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ORIGINAL ARTICLE

Either taking it easy or feeling too tired: old Cory's Shearwaters display reduced activity levels while at sea

**Paulo Catry · José Pedro Granadeiro ·
Jaime Ramos · Richard A. Phillips ·
Paulo Oliveira**

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Abstract It has long been known that birds change their behaviour, reproductive performance and survival as they mature, including in the first few years after recruitment into the breeding population. However, and contrasting with the description of patterns of actuarial and reproductive senescence in later years, there are surprisingly few studies documenting changes in behaviour in old individuals. Such studies are important, as birds provide particularly interesting models for studying the biology of senescence. It has been suggested that, unlike mammals, birds may remain physically fit until an advanced age, yet this has limited empirical support. In this paper, we used activity (immersion) loggers to show that old (>26 years) Cory's Shearwaters *Calonectris diomedea* are less active when foraging at sea, spend more time resting on the water and have a smaller number of take-offs and landings during darkness, when compared to experienced mid-aged individuals (13–20 years old). Old individuals also tended to have reduced immune response against an experimental challenge using phytohaemagglutinin. These results are in line with observed reductions in activity levels with age in a wide range of non-avian taxa, and may suggest that old seabirds are physically less fit than younger individuals. Alternatively, old birds might simply be more experienced and their reduction in activity might reflect a strategic regulation of investment in different activities. Our study illustrates the potential for gaining insights into avian aging patterns and processes by looking into the behaviour of model organisms. We therefore encourage more research focusing on behavioural parameters that may reflect variations in physical condition or strategic choices, during both the breeding and non-breeding seasons.

Keywords *Calonectris diomedea* · Senescence · Age · Long-lived bird · Selvagem

Zusammenfassung Es ist bereits seit längerem bekannt, dass sich das Verhalten, der Bruterfolg und die Überlebensrate von Vögeln mit zunehmendem Alter verändert. Trotz der Beschreibung solcher Muster von Sterblichkeits- und reproduktiver Vergreisung in späteren Jahren gibt es erstaunlich wenige Studien, die eine derartige Veränderung im Verhalten alter Individuen dokumentieren. Solche Studien sind wichtig, weil Vögel ein besonders interessantes Modellsystem für die Untersuchung der Biologie von Vergreisung darstellen. Anders als bei Säugetieren wurde

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P. Catry (✉)
Eco-Ethology Research Unit, ISPA, Rua Jardim do Tabaco 34,
1149-041 Lisbon, Portugal
e-mail: paulo.catry@gmail.com

P. Catry
Museu Nacional de História Natural, Rua da Escola Politécnica,
Lisbon, Portugal

J. P. Granadeiro
CESAM, Museu Nacional de História Natural,
Rua da Escola Politécnica, Lisbon, Portugal

J. Ramos
IMAR-Institute of Marine Research, Department of Zoology,
University of Coimbra, Coimbra, Portugal

R. A. Phillips
British Antarctic Survey, Natural Environment Research
Council, High Cross, Madingley Road,
Cambridge CB3 0ET, UK

P. Oliveira
Serviço do Parque Natural da Madeira, Secretaria Regional do
Ambiente e dos Recursos Naturais, Funchal, Portugal

vorgeschlagen, dass Vögel bis ins hohe Alter physisch gesund bleiben. Dies wird jedoch nur im begrenzten Maße von empirischen Daten unterstützt. In der vorliegenden Studie verwendeten wir Aktivitätslogger, um zu zeigen, dass 26-jährige Gelbschnabel-Sturmtaucher *Calonectris diomedea* weniger aktiv sind, während sie auf See furagieren. Sie haben kürzere Ruhepausen auf dem Wasser und eine geringere Anzahl Starts und Landungen während der Dunkelheit, im Vergleich mit erfahrenen mittel alten Individuen (13–20 Jahre alt). Alte Individuen neigten auch zu einer reduzierten Immunreaktion auf eine experimentelle Injektion von Phytohaemagglutinin. Diese Ergebnisse stimmen im Wesentlichen überein mit der beobachteten Abnahme von Aktivität mit zunehmendem Alter in einer großen Anzahl anderer Tiergruppen. Es kann sein, dass alte Seevögel physisch weniger fit sind als jüngere. Alternativ könnten ältere Vögel auch erfahrener sein, und die Aktivitätsreduktion könnte eine strategische Regulierung der Allokation von Investment in unterschiedliche Aktivitäten sein. Unsere Untersuchung zeigt, dass detaillierte Studien des Verhaltens von Modellorganismen das Potential haben, Muster und Alterungsprozesse bei Vögeln zu erklären. Wir regen deshalb mehr Verhaltensstudien an, die die Variation in der physischer Kondition oder verschiedene strategischen Entscheidungen reflektieren, und dies sowohl in wie außerhalb der Brutsaison.

Introduction

In recent decades, many studies have focused on age-related changes in the behaviour and fitness of birds. Some general trends are now relatively well established. For example, in the first months or years of life, birds apparently improve their foraging efficiency (Wunderle 1991), dominance-mediated competitive ability (Sergio et al. 2009), migratory performance (Thorup et al. 2003), and breeding success and survival (Newton 1989). Such changes are apparent in cross-sectional studies and result not only from the selective appearance and disappearance of phenotypes but also, as longitudinal analyses indicate, from the acquisition of relevant experience (Forslund and Pärt 1995).

Changes in behaviour may also occur at a more advanced age and could result from strategic choices, as predicted by classic life-history theory. This includes, for example, that, in their last breeding attempt, individuals should raise their reproductive effort in order not to waste unused resources (Stearns 1992). However, recent theoretical research suggests that increased parental investment may not be adaptive before the terminal breeding attempt, and that instead, a reduction in reproductive effort should be typical response to an advancing age (McNamara et al. 2009). Furthermore, in the last breeding attempt, it is possible that birds are already somewhat debilitated by a rapidly advancing terminal disease (Ricklefs 2000, 2008; Coulson and Fairweather 2001), which would hinder the detection of an increased terminal effort. In fact, only a handful of experimental studies have found evidence for the terminal investment hypothesis (e.g. Hanssen 2006; Velando et al. 2006).

Studies to date have either documented actuarial senescence (Ricklefs 2000), or, if they dealt with loss of function in old individuals, have mostly focused on reproduction (e.g. Bennett and Owens 2002; Jones et al. 2008). This reflects the desire to understand age-specific reproductive performance in relation to life-history theory, and also the relative ease with which relevant parameters can be measured. However, reproductive performance may be affected by a number of external factors, such as the quality of the nesting partner or changes in the environment, which confound interpretation (Nisbet 2001). Therefore, measuring other aspects of individual state and performance may contribute to a better understanding of the mechanisms of aging, and hence of the biology of senescence. Although there has been recent research focusing on hormonal, physiological and cellular parameters (Haussmann et al. 2005; Vleck et al. 2007), surprisingly few studies have explored the effects of aging of wild animals on traits such as foraging behaviour and efficiency (but see Catry et al. 2006; MacNulty et al. 2009; Lecomte et al. 2010). Such traits are highly relevant because they influence the rate of resource acquisition, and hence have major implications for fitness correlates that include reproductive output and survival.

Declines in activity levels of old individuals have been described for taxa ranging from nematodes and insects, to rodents, dogs and primates (e.g. Emborg et al. 1998; Fernández et al. 1999; Siwak et al. 2002; see Sallis 2000; Ingram 2000 for reviews). Such declines are more obvious for demanding actions that require higher energetic expenditure or greater motor coordination, and, at least in mammals, seem to have a biological basis, resulting from impaired motor and neurobiological function, rather than a simple adaptive reduction in motivation or as an effect of social influences (Emborg et al. 1998; Ingram 2000; Carter et al. 2002; Némoz-Bertholet and Aujard 2003). Few studies of wild birds have attempted to measure activity levels in relation to aging, but very old male Grey-headed Albatrosses *Thalassarche chrysostoma* were reported to display reduced foraging efficiency when compared to mid-aged individuals, which suggests a deterioration in physical performance (Catry et al. 2006). Furthermore, in Wandering Albatrosses *Diomedea exulans*, differences were found in the at-sea activity budgets and distribution of mid-age and old male individuals, and old birds had higher levels of the stress hormone corticosterone after a foraging trip (Lecomte et al. 2010). These results contrasts with recent suggestions that birds remain physically fit into old age (Ricklefs 2000, 2008). Clearly, this is an interesting question that deserves further attention.

New data logger systems are revolutionising our ability to continuously monitor bird behaviour, including in species such as seabirds whose pelagic lifestyles were formerly largely unknown (Ropert-Coudert and Wilson 2005). Seabirds are particularly useful models for studying age-related changes in ecology and behaviour, given their unusual longevity and the ease with which they can be marked (ringed), such that many individuals are of known age in populations subject to long-term study (Wooller et al. 1992). Cory's Shearwaters *Calonectris diomedea* are medium-sized seabirds that typically forage for fish and squid in the upper levels of the pelagic domain. While one bird incubates, the partner engages in long foraging trips that normally last for several days and can take the off-duty individual hundreds of kilometres from the nesting site. Here, we report a study on the activity levels and water mass selection of foraging Cory's Shearwaters of known age.

We were particularly interested in exploring the possibility that old individuals might suffer from some form of physical senescence effects that could affect their at-sea distribution or foraging behaviour. If so, we would make the following predictions: (1) old individuals should spend more time resting on the water during a foraging trip (Passos et al. 2010), and (2) old birds should perform a smaller number of take-offs and landings, as these are known to be energy-demanding activities in medium to large sized petrels (Weimerskirch et al. 2000; Shaffer et al. 2001). If the first two predictions are confirmed, we would also predict as a corollary that (3) old individuals should take longer to recover body mass lost in incubation and hence make longer foraging trips. It is important to note from the outset that similar patterns (predictions 1 and 2) could be observed if old birds were simply more efficient, allowing them more discretionary resting time than mid-aged individuals. Hence, in this respect our study is exploratory, as to attribute any detected changes to senescence requires more detailed, longitudinal analyses. Our aim is therefore primarily to identify variables that deserve scrutiny in future research.

Methods

This study took place at Selvagem Grande, Savage islands (30°09′N, 15°52′W), where a large colony (currently ca. 30,000 pairs) of Cory's Shearwaters has been the object of long-term research (Mougin et al. 2000; Granadeiro et al. 2006). Cory's Shearwaters nest in burrows and incubate their single egg for a period of ca. 54 days (Thibault et al. 1997). In some parts of the colony, chicks and breeding adults have been marked with monel rings on the leg since 1977. In June 2007, during early incubation, we searched those sectors for individuals ringed as chicks, and therefore of known age. To increase sample sizes, we also selected birds that had been ringed as adults in 1977–1987 and hence were of considerably advanced age. On average, Cory's Shearwaters start nesting at 8.9 ± 1.7 years and fewer than 1% of the individuals do so before the age of 6 (Mougin et al. 2000), hence these birds would have been at least 26 years old by the time of our study. Based on previous studies of senescence in this population that reported declines in breeding success for birds older than 25 years (Mougin 2002), we defined two groups of ringed birds, as follows: "Old" individuals were those ringed as chicks (40%) or adults (60%) and, respectively, known or assumed to be at least 26 years old, and "Mid-aged" individuals were those aged 13–20 years (the majority were 13–16 years old). These groups were defined a priori (i.e., before subsequent study).

In the last week of June 2007, we deployed activity and temperature loggers on incubating birds. The loggers (Mk 7; British Antarctic Survey, Cambridge) weigh only 3.5 g and were attached to the monel ring using a plastic, weather-resistant cable-tie. These loggers record a single sea-surface temperature (SST) value after 20 min of continuous immersion, and will only record a new value after a subsequent dry period, followed by immersion for a further 20 min. They also record the timings of all changes of state (from wet to dry, and vice versa) of 6 s or more, allowing the reconstruction of detailed activity patterns. These loggers are not known to have any significant deleterious effects (Igual et al. 2005). Loggers were recovered 3–4 weeks later, by which time all individuals had performed at least one foraging trip. The recovery rate was 96%.

The approximate start and end date of each foraging trip (which typically lasted several days; see "Results") could be estimated from the first and last wet event between incubation stints (Edwards et al. 2007). However, after leaving its nest, a bird could potentially fly for several hours before landing on the water, which would be indistinguishable from time spent at the nest, as would the last flight at the end of the foraging trip. Hence, when estimating number of hours flying or resting on the water per day, we excluded information on the first and the last day of the foraging trip. During a foraging trip, birds spent most of the night on the water. On rare occasions, loggers recorded a long continuous dry period during the night, which could result from the bird attending the colony rather than represent time in flight. To avoid the disproportionate influence of these rare events, we used median values, rather than means, when calculating summary statistics for individuals.

Shearwater at-sea nocturnal activity may be influenced by variation in ambient light levels related to the moon phase (Yamamoto et al. 2008). To assess if this factor might confound our results, we compared the likely light levels experienced by Mid-aged and Old individuals by the use of a moon score. A night with full moon was given a score of 15, while the new moon had a score of 0, with intermediate dates having intermediate scores, between 1 and 14. We then calculated the median score experienced by each individual during the nights it was out at sea and finally compared the two age-groups. This analysis is unlikely to be further confounded by cloud-cover, as only thin clouds were occasionally present during the study. Furthermore, departure date had no influence on the behavioural variables measured, and when we repeated the analyses statistically controlling for departure date, the patterns reported in this paper remained unchanged.

To assess potential differences in selection of foraging areas, we calculated the mean logger SST value for each bird during darkness (to avoid direct effects of sunlight on the loggers) on each day, took the mean of those values during each foraging trip, and then compared this between between Old and Mid-aged groups.

In our analyses, we deliberately excluded birds that might be affected by an advanced terminal illness (Catry et al. 2006). Survival rates of Cory's Shearwaters are typically high and only a few individuals were not resighted in the following year. These birds may have died in the intervening period, or be deferring breeding. This small sample was insufficient for exploring patterns relating to terminal investment, but could introduce considerable noise in the datasets. Hence, analyses presented here focus exclusively on birds that were resighted in the season following our field measurements.

Phytohaemagglutinin skin-test

Mougin (2002) has shown that Cory's Shearwaters aged above 25 years old displayed a decline in reproductive function consistent with senescence. To further assess whether our group of Old birds showed physiological evidence of senescence, we evaluated their immune status by means of the phytohaemagglutinin (PHA) test (Smits et al. 1999; Haussmann et al. 2005; Kennedy and Nager 2006). This test consists of injecting a mitogen (PHA) and measuring the swelling at the injection site 24 h later. The swelling results from a perivascular accumulation of T lymphocytes followed by macrophage infiltration (Smits et al. 1999), and its measurement is thought to provide an indication of the T cell-mediated immune response.

We attempted to use the same procedure as Forero et al. (2006), which involved the injection of a solution of PHA into the foot-web and measurement of subsequent swelling. However, we were unsuccessful at web injections and instead injected 0.05 ml of 2 mg ml^{-1} PHA (Sigma) in phosphate-buffered saline (PBS) at a marked point on the tarsus. Three measurements of tarsus thickness over the injection point were made before and 24 h after the injection using an electronic Mitutoyo micrometer ($\pm$0.01 mm). From these, we calculated three different PHA response measures to assess the repeatability of our estimates, which was high ($r = 0.87$, $F_{64,194} = 20.1$, $P < 0.001$). We then averaged the three measurements before and the three measurements after and calculated a final PHA response value based on this difference.

Study birds were sexed using a discriminant function based on bill measurements (Granadeiro 1993). Individuals with a score >0.1 were classified as males and those with a score <−0.1 as females. Birds with intermediate values were sexed if paired with an individual of known sex, or if their distinctive vocalizations (Thibault et al. 1997) were heard during handling. By using these criteria, and cross-validation with nesting partners, sex classification accuracy was >99% (unpublished data).

Variables related to the number of take-offs and landings were log-transformed to meet the requirements of normality and homogeneity of variances. Means are presented ±SD.

Results

Sex had no influence on foraging trip variables reported below and hence this factor was excluded from all models. During foraging trips, Mid-aged individuals took off and landed more often than did Old individuals (Fig. 1). This difference was only significant during darkness (Table 1). The proportion of time spent resting on the water was higher in Old individuals, again with the most pronounced differences observed during darkness (Table 1). There were no differences between age groups in foraging trip duration, mean daily SST values or absolute minimum SST values attained during the trip (Table 1). Trip duration correlated negatively with minimum SST values ($r = -0.53$, $n = 33$, $P = 0.001$), indicating that only on longer trips did birds reach the cold waters of the Canaries upwelling, near the African coast (own unpublished data). This illustrates the usefulness of SST as an indicator of foraging region.

Sex had no influence on PHA response and hence was excluded from the model. Cory's Shearwaters from the Old group had a weaker PHA response (0.663 ± 0.423 mm, $n = 33$) than Mid-aged individuals (0.853 ± 0.451 mm, $n = 32$; ANOVA $F_{1,64} = 3.06$, $P = 0.085$). Note that the difference is significant if we adopt a one-tailed test, in accordance with our directional prediction that senescent animals should show a depressed immune response.

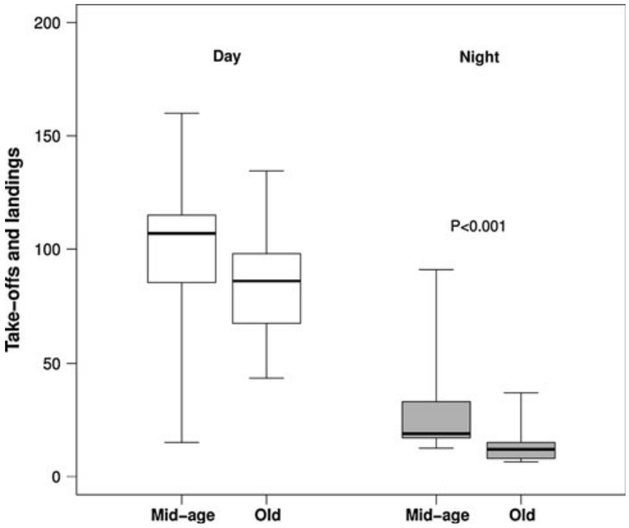

Fig. 1 *Box-plots* depicting the number of take-offs and landings (per day or night) of Old ($N = 18$) and Mid-aged ($N = 17$) Cory's Shearwaters *Calonectris diomedea*. Differences were tested on log-transformed data (see Table 1 for statistics)

Discussion

The concept that, unlike mammals such as humans, birds may remain physically fit until old age (Ricklefs 2000, 2008) has seldom been tested (but see Coulson and Fairweather 2001; Catry et al. 2006), despite its importance in the context of the biology of senescence. The results from the present work, and those from a recent study with albatrosses (Lecomte et al. 2010), suggest that old, free-living seabirds display a reduction in activity levels that parallels patterns reported for a diversity of other taxa (e.g. Emborg et al. 1998; Fernández et al. 1999; Ingram 2000; Siwak et al. 2002; Némoz-Bertholet and Aujard 2003). The causes for such a reduction in activity levels are so far unknown, but circumstantial evidence suggests that senescence due to progressive wear and tear (somatic deterioration) of aging bodies is a strong candidate explanation.

For medium to large petrels that rely on wind-assisted dynamic soaring for travel, flight is often considered to be a relatively economical activity, only slightly more costly than resting: instead, most of the variation in energy expenditure during foraging trips of albatrosses is explained by the number of take-offs, which are energetically expensive (Bevan et al. 1995; Weimerskirch et al. 2000; Shaffer et al. 2001). However, those studies involved birds that proceed by flap-gliding in the windy southern ocean, and it is likely that flight is much more costly for Cory's Shearwaters, which are frequently seen using flapping flight.

The discovery that Old Cory's Shearwaters differed from Mid-aged individuals mostly in the number of take-offs and landings fits well with evidence from other taxa that declines in spontaneous activity are more pronounced in the frequency of demanding physical tasks. For example, in Grey Mouse Lemurs *Microcebus murinus*, differences between young and old adults were clearest in activities such as difficult jumps, where an intense physical effort was required (Némoz-Bertholet and Aujard 2003).

Petrels are known to both travel and forage during darkness as well as daylight, although they tend to be more

Table 1 Characteristics of foraging trips carried out by Mid-aged and Old Cory's Shearwaters *Calonectris diomedea* during incubation

	Mid-aged birds ($n = 17$)	Old birds ($n = 18$)	Statistical comparison
Wet-dry changes during darkness	30.8 ± 24.0	13.4 ± 7.2	$F_{1,34} = 12.6$ $P < 0.001$
Wet-dry changes in daylight	100.8 ± 32.7	84.7 ± 24.5	$F_{1,34} = 0.84$ $P = 0.34$
Proportion time resting in water	0.46 ± 0.13	0.55 ± 0.13	$F_{1,34} = 3.67$ $P = 0.06$
Resting in water during darkness	0.72 ± 0.18	0.83 ± 0.20	$F_{1,34} = 3.96$ $P = 0.05$
Resting in water during daylight	0.38 ± 0.14	0.44 ± 0.12	$F_{1,34} = 1.89$ $P = 0.18$
Mean SST (°C)	18.65 ± 1.10	18.59 ± 0.62	$F_{1,34} = 0.45$ $P = 0.83$
Minimum SST (°C)	17.12 ± 1.25	17.26 ± 1.16	$F_{1,34} = 0.14$ $P = 0.71$
Foraging trip duration (days)	9.23 ± 2.69	8.52 ± 1.93	$F_{1,34} = 0.76$ $P = 0.39$
Light levels (median moon score)	7.5	9.0	M-W U = 100.5 $P = 0.20$

Number of take-offs and landings and mean sea surface temperature (*SST*) are means of mean daily values per individual. Proportions of time resting are means of medians of daily values per individual. See text for details active during the latter (Catry et al. 2004; Phalan et al. 2007; this study). The disproportionate reduction of activity among old Shearwaters during darkness might reflect a strategy to avoid demanding activities when they are less likely to yield a benefit, given that foraging at night seems to be less profitable for visual predators such as seabirds (Catry et al. 2004). An experimental study with Cory's Shearwaters showed that handicapped birds (carrying extra mass) also reduced their activity levels (less time spent flying) during darkness (Passos et al. 2010). It seems less likely that Old birds sleep more during darkness, as sleep is more often interrupted in aged animals (e.g. Hornung et al. 2005), including birds (Paredes et al. 2006). That sea surface temperatures in feeding areas and foraging trip duration were similar in Mid-aged and Old individuals suggests that differences in activity levels between age groups cannot be explained by disparate habitat preferences.

The decline in the PHA response by aged Cory's Shearwaters is consistent with results from recent studies indicating that immunosenescence may be common in both short and long-lived bird species (Haussmann et al. 2005; Vleck et al. 2007). It also suggests that Old birds in our study had reached an age where senescence effects might be apparent (see also Mougin 2002).

There are alternative explanations to deterioration in physical function for the observed declines in activity. Old individuals were not forced to prolong their foraging trips as a result of their lower activity levels, and it is therefore possible that they were more efficient at foraging as a result of accumulated experience. In this context, it should be mentioned that the handicapped (carrying extra mass) Cory's shearwaters studied by Passos et al. (2010), and alluded to above, did make longer foraging trips, which may suggest that this is a relevant variable when studying performance during foraging movements.

Both the activity and the immune response trends presented in this paper result from cross-sectional analyses. Cross-sectional studies have limitations, because patterns may result from cohort heterogeneity or even individual heterogeneity in longevity and other parameters of interest (Nisbet 2001). However, as far as we are aware, no study has demonstrated that differential mortality of phenotypes is responsible for apparent senescence in breeding performance in long-lived birds. Hence, despite this being a possibility, it is relatively unlikely to have influenced our results. Nevertheless, the hypotheses tested in this study should be further evaluated using longitudinal datasets. Neither can we discard the idea that old individuals might be strategically reducing their parental effort (McNamara et al. 2009). This explanation could be ruled out in our case by determining if differences in individual activity patterns persist during the nonbreeding season.

In conclusion, our study demonstrates the potential for gathering insights into avian senescence patterns and processes by looking beyond the classical variables of adult mortality and breeding output. We would therefore encourage more research focusing on parameters that reflect physical performance and behaviour, both in the breeding and non-breeding seasons.

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