered by their ecology and life history (Bridge 2006). Their pelagic lifestyles make them relatively inaccessible during the non-breeding season, when moulting usually takes place (Weimerskirch 1991; Monteiro and Furness 1996; Bridge 2006). Observations at sea can provide important information on seabird moult, as moult can be observed from photographs of birds in flight (Camphuysen and Van Der Meer 2001; Keijl 2011; Ryan et al. 2020), or from dead specimens, either killed incidentally on fishing gear (Ryan 1999; Edwards and Rohwer 2005), washed ashore (Bugoni et al. 2007), or collected (Brown 1988) or captured at sea (Bugoni et al. 2008, 2014).

White-chinned Petrels are the largest members of the Procellariidae other than the giant petrels. They breed on sub-Antarctic islands during the austral summer (Marchant and Higgins 1990) and are listed as Vulnerable (BirdLife International 2022) because they are the seabird most often killed on longlines in the Southern Ocean and adjacent temperate waters (Robertson et al. 2006; Petersen et al. 2009; Delord et al. 2010; Rollinson et al. 2017) and are also impacted by other fisheries (Waugh et al. 2008; Watkins et al. 2008; Ryan et al. 2012). Adults return to their breeding colonies in early/mid-September, lay a single egg from early November to mid-December, and successful breeders depart for their wintering grounds in April; failed breeders depart earlier (Marchant and Higgins 1990; Phillips et al. 2006; Péron et al. 2010; Ryan et al. 2012). Ryan (1999) found that adults do not moult while breeding, but Bugoni et al. (2014) reported that all Spectacled Petrels *Procellaria conspicillata*, sister species to the White-chinned Petrel, caught at sea off Brazil during the chick-rearing period in February, were in primary moult. Some studies have reported rapid primary moult in White-chinned Petrels (of unknown age, Marchant and Higgins 1990; and adults, Ryan 1999) but not among immatures (Ryan 1999). Chastel (1995) reported that many White-chinned Petrels replace all their rectrices at once, whereas Bugoni et al. (2014) found that Spectacled Petrels typically replaced alternate tail feathers, with no clear pattern across the tail. Body moult is protracted, with an overlap between primary, tail and body moult (Bugoni et al. 2014).

In this study, I describe the moult pattern (timing, duration, sequence and symmetry) of flight feathers in White-chinned Petrels incidentally killed by fishing vessels off southern Africa. I augment these data with observations of adults attending breeding colonies on Marion Island to confirm when breeding adults start to moult, and use photographs of non-moulting petrels in flight to demonstrate that secondary moult is incomplete in some birds. Finally, I assess whether moult impacts the proportion of time spent in flight based on data from adult

White-chinned Petrels tracked with Global Location Sensor (GLS) loggers equipped with activity sensors (Rollinson et al. 2018).

Methods

White-chinned Petrels incidentally caught by long-line fishing vessels off southern Africa were frozen and returned to port for examination. Initial fishing effort (1996–2005) mainly targeted Patagonian Toothfish *Dissostichus eleginoides* around the Prince Edward Islands in the southwest Indian Ocean, where most captures were of breeding adults caught during the austral summer (Ryan 1999). However, from 2002 to 2020, most fishing effort monitored was by foreign-flagged vessels targeting tunas (*Thunnus*) and Swordfish (*Xiphias gladius*) in oceanic waters around southern Africa (Petersen et al. 2009; Rollinson et al. 2017). These vessels mainly fish in southern Africa waters from April–November, so most samples were from the austral winter. After defrosting, the petrels were sexed by inspection of the gonads, aged and scored for flight feather moult (Ryan 1999). Juveniles were identified by smooth, pale grey bills, lacking any moult scarring (cf. Marchant and Higgins 1990) as well as greatly reduced gonads. Adults were identified by ivory yellow bills with extensive moult scarring, and well-developed gonads in females (year-round) and males (pre-breeding and early breeding season only, September-November). Immatures were inferred by intermediate bill scarring and gonad development, but could not always be reliably identified, especially in males outside the early breeding season. Birds of unknown age were included in the overall moult patterns (i.e. when not separating by age), but excluded when reporting patterns for adults and immatures.

To confirm the onset of wing moult in breeding adults, birds returning to colonies on Marion Island, southwest Indian Ocean were checked for primary moult at the end of the breeding season over five years from 2009 to 2018. Observations were made from 6 April to 12 May, with most in mid- to late-April each year. The start of primary moult is readily detected in birds in flight as typically two or more inner primaries are shed at once.

Moult data

White-chinned Petrels have 10 functional primaries, 24–26 secondaries and 12 tail feathers. Moult of flight feathers was scored (cf. Ginn and Melville 1983) where old feathers = 0, growing feathers = 1 to 4 for increasing stages of development, and fully-grown new feathers = 5. However, differences in age among fully grown feathers were hard to discern, especially among secondaries and rectrices, because the plumage of all birds was thoroughly waterlogged as a result of drowning on longlines. Accordingly, it was not possible to age most fully-grown secondaries and rectrices, and birds with no active moult were simply scored as fully grown. To assess the extent of incomplete moult in the secondaries, I examined photographs of White-chinned Petrels in flight taken at sea, mostly off the Western Cape, from April 2005 to May 2021. Wear contrasts were used to infer the extent of secondary and greater covert moult among birds not in active wing moult. Old feathers, not replaced during the most recent wing moult, are distinctly paler and browner than newer feathers (e.g. Onley and Scofield 2007; Supplemental Figure 3.1). I excluded obvious juveniles in fresh plumage from the sample sizes of birds checked as they have uniform-age wings, but some older juveniles with worn plumage may have been included.

Primaries were numbered from P1 (innermost) to P10 (outermost); secondaries from S1 (outermost) to S26 (but ranges from 24–26); and rectrices from T1 (central pair) to T6 on each side of the tail. The Primary Moult Score (PMS) was calculated for each bird as the sum of the moult scores of the ten primaries on the wing in best condition to score (range 0–50). Similarly, I calculated Secondary Moult Score (SMS, range 0–130 for a bird with 26 secondaries) but given variations in the number of secondaries, I standardised SMS scores from 0–1 by dividing by the maximum total score; and a Tail Moult Score (TMS) for the entire tail (range 0–60). Not all birds were scored for secondary and tail moult. The presence of wing covert and body moult were also recorded for some individuals.

PMS, SMS and TMS were converted into Percentage Feather Mass Grown (PFMG) using the relative masses of primaries, secondaries and rectrices, respectively (Underhill and Joubert 1995). Feather masses were obtained by collecting flight feathers from four White-chinned Petrels killed on longlines. After plucking, the feathers were air dried for several days then measured (flattened total length to the nearest 1 mm) and weighed (to the nearest 1 mg). The average mass of each primary, secondary and rectrix (Supplemental Table 4.1) was used to calculate relative feather mass for each tract (Underhill and Joubert 1995).

Symmetry of moult

Symmetry of feather growth was assessed by comparing the moult scores of each feather pair on either side of the bird (all tails were scored on both sides, but not all birds were scored for both wings). A simple index of asymmetry was calculated as the standardised moult score asymmetry (i.e. asymmetry score/50 for primaries, asymmetry score/120 or 125 or 130 for secondaries and asymmetry score/30 for rectrices, expressed as %), given that the maximum possible asymmetry would have a summed moult score difference of 50 for primaries (all primaries on one wing old, and those on the other wing new), 120–130 for secondaries and 30 for rectrices. Differences in moult score of 1 between a pair of tail feathers were regarded as 'minor' asymmetries (i.e. 0–1, 1–2, 2–3, 3–4 and 4–5); differences of 2–3 as 'intermediate' (i.e. 0–2, 0–3, 1–3, 1–4, 2–4, 2–5, 3–5) and of 4–5 as 'major' asymmetries (i.e. 0–4, 0–5, 1–5). To test whether asymmetry at a feather position is random, I used Pearson's chi-squared goodness-of-fit tests with Yates' correction for continuity to compare the observed frequency of asymmetry with that expected by chance (assuming random replacement) for a given likelihood that a given feather is in active moult (cf. Adekola et al. 2021a, b). The degree of moult asymmetry depends on the proportion of feathers in moult, because if no feathers are in moult, the moult pattern will be symmetrical. As a result, differences in the proportion of feathers in active moult must be controlled for when comparing asymmetry across feathers (Adekola et al. 2021a, b).

Activity data linked to moult

To assess whether flight feather moult affects the proportion of time spent in flight (cf. Cherel et al. 2016), I used immersion state time series (wet/dry) to calculate the percentage of each day spent sitting on the water (Gutowsky et al. 2014) by six breeding adult White-chinned Petrels tracked with GLS loggers between 2010 and 2012 (Rollinson et al. 2018). Activity data were missing for some months: September to November (for birds A and C; Supplemental Figure 4.2; August to November (for bird B; Supplemental Figure 4.2); June to November (for bird D; Supplemental Figure 4.2); October and November (for bird E; Supplemental Figure 4.2); and July to November (for bird F; Supplemental Figure 4.2). I assumed that moult of adults would occur during the months it was observed in birds killed on long-lines.

Data analyses

Annual estimates of flight feather moult start date and duration (± standard deviation, SD) were obtained using the combined PFMG of all flight feathers in the 'moult' package in R (Erni et al. 2013). Mean start date and duration of adult moult were estimated by modelling PFMG values against Julian day from 1 December (outside the primary moult period in adult White-chinned Petrels; Ryan 1999). I ran basic models that make use of non-moulting as well as moulting birds, fitting the model using the maximum likelihood method (Underhill and Zucchini 1988; Newton 2009) and calculated 95% confidence limits for moult parameters following Erni et al. (2013). These models give estimates of moult duration, average start and end dates, and their standard errors. Models were compared using Akaike Information Criteria (AIC), and significant differences between models were tested using log-likelihood ratio tests (Burnham and Anderson 2002). To test whether moult tends to be symmetrical across flight feathers, I compared observed values of asymmetry to those expected assuming moult is random with respect to location (Brommer et al. 2003; Adekola et al. 2021a, b). I used general linear models to assess differences in number of growing feathers and active moult centres between ages and sexes among moulting birds. I also used chi-square (contingency table) to test differences in number of birds in moult across ages and sexes. All statistical analyses were performed in the R statistical environment (R Core Team 2019).

Results

I scored moult from 2431 White-chinned Petrels incidentally caught by vessels fishing off southern Africa between 1996 and 2020 (268 from the toothfish fishery and 2163 from the tuna fishery). Some of the 156 juveniles were moulting body feathers, but none had started to replace any primaries, secondaries or tail feathers and so are not considered further. Additional data on the moult extent among the remiges, and greater and median secondary coverts, was obtained from photographs of 88 post-juvenile birds in flight taken at sea (67 that had completed moult, and 21 in active wing moult).

Primary moult

Of the 2276 non-juvenile birds scored for primary moult, 1294 (57%) were scored as adults, 845 (37%) immatures and 137 (6%) of unknown age. More adults (36%, n = 470) were moulting primaries than immatures (6%, n = 51). The proportion of adults in primary moult increased from March to May and then decreased until September (Figure 4.1A), while immatures were mostly in moult between December and May (Figure 4.1B), explaining the lower proportion in moult than adults (given that most immature birds were caught during winter). The few adults moulting in summer presumably were failed breeders, because all but one adult caught at the Prince Edward Islands were not moulting; the exception was a female just starting moult on 21 March. Virtually all adults visiting colonies at the end of the breeding season were yet to start moulting. The first adult seen in primary moult at Marion Island was on 25 April, when most chicks have fledged. The Underhill-Zucchini model estimated the mean start and end of adult primary moult as 7 May (± 8 days SD) to 20 August (± 10 days SD), suggesting that primary moult lasts 103 days (Figure 3.2). Males started (4 May ± 14 days) and finished moulting (14 August ± 12 days), roughly 10 days before females (14 May ± 10 days to 26 August ± 15 days). However, some adults (7 males and 4 females, all with well-developed gonads) were still completing growth of P9 and P10 in late September.

Most White-chinned Petrels showed a sequential and descendent moult, starting from P1 and proceeding to P10, but six of 25 birds moulting inner primaries apparently dropped P2 or P2 and P3 before P1 (Supplemental Table 4.2). Primaries only had one active moult centre (apart from one bird growing P8 and P10, but this was on one wing only). Females (2.3 ± 1.1 growing feathers) and males (2.2 ± 1.1) replaced similar numbers of primaries at once, but moult was more intense in adults (2.3 ± 1.1) than immatures (1.9 ± 1.2; $F_{2,521} = 4.07$, $p = 0.02$). Among all birds, 30% were growing one primary, 26% were growing two, 35% were growing three, 5% were growing four, 3% were growing five, and 1% were growing six primaries ($n = 538$). Among moulting adults, 303 (65%) were females, 166 (35%) males, with one of unknown sex (Supplemental Table 4.3). In moulting immatures, 35 (67%) were females and 17 (33%) were males (Supplemental Table 4.3). Although males predominated among all birds killed (57% of adults and 59% of immatures), females were more often in primary moult than males for both adults (33% males, 58% females; $\chi^2 = 6.33$, $p = 0.01$) and immatures (4% males, 11% females; $\chi^2 = 2.40$, $p = 0.04$).

Secondary moult

Most White-chinned Petrels (75%) had 24 secondaries; 19% had 25 and 6% had 26. Of the 906 birds scored for secondary moult, 490 (54%) were adults, 363 (40%) immatures and 53 (6%) unknown age. Secondary moult was recorded in 284 (58%) adults and 29 (8%) immatures (Supplemental Table 4.4). The numbers of males and females examined for secondary moult were similar (χ^2 = 0.52, p = 0.43), with females more likely to be in secondary moult in immatures (14% females, 5% males; χ^2 = 3.39, p = 0.04) but not in adults (65% females, 50% males; χ^2 = 1.70, p = 0.13). Among adults, secondary moult started in March and peaked in May. The mean starting day was estimated to be 21 May ± 9 days, two weeks after the start of primary moult, and lasted for 114 days, ending on 11 September ± 15 days. However, some adults were still growing secondaries in late October, shortly before the start of egg laying (Figure 4.1C). Secondary moult in immatures started slightly earlier than adults, peaking in April (Figure 4.1D). Moult of secondary feathers mainly overlapped with the latter half of primary moult in both adults (Figure 4.3A) and immatures (Figure 4.3B). A few birds completing primary moult were not moulting any secondaries (3% of 79 birds with PMS 30–39 and 26% of 265 birds with PMS 40–49), suggesting that they may not replace any secondaries in some years, but all 19 birds with PMS 20-30 were in secondary moult. Photographs of birds at sea show that 27% of 67 post-juvenile birds only replaced a subset of secondaries, retaining 8.1 ± 2.5 old feathers (range 4–14).

The secondaries were replaced from 2.7 ± 1.3 active moult centres (range 1–6), replacing 4.6 ± 2.7 secondaries at once (range 1–13). Females (2.8 ± 1.3 active centres) tended to have more active centres than males (2.5 ± 1.3), and adults (2.7 ± 1.3) to have more active centres than immatures (2.4 ± 1.4) but these differences were not significant for either sex (t = 1.4, df = 223.0, p = 0.15) or age (t = 1.2, df = 33.0, p = 0.24). Secondary moult was more intense in adults (4.7 ± 2.8 growing feathers) than immatures (3.6 ± 2.3; $F_{2,309}$ = 2.59, p = 0.05). Immature females (4.0 ± 2.3) grew more secondaries at once than immature males (2.3 ± 1.8; t = 2.2, df = 16.8, p = 0.03), but there was no difference between the sexes in adults (females 4.7 ± 2.7, males 4.8 ± 2.8; t = -0.2, df = 197.5, p = 0.83; Supplemental Table 4.4). Among all birds, 21% had one active centre, 28% had two, 24% had three, 17% had four, 8% had five, and 2% had six (n = 323). Three main nodal sites were identified: the innermost secondaries

(S17–S21) and S1 and S5. Moult started in the innermost secondaries, then inwards from S1–S4, and from S5–S16. There was considerable variation in the intensity of secondary moult: 14% of birds were growing one secondary, 10% two, 17% three, 12% four, 11% five, 10% six, 8% seven, 6% eight, 7% nine, 3.2% ten, 1.2% 11 and 0.6% were growing 13 secondaries (n = 323).

Tail moult

Of the 811 birds scored for tail moult, 436 (54%) were adults, 329 (40%) immatures and 46 (6%) unknown age. Rectrix moult was recorded in 195 (45%) adults and 59 (18%) immatures (Supplemental Table 4.5). In moulting adults, 116 (59%) were females and 79 (41%) were males, whereas 33 (56%) of moulting immatures were females and 26 (44%) were males (Supplemental Table 4.5). The numbers of males and females examined for tail moult were similar ($\chi^2 = 0.43$, $p = 0.49$), and females were more likely to be in tail moult in immatures (24% females and 13% males; $\chi^2 = 2.70$, $p = 0.04$) but not in adults (45% females and 42% males; $\chi^2 = 0.05$, $p = 0.41$). The proportion of adults in active tail moult was highest in July and decreased until September (Figure 4.1E), while immatures were in active moult from March and decreased to September (Figure 4.1F). Tail moult overlapped with the end of primary moult (Figure 4.4A) and usually coincided with the start of secondary moult (Figure 4.4B). The mean starting day estimated for replacing rectrices in adults was 27 May ± 11 days. Rectrix moult mostly started at the central feathers (T6), but this was quite variable, and 2% of adults replaced all rectrices at once (Figure 4.5). Only 14% of birds followed an alternating pattern of tail moult.

Rectrices were replaced from 2.9 ± 1.4 active moult centres (range 1–6), growing 4.8 ± 3.1 rectrices at once (range 1–12). Sex had no influence on the number of active centres (males 2.9 ± 1.5, females 2.8 ± 1.3; $t = -0.8$, $df = 205.0$, $p = 0.5$). However, adults had more active centres (3.0 ± 1.4) and were growing more rectrices (4.9 ± 3.1) than immatures (2.3 ± 1.0; $F_{2,251}$

= 6.92, $p < 0.001$, and 4.2 ± 3.2; $F_{2,251} = 1.25$, $p = 0.29$, respectively). Among all birds, 21% had one active centre, 23% had two, 21% had three, 22% had four, 11% had five and 2% had six active centres, and 18% of birds were growing one rectrix, 17% two, 7% three, 12% four, 8% five, 8% six, 8% seven, 9% eight, 5% nine, 5% ten, 2% eleven, and 2% were growing all their rectrices at once (n = 261).

Wing covert and body moult

Although a few birds just starting to replace their greater secondary coverts had only dropped 1-2 feathers, most birds were growing 60-100% of coverts at once (mean 0.82 ± 0.34 proportion of greater coverts in moult, n = 67). The greater coverts were replaced just as primary moult started; among bycatch birds, 73% of birds replacing greater coverts were growing 3–6 inner primaries (n = 43). Twelve of 17 birds photographed in early primary moult were replacing most or all of their greater secondary coverts (Supplemental Figure 4.3). Greater secondary covert moult was mainly observed in April and May, but some individuals (presumably immatures) were replacing greater coverts in October. Moult of the median secondary coverts generally only started when most greater coverts had been replaced.

Most birds examined in early winter were moulting body feathers (91% of birds killed from April to June, n = 206). This proportion decreased until the start of the breeding season in October (68%, n = 25; small samples between November and January).

Intensity of moult

Birds replacing 5–6 primaries at the same time reduced the total length of their primaries by 40–51% and the total mass by 28–39% (Supplemental Table 4.1). Expressed as a proportion of all wing and tail feathers combined, birds growing 5–6 primaries were simultaneously replacing 13–17% of their length and 14–19% of their mass. Replacing 13 secondaries at the same time amounted to 54% of their total length and mass, and 23% of the total length and

14% of the mass of all flight feathers (Supplemental Table 4.1). Replacing 11–12 rectrices at the same time equated to 92–100% of their total length and 92–100% of their total mass, or 22–24% of the overall length and 23–25% of the overall mass of all flight feathers (Supplemental Table 4.1).

Symmetry of moult

Of the 39 birds sampled for both wings, almost all moult in the primaries was symmetrical (84%; Table 4.1). Primary asymmetry (minor or intermediate, but not major) tended to be greater among the outer primaries (P8–P10: 16–26%) than inner primaries (P1–P7: 5–11%), but this simply reflected the lower proportion of active moult in the inner primaries (P_{moult} for P1–P7: 0.01–0.06) than in the outer primaries (P8–P10: 0.10–0.17; Table 4.1). Moult symmetry among the secondaries (65%; Table 4.2) and rectrices (68%; Table 4.3) was less than among the primaries (Table 4.1). Secondary asymmetry tended to be greater among the inner and outer secondaries (Table 4.2). There was strong selection for symmetry across all rectrices ($p < 0.05$; Table 4.3). Asymmetry tended to be greater among adults (T1: 28%; T2–T6: 20–24%) than immatures (T1–T6: 4–8%), but again this merely reflected the greater proportion of adults in tail moult (0.17–0.20) than immatures (0.05–0.08; Table 4.3).

Activity data linked to moult

There was no clear increase in time on the water (i.e. reduced flight activity) during the inferred moult period among adults fitted with leg-mounted activity loggers (Supplemental Figure 4.2).

Discussion

Despite being one of the largest petrels, White-chinned Petrels show no evidence of overlap between moulting and breeding (Ryan 1999). Among the closely-related Spectacled Petrel, Bugoni et al. (2014) suggested that primary moult started during chick rearing, because all birds caught off Brazil in February were in primary moult. However, it is likely that these birds were all immatures or failed breeders, as Bugoni et al. (2014) found two distinct groups of moulters in winter (April-August): some birds had completed primary moult, but most (presumably breeding adults) were only just starting moult. I found that adult moult among White-chinned Petrels only commenced after breeding, although a few birds still visiting their breeding colonies in late April had dropped their inner primaries.

The duration of primary moult varies considerably among petrels (Hunter 1984; Monteiro and Furness 1996; Bridge 2006; Ryan et al. 2020), largely determined by the intensity of moult (Brown 1988; Cherel et al. 2016). The duration and extent of moult in albatrosses is directly linked to timing and duration of interbreeding period (Weimerskirch 1991), but among petrels all primaries are replaced each year, irrespective of the time between breeding attempts (Marchant and Higgins 1990). Adult White-chinned Petrels manage to complete their flight feather moult during the non-breeding period by having a fairly intense primary moult (Marchant and Higgins 1990), and overlapping this with secondary, tail and wing covert moult. Rapid growth of the inner primaries has been reported in *Ardenna* shearwaters (Brown 1988; Cooper et al. 1991) and *Oceanodroma* storm-petrels (Ainley et al. 1976). Five to six inner primaries are usually replaced simultaneously (Brown 1988), with one or two outer primaries replaced at once (Bugoni et al. 2014). I found up to 3-4 outer primaries growing at once in White-chinned Petrels.

The results confirm that White-chinned Petrel primary moult is complete, progressing in a simple wave from inner to outer primaries, as observed in other petrels (Brooke 1981; Hunter 1984; Marchant and Higgins 1990; Cooper et al. 1991; Warham 1996; Monteiro and Furness 1996; Ryan 1999; Ramos et al. 2009; Bugoni et al. 2014). However, in almost one quarter of all birds, P1 probably was dropped after P2 and even P3, which has been reported in other petrels (e.g. Northern Fulmars *Fulmarus glacialis*, Thompson et al. 2000; Allard et al. 2008; Sooty Shearwaters *A. grisea*, Thompson et al. 2000) and storm petrels (Ainley et al.

1976). Males started and finished moulting before females, as reported in some fulmarine petrels (e.g. Hunter 1984; Alonso et al. 2009; Grissot et al. 2020), and might be a general pattern among Procellariiformes. For example, male albatrosses tend to moult more primaries each year than females (Weimerskirch 1991; Prince et al. 1997), suggesting that they start moult earlier than females. This sex-related difference could in part be linked to differences in parental investment (Svensson and Niisson 1997; Alonso et al. 2009; Ramos et al. 2009). The female-biased sex ratio in the proportion of moulting birds could in part be due to females moulting later than male White-chinned Petrels. Generally, adult moult was more intense than immature moult, replacing more flight feathers at once, which presumably results from immatures having more time to moult, and thus can afford to replace fewer feathers at once (Adekola et al. 2021a).

Secondaries showed a complex moulting pattern. The presence of several nodal sites of moult in the secondaries is a common pattern in birds with long wings (e.g. Edelstam 1984), including Procellariiformes such as giant petrels (Stresemann and Stresemann 1966; Hunter 1984), Cory’s Shearwaters (Ramos et al. 2009), albatrosses (Prince et al. 1993, 1997) and even storm petrels (Ainley et al. 1976), presumably to minimize large gaps in the wing (Arroyo et al. 2004). Secondary moult typically commenced after some inner primaries had been dropped (Hunter 1984; Ramos et al. 2009). It started at the innermost secondaries, probably because these feathers are subjected to more exposure and faster wear rates than the central secondaries (Zuberogoitia et al. 2013; Adekola et al. 2021a; Osborne and Ryan 2021). Carvalho et al. (2022) also reported complex secondary moult pattern for both Great and Sooty shearwaters and started at three points: S21 outward, S5 and S1 inward, with S4 usually moulting last. Thompson et al. (2000) found secondary moult started at an inner node and S5 in Sooty Shearwaters and Northern Fulmars, and secondary moult in storm petrels is similar to White-chinned Petrels, with nodes at S1 and S5 and the inner secondaries (Ainley et al. 1976).

Tail moult overlapped with the end of primary moult and usually commenced with the start of secondary moult. In other petrels, rectrices tend to be replaced when primary moult is almost complete (Warham 1996; Bugoni et al. 2014), suggesting that birds try not to grow primaries and rectrices simultaneously (Bugoni et al. 2014). Unlike other petrels, the intensity of tail moult varied greatly among individuals. On average, adults tended to replace slightly more rectrices at once than immatures, but both age groups show marked variation from 1-12 feathers growing at once (Chastel 1995). In terms of moult sequence, I found no fixed sequence in rectrix replacement. Bugoni et al. (2014) reported a tendency for alternating feathers to be replaced in the closely-related Spectacled Petrel, but this was only found in 14% of birds in active tail moult among White-chinned Petrels.

Body moult largely overlapped with primary moult, as found in Spectacled Petrels (Bugoni et al. 2014). In most petrel species, body feathers are replaced over several months, especially during the non-breeding period (Monteiro and Furness 1995; Thompson and Furness 1995; Warham 1996; Bugoni et al. 2014). My findings suggest that most White-chinned Petrels suspend body feather moult while breeding (but see Ramos et al. 2009).

Moult symmetry was higher in the primaries than in the secondaries and rectrices, as reported in other seabirds (e.g. Cape Gannets; Adekola et al. 2021a). Asymmetry in flight feathers has associated aerodynamic costs, and is thought to reduce manoeuvrability (Thomas 1993). The higher percentage of symmetrical moult in the primaries compared to the secondaries and rectrices supports the notion that birds minimise asymmetry in tracts with the greatest functional importance (Møller and Swaddle 1997; Arroyo et al. 2004; Bugoni et al. 2007). As petrels spend long periods gliding while foraging, synchrony in wing feather moult is probably under stronger stabilizing selection than tail feathers (Ramos et al. 2009).

The use of activity data can reveal novel insights on moult timing, especially among seabirds (Bridge 2011; Gutowsky et al. 2014; Grissot et al. 2020). Several petrels (Cherel et al.

2016; Jones et al. 2020) and a range of other seabirds including skuas (Phillips et al. 2007; Magnusdottir et al. 2014; Weimerskirch et al. 2015), alcids (Mosbech et al. 2012) and sulids (Garthe et al. 2012) all exhibit reduced flight activity while moulting. However, I found no evidence of an increase in the proportion of time spent sitting on the water in adult White-chinned Petrels during their moult period, which is surprising given their intensity of moult.

Although most studies of flight feather moult focus on the primaries, greater attention is needed on secondary moult in long-winged species, which can have two to more than three times as many secondaries as primaries to replace. Among White-chinned Petrels, the early replacement of the greater secondary coverts, at the same time as the innermost primaries, combined with the long length of the greater coverts (Bridge 2004), allows individuals to replace up to half of their secondaries at once without becoming flightless. In effect, delaying the replacement of the secondaries until the greater coverts have been replaced largely offsets the loss of wing area created by replacing a large number of secondaries at once (Ryan et al. 2020; Chapter 7). However, not all secondaries are replaced each year. Further studies are needed to determine which factors determine the extent of secondary moult, and assess whether such incomplete moult has any fitness implications (Fayet et al. 2016).

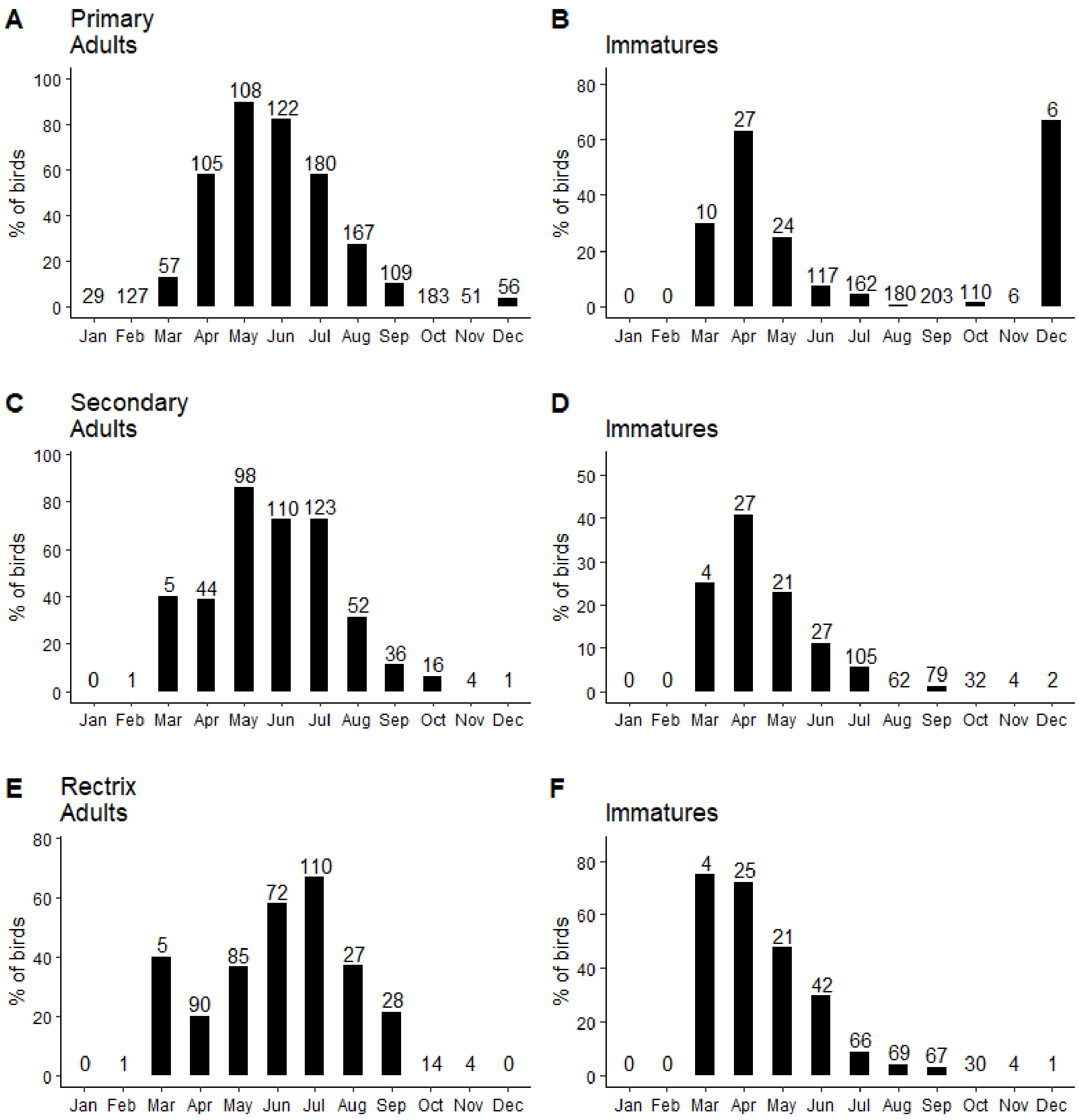


Figure 4.1: Monthly proportions of (A) adult and (B) immature White-chinned Petrels in primary moult; (C) adult and (D) immature White-chinned Petrels in secondary moult; (E) adult and (F) immature White-chinned Petrels in rectrix moult. Numbers above bars = sample sizes.

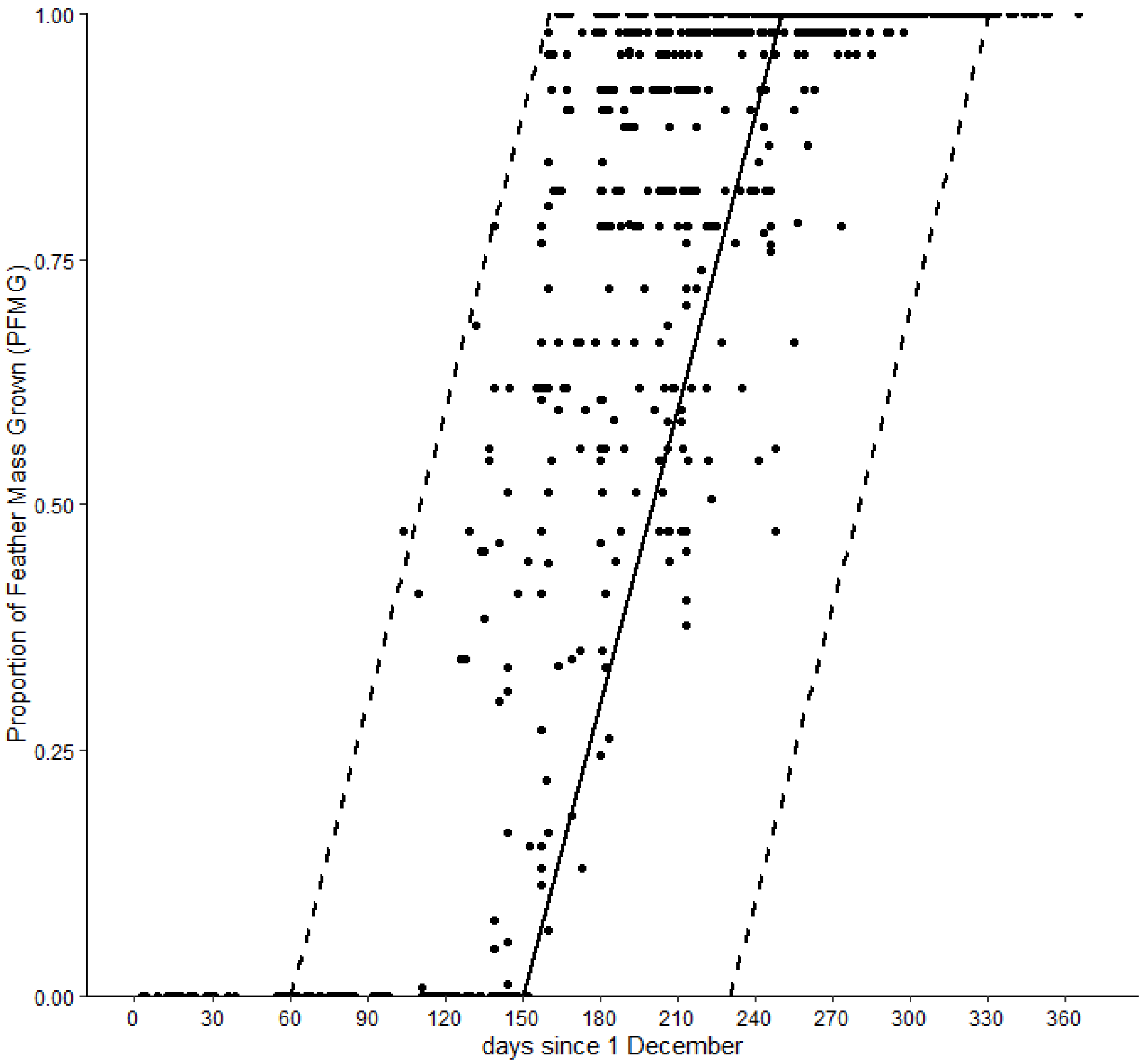


Figure 4.2: Temporal distribution of the proportion of primary feather mass grown (PFMG) of adult White-chinned Petrels incidentally caught by fishing vessels off southern Africa. The continuous line shows the average moult trajectory, dashed lines show 95% confidence intervals.

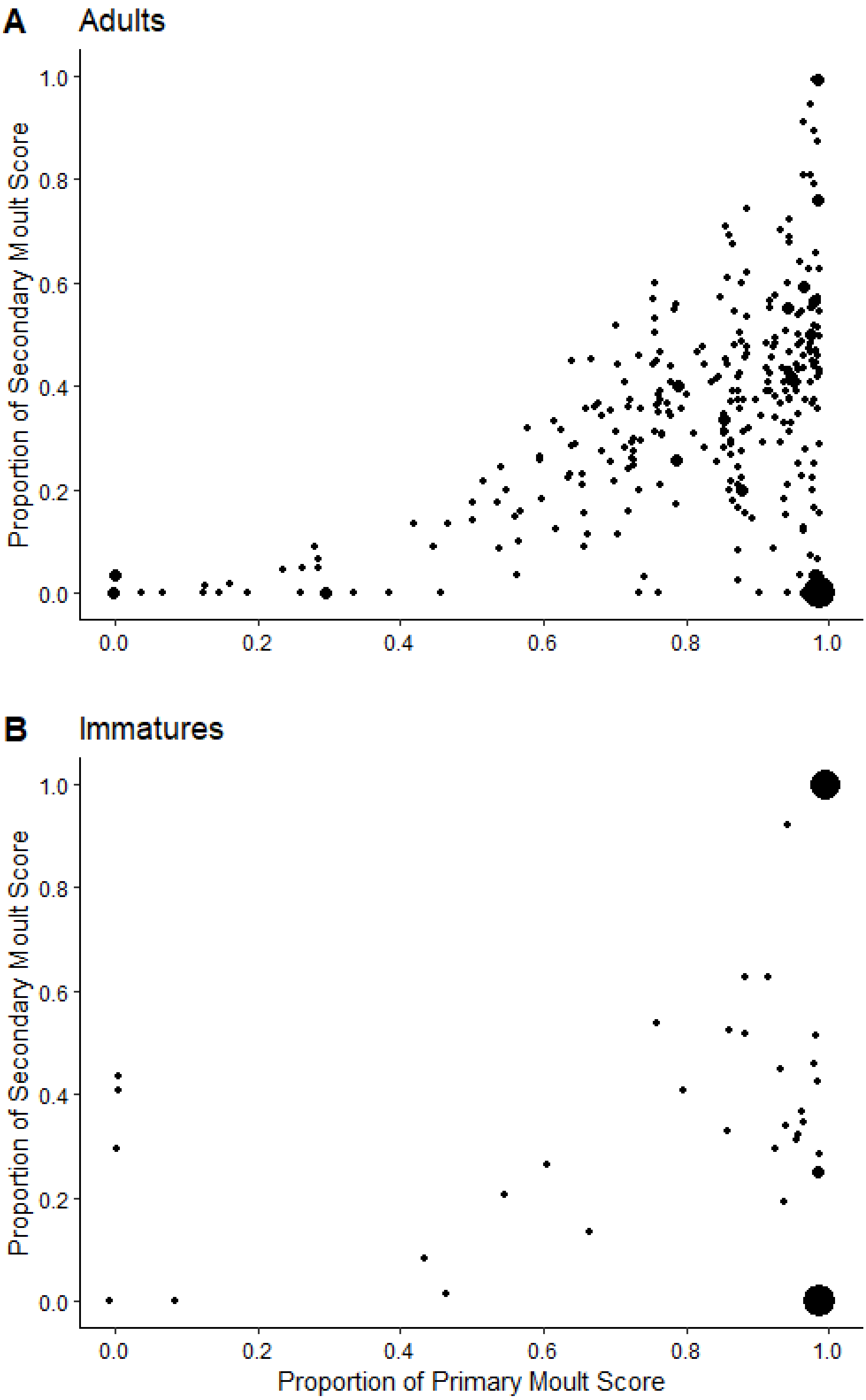


Figure 4.3: Proportion of secondary moult scores in relation to primary moult scores of (A) adult and (B) immature White-chinned Petrels incidentally caught by fishing vessels off southern Africa. Sample sizes for the largest sample point in (A) is 168 and in (B) is 88.

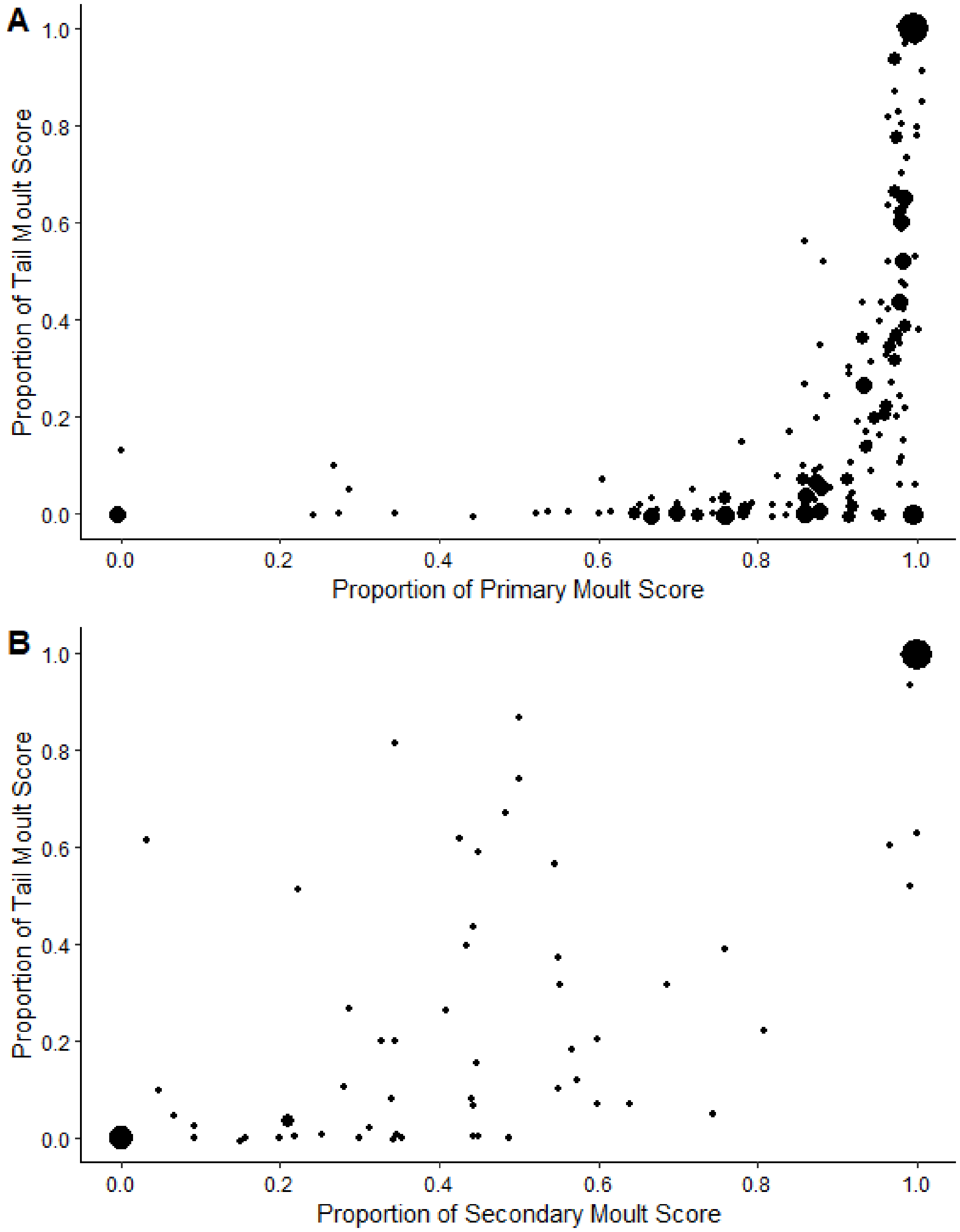


Figure 4.4: Proportion of moult scores of rectrices in relation to (A) primary moult scores; and (B) secondary moult score of White-chinned Petrels incidentally caught by fishing vessels off southern Africa. Sample sizes for the largest sample point in (A) is 148 and in (B) is 75.

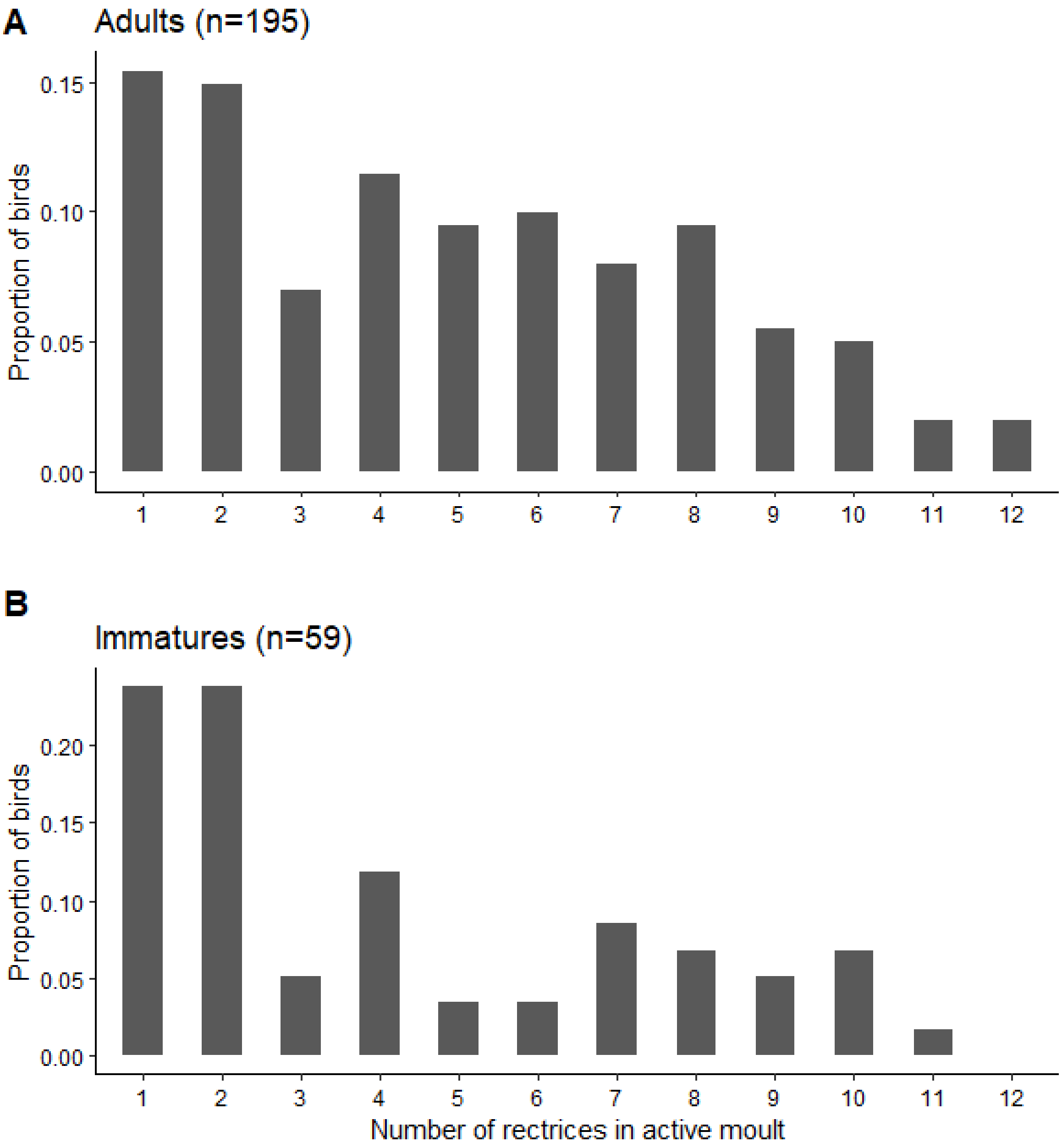


Figure 4.5: Proportions of (A) adult and (B) immature White-chinned Petrels showing number of rectrices in active moult.

Table 4.1: Proportion of primaries in active moult (P_{moult}) among White-chinned Petrels (n = 2276 post-juvenile birds), and the comparison between observed and expected asymmetry (see Methods for details).

Primary	**$P_{(moult)}$**	**Symmetry (%)**	**Asymmetry (%)**	**Expected % (null model)**	**χ^2 values**	**P**
P10	0.17	78.9	21.1	45.0	18.58*	< 0.001
P9	0.12	73.7	26.3	49.9	16.95*	< 0.001
P8	0.10	84.2	15.8	48.8	16.18*	< 0.001
P7	0.06	89.5	10.5	43.2	12.75*	< 0.001
P6	0.04	94.7	5.3	38.8	10.46*	< 0.001
P5	0.03	89.5	10.5	14.5	0.68	0.35
P4	0.02	89.5	10.5	10.0	1.14	0.21
P3	0.01	94.7	5.3	0.00	–	–
P2	0.01	94.7	5.3	0.00	–	–
P1	0.01	94.7	5.3	10.0	1.14	0.21

* $p < 0.001$

Table 4.2: Proportion of secondaries in active moult (P_{moult}) among White-chinned Petrels (n = 906 post-juvenile birds), and the comparison between observed and expected asymmetry (see Methods for details).

Primary	**$P_{(moult)}$**	**Symmetry (%)**	**Asymmetry (%)**	**Expected % (null model)**	**χ^2 values**	**P**
S1	0.06	66.7	33.3	67.5	1.42	0.16
S2	0.10	66.7	33.3	16.9	5.69*	0.01
S3	0.08	41.7	58.3	52.0	0.11	0.14
S4	0.09	75.0	25.0	33.0	0.29	0.64
S5	0.05	50.0	50.0	20.8	0.59	0.39
S6	0.04	66.7	33.3	52.0	0.08	0.36
S7	0.04	58.3	41.7	75.0	0.04	0.11
S8	0.04	83.3	16.7	33.0	3.34*	0.04
S9	0.04	58.0	42.0	75.0	1.42	0.16
S10	0.05	75.0	25.0	19.0	0.62	0.37
S11	0.05	66.7	33.3	33.0	0.29	0.64
S12	0.05	75.0	25.0	19.0	0.62	0.37
S13	0.09	75.0	25.0	19.0	0.62	0.37
S14	0.05	83.3	16.7	2.00	0.24	0.73
S15	0.06	83.3	16.7	2.00	0.24	0.73
S16	0.07	75.0	25.0	8.00	0.07	0.44
S17	0.12	66.7	33.3	75.0	0.00	0.22
S18	0.13	66.7	33.3	52.0	0.08	0.36
S19	0.10	58.3	41.7	13.3	0.23	0.73
S20	0.08	41.7	58.3	16.9	0.01	0.50
S21	0.05	50.0	50.0	46.9	5.69*	0.01
S22	0.04	50.0	50.0	40.8	3.71*	0.03
S23	0.04	58.3	41.7	67.5	0.00	0.31
S24	0.04	66.7	33.3	75.0	1.42	0.16

* $p < 0.001$

Table 4.3: The proportion of tail feathers in active moult at time of sampling among adult and immature White-chinned Petrels, and the comparison between observed and expected asymmetry (see Methods for details).

Parameters	**R1**	**R2**	**R3**	**R4**	**R5**	**R6**
Adults (n = 436)						
Proportion in moult	0.20	0.17	0.19	0.19	0.20	0.20
Symmetry (%)	72.0	80.1	78.0	77.3	78.4	75.8
Asymmetry: major (%)	8.1	5.1	5.7	4.8	5.7	8.4
intermediate (%)	11.1	7.1	8.6	8.4	8.1	7.7
minor (%)	8.8	7.7	7.7	9.5	7.8	8.1
Total asymmetry (%)	28.0	19.9	22.0	22.7	21.6	24.2
Expected % (null model)	38.6	31.1	36.0	34.7	31.3	36.3
χ^2 values	81.51*	68.71*	97.61*	86.08*	71.28*	99.38*
Immatures (n = 329)						
Proportion in moult	0.05	0.08	0.07	0.05	0.08	0.07
Symmetry (%)	93.1	92.0	94.5	95.6	92.5	93.3
Asymmetry: major (%)	3.1	3.3	1.1	0.9	2.6	2.2
intermediate (%)	1.6	2.9	2.2	2.4	3.3	2.3
minor (%)	2.2	1.8	2.2	1.1	1.6	2.2
Total asymmetry (%)	6.9	8.0	5.5	4.4	7.5	6.7
Expected % (null model)	14.5	15.8	14.3	13.9	14.3	15.1
χ^2 values	34.48*	30.47*	45.31*	43.25*	29.02*	38.99*

* $p < 0.01$

Supplemental material

Supplemental Table 4.1: The average (± SD) mass (mg) and length (mm) of fully grown White-chinned Petrel primaries, secondaries and rectrices (n = 4) killed by fishing operations.

Feathers	Mass (mg)	Length (mm)
	Primaries	
P10	825 ± 46.6	282 ± 15.9
P9	946 ± 35.7	288 ± 10.9
P8	777 ± 21.1	278 ± 7.6
P7	681 ± 15.6	262 ± 6.0
P6	548 ± 14.5	246 ± 6.5
P5	472 ± 20.1	225 ± 9.6
P4	354 ± 24.9	198 ± 13.9
P3	270 ± 20.3	174 ± 13.1
P2	207 ± 15.6	152 ± 11.4
P1	173 ± 5.1	138 ± 4.1
Total	**5253 ± 219.5**	**2243 ± 99.0**
	Secondaries	
S1	172 ± 11.1	130 ± 8.4
S2	140 ± 13.2	120 ± 11.3
S3	127 ± 2.6	110 ± 2.3
S4	117 ± 5.3	118 ± 5.4
S5	121 ± 5.8	119 ± 5.7
S6	115 ± 2.9	120 ± 3.0
S7	107 ± 5.4	121 ± 6.1
S8	104 ± 2.7	121 ± 3.1
S9	108 ± 5.5	119 ± 6.1
S10	105 ± 5.5	120 ± 6.3
Feathers	**Mass (mg)**	**Length (mm**
	Secondaries (continued)	
S11	105 ± 5.5	123 ± 6.5
S12	106 ± 5.6	124 ± 6.5
S13	107 ± 5.5	125 ± 6.4
S14	110 ± 8.5	124 ± 9.5
S15	118 ± 8.6	126 ± 9.2
S16	119 ± 13.8	126 ± 14.7
S17	123 ± 16.4	126 ± 16.8
S18	131 ± 16.4	127 ± 15.9
S19	140 ± 11.2	128 ± 10.2
S20	151 ± 14.5	128 ± 12.3
S21	144 ± 29.4	130 ± 26.5
S22	130 ± 30.2	123 ± 28.6
S23	93 ± 23.8	110 ± 28.2
S24	55 ± 15.7	88 ± 25.1
Total	**2848 ± 265.2**	**2906 ± 274.1**
	Rectrices	
R1	232 ± 10.5	142 ± 6.5
R2	227 ± 14.6	139 ± 8.9
R3	227 ± 10.6	140 ± 6.5
R4	225 ± 8.2	138 ± 5.0
R5	222 ± 8.2	137 ± 5.1
R6	211 ± 9.6	134 ± 6.1
Total	**1344 ± 61.7**	**830 ± 38.1**

Supplemental Table 4.2: Moult scores of White-chinned Petrels growing inner primaries (n = 25) where replacement may not have been sequential from P1 outwards. Scores follow Ginn and Melville (1983): 0 = old feathers, 1–4 = growing feathers at increasing stages of development, and 5 = fully-grown new feathers.

	Age	**Sex**	**P1**	**P2**	**P3**	**P4**	**P5**	**P6**	**P7**
Bird 1	adult	female	0	1	1	0	0	0	0
Bird 2	adult	male	1	2	1	0	0	0	0
Bird 3	immature	male	1	2	1	0	0	0	0
Bird 4	immature	female	1	3	2	0	0	0	0
Bird 5	adult	female	2	3	3	1	0	0	0
Bird 6	adult	male	4	5	4	4	3	2	0

Supplemental Table 4.3: The number of adult and immature, and female and male White-chinned Petrels growing primaries, among 538 non-juvenile birds incidentally caught by fishing vessels off southern Africa from 2002-2020.

	Number of growing primaries						**Total**
	1	2	3	4	5	6	
Adults	130	125	176	24	9	6	**470**
Female	77	80	123	14	4	5	303
Male	53	45	52	10	5	1	166
Unknown sex	0	0	1	0	0	0	1
Immatures	27	12	11	3	1	1	**55**
Female	15	8	10	3	1	0	37
Male	12	4	1	0	0	1	18
Unknown age	5	5	3	0	0	0	**13**
Female	4	0	2	0	0	0	6
Male	1	2	1	0	0	0	4
Unknown sex	0	3	0	0	0	0	3
Total	162	142	190	27	10	7	**538**

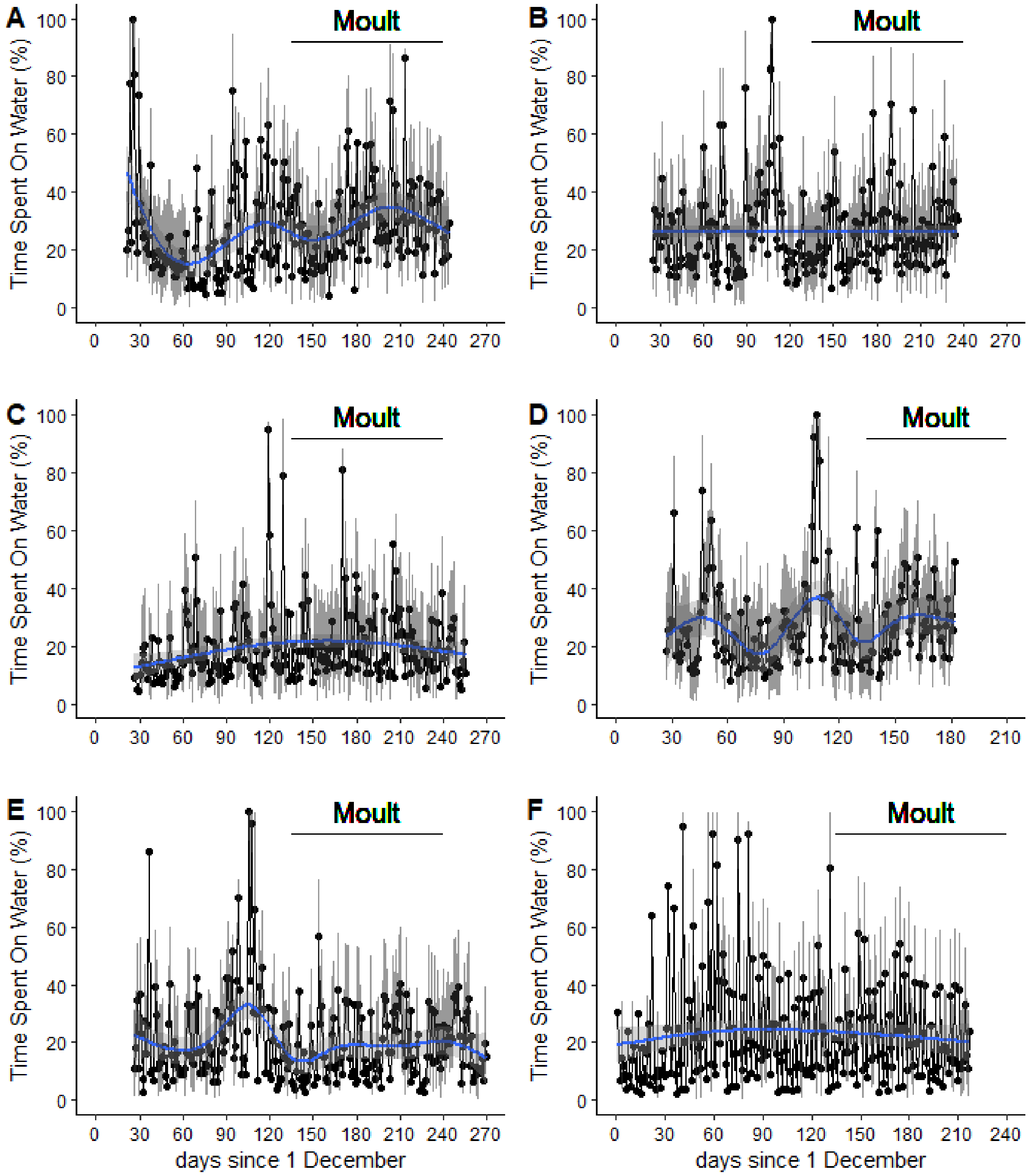
Supplemental Table 4.4: The number of adult and immature, and female and male White-chinned Petrels growing secondaries, among 323 non-juvenile birds incidentally caught by fishing vessels off southern Africa from 2002-2020.

	Number of growing secondaries													**Total**
	1	2	3	4	5	6	7	8	9	10	11	12	13	
Adults	35	30	49	34	32	28	22	17	22	10	3	0	2	**284**
Female	21	20	32	23	26	19	11	8	13	7	2	0	2	184
Male	14	10	17	11	6	9	11	9	8	3	1	0	0	99
Unknown sex	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Immatures	8	3	5	4	2	3	2	2	0	0	0	0	0	**29**
Female	4	2	3	4	2	2	2	2	0	0	0	0	0	21
Male	4	1	2	0	0	1	0	0	0	0	0	0	0	8
Unknown age	2	0	1	2	0	0	2	1	0	1	1	0	0	**10**
Female	2	0	0	0	0	0	0	0	0	1	1	0	0	4
Male	0	0	0	1	0	0	1	1	0	0	0	0	0	3
Unknown sex	0	0	1	1	0	0	1	0	0	0	0	0	0	3
Total	45	33	55	40	34	31	26	20	22	11	4	0	2	**323**

Supplemental Table 4.5: The number of adult and immature, and female and male White-chinned Petrels growing rectrices, among 261 non-juvenile birds incidentally caught by fishing vessels off southern Africa from 2002-2020.

	Number of growing rectrices												**Total**
	1	2	3	4	5	6	7	8	9	10	11	12	
Adults	31	27	13	23	19	19	16	19	11	10	3	4	**195**
Female	19	18	8	11	10	9	12	14	5	8	1	1	116
Male	12	9	5	12	9	10	4	5	6	2	2	3	79
Immatures	14	14	3	7	2	2	5	4	3	4	1	0	**59**
Female	4	10	3	4	1	1	3	3	1	2	1	0	33
Male	10	4	0	3	1	1	2	1	2	2	0	0	26
Unknown age	0	3	1	1	0	1	0	0	0	0	1	0	**7**
Female	0	1	1	0	0	0	0	0	0	0	1	0	3
Male	0	2	0	0	0	1	0	0	0	0	0	0	3
Unknown sex	0	0	0	1	0	0	0	0	0	0	0	0	1
Total	45	44	17	31	21	22	21	23	14	14	5	4	**261**

Supplemental Figure 4.1: Mixture of new and old secondaries and secondary coverts in a non-moulting White-chinned Petrel (photo Peter Ryan).



Supplemental Figure 4.2: Average daily time spent on water (%) by six adult White-chinned Petrels tracked over three years (2010 to 2012) in relation to the adult moult period. Values are daily means ± SD; regression lines are generated using geom_smooth (method = "gam").

Supplemental Figure 4.3: White-chinned Petrels in early primary moult replacing most of their greater secondary coverts before the start of secondary moult (photos Peter Ryan).

CHAPTER 5

Timing, intensity and symmetry of flight feather moult in White-capped Albatrosses

Abstract

Many seabirds have complex moult strategies. Albatrosses, for example, typically only replace a subset of flight feathers each year. Moult was scored from over 600 White-capped/Shy Albatrosses killed by longline fisheries off South Africa between 1999 and 2020. Despite being on their non-breeding grounds, less than 40% of birds were either moulting their wing or tail feathers. Although a few birds exhibited intense moult, replacing up to six primaries and 14 secondaries at once, the norm was for replacing only 1-2 primaries (mean ± SD, 1.9 ± 1.2), and 2-6 secondaries (3.9 ± 3.0) at once, which is surprising given the expectation that large, long-winged birds should be under time pressure to complete their moults. This occurs as adults typically take a year off between successful breeding attempts, seemingly allowing time for a more protracted moult. The primaries had two active centres in the inner and outer primaries in 13% of birds in active moult (two adults and eight immatures) and secondaries with multiple moult centres (2.4 ± 1.7, 1–9). Secondary moult overlaps with primary moult and progresses from three nodal sites: first dropping the innermost five to eight secondaries, followed by the outermost four secondaries and almost simultaneously with S16–S22 and S4–S7, ending with the middle secondaries (although not all moulted each year). Adults had more active centres (3.4 ± 2.3) and replaced more secondaries at once (5.7 ± 3.7) than immatures (2.0 ± 1.4 centres, 3.3 ± 2.6 feathers). Females had more active centres (2.5 ± 1.9) and were moulting more secondaries (4.1 ± 3.4) than males (2.1 ± 1.3 centres, 3.5 ± 3.5). Tail moult commences at the start of primary moult, with multiple active centres (2.7 ± 1.6; 1–6) and 3.8 ± 2.9 feathers growing at the same time (range 1–11). The number of active centres and growing rectrices were independent of age or sex. Rectrix asymmetry and probability of replacement were similar among adults and immatures. Most birds replaced their rectrices in pairs, starting from the central feathers, but some birds replaced alternate feathers, or replaced almost all rectrices at once. Age and sex differences in moult intensity may be due to time constraints. The low

proportion of moulting birds on their non-breeding grounds might suggests that moult in White-capped Albatrosses is more constrained during the non-breeding period in southern African waters.

Introduction

Moult is an important element in the annual cycle of birds (Bridge 2006; Newton 2009; Zuberogoitia et al. 2018). Despite the energetic costs of moulting, most birds undertake at least one complete moult each year (Beltran et al. 2018). However, birds with large wings that need to maintain flight performance year round struggle to completely replace all their flight feathers each year (Rohwer et al. 2009). The more feathers that a bird replaces at once, the faster it completes its moult, but intensive moult also decreases flight efficiency (Langston and Rohwer 1996). As a result, most birds do not replace feathers while breeding or migrating (King 1981; Walsberg 1983). Many large birds have evolved complex strategies for replacing their flight feathers, apparently in response to these constraints (Rohwer 1999). Albatrosses are among the longest-winged birds in the world and do not moult flight feathers while breeding (Brooke 1981; Furness 1988; Weimerskirch 1991; Prince et al. 1997). As a result, many only replace some of their flight feathers each year, and have some of the most complex and unusual moult patterns (Langston and Rohwer 1995; Weimerskirch 1991; Prince et al. 1997; Furness 1988; Bugoni et al. 2014), which can be linked to the age and breeding success of the individual (Prince et al. 1993).

Many albatrosses alternate moulting their inner and outer primaries (Prince et al. 1993; Langston and Rohwer 1995; Prince et al. 1997; Flood and Ryan 2016; 2018). The timing and extent of moults in albatrosses are further complicated by individual variation with age and breeding status or breeding history (Prince et al. 1993; Bridge 2006). *Thalassarche* albatrosses only replace a subset of primaries each year, using a descendant wave moult, but most do not moult each year (e.g., pre-breeding and breeding Black-browed Albatrosses *T. melanophris* and pre-breeding and failed breeding Grey-headed Albatrosses *T. chrysostoma*, Prince et al. 1993; adult Atlantic Yellow-nosed Albatrosses *T. chlororhynchos*, Furness 1988).

Incomplete moult is a common strategy among large seabirds, in which replacement of the primaries is interrupted by breeding (Stresemann and Stresemann 1966; Langston and Rohwer 1995) and other events, such as dispersal (Clay et al. 2016). Conventionally, incomplete moult and unusual breeding frequencies are driven by trade-offs between the time allocated to moult and breeding, and these trade-offs develop because of a physiological constraint in the rate at which individual feathers can be generated (Langston and Rohwer 1995). Selective pressures for efficient moult patterns are strongest in species where time is most constrained (Langston and Rohwer 1995). This moult strategy forces birds to retain worn feathers in the wing, which may have important reproductive consequences (Langston and Rohwer 1996).

Immatures switch between moulting their outer primaries and some combination of the innermost primaries in one year and moulting their mid-inner primaries and innermost primaries in the next year. Prince et al. (1993) found that the moult cycle starts with the outer three and some innermost primaries before starting the inner primaries the next year in two mollymawk species. In White-capped/Shy Albatrosses, the adults normally follow an annual moult cycle linked to the breeding cycle, while juveniles moult in summer (Flood and Ryan 2016; 2018). Immatures usually synchronise the timing of moult cycles with adults at about the fifth cycle (Flood and Ryan 2016; 2018).

White-capped Albatrosses *Thalassarche steadi* are the largest of the mollymawks (Flood and Ryan 2016) and are listed as near-threatened, mainly due to incidental mortality on fishing gear (BirdLife International 2022). After White-chinned Petrels, they are the second most frequently killed seabird on longlines off South Africa (Petersen et al. 2009; Rollinson et al. 2017). They can only be separated reliably from the Shy Albatross *T. cauta* by genetic markers (Abbott et al. 2006). Both species are killed on longlines off South Africa, but of 258 bycatch birds tested, 255 could be allocated with confidence to taxon (13 to *cauta* and 242 to *steadi*;

Flood and Ryan 2018). Most White-capped Albatrosses (95%) breed at the Auckland Islands, south of New Zealand, usually between September and April (Marchant and Higgins 1990; BirdLife International 2022). Moult studies of White-capped/Shy Albatrosses have focused mainly on primaries, which occurs during the austral winter in adults and mostly during summer in immatures (Kinsky 1968; Brooke 1981; Melville 1991; Flood and Ryan 2018). Few studies have explored secondary, tail and body moult in *Thalassarche* albatrosses (Prince et al. 1993; Bugoni et al. 2014; Osborne and Ryan 2021). The study extends the analysis reported by Flood and Ryan (2018), adding more birds and describing the timing of secondary and rectrix moult, the intensity of flight feather moult and assessing symmetry of rectrix moult. I also explore the proportion of birds in active wing and tail moult during non-breeding season in southern African waters.

Methods

Data collection

White-capped/Shy Albatrosses incidentally caught by long-line fishing vessels off southern Africa were collected, sexed, aged and scored for flight feather moult (Ryan 1999; Flood and Ryan 2018). Most fishing effort monitored was by foreign-flagged vessels, which mainly fish in southern Africa waters from April–November (Petersen et al. 2009; Rollinson et al. 2017), so most samples were from the austral winter. Age-related differences have been reported in the timing of primary moult in Shy Albatross, where they are presented in terms of moult cycles from juvenile and adult (Flood and Ryan 2018). While the 1st cycle starts with a complete prebasic moult in the nest, the 2nd cycle and other cycles involve head, body, and rectrix moult. The 3rd and all subsequent cycles involve wing moult (Flood and Ryan 2018). Tickell (2000) reported that mollymawks typically moult in cycles, replacing some of their primaries each year from the 3rd cycle onwards. Adult mollymawks follow an annual moult cycle related to the breeding cycle while young immatures moult earlier than adults, whereas old immatures replace feathers at the same time with adults (Flood and Fisher 2016; Flood and Ryan 2018). Distinguishing 6th cycle birds and adults was sometimes tricky (Flood and Ryan 2018).

Moult data

Shy Albatrosses have 10 functional primaries, 29–31 secondaries and 12 tail feathers. Moult of flight feathers was scored (cf. Ginn and Melville 1983), where old feathers = 0, growing feathers = 1 to 4 for increasing stages of development, and fully-grown new feathers = 5. However, many fully-grown secondaries and rectrices could not be aged reliably, as they were waterlogged and/or damaged post-mortem. Moult of the wings was roughly symmetrical, so the moult score of one wing (10 primaries, 29–31 secondaries), usually the right wing (unless it was damaged), was recorded. However, some birds had both wings scored. Tail moult usually was scored for all 12 rectrices. In some birds, moult of other feather tracts was checked, including body moult and especially the greater upper- and underwing coverts. Primaries were numbered from P1 (innermost) to P10 (outermost); secondaries from S1 (outermost) to S31 (but ranges between 29–31); and rectrices from T1 (central pair) out to T6 on each side of the tail.

Feather masses were obtained by collecting flight feathers from nine Shy Albatrosses killed incidentally during fishing operations. After plucking, the feathers were air dried for several days then measured (flattened total length to the nearest 1 mm) and weighed (to the nearest 1 mg).

Symmetry of rectrix moult

Symmetry of rectrix moult was assessed by comparing the moult scores of each feather pair on either side of the bird. A simple index of asymmetry was calculated as the standardised moult score asymmetry (i.e. asymmetry score/30 for rectrices, expressed as %), given that the maximum possible asymmetry would have a summed moult score difference of 30 for rectrices (all rectrices on one side old, and those on the other side new). Differences in moult score of 1 between a pair of feathers were regarded as ‘minor’ asymmetries (i.e. 0–1, 1–2, 2–3, 3–4 and 4–5); differences of 2–3 as ‘intermediate’ (i.e. 0–2, 0–3, 1–3, 1–4, 2–4, 2–5, 3–5) and of 4–5 as ‘major’ asymmetries (i.e. 0–4, 0–5, 1–5). The degree of partial-moult asymmetry depends on the number of feathers moulted, because if no feather, or all feathers are moulted, the moult pattern will be symmetrical. The potential for moult asymmetry peaks when half the feathers are moulted (in the most extreme case, one side is replaced and the other is not, giving an asymmetry score of 1), with a range of possible maximum asymmetry values between these extremes. As a result, differences in the proportion of feathers moulted must be controlled for when comparing asymmetry across feathers (cf. Adekola et al. 2021a).

Data analyses

To test whether asymmetry at a feather position is random, I used Pearson’s chi-squared goodness-of-fit tests with Yates’ correction for continuity to compare the observed frequency of asymmetry with that expected by chance (assuming random replacement) for a given level of feather replacement (Brommer et al. 2003; Adekola et al. 2021a). I used general linear models to assess differences in number of growing feathers and active moult centres between ages and sexes among moulting birds. The average masses for each primary, secondary and rectrix (Supplemental Table 5.1) was used to calculate moult intensity of flight feathers (Adekola et al. 2021a). Variance terms are SD unless otherwise indicated. All statistical analyses were performed in the R statistical environment (R Core Team 2019).

Results

Moult was scored from 644 Shy Albatrosses incidentally caught on longlines off southern Africa between 1999 and 2020: 198 adults, 332 immatures, 112 juveniles and 2 of unknown age. None of the juveniles examined exhibited any moult of primaries, secondaries or rectrices. Most captures (89%) were recorded between March and December.

Primary moult

The proportion of moulting adults and immatures was low: of the 198 adults scored for primary moult, 27 (14%) were moulting primaries, and 30 (9%) of the 332 immatures sampled were moulting primaries. Shy Albatrosses showed a descendent moult, starting from P1 and proceeding to P10. The average number of growing primaries was 1.9 ± 1.2 (range 1–6). Most birds (87%) had a single active centre, but a few (13%) had two (always in the outer and inner primaries). Age and sex had no influence on the average number of moult centres, or growing primaries (Table 5.1). Although a few birds were moulting up to six primaries at once, the modal number replaced among both adults and immatures was only one (Table 5.1): Forty (53%, n = 77) were growing one primary, 24% were growing two, 13% were growing three, 6% were growing four, 3% were growing five, and 1% were growing six primaries (Table 5.1).

Secondary moult

Most Shy Albatrosses had 30 secondaries (97%; 2% had 31 and 1% had 29). Of the 241 birds scored for secondary moult, 25% of 52 adults and 75% of 53 immatures were moulting secondaries. The number of males and females moulting secondaries were similar in both adult and immature birds (Table 5.2). The proportion of adults moulting secondaries was similar to the proportion replacing primaries (14%; $\chi^2 = 0.72$, df =1, p = 0.33). However, the proportion of immatures moulting secondaries was greater than the proportion replacing primaries (9%; $\chi^2 = 3.69$, df = 1, p = 0.03). Adults were in active secondary moult between April and December, while the proportion of immatures in secondary moult decreased from March until December (Figure 5.1, although no adults or immatures were sampled in January or February). Secondaries were replaced from multiple moult centres (2.4 ± 1.7, 1–9), with up to 14 feathers growing at once (3.9 ± 3.0, 1–14). Females had more active centres (2.5 ± 1.9) than males (2.1 ± 1.3), and adults had more active centres (3.4 ± 2.3) than immatures (2.0 ± 1.4; $F_{2,50} = 3.81$, p = 0.03). Females also replaced more secondaries at once (4.1 ± 3.4) than males (3.5 ± 3.5); and adults were growing more secondaries (5.7 ± 3.7) than immatures (3.3 ± 2.6; $F_{2,50} = 3.72$, $p = 0.03$). Across all birds, 38% had one active centre, 34% had two, 8% had three, 8% had four, 6% had five, 2% had six, 2% had seven and 2% had nine active centres ($n = 53$). Three different nodal sites were dominant: first dropping the innermost eight secondaries (S23–S30); followed by the outermost (S1–S3) and almost simultaneously with S16–S22 and S4–S7; and finally, the middle secondaries (S8–S15). Although a few adults were moulting up to 14 secondaries at once, the modal number replaced was only one (among immatures) (Table 5.2): Thirteen (25%) were growing one secondary, 19% were growing two, 17% were growing three, 6% were growing four, 9% were growing five, 6% were growing six, 6% were growing seven, 6% were growing eight, 4% were growing ten, 2% were growing 11 and 2% were growing 14 secondaries ($n = 53$; Table 5.2).

Tail moult

Tail moult was more frequent than primary and secondary moult among adults (62% of 39 birds, $\chi^2 = 12.99$, $p < 0.001$ for primaries and $\chi^2 = 14.90$, $p < 0.001$ for secondaries), and than primary moult among immatures (42% of 169 birds, $\chi^2 = 20.08$, $p < 0.001$) but less frequent than immature secondary moult (41% of 156 birds, $\chi^2 = 8.75$, $p < 0.01$). Adults were in active rectrix moult between April and November (although no adults were sampled for tail moult between December and March; Figure 5.1C), while the proportion of immatures in rectrix moult decreased from March until November (but no immatures were sampled in January or February; Figure 5.1D). Most birds replaced their rectrices in pairs, starting from the central feathers, but some birds replaced alternate feathers, or replaced almost all rectrices at once. Adult and immature White-capped Albatrosses replaced tail feathers throughout the year (Figure 5.2). The rectrices typically had multiple active centres (2.7 ± 1.6; 1–6), growing up to 11 feathers at once (3.8 ± 2.9). Females had a similar number of active centres (2.9 ± 1.7) as males (2.5 ± 1.5); and adults had a similar number (3.0 ± 1.8) as immatures (2.6 ± 1.5; $F_{2,92} =$

1.11, p = 0.33). There also was no difference in the number of growing feathers between females (3.7 ± 2.6) and males (3.9 ± 3.2), or between adults (4.0 ± 2.8) and immatures (3.7 ± 2.9; $F_{2,92} = 0.23$, p = 0.79). Among all birds, 36% (n = 95) had one active centre, 15% had two, 15% had three, 18% had four, 14% had five and 2% had six active centres. Overall, 33 birds (35%) were growing one rectrix, 12% two, 12% three, 4% four, 6% five, 12% six, 6% seven, 6% eight, 4% nine, 1% ten, and 2% were growing 11 rectrices (n = 95; Figure 5.2, Table 5.3).

Body and covert moult

Of the 107 birds scored for body moult, 25% had extensive body moult, 72% had some moult, and only 3% had no visible moult (only in July; Supplemental Table 5.2). Birds moulting body feathers increased from May to October (Supplemental Table 5.2). All 10 albatrosses growing greater secondary coverts were replacing large numbers of coverts (between 15 and 21 feathers at once) at the same time as the inner primaries, before the start of secondary moult.

Moult intensity of flight feathers

Birds replacing 5–6 primaries at the same time reduced the total length of all their primaries by 39–49% and the total mass by 26–37% (Supplemental Table 5.1). Expressed as a proportion of all flight feathers, birds growing 5–6 primaries were replacing 10–13% of their overall length and 12–16% of their overall mass. Replacing 13–14 secondaries at the same time amounted to 41–44% of secondary length and 42–45% of secondary mass, and 19–21% of the total length and 11–12% of the mass of all flight feathers (Supplemental Table 5.1). Replacing 10–11 rectrices at the same time equated to 84–92% of their total length and 83–92% of their total mass, or 21–23% of the overall length and 24–26% of the overall mass of all flight feathers (Supplemental Table 5.1).

Symmetry of moult

Even though there was some asymmetry in tail moult pattern, there was strong selection for symmetry across all the rectrices, especially among immature White-capped Albatrosses ($p < 0.001$; Table 5.4). Major asymmetry at the rectrices tended to be higher at the central and outer tail feathers among adults (T1–T2: 6.0%–10.9%; T6: 9.4%) and immatures (T1–T2: 4.2%–7.2%; T6: 3.1%) compared to the other feather tracts (Table 5.4). Rectrix asymmetry tended to be similar among adults (T1–T2: 20–23%; T3–T5: 16–18%; T6: 21%) and immatures (T1–T2: 20–22%; T3–T5: 15–18%; T6: 20%), with similar probability of feather replacement among adults (0.82–0.90) and immatures (0.86–0.89; Table 5.4).

Discussion

Surprisingly, moult in White-capped Albatrosses is more constrained during the non-breeding period in southern Africa. The low proportion of birds in active moult during the non-breeding season is intriguing. Although the lack of breeding data on the birds sampled complicates interpretation, the low intensity of moult could probably suggest that most adult White-capped/Shy Albatrosses moult some feathers in winter after breeding successfully, and then some feathers the following year (as reported in Grey-headed Albatrosses; Prince et al. 1993). The few birds moulting more feathers might be failed breeders in a rush to get back into shape before attempting to breed again the following year. Further studies are needed to explore the factors determining the low proportion of White-capped Albatrosses in active moult during their non-breeding season in southern African waters.

Adult White-capped Albatrosses mainly moult their primaries during winter and suspend in late spring (Kinsky 1968; Brooke 1981; Melville 1991; Flood and Ryan 2018). Immatures might have to start moulting earlier than adults to complete moult before the end of summer, presumably when food is easiest to come by, whereas adults breed then, and are constrained to moult outside the time of easiest foraging. Flood and Ryan (2018) found that young immatures moult earlier than adults, with moult becomes progressively later for older immatures until it synchronizes with adults. Inexperienced adult albatrosses delay primary moult compared to experienced birds (Furness 1988; Weimerskirch 1991). I found no evidence for age differences in number of growing primaries, unlike in White-chinned Petrels, where adults moult more intensively than immatures (Chapter 4), probably because White-capped Albatrosses are biennial breeders, so have a whole year to moult after a successful breeding attempt.

Wing moult is variable in White-capped Albatrosses, with a few birds having intense moult, growing up to six primaries at the same time. This occurs despite the birds typically taking a year off between successful breeding attempts, allowing them additional time for a potentially more protracted moult (Prince et al. 1997). On the other hand, the more intense moulters could be failed breeders, trying to breed again without skipping a year. The few individuals with two moult centres were growing both inner or outer primaries. In three species of albatrosses, the primary feathers show strong biennial patterns of replacement, suggesting that an intrinsic, biennial cycle governs which series initiate moult each year (Prince et al. 1993; Prince et al. 1997). Atlantic Yellow-nosed Albatrosses replace their inner primaries less frequently than their outer primaries (Furness 1988). Male and female Shy Albatrosses replaced similar number of flight feathers (as in, Grey-headed Albatrosses; Cobley and Prince 1998). However, some albatrosses showed sexual differences in number of feathers replaced, as males usually replace more feathers than females (Weimerskirch 1991; Langston and Rohwer 1995).

Secondary moult was more variable than primaries in White-capped Albatrosses (Flood and Ryan 2016), with few birds growing up to 14 secondaries at the same time. The presence of several nodal sites of moult in the secondaries is a common pattern in birds with long wings (e.g., Edelstam 1984), including gannets (Chapter 3), Procellariiformes (Stresemann and Stresemann 1966; Chapter 4), with multiple waves of moult (Ainley et al. 1976; Hunter 1984;

Ramos et al. 2009; Adekola et al. 2021a), and may reflect strategy to minimize gaps in the wing (Arroyo et al. 2004; Adekola et al. 2021a). Secondary moult was observed starting rapidly from the innermost and the outermost feathers, probably because these feathers are more exposed and wear faster (Zuberogoitia et al. 2013; Adekola et al. 2021a; Osborne and Ryan 2021). Secondary moult was more intense among adults than immature birds, probably due to time constraints to carry out other activities.

The incidence of tail moult was seemingly higher than primary or secondary moult, with most birds replacing their rectrices in pairs. Some individuals were replacing almost all of their tail feathers at the same time. Bugoni et al. (2014) reported up to seven tail feathers growing simultaneously in the Atlantic Yellow-nosed Albatrosses. I found no age and sex differences in moult centres and number of growing feathers at the tail. The annual replacement of tail feathers in albatrosses was also confirmed (Prince 1993; Tickell 2000).

Body moult mostly occurred during winter in White-capped Albatross. This is consistent with the findings of Marchant and Higgins (1990) who reported that most species of albatrosses undergo body moult during winter. As found in White-chinned Petrels (Chapter 4), White-capped Albatrosses also prioritized the replacement of greater secondary coverts at the same time as the inner primaries, before the start of secondary moult, to compensate for the loss of wing area created by replacing a many secondary feathers at once (Ryan et al. 2020; Chapter 7).

Moult of primaries and secondaries is normally symmetrical in both wings (Brooke 1981). Despite the much greater probability of being moulted than other rectrices, the central (T1) had the lowest symmetry in both adult and immature White-capped/Shy Albatrosses. Tail moult in albatrosses was asymmetrical and several feathers could moult simultaneously, even for breeding birds, in agreement with their lesser importance in flight (Bugoni et al. 2007).

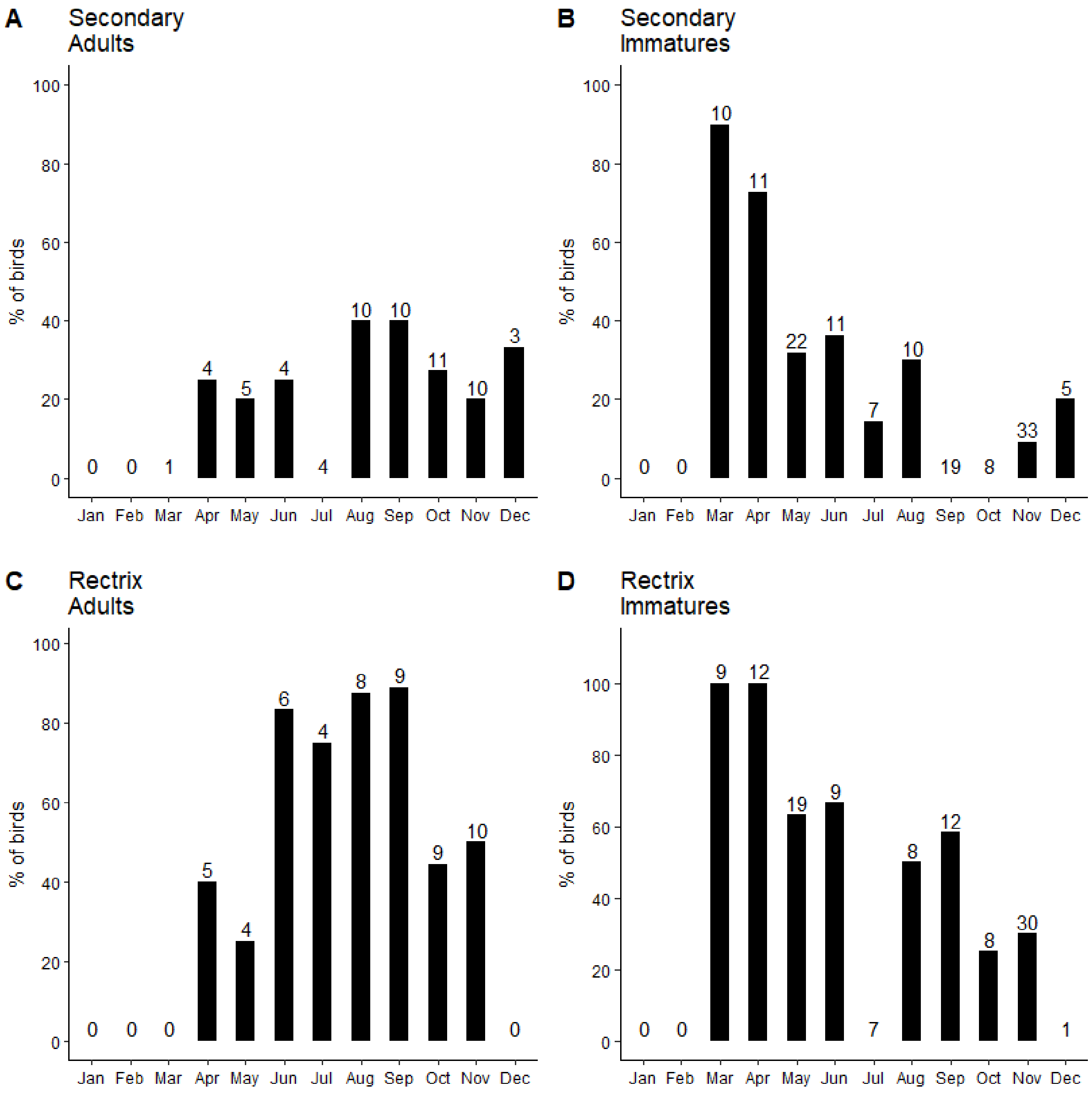


Figure 5.1: Monthly proportions of adult (A, C) and immature (B, D) White-capped/Shy Albatrosses in secondary and rectrix moult. The numbers above the bars are the sample sizes.

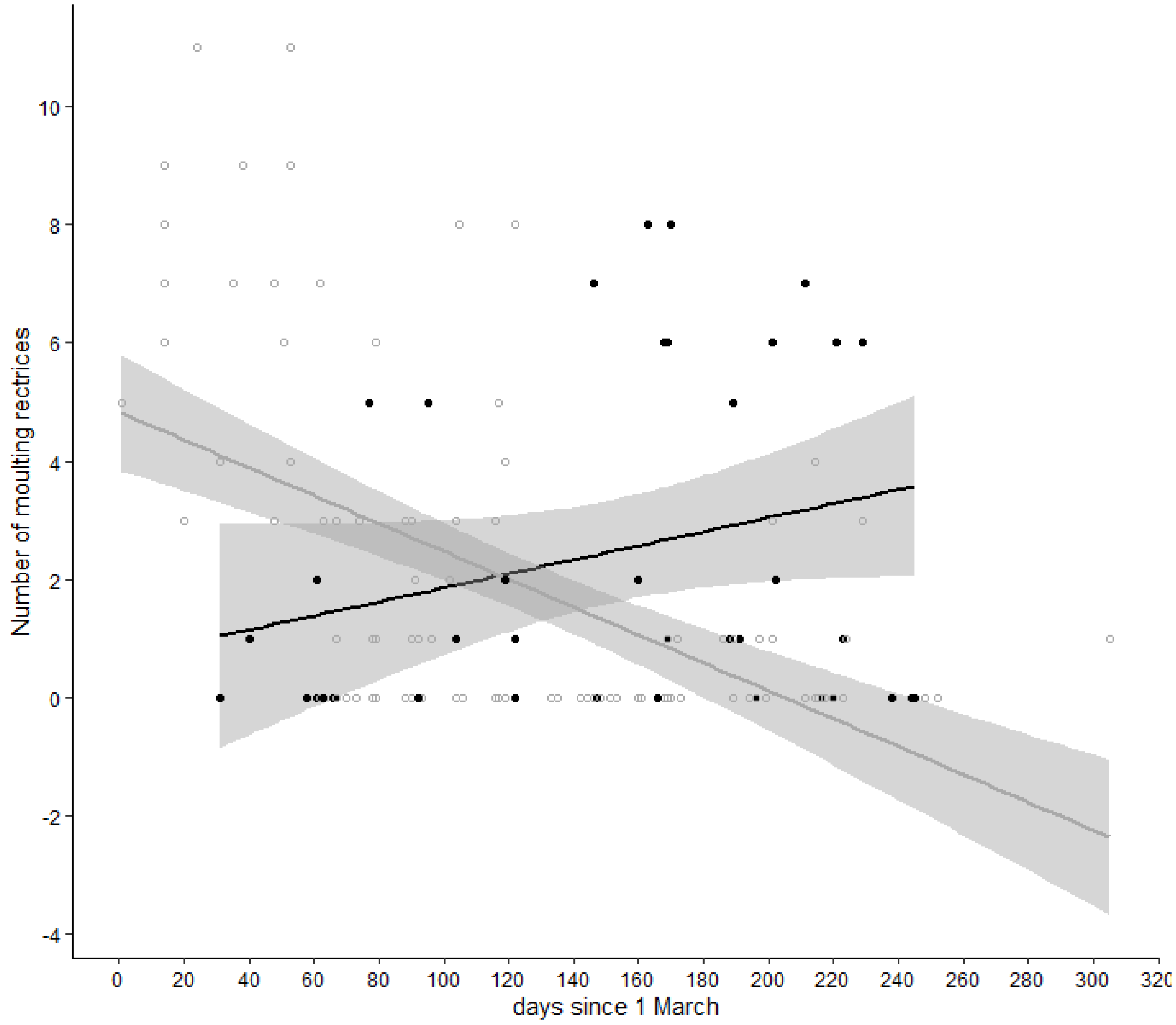


Figure 5.2: Proportions of adult (n = 41; black) and immature (n = 117; grey) White-capped/ Shy Albatrosses (n = 158) moulting different numbers of tail feathers (0-11) from March to December.

Table 5.1: The number of primaries being grown at once by White-capped/Shy Albatrosses, based on birds incidentally caught by fishing vessels off southern Africa from 1999-2020.

	1	**2**	**3**	**4**	**5**	**6**	**Total**
Adults	11	7	5	3	0	1	**27**
Female	6	5	2	3	0	1	17
Male	5	2	3	0	0	0	10
Immatures	29	11	5	2	2	1	**50**
Female	16	6	1	1	2	0	26
Male	13	5	4	1	0	1	24
Total	40	18	10	5	2	2	**77**

Table 5.2: The number of secondaries being grown at once by White-capped/Shy Albatrosses, based on birds incidentally caught by fishing vessels off southern Africa from 1999-2020.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**10**	**11**	**14**	**Total**
Adults	0	2	4	0	0	3	1	1	0	1	1	**13**
Female	0	0	3	0	0	2	1	0	0	1	1	8
Male	0	2	1	0	0	1	0	1	0	0	0	5
Immatures	13	8	5	3	5	0	2	2	2	0	0	**40**
Female	8	6	3	2	2	0	1	1	2	0	0	25
Male	5	2	2	1	3	0	1	1	0	0	0	15
Total	13	10	9	3	5	3	3	3	2	1	1	**53**

Table 5.3: The number of rectrices being grown at once by White-capped/Shy Albatrosses, based on birds incidentally caught by fishing vessels off southern Africa from 1999-2020.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**Total**
Adults	8	3	0	0	3	7	0	2	0	1	0	**24**
Female	5	1	0	0	3	5	0	0	0	1	0	15
Male	3	2	0	0	0	2	0	2	0	0	0	9
Immatures	25	8	11	4	3	4	6	4	4	0	2	**71**
Female	13	4	7	3	2	4	3	2	0	0	1	39
Male	12	4	4	1	1	0	3	2	4	0	1	32
Total	33	11	11	4	6	11	6	6	4	1	2	**95**

Table 5.4: Probabilities of rectrix replacement among White-capped/Shy Albatrosses and comparison between observed and expected asymmetry (see Methods for details).

Parameters	**T1**	**T2**	**T3**	**T4**	**T5**	**T6**
Adults (n = 38)						
Probability of replacement	0.90	0.86	0.85	0.82	0.84	0.90
Symmetry (%)	76.8	79.9	83.0	84.5	82.5	79.4
Asymmetry: major (%)	10.9	6.0	2.3	3.4	3.9	9.4
intermediate (%)	5.5	6.0	6.8	5.2	9.7	3.7
minor (%)	6.8	8.0	7.9	6.9	3.9	7.5
Total asymmetry (%)	23.2	20.1	17.0	15.5	17.5	20.6
Expected (null model) (%)	18.7	23.8	26.0	29.2	27.1	17.4
χ^2 values	0.26	3.68	1.03	4.81	0.58	2.44
p-value	0.68	0.03	0.24	0.02	0.39	0.08
Immatures (n = 170)						
Probability of replacement	0.89	0.86	0.87	0.86	0.86	0.88
Symmetry (%)	77.7	79.6	84.0	85.0	81.6	79.6
Asymmetry: major (%)	7.2	4.2	2.4	2.6	2.5	3.1
intermediate (%)	5.8	7.8	3.2	4.6	6.1	8.7
minor (%)	9.4	8.4	10.4	7.8	9.8	8.7
Total asymmetry (%)	22.3	20.4	16.0	15.0	18.4	20.4
Expected (null model) (%)	20.1	24.1	23.4	24.2	24.0	21.0
χ^2 values	21.10	15.17	20.39	32.00	11.79	19.44
p-value	0.00	0.00	0.00	0.00	0.00	0.00

Supplemental material

Supplemental Table 5.1: The average (± SD) mass (mg) and length (mm) of White-capped/Shy Albatross primaries, secondaries and rectrices.

Feathers	**Mass (mg)**	**Length (mm)**	**Feathers**	**Mass (mg)**	**Length (mm)**
	Primaries (n = 9)			Secondaries (continued)	
P10	2725 ± 107.0	409 ± 7.0	S15	262 ± 33.9	178 ± 5.5
P9	2693 ± 88.0	417 ± 8.1	S16	270 ± 30.0	179 ± 4.4
P8	2412 ± 134.1	403 ± 9.3	S17	273 ± 29.9	180 ± 4.8
P7	2011 ± 201.3	365 ± 40.6	S18	274 ± 30.2	180 ± 4.8
P6	1657 ± 147.8	345 ± 10.5	S19	278 ± 28.8	181 ± 4.6
P5	1272 ± 134.4	306 ± 10.1	S20	278 ± 32.4	182 ± 5.1
P4	950 ± 89.5	268 ± 8.0	S21	291 ± 36.7	183 ± 4.7
P3	733 ± 84.7	235 ± 6.8	S22	305 ± 21.1	185 ± 4.9
P2	584 ± 64.8	211 ± 5.9	S23	312 ± 18.0	187 ± 4.9
P1	537 ± 54.2	194 ± 4.6	S24	330 ± 16.7	189 ± 4.9
Total	**15574 ± 1106**	**3153 ± 111**	S25	361 ± 17.1	192 ± 5.2
	Secondaries (n = 5)		S26	393 ± 19.1	196 ± 5.1
S1	445 ± 36.3	185 ± 3.4	S27	426 ± 41.0	198 ± 5.5
S2	408 ± 39.0	176 ± 4.2	S28	401 ± 93.0	195 ± 11.2
S3	364 ± 32.1	170 ± 3.1	S29	388 ± 24.2	198 ± 4.4
S4	336 ± 25.9	169 ± 2.6	S30	262 ± 18.5	167 ± 4.1
S5	294 ± 34.3	172 ± 2.8	S31	168 ± 12.5	137 ± 2.2
S6	278 ± 34.4	173 ± 5.0	**Total**	**9518 ± 944**	**5549 ± 139**
S7	274 ± 33.5	172 ± 4.4		Rectrices (n = 9)	
S8	267 ± 31.3	173 ± 4.1	T1	814 ± 88.9	250 ± 8.6
S9	264 ± 29.2	174 ± 4.2	T2	833 ± 83.9	250 ± 8.3
S10	255 ± 21.1	172 ± 2.3	T3	838 ± 117.0	247 ± 7.0
S11	264 ± 31.8	175 ± 3.4	T4	846 ± 84.0	247 ± 9.4
S12	264 ± 28.5	176 ± 3.9	T5	891 ± 98.5	242 ± 7.7
S13	267 ± 32.6	177 ± 4.0	T6	838 ± 82.3	231 ± 8.5
S14	266 ± 30.6	178 ± 5.1	**Total**	**5060 ± 555**	**1467 ± 49**

Supplemental Table 5.2: Monthly variation in body moult (0 = no moult, 1 = some moult and 2 = heavy moult) across different months in 107 White-capped/Shy Albatrosses incidentally caught by fishing vessels off southern Africa from 1999-2020.

Month	**Absent**	**Slight**	**Heavy**	**Total**
January				
February				
March		1	5	6
April		3	2	5
May		17	4	21
June		16	2	18
July	3	14		17
August		6	3	9
September		11	7	18
October		8	4	12
November		1		1
December				
Total		77	27	107

CHAPTER 6

Extent and symmetry of tail moult in Amur Falcons

Abstract

Amur Falcons undergo one of the most extreme migrations of any raptor, crossing the Indian Ocean between their Asian breeding grounds and non-breeding areas in southern Africa. Adults are thought to replace all their flight feathers on the wintering grounds, but juveniles only replace some tail feathers before migrating. I compare the extent and symmetry of flight feather moult in a large sample of Amur Falcons killed at communal roosts during two hailstorms in KwaZulu-Natal, South Africa in March 2019, shortly before their northward migration. Most adults had completed replacing their remiges, with only a few still growing 1–3 feathers (mainly secondaries), but most were still growing their tail feathers. Juveniles only replaced tail feathers. Moult typically was distal from the central rectrices, but 25% of adults and 1% of juveniles replaced the outer tail first, and a few individuals exhibited other moult patterns (simultaneous moult across the tail, or among the inner and outer feathers). These different moult strategies were independent of sex. Adults that replaced the outer tail first typically had replaced a greater proportion of the rectrices (mean ± SD; 0.81 ± 0.19) than adults starting from the central tail (0.17 ± 0.08). Proportionally fewer distal moulting adults were killed on 9 March than 21 March, resulting in the average proportion of rectrices replaced by adults decreasing between the two storm events from 0.52 ± 0.26 to 0.43 ± 0.23. By comparison, juvenile tail moult increased from 9 March (0.34 ± 0.18) to 21 March (0.40 ± 0.15). Overall, the probability of replacement for T1 was similar for adults (0.82) and juveniles (0.83), but adults were more likely to have replaced T2–6 (0.40–0.45) than juveniles (0.18 for T2 and 0.04–0.07 for T3–6). Asymmetry in tail moult was greater at T1 for adults (15%) than juveniles (10%), but asymmetry for T2 to T6 was greater in juveniles (3–10%) than adults (1–4%), especially given the greater probability of feather replacement in adults. Despite these differences, the degree of asymmetry was less than expected by random replacement across all rectrices in both age classes. Interestingly, moult tended to be more advanced on the left than right side of the tail.

The extent of tail moult was correlated with body condition in adults and juveniles, suggesting that moult pattern might be used as an indicator of fitness in falcons.

Introduction

Knowledge of moult extent in birds reveals vital information about the life processes of a given individual or population (Zuberogoitia et al. 2018). Many factors, such as environmental and body conditions influence available time and resources for moult (Beltran et al. 2018), and may affect the extent of moult and its duration (Bojarinova et al. 1999; Kiat and Sapir 2018). Extent of moult has been suggested to correlate with the future performance of birds (Minias and Iciek 2013). Delayed moult can lead to increased winter mortality (Svensson and Nilsson 1997; Verhulst 1998; Verhulst and Nilsson 2008), and the accumulation of old feathers can even impact future breeding probability (Rohwer et al. 2011). Individual variation in moult sequence, duration and extent also depend on age, sex and climate (Zuberogoitia et al. 2018). In most migratory birds, moulting is suspended during migration (e.g. Berthold 1975; Ferguson-Lees and Christie 2001; Ramirez and Panuccio 2019), but there are exceptions (e.g. Palearctic-breeding migrant harriers, Kjellen 1992).

Adult falcons (Falconidae) typically moult their flight feathers in one moult cycle (Pyle 2005; Zuberogoitia et al. 2018), but the timing and extent of juvenile flight feather moult varies among species (Zuberogoitia et al. 2016). Juvenile falcons have distinct juvenile plumages, differing from adults in terms of colour and pattern, and with sexual differences in plumage among several species (Hailman et al. 1972). Post-juvenile body moult (preformative moult) is staggered between 6-12 months after fledging (Zuberogoitia et al. 2016). As a result, the timing and extent of post-juvenile moult determines the appearance of the individual, influencing its attractiveness, social status and camouflage (Kiat et al. 2019). Most juvenile falcons only start to replace their flight feathers when they are around one year old, but some Sooty Falcons *Falco concolor* might replace all their flight feathers in their first winter (Cramp and Simmons 1977). The Sooty Falcon is a long-distance migrant, so moulting during its first winter might be particularly important if juvenile flight feathers are of lesser quality (i.e. prone to wear faster than adult feathers), as is known to be the case for body feathers in juvenile birds (Rohwer and Rohwer 2013; Zuberogoitia et al. 2018). However, juveniles of other long-distance migrant falcons do not moult their flight feathers on their wintering grounds. Eurasian Hobbies *F. subbuteo* and Eleonora's Falcons *F. eleonorae* undergo a similar migration to Sooty Falcons, yet only moult in their second summer (Cramp and Simmons 1977; Zuberogoitia et al. 2018). Other migratory species, such as Lesser Kestrel *F. naumanni* and Red-footed Falcon *F. vespertinus*, only moult a variable number of tail feathers on their wintering grounds, retaining all juvenile primaries and secondaries (Corso 2001). The factors related to the extent of tail moult in these species are unknown.

In addition to moult extent, moult symmetry has been proposed as a predictor of fitness in birds (Minias and Iciek 2013), not least because asymmetry in feather moult might reduce flight efficiency (Thomas 1997; Brommer et al. 2003). Moult asymmetry consists of two types; Type I is the short-term temporal mismatch between feather replacement within a single moult event (Arroyo et al. 2004), whereas Type II asymmetry is retained across moult seasons in species that undergo a partial moult (Weimerskirch 1991). Apart from the impact on individual fitness, the time and energy allocated to a single episode of moult can affect feather quality, with rapid moult resulting in lower-quality feathers (Nilsson and Svensson 1996; Dawson et al. 2000; Serra et al. 2007). Thus birds that accelerate the rate of feather growth may suffer costs in feather quality, which is disadvantageous to annual survival, compared to birds that grow high-quality feathers (Rohwer and Rohwer 2013).

The Amur Falcon *F. amurensis* is an abundant migrant that breeds in eastern Asia and winters in southern Africa (Alexander and Symes 2016). They travel some 14500 km, one of the longest migration routes of any raptor, and are unusual in undertaking a long trans-oceanic migration, with most individuals crossing the Indian Ocean between India and the east coast of Africa (Meyburg et al. 2017). In most migratory falcons, adults usually start their wing-moult on the breeding grounds before moult is suspended for autumn migration. After migration, primary moult is resumed and finished in the winter quarters, long before spring migration (Cramp and Simmons 1977). Although it is claimed that Amur Falcons are unusual in moulting their flight feathers entirely on their wintering grounds (Symes and Woodborne 2010), some adults initiate moult while still on the breeding grounds, suspend during migration and resume on the wintering grounds (Dement'ev and Gladov 1951; Schafer 2003). Juveniles start post-juvenile moult during their first winter, replacing a variable number of tail feathers as well as some head and body feathers, but their juvenile remiges and usually some outer rectrices are retained (Ferguson-Lees and Christie 2001).

I report moult intensity and symmetry in Amur Falcons based on large numbers of birds killed on their wintering grounds at their communal roosts by two hailstorms in March 2019. The two events occurred 12 days apart, which gave an insight into moult progression. I also report whether the extent of tail moult correlates with body moult in juvenile males, whether there is a relationship between adult wing and tail moult, and test whether moult extent is related to body condition.

Methods

I scored moult in Amur Falcons killed at their roosts during two exceptional nocturnal hailstorms in KwaZulu-Natal, South Africa, in 2019: one near Mooi River (29.21°S, 30.00°E) on 9 March and another near Newcastle (27.72°S, 30.00°E) on 21 March. The number of birds killed outright at Mooi River (or which died shortly thereafter in captivity) was 836 and an additional 1000 were rescued after being battered to the ground and were released once they had recovered (Allan 2019). During the Newcastle hailstorm 1155 birds were killed and an additional 900 were rescued and released. All dead birds were aged and sexed by plumage characters (Cramp and Simmons 1977). Juveniles were readily distinguished by their buffy-edged upperpart feathers and pale buff cheeks and throat. However, I was unable to reliably differentiate second-year birds from adults, so I only recognised two age classes: adults and juveniles. The following measurements were taken from all birds: mass (to the nearest 0.1 g for birds not too badly damaged in the storm), bill length (from nostril to the bill tip) and depth (of both mandibles in line with the nostril), head length and tarsus length, all to the nearest 0.1 mm (using digital Vernier callipers), and wing (flattened chord) and tail length (both to the nearest 1 mm).

I scored flight feather moult according to Ginn and Melville (1983), where old feathers were scored as 0, growing feathers as 1 to 4 for increasing stages of development, and fully-grown new feathers as 5. Primaries were numbered from P1 (the innermost) to P10 (the outermost); major secondaries were numbered from S1 (outermost) to S11 (innermost); and rectrices were numbered in pairs, from the central feathers (T1) outwards to T6. I expressed the extent of flight feather moult as the moult index (range 0 – 1), calculated as the sum of moult scores for both wings and both sides of the tail (primaries divided by 100; secondaries divided by 110, given 11 major secondaries; and rectrices divided by 120; cf. Minias and Iciek 2013).

The number of tail feathers replaced in adults was bimodal, with no birds having replaced 6 or 7 rectrices (Figure 6.1). I termed those that had moulted 8–12 feathers ‘early’ tail moulters, and those that had replaced 0–5 feathers as ‘late’ tail moulters. Attempts to create moult summary tables (*sensu* Rohwer and Rohwer 2018) for tail moult were confounded by individual variation in nodal and terminal feathers. I recognized five moult ‘strategies’: (i) Outward: moult starts at the centre (usually T1 but occasionally T2) and proceeds outwards; (ii) Inward: moult starts from the outer rectrices (usually T6 but occasionally T5) and proceeds inwards; (iii) Out/In: moult starts at both the inner and outer rectrices; (iv) Simultaneous: all rectrices moulted together; and (v) Mixed: moulting at multiple positions with no clear pattern or order. Each side of the tail was scored independently for all individuals, and birds also could have all rectrices new (New) or old (Old). I identified nodes (early in moult, where one new feather was clearly older than any other new feathers) and terminal feathers (late in moult, where one feather was clearly the last to be replaced) (Supplemental Table 6.2).

Tail raggedness was calculated as the sum of values for each tail feather, where 0 indicates a feather of full length (whether old or new), 4 indicates a feather at the first stage of growth (moult score 1), 3 a feather with moult score 2, 2 a feather with moult score 3, and 1 a feather with moult score 4 (cf. Arroyo and King 1996). Juvenile Amur Falcons undergo a partial body moult on the wintering grounds (Symes and Woodborne 2010), but the extent of new feathers was only readily apparent in males, which moult into the distinctive blue-grey adult male plumage. Accordingly, I scored body moult for males on a scale from 0–4 based on the extent of adult plumage acquired (Supplemental Figure 6.1).

Symmetry of tail feather moult was assessed by comparing the moult scores of each feather pair. A simple index of asymmetry was calculated as the standardised moult score asymmetry (i.e. asymmetry score/30, expressed as %), given that the maximum possible tail asymmetry would have a summed moult score difference of 30 (all feathers on one side of the tail old, and those on the other side new). Differences in moult score of 1 between a pair of feathers (right and left rectrices; 6 on each side) were regarded as ‘minor’ asymmetries (i.e. 0/1, 1/2, 2/3, 3/4 and 4/5); differences of 2 – 3 as ‘intermediate’ (i.e. 0/2, 0/3, 1/3, 1/4, 2/4, 2/5, 3/5) and of 4 – 5 as ‘major’ asymmetries (i.e. 0/4, 0/5, 1/5). To test whether asymmetry at a feather position is random, I used Pearson’s Chi-squared goodness-of-fit tests with Yates’ correction for continuity to compare the observed frequency of asymmetry with that expected by chance (assuming random replacement) for a given level of feather replacement. The degree of asymmetry is constrained by the likelihood of moult, because if no rectrices, or all rectrices are moulted, the moult pattern will be symmetrical. The potential for moult asymmetry peaks when half the feathers are moulted (in the most extreme case, one side is replaced and the other is not, giving an asymmetry score of 1), with a range of possible maximum asymmetry values between these extremes. As a result, differences in the proportion of feathers moulted must be controlled for when comparing asymmetry across feathers. To test whether tail moult tends to be symmetrical, I compared observed values of asymmetry to those expected assuming moult is random with respect to location (Brommer et al. 2003).

Traditionally in avian studies, body condition is calculated as the ratio of body mass to tarsus length (e.g. Izhaki and Maitav 2008). An alternative is the Scaled Mass Index (SMI, Peig and Green 2009) which avoids the problems associated with residual-based measures of 'condition' (Labocha and Hayes 2012). SMI scales each individual's body mass to the value expected if all birds were all of identical skeletal size, by using the inherent power relationship between mass and size modelled from the data (Peig and Green 2009). I used body mass and wing length measures and scaled the masses to the mean wing length, although the results when tarsus length (rather than wing length) was used, do not differ significantly. I used body mass and wing length for scaling because reverse sexual dimorphism holds for all measures except tarsus length (where males > females; Supplemental Table 6.1). Also, for a long-distance migrant like Amur Falcon, wing length would be better measure for body condition than tarsus. Juveniles are significantly smaller than adults within each sex (Supplemental Table 6.1), so separate values were used for each age-sex combination. I scaled the masses to the mean wing length of 239.9 mm (male) and 240.4 mm (female) for adults, and mean wing length of 233.8 mm (male) and 236.2 mm (female) for juveniles, using a Secondary Major Axis slope of 3.22 (for adults) and 1.54 (for juveniles) (Peig and Green 2009).

Due to non-linearity of the response variable (extent of tail moult) for adult birds, Mann-Whitney U-tests were used to compare means between time of event and sex. General linear models were used to explain the extent of tail moult in relation to event, sex, age, body condition and the interactions between these variables. Akaike's Information Criterion (AIC) was used to select the best model. The effect of body condition on the extent of tail moult in adults and juveniles was analysed. In adults, I also explored the effect of moulters (early and late moulters) on body condition. All statistical estimates were reported as means ± standard deviation (SD), apart from Figure 6.2 showing median and Interquartile Range (IQR). All statistical analyses were performed within the R statistical environment (R Core Team 2019).

Results

I scored moult from 1215 adult and 732 juvenile Amur Falcons killed in two hailstorms in KwaZulu-Natal (Table 6.1). The second event at Newcastle was more devastating than the first, with ~54% of the affected birds being rescued alive after the first event at Mooi River whereas only ~44% of birds survived the second event at Newcastle. The sex ratio of individuals killed was significantly male-biased in the second event (adults: $\chi^2 = 93.82$, $p < 0.001$, juveniles: $\chi^2 = 4.85$, $p = 0.02$) but female-biased in juveniles killed during the first event ($\chi^2 = 3.90$, $p = 0.03$; Table 6.1).

Adult flight feather moult

Most adults had completed replacement of remiges (their definitive prebasic moult) by mid-March. All adults had completed primary and secondary moult on 21 March, but 4% killed on 9 March were still finishing growing primary 10 (average proportion of primaries grown = 0.98 ± 0.01) and 32% were growing their outer secondaries (0.96 ± 0.03), with 27% growing only S1 and 5% growing S1 and S2. Most adults still growing P10 were also growing secondaries (63%), but this was not significantly different from random ($\chi^2 = 1.20$, d.f. = 1, $p = 0.32$).

By comparison, half of adults (50%) were actively moulting their tails, with 20% having completed tail moult and 30% yet to start (n = 1930). Males (0.52 ± 0.25) had more advanced tail moult than females (0.42 ± 0.22; U = 147791, $p < 0.001$; Table 6.2), but surprisingly tail moult was more advanced among birds killed on 9 March (0.52 ± 0.26) than 21 March (0.43 ±

0.23; U = 193851, $p < 0.001$; Table 6.2). This resulted from the strongly bimodal distribution of moult progression in adults, with 32% ‘early’ tail moulters and 68% ‘late’ tail moulters (Figure 6.1). Adult tail moult was more advanced in birds killed on 9 March because 45% of birds killed in this event were ‘early’ moulters compared to only 24% killed on 21 March. There was a significant difference between early and late tail moulters in terms of the progression of primary and secondary moult, with early tail moulters on average more advanced (0.99 ± 0.05) than late tail moulters (0.98 ± 0.10; U = 128259, $p < 0.001$).

Tail raggedness is linked to moult intensity, and thus the degree of raggedness tended to be higher (0.52 ± 0.48) in birds killed in the first event than in those from the second event (0.43 ± 0.39) (t = 1.74, d.f. = 1017, p = 0.04). The maximum tail raggedness score among adults was 18 in the first event and 20 in the second event.

Juvenile tail and body moult

Flight feather moult in juveniles (preformative moult) was restricted to the rectrices. Overall, juvenile tail moult was less advanced than that of adults, and may well be only a partial moult in most juveniles. However, there was considerable variation among individuals; 2% of juveniles had completed tail moult, 83% were in active moult, and 15% had not yet started to moult (n = 742). The proportion to have completed moult was significantly less than adults (20%), but the proportion not yet started to moult also was less than adults (30%; $\chi^2 = 243.4$, d.f. = 2, $p < 0.001$). Moult typically started with the central rectrices in both age classes (see below), with the probability of replacement for T1 similar for adults (0.82) and juveniles (0.83; Table 6.3). However, adults were more likely to have replaced their other rectrices (0.40–0.45) than juveniles (0.18 for T2 and 0.04–0.07 for T3–T6; Table 6.3). Among juveniles, the distribution of tail moult was unimodal (Figure 6.1) and as expected, moult extent in juveniles increased slightly from birds killed on 9 March (0.34 ± 0.18) to those on 21 March (0.40 ± 0.15; U = 55334, $p < 0.001$; Table 6.2). Tail moult was more advanced among females (0.38 ±

0.26) than males (0.35 ± 0.27; Table 6.2), although this effect was only significant in the second event ($F_{1,420} = 12.86$, $p < 0.001$). However, there was considerable variation among individuals, with a few birds (three adults and one juvenile) dropping all 12 rectrices at once. There was a positive relationship between the extent of tail moult and body moult in juvenile males ($F_{4,368} = 14.96$, $p < 0.001$; Figure 6.2). Because moult was further advanced among juveniles killed in the second event, the degree of raggedness was also higher (0.68 ± 0.39) than in the first event (0.42 ± 0.31; $t = -3.96$, d.f. = 737.23, $p < 0.001$). Maximum tail raggedness among juveniles was 24 in the first event and 18 in the second event.

Pattern and symmetry of tail moult

In birds just starting tail moult, the nodal point where moult was initiated was typically T1 (89% of 400 adults; 99% of 572 juveniles; Supplemental Table 6.2), followed by T2 (8% adults; 1% juveniles; Supplemental Table 6.2). However, in adults completing tail moult, the terminal feather also was mostly T1 (72%, n = 117) followed by T2 (24%; Supplemental Table 6.2). This is because 24% of adults moulted their tail inwards rather than outwards (Table 6.4), and these birds formed the majority of 'early' adult moulters. There was thus a marked difference in tail moult scores between strategies: Outward (0.17 ± 0.08), Inward (0.81 ± 0.19), and other strategies (0.41 ± 0.22; $F_{2,1157} = 2088$, $p < 0.001$). There was no evidence that moult strategy was linked to sex ($\chi^2 = 0.90$, d.f. = 2, $p = 0.32$).

Among birds with some active tail moult, 39% of adults (n = 590) and 27% of juveniles (n = 617) exhibited some asymmetry in tail moult. The average asymmetry scores (AS) were very similar for adults (3.9 ± 7.2%) and juveniles (4.0 ± 10.6%) but juveniles had more extreme asymmetry than adults. Significantly more juveniles (n = 18) had AS > 33% than adults (n = 4; $\chi^2 = 7.25$, $p < 0.01$). Three juveniles had AS of 83%, having completely replaced all rectrices on the left side of the tail, but only T1 on the right. Another juvenile had replaced T1-4 and T6 was almost fully grown on the left side of the tail, while the right side was still all old (AS =

80%). By comparison, the highest AS for an adult was 67% (T3-6 replaced on the left side; all old on the right side). Interestingly, there was a slight tendency for moult to be more advanced on the left side of the tail more often (56% of adults and 54% of juveniles) than on the right ($\chi^2 = 4.27$, d.f. = 1, $p = 0.02$ for all birds combined). Among birds with the typical outward moult pattern, the left side of the tail started to moult first more often than the right side in both adults ($\chi^2 = 6.11$, d.f. = 1, $p < 0.01$) and juveniles ($\chi^2 = 6.50$, d.f. = 1, $p < 0.01$; Table 6.4).

Type I asymmetry was greater at T1 for adults (15%) than juveniles (10%), but asymmetry for T2 to T6 was less in adults (1–4%) than juveniles (3–10%; Table 6.3), especially given the greater probability of feather replacement in adults. Despite these differences, the degree of asymmetry was less than expected by random replacement across all rectrices in both age classes (Table 6.3).

Correlations with body condition

The extent of tail moult correlated with body condition in both adults and juveniles. In adults, early moulters were in better condition than late moulters, and females were in better condition than males (Table 6.5). Birds killed in the second event were in better condition than in the first event for both adults (second event: 149.10 ± 73.32 vs first event: 139.38 ± 78.26; $t = 9.67$, d.f. = 815.56, $p < 0.001$) and juveniles (second event: 138.84 ± 61.42 vs first event: 131.02 ± 59.62; $t = 6.93$, d.f. = 585.66, $p < 0.001$). After controlling for this effect, both indices of body condition were related to the extent of tail moult in adults and juveniles: SMI (adults: $F_{1,1138} = 11.74$, $p < 0.001$; juveniles: $F_{1,739} = 1.76$, $p = 0.04$; Figure 6.3) and mass/tarsus length (adults: $F_{1,1138} = 14.05$, $p < 0.001$; juveniles: $F_{1,739} = 2.07$, $p = 0.03$). Birds with better body condition tended to moult more tail feathers, with considerable variation among individuals (Figure 6.3). Females were significantly larger than males in all measurements except tarsus length (Supplemental Table 6.1).

Discussion

The two mass mortality events affected almost 4000 Amur Falcons at their communal roosts in March 2019, with 1991 killed and about 1900 injured severely enough to be temporarily taken into captivity (Allan 2019). Similar mass mortality events have been linked to severe hail storms (Bernitz 2006; Pietersen and Symes 2010), and it is interesting to speculate whether the risk of such events is likely to increase as climate change is predicted to increase storm frequency and severity. The greater mortality of male Amur Falcons might reflect a male-biased adult sex ratio, which is common across many bird species (Morrison et al. 2016), particularly in threatened species (Donald 2007) and in small or fragmented populations (Fretwell and Calver 1969; Dale 2001; Woolfenden et al. 2001; Zanette 2001). However, male-biased mortality might also result from the smaller size and lighter weight of the males, possibly making them more vulnerable to hailstones and allowing them to roost on more peripheral branches than females (which might obtain more protection from hailstones by roosting on more central branches; Jenni 1993; Donazar and Feijoo 2002). The unexpected finding that males have longer tarsus lengths than females may relate to a more aerial hunting pattern in males, possibly related to the provisioning by males of females and young during the breeding period (Jenkins 1995).

The two mass mortality events gave me the opportunity to not only report the extent of flight feather moult but to explore individual variation between events and symmetry of tail moult in adult and juvenile Amur Falcons. The duration and extent of moult is constrained by energy invested (Pietiainen et al. 1984), and I found that extent of tail moult differed between event, sex and age (Zuberogoitia et al. 2018). Perhaps the most surprising result was that adults killed in the first event had moulted more tail feathers than those killed 12 days later, even though moult in the primaries and secondaries was more advanced in the second event. The more advanced tail moult on 9 March was linked to a higher proportion of ‘early’ moulters during the first event compared with the second. Which begs the question, why is adult tail moult bimodal? ‘Late’ moulters might be second-year birds, and their proportion could be higher in the second event if some full adults had already departed KwaZulu Natal by 20 March. Of 6 adults fitted with PTT satellite-trackers; departure dates ranged from 3 March to 24 April (median 29 March), with 3 of 13 departure dates before 20 March (Z. Bernitz unpubl. data). This suggests that some older adults might have departed by the time of the second event on 20 March, which might at least in part account for the higher proportion of ‘late’ tail moulters killed in the second event. The first event may have comprised a mix of adults that had more-or-less finished moulting and were preparing to migrate, and those adults with poorer body condition than the expected, showing a delayed moult (related to the energy-body condition) trying to finish it before migrating. However, the high proportion of ‘late’ moulters overall, and the fact that most ‘early’ moulters follow a different replacement strategy (inwards from the outer tail) suggests that there is a more complex explanation for this unexpected result.

Adult males had slightly more advanced tail moult than females. This is consistent with other studies on sex-linked differences in timing of moult especially for migrants (Barshep 2011; Barshep 2013; Morbey et al. 2017) where males start moult earlier than females, because they are more active in territory defence and need full-grown flight feathers early as they are under pressure to get to the breeding grounds first to establish breeding sites in spring (Svensson and Nilsson 1997; Hemborg 1999; Newton 2011; Lehikoinen 2017). Also, breeding adult female raptors (Newton and Marquiss 1982) and other birds (Svensson and Nilsson 1997) often moult later than breeding males due to more-extensive chick-feeding responsibilities (Hemborg 1999). However, there was no evidence of sex-linked differences in tail moult strategies among adults, with almost as many females as males moulting inwards rather than the more common outwards pattern. Unlike the adults, juvenile female Amur Falcons had more advanced tail moult than juvenile males. The extent of post-juvenile moult advanced more in females than males in response to historical climate warming trends (Kiat et al. 2019), suggesting that moult in juvenile females may be more sensitive to environmental variation (Delhey et al. 2020).

There are often age-related differences in the extent and timing of moult (Zuberogoitia et al. 2016). Juveniles require more energy to obtain the same food intake as adults and are not constrained by breeding activities, and thus normally start moulting later than adults. As birds gain experience, they can mobilise more energy, which enables them to start moult earlier and potentially moult more intensively than younger, less-experienced birds. Immature vultures, for example, need three moult cycles to complete moult, whereas adults can complete their moult in two cycles (Zuberogoitia et al. 2016). Fewer juvenile Amur Falcons had completed tail moult (2%) than adults (20%), suggesting that perhaps some juveniles only replace a subset of tail feathers before migrating. However, most replace at least some tail feathers, with the proportion yet to start tail moult by mid-March (15%) less than among adults (30%). Quite surprising that four birds were replacing all their 12 rectrices at once, which could suggest the possibility of such extreme moult resulting from shock moult. Examination of juveniles on migration or on arrival at the breeding grounds is needed to confirm whether tail moult is partial in some birds. One possible reason for juveniles replacing tail feathers rather than primaries may be related to the fact that Amur Falcons feed on the wing, and juveniles that have fresh rectrices should be better able to swerve to catch agile dragonflies in pursuit during migration (Hedlund 2019).

Moult tables summarise the adequacy of the data for making inferences about the direction of moult replacement and to clarify differences in moult strategies (Pyle 2013; Rohwer and Rohwer 2018). I confirmed previous findings that moult in Amur Falcons typically starts with the central tail feathers (Louette 2007; Bugoni et al. 2014); most juveniles and ‘late’ adult moulters start replacing their rectrices at the centre and proceed outwards. However, one quarter of adults apparently start moult at the outer tail and proceed inwards; these made up most of the 'early' moulters that were close to completing tail moult in mid-March. This variation in moult sequence may suggests moult plasticity and may be an adaptive response to the problem of optimal timing of moult of differing feathers within the same feather tract (Barta et al. 2006). Pyle (2013) reported that moult initiation nodes in the wings of falcons may be plastic, perhaps as an adaptive response to differences in wing shape and the time it takes to replace inner and outer primaries. In some other species, the node varies in the remiges and in some rectrices, e.g. Savi's Warbler *Locustella luscinioides* (Neto and Gosler 2006), Rufous Fantail *Rhipidura rufifrons* (Junda et al. 2012), Greater Flamingos *Phoenicopterus roseus* (Studer-Thiersch 2000), European Stonechats *Saxicola rubicola (*Flinks et al. 2008) and some tropical hummingbirds (Stiles 1993). Even within monotypic species such as the Grey Plover *Pluvialis squatarola,* the moult sequence can vary substantially according to the latitude or hemisphere of a bird's winter grounds, due to varying environmental constraints (Serra et al. 1999). This variation can also be driven by hormonal endocrinological processes, available nutritional resources and light regimes (Payne 1972; Dawson 2006). Further study is needed to investigate the causes and consequences of the various tail moult strategies found in Amur Falcons.

Despite their greater probability of being moulted than other tail feathers, the central feathers (T1) had the lowest symmetry in adult and shared lowest symmetry with T2 in juvenile Amur Falcons. The greater asymmetry among juvenile tail moult (apart from the central pair of rectrices) might indicate selection for birds with greater symmetry. Birds of higher intrinsic quality might be expected to moult in a more symmetrical manner (Minias and Iciek 2013), as this is the ideal state for bilateral structures (Leamy and Klingenberg 2005). Generally, moult tends to be symmetrical between both wings and tail in those species that follow a simple moult pattern, with asymmetry increasing in proportion to the intricacy of the moult pattern and the age of the individual (Zuberogoitia et al. 2016). Thus, the ability to carry out selective replacement of damaged feathers and/or arrest the moult process increases asymmetry (Ellis et al. 2016). The high level of symmetry maintained by individuals, and the cost of asymmetry in terms of reduction in survival probability, suggest that developmental homeostasis in partial moult is maintained by stabilising selection (Brommer et al. 2003).

Asymmetrical moulting confers energetic costs and might reduce turning performance, impacting flight manoeuvrability (Thomas 1993). I found evidence of selection for symmetrical moult across all rectrices, but the central rectrices moult less symmetrically than outer rectrices. High levels of asymmetry of the central rectrices have been reported in several other birds (Wetmore 1915; Stresemann and Stresemann 1968; Henny et al. 1985; Kemp 1995; Pyle 1995; Louette 2007). The central rectrices are subject to heavy wear and this process may enhance asymmetry, due to physiological constraints (as growth of rectrices would require high levels of energy for replacement). The finding that moult tended to initiate on the left side of the tail first was unexpected; I found no other evidence of handedness in moult.

The link between body condition and 'early' versus 'late' tail moulters vis-à-vis extent of tail moult and body condition suggests that extent of tail moult correlates with body condition. Birds killed during the second mass mortality event had greater body condition than those in the first event, presumably because they were preparing for migration and thus accumulating fat reserves. I confirmed that the extent of tail moult was correlated with body condition in both adults and juveniles, similar to the pattern found in several passerines (Gosler 1991; López et al. 2005; Senar et al. 2008; Minias and Iciek 2013). In some passerines, the extent of juvenile moult ranges from no replacement of flight feathers to complete replacement depending on the time of hatching (Jenni and Winkler 1996; Bojarinova et al. 1999). The extent of moult can correlate with the future performance of birds, reflecting nutritional status of birds at the time of moulting (Senar et al. 2008). The effects of extent of post-juvenile moult on future performance has been linked to feather quality which may affect flight efficiency (Jenni and Winkler 1996). Amur Falcons in better condition moulted more tail feathers (and at least for juvenile males, more body feathers), suggesting that moult pattern might be used as an indicator of fitness in falcons.

Table 6.1: Sample size (and %) of adult and juvenile Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa, in March 2019.

Events	**Adults**		%	**Juveniles**		%	**Total**	%
	Male	Female	Male	Male	Female	male		male
First event	281	230	55%	139	175	44%	825	51%
Second event	481	223	68%	232	186	56%	1122	64%
Total	762	453	63%	371	361	51%	1947	58%

Table 6.2: Differences in the mean extent of tail moult (mean ± SD moult index) between event, sex, and age of Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa, in March 2019.

Parameters		Tail moult extent	F	P
Event				
	First	0.43 ± 0.24	11.59	0.001
	Second	0.41 ± 0.19		
Sex				
	Male	0.44 ± 0.23	9.44	0.002
	Female	0.40 ± 0.25		
Age				
	Adult	0.47 ± 0.17	33.04	<0.001
	Juvenile	0.37 ± 0.20		
Event*Sex				
	First – Male	0.49 ± 0.21	57.92	<0.001
	Second – Male	0.38 ± 0.16		
	First – Female	0.37 ± 0.22		
	Second – Female	0.44 ± 0.20		
Event*Age				
	First – Adult	0.52 ± 0.26	24.77	<0.001
	Second – Adult	0.43 ± 0.23		
	First – Juvenile	0.34 ± 0.18		
	Second – Juvenile	0.40 ± 0.15		
Sex*Age				
	Male – Adult	0.52 ± 0.25	12.86	<0.001
	Female – Adult	0.42 ± 0.22		
	Male – Juvenile	0.35 ± 0.27		
	Female – Juvenile	0.38 ± 0.26		
Event*Sex*Age			24.87	<0.001

* $F_{7,1920} = 24.93$

Table 6.3: Probabilities of rectrix replacement among 1215 adult and 732 juvenile Amur Falcons and comparison between observed and expected asymmetry (see Methods for details).

Parameters	**T1**	**T2**	**T3**	**T4**	**T5**	**T6**
Adults						
Probability of replacement	0.82	0.40	0.40	0.40	0.40	0.45
Symmetry (%)	85.2	96.5	97.9	98.7	99.2	99.0
Asymmetry: major (%)	1.1	0.9	1.0	0.6	0.4	0.8
intermediate (%)	6.2	1.2	0.7	0.4	0.2	0
minor (%)	9.7	1.4	0.4	0.3	0.2	0.2
Total asymmetry (%)	14.8	3.5	2.1	1.3	0.8	1.0
Expected (null model) (%)	30.0	48.0	48.1	48.1	48.0	49.5
χ^2 values*	26.47	715.84	859.61	865.07	882.10	1034.74
Juveniles						
Probability of replacement	0.83	0.18	0.07	0.06	0.04	0.05
Symmetry (%)	90.0	89.8	95.8	95.8	96.9	96.6
Asymmetry: major (%)	3.4	4.4	2.2	3.2	2.3	2.1
intermediate (%)	3.3	1.5	1.0	0.5	0.4	1.0
minor (%)	3.3	4.3	1.0	0.5	0.4	0.3
Total asymmetry (%)	10.0	10.2	4.2	4.2	3.1	3.4
Expected (null model) (%)	28.1	29.2	12.4	10.9	7.1	9.6
χ^2 values*	217.65	163.52	50.13	38.75	23.16	35.91

* d.f. = 1935, all $p < 0.001$

Table 6.4: Moult summary matrix table for 1188 adult and 732 juvenile Amur Falcons.

		Right side						
Adults		Outward	Inward	Out/In	Simultaneous	Mixed	New	Old
Left side	Outward	335		3		6		36
	Inward		120	1			11	2
	Out/In	4	1	10				
	Simultaneous				3			
	Mixed	5	3			8	1	4
	New		13	1			242	
	Old	17	2			3		355
Juveniles								
Left side	Outward	543		9		8	1	20
	Inward		3					
	Out/In	4		11				1
	Simultaneous				1			
	Mixed	2				1	1	2
	New	3					13	
	Old	6	1					112

Table 6.5: Differences in the mean body condition (± SD) between 'early' versus 'late' tail moulters, event and sex of adult Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa, in March 2019.

Parameters		**Body condition**	**F**	**P**
Moulter				
	Early	147.46 ± 86.36	17.03	<0.001
	Late	143.05 ± 63.16		
Event				
	First	139.38 ± 78.26	93.99	0.002
	Second	149.10 ± 73.32		
Sex				
	Male	140.51 ± 83.17	56.94	<0.001
	Female	149.34 ± 67.21		
Moulters*Event				
	Early – First	139.57 ± 59.21	8.92	0.01
	Late – First	139.19 ± 74.50		
	Early – Second	154.53 ± 82.11		
	Late – Second	146.23 ± 53.10		
Moulters*Sex				
	Early – Male	143.10 ± 90.11	0.25	0.62
	Late – Male	137.62 ± 86.33		
	Early – Female	150.64 ± 84.14		
	Late – Female	148.12 ± 71.62		
Moulters*Event*Sex			0.49	0.49

* $F_{7,1081} = 21.46$

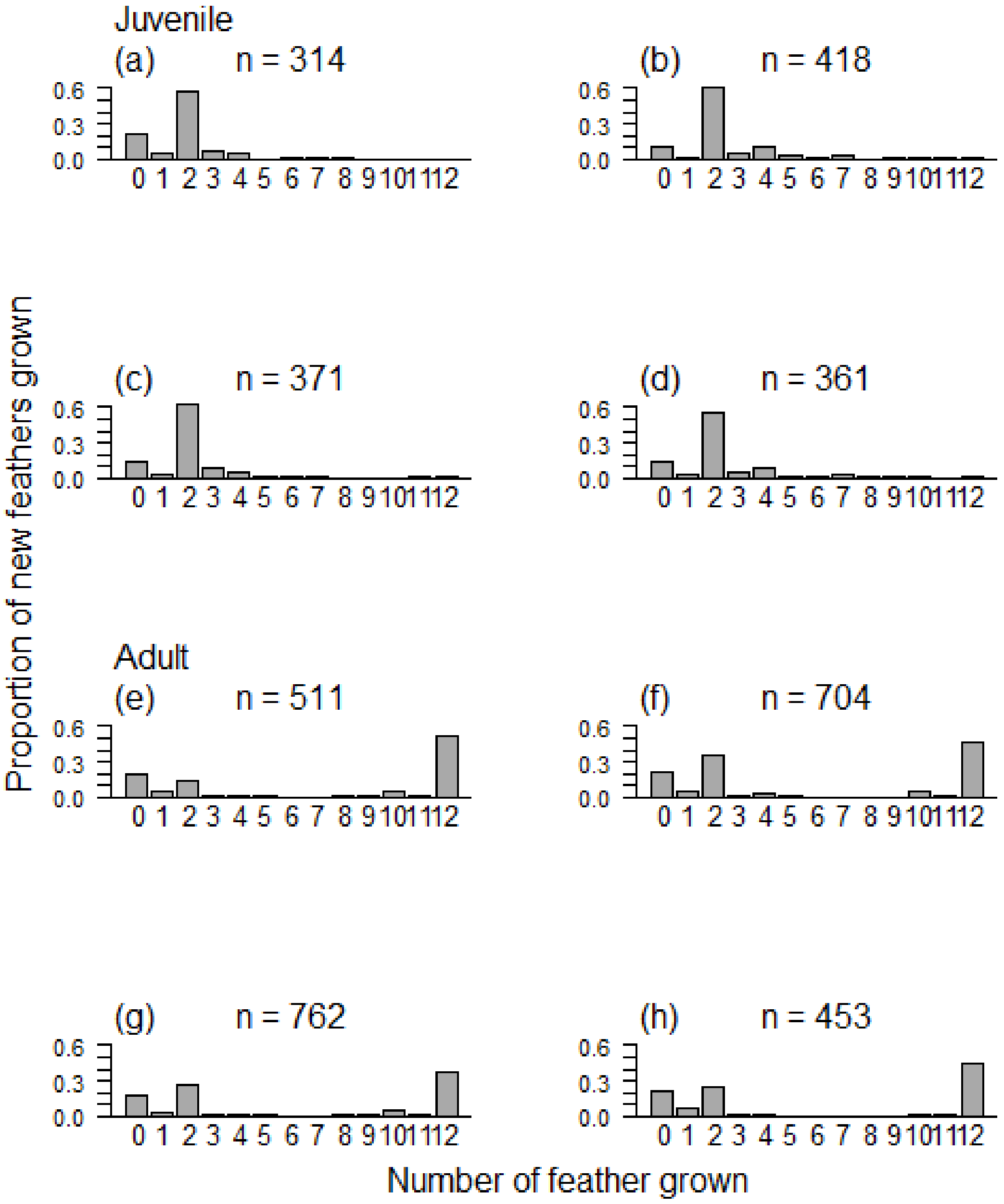


Figure 6.1: Number of tail feathers moulted by juvenile (a) first event; (b) second event; (c) males; (d) females; and adult Amur Falcons in (e) first event; (f) second event; (g) males; (h) females.

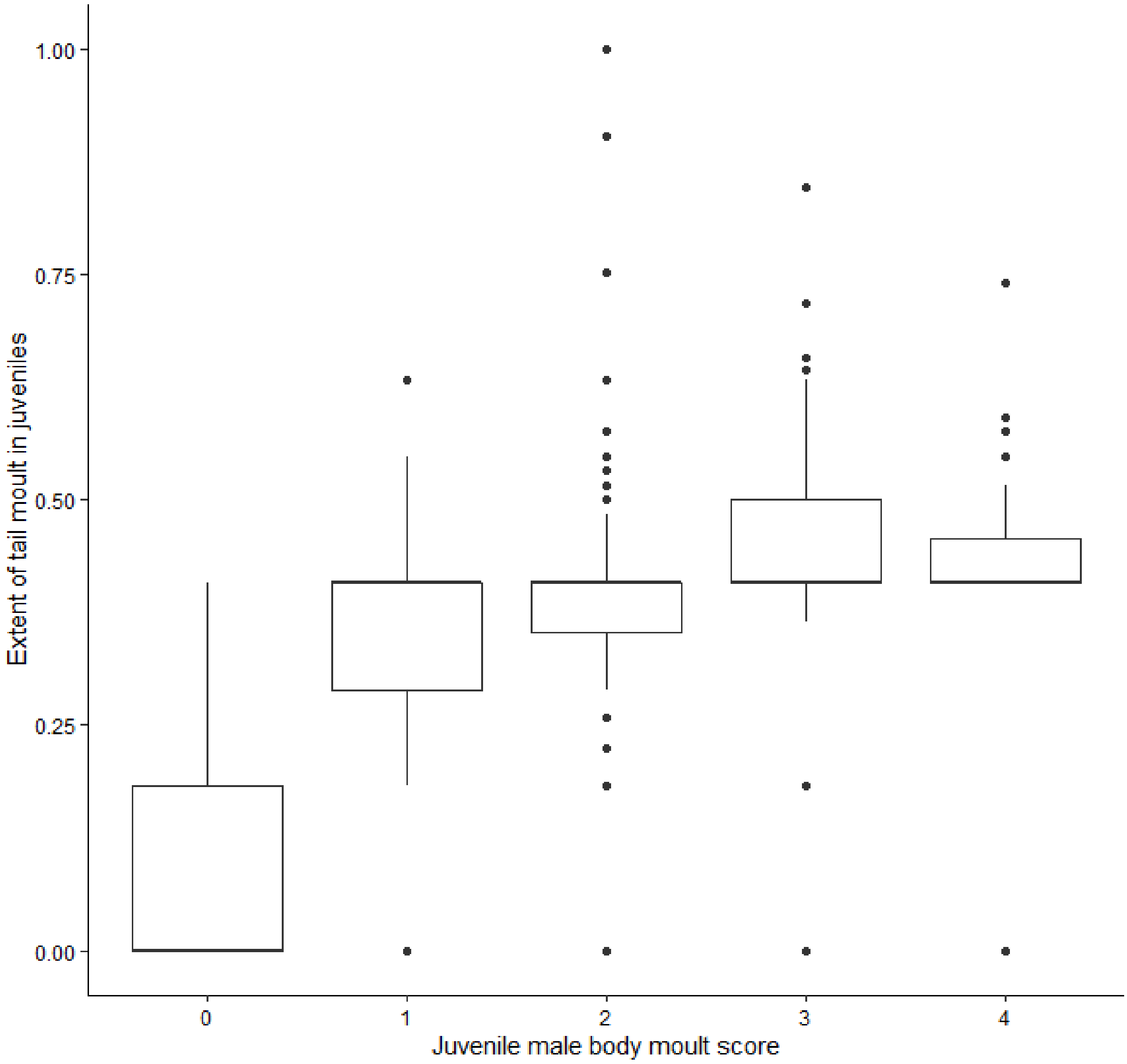


Figure 6.2: Extent of tail moult and body moult of juvenile male Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa, in March 2019 (Bold line – Median extent of tail moult for juvenile male body moult; Boxes 25th to 75th percentile; Whiskers 10th/90th percentile).

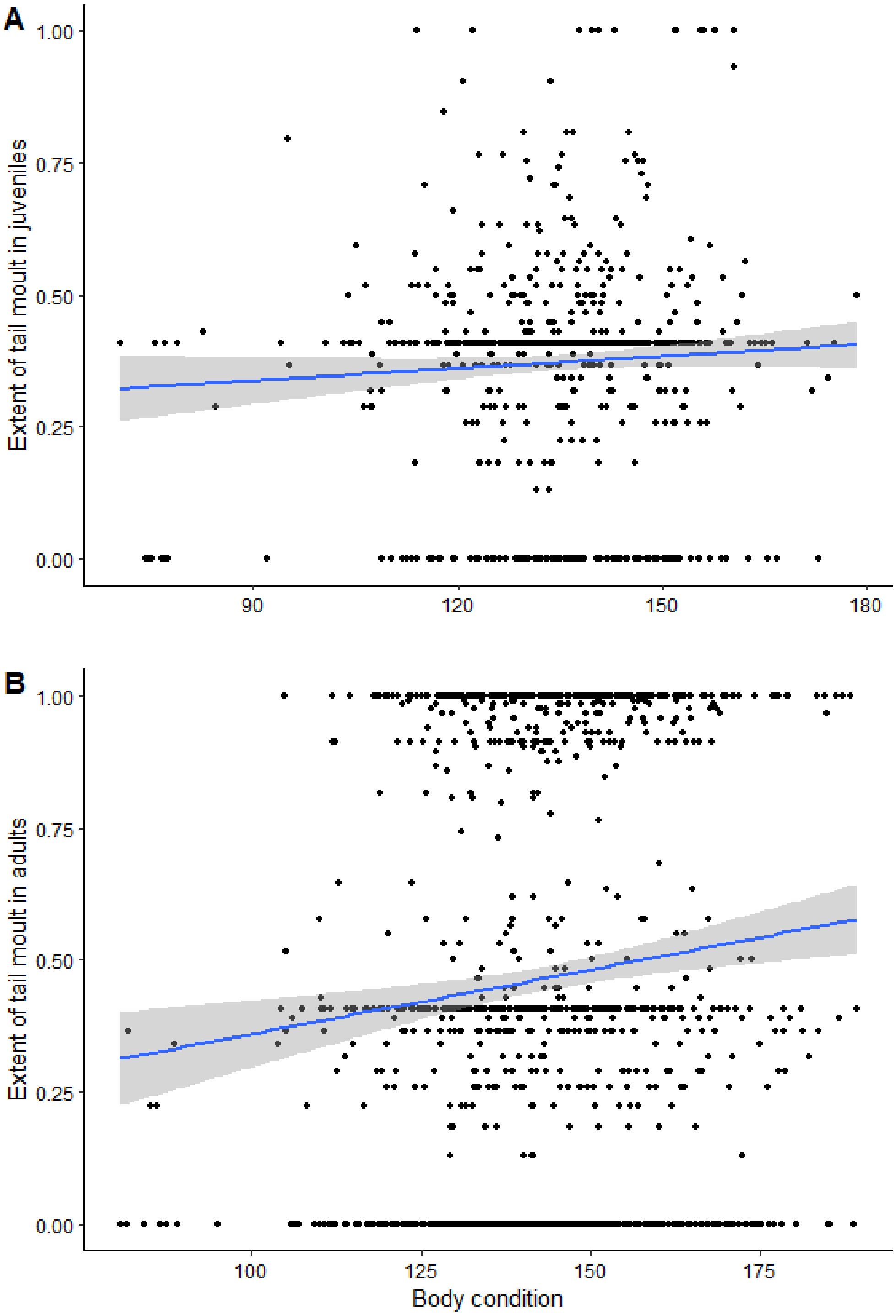


Figure 6.3: Relationship between extent of tail moult (proportion of feathers replaced) and body condition in (A) juvenile and (B) adult Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa, in March 2019.

Supplemental material

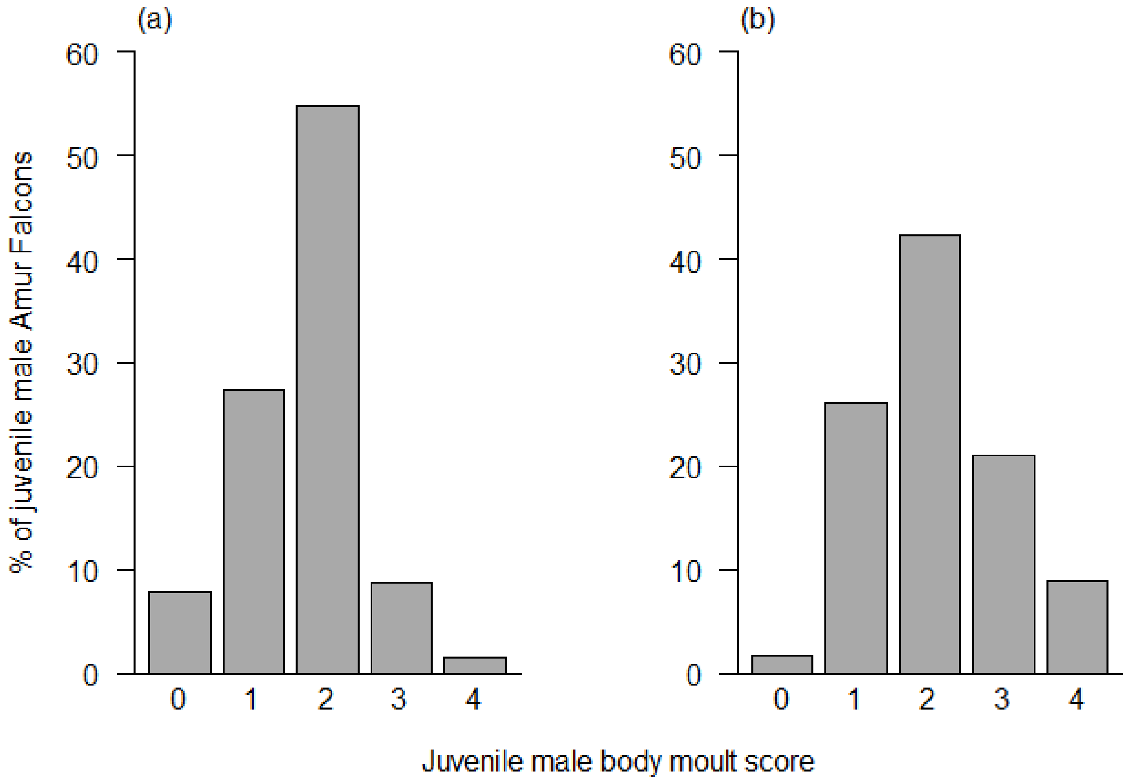
Supplemental Table 6.1: Mean morphological measurements (± SD) of juvenile and adult Amur Falcons killed by hailstorms in KwaZulu-Natal, South Africa, in March 2019. p values refer to results of t-tests comparing sexes within age groups.

Age/Sex	**Mean ± SD**	**t**	**d.f.**	**P**
Mass (g)				
Juvenile males	130.1 ± 14.7	8.07	738.73	<0.001
Juvenile females	138.7 ± 14.5			
Adult males	141.3 ± 15.1	4.93	809.63	<0.001
Adult females	146.1 ± 14.8			
Bill length (mm)				
Juvenile males	13.4 ± 0.5	4.29	739.58	<0.001
Juvenile females	13.5 ± 0.5			
Adult males	13.6 ± 0.6	10.68	842.13	<0.001
Adult females	13.9 ± 0.6			
Head length (mm)				
Juvenile males	41.3 ± 1.1	-1.04	739.49	0.30
Juvenile females	41.2 ± 1.1			
Adult males	41.2 ± 1.2	5.10	887.54	<0.001
Adult females	41.6 ± 1.3			
Tarsus length (mm)				
Juvenile males	28.1 ± 0.9	-8.91	728.40	<0.001
Juvenile females	27.5 ± 1.0			
Adult males	28.3 ± 1.2	-8.18	839.74	<0.001
Adult females	27.8 ± 1.0			
Left wing length (mm)				
Juvenile males	233.8 ± 5.7	5.51	735.43	<0.001
Juvenile females	236.2 ± 6.0			
Adult males	239.9 ± 5.9	1.45	850.59	0.15
Adult females	240.4 ± 6.0			
Right wing length (mm)				
Juvenile males	233.9 ± 5.9	5.35	736.83	<0.001
Juvenile females	236.2 ± 6.1			
Adult males	240.0 ± 6.1	1.56	861.39	0.12
Adult females	240.5 ± 6.2			
Tail length (mm)				
Juvenile males	119.0 ± 5.3	2.65	736.69	0.01
Juvenile females	120.0 ± 4.8			
Adult males	125.8 ± 5.1	0.54	866.09	0.60
Adult females	126.0 ± 5.1			
Bill depth (mm)				
Juvenile males	9.4 ± 0.3	3.47	720.93	0.001
Juvenile females	9.5 ± 0.2			
Adult males	9.5 ± 0.3	2.94	926.52	0.01
Adult females	9.6 ± 0.3			

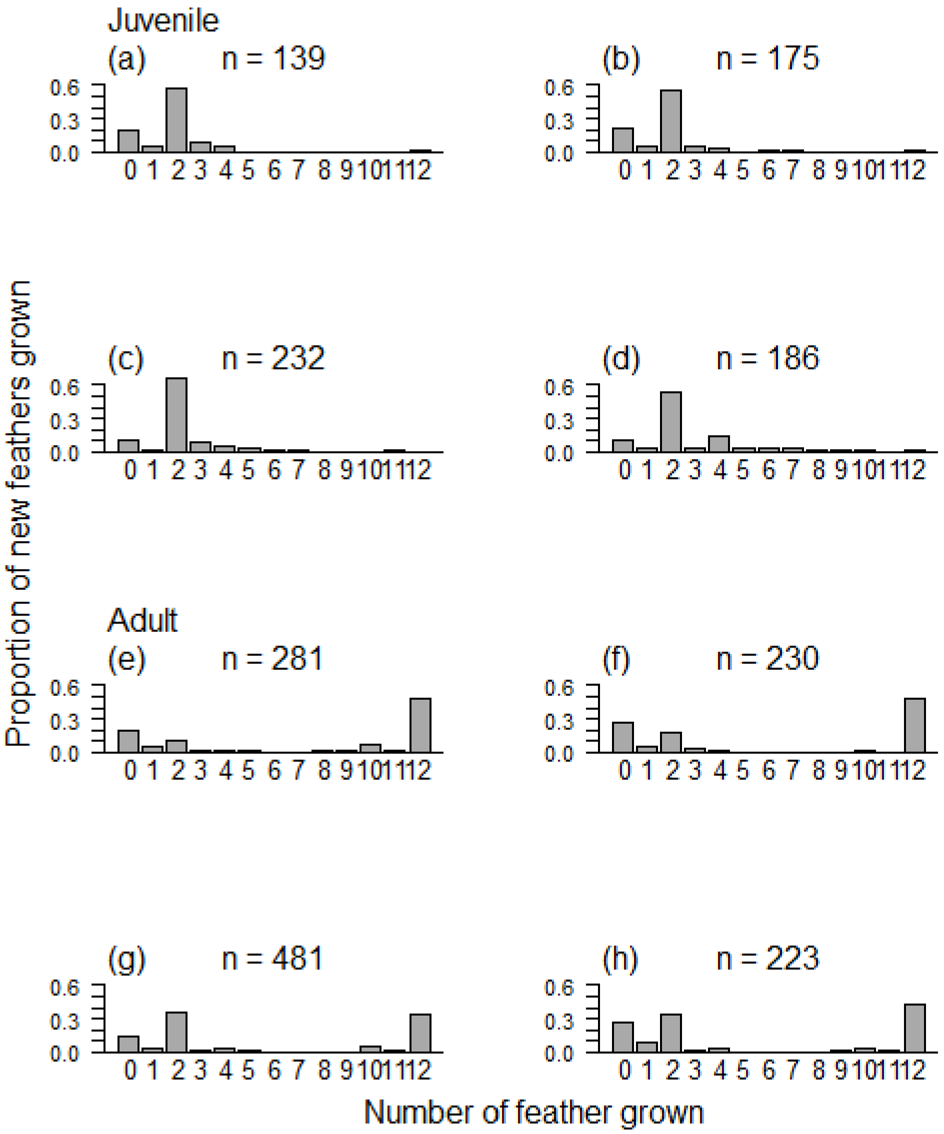
Supplemental Table 6.2: Moult summary table (showing nodal and terminal sites) for 1188 adult and 732 juvenile Amur Falcons.

	T1	**T2**	**T3**	**T4**	**T5**	**T6**
Adults						
Nodal feathers	354	31	8	4	0	3
Terminal feathers	84	28	3	1	1	0
Juveniles						
Nodal feathers	566	5	0	1	0	0
Terminal feathers	1	1	2	0	3	0

Supplemental Figure 6.1: Four juvenile male Amur Falcons showing increasing progression of body moult into adult male plumage (from left, stage 1 to right stage 4). Note: New central rectrices for birds in stages 2 and 4.



Supplemental Figure 6.2: Percentage of juvenile male Amur Falcons with different body moult scores during (a) first event (n = 139); (b) second event (n = 234).



Supplemental Figure 6.3: Number of tail feathers moulted by juvenile (a) first event males; (b) first event females; (c) second event males; (d) second event females; and adult Amur Falcons in (e) first event males; (f) first event females; (g) second event males; (h) second event females.

CHAPTER 7

Synthesis and conclusions

Moult is one of three energy-demanding events in the annual cycle of birds, alongside breeding and migration. Unlike breeding and migration, moult is indispensable, and its patterns vary considerably among species. Despite the importance of moult, it has been relatively less studied compared with breeding and migration. In addition, feather replacement is more challenging in large birds compared to smaller birds, due to the time required to grow their long wing feathers (Rohwer et al. 2009; Rohwer and Rohwer 2013). In this thesis I explored how different birds balance moult with other aspects of their annual cycles. In particular, I assessed how large, long-winged birds manage to replace their large number of secondaries. I also explored whether nestlings could grow flight feathers of equal quality as adults in a long-distance migratory raptor. The costs of moult and compromised feather quality pose substantial selection pressures (Minias et al. 2015).

The main results of my research are as follows:

1. *Juvenile flight feathers are not significantly compromised in terms of quality*

In Chapter 2, I showed that juvenile flight feathers are not significantly compromised in terms of quality, despite seemingly rapid growth rates and lighter mass per unit length. Contrary to the previous studies indicating that rapid growth of feathers reduces their quality, I found that juveniles are able to grow equally complex structures as adults. Age and sometimes sex are significant factors in determining the quality of feathers in birds (Pap et al. 2007; Butler et al. 2008).

2. *Feather traits could be used as reliable indicators of a bird's health*

In Chapter 2, I showed that adult and juvenile Amur Falcons with better body condition tended to have longer and heavier feathers, with limited variations across feather tracts, suggesting that feather traits could be used as reliable indicators of a bird's health. Pap et al. (2008) showed that feather deformities is linked to low body condition, showing that birds in poor condition during moult grow lower quality remiges which became more rapidly damaged. Vágási et al. (2012) also reported that body condition was positively associated with feather traits. Patanella (2018) also reported relationship between feather quality and body condition of Eastern Bluebirds from two urban and two rural sites, showing that the ratio of rectrix mass to length and barbule density increased with body measurements.

3. *Moult duration and symmetry might be used as an index of condition*

In Chapter 3, I showed that moult duration and symmetry, but not timing, differed between two neighbouring breeding colonies of Cape Gannets. I concluded that differences in moult duration and perhaps asymmetry between the breeding colonies may be linked to foraging conditions, given that gannets breeding at Lambert's Bay are thought to be under greater food stress than those breeding on Malgas Island. This suggests that moult can be used as an index of condition. Different populations of a species can have different moult strategies (e.g., Dunlin *Calidris alpina*; Greenwood 1983).

4. *Moult pattern might be used as an indicator of fitness*

In Chapter 6, I showed that extent of tail moult was correlated with body condition in adult and juvenile Amur Falcons, suggesting that moult pattern might be used as an indicator of fitness in falcons. In several passerines, extent of moult correlates with body condition (Gosler 1991; López et al. 2005; Senar et al. 2008; Minias and Iciek 2013). The extent of moult can correlate with the future performance of birds, reflecting nutritional status of birds at the time of moulting (Senar et al. 2008). The effects of extent of post-juvenile moult on future performance has been linked to feather quality which may affect flight efficiency (Jenni and Winkler 1996).

5. *Little evidence of reduced flight activity during moult period*

In Chapter 4, I showed that unlike many smaller petrels, there was little evidence that adult White-chinned Petrels reduced the time spent flying while moulting, despite the intense nature of wing and tail moult. Several petrels (Cherel et al. 2016; Jones et al. 2020) and a range of other seabirds including skuas (Phillips et al. 2007; Magnusdottir et al. 2014; Weimerskirch et al. 2015), alcids (Mosbech et al. 2012) and sulids (Garthe et al. 2012) all exhibit reduced flight activity while moulting. Other species, some diving petrels and alcids, even becoming flightless (Bridge 2004).

6. *Moult intensity varies considerably among seabirds*

In Chapters 3-5, I showed that moult is intense in adults of annual breeders with large, long wings, but less intense in biennial breeder. Moult was particularly intense in the secondaries of the two Procellariiformes studied: White-capped/Shy Albatross grow up to 48% of their secondaries at once (Chapter 5) and White-chinned Petrels up to 54% of their secondaries (Chapter 4), compared to only 31% secondaries at once in Cape Gannets (Chapter 3). This rapid replacement of secondaries was coupled with often intense moult of other flight feathers, with White-chinned Petrels growing up to six primaries and all their rectrices at once. Interestingly, White-chinned Petrels and White-capped/Shy Albatrosses don't replace all secondaries each year. Large birds tend to grow more feathers simultaneously and thus decreasing the time required for feather replacement (Langston and Rohwer 1996; Bridge 2006; Rohwer and Rohwer 2013). Stepwise replacement of the remiges occurs in many large birds (Stresemann and Stresemann 1966; Bridge 2006). Intensive moult and several loci of secondary moult is a common pattern in birds with long wings (Edelstam 1984; Ryan et al. 2020), including Procellariiformes such as giant petrels (Stresemann and Stresemann 1966; Hunter 1984), Cory's Shearwaters (Ramos et al. 2009), albatrosses (Prince et al. 1993, 1997) and even storm petrels (Ainley et al. 1976), presumably to minimize large gaps in the wing (Arroyo et al. 2004).

Secondary moult

There is lack of focus on secondary moult relative to primary moult, and one key finding from this thesis was the presence of rapid secondary moult in many seabirds. All three seabirds studied had a greater total length of secondaries than primaries (23-43% longer; Supplemental Tables 3.1, 4.1 and 5.1), which given the relatively invariant rate of feather growth (Jenni et al. 2020), emphasises the need for greater focus on secondary moult strategies. One way long-winged seabirds may be able to moult many secondaries at the same time is to replace the greater secondary coverts before starting secondary moult (Chapters 4 and 5, also found in Blue Petrels, Ryan et al. 2020, Kelp Gulls *Larus dominicanus* (Figure 7.1) and other petrels (e.g. Soft-plumaged Petrel *Pterodroma mollis*; Figure 7.2) and having long secondary coverts that overlap extensively with the secondaries. Together, these two measures greatly reduce the loss of wing area during secondary moult, allowing more secondaries to be replaced at once.

To test whether large, long-winged seabirds differ from other birds in terms of wing structure, I explored the importance of secondaries (area protruding beyond the upper greater coverts) relative to wing area in 102 bird species from 52 families, ranging in body mass from 9.5 to 8300 g. Of these, 27 were seabirds from six families (Supplemental Table 7.1). Wing area is crucial for flight and a key variable for studies of avian comparative ecology (Malo and Mata 2021), which is important in understanding mechanics and energetics of flight (Spedding and Pennycuick 2001). Wing area and body mass are primary measures and widely used in studies of animal flight morphology (Warham 1977; Vágási et al. 2016), which can be used as predictors of habitat quality (Jaksic and Carothers 1985).

Until recently, there have been few studies on the relationship between wing structure and evolutionary history (Baumgart et al. 2021). To explore this subject, the wing area of dead birds was recorded with and without their secondaries. Birds were obtained from a variety of sources: powerline collisions, incidental fisheries bycatch, roadkill, or just found dead. Wing area was measured by tracing the fully extended and flattened wing onto a sheet of paper. The secondaries were then plucked, and the wing overlaid on the same tracing and the new outline of the trailing edge of the wing recorded. The tracing was then cut out (total wing, and the area accounted for just by the secondaries) and weighed to the nearest 0.1 mg and compared to the mass of a reference square of the same paper of known area (typically around 20-50% of the area of the wing tracing; cf. Pennycuick 1989; Stiles 1995). The mass of each bird was also measured (to the nearest 1 g) for birds in good condition. However, most birds were in too poor condition to weigh, so masses were taken from Dunning (2007). Average body mass was used unless there was strong sexual dimorphism, in which case average male or female mass was used, depending on the sex of the bird sampled. A general liner model was used to explain the proportion of secondary wing area in relation to body mass, total wing area, secondary wing area and different bird groups within the R statistical environment (R Core Team 2019).

I found a positive relationship between secondary wing area and total wing area (Figure 7.3 and Supplemental Figure 7.1) and between proportion of secondary wing area and body mass (Figure 7.3, Supplemental Figure 7.1, Supplemental Table 7.2). These results differed across different bird groups (Figure 7.3 and Supplemental Figure 7.1) with a marked difference between seabirds and other groups of birds (Supplemental Figure 7.1). Among seabirds, only cormorants (Phalacrocoracidae) differed from other families in having relatively large proportions of their wing area dependent on their secondaries (Figure 7.3 and Supplemental Figure 7.1). They probably manage to do this because they are not very aerial as they forage close to land and mostly roost ashore between foraging bouts (Siegfried et al. 1975; White et al. 2007).

Species that replace numerous secondary feathers at once have a relatively small secondary area not covered by greater coverts (Supplemental Table 7.1), suggesting that long-winged birds and especially larger species that struggle to moult rapidly have responded by reducing the area not covered by the coverts. In the light of reduced wing area and often intense nature of moult, long-winged birds also moult all the greater secondary coverts, which presumably aid simultaneous replacement of large numbers of secondary feathers later in the moult cycle (Ryan et al. 2020). The greater secondary coverts are remarkably long in Procellariiformes (petrels and albatrosses) and once they have been replaced, they help to reduce wing gaps by the replacement of the secondaries (Ryan et al. 2020).

I surmise that the relatively small secondary area not covered by greater coverts in long-winged seabirds allows these species to replace large numbers of secondaries at once. At least in petrels and some gulls, this adaptation is facilitated by the near-simultaneous replacement of most greater secondary coverts at the start of primary moult, so the secondary coverts are already replaced once secondary moult starts.

Conclusions

In this thesis, I have presented novel findings in support of much-needed study related to how birds fit moult into their life-history activities. Specifically, I showed how large birds balance moult with other aspects of their annual cycles (despite some intense moult). I consider that this study contributes to a better understanding of moult strategies and feather quality, with important implications for conservation and management. My research challenges the findings of some previous studies, such as (i) intense moult resulting in reduced flight ability, (ii) incomplete moult and unusual breeding frequencies being driven by trade-offs between the time allocated to moult and breeding, (iii) juvenile flight feathers are of lesser quality than adults due to fast growth of feathers. I provided several lines of evidence that moult may be used as an index of condition and ultimately as an indicator of fitness. Further studies are needed to better understand the variation and evolution of different moult strategies and feather quality, and their implications on fitness.

Figure 7.1: An immature Kelp Gull *Larus dominicanus* in heavy wing moult. In addition to growing primaries 5-8, it is replacing almost all its secondaries, having already grown a fresh set of greater secondary coverts (photo Peter Ryan).

Figure 7.2: A Soft-plumaged Petrel *Pterodroma mollis* in wing moult, showing growing primaries and secondaries, with new secondary coverts (photo Peter Ryan).

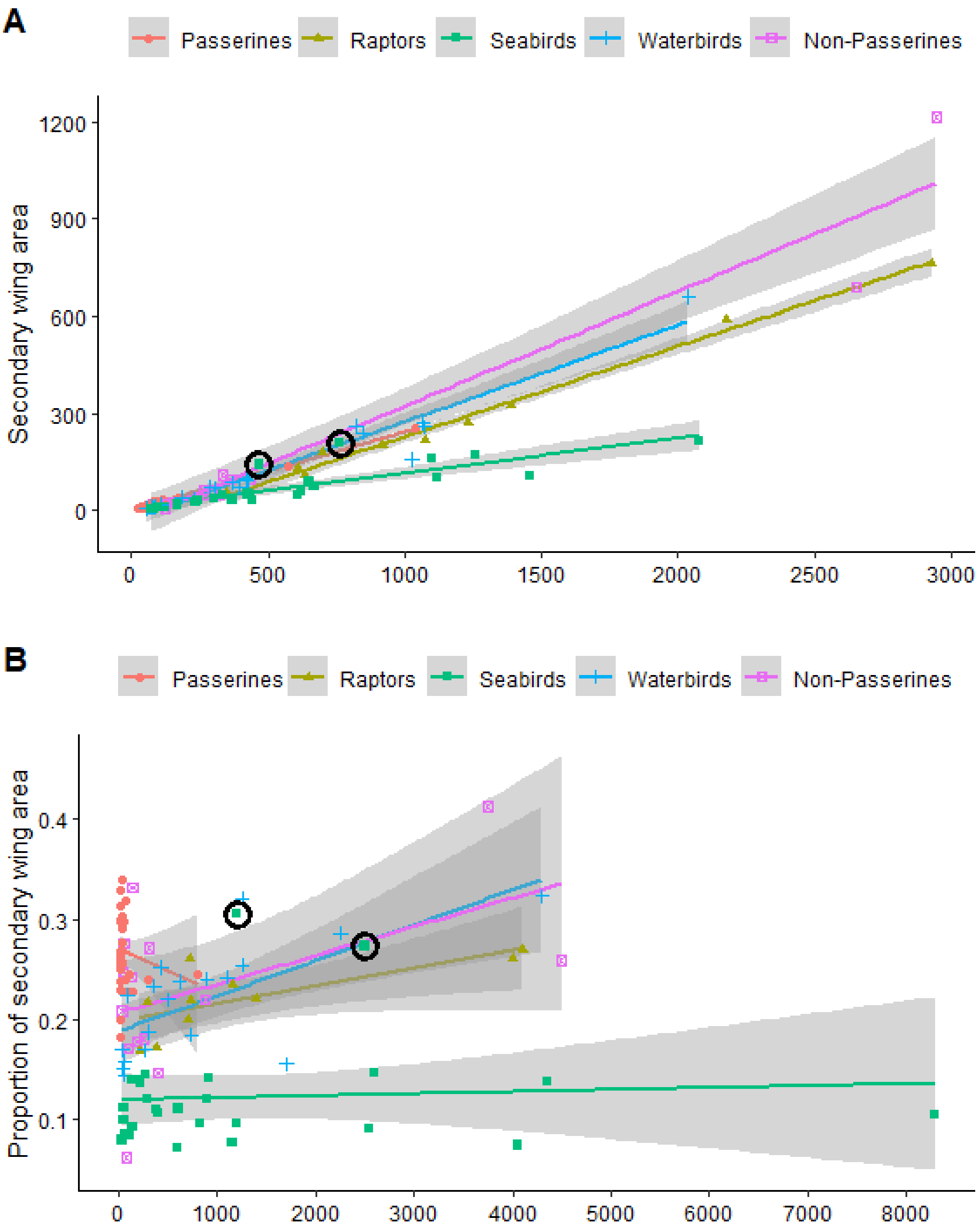
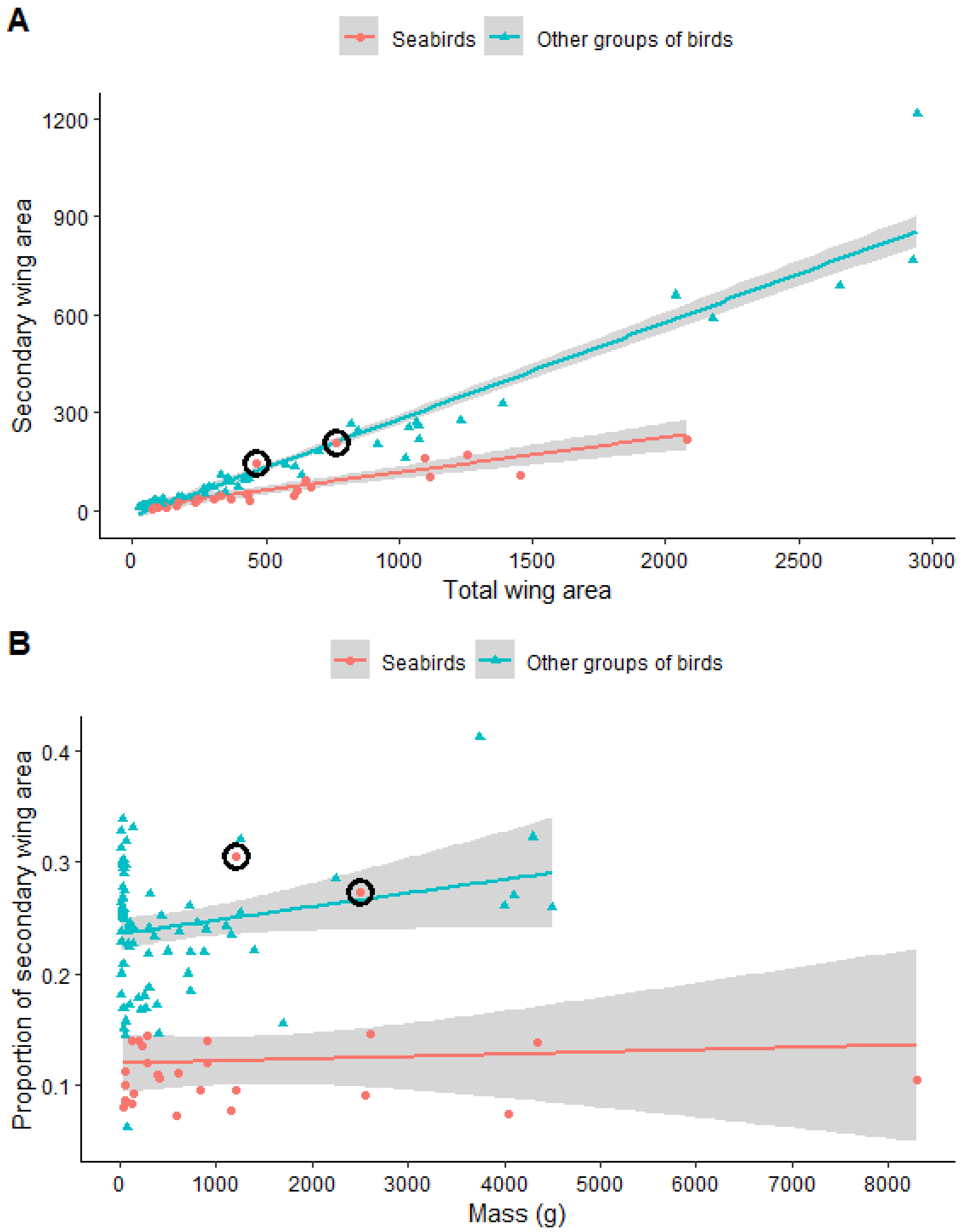


Figure 7.3: Relationship between (A) secondary wing area (protruding beyond the greater secondary coverts) and total wing area among passerines, raptors, seabirds, fresh-water birds and other non-passerines; (B) proportion of secondary wing area and mass across non-passerines, passerines, raptors, seabirds and waterbirds. The black circled points are for the two cormorant species (Cape and White-breasted Cormorants), which differ from other seabird species.

Supplemental material



Supplemental Figure 7.1: Relationship between (A) secondary wing area and total wing area among seabirds and other groups of birds; (B) proportion of secondary wing area and mass among seabirds and other groups of birds. The black circled points are for the two cormorant species (Cape and White-breasted Cormorants), which differ from other seabird species.

Supplemental Table 7.1: The Proportion of Secondary Wing Area (SWA) across different bird families/groups

Group/family	Species	Mass (g)	SWA
Raptors			
Accipitridae	Verreaux's Eagle *Aquila verreauxii*	4100	0.27
Accipitridae	Martial Eagle *Polemaetus bellicosus*	4000	0.26
Accipitridae	Jackal Buzzard *Buteo rufofuscus*	1155	0.23
Accipitridae	Steppe Buzzard *Buteo vulpinus*	730	0.22
Accipitridae	Black Sparrowhawk *Accipiter melanoleucus*	720	0.26
Strigidae	Spotted Eagle-owl *Bubo africanus*	700	0.20
Tytonidae	Barn Owl *Tyto alba*	385	0.17
Falconidae	Southern Caracara *Caracara plancus*	1400	0.22
Falconidae	Chimango Caracara *Milvago chimango*	295	0.22
Falconidae	Rock Kestrel *Falco rupicolus*	215	0.17
Seabirds			
Phalacrocoracidae	White-breasted Cormorant *Phalacrocorax carbo*	2500	0.27
Phalacrocoracidae	Cape Cormorant *Phalacrocorax capensis*	1200	0.31
Laridae	Kelp Gull *Larus dominicanus*	910	0.14
Laridae	Greater Crested Tern *Sterna bergii*	385	0.11
Laridae	Hartlaub's Gull *Chroicocephalus hartlaubii*	280	0.14
Laridae	Common Tern *Sterna hirundo*	125	0.14
Laridae	Damara Tern *Sternula balaenarum*	52	0.10
Laridae	Sooty Tern *Onychoprion fuscatus*	180	0.11
Sulidae	Cape Gannet *Morus capensis*	2600	0.15
Diomedeidae	Indian Yellow-nosed Albatross *Thalassarche carteri*	2550	0.09

Diomedeidae	Wandering Albatross *Diomedea exulans*	8300	0.10
Diomedeidae	Shy Albatross *Thalassarche cauta*	4050	0.07
Procellariidae	Southern Giant Petrel *Macronectes giganteus*	4350	0.14
Procellariidae	White-chinned Petrel *Procellaria aequinoctialis*	1200	0.10
Procellariidae	Spectacled Petrel *Procellaria conspicillata*	1150	0.08
Procellariidae	Great Shearwater *Ardenna gravis*	900	0.12
Procellariidae	Sooty Shearwater *Ardenna grisea*	825	0.10
Procellariidae	Cory’s Shearwater *Calonectris borealis*	600	0.11
Procellariidae	Great-winged Petrel *Pterodroma macroptera*	590	0.07
Procellariidae	Manx Shearwater *Puffinus puffinus*	400	0.11
Procellariidae	Soft-plumaged Petrel *Pterodroma mollis*	285	0.12
Procellariidae	Subantarctic Shearwater *Puffinus elegans*	225	0.14
Procellariidae	Broad-billed Prion *Pachyptila vittata*	190	0.14
Procellariidae	Fairy Prion *Pachyptila turtur*	140	0.09
Procellariidae	Common Diving Petrel *Pelecanoides urinatrix*	115	0.08
Oceanitidae	White-bellied Storm Petrel *Fregetta grallaria*	54	0.09
Oceanitidae	White-faced Storm Petrel *Pelagodroma marina*	50	0.11
Oceanitidae	Grey-backed Storm Petrel *Garrodia nereis*	35	0.08
Waterbirds			
Anatidae	Spur-winged Goose *Plectropterus gambensis*	4300	0.32
Anatidae	Egyptian Goose *Alopochen aegyptiaca*	2250	0.29
Anatidae	South African Shelduck *Tadorna cana*	1250	0.32
Anatidae	Yellow-billed Duck *Anas undulata*	890	0.24
Anatidae	Cape Shoveler *Spatula smithii*	615	0.24
Anatidae	Cape Teal *Anas capensis*	425	0.25

Phoenicopteridae	Lesser Flamingo *Phoeniconaias minor*	1700	0.16
Threskiornithidae	Sacred Ibis *Threskiornis aethiopicus*	1250	0.25
Ardeidae	Black-headed Heron *Ardea melanocephala*	1100	0.24
Podicipedidae	Black-necked Grebe *Podiceps nigricollis*	300	0.19
Rallidae	Red-knobbed Coot *Fulica cristata*	730	0.18
Rallidae	Common Moorhen *Gallinula chloropus*	265	0.17
Rallidae	Red-chested Flufftail *Sarothrura rufa*	38	0.15
Burhinidae	Spotted Thick-knee *Burhinus capensis*	495	0.22
Burhinidae	Water Thick-knee *Burhinus vermiculatus*	355	0.23
Glareolidae	Double-banded Courser *Rhinoptilus africanus*	90	0.22
Scolopacidae	Curlew Sandpiper *Calidris ferruginea*	60	0.14
Scolopacidae	Sanderling *Calidris alba*	58	0.16
Charadriidae	Three-banded Plover *Charadrius tricollaris*	34	0.17
Other non-passerines			
Phasianidae	Cape Spurfowl *Pternistis capensis*	875	0.22
Otididae	Ludwig’s Bustard *Neotis ludwigii*	4500	0.26
Bucorvidae	Southern Ground Hornbill *Bucorvus leadbeateri*	3750	0.41
Musophaginae	Knysna Turaco *Tauraco corythaix*	310	0.27
Bucerotidae	Red-billed Hornbill *Tockus rufirostris*	140	0.33
Coraciidae	European Roller *Coracias garrulus*	128	0.24
Coliidae	Speckled Mousebird *Colius striatus*	50	0.28
Coliidae	White-backed Mousebird *Colius colius*	44	0.25
Cuculidae	Diderik Cuckoo *Chrysococcyx caprius*	34	0.21
Columbidae	Rock Dove *Columba livia*	400	0.15
Columbidae	Red-eyed Dove *Streptopelia semitorquata*	250	0.18

Columbidae	Laughing Dove *Spilopelia senegalensis*	100	0.17
Pteroclididae	Namaqua Sandgrouse *Pterocles namaqua*	190	0.18
Apodidae	Alpine Swift *Tachymarptis melba*	75	0.06
Passerines			
Corvidae	White-necked Raven *Corvus albicollis*	800	0.25
Corvidae	House Crow *Corvus splendens*	300	0.24
Hirundinidae	Rock Martin *Ptyonoprogne fuligula*	15	0.20
Hirundinidae	Brown-throated Martin *Riparia paludicola*	13	0.24
Hirundinidae	House Martin *Delichon urbicum*	13	0.18
Sturnidae	Red-winged Starling *Onychognathus morio*	135	0.23
Sturnidae	Common Starling *Sturnus vulgaris*	78	0.23
Turdidae	Tristan Thrush *Turdus eremita*	100	0.25
Malaconotidae	Bokmakierie *Telophorus zeylonus*	63	0.32
Thraupidae	Gough Bunting *Rowettia goughensis*	53	0.30
Muscicapidae	Ant-eating Chat *Myrmecocichla formicivora*	42	0.26
Muscicapidae	Marico Flycatcher *Melaenornis mariquensis*	24	0.27
Muscicapidae	Karoo Robin *Cercotrichas coryphaeus*	19	0.30
Pycnonotidae	Cape Bulbul *Pycnonotus capensis*	38	0.29
Pycnonotidae	Sombre Greenbul *Andropadus importunus*	31	0.34
Laniidae	Southern Fiscal *Lanius collaris*	38	0.30
Promeropidae	Cape Sugarbird *Promerops cafer*	35	0.29
Ploceidae	Southern Masked Weaver *Ploceus velatus*	33	0.28
Ploceidae	Scaly-feathered Finch *Sporopipes squamifrons*	11	0.26
Muscicapidae	Cape Robin-chat *Cossypha caffra*	30	0.30
Macrosphenidae	Cape Grassbird *Sphenoeacus afer*	30	0.27

Passeridae	Cape Sparrow *Passer melanurus*	29	0.29
Alaudidae	Karoo Lark *Calendulauda albescens*	28	0.30
Alaudidae	Red-capped Lark *Calandrella cinerea*	23	0.25
Alaudidae	Grey-backed Sparrowlark *Eremopterix verticalis*	17	0.25
Platysteiridae	White-tailed Shrike *Lanioturdus torquatus*	28	0.26
Motacillidae	African Pipit *Anthus cinnamomeus*	25	0.26
Fringillidae	Cape Canary *Serinus canicollis*	17	0.30
Fringillidae	Yellow Canary *Crithagra flaviventris*	17	0.23
Nectariniidae	Malachite Sunbird *Nectarinia famosa*	17	0.26
Zosteropidae	Cape White-eye *Zosterops virens*	11	0.33
Sylviidae	Dartford Warbler *Sylvia undata*	9.5	0.31

Supplemental Table 7.2: Mean differences between the proportion of secondary wing area between non-passerines, passerines, raptors, seabirds and waterbirds (and effect on mass, total wing area and secondary wing area).

Parameters	Estimate ± SE	t-value	p-value	F $_{(7,94)}$	R^2
			<0.001	**40.37**	**0.73**
Intercept	0.21 ± 0.01	19.66	<0.001		
Mass	0.00 ± 0.00	2.96	0.00		
Total wing area	-0.00 ± 0.00	-4.60	<0.001		
Secondary wing area	0.00 ± 0.00	6.90	<0.001		
Passerines	0.06 ± 0.01	5.22	<0.001		
Raptors	0.02 ± 0.02	1.01	0.31		
Seabirds	-0.07 ± 0.01	-4.83	<0.001		
Waterbirds	0.00 ± 0.01	0.19	0.85		

References

Abbott CL, Double MC, Gales R, Baker GB, Lashko A, Robertson CJR & Ryan PG (2006). Molecular provenance analysis for Shy and White-capped Albatrosses killed by fisheries interactions in Australia, New Zealand and South Africa. Conservation Genetics 7:531-542

Achache Y, Sapir N & Elimelech Y (2018). Hovering hummingbird wing aerodynamics during the annual cycle. ll. Implications of wing feather moult. *Royal Society Open Science* 5:171766

Adekola OE, Allan DG, Bernitz Z, Dlungwana W & Ryan PG (2021a). Extent and symmetry of tail moult in Amur Falcons. *Journal of Ornithology* 162:655–667

Adekola OE, Crawford RJM, Dyer BM, Makhado AB, Upfold L & Ryan PG (2021b). Timing, duration and symmetry of moult in Cape Gannets. *Ostrich* 92:295–306

Ainley DG, Lewis TJ & Morrell S (1976). Molt in Leach's and Ashy Storm-Petrels. *Wilson Bulletin* 88:76–95

Ainley DG & Boekelheide RJ (eds) (1991). *Seabirds of the Farallon Islands. Ecology, dynamics, and structure of an upwelling-system community*. Stanford University Press, Palo Alto

Alexander J & Symes CT (2016). Temporal and spatial dietary variation of Amur Falcons *Falco amurensis* in their South African nonbreeding range. *Journal of Raptor Research* 50:276-288

Allan D (2019). Annihilation. *African Birdlife* 7:22-25

Allard KA, Mallory ML, Wilcox KL & Mark R (2008). Forbes Prebasic molt initiation and progress in northern fulmars of the High Arctic: do molt and breeding overlap? *Polar Biology* 31:181–188

Alonso H, Matias R, Granadeiro JP & Catry P (2009). Moult strategies of Cory's Shearwaters *Calonectris diomedea borealis*: the influence of colony location, sex and individual breeding status. *Journal of Ornithology* 150:329–337

Arroyo BE & King JR (1996). Age and sex differences in molt of the Montagu's Harrier *Circus pygargus*. *Journal of Raptor Research* 30:161-184

Arroyo B, Mínguez E, Palomares L & Pinilla J (2004). The timing and pattern of moult of flight feathers of European storm-petrel *Hydrobates pelagicus* in Atlantic and Mediterranean breeding areas. *Ardeola* 51:365–373

Ausems ANMA, Wojczulanis-Jakubas K & Jakubas D (2019). Differences in tail feather growth rate in storm-petrels breeding in the Northern and Southern Hemisphere: a ptilochronological approach. *PeerJ* 7:e7807

Austin JE & Fredrickson LH (1987). Body and organ mass and body composition of postbreeding female Lesser Scaup. *Auk* 104:694–699

Bachmann T, Emmerlich J, Baumgartner W, Schneider JM & Wagner H (2012). Flexural stiffness of feather shafts: geometry rules over material properties. *Journal of Experimental Biology* 215:405–415

Barbraud C & Chastel O (1998). Southern fulmars molt their primary feathers while incubating. *Condor* 100:563–566

Barrientos R, Barbosa A, Valera F & Moreno E (2007). Temperature but not rainfall influences timing of breeding in a desert bird, the trumpeter finch *Bucanetes githagineus*. *Journal of Ornithology* 148:411–416

Barshep Y, Mínton C, Underhill LG & Remisiewicz M (2011). The primary moult of Curlew Sandpipers *Calidris ferruginea* in north-western Australia shifts according to breeding success. *Ardea* 99:43–51

Barshep Y, Mínton C, Underhill LG, Erni B & Tomkovich P (2013). Flexibility and constraints in the molt schedule of long-distance migratory shorebirds: causes and consequences. *Ecology and Evoltion* 3:1967–1976

Barta Z, Houston AI, McNamara JM & Welham RK (2006). Annual routines of non-migratory birds: Optimal moult strategies. *Oikos* 112:580-593

Baumgart SL, Sereno PC & Westneat MW (2021). Wing shape in waterbirds: morphometric patterns associated with behavior, habitat, migration and phylogenetic convergence. *Integrative Organismal Biology* 3:1-20

Beltran RS, Burns JM & Breed GA (2018). Convergence of biannual moulting strategies across birds and mammals. *Proceedings of the Royal Society of London Series B* 285:20180318

Bernitz Z (2006). Mass die-off of migrating kestrels: Ventersdorp. *Gabar* 17:2-4

Berruti A, Underhill LG, Shelton PA, Moloney C & Crawford RJM (1993). Seasonal and interannual Variation in the diet of two colonies of the Cape Gannet *Morus capensis* between 1977-78 and 1989. *Waterbird* 16:158–175

Berthold P (1975). *Migration: control and metabolic physiology*. In: Farner DS & King JR (eds). Avian Biology, Volume 5:77–128. Academic Press, New York

BirdLife International (2021). *Morus capensis*. In IUCN Red List of Threatened Species (www.redlist.org)

BirdLife International (2022). Species factsheets: *Procellaria aequinoctialis* and *Thalassarche cauta steadi*. Downloaded from http://www.birdlife.org on 21/03/2022

Bodde SG, Meyers MA & McKittrick J (2011). Correlation of the mechanical and structural properties of cortical rachis keratin of rectrices of the Toco Toucan *Ramphastos toco*. *Journal of Mechanical, Behavioral and Biomedical Materials* 4:723–732

Bojarinova JG, Lehikoinen E & Eeva T (1999). Dependence of postjuvenile moult on hatching date, condition and sex in the Great Tit. *Journal of Avian Biology* 30:437-446

Bonser RHC (1996). The mechanical properties of feather keratin. *Journal of Zoology* 239:477-484

Booth DT, Clayton DH & Block BA (1993). Experimental demonstration of the energetic cost of parasitism in free-ranging hosts. *Proceedings of the Royal Society of London Series B* 253:125-129

Borras A, Cabrera T, Cabrera J & Senar JC (2004). Interlocality variation in speed of moult in the Citril Finch *Serinus citrinella*. *Ibis* 146:14–17

Bridge ES (2003). Effects of simulated primary moult on pigeon flight. *Ornis Fennica* 80:121–129

Bridge ES (2004). The effects of intense wing molt on diving in alcids and potential influences on the evolution of molt patterns. *Journal of Experimental Biology* 207:3003–3014

Bridge ES & Nisbet ICT (2004). Wing molt and assortative mating in Common Terns: A test of the molt-signaling hypothesis. *Condor* 106:336–343

Bridge ES (2006). Influences of morphology and behavior on wing-molt strategies in seabirds. *Marine Ornithology* 34:7–19

Bridge ES (2011). Mind the gaps: what's missing in our understanding of feather molt. *Condor* 113:1–4

Broggi J, Gamero A, Hohtola E, Orell M & Nilsson JÅ (2011). Interpopulation variation in contour feather structure is environmentally determined in great tits. *PLoS ONE*. 6:e24942

Brommer JE, Pihlajamäki O, Kolunen H & Pietiäinen H (2003). Life-history consequences of partial-moult asymmetry. *Journal of Animal Ecology* 72:1057-1063

Brooke RK (1981). Modes of moult of flight feathers in albatrosses. *Cormorant* 9: 13–18

Brown RGB (1988). The wing-moult of fulmars and shearwaters (Procellariidae) in Canadian Atlantic waters. *Canadian Field Naturalist* 102:203–208

Bugoni L, Sander M & Costa ES (2007). Effects of the first southern Atlantic hurricane on Atlantic petrels *Pterodroma incerta*. *Wilson Journal of Ornithology* 119:725–729

Bugoni L, Neves TS, Peppes FV & Furness RW (2008). An effective method for trapping scavenging seabirds at sea. *Journal of Field Ornithology* 79:308–313

Bugoni L, Naves LC & Furness RW (2014). Moult of three Tristan da Cunha seabird species sampled at sea. *Antarctic Science* 27:240-251

Burnham KP & Anderson DR (2002). Model selection and multimodel inference: A practical information-theoretic approach. *Journal of Wildlife Management* 67:655

Butler LK, Rohwer S & Speidel MG (2008). Quantifying structural variation in contour feathers to address functional variation and life history trade-offs. *Journal of Avian Biology* 39:629–639

Camphuysen CJ & Van Der Meer J (2001). Pelagic distribution, moult and (sub-) species status of Cory's shearwaters *Calonectris diomedea borealis* wintering off southern Africa. *Marine Ornithology* 29:89–96

Carbonell R & Tellerfa JL (1999). Feather traits and ptilochronology as indicators of stress in Iberian blackcaps *Sylvia atricapilla*. *Bird Study* 46:234-248

Carr JM & Lima SL (2012). Heat-conserving postures hinder escape: a thermoregulatin-predation trade-off in wintering birds. *Behavioral Ecology* 23:434-441

Carvalho PC, Ronconi RA, Bugoni L & Davoren GK (2022). Moult chronology and strategies of sympatric Great (*Ardenna gravis*) and Sooty (*A. grisea*) Shearwaters based on stable isotope analysis. Ibis 164:998–1012

Chastel O (1995). Influence of reproductive success on breeding frequency in four southern petrels. *Ibis* 137:360–363

Chen C, Foley J, Tang P, Li A, Jiang TX, Wu P, Widelitz RB & Chuong CM (2015). Development, regeneration and evolution of feathers. *Annual Review of Animal Biosciences* 3:169-195

Cherel Y, Phillips RA, Hobson KA & McGill R (2006). Stable isotope evidence of diverse species-specific and individual wintering strategies in seabirds. *Biology Letters* 2:301–303

Cherel Y, Quillfeldt P, Delord K & Weimerskirch H (2016). Combination of at-sea activity, geolocation and feather stable isotopes documents where and when seabirds molt. *Frontiers in Ecology and Evolution* 4:3

Cincotta A, Nicolaï M, Campos HBN, McNamara M, D'Alba L, Shawkey MD, Kischlat E, Yans J, Carleer R, Escuillié F & Godefroit P (2022). Pterosaur melanosomes support signalling functions for early feathers. *Nature* 604: 684–688

Clark CJ, Elias DO & Prum RO (2011). Aeroelastic flutter produces hummingbird feather songs. *Science* 333:1430-1433

Clark WS (2004). Wave molt of the primaries of Accipitrid raptors, and its use in ageing. In, Chancellor RD & Meyburg BU. (eds). *Raptors worldwide: Proceedings of the V World Conference on Birds of Prey*, pp 795-804. World Working Group on Birds of Prey, Berlin

Clay T, Manica A, Ryan PG, Silk J, Croxall JP, Ireland L, Phillips RA (2016). Proximate drivers of spatial segregation in non-breeding albatrosses. *Scientific Reports* 6:29932

Clayton DH (1990). Mate choice in experimentally parasitized rock doves: lousy males lose. *American Zoology* 30:251–262

Cobley ND & Prince PA (1998). Factors affecting primary molt in the Gray-headed Albatross. *Condor* 100:8-17

Cohen LA, Pichegru L, Grémillet D, Coetzee J, Upfold L & Ryan PG (2014). Changes in prey availability impact the foraging behaviour and fitness of Cape gannets over a decade. *Marine Ecology Progress Series* 505:281–293

Conroy JWH (1972). Ecological aspects of the biology of the giant petrel *Macronectes giganteus* (Gmelin) in the maritime Antarctic. *British Antarctic Survey Scientific Report* 75:1–74

Cooper J, Underhill LG & Avery G (1991). Primary molt and transequatorial migration of the Sooty Shearwater. *Condor* 93:724–730

Corso A (2001). Notes on the moult and plumages of Lesser Kestrel. *British Birds* 94:409-418

Cramp S & Simmons KEL (eds) (1977). *Handbook of the Birds of the Western Palearctic.* Oxford University Press, Oxford

Cramp S & Simmons KEL (eds) (1980). *The Birds of the Western Palearctic.* Vol. II. Oxford University Press, Oxford

Crawford RJM, Shelton PA, Cooper J & Brooke RK (1983). Distribution, population size and conservation of the Cape Gannet *Morus capensis. South African Journal of Marine Science* 1:153–174

Crawford RJM, Dundee BL, Dyer BM, Klages NTW, Meÿer MA & Upfold L (2007). Trends in numbers of Cape Gannets *Morus capensis*, 1956/1957-2005/2006, with a consideration of the influence of food and other factors. *ICES Journal of Marine Science* 64:169–177

Crawford RJM, Sydeman WJ, Thompson SA, Sherley RB, Makhado AB (2019). Food habits of an endangered seabird indicate recent poor availability of abundant forage resources. *ICES Journal of Marine Science* 76:1344–1352

Dale S (2001). Female-biased dispersal, low female recruitment, unpaired males, and the extinction of small and isolated bird populations. *Oikos* 92:344-356

Dawson A, Hinsley SA, Ferns PN, Bonser RHC & Eccleston L (2000). Rate of moult affects feather quality: A mechanism linking current reproductive effort to future survival. *Proceedings of the Royal Society Series B* 267:2093-2098

Dawson A (2006). Control of molt in birds: association with prolactin and gonadal regression in starlings. *General and Comparative Endocrinology* 147:314-322

Dawson A (2015). *Avian molting.* In: Scanes, Colin G (ed) Sturkie's Avian Physiology, pp. 907-917. Academic Press, Amsterdam

de La Hera I, Perez-Tris J & Luis Telleria J (2009). Repeatable length and mass but not growth rate of individual feathers between moults in a passerine bird. *Acta Ornithology* 44:95–99

de La Hera I, Pérez-Tris J & Tellería JL (2010). Migratory behavior and differential resource allocation between wing and tail feathers in a passerine bird. *Auk* 127:647-652

de La Hera I, DeSante DF & Milá B (2012). Feather growth rate and mass in nearctic passerines with variable migratory behavior and molt pattern. *Auk* 129:222–230

de la Hera I, Hernández-Téllez I, Pérez-Rigueiro J, Pérez-Tris J, Rojo FJ & Tellería JL (2020). Mechanical and structural adaptations to migration in the flight feathers of a Palaearctic passerine. *Journal of Evolutionary Biology* 33:979-989

del Hoyo J & Collar NJ (2016). *HBW and BirdLife International Illustrated Checklist of the Birds of the World.* Volume 2. Lynx Edicions, Barcelona

Delhey K, Guallar S, Rueda-Hernandez R, Valcu M, Wang D & Kempenaers B (2020). Partial or complete? The evolution of post-juvenile moult strategies in passerine birds. *Journal of Animal Ecology* 89:2896-2908

Delord K, Cotté C, Péron C, Marteau C, Pruvost P, Gasco N, Duhamel G, Cherel Y & Weimerskirch H (2010). At-sea distribution and diet of an endangered top predator: relationship between white-chinned petrels and commercial longline fisheries. *Endangered Species Research* 13:1–16

Dement'ev GP & Gladkov NA (eds) (1951). (Birds of the Soviet Union, vol. 1). Gosudarstvennoe Izdatel'stvo., "Sovetskaya Nauka," Moscow [in Russian]

DesRochers DW, Reed JM, Awerman J, Kluge JA, Wilkinson J, van Griethuijsen LI, Aman J & Romero LM (2009). Exogenous and endogenous corticosterone alter feather quality. *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology* 152:46-52

Dial TR, Heers AM & Tobalske BW (2012). Ontogeny of aerodynamics in mallards: Comparative performance and developmental implications. *Journal of Experimental Biology* 215:3693-3702

Donald PF (2007). Adult sex ratios in wild bird populations. *Ibis* 149:671-692

Donazar JA & Feijoo JE (2002). Social structure of Andean Condor roosts: Influence of sex, age, and season. *Condor* 104:832–837

Dorward DF (1962). Comparative biology of the White Booby and the Brown Booby *Sula* spp. at Ascension. *Ibis* 103:174–220

Dunning Jr. JB (2007). *CRC Handbook of Avian Body Masses.* CRC Press, Boca Raton

Echeverry-galvis MA & Hau M (2013). Flight Performance and Feather Quality: Paying the Price of Overlapping Moult and Breeding in a Tropical Highland Bird. *PLoS ONE.* 8:e61106

Edelstam C (1984). Patterns of moult in large birds of prey. *Annales Zoologici Fennici* 21:271–276

Edwards AE & Rohwer S (2005). Large-scale patterns of molt activation in the flight feathers of two albatross species. *Condor* 107:835–848

Ellis DH, Rohwer VG & Rohwer S (2016). Experimental evidence that a large raptor can detect and replace heavily damaged flight feathers long before their scheduled moult dates. *Ibis* 159:217-220

Ennos A, Hickson J & Roberts A (1995). Functional morphology of the vanes of the flight feathers of the pigeon *Columba livia*. *Journal of Experimental Biology* 198:1219-1228

Erni B, Bonnevie BT, Oschadleus HD, Altwegg R & Underhill LG (2013). Moult: An R package to analyze moult in birds. *Journal of Statistical Software* 52:1–23

Espie RH, James PC, Warkentin IG & Oliphant LW (1996). Ecological correlates of molt in Merlins *Falco columbarius*. *Auk* 113:363-369

Fayet AL, Freeman R, Shoji A, Kirk HL, Padget O, Perrins CM & Guilford T (2016). Carry-over effects on the annual cycle of a migratory seabird: an experimental study. *Journal of Animal Ecology* 85:1516–1527

Ferguson-Lees J & Christie DA (2001). *Raptors of the World.* Houghton Mifflin Company, New York

Filardi CE & Rohwer S (2001). Life history implications of complete and incomplete primary molts in pelagic cormorants. *Condor* 103:555-569

Flinks H, Helm B & Rothery P (2008). Plasticity of moult and breeding schedules in migratory European Stonechats *Saxicola rubicola. Ibis* 150:687-697

Flood RL & Fisher E (2016). *Multimedia Identification Guide to North Atlantic Seabirds: Albatrosses and Fulmarine Petrels*. Scilly Pelagics, Scilly

Flood RL & Ryan PG (2016). Ageing criteria for the Shy Albatrosses. *African Birdlife* 4:49–53

Flood RL & Ryan PG (2018). Age-related timing of primary moult in Shy Albatross *Thalassarche [c.] cauta/steadi* longline casualties from South Africa. *Marine Ornithology* 46:197-202

Forsman D (2016). *Flight identification of Raptors of Europe, North Africa and the Middle East*. Bloomsbury, Christopher Helm, Barcelona

Freed LA & Cann RL (2012). Changes in timing, duration and symmetry of molt of Hawaiian forest birds. *PLoS One* 7:e29834

Fretwell SD & Calver JS (1969). On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19:37-44

Furness RW (1988). Influences of status and recent breeding experience on the moult strategy of the Yellow-nosed Albatross *Diomedea chlororhynchos*. *Journal of Zoology* 215:719–727

Furness RW, Thompson DR & Becker PH (1995). Spatial and temporal variation in mercury contamination of seabirds in the North Sea. *Helgoländer Meeresuntersuchungen* 49:605–615

Galvan I (2011). Feather microstructure predicts size and colour intensity of a melanin-based plumage signal. *Journal of Avian Biology* 42:473-479

Gamero A, Senar JC, Hohtola E, Nilsson JÅ & Broggi J (2015). Population differences in the structure and coloration of great tit contour feathers. *Biological Journal of the Linnean Society*. 114:82-91

Garthe S, Ludynia K, Hüppop O, Kubetzki U, Meraz JF & Furness RW (2012). Energy budgets reveal equal benefits of varied migration strategies in Northern Gannets. *Marine Biology* 159:1907–1915

Ginn HB & Melville DS (1983). *Moult in Birds*. BTO Guide 19. British Trust for Ornithology, Tring

Ginn HB & Melville DS (2007). *Moult in Birds*. BTO Guide 19. Page Brothers, Norwich

Gosler AG (1991). On the use of greater covert moult and pectoral muscle as measures of condition in passerines with data for the Great Tit *Parus major*. *Bird Study* 38:1-9

Greenwood JG (1983). Post-nuptial primary moult in Dunlin *Calidris alpina*. *Ibis* 125:223–228

Grémillet D, Pichegru L, Kuntz G, Woakes AG, Wilkinson S, Crawford RJM & Ryan PG (2008). A junk-food hypothesis for gannets feeding on fishery waste. *Proceedings of the Royal Society London Series B* 275:1149–1156

Grémillet D, Collet J, Weimerskirch H, Courbin N, Ryan PG & Pichegru L (2019). Radar detectors carried by Cape Gannets reveal surprisingly few fishing vessel encounters. *PLoS ONE* 14:e0210328

Griggio M, Devigili A, Hoi H & Pilastro A (2009). Female ornamentation and directional male mate prefernce in the Rock Sparrow. *Behavioral Ecology* 20:1072-1078

Grissot A, Graham IM, Quinn L, Brathen VS & Thompson PM (2020). Breeding status influences timing but not duration of moult in the Northern Fulmar *Fulmarus glacialis*. *Ibis* 162:446−459

Gutowsky SE, Gutowsky LFG, Jonsen ID, Leonard ML, Naughton MB, Romano MD & Shaffer SA (2014). Daily activity budgets reveal a quasi-flightless stage during non-breeding in Hawaiian albatrosses. *Movement Ecology* 2:23

Gwinner E (1996). Circadian and circannual programmes in avian migration. *Journal of Experimental Biology* 199:39-48

Hagelin JC (2007). The citrus-like scent of crested auklets: Reviewing the evidence for an avian olfactory ornament. *Journal of Ornithology* 148:195

Hailman JP, Brown L & Amadon D (1972). *Eagles, Hawks and Falcons of the World.* Bird-Banding

Harrison XA, Blount JD, Inger R, Norris DR & Bearhop S (2011). Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology* 80:4–18

Harrison P, Perrow M & Larsson H (2021). *Seabirds: The New Identification Guide*. Lynx Edicions, Barcelona

Haukioja E (1971). Flightlessness in some moulting passerines in nothern Europe. *Ornis Fennica* 48:101-116

Hedenström A & Sunada S (1999). On the aerodynamics of moult gaps in birds. *Journal of Experimental Biol*ogy 202:67-76

Hedlund J (2019). Ecosystem in the sky - species interaction during migration over the Indian Ocean. *2019 International Congress of Odonatology,* Austin

Helm B & Gwinner E (2006). Migratory restlessness in an equatorial nonmigratory bird. *PLoS Biology* 4:e110Hemborg C (1999). Sexual differences in moult-breeding overlap and female reproductive costs in pied flycatchers *Ficedula hypoleuca. Journal of Animal Ecology* 68:429-439

Henny CJ, Olson RA & Fleming TL (1985). Breeding chronology, molt, and measurments of Accipiter Hawks in northeastern Oregon. *Journal of Field Ornithology* 56:97-212

Hernández-Téllez I, Aguirre JI, de La Hera I, Onrubia A & Tellería JL (2021). Feather traits in four southern populations of the Eurasian blackcap *Sylvia atricapilla*: do altitudinal movements explain the differences? *Journal of Avian Biology* 52:e02832

Hockey PAR, Dean WJR, Ryan PG (eds). (2005). *Roberts Birds of southern Africa* (7th edn). Trustees of the John Voelcker Bird Book Fund, Cape Town

Hope SF, Stabile FA & Butler LK. (2016). Urban living alters moult dynamics in a passerine. *Journal of Avian Biology* 47:304-311

Howell SNG & Pyle P (2015). Use of "definitive" and other terms in molt nomenclature: A response to Wolfe et al. (2014). *Auk* 132:365-369

Hunter S (1984). Moult of the giant petrels *Macronectes halli* and *M. giganteus* at South Georgia. *Ibis* 126:119–132

Izhaki I & Maitav A (2008). Blackcaps *Sylvia atricapilla* stopping over at the desert edge; inter- and intra-sexual differences in spring and autumn migration *Ibis*. 140:234-243

Jaksic FM & Carothers JH (1985). Ecological, morphological and bioenergetic correlates of hunting mode in hawks and owls. *Ornis Scandinavica* 16:165-172

Jenkins AR (1995). Morphometrics and flight performance of southern African Peregrine and Lanner Falcons. *Journal of Avian Biology* 26:49-58

Jenni L (1993). Structure of a Brambling *Fringilla montifringilla* roost according to sex, age and body-mass. *Ibis* 135:85–90

Jenni L & Winkler R (1996). *Moult and ageing of European Passerines.* Oxford University Press, Oxford

Jenni L, Ganz K, Milanesi P & Winkler R (2020). Determinants and constraints of feather growth. PLoS ONE 15:e0231925

Jones CW, Phillips RA, Grecian WJ & Ryan PG (2020). Ecological segregation of two superabundant, morphologically similar, sister seabird taxa breeding in sympatry. *Marine Biology* 167:45

Junda J, Crary AL & Pyle P (2012). An age-specific, bivariate pattern to replacement of primaries during the prebasic molt in Rufous Fantail *Rhipdura rufifrons. Journal of Ornithology* 124:680-685

Karell PK, Karstinen AT, Kolunen H, Siitari H & Brommer JE (2011). Blood parasites mediate morph-specific maintenance costs in a colour polymorphic wild bird. *Journal of Evolutionary Biology* 24:1783-1792

Keijl GO (2011). Sooty shearwaters *Puffinus griseus* in the north atlantic - moult studies using digital cameras. *Marine Ornithology* 39:141–142

Kemp AC (1995). Aspects of the breeding biology and behaviour of the Secretary Bird *Sagittarius serpentarius* near Pretoria, South Africa. *Ostrich* 66:61-68

Kiat Y & Sapir N (2018). Life-history trade-offs result in evolutionary optimization of feather quality. *Biological Journal of the Linnean Society* 125:613-624

Kiat Y, Vortman Y & Sapir N (2019). Feather moult and bird appearance are correlated with global warming over the last 200 years. *Nature Communications* 10:2540

King JR (1981). Energetics of avian molt. *Proceedings of the XVII International Ornithological Congress* 312-317

Kinsky FC (1968). An unusual seabird mortality in the southern North Island (New Zealand). *Notornis* 15:143–155

Kjellen N (1992). Differential timing of autumn migration between sex and age groups in raptors at Falsterbo, Sweden. *Ornis Scandinavica* 23:420–434

Korpimäki E & Hakkarainen H (2012). *The Boreal Owl. Ecology, behaviour and conservation of a forest-dwelling predator*. Cambridge University Press, Cambridge

Labocha MK & Hayes JP (2012). Morphometric indices of body condition in birds: A review. *Journal of Ornithology* 153:1-22

Langston NE & Rohwer S (1995). Unusual patterns of incomplete primary molt in Laysan and Black-footed Albatrosses. *Condor* 97:1–19

Langston NE & Rohwer S (1996). Molt-breeding tradeoffs in albatrosses: Life history implications for big birds. *Oikos* 76:498–510

Leamy LJ & Klingenberg CP (2005). The genetics and evolution of fluctuating asymmetry. *Annual Review of Ecology, Evolution, and Systematics* 36:1-21

Lee E, Aoyama M & Sugita S (2009). Microstructure of the feather in Japanese Jungle Crows *Corvus macrorhynchos* with distinguishing gender differences. *Anatomical Science International* 84:141-147

Lees J, Garner T, Cooper G & Nudds R (2017). Rachis morphology cannot accurately predict the mechanical performance of primary feathers in extant (and therefore fossil) feathered flyers. *Royal Society Open Science* 4:160927

Lehikoinen A, Santaharju J & Moller AP (2017). Sex-specific timing of autumn migration in birds: the role of sexual size dimorphism, migration distance and differences in breeding investment. *Ornis Fennica* 94:53-65

Leisler B & Winkler H (2003). *Morphological consequences of migration in passerines.* In: Berthold P, Gwinner E & Sonnenschein E (eds) Avian Migration. Springer, Berlin, Heidelberg

Lenth R. (2020). emmeans: estimated marginal means, aka least-squares means. *R Package Version 1.4.5*

Leu M & Thompson CW (2002). The potential importance of migratory stopover sites as flight feather molt staging areas: a review for neotropical migrants. *Biological Conservation* 106:46-56

López G, Figuerola J, Varo N & Soriguer R (2005). White Wagtails *Motacilla alba* showing extensive post-juvenile moult are more stressed. *Ardea* 93:237-244

Louette M (2007). Moult patterns in the Long-tailed Hawk *Urotriorchis macrourus*. *Ostrich* 78:577-582

MacLeod R, Barnett P, Clark JA & Cresswell W (2005). Body mass change strategies in blackbirds *Turdus merula*: the starvation-predation risk trade-off. *Journal of Animal Ecology* 74:292-302

Magnusdottir E, Leat EHK, Bourgeon S, Jónsson JE, Phillips RA, Strøm H, Petersen A, Hanssen SA, Bustnes JO & Furness RW (2014). Activity patterns of wintering Great Skuas *Stercorarius skua*. *Bird Study* 61:301–308

Malo JE & Mata C (2021). Web databases of feather photographs are useful tools for avian morphometry studies. *Ecology and Evolution* 11:7677–7684

Marchant S & Higgins P (eds) (1990). *Handbook of Australian, New Zealand & Antarctic Birds – Volume 1, Raties to ducks.* Oxford University Press, Melbourne

Mares R, Doutrelant C, Paquet M, Spottiswoode CN & Covas R (2017). Breeding decisions and output are correlated with both temperature and rainfall in an arid-region passerine, the sociable weaver. *Royal Society open science* 4:170835

Marra PP, Cohen EB, Loss SR, Rutter JE & Tonra CM (2015). A call for full annual cycle research in animal ecology. *Biology Letters* 11:20150552

Marzal A, Asghar M, Rodriguez L, Reviriego M, Hermosell IG, Balbontin J, Garcia-Longoria L, de Lope F & Bensch S (2013). Co-infections by malaria parasites decrease feather growth but not feather quality in house martin. *Journal of Avian Biology* 44:437-444

Meillère A, Brischoux F, Henry PY, Michaud B, Garcin R & Angelier F (2017). Growing in a city: Consequences on body size and plumage quality in an urban dweller, the house sparrow P*asser domesticus*. *Landscape and Urban Planning* 160:127-138

Melville DS (1991). Primary moult in Black-browed and Shy Mollymawks. *Notornis* 38:51–59

Merilä J & Hemborg C (2000). Fitness and feather wear in the collared flycatcher *Ficedula albicollis. Journal of Avian Biology* 31:504-510

Meyburg BU, Howey P, Meyburg C & Pretorius R (2017). Year-round satellite tracking of Amur Falcon *Falco amurensis* reveals the longest migration of any raptor species across the open sea. *From Avian Tracking to Population Processes,* British Ornithologists' Union Annual Conference, University of Warwick (poster)

Minias P & Iciek T (2013). Extent and symmetry of post-juvenile moult as predictors of future performance in Greenfinch *Carduelis chloris*. *Journal of Ornithology* 154:465-468

Minias P, Włodarczyk R, Surmacki A & Iciek T (2015). Silver spoon effects on plumage quality in a passerine bird. *Royal Society Open Science* 2:140459

Møller AP & Swaddle JP (1997). *Asymmetry, Developmental Stability and Evolution.* Oxford University Press, Oxford

Moloto DJ (2019). *Are there structural differences in the flight feathers among Procellariiformes related to the use of wings for underwater propulsion?* MSc thesis, University of Cape Town, Cape Town

Monaghan P, Metcalfe NB & Torres R (2009). Oxidative stress as a mediator of life history trade-offs: mechanisms, measurements and interpretation. *Ecology Letters* 12:75–92

Monteiro LR & Furness RW (1995). Seabirds as monitors of mercury in the marine environment. *Water, Air and Soil Pollution* 80:851–870

Monteiro LR & Furness RW (1996). Molt of Cory's Shearwater during the breeding season. *Condor* 98:216–221

Morbey YE, Guglielmo CG, Taylor PD, Maggini I, Deakin J, Mackenzie SA, Brown JM & Zhao L (2017). Evaluation of sex differences in the stopover behavior and postdeparture movements of wood-warblers. *Behavioral Ecology* 29:117-127

Moreno-Rueda G (2011). House Sparrows Passer domesticus with larger uropygial glands show reduced feather wear. *Ibis* 153:195-198

Moreno-Rueda G (2017). Preen oil and bird fitness: a critical review of the evidence. *Biological Reviews* 92:2131-2143

Morrison CA, Robinson RA, Clark JA & Gill JA (2016). Causes and consequences of spatial variation in sex ratios in a declining bird species. *Journal of Animal Ecology* 85:1298-1306

Mosbech A, Johansen KL, Bech NI, Lyngs P, Harding AMA, Egevang C, Phillips RA & Fort J (2012). Inter-breeding movements of litte auks *Alle alle* reveal a key post-breeding staging area in the Greenland Sea. *Polar Biology* 35:305–311

Moseley C, Grémillet D, Connan M, Ryan PG, Mullers RHE, van der Lingen CD, Miller TW, Coetzee JC, Crawford RJM, Sabarros P, McQuaid CD & Pichegru L (2012). Foraging ecology and ecophysiology of Cape gannets from colonies in contrasting feeding environments. *Journal of Experimental Marine Biology and Ecology* 422–423:29–38

Mullers RHE, Navarro RA, Crawford RJM & Underhill LG (2009). The importance of lipid-rich fish prey for Cape gannet chick growth: Are fishery discards an alternative? ICES Journal of *Marine Science* 66: 2244–2252

Murphy ME & King JR (1991). Nutritional aspects of avian molt. *Proceedings XX International Ornithological Congress*, 2186-2193

Murphy ME & King JR (1992). Energy and nutrient use during moult by White-crowned Sparrows *Zonotrichia leukophrys gambelii*. *Ornis Scandinavica* 23:304–313Murphy ME (1996). Energetics and nutrition of molt. In: Carey C (ed.), *Avian energetics and nutritional ecology*. Chapman & Hall, New York, 158–198

Nelson JB (1966). The breeding biology of the Gannet *Sula bassana* on the Bass Rock, Scotland. *Ibis* 108:584–626

Nelson JB (1978). *The Sulidae, Gannets and Boobies.* Oxford University Press, Oxford

Neto JM & Gosler AG (2006). Post-juvenile and post-breeding moult of Savi's Warblers *Locustella luscinioides* in Portugal. *Ibis* 148:39-49

Newton I & Marquiss M (1982). Moult in the Sparrowhawk. *Ardea* 70:163-172

Newton I (2009). Moult and plumage. *Ringing and Migration* 24:220–226

Newton I (2011). Migration within the annual cycle: species, sex and age differences. *Journal of Ornithology* 152:169-185

Nilsson JA & Svenssonn E (1996). The cost of reproduction: A new link between current reproductive effort and future reproductive success. *Proceedings of the Royal Society Series B* 263:711-714

Norberg U (1990). Vertebrate Flight: mechanics, physiology, morphology, ecology and evolution. *Zoophysiology Series 27*. Springer, New York

Norell MA & Xu X (2005). Feathered dinosaurs. *Annual Review of Earth and Planetary Sciences* 33:277–299

Okes NC, Hockey PAR, Pichegru L, van der Lingen CD, Crawford RJM & Grémillet D (2009). Competition for shifting resources in the southern Benguela upwelling: Seabirds versus purse-seine fisheries. *Biological Conservation* 142:2361–2368

Olle A & Estrada V (2017). Halcones peregrinos nórdicos: cómo son y de dónde vienen. *Quercus* 371:12-18

Onley DJ & Scofield RP (2007). *Field guide to the Albatrosses, Petrels and Shearwaters of the World.* Christopher Helm, London

Ontiveros D (1995). Velocidad de crecimiento de rémiges y rectrices en *Milvus migrans* y *Buteo buteo* durante la muda. *Ardeola* 42:183-189

Osborne A & Ryan PG (2021). Using digital photography to study moult extent in breeding seabirds. *Ostrich* 92:225–228

Osváth G, Daubner T, Dyke G, Fuisz TI, Nord A, Pénzes J, Vargancsik D, Vágási CI, Vincze O & Pap PL (2018). How feathered are birds? Environment predicts both the mass and density of body feathers. *Functional Ecology* 32:701-712

Pan Y, Zheng W, Sawyer RH, Pennington MW, Zheng X, Wang X, Wang M, Hu L, O'Connor J, Zhao T, Li Z, Schroeter ER, Wu F, Xu X, Zhou Z & Schweitzer MH (2019). The molecular evolution of feathers with direct evidence from fossils. *Proceedings of the National Academy of Sciences USA* 116:3018-3023

Pap PL, Barta Z, Tökölyi J & Vágási IC (2007). Increase of feather quality during moult: A possible implication of feather deformities in the evolution of partial moult in the great tit *Parus major*. *Journal of Avian Biology* 38:471-478

Pap PL, Vágási CI, Czirják GÁ & Barta Z (2008). Diet quality affects postnuptial molting and feather quality of the House Sparrow *Passer domesticus*: Interaction with humoral immune function? *Canadian Journal of Zoology* 86:834-842

Pap PL, Osváth G, Sándor K, Vincze O, Bărbos L, Marton A, Nudds RL & Vágási CI (2015). Interspecific variation in the structural properties of flight feathers in birds indicates adaptation to flight requirements and habitat. *Functional Ecology* 29:746–757

Pap PL, Vincze O, Vágási CI, Salamon Z, Pándi A, Bálint B, Nord A, Nudds RL & Osváth G (2019). Vane macrostructure of primary feathers and its adaptations to flight in birds. *Biological Journal of the Linnean Society* 126:256-267

Patanella KR (2018). *Birds of a feather: indicators of quality in urban versus rural Eastern bluebirds Sialia sialis*. MSc thesis, Western Carolina University, Cullowhee, North Carolina

Payne RB (1972). Mechanisms and control of molt. In: Farner DS, King JR (eds). Avian Biology, Volume 2:103-105. Academic Press, New York

Peig J & Green AJ (2009). New perspectives for estimating body condition from mass/length data: The scaled mass index as an alternative method. *Oikos* 118:1883-1891

Pennycuick CJ (1989). *Bird Flight Performance: A practical calculation manual*. Oxford University Press, Oxford

Pennycuick CJ (2008). *Modelling the flying bird*. Academic Press, London

Péron C, Delord K, Phillips RA, Charbonnier Y, Marteau C, Louzao M & Weimerskirch H (2010). Seasonal variation in oceanographic habitat and behaviour of White-chinned Petrels *Procellaria aequinoctialis* from Kerguelen Island. *Marine Ecology Progress Series* 416:267–284

Petersen SL, Honig MB, Ryan PG & Underhill LG (2009). Seabird bycatch in the pelagic longline fishery off southern Africa. *African Journal of Marine Science* 31:191–204

Phillips RA, Silk JRD, Croxall JP & Afanasyev V (2006). Year-round distribution of white-chinned petrels from South Georgia: relationships with oceanography and fisheries. *Biological Conservation* 129:336–347

Phillips RA, Croxall JP, Silk JRD & Briggs DR (2007). Foraging ecology of albatrosses and petrels from South Georgia: two decades of insights from tracking technologies. *Aquatic Conservation: Marine and Freshwater Ecosystems* 17:S6–S21

Pietersen DW & Symes CT (2010). Assessing the diet of Amur Falcon *Falco amurensis* and Lesser Kestrel *Falco naumanni* using stomach content analysis. *Ostrich* 81:39-44

Pietiainen H, Saurola P & Kolunen H (1984). The reproductive constraints on moult in the Ural Owl *Strix uralensis*. *Annales Zoologici Fennici* 21:277-281

Podlaszczuk P, Kamiński M, Włodarczyk R, Kaczmarek K, Janiszewski T & Minias P (2016). Plumage quality mediates a life-history trade-off in a migratory bird. *Frontiers in Zoology* 13:47

Prevost Y (1983). Moult in the Osprey *Pandion haliaetus*. *Ardea* 71:199-209

Price TD (2006). Phenotypic plasticity, sexual selection and the evolution of colour patterns. *Journal of Experimental Biology*. 209:2368-2376

Prince PA, Rodwell S, Jones M & Rothery P (1993). Moult in Black-browed and Grey-headed Albatrosses *Diomedea melanophris* and *D. chrysostoma. Ibis* 135:121–131

Prince PA, Weimerskirch H, Huin N & Rodwell S (1997). Molt, maturation of plumage and ageing in the Wandering Albatross. *Condor* 99:58–72

Prum RO (1999). Development and evolutionary origin of feathers. *Journal of Experimental Zoology* 285:291–306

Pyle P (1995). Incomplete flight feather molt and age in certain North American non-passerines. *North American Bird Bander* 20:15-26

Pyle P (2005). Remigial molt patterns in north American falconiformes as related to age, sex, breeding status, and life-history strategies. *Condor* 107:823-834

Pyle P (2008). *Identification Guide to North American Birds*. Part 2. Slate Creek Press, Point Reyes, CA

Pyle P (2009). Age determination and molt strategies in North American alcids. *Marine Ornithology* 37:219-225

Pyle P (2013). Evolutionary implications of synapomorphic wing-molt sequences among falcons (Falconiformes) and parrots (Psittaciformes). *Condor* 115:593-602

R Core Team (2019). R: A language and environment for statistical computing. R foundation for statistical computing, Vienna

Raikow RJ, Stettenheim PR & Lucas AM (1974). Avian Anatomy--Integument. *Bird-Banding* 45:76-79

Ramirez J & Panuccio M (2019). Flight feather moult in Western Marsh Harriers during autumn migration. *Avian Research* 10:1-6

Ramos R, Militão T, González-Solís J & Ruiz X (2009). Moulting strategies of a long-distance migratory seabird, the Mediterranean Cory's Shearwater *Calonectris diomedea diomedea*. *Ibis* 151:151–159

Reynolds SJ, Martin GR, Dawson A, Wearn CP & Hughes BJ (2014). The Sub-Annual breeding cycle of a tropical seabird. *PLoS One* 9:e93582

Robertson G, McNeill M, Smith N, Wienecke B, Candy S & Olivier F (2006). Fast sinking (integrated weight) longlines reduce mortality of white-chinned petrels (*Procellaria* *aequinoctialis*) and sooty shearwaters (*Puffinus griseus*) in demersal longline fisheries. *Biological Conservation* 132:458–471

Rohwer S (1999). Time constraints and moult-breeding tradeoffs in large birds. In: Adams NJ & Slotow RH (eds) Proceedings XXII International Ornithological Congress, Durban: 568–581. BirdLife South Africa, Johannesburg

Rohwer S (2008). A primer on summarizing molt data for flight feathers. *Condor* 110:799–806

Rohwer S, Ricklefs RE, Rohwer VG & Copple MM (2009). Allometry of the duration of flight feather molt in birds. *PLoS Biology* 7:e1000132

Rohwer S, Viggiano A & Marzluff JM (2011). Reciprocal tradeoffs between molt and breeding in albatrosses. *Condor* 113:61-70

Rohwer VG & Rohwer S (2013). How do birds adjust the time required to replace their flight feathers? *Auk* 130:699–707

Rohwer S & Rohwer VG (2018). Primary molt in Gruiforms and simpler molt summary tables. *PeerJ* 6:e5499

Rollinson DP, Wanless RM & Ryan PG (2017). Patterns and trends in seabird bycatch associated with the pelagic longline fishery off South Africa. *African Journal of Marine Science* 39:9–25

Rollinson DP, Dilley BJ, Davies D & Ryan PG (2018). Year-round movements of white-chinned petrels from Marion Island, southwestern Indian Ocean. *Antarctic Science* 30:183–195

Ryan PG (1999). Sexual dimorphism, moult and body condition of seabirds killed by longline vessels around the Prince Edward Islands, 1996–97. *Ostrich* 70:187–192

Ryan PG, Dilley BJ & Jones MGW (2012). The distribution and abundance of white-chinned petrels breeding at the sub-Antarctic Prince Edward Islands. *Polar Biology* 35:1851–1859

Ryan PG, Lee J & Bouard F (2020). Moult intensity in blue petrels and a key moult site off West Antarctica. *Antarctic Science* 32:1–9

Saino N, Romano M, Caprioli M, Lardelli R, Micheloni P, Scandolara C, et al. (2013). Molt, feather growth rate and body condition of male and female Barn Swallows. *Journal of Ornithology* 154:537–547

Schafer S (2003). Study on a Mongolian breeding population of the Amur Falcon *Falco amurensis*. PhD Thesis, Martin Luther University, Halle-Wittenberg

Selman C, Blount JD, Nussey DH & Speakman JR (2012). Oxidative damage, ageing, and life-history evolution: where now? *Trends in Ecology and Evolution* 27:570–577

Senar JC, Copete JL & Martin AJ (2008). Behavioural and morphological correlates of variation in the extent of postjuvenile moult in the Siskin *Carduelis spinus*. *Ibis* 140:661-669

Serra L, Whitelaw DA, Tree AJ & Underhill LG (1999). Moult, mass and migration of Grey Plovers *Pluvialis squatarola* wintering in South Africa. *Ardea* 87:71-81

Serra L, Griggio M, Licheri D & Pilastro A (2007). Moult speed constrains the expression of a carotenoid-based sexual ornament. *European Society for Evolutionary Biology*

20:2028–2034

Shawkey MD & Hill GE (2005). Carotenoids need structural colours to shine. *Biology Letters* 1:121-124

Sheard C, Neate-Clegg MHC, Alioravainen N, Jones SEI, Vincent C, MacGregor HEA, Bregman TP, Claramunt S & Tobias JA (2020). Ecological drivers of global gradients in avian dispersal inferred from wing morphology. *Nature Communications* 11:2463

Sherley RB, Crawford RJM, Dyer BM, Kemper J, Makhado AB, Masotla M, Pichegru L, Pistorius PA, Roux JP, Ryan PG, Tom D, Upfold L & Winker H (2019). The status and conservation of the Cape Gannet *Morus capensis*. *Ostrich* 90:335–346

Shugart GW & Rohwer S (1996). Serial descendant primary molt or *Staffelmauser* in Black-crowned Night-herons. *Condor* 98:222–233

Siefferman L & Hill GE (2003). Structural and melanin coloration indicate parental effort and reproductive success in male eastern bluebirds. *Behavioral Ecology* 14:855-861

Siegfried WR, Williams AJ, Frost PGH & Kinahan JB (1975). Plumage and ecology of cormorants. *African Zoology* 10:183-192

Sild E, Sepp T, Männiste M & Hõrak P (2011). Carotenoid intake does not affect immune-stimulated oxidative burst in greenfinches. *Journal of Experimental Biology* 214:3467-3473

Spedding GR & Pennycuick CJ (2001). Uncertainty calculations for theoretical flight power curves. *Journal of Theoretical Biology* 208:127-139

Staverees L, Crawford RJM & Underhill LG (2008). Factors influencing the breeding success of Cape Gannets *Morus capensis* at Malgas Island, 2002/03. *Ostrich* 79:67–72

Stettenheim PR (2000). The integumentary morphology of modern birds - an overview. *American Zoologist* 40:461-477

Stiles FG (1995). Intraspecific and interspecific variation in molt patterns of some tropical hummingbirds. *Auk* 112:118-132

Stresemann E & Stresemann V (1966). Die Mauser der Vögel. *Journal für Ornithologie* 107: 313–317

Stresemann E & Stresemann V (1968). The moult of Tawny Pipit *Anthus campestris* and Richard's Pipit *Anthus richardi*. *Journal of Ornithology* 109:17-21

Strochlic DE & Romero LM (2008). The effects of chronic psychological and physical stress on feather replacement in European starlings *Sturnus vulgaris*. *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology* 149:68-79

Studer-Thiersch A (2000). What 19 years of observation on captive Greater Flamingos suggests about adaptations to breeding under irregular conditions. *Waterbirds* 23:150-159

Svensson E & Nilsson JÅ (1997). The trade-off between molt and parental care: A sexual conflict in the blue tit? *Behavioral Ecology* 8:92-98

Swaddle JP & Witter MS (1997). The effects of molt on the flight performance, body mass and behavior of European starlings *Sturnus vulgaris*: An experimental approach. *Canadian Journal of Zoology* 75:948–953

Symes CT & Woodborne S (2010). Migratory connectivity and conservation of the Amur Falcon *Falco amurensis*: a stable isotope perspective. *Bird Conservation International* 20:134-148

Szép T, Dobránszky J, Møller AP, Dyke G & Lendvai ÁZ (2019). Older birds have better feathers: A longitudinal study on the long-distance migratory Sand Martin, *Riparia riparia*. *PLoS ONE* 14:e0209737

Takaki Y, Eguchi K & Nagata H (2001). The growth bars on tail feathers in the male Styan's Grasshopper Warbler may indicate quality. *Journal of Avian Biology* 32:319–325

Tellería JL, de la Hera, I & Pérez-Tris J (2013). Morphological variation as a tool for monitoring bird populations: A review. *Ardeola* 60:191-224

Thomas ALR (1993). The aerodynamic costs of asymmetry in the wings and tail of birds: asymmetric birds can't fly round tight corners. *Proceedings of the Royal Society Series B* 254:181-189

Thomas ALR (1997). On the tails of birds. *Bioscience* 47:215–225

Thompson TJ & Powers HH (1924). The variation of certain blood constituents of chickens during the molting season. *Poultry Science* 4:186–188

Thompson DR & Furness RW (1995). Stable isotope ratios of carbon and nitrogen in feathers indicate seasonal dietary shifts in Northern Fulmars. *Auk* 112:493–498

Thompson CW, Hatch SA, Leu M, Brennan K, Roca B & Krausse B (2000). Novel sequences of flight feather molt in Sooty Shearwaters and Northern Fulmars. *Pacific Seabirds* 27:50

Tickell WLN (2000). *Albatrosses.* Pica Press, Robertsbridge, UK

Underhill LG & Zucchini W (1988). A model for avian primary moult. *Ibis* 130:358–372

Underhill LG & Joubert A (1995). Relative masses of primary feathers. *Ringing and Migration* 16:109–116

Vágási CI, Pap PL, Vincze O, Benko Z, Marton A & Barta Z (2012). Haste makes waste but condition matters: Molt rate-feather quality trade-off in a sedentary songbird. *PLoS ONE* 7:e40651

Vágási CI, Pap PL, Vincze O, Osváth G, Erritzøe J & Møller AP (2016). Morphological adaptations to migration in birds. *Evolutionary Biology* 43:48-59

Verhulst S (1998). Multiple breeding in the Great Tit, II. The costs of rearing a second clutch. *Functional Ecology* 12:132-140

Verhulst S & Nilsson JÅ (2008). The timing of birds' breeding seasons: A review of experiments that manipulated timing of breeding. *Philosophical Transactions of the Royal Society Series B* 363:399-410

Videler JJ (2005). *Avian flight*. Oxford University Press, New York

Walsberg GE (1983). Avian ecological energetics. *Avian Biol.* 7:161-220

Wang X, Nudds RL, Palmer C & Dyke GJ (2012). Size scaling and stiffness of avian primary feathers: implications for the flight of Mesozoic birds. *Journal of Evolutionary Biology* 25:547–555

Warham J (1977). Wing loadings, wing shapes, and flight capabilities of Procellariiformes. *New Zealand Journal of Zoology* 4:73–83

Warham J (1996). *The Behaviour, Population Biology and Physiology of the Petrels.* Academic Press, London

Watkins BP, Petersen SL & Ryan PG (2008). Interactions between seabirds and deep-water hake trawl gear: an assessment of impacts in South African waters. *Animal Conservation* 11:247–254

Waugh SM, Baker G, Gales R and Croxall JP (2008). CCAMLR process of risk assessment to minimise the effects of longline fishing mortality on seabirds. *Marine Policy* 32:442–454

Weber TP, Borgudd J, Hedenstrom A, Persson K & Sandberg G (2005). Resistance of flight feathers to mechanical fatigue covaries with moult strategy in two warbler species. *Biology Letters* 1:27–30

Weber TP, Kranenbarg S, Hedenström A, Waarsing JH & Weinans H (2010). Flight feather shaft structure of two warbler species with different moult schedules: a study using high-resolution X-ray imaging. RID A-5648-2009 RID F-5377-2010. *Journal of Zoology* 280:163–170

Weimerskirch H. (1991). Sex-specific differences in molt strategy in relation to breeding in the Wandering Albatross. *Condor* 93:731–737

Weimerskirch H, Tarroux A, Chastel O, Delord K, Cherel Y & Descamps S (2015) Population-specific wintering distributions of adult south polar skuas over the three oceans. *Marine Ecology Progress Series* 538:229–237

Wetmore S (1915). A Peculiarity in the growth of the tail feathers of the Giant Hornbill *Rhinoplax vigil*. *Auk* 32:113-114

White CR, Day N, Butler PJ & Martin GR (2007). Vision and foraging in cormorants: More like herons than hawks? *PLoS ONE* 2:e639

Wikelski M, Martin LB, Scheuerlein A, Robinson MT, Robinson ND, Helm B, Hau M & Gwinner E (2008). Avian circannual clocks: Adaptive significance and possible involvement of energy turnover in their proximate control. *Philosophical Transactions of the Royal Society Series B* 363:411-423

Williams EV & Swaddle JP (2003). Moult, flight performance and wingbeat kinematics during take-off in European Starlings *Sturnus vulgaris*. *Journal of Avian Biology* 34:371–378

Wilson RP (1992). Environmental monitoring with seabirds: do we need additional technology? *South African Journal of Marine Science* 12:919-926

Wolfe JD, Pyle P & Ralph CJ (2009). Breeding seasons, molt patterns, and gender and age criteria for selected northeastern Costa Rican resident landbirds. *Wilson Journal of Ornithology* 121:556–567

Wolfe JD, Johnson EI & Terrill RS (2014). Searching for consensus in molt terminology 11 years after Howell et al. "first basic problem". *Auk* 131:371-377

Woolfenden BE, Gibbs HL & Sealy SG (2001). Demography of Brown-headed Cowbirds at Delta Marsh, Manitoba. *Auk* 118:156-166

Zanette L (2001). Indicators of habitat quality and the reproductive output of a forest songbird in small and large fragments. *Journal of Avian Biology* 32:38-46

Zuberogoitia I, De La Puente J, Elorriaga J, Alonso R, Palomares LE & Martínez JE (2013). The flight feather molt of Griffon Vultures *Gyps fulvus* and associated biological consequences. *Journal of Raptor Research* 47:292–303

Zuberogoitia I, Gil JA, Martínez JE, Erni B, Aniz B & López-López P (2016). The flight feather moult pattern of the Bearded Vulture *Gypaetus barbatus*. *Journal of Ornithology* 157:209-217

Zuberogoitia I, Zabala J & Martínez JE (2018). Moult in birds of prey: A review of current knowledge and future challenges for research. *Ardeola* 65:183-207

Supplemental Material 8: Contribution to co-authored publications

I confirm that the first author of the underlisted articles was principal in the work done towards publishing the articles:

i. **Oluwadunsin E. Adekola**, Robert J. M. Crawford, Bruce M. Dyer, Azwianewi B. Makhado, Leshia Uphold and Peter G. Ryan (2021a). Timing, duration and symmetry of moult in Cape Gannets. *Ostrich: Journal of African Ornithology* 92: 1-12 https://doi.org/10.2989/00306525.2021.1988745.

ii. **Oluwadunsin E. Adekola**, David G. Allan, Zephne Bernitz, Wiseman Dlungwana and Peter G. Ryan (2021b). Extent and Symmetry of tail moult in Amur Falcons. *Journal of Ornithology* 162: 655-667 https://doi.org/10.1007/s10336-021-01874-0.

Oluwadunsin E. Adekola was principal in designing the research and autonomously conducted the laboratory works and analysed the data. He wrote the manuscripts and addressed editorial comments. The co-authors contributed to the work through expertise, funds, data collections, and reviewing of the manuscripts.

Prof. Peter G. Ryan

20 May 2022