Continuous behavioural monitoring reveals increased feeding time during wing moult in free-ranging Pacific Black Ducks *Anas superciliosa*

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Abstract

Many waterfowl species go through a wing moult where all flight feathers are lost simultaneously, rendering the birds flightless while their feathers are regrowing. This puts constraints on the birds during this energetically and nutritiously demanding phase in their annual cycle. Previously, it has been proposed that ducks either decrease activity levels to allocate more resources to wing feather moult, or that they increase feeding activity to match the increased nutritional demands. To study how ducks adjust their time-activity budgets during this challenging life-history stage, we evaluated continuous remotely-sensed time-activity budgets in Pacific Black Ducks *Anas superciliosa* in southeast Australia, prior to, during and after their annual moult. We tracked three ducks using trackers that recorded one of six different behaviours every 2 sec in addition to hourly GPS locations. Rather than reducing their activity levels, all three ducks increased their daily feeding time and decreased daily resting time. Although the sample size was limited, these data provide support for the hypothesis that moult in ducks is a period of enhanced energy expenditure where they feed more to meet the demands for feather regrowth and possibly also compensate for the potentially reduced foraging efficiency due to flightlessness.

Key words: accelerometry, overall dynamic body acceleration (ODBA), on-board behaviour classification, time-activity budget, wildlife tracking.

Bird feathers need to be replaced through the process of moult to compensate for tear and wear and guarantee their functionality (Portugal *et al*. 2018; Rohwer *et al*. 2009). As regrowing feathers is energetically and nutritiously demanding (Klaassen 1995) most birds time their moult during periods of the year where food availability is high and there is no conflict with other demanding life-history phases such as reproduction and migration. In many waterfowl (Anatidae) species, the period of moult comes with the additional challenge of flightlessness. These birds typically moult all flight feathers simultaneously, rendering them flightless for several weeks (Adams *et al.* 2000; Hohman *et al.* 1992). In such a situation, moult may thus require birds to occupy specific habitats where food and safety can be found in close proximity, potentially involving moult migration, where birds fly to a moulting site separate from their breeding or wintering sites (Salomonsen 1968). Given the specific constraints on moulting ducks, two alternative hypotheses have been raised as to how waterfowl might modify their behaviour during wing moult to meet the energetic and nutritional demands of moult, in which birds may either: (1) become less active during moult in order to preserve more resources for feather regrowth, or (2) feed more intensively to meet the elevated resource needs for moult (Fox *et al.* 2014). In many bird species, including ducks, individuals utilise a substantial portion of their body mass during moult, using these stores to provide additional energy and/or nutrients to meet the demands of moult and allow for reduced feeding activity (Fox *et al.* 2014).

To investigate these two alternative hypotheses, time budget studies to date have been undertaken mostly on moulting migratory waterfowl in the northern hemisphere (Fox *et al.* 2014). Harlequin Ducks *Histrionicus histrionicus* in the Gennet Islands (Canada) spend less time foraging during wing moult and more time out of the water and resting (Adams *et al.* 2000). Portugal *et al.* (2009) similarly found that captive Common Eiders *Somateria mollissima* and Garganeys *Anas querquedula* at Slimbridge (UK) devote less time to foraging and more time to resting during wing moult.

We studied time-activity budgets in a southern hemisphere waterfowl species – the Pacific Black Duck (hereafter PBD) *Anas superciliosa*. PBDs have been found throughout Australia and with extended distribution into New Guinea, Indonesia and New Zealand (Frith 1967; McEvoy *et al.* 2015). This species occupies a great range of habitats from small farm dams to relatively deep and permanent water bodies (Frith 1967). Although some PBDs make long-distance journeys, such as from southern New South Wales to northern Queensland or from New Zealand to Australia, in general they are relatively sedentary in mild temperate coastal regions (Frith 1967) where water availability is rather stable and more predictable than in arid central Australia (Kingsford & Norman 2002). In contrast to most previous studies that relied on human observations to record time-activity budgets (*e.g.* Adams *et al.* 2000; Portugal *et al.* 2009), we used newly-developed smart trackers attached to individual birds to record the PBDs' behaviours continuously, in addition to regularly noting their positional data, to test the above-mentioned hypotheses on PBDs by assessing whether they became less active or feed more during wing moult.

Methods

Eighteen PBDs were captured in tapered funnel traps on a small water body in Wallington, Victoria, Australia (38.23°S, 144.53°E): eight during December 2019–January 2020 and 10 during September 2020–February 2021. PBDs are monomorphic and the sex of the ducks was not determined. The ducks were fitted with backpack-mounted GPS trackers (Lego tracker from Druid Technology Co., Ltd) that transmitted data through either the 3G mobile network (typically once a day) or Bluetooth (using a mobile phone device and only when at a distance of < 70 m). For details on the deployment, functionality and use of the trackers see Yu *et al.* (2022). In brief, aside from a GPS device recording the ducks' positions at hourly intervals, the trackers contained a tri-axial accelerometer (ACC) with a 25 Hz sampling rate. Unlike most ACC-trackers used previously (which log raw ACC data), these trackers processed the data on board, yielding two different sets of information. Firstly, every 10 min, ACC data was summarised into a single mean overall dynamic body acceleration value (meanODBA, which is the mean of 100 ODBA values measured at 6 sec intervals), following Wilson *et al.* (2006). Although lacking empirical data to relate meanODBA values to ducks' true energy expenditure, higher meanODBA values are indicative of higher energy expenditure (Weegman *et al.* 2017). Secondly, every 2 sec, ACC data was processed by an on-board machine learning classifier (*i.e.* extreme gradient boosting, following Yu & Klaassen 2021) and assigned to one of eight behaviour types. These behaviours were "dabbling/swimming", "floating", "feeding", "resting", "flying", "preening", "walking" and "running". In this study, we grouped four behaviour types serving similar ecological purposes grouping "floating" with "resting" and combining "walking" and "running" into "locomotion", yielding a total of six behaviour types.

For all 18 ducks, meanODBA data were obtained after deployment. Following development of the behaviour classifier (Yu *et al.* 2022), we uploaded the process to six of the 18 trackers. The period of wing moult in each duck was assessed using daily total time "flying", with a consistent daily amount of flying time of < 200 sec considered to be indicative of moult. Because wing flapping behaviours of ducks on land or water were also recorded as "flying", the threshold value of 200 sec rather than 0 sec was required to account for these occasional flapping behaviours during the moulting period. Further confirmation that the birds were indeed moulting came from GPS fixes indicating that no major displacements took place during this period. Three of the six PBDs (D5210, D5239 and D5246) yielded complete data records throughout wing moult and were used in this study. The remaining three ducks for which we have behavioural records did not show evidence of wing moult during tracking. The capture, tagging and observing protocols were approved by Deakin Animal Ethics Committee (approval reference: B13-2019).

For each duck, meanODBAs and behaviour records during the wing-moult period (henceforth "moult" stage) and a variable period of time outside the moulting stage (henceforth "pre-moult" stage for the time period before wing moult and "post-moult" for the time period after wing moult) were used in the analyses. For duck D5210 the pre-moult and post-moult stages both lasted 30 days. Limitations in data availability (caused by the timing of uploading of the behaviour classifier and low battery levels) resulted in shorter pre-moult and post-moult stages of 2 and 22 days for duck D5239, while for duck D5246 these periods were 21 and 16 days, respectively. MeanODBAs were summarised into daily mean values (the dailyODBA). The continuous behaviour data recorded for each bird were summarised as daily total times for each of the six behaviour categories. For each duck, their daily total times for each behaviour, as well as their dailyODBAs, were compared between the pre-moult, moult and post-moult stages. Nonparametric Wilcoxon rank sum tests were used for the analyses because of non-normality of the data, resulting in 21 comparisons for each duck. Additionally, to test whether ducks spend more time feeding at night during the moult, each date was partitioned into day (time between sunrise and sunset) and night (time before sunrise and time after sunset). The daily total times spent feeding by each duck in day and night during the pre-moult, moult and post-moult stages were then compared using Wilcoxon rank sum tests, resulting in six comparisons for each of the tracked birds. To test whether the ducks exercised their breast muscles to promote muscle resynthesis during the late wing moult period, we used a nonparametric Mann-Kendall trend test on daily total "wing-flapping" (*i.e.* simulating flying) time over the last 20 days of wing moult. All analyses were performed using R 4.0.5 (R Core team 2021) within the Rstudio platform.

Results

D5210 was tracked from 23 September 2020 until 30 March 2022, D5239 from 31 January 2020 until 6 October 2021 and D5246 from 3 February 2021 until 1 May 2021. Within this period, D5210 moulted at Reedy Lake (10 km west of the catch site; Fig. 1) from 8 March–16 April 2021. It also flew to Reedy Lake on the night of 17 February 2021 (*i.e.* 18 days before moulting commenced) and spent around 4 days at this site, in what might have been an exploratory trip. D5239 moulted from 25 December 2020 to 26 January 2021 at a local farm dam, where it had not previously been recorded and did not visit again during the post-moult period. Compared to the sites used by D5239 outside of the moult period, the moulting site was more secluded and had fewer houses in the immediate vicinity. D5246 flew across Port Phillip Bay to moult at a local farm dam (*c.* 50 km east of the catch site) from 24 February–24 March 2021. This moulting site was also more secluded, with fewer houses nearby, and provided more vegetation cover than the sites used by D5246 at other times of the year.

Wilcoxon rank sum tests showed that in four of the six comparisons dailyODBAs were higher during moult than during either the pre-moult or post-moult stages (Fig. 2, Supporting Materials Table S1). Only in one case, for D5210, was daily mean ODBA higher during the post-moult compared to the moult stage. The time-activity budgets in all three ducks show clear behavioural modifications during wing moult (Fig. 3, Supporting Materials Table S2). Most strikingly, all three ducks seemingly spent

Figure 1. Moulting (yellow) and non-moulting (light blue) locations based on hourly GPS fixes of the three ducks included in this study. A blue pin marks the catching site for each of the three birds. The base map shows locations of D5246.

more time feeding during moult compared to pre- and post-moult (significant in five out of six comparisons) and significantly less time resting (significant in five out of six comparisons). Closer inspection of the feeding time suggested that in most cases the feeding time during moult increased similarly during both day (significant in five out of six comparisons) and night-time (significant in five out of six comparisons) (Fig. 4, Supporting Materials Table S3). Mann-Kendall trend tests indicate that all three ducks progressively increased wing flapping during the last 20 days of wing moult (Fig. 5).

Discussion

Although our study is based on data from only three individuals, we deem that the uniqueness of the data and consistency of the results warrants our consideration. All three of the tracked PBDs made clear behavioural modifications in relation to their wing moult, including selecting a specific moulting site and changes in their time-activity budgets. As a relatively sedentary duck species (Frith 1967), all three individuals stayed relatively close (≤ 50 km) to their tracker deployment site over the period in which they were tracked. However, all three ducks chose moulting sites different from the sites they typically frequented prior to and after moult. The moulting sites chosen appeared to differentiate themselves from non-moulting sites in being more secluded and offering more shelter, presumably to reduce predation risk (Nilsson *et al.* 2001; Salomonsen 1968). The variation in the duration of wing moult at different moulting sites among the three ducks, ranging from 29–40 days, might indicate site differences in food availability and predation. Possibly, the longer stay of D5210 on its moulting site indicates

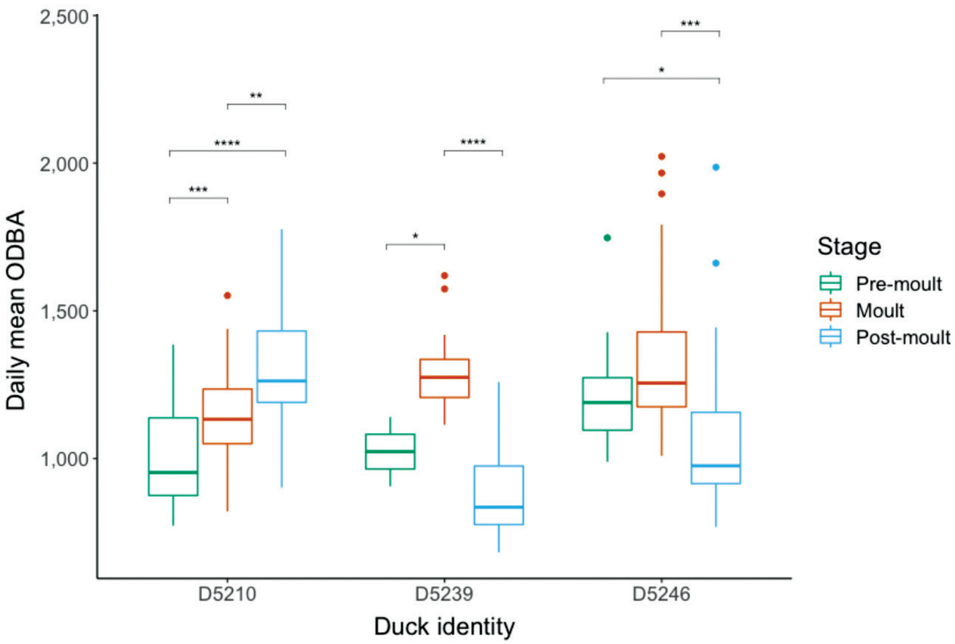

Figure 2. Box plots of daily mean ODBAs (*i.e.* Overall Dynamic Body Acceleration) of three Pacific Black Ducks during their moult (red), pre-moult (green) and post-moult (blue) stages. In the box plots, the lower and upper hinges of each box indicate the 25th and 75th percentiles of the data and the line within each box indicates the median. The upper and lower whiskers from the hinge to the largest and lowest value, respectively, extend no further than 1.5 times the inter-quartile range (which is the distance between the 25th and 75th percentiles), with outliers beyond these ranges depicted as dots. Horizontal bars above box plots indicate significant differences between the 3 stages using Wilcoxon rank sum tests: * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$ and **** = $P \leq 0.0001$ (for detailed statistics see Supplementary Materials Table S1).

particularly low predation risk and/or high food availability at that site compared to the sites used by D5239 and D5246. Also striking was the variation in the timing of the onset of moult across the three individuals. This is likely a reflection of the more opportunistic life history characteristic of many Australian ducks compared to related species in the northern hemisphere (Frith 1967).

The PBDs mostly had higher dailyODBAs when in moult. Therefore, the first hypothesis that ducks became less active to preserve more energy for feather regrowth was not supported. Contrary to some previous studies in moulting ducks (*e.g.* Adams *et al.* 2000; Portugal *et al.* 2009), we found that the PBDs tended to spend more time feeding and less time resting during wing moult. This suggests that they increased feeding time to compensate for the higher nutrient and energy requirements associated with moult (Klaassen 1995; Portugal *et al.* 2018), for lower food

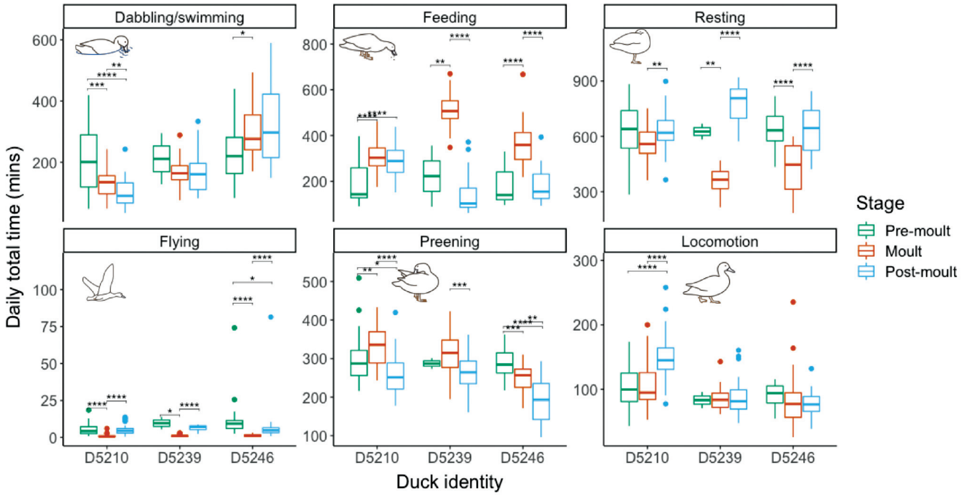

Figure 3. Box plots of the time-activity budgets for three Pacific Black Ducks during their moult (red), pre-moult (green) and post-moult (blue) stages. For explanation of the box plots see Fig. 2 caption. For detailed statistics see Supplementary Materials Table S2.

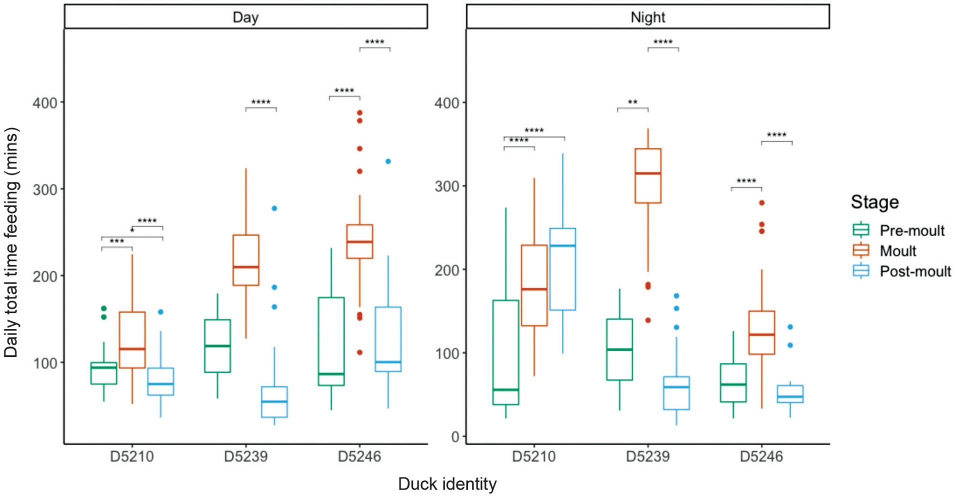

Figure 4. Box plots of the total feeding time during day (left panel) and night (right panel) and during their moult (red), pre-moult (green) and post-moult (blue) stages in three Pacific Black Ducks. For explanation of the box plots see Fig. 2 caption. For detailed statistics see Supplementary Materials Table S3.

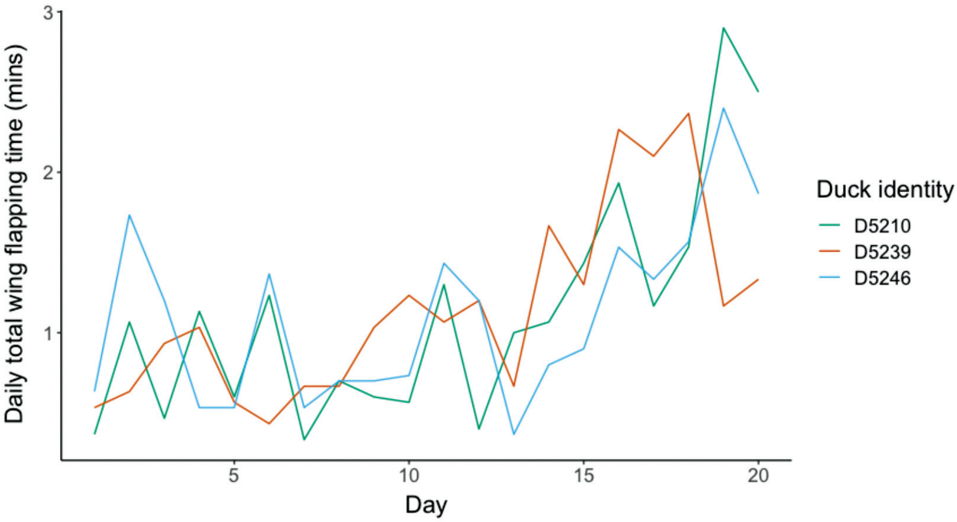

Figure 5. Daily total wing-flapping time recorded for each duck during the last 20 days of the wing moult. Mann-Kendall trend tests for the three ducks indicate a significant increase in wing-flapping activity (D5210: Kendall's tau = 0.529, $P < 0.05$; D5239: Kendall's tau = 0.638, $P < 0.01$; D5246: Kendall's tau = 0.411, $P < 0.05$).

availability at their moulting site, or for both of these factors. At any rate, the increase in feeding time apparently came at the expense of resting time and was seemingly in support of the second hypothesis, that waterfowl feed more to meet elevated needs of moult. The increases in feeding time seemingly differed between the individual ducks, which might reflect differences in food availability between their respective moulting and non-moulting sites, and possible differences in the ducks' physical condition. From the tracking data, we could not tell if the three ducks had bred prior to wing moult, and the sex of each bird was also unknown. Therefore, we were also unable to evaluate whether the time activity budgets of the three ducks were potentially influenced by a carryover effect of breeding. During moult, the PBDs showed increases in their feeding time during both day and night. Thus, although flightless and one might have expected diurnal activity to be moderated to mitigate predation risk, that notion was not supported by our observations. Moreover, we found a progressive increase in wing flapping towards the end of wing moult (Fig. 5) suggesting that the ducks exercise their breast muscles to stimulate their redevelopment (Piersma 1988). Since we only had three individuals in this study, however, the conclusions drawn should be considered preliminary rather than conclusive, with further analysis of ACC and ODBA data recorded for PBDs and other species required to clarify the situation.

Other than the ecological explanations of increased feeding time of PBDs during wing moult, which is consistent with the findings of Fox *et al.* (2007), the discrepancy between our observations on moulting ducks and those published to date could be due to our use of continuous behavioural observations using a modified tracker rather than intermittent visual observation. In most previous studies (*e.g.* Adams *et al.* 2000; Döpfner *et al.* 2009; Portugal *et al.* 2009), each day was divided into two (*i.e.* morning and afternoon) or three (*i.e.* morning, afternoon and evening) periods, with night-time observations being absent in all cases. In other cases it involved birds in captivity that may not have been as hard-pressed to find food under safe and optimal foraging conditions. For instance, while Portugal *et al.* (2009) studying captive Common Eiders *Somateria mollissima* reported that these reduced daily foraging time while moulting, Guillemette *et al.* (2007) using data loggers on wild Common Eiders found no such reduction. In this study, the PBDs' behaviour was continuously recorded at 2 sec intervals, resulting in 43,200 behaviour records daily. Although the on-board classifier is not perfect, given an estimated accuracy of 92%, the long-term time-activity budgets drawn from the data can be considered more reliable than most non-continuous visual observation strategies, especially because it allows for recordings at night. We hope this new technique promotes more research into the study of avian wing moult and animal behaviour in general.

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Photograph: Pacific Black Duck in moult, by Hui Yu.

