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Seasonal activity levels of a farm-island population of striated caracaras (*Phalcoboenus australis*) in the Falkland Islands

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Abstract

Background: Animals need adaptive strategies to cope with seasonal changes in prey availability to survive and reproduce, which can include migrating, prey-switching, or reducing metabolic needs. Human settlements can disrupt spatiotemporal patterning in resource availability, which can affect animals' foraging success, particularly for juveniles who are behaviorally developing and learning efficient foraging skills. Here, we investigate behavioral responses of juvenile striated caracaras, a near-threatened scavenging falconid, to seasonally migratory seabird prey and a farm settlement on Saunders Island, Falklands. We deployed accelerometer–GPS dataloggers ($n = 27$) to measure seasonal differences in daily and hourly vectorial dynamic body acceleration (VeDBA; an activity index measured in gravitational g) and space use, and investigated seasonal variation in body mass of the tagged subset and an additional 65 caracaras.

Results: Juvenile caracaras were overall similarly active in winter and summer. However, during winter, caracaras made the most of limited daylight by increasing average daytime activity (winter males: 0.16 ± 0.03 g, summer males: 0.09 ± 0.01 g, winter females: 0.12 ± 0.02 g, summer females: 0.08 ± 0.01 g). During winter, both sexes increased the percentage of daylight spent in high activity (winter males: $35 \pm 5\%$, summer males: $21 \pm 3\%$, winter females: $25 \pm 6\%$, summer females: $16 \pm 3\%$, $p < 0.001$) and ranged nearly 4 times farther (95% kernel density estimate winter: 2.36 ± 0.96 km², summer: 0.61 ± 0.20 km²; $p < 0.001$). Furthermore, on a daily scale, males were 21% more active than females year-round (24-h average VeDBA: males 0.07 ± 0.01 g, females 0.06 ± 0.01 g; $p < 0.01$). We did not observe a significant seasonal difference in mass.

Conclusion: That caracaras' daily activity and body mass did not vary between seasons suggests that wintering birds on Saunders are meeting resource requirements despite the absence of seasonally migratory prey. We hypothesize that human subsidies may mitigate the effect of seasonal food limitations. Further research should include studies on seasonal energetics to improve our understanding of baseline body condition, and comparative studies on other islands and including adults to understand the importance of human subsidies.

Keywords: Falconid, Hidden Markov model, Migratory prey, Seabirds, South Atlantic, Vectorial dynamic body acceleration

Background

Many predators face seasonal fluctuations in resource availability, due for instance to migratory prey [1], changes in prey vulnerability [2], or pulsed resources [3]. Life-history theory predicts that animals have adaptive

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strategies to cope with changes in prey availability [4, 5], such as migrating to more productive resource patches [6–8], prey-switching [9–11], or reducing metabolic needs [12, 13]. The introduction of human settlements to a landscape can disrupt naturally occurring spatial and temporal variation to which an animal is well-adapted [14], by suppressing natural food resources (e.g., hunting potential prey) or providing resources where historically there were none (hereafter “human subsidies”; i.e., subsidies sensu [15]).

While the effects of seasonal food availability have been investigated at the population level for several species [14, 16–20], less is known about the impact on individual life-history strategies [14], particularly during the juvenile stage when individuals are still behaviorally developing, learning judicious time–energy management, efficient foraging skills, and competitive strategies [21, 22]. Across many mammalian and bird species, juvenile mortality can be high [21, 23, 24], thus making it an important age class to study as impacts extend to population level effects. Here, we report on seasonal juvenile behavioral patterns of an endemic island predator in a system with fluctuating seabird prey and a relatively recent introduction of humans (i.e., since the mid-nineteenth century).

Striated caracaras (*Phalcoboenus australis*) are near-threatened falconids that inhabit the southern coasts of Patagonia and the outer Falkland Islands [25–27]. They are long-lived [Amy Wallace pers. comm] with extended periods of adolescence [28] and exhibit reverse sexual size dimorphism [KH unpubl. data]. During austral summer, caracaras primarily feed on eggs, chicks, and dead or dying adults of breeding colonial seabirds, the after-birth, feces, and carrion of resident pinnipeds, and invertebrates including limpets and kelp fly larvae [17, 28–30]. During austral winter, when most seabirds migrate offshore, caracaras’ diets include native upland geese (*Chloephaga picta*), the feces and carrion of resident southern fur seals (*Arctocephalus australis*), southern sea lions (*Mirounga leonina*) and gentoo penguins (*Pygoscelis papua*), as well as beetles and subsidies provided by farms [17, 28, 31]. Since human occupation began in the Falklands in the mid-nineteenth century, many islands’ vegetation has changed dramatically due to farming [32], resident pinniped populations suffered a population decline from the sealing industry [33], and caracaras were persecuted to the point of near extinction [25, 34]. While the caracaras in the Falklands are now protected, a previous study posited that population recovery may be limited by winter food stress [31].

Animals must maintain a positive energy balance to survive [35] and partition their daily activities to do so; therefore, time–energy allocation and activity budgets provide valuable tools for assessing animals’ response to

their environment [36]. Advancements in animal-borne datalogger technology now allow researchers to investigate fine-scale behavioral responses of wild animals [37–39]. Accelerometers, for example, record high-resolution three-dimensional movement, which can be used to calculate an index of activity, such as vectorial dynamic body acceleration (VeDBA, measured in gravitational g) [40, 41]. Furthermore, an animal’s time-activity budget can be estimated using a hidden Markov model (HMM) to decode behavioral state from acceleration [42, 43].

Our objective was to study juvenile caracaras’ activity levels in the presence and absence of seasonally migratory prey on Saunders Island, Falklands, which supports seven species of breeding seabirds during summer (hereafter the “seabird colonies site”) and has a farm settlement that provides human subsidies (e.g., animal feed, offal, and compost) year-round. To do this, we deployed animal-borne accelerometer and GPS dataloggers on 27 juvenile caracaras during summer and winter and investigated seasonal variation in body mass of the tagged subset and an additional 65 caracaras. If juvenile caracaras were food stressed and unable to forage optimally during winter, we predicted that caracaras would (1) have a higher daily activity index (i.e., 24-h average VeDBA); (2) engage in higher intensity daytime activity (i.e., average VeDBA during daylight); (3) range farther; and (4) have lower mass than during summer.

Results

Daily time–activity allocation

On a daily scale, caracaras were similarly active in winter and summer. We found no seasonal difference in the overall daily activity index (i.e., 24-h average VeDBA) for either sex. However, during winter, caracaras made the most of limited daylight by increasing their average daytime activity by 71% for males and 60% for females (winter males: 0.16 ± 0.03 g [$n=5$], summer males: 0.09 ± 0.01 g [$n=5$], winter females: 0.12 ± 0.02 g [$n=7$], summer females: 0.08 ± 0.01 g [$n=7$]; ANOVA, $p < 0.001$, $t = 7.05$). Furthermore, on a daily basis, males appear to be 21% more active than females year-round (24-h average VeDBA: males: 0.07 ± 0.01 g, females: 0.06 ± 0.01 g; ANOVA, $p < 0.01$, $t = 3.35$; Fig. 1). Tag version had a significant effect in both models; however, for the daily index (i.e., 24-h average VeDBA) tag version only accounted for an additional 13% of the variation ($p = 0.039$, $t = 2.20$), and for the daytime average VeDBA, tag version only accounted for an additional 6% of the variation ($p < 0.05$, $t = 2.24$).

Daily activity budgets

Hidden Markov models (HMMs) are dependent mixture models in which several distributions are used to account

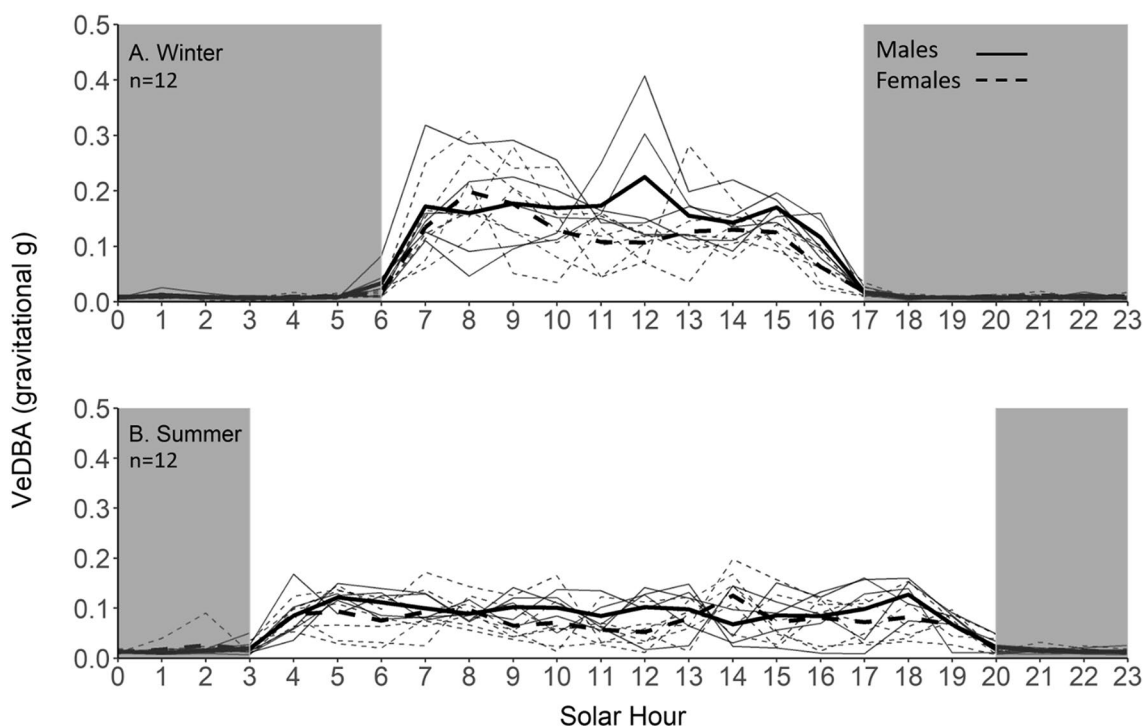


Fig. 1 Seasonal sex differences in 24-h average VeDBA per bird ($n = 12$ per season). VeDBA was binned by solar hour (i.e., 0–23) to show 24-h patterns in average VeDBA. Thin lines represent 1 day of data for individual males (solid) and females (dashed). Thick lines represent the mean average VeDBA for males (solid) and females (dashed). Gray shading denotes night (solar dusk to dawn). During daylight, winter VeDBA increased by 71% for males and 60% for females (Fig. 1a) in comparison to summer (Fig. 1b)

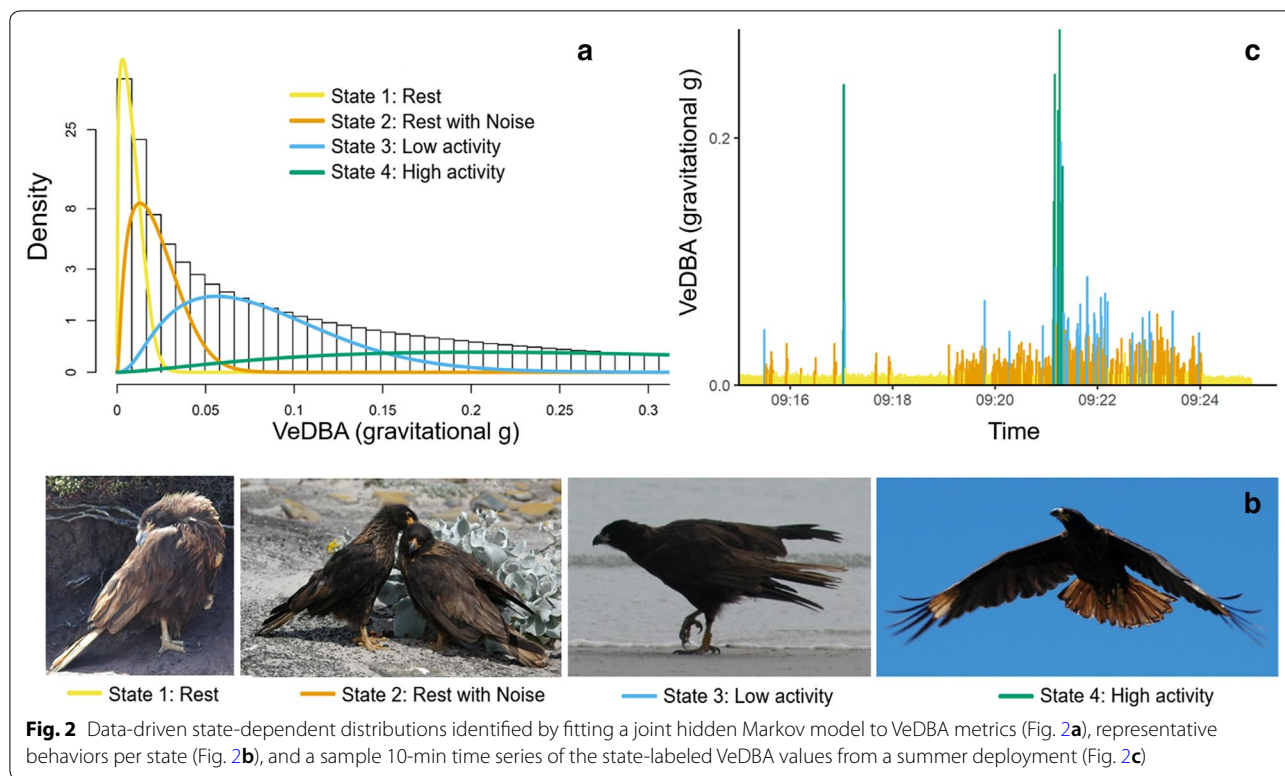
for an animal's behavioral modes [42]. We found that a 4-state HMM fit the data best (Fig. 2a) while comprising clearly interpretable states: (1) rest (e.g., sleep or a similar motionless posture); (2) rest with noise (e.g., preening or daytime rest); (3) low activity (e.g., walking or raking); and (4) high activity (e.g., flight, running, or antagonistic behavior) (Fig. 2b). When coupled with the GPS data, resting states clustered at known roost sites and the highest activity seemingly occurred in flight (e.g., coming and going from the roost site).

Using the state-labeled data, we found that during both seasons, over 90% of night was spent in resting states (i.e., states 1 and 2), even though winter nights were nearly two times longer (winter 13.2 h, summer = 7.2 h [mean]). Nearly all activity occurred during daylight hours (Fig. 1), thus we focused the remainder of our analysis only on daytime. Year-round, males spent a greater percentage of daylight hours in state 4 (i.e., high activity) than females (Fig. 3b); moreover, during winter, both sexes increased the percentage of daylight hours spent in state 4 (winter males: $35 \pm 5\%$, summer males: $21 \pm 3\%$, winter females: $25 \pm 6\%$, summer females: $16 \pm 3\%$; ANOVA, $p < 0.001$, $t = 6.12$; Fig. 3b). Similarly, we found that males spent a greater percentage of daylight hours in state 3 (i.e., low

activity) year-round (males: $29\% \pm 5\%$, females: $24\% \pm 5\%$; ANOVA, $p = 0.01$, $t = 2.75$), though during winter both sexes increased the percentage of daylight hours spent in state 3 (winter males: $30 \pm 5\%$, summer males: $28 \pm 3\%$, winter females: $27 \pm 6\%$, summer females: $21 \pm 2\%$; ANOVA, $p < 0.05$, $t = 2.25$; Fig. 3b).

Daily space use

Caracaras ranges expanded significantly in winter. The winter daily range size (i.e., 95% kernel density estimate, KDE) was nearly 4 times larger than during summer (winter $2.36 \pm 0.96 \text{ km}^2$, summer $0.61 \pm 0.20 \text{ km}^2$; Wilcoxon rank sum test, $p < 0.001$), while their winter kernel core area of use (i.e., 50% KDE) increased by 58% (winter $0.19 \pm 0.02 \text{ km}^2$, summer $0.12 \pm 0.04 \text{ km}^2$; two-sample t test, $p < 0.001$; Fig. 4). For comparison, the mean 100% minimum convex polygon (MCP) for winter was an order of magnitude larger than during summer (winter: $10.8 \pm 14.5 \text{ km}^2$, summer: $0.45 \pm 0.42 \text{ km}^2$; Wilcoxon rank sum test, $p < 0.01$). During summer all tagged birds remained tightly clustered at the seabird colonies site (Fig. 4b), while in winter, caracaras were more loosely clustered at the farm settlement (Fig. 4a, lower right) and one bird traveled 16 km northwest to the seabird colonies



site (blue points, Fig. 4b). Caracaras slept in social roosts at night during both seasons, though GPS tracks suggest interindividual variation in daytime space use.

Seasonal mass

Contrary to our prediction, we found no statistically significant seasonal difference in juvenile caracaras’ mass, although there was a trend for both males and females to weigh less in winter (males summer: 1498 ± 169 g [$n=11$], males winter: 1424 ± 104 g [$n=33$]; females summer: 1772 ± 108 g [$n=19$], females winter: 1717 ± 121 g [$n=29$]). Males weighed 17% less than females throughout the year (males: 1443 ± 125 g, $n=44$, females: 1739 ± 118 g, $n=48$; ANOVA, $p < 0.05$, $F=5.48$).

Discussion

Juvenile striated caracaras on Saunders Island remain as active in winter as they are in summer, though they compress their activity into winter’s shorter daylight hours. These results suggest that during winter, juvenile caracaras on Saunders do not employ the energy-saving strategies that some species exhibit when faced with seasonal food scarcity [44–47]. Moreover, we found that male caracaras are more active than females in both seasons, a possible behavioral expression of the reverse sexual size dimorphism common in the Falconidae family [48, 49].

In the present study, not enough males wore GPS transmitters in winter to draw a statistically significant conclusion about differences in space use by sex. However, the one male sampled during winter traveled from the farm settlement to the seabird colonies, increasing his 95% KDE twofold over the ranges of females who remained at the settlement (male 95% KDE: 3.85 km^2 , female 95% KDE: $1.98 \pm 0.54 \text{ km}^2$ [$n=4$]). On average, male caracaras in the Falklands weigh 200 g less than females, and as cost of transport scales positively with mass, we hypothesize their smaller size could facilitate their higher activity levels [50–52]. Since these are juvenile birds, they are not involved in breeding activity, so this cannot be due to nest provisioning. Notably, the seasonal daily ranges we measured were comparable to the multiday ranges reported in Harrington et al. (2018), which tracked 6 birds with GPS dataloggers over 5–20 days during December 2010 and 5 birds over 3–9 days during July–August 2012 and 2017.

That the caracaras’ daily activity and overall body mass did not vary between the seasons suggests that wintering birds on Saunders Island are meeting their resource requirements despite the absence of seasonally migratory seabird prey. We hypothesize that resources available at the nearby farm settlement may be mitigating the effect of seasonal food limitations.

However, juvenile caracaras appear to respond atypically to human subsidies. While human subsidies are

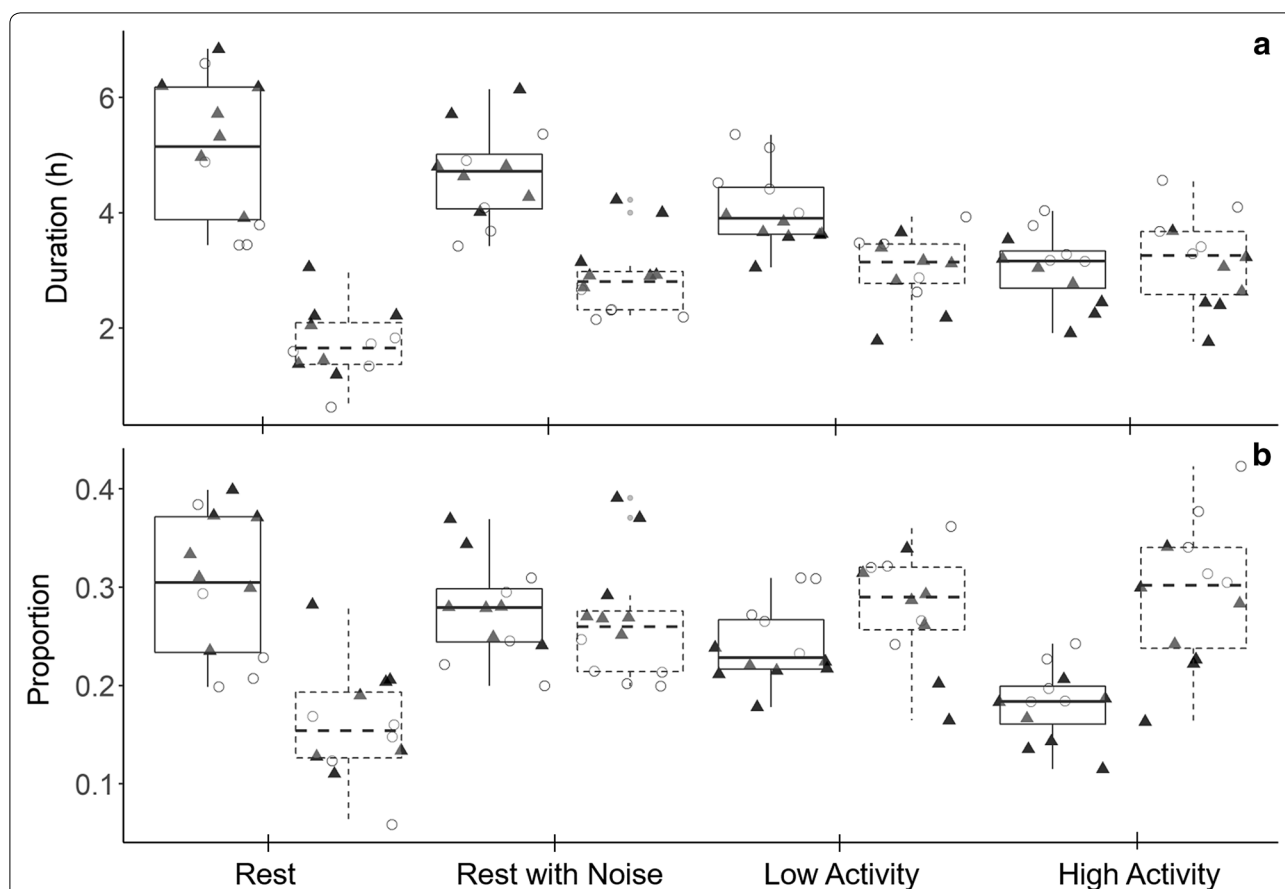
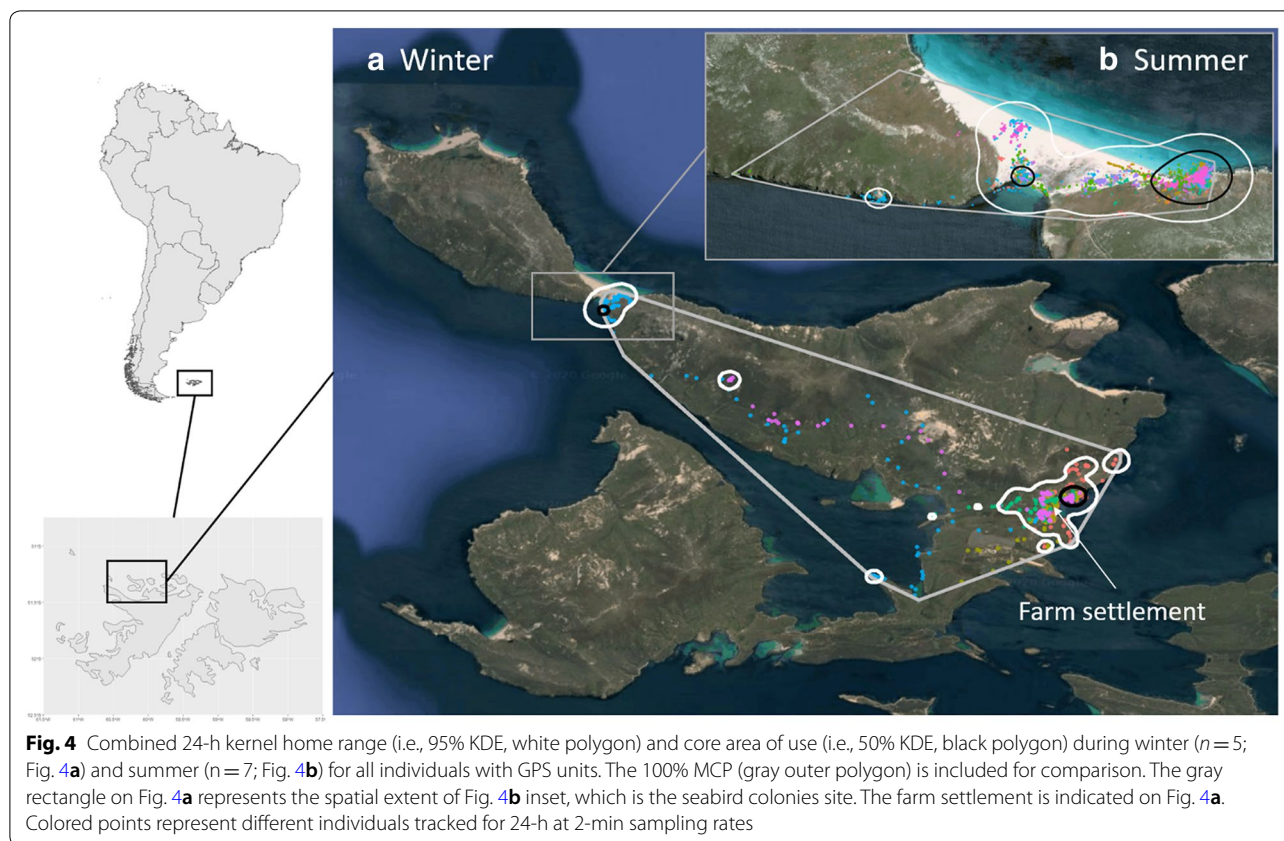


Fig. 3 Boxplots show duration (Fig. 3a) and corresponding percentage (Fig. 3b) of daytime (i.e., solar dawn to solar dusk) spent in each activity state for summer (solid) and winter (dashed). Open circles (males) and triangles (females) reveal sex differences within corresponding boxplots. Year-round, males spent a greater proportion of daylight hours in states 3 and 4 than females. During winter, both sexes increased their proportion of time spent in states 3 and 4. Caracaras appear to spend the extra daylight of longer summer in resting states (Fig. 3a). Boxplot whiskers extend to the largest and smallest values (at most 1.5 * IQR [inter-quartile range])

available year-round at the Saunders settlement, juvenile caracaras only gather and roost at the farm settlement when resources associated with the breeding seabird colonies dwindle. For other species, predictable food resources have encouraged residency (e.g., [16, 53, 54]). Human subsidies have also encouraged corvids—scavenging predators that fill a similar ecological niche as the caracaras—and canids to reduce and shift their home ranges closer to subsidized resources [55, 56]. Caracaras on Saunders Island, on the other hand, have not become year-round residents at the settlement or reduced their home range to remain near the subsidies. Instead, they have increased winter ranges and leave the settlement as soon as their natural food supply increases (i.e., when the seabirds return to breed). This suggests that the human subsidies are less attractive to the birds than naturally available resources. Additionally, not all caracaras in the Falklands overwinter at farm settlements. For example, a 2012 austral winter

survey counted 274 caracaras of all age classes on Steeple Jason Island, a nature preserve 80 km northwest of Saunders, where the caracaras were observed hunting terrestrial invertebrates, foraging in the intertidal and kelp wrack, and scavenging at gentoo colonies [57].

One limitation to our study was the use of two versions of our datalogger. While tag version was significant in modeling daily average VeDBA and daytime average VeDBA, when comparing *R*-squared values, we determined tag version did not explain an ecologically relevant proportion of the data. Biological factors explained 32% of the daily average VeDBA and 72% of the daytime average VeDBA, while tag version only explained an additional 13% and 6%, respectively. Additionally, when comparing between seasons measured by the same tag version, we achieved similar results. It is possible the effect was due to year and not tag version, though we were unable to include year and



tag version in the same model because we did not use both tag versions in all years.

Conclusions

We used animal-borne dataloggers to better understand behavioral response to seasonal resource fluctuation. Combining GPS data with high-resolution accelerometry is especially useful for understanding activity states in an ecological context. In addition, HMMs provide a data-driven framework for evaluating unobserved activity states. While we did not find behavioral evidence of food stress, further research should include studies on seasonal energetics to improve our understanding of baseline body condition, and comparative studies of adult caracaras and islands without human subsidies. As many island-restricted species will likely face increased variation in resource availability in response to changing conditions including rising sea levels and human population expansion, we suggest that conservation managers consider seasonal activity budgets when developing species management plans.

Methods

Study area

This study was conducted on Saunders Island (51.37°S 60.09°W), a 127-km² island in the northwest Falkland Islands archipelago that supports an estimated 50 to 100 caracaras year-round [31, KH unpubl. data]. During austral summer, the island supports over 25,000 breeding seabirds (see [17] for description) at the northwest end of the island. Following the breeding season, all seabirds at the colonies site—except the gentoos who roost near their breeding colonies throughout the year—migrate offshore. When this happens, caracaras vacate their summer roost and move 16 km SE to the 2.5-km² farm settlement, where they overwinter at a roost adjacent to the settlement. The farm is owned and operated by a family of four and 2 co-workers who maintain approximately 6500 sheep, 200 dairy and beef cattle, approximately 400 cage-free chickens and ducks, and 22 farm dogs. Five sheep are processed each week for family use, and offal is left for the scavenging birds. The family also keeps two pigs in a small, open-air pigpen, which are fed two upland geese (*Chloephaga picta*) daily; many caracaras attend the feeding during winter and feed on scraps as available. The pig

feeding, weekly sheep processing, and dogs' bones appear to be the primary draw for the caracaras in winter [17]. The farmers have not observed caracaras preying on the free-ranging farm animals at the settlement, although they have seen caracaras approach and pick at the nose and tails of recently birthed lambs [KH pers. comm.]. No seabirds roost or breed at the settlement.

Animal handling and instrumentation

From 2017 to 2019, we trapped 92 juvenile caracaras (*Phalacrocorax australis*, Gmelin 1788), 62 at the seabird colonies site during austral summer (December–February) and 30 at the farm site during austral winter (June–August). We targeted juvenile caracaras (i.e., second year birds, aged by plumage per [28]) to remove the effect of breeding on seasonal movement, activity levels, and mass. It was not possible to trap at both sites during the same season, because the birds seasonally migrate between the two sites [17]. Caracaras were trapped using a mutton-baited monofilament snare carpet that pulls tight around their metatarsus as the birds walk through the trap [58]. The trap is monitored continuously, and caracaras are removed immediately after snaring. All captured caracaras were weighed to the nearest 50 g using a hand-held scale and banded with colored alphanumeric plastic leg bands [17]. Approximately 50 μ L of blood was collected from the brachial vein using a sterile 21 gauge hypodermic needle [59] and transferred immediately onto an 8- μ m filter paper [60] for molecular sexing (modified protocol from [61]). Caracaras have distensible crops, thus we visually assessed crop size and categorized as not distended, partially distended, or distended, which allowed us to control for the added mass of food storage by restricting our mass analysis to birds that did not have

distended crops. We observed no adverse effects of trapping and handling, with many individuals continuing to feed immediately upon release.

To 27 of those caracaras—13 at the seabird colonies site and 14 at the farm settlement—we attached custom-built Arduino-based archival dataloggers (TWLogger; [62]). We attached the loggers to the bird's two central feathers using Tesa 4651 adhesive tape (Norderstedt, Germany) [63] (Fig. 5). The dataloggers were <2% of birds' body mass (1649.44 ± 177.08 g, mean \pm SD [$n = 27$]); and we assumed that any unexpected behavioral effect of the dataloggers would be pervasive across our sample and thus not affect our comparative index. For all deployments, loggers recorded tri-axial acceleration (50-Hz sampling rate) data, which were used to calculate VeDBA and decode behavioral states. For 2018 and 2019 deployments, loggers also recorded GPS positions (2-min sampling rate), which were used to help validate behavioral state classifications and estimate utilization distributions and core areas of use. Prior to deployment, we spherically rotated all loggers to pass through all combinations of pitch and roll to record reference values to calibrate accelerometer data to account for inherent sensor variability (i.e., due to manufacturing) [64]. After deployment, all instrumented individuals resumed normal activity.

The present study occurred concurrently with TWLogger development, which was an iterative process. Tags deployed in 2017 (dimensions: L52 \times W23 \times H10 mm) used an inertial movement unit (IMU) that included a gyroscope in addition to accelerometer sensors and did not include a GPS module. Tags deployed in 2018 and 2019 were slightly larger (dimensions: L52 \times W23 \times H17 mm), included a GPS, and used a smaller IMU that omitted the gyroscope; this version consumed less power



Fig. 5 The TWLogger inertial movement datalogger with GPS prior to encapsulating in heat shrink for deployment (Fig. 5a), and a banded caracara wearing a tail-mounted TWLogger (Fig. 5b) while feeding on a gentoo penguin carcass at the seabird colonies site

while maintaining similar accelerometer sensitivities. While the 2018/2019 tags weighed slightly more (2017: 20 g; 2018/2019: 25 g), both versions comprised a similar percentage of the average caracaras' mass (2017: 1.2%; 2018/19: 1.5%).

To retrieve loggers, we recaptured birds using a nut-baited single snare. Deployment durations ranged from 1.0 to 12.2 days (4.3 ± 3.6 days, mean \pm SD), though logger battery durations ranged from 26 to 40 h. All but two loggers were recovered. Despite intensive efforts, we were unable to relocate one bird tagged during austral summer 2017 and another tagged during austral winter 2018. In both cases, the loggers would have been shed during their natural molt (Nov–Jan), if not before, preventing long-term consequences for the birds. Only one of 25 recovered loggers failed to record data.

Data processing

We obtained 24 complete datasets of tri-axial acceleration (winter $n=12$, summer $n=12$). Of these, 12 loggers also recorded GPS data (winter $n=5$, summer $n=7$). Each dataset represented one individual; thus, all observations were independent.

Prior to analysis, we processed acceleration data using purpose-written scripts in R (R v. 3.5.2). First, we used the spherical calibration function in the tagtools package [65] in R to calibrate the data using the reference values recorded prior to deployment. This allowed us to convert raw sensor values to acceleration in m s^{-2} while accounting for inherent sensor variability due to manufacturing effects. Next, we corrected any sampling rate variability, which accounted for less than 0.001% of the data. Because we were assessing hourly and daily scales and lower resolution acceleration data maintains high accuracy [66], we down sampled the data to 10-Hz to improve data processing speeds [67]. From the 2018 and 2019 deployments that included GPS units, we obtained 12 complete sets of tri-axial acceleration and GPS data. All GPS data were processed using an SDA filter (i.e., speed–distance–angle filter) [68] in R to remove aberrant positions, as environmental conditions may have affected accuracy of satellite fixes. GPS data were then rejoined to the dataset.

All dataloggers recorded data for greater than 24 h; although to ensure data were comparable on a daily scale and to minimize the effects of tag deployment, we clipped from the beginning of each dataset to make all files 24 h in length.

We classified each data point as day or night to assess diel patterning and standardize statistics such as daytime hourly VeDBA rates. We calculated solar periods (i.e., dawn, day, dusk, and night) using the maptools package in R [69] that performs sun ephemerides calculations

using algorithms developed by the National Oceanic & Atmospheric Administration (NOAA). Solar dawn and dusk are defined as the time when the solar positioning is between 0 and 12 degrees below the horizon (nautical twilight). Night is defined as the time when the solar positioning is below 12 degrees on the horizon. For this analysis, “daytime” comprises dawn, day, and dusk periods. We calculated daytime length as the period between solar dawn and dusk and created 1-h solar time bins from zero to 23 beginning at solar midnight to facilitate seasonal comparisons.

VeDBA calculations

To calculate VeDBA (as described by [41]), we first calculated dynamic acceleration from each axis by subtracting static acceleration (i.e., smoothed acceleration over a 2-s window) from raw acceleration values. We then found the square root of the sum of squared dynamic acceleration of each axis. Using the 10-Hz VeDBA values, we calculated 24-h average VeDBA (i.e., daily activity index) and average daytime VeDBA per individual (i.e., VeDBA index subset to daylight hours and divided by day length). We reported VeDBA metrics in gravitational g .

State classifications

We used hidden Markov models (HMMs) to infer behavioral states from the 10-Hz acceleration data as they allow identification of relevant changes in behavioral intensity, i.e., activity versus rest, taking into account the serial dependence between observations [42, 70]. HMMs require an input metric that can be used to distinguish between movements that represent likely states. We selected VeDBA as our input metric [40, 42, 71]. Since VeDBA values are positive and continuous, we used gamma state-dependent distributions within the HMM.

For animal behavior data, formal model selection techniques tend to select more HMM states than seem biologically reasonable (i.e., additional states compensate for the inability to capture all the structure in such complex data); therefore, we first considered a simple (2-state) model and then built up complexity until a reasonable goodness-of-fit was achieved, but such that the model states were still biologically interpretable [72].

We used ecological knowledge (i.e., 675 h of observations over 3.5 years) and GPS positions to validate the model's state classifications (e.g., known overnight roost sites where caracaras should be in a resting state). For daylight hours, we calculated absolute state durations (hours) and proportion of time spent in each state.

GPS calculations

We used the GPS data to calculate KDEs [73, 74] of the 95% home range and 50% core areas of use of all recorded

locations for each individual bird (winter $n = 5$, summer $n = 7$) using the `kernelUD` and `kernel.area` functions in the `adehabitatHR` package in R [75]. To allow comparison between seasonal home ranges of different sizes, we used a fixed value smoothing parameter h (i.e., bandwidth) for each study area. To determine our smoothing parameters, we first subset the data by season and used the `href` method in the `kernelUD` function to calculate h per individual within a season. We then used the median h per season as our smoothing parameter [76]. For comparison, we also calculated 100% MCPs [77, 78] per bird using the `mcp` and `mcp.area` function from the `adehabitatHR` package.

Statistical analyses

We ran all statistical analyses in R (R v. 3.5.2). We tested for seasonal differences in 24-h average VeDBA, average daytime VeDBA, proportion of daylight hours spent in each behavioral state, and body mass using analyses of variance with season, sex, and device model as covariates. We selected the most parsimonious model to our data by comparing our initial model to subsequent models after removing non-significant fixed terms using likelihood-ratio tests. We report best model with tag version, but compare R -squared with and without tag version to understand importance. To compare KDEs and MCPs between seasons, we used two-sample t -tests and a Wilcoxon rank sum test, as our dataset contained only one year per treatment.

Abbreviations

GPS: Global Position System; HMM: Hidden Markov model; IMU: Inertial movement unit; KDE: Kernel density estimate; MCP: Minimum convex polygon; VeDBA: Vectorial dynamic body acceleration.

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Authors' contributions

KH, JF, and BM conceptualized this study. KH and JF designed the dataloggers used in this study. KH conducted fieldwork. JH analyzed genetic data. KH, JF, RL and BM analyzed accelerometry data. KH wrote and prepared the original manuscript. KH, JF, RL, JFT, JH and BM reviewed and edited the manuscript. KH administered the project. KH obtained project funding. All authors read and approved the final manuscript.

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Availability of data and materials

R scripts and TWLogger details are available on GitHub (<http://github.com/Fahlbusch-Harrington/TWLogger>). Raw data are available by email upon request to the corresponding author.

Ethics approval and consent to participate

Caracara capture, handling, and instrumentation methods were conducted under Institutional Animal Care and Use Committee protocol (#1054) and complied with the conservation of Wildlife and Nature Ordinance of 1999, Section 9, License to carry out Scientific Research permit (#R22/2015, Falkland Islands Government).

Consent for publication

All authors agree consent to publish this work to *Animal Biotelemetry*.

Competing interests

The authors declare no competing or financial interests.

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References

1. Elbroch LM, Lendrum PE, Newby J, Quigley H, Craighead D. Seasonal foraging ecology of non-migratory cougars in a system with migrating prey. *PLoS ONE*. 2013;8:e83375.
2. Metz MC, Smith DW, Vucetich JA, Stahler DR, Peterson RO. Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park. *J Anim Ecol*. 2012;81:553–63.
3. Ostfeld RS, Keesing F. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends Ecol Evol*. 2000;15:232–7.
4. Roff DA. *The evolution of life histories*. New York: Chapman & Hall; 1992.
5. Stearns SC. *The evolution of life histories*. Oxford: Oxford University Press; 1992.
6. Alerstam T, Hedenström A, Åkesson S. Long-distance migration: evolution and determinants. *Oikos*. 2003;103:247–60.
7. Richter HV, Cumming GS. Food availability and annual migration of the straw-colored fruit bat (*Eidolon helvum*). *J Zool*. 2006;268:35–44.
8. Wysujack K, Greenberg LA, Bergman E, Olsson IC. The role of the environment in partial migration: food availability affects the adoption of a migratory tactic in brown trout *Salmo trutta*. *Ecol Freshw Fish*. 2009;18:52–9.
9. Bailey KM, Ainley DG. The dynamics of California sea lion predation on Pacific hake. *Fish Res*. 1981;1:163–76.
10. Harper GA. Numerical and functional response of feral cats (*Felis catus*) to variations in abundance of primary prey on Stewart Island (Rakiura). *New Zealand Wildlife Res*. 2005;32:597–604.
11. Sigler MF, Tollit DJ, Vollenweider JJ, Thedinga JF, Csepp DJ, Womble JN, Wong MA, Rehberg MJ, Trites AW. Steller sea lion foraging response to seasonal changes in prey availability. *Mar Ecol Prog Ser*. 2009;388:243–61.
12. Doucette LI, Brigham RM, Pavey CR, Geiser F. Prey availability affects daily torpor by free-ranging Australian owllet-nightjars (*Aegotheles cristatus*). *Oecologia*. 2012;169:361–72.
13. Geiser F. Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annu Rev Physiol*. 2004;66:239–74.
14. Oro D, Genovart M, Tavecchia G, Fowler MS, Martínez-Abraín A. Ecological and evolutionary implications of food subsidies from humans. *Ecol Lett*. 2013;16:1501–14.

15. Polis GA, Hurd SD. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *Am Nat.* 1996;147:396–423.
16. Gilbert NI, Correia RA, Silva JP, Pacheco C, Cattray I, Atkinson PW, Gill JA, Franco AM. Are white storks addicted to junk food? Impacts of landfill use on the movement and behaviour of resident white storks (*Ciconia ciconia*) from a partially migratory population. *Mov Ecol.* 2016;4:7.
17. Harrington KJ, Pole-Evans S, Reeves M, Bechard M, Bobowski M, Barber DR, Rexer-Huber K, Lecomte N, Bildstein KL. Seasonal micro-migration in a farm-island population of striated caracaras (*Phalacrocorax australis*) in the Falkland Islands. *Mov Ecol.* 2018;6:4.
18. Donazar JA, Gangoso L, Forero MG, Juste J. Presence, richness and extinction of birds of prey in the Mediterranean and Macaronesian islands. *J Biogeogr.* 2005;32:1701–13.
19. Duhem C, Roche P, Vidal E, Taton T. Effects of anthropogenic food resources on yellow-legged gull colony size on Mediterranean islands. *Popul Ecol.* 2008;50:91–100.
20. Parra J, Tellería JL. The increase in the Spanish population of Griffon Vulture *Gyps fulvus* during 1989–1999: effects of food and nest site availability. *Bird Conserv Int.* 2004;14:33–41.
21. Wunderle JM. Age-specific foraging proficiency in birds. *Curr Ornithol.* 1991;8:273–324.
22. Greig SA, Coulson JC, Monaghan P. Age-related differences in foraging success in the Herring Gull (*Larus argentatus*). *Anim Behav.* 1983;31:1237–43.
23. Caughley G. Mortality patterns in mammals. *Ecology.* 1966;47:906–18.
24. Lack D. The natural regulation of animal numbers. *The Natural Regulation of Animal Numbers.* Oxford: Clarendon Press; 1954.
25. Woods RW, Woods A. Atlas of breeding birds of the Falkland Islands. Oswestry: Anthony Nelson; 1997.
26. Balza U, Lois NA, Raya Rey A. Status and reproductive outcome of the breeding population of Striated Caracaras (*Phalacrocorax australis*) at Franklin Bay, Staten Island, Argentina. *Wilson J Ornithol.* 2017;129:890–8.
27. Reeves M, Bildstein KL. Distribution and abundance of breeding striated caracaras in the Falkland Islands (Malvinas). *J Raptor Res.* 2018;52:309–16.
28. Strange IJ. The Striated Caracara *Phalacrocorax australis* in the Falkland Islands. Warrington: Philip Myers; 1996.
29. Harrington KJ, Bildstein KL. Predation of Southern Red Octopus (*Enterocottopus megalocytus*) by Striated Caracaras (*Phalacrocorax australis*) in the Falkland Islands. *J Raptor Res.* 2019;53:220–2.
30. Cattray P, Lecoq M, Strange IJ. Population growth and density, diet and breeding success of striated caracaras *Phalacrocorax australis* on New Island, Falkland Islands. *Polar Biol.* 2008;31:1167–74.
31. Rexer-Huber K, Bildstein KL. Winter diet of Striated Caracara *Phalacrocorax australis* (Aves, Polyborinae) at a farm settlement on the Falkland Islands. *Polar Biol.* 2013;36:437–43.
32. Tourangeau W, Sherren K, Delignières M. 'We secured the tussac': accounts of ecological discovery, exploitation and renewal in the Falkland Islands. *People Nat.* 2019;1:548–61.
33. Baylis AM, Orben RA, Arnould JP, Christiansen F, Hays GC, Staniland IJ. Disentangling the cause of a catastrophic population decline in a large marine mammal. *Ecology.* 2015;96:2834–47.
34. Cawkell EM, Hamilton JE. The birds of the Falkland Islands. *Ibis.* 1961;103:1–27.
35. Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. Toward a metabolic theory of ecology. *Ecology.* 2004;85:1771–89.
36. Christiansen F, Rasmussen MH, Lusseau D. Inferring activity budgets in wild animals to estimate the consequences of disturbances. *Behav Ecol.* 2013;24:1415–25.
37. Brown DD, Kays R, Wikelski M, Wilson R, Klimley AP. Observing the unwatchable through acceleration logging of animal behavior. *Animal Biotelemetry.* 2013;1:20.
38. Nathan R, Spiegel O, Fortmann-Roe S, Harel R, Wikelski M, Getz WM. Using tri-axial acceleration data to identify behavioral modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. *J Exp Biol.* 2012;215:986–96.
39. Shepard EL, Wilson RP, Quintana F, Laich AG, Liebsch N, Albareda DA, Halsey LG, Gleiss A, Morgan DT, Myers AE, Newman C. Identification of animal movement patterns using tri-axial accelerometry. *Endanger Species Res.* 2008;10:47–60.
40. Qasem L, Cardew A, Wilson A, Griffiths I, Halsey LG, Shepard EL, Gleiss AC, Wilson R. Tri-axial dynamic acceleration as a proxy for animal energy expenditure; should we be summing values or calculating the vector. *PLoS ONE.* 2012;7:e31187.
41. Bidder OR, Qasem LA, Wilson RP. On higher ground: how well can dynamic body acceleration determine speed in variable terrain. *PLoS ONE.* 2012;7:e50556.
42. Leos-Barajas V, Photopoulou T, Langrock R, Patterson TA, Watanabe YY, Murgatroyd M, Papastamatiou YP. Analysis of animal accelerometer data using hidden Markov models. *Methods Ecol Evol.* 2017;8:161–73.
43. Papastamatiou YP, Watanabe YY, Demšar U, Leos-Barajas V, Bradley D, Langrock R, Weng K, Lowe CG, Friedlander AM, Caselle JE. Activity seascapes highlight central place foraging strategies in marine predators that never stop swimming. *Mov Ecol.* 2018;6:9.
44. Giroud S, Blanc S, Aujard F, Bertrand F, Gilbert C, Perret M. Chronic food shortage and seasonal modulations of daily torpor and locomotor activity in the grey mouse lemur (*Microcebus murinus*). *Am J Physiol Regul Integr Comp Physiol.* 2008;294:1958–67.
45. Vuarin P, Dammhahn M, Kappeler PM, Henry PY. When to initiate torpor use? Food availability times the transition to winter phenotype in a tropical heterotherm. *Oecologia.* 2015;179:43–53.
46. Cuyler LC, Øritsland NA. Metabolic strategies for winter survival by Svalbard reindeer. *Can J Zool.* 1993;71:1787–92.
47. Riek A, Brinkmann L, Gaulty M, Perica J, Ruf T, Arnold W, Hambly C, Speakman JR, Gerken M. Seasonal changes in energy expenditure, body temperature and activity patterns in llamas (*Lama glama*). *Sci Rep.* 2017;7:7600.
48. Bechard MJ, Sarasola JH, Helbig AJ. Morphometric Measures of male and female Spot-winged Falconets *Spizapteryx circumcinctus* sexed using PCR Amplification Methods. In: Chancellor RD, Meyburg BU, editors. *Raptors Worldwide.* World Working Group on Birds of Prey and Owls & MME/ BirdLife Hungary, Budapest; 2004.
49. Newton I. Population ecology of raptors. London: A&C Black; 2010.
50. Goldstein DL. Estimates of daily energy expenditure in birds: the time-energy budget as an integrator of laboratory and field studies. *Am Zool.* 1988;28:829–44.
51. Pennycuik CJ. Mechanics of flight. In: Farner DS, King JR, editors. *Avian Biology*, vol. 5. New York: Academic Press; 1975. p. 1–75.
52. Krüger O. The evolution of reversed sexual size dimorphism in hawks, falcons and owls: a comparative study. *Evol Ecol.* 2005;19:467–86.
53. Plummer KE, Siriwardena GM, Conway GJ, Risely K, Toms MP. Is supplementary feeding in gardens a driver of evolutionary change in a migratory bird species? *Glob Chang Biol.* 2015;21:4353–63.
54. Baskin Y. Trumpeter swans relearn migration. *Bioscience.* 1993;43:76–9.
55. Kristan WB III, Boorman WI. Effects of anthropogenic developments on common raven nesting biology in the west Mojave Desert. *Ecol Appl.* 2007;17:1703–13.
56. Marzluff JM, Neatherlin E. Corvid response to human settlements and campgrounds: causes, consequences, and challenges for conservation. *Biol Conserv.* 2006;130:301–14.
57. Woods RW, Meiburg JA, Galloway D. Striated Caracaras *Phalacrocorax australis* on Steeple Jason, Falkland Islands: winter population, diet, feeding behaviour and potential problems of mouse eradication August–September 2012. Falkland Islands: Falklands Conservation survey report to F.I. Government. Stanley; 2012.
58. Collister A. Simple noose trap. *Western Bird Bander.* 1967;42.
59. Owen JC. Collecting, processing, and storing avian blood: a review. *J Field Ornithol.* 2011;82:339–54.
60. Smith LM, Burgoyne LA. Collecting, archiving and processing DNA from wildlife samples using FTA® databasing paper. *BMC Ecol.* 2004;4:4.
61. Griffiths R, Double M, Orr K, Dawson R. A DNA test to sex most birds. *Mol Ecol.* 1998;7:1071–6.
62. Fahlbusch JA, Harrington KJ. A low-cost, open-source inertial movement GPS logger for eco-physiology applications. *J Exp Biol.* 2019;222.
63. Wilson RP, Pütz K, Peters G, Culik B, Scolaro JA, Charrassin JB, Ropert-Coudert Y. Long-term attachment of transmitting and recording devices to penguins and other seabirds. *Wildl Soc Bull (1973-2006).* 1997;25:101–6.
64. Wilson RP, White CR, Quintana F, Halsey LG, Liebsch N, Martin GR, Butler PJ. Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *J Anim Ecol.* 2006;75:1081–90.

65. DeRuiter S. tagtools: Tools for Working with Data from High-Resolution Biologging Tags. R package version R 3.4.3. 2018. <http://www.animaltags.org/doku.php>.
66. Ladds MA, Salton M, Hocking DP, McIntosh RR, Thompson AP, Slip DJ, Harcourt RG. Using accelerometers to develop time-energy budgets of wild fur seals from captive surrogates. *PeerJ*. 2018;6:e5814.
67. Halsey LG, Green JA, Wilson RP, Frappell PB. Accelerometry to estimate energy expenditure during activity: best practice with data loggers. *Physiol Biochem Zool*. 2009;82:396–404.
68. Freitas C, Lydersen C, Ims RA, Fedak MA, Kovacs KM. A simple new algorithm to filter marine mammal Argos locations. *Marine Mammal Sci*. 2008;24:315–25.
69. Bivand R, Lewin-Koh N. mapproj: tools for reading and handling spatial objects. R package version 0.8-39. 2016. <https://CRAN.R-project.org/package=mapproj>.
70. Patterson A, Gilchrist HG, Chivers L, Hatch S, Elliott K. A comparison of techniques for classifying behavior from accelerometers for two species of seabird. *Ecol Evol*. 2019;9:3030–45.
71. Beltramino LE, Venerus LA, Trobbiani GA, Wilson RP, Ciancio JE. Activity budgets for the sedentary Argentine sea bass *Acanthistius patachonicus* inferred from accelerometer data loggers. *Austral Ecol*. 2019;44:397–408.
72. Pohle J, Langrock R, van Beest FM, Schmidt NM. Selecting the number of states in hidden Markov models: pragmatic solutions illustrated using animal movement. *J Agric Biol Environ Stat*. 2017;22:270–93.
73. Worton BJ. Kernel methods for estimating the utilization distribution in home-range studies. *Ecol*. 1989;70:164–8.
74. Worton BJ. Using Monte Carlo simulation to evaluate kernel-based home range estimators. *J Wildl Manage*. 1995;794–800.
75. Calenge C. The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. *Ecol Modell*. 2006;197:516–9.
76. Peris A, Closa F, Marco I, Acevedo P, Barasona JA, Casas-Díaz E. Towards the comparison of home range estimators obtained from contrasting tracking regimes: the wild boar as a case study. *Eur J Wildl Res*. 2020;66:1–10.
77. Odum EP, Kuenzler EJ. Measurement of territory and home range size in birds. *Auk*. 1955;72:128–37.
78. Nilsen EB, Pedersen S, Linnell JD. Can minimum convex polygon home ranges be used to draw biologically meaningful conclusions? *Ecol Res*. 2008;23:635–9.

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