First three-dimensional tracks for the Ascension Frigatebird *Fregata aquila* highlight the importance of altitude for behavioural studies

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Abstract

Identifying at-sea foraging areas is a longstanding goal for seabird ecology and conservation. GPS tracks can reveal behaviour because slow, tortuous flight often indicates searching linked to feeding attempts, but two-dimensional (2D) paths may oversimplify three-dimensional (3D) flight. Here, we present the first 3D tracks for Ascension Frigatebirds *Fregata aquila* and assess whether incorporating flight altitude improves our ability to describe putative behavioural states. We compare results using altitude derived from GPS loggers and barometric altimeters deployed simultaneously. Tracked birds (three females) travelled at a mean altitude of 178 m and attained maximum heights of 1,658–1,871 m (measured by barometric altimeters). Hidden Markov models based on 2D tracks defined three states (interpreted as 'search', 'slow travel' and 'fast travel'). However, with 59.5% of locations defined as 'search', identifying the most important foraging hotspots would be challenging. Including altitude was informative, allowing models to define two further states by introducing high-altitude 'soaring/thermalling' behaviour (3.4% of locations) and dividing 'search' into mid-altitude (44.7%) and low-altitude (12.2%), the latter being more likely to represent prey capture. Barometric altitude was less prone to large errors than GPS, but GPS altitude was highly correlated ($r = 0.94$) and state assignments overlapped by 88% overall. Using GPS altitude would reduce potential tag effects and allow us to model tracks in 3D for males and lighter females, which are too small to carry both loggers. Overall, incorporating flight height from either barometric altimeters or GPS loggers into behavioural models improved our ability to distinguish putative foraging events from high-altitude flight.

Introduction

Breeding seabirds are central place foragers that can travel vast distances from the nest to feed. Many factors influence the distance travelled to forage, including species ecology (Thaxter *et al*. 2012; Oppel *et al*. 2018), prey availability (Hamer *et al*. 2007; Paiva *et al*. 2013; Thorne *et al*. 2015), and competition (Ashmole 1963; Lewis *et al*. 2001; Wakefield *et al*. 2013; Oppel *et al*. 2015; Corman *et al*. 2016). Our understanding of the patterns and processes involved in determining foraging behaviour is crucial to conserving seabirds both at their breeding colonies and their often-distant foraging areas (Croxall *et al*. 2012; Lewison *et al*. 2012). A key goal is to identify geographical areas or predictable environmental features associated with foraging to prioritise areas for conservation measures (BirdLife International 2010). Foraging is often classified from tracking data by identifying slow and tortuous flight as searching behaviour associated with feeding attempts (Andersson 1981; Fauchald & Tveraa 2003). However, this approach generally operates within a two-dimensional (2D) plane, whereas aerial and marine species move in three dimensions (3D) (Bailleul *et al*. 2010; Belant *et al*. 2012). Many wide-ranging species have evolved strategies such as thermalling and dynamic soaring that improve flight efficiency when travelling over large distances (Weimerskirch *et al*. 2003; Sachs *et al*. 2012; Yonehara *et al*. 2016). These movements may not follow the direct trajectories that many species exhibit during transit behaviour, so additional data streams may be needed to confidently interpret behavioural patterns (McClintock *et al*. 2017).

Identifying important areas for seabirds is particularly challenging in the tropics, where low productivity and unpredictable prey distributions mean that foraging is often diffuse and not linked to stable environmental features (Ashmole 1963; Boekelheide & Ainley 1983; Weimerskirch 2007). Frigatebirds provide an example of extreme specialisation to such sparse environments. They are the only marine animals that are physically unable to enter the water despite relying entirely on marine resources, such as flying fish and squid (Weimerskirch *et al*. 2003, 2010), which can be brought to the surface by other aquatic predators (Au & Pitman 1986; Miller *et al*. 2018). Frigatebirds may also predate on seabird chicks or turtle hatchlings and feed through kleptoparasitism, but this is more common in immature birds (Stonehouse & Stonehouse 1963; Osorno *et al*. 1992; Lagarde *et al*. 2001). As their plumage is not waterproof and they cannot reliably take off when wet (Mahoney 1984), they cannot rest on the water and must remain in flight for the duration of a foraging trip (Weimerskirch *et al*. 2003; De Monte *et al*. 2012; Weimerskirch *et al*. 2016). Consequently, frigatebirds have extremely low wing loadings, allowing them to remain airborne for many days with very low energetic output (Brewer & Hertel 2007). They use thermals to reach high altitudes, allowing them to glide and soar to efficiently cover large distances (Weimerskirch *et al*. 2016), even sleeping on the wing in rising air currents (Rattenborg *et al*. 2016). However, foraging can only take place when birds are near to sea level, and so altitude data is likely to provide relevant information for behavioural models.

The Ascension Frigatebird *Fregata aquila* is endemic to Ascension Island, an isolated peak in the central tropical Atlantic, 1,300 km from the nearest land. The species is regarded as 'vulnerable' due to its restricted range (BirdLife International 2018a). The Ascension Frigatebird only recently recolonised the main island from Boatswainbird Islet after the successful eradication of Feral Cats *Felis catus* in 2006 (Ratcliffe *et al*. 2008, 2010). A previous study described the at-sea foraging distributions of this species, showing them to roam over a large marine area with some trips extending up to 1,100 km from the colony (Oppel *et al*. 2017). However, more detailed behavioural analyses are required to locate foraging hotspots within this very large area. In this study, we use a combination of GPS and barometric altimeter data to reconstruct the first 3D foraging tracks of the Ascension Frigatebird. GPS altitude is less accurate than latitude and longitude because four satellites are required for 3D positions, compared to three for 2D positions, and the location of those satellites affects accuracy (Dussault *et al*. 2019). These GPS altitude errors can occur at the scale of frigatebird flight (De Monte *et al*. 2012). Barometric pressure loggers are less prone to large errors but are affected by changing sea level air pressure (Berberan-Santos *et al*. 1997). Consequently, we first compare the distribution of error in the altitude recorded at a fixed point by GPS loggers and barometric pressure loggers. We then evaluate the implications of incorporating altitude into behavioural classifications performed using hidden Markov models (HMMs): a commonly used technique for decomposing tracking data into discrete movement patterns based primarily on speed and turning angle (Michelot *et al*. 2016; Bennison *et al*. 2017). Finally, we assess whether altitudes recorded by GPS loggers can be reliably used in place of barometric pressure data in future studies of this species (e.g. Rattenborg *et al*. 2016; Weimerskirch *et al*. 2016; Parr *et al*. 2017).

Methods

Study site and sampling: We studied Ascension Frigatebirds on the Letterbox Peninsula, Ascension Island (7°56'S 14°18'W), in September and October 2018. We caught five incubating females by hand on the nest and sheltered eggs from the sun during processing. Birds were first weighed to the nearest 10 g and only tagged if the logger and attachment weight was less than 3% of body mass. Due to considerable sexual dimorphism (Fairbairn & Shine 1993), males were too light to carry both a GPS and altimeter. Modular Signal Recorder (MSR) 145W air pressure and temperature loggers weighing 18 g and scheduled to record at 1 Hz, were attached to the underside of four central tail feathers using Tesa® tape. GPS loggers (iGot-U GT-120, Mobile Action Technology) waterproofed with heatshrink plastic, weighing 18.5 g or 15.3 g (different battery sizes) and scheduled to record at five-minute intervals, were attached to the top of four central tail feathers using Tesa® tape. Three birds were tagged with large battery loggers; a total logger weight of 36.5 g (2.25–2.77% of body mass) and two birds with small battery loggers; a total logger weight of 33.3 g (2.73% and 2.67% of body mass). Handling time was limited to 10 minutes. Due to issues with marking frigatebirds with leg rings owing to their short tarsus (Stonehouse & Stonehouse 1963; Schreiber 1999) or wing tags that reduce breeding success (Trefry *et al*. 2013), we marked birds on the forehead using gold nail varnish for re-sighting. Tagged individuals were recaptured after 7–14 days, and after logger removal, individuals were weighed to assess the impact of tagging on body mass. Three control birds of the same breeding stage and broad location were captured and processed using the same protocol. Both control and study nests were monitored throughout the study period, and after recapture if possible.

GPS data: We located individual nests by taking the modal latitude and longitude of GPS locations within 3 km of the colony (rounded to four decimal places), checked against locations from a handheld GPS. Using the 'geosphere' (Hijmans

2017) and 'raster' (Hijmans 2018) R packages, we split GPS tracks into trips when the bird crossed a radius of 500 m from the nest, with one additional GPS location at the start of each trip and the end of complete trips. We checked for erroneous positions by visually assessing plots, and by calculating the ground speed between each successive location. The maximum ground speed was 19.17 ms^{-1}, which was substantially lower than the 27.3 ms^{-1} used in a maximum velocity filter for Christmas Island Frigatebirds *F. andrewsi* (Hennicke *et al.* 2015). We corrected the GPS altitude for the difference between the ellipsoid and the local geoid using the Earth Gravitation Model 2008-WGS84 version in a 2.5 x 2.5-minute grid (Pavlis *et al.* 2012; downloaded from https://earth-info.nga.mil/GandG/wgs84/gravitymod/egm2008/egm08_gis.html). We used the extract function from the 'raster' package with a bilinear method that interpolates between the four nearest cells (Hijmans 2018). For each bird, we calculated the track duration, total distance travelled, and the maximum distance reached from the colony.

Barometric pressure data: Pressure data at 1 Hz were smoothed across the previous five and next five records (an 11-second window) to reduce the impact of very short-lived pressure changes, such as those caused by turbulence (Cleasby *et al.* 2015). We used the barometric formula to estimate altitude in meters above sea level (Berberan-Santos *et al.* 1997). Sea level pressure was calibrated using the mean temperature and air pressure recorded by the loggers at the nest for 48 hours before the foraging trip, and the altitude of the nest as the modal value recorded by the GPS loggers (rounded to one decimal place). We calculated the error for each altitude record from the fixed altitude at the nest within the 48-hour period measured by both loggers. The relatively stable air pressure in the tropics allows for birds to travel long distances from the calibration point without substantial changes to sea level pressure. 3D tracks were visualised using the 'rayshader' R package (Morgan-Wall 2019).

Behavioural modelling: Hidden Markov models (HMMs) implemented in the R package 'momentuHMM' (McClintock & Michelot 2018) were used to differentiate between discrete behavioural states in 2D (speed and turning angle) and 3D tracks (speed, turning angle and altitude; see R code available at doi.org/10.5281/zenodo.3672124). We linearly interpolated the GPS data to the five-minute sampling frequency to regularise the data. To make GPS and barometric altitudes comparable, we linearly interpolated barometric altitudes between each GPS position. Frigatebirds are unable to dive or rest on the water so for the purposes of HMM-fitting we adjusted barometric and GPS altitudes <= 0 m to a nominal height of 0.1 m. This was a modelling constraint imposed by the positive continuous gamma distribution used to model flight altitude and affected a small proportion of locations (barometric: n = 11, 0.2%; GPS: n = 29, 0.6%; values below zero are included in all other calculations of summary statistics and plots unless otherwise stated). A *k*-means clustering algorithm (with *k* = number of states, 1–5) was used to select appropriate starting values for the state-dependent probability distribution parameters of each data stream (Dean *et al.* 2013), assuming a gamma distribution for speed and altitude, and a von Mises distribution with a mean of zero for turning angle. Starting values were then randomly perturbed over 10 optimisations to evaluate the impact on model likelihood and help avoid convergence towards local maxima (McClintock & Michelot, 2018). For both 2D and 3D analyses, we compared the fitted models with 1–5 putative latent behavioural states based on their Akaike Information Criterion (AIC) and used an 'elbow criterion' (i.e. the point at which adding additional states results in more marginal reductions in AIC) to select the best trade-off between minimising errors on state parameters and overfitting (Dean *et al*. 2013). The Viterbi algorithm was then used to decode the most probable sequence of underlying states from the selected model for each individual track (McClintock & Michelot, 2018). To assess how state assignments based on barometric altitude measurements compare with those based on GPS-derived altitudes we refitted the 3D HMM using the same starting parameters but with barometric altitude substituted by GPS altitude in the vertical dimension. We then calculated the state confusion matrix and overall assignment accuracy using the 'confusionMatrix' function in 'caret' R package (Kuhn *et al*. 2019).

Statistics: To quantify the correlations between altitude derived from barometric pressure and from GPS, and between altitude and speed in travelling states, we first subsampled data locations to 50 minute intervals to provide altitude measures that were no longer autocorrelated. We then used Spearman's rank tests performed in R (R Core Team 2019).

Results

Data recovery and tag effects: We recaptured all five of the tagged individuals and successfully recovered loggers from four, the fifth having shed the loggers along with the central tail feathers. One individual remained at the nest for 5–7 days after deployment, meaning that the GPS logger battery was exhausted before the foraging trip started. Three foraging trips were therefore available for analysis. One control bird abandoned during the study, but this is unlikely to have been a handling response as the bird was observed on the nest for 14 days after the initial capture. The other two control nests were attended for at least 7–17 days after initial capture. We recorded no substantial difference in body mass before and after tagging (before: 1,160 g, 1,620 g, 1,400 g and 1,320 g; after: 1,250 g, 1,420 g, 1,400 g and 1,380 g respectively; mean change -12.5 ± 65.2 g S.E., n = 4).

Table 1. Summary of partial foraging trips for Ascension Frigatebirds *Fregata aquila* tracked using GPS loggers and barometric altimeters simultaneously. Means are given ± 1 S.E.

Individual	Mean altitude (m)	Maximum altitude (m)	Period recorded (days)	Total distance (km)	Maximum distance from the colony (km)
Bird 1	164	1,825	2.69	908	376
Bird 2	175	1,658	9.52	3,644	411
Bird 3	183	1,871	6.09	2,169	677
Mean ± SE	**189 ± 2.4**	**1,678 ± 22**	**6.10 ± 1.97**	**2,240 ± 791**	**488 ± 95**

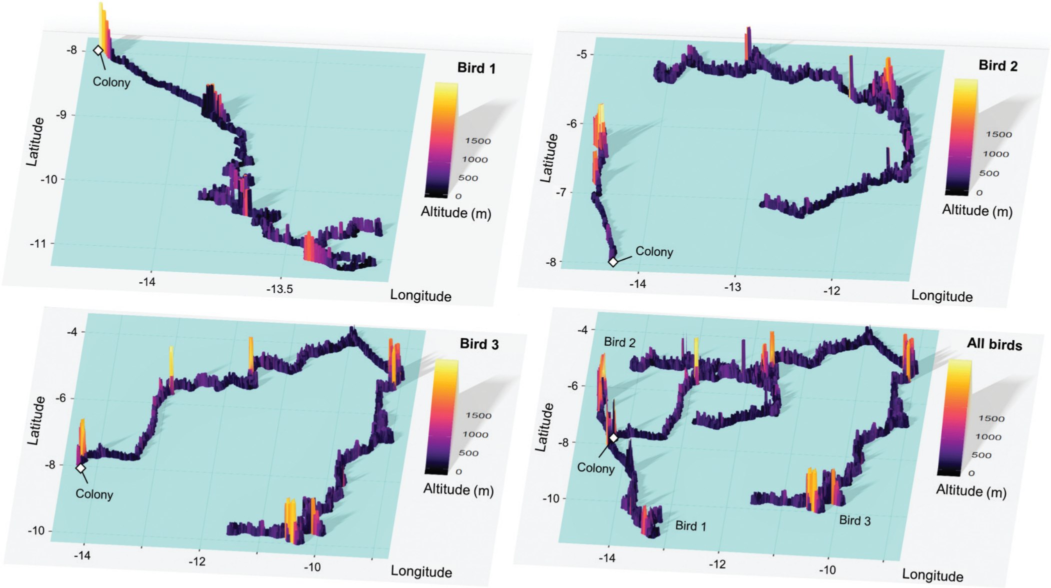


Figure 1. Three-dimensional tracks for three Ascension Frigatebirds *Fregata aquila* showing latitude and longitude recorded by GPS loggers and altitude derived from barometric pressure loggers. The gap for Bird 2 was due to missing GPS data.

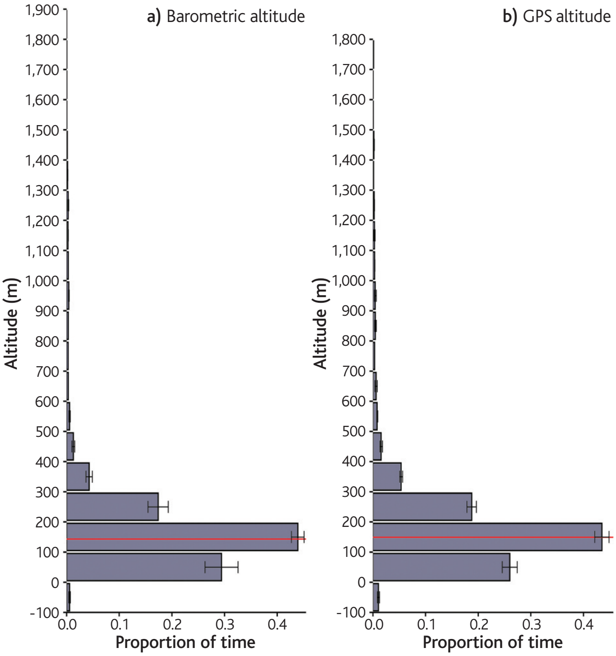


Figure 2. Vertical utilisation distributions of Ascension Frigatebirds *Fregata aquila* tracked with a) barometric altimeters and b) GPS loggers showing the mean (± 1 S.E.) proportion of time spent in 100 m altitude bands. The median flight height (144 m for barometric and 150 m for GPS) is marked with a red line.

Foraging trip characteristics: We recorded a total of 18.3 days of the at-sea foraging trips for three Ascension Frigatebirds (Figure 1), during which they travelled a total of 6,721 km, reaching up to 677 km from the colony (Table 1). These foraging trips fell within the range of Ascension Frigatebirds tracked from the main breeding colony on Boatswainbird Island (260 m off the coast of Ascension Island near to the Letterbox Peninsula) in 2013 and 2014 (Oppel *et al.* 2017), so are likely to represent normal foraging behaviour for the species. Frigatebirds largely travelled within 100–200 m altitude (Figure 2), and we recorded similar mean altitudes (164–183 m) and maximum altitudes (1,658–1,872 m) among individuals.

Behavioural models: Inspection of model AICs suggested that a three-state HMM adequately described the dominant behavioural patterns in 2D Ascension Frigatebird tracks, with state parameter estimates that were qualitatively similar to those recently reported by Austin *et al*. (2019) for the Magnificent Frigatebird *F. magnificens*. These consisted of: 1) a 'travelling' state characterised by sustained, directed flight with high speeds and low variance in turning angle; 2) an intermediate state with similarly low turning angle variance but lower travel speeds which Austin *et al*. (2019) described as 'search/rest' (which included resting on land) but which we refer to as 'slow travel' (as Ascension Frigatebirds have no access to land away from the colony); and 3) an 'area restricted search' type behaviour characterised by slow speeds and high variance in turning angle, which includes putative foraging events (Table 2; Austin *et al*. 2019).

Our ability to discriminate potential foraging events was substantially improved when altitude derived from barometric pressure was also included in the model (Figures 3–5). In the 3D case, model AICs supported fitting a more complex five-state HMM. Parameter estimates maintained the two 'travel' classes identified in the 2D model with the additional distinction that 'fast travel' was associated with higher elevations than 'slow travel'. This association was underscored by the significant positive correlation between flight altitude and travel speed across travel-associated locations (Spearman's $r = 0.22$, $S = 1,231,694$, $P = 0.001$). A third high-speed state characterised by very high flight altitudes and more variable turning angles was also identified, which we interpret as the 'thermalling/gliding' or soaring behaviour described in other frigatebird species (Weimerskirch *et al*. 2003, 2016), along with two area-restricted search (ARS) states: a 'mid-altitude ARS' with a mean elevation of 155 m and a 'low-altitude ARS' with a mean

Table 2. Parameter estimates of the state-dependent probability distributions from hidden Markov models fitted to 2D and 3D Ascension Frigatebird *Fregata aquila* tracks, along with the proportion of time spent in each behavioural state. Estimates for speed and altitude (derived from barometric pressure unless labelled as GPS) are presented as means ± 1 S.D., while turning angle as the concentration parameter (κ) of a von Mises distribution with mean = 0 (higher values of κ indicate less variable angles and thus more directed flight).

Model	Behavioural mode	Speed (kph)	Angle (κ)	Altitude (m)	% locations
2D	Travel (fast)	27.9 ± 8.9	5.1	-	15.0
	Travel (slow)	15.7 ± 4.2	4.1	-	25.5
	Search	9.6 ± 5.6	0.7	-	59.5
3D	Thermal/glide	23.3 ± 10.5	2.7	908 ± 327	3.4
	Travel (fast/high)	21.6 ± 10.9	1.9	255 ± 72	19.2
	Travel (slow/mid)	17.9 ± 5.9	4.9	120 ± 41	20.4
	Mid-altitude search	9.8 ± 5.5	0.7	155 ± 50	44.7
	Low-altitude search	7.9 ± 4.3	1.0	64 ± 44	12.2
3D GPS	Thermal/glide	22.6 ± 10.9	2.6	890 ± 321	3.4
	Travel (fast/high)	21.0 ± 10.9	1.8	263 ± 76	19.2
	Travel (slow/mid)	18.0 ± 5.9	5.2	127 ± 45	20.4
	Mid-altitude search	9.7 ± 5.4	0.7	156 ± 54	44.7
	Low-altitude search	7.8 ± 4.1	1.1	58 ± 51	12.2

elevation of 64 m coupled with very slow speeds and highly variable turning angles. Of the 5,169 regularised track locations, 3,074 (59.6%) were classified as ARS in the 2D model, of which, 408 (13.3%) were above the maximum flight height of low-altitude ARS (232 m), and 95 (3.1%) were above the maximum flight height of both ARS states (344 m). Furthermore, the 2D model identified 36 records in the lowest 5% of altitude measures (below 38 m) as travel, while the 3D model classed 20 as travel. This suggests that the 2D model is a poorer predictor of the distribution of potential prey capture events.

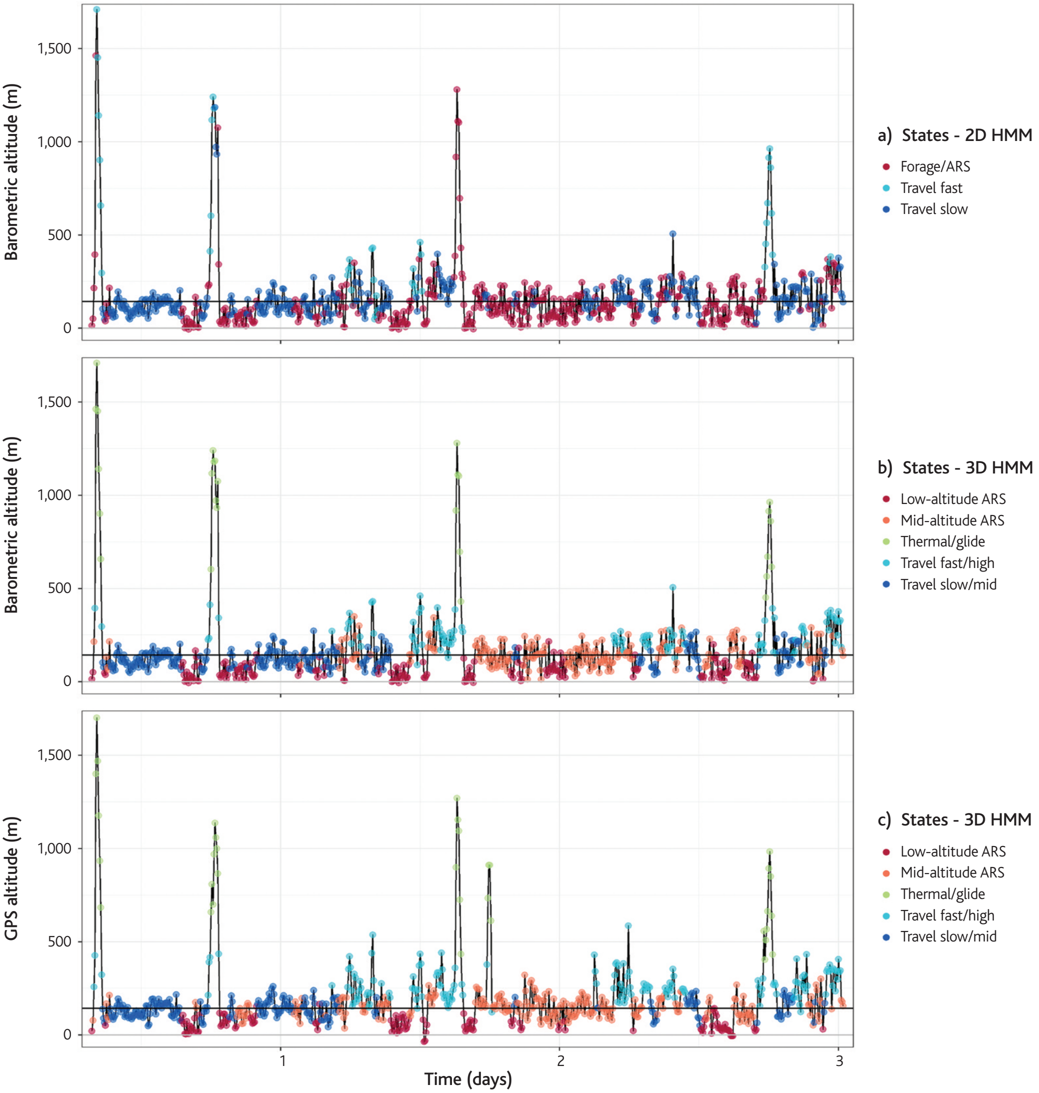


Figure 3. Flight altitude recorded for the foraging trip of Ascension Frigatebird *Fregata aquila* 1, with circle colour indicating behavioural classification for each GPS location from a) a 2D hidden Markov model (HMM) and b) a 3D HMM using barometric altitude and c) a 3D HMM using GPS altitude. The black horizontal line shows the median altitude across all three birds (144 m).

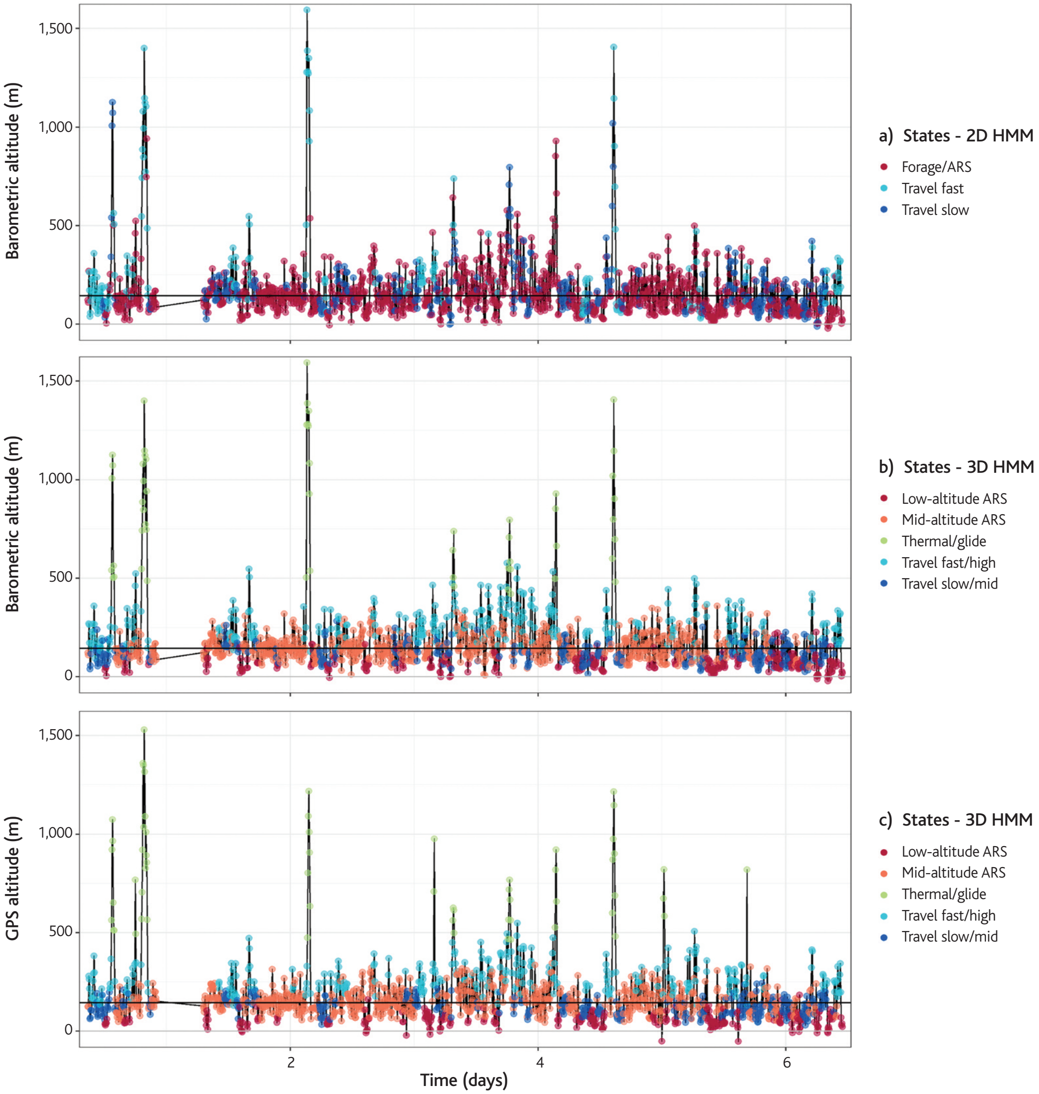


Figure 4. Flight altitude recorded for the foraging trip of Ascension Frigatebird *Fregata aquila* 2, with circle colour indicating behavioural classification for each GPS location from a) a 2D hidden Markov model (HMM), b) a 3D HMM using barometric altitude, and c) a 3D HMM using GPS altitude. The black horizontal line shows the median altitude across all three birds (144 m).

Comparison of GPS and pressure-derived altitudes: GPS altitude had a similar mean error from the reference point at the nest to barometric altitude (7.2 m and 8.0 m, respectively; Table 3), but a much greater standard deviation (18.0 m and 4.9 m), minimum error (-236.1 m and -19.3 m) and maximum error (675.3 m and 23.2 m). GPS altitude had a mean difference compared to barometric altitude of 5.7 m ± 59.3 SD (range: -1,397–1,219 m). However, the two altitude measures were highly correlated with a Spearman's correlation coefficient of $r = 0.94$ ($S = 1,168,360$, $P < 0.001$; Figure 6). Refitting the 3D HMM with GPS-derived altitude resulted in an overall

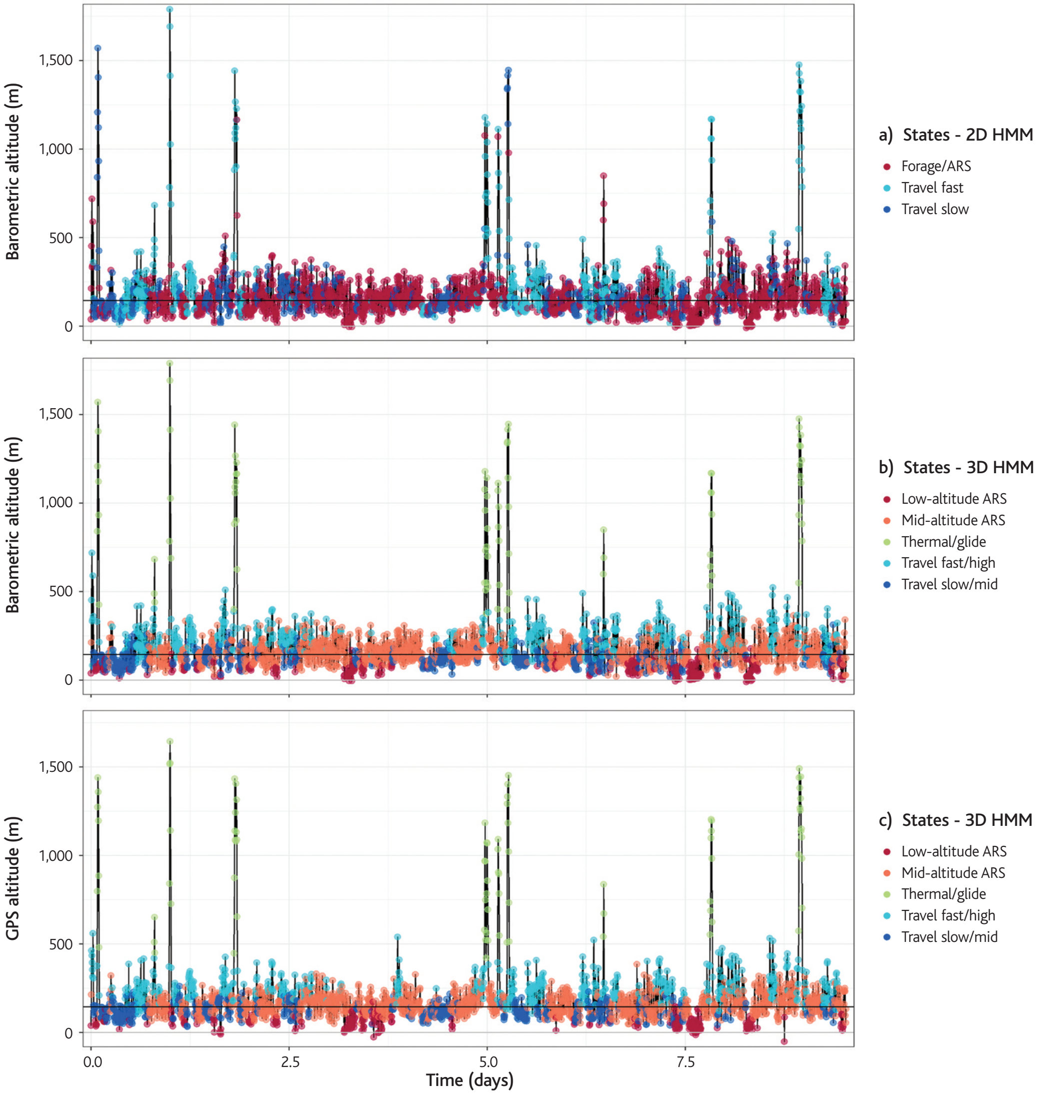


Figure 5. Flight altitude recorded for the foraging trip of Ascension Frigatebird *Fregata aquila* 3, with circle colour indicating behavioural classification for each GPS location from a) a 2D hidden Markov model (HMM), b) a 3D HMM using barometric altitude, and c) a 3D HMM using GPS altitude. The black horizontal line shows the median altitude across all three birds (144 m).

state assignment accuracy of 87.9% (95% CI = 86.9–88.7) compared to those based on barometric pressures (Figure 7). Of the inferred 'low-altitude search' behaviours, which includes putative foraging events, 74.3% were correctly identified using GPS altitude along with 97.6% of apparent thermalling behaviour. Using GPS altitude identified 26 bouts of thermalling/soaring compared to 21 for barometric altitude, which relates to 21 matching bouts and 4 additional bouts that may relate to GPS error given that they all contain only 1–3 locations (Figure 3–5). The most common state confusions occurred between low-altitude and mid-altitude 'search' states.

Table 3. Measures of altitude at the nest during a 48-hour period before the start of the foraging trip. Means and standard deviations (SD) were calculated as the mean absolute difference (error) from the nest altitude (the modal value from the GPS and the measurement).

	GPS altitude error (m)				Barometric altitude error (m)			
Individual	mean	SD	min	max	mean	SD	min	max
Bird 1	11.9	27.1	-236.1	385.1	9.4	6.4	-19.3	23.2
Bird 2	5.5	21.5	-66.7	675.3	7.0	4.1	-16.8	16.5
Bird 3	4.1	5.5	-46.4	70.3	7.6	4.1	-17.1	14.3
All birds	**6.9**	**21.1**	**-236.1**	**675.3**	**8.0**	**5.1**	**-19.3**	**23.2**

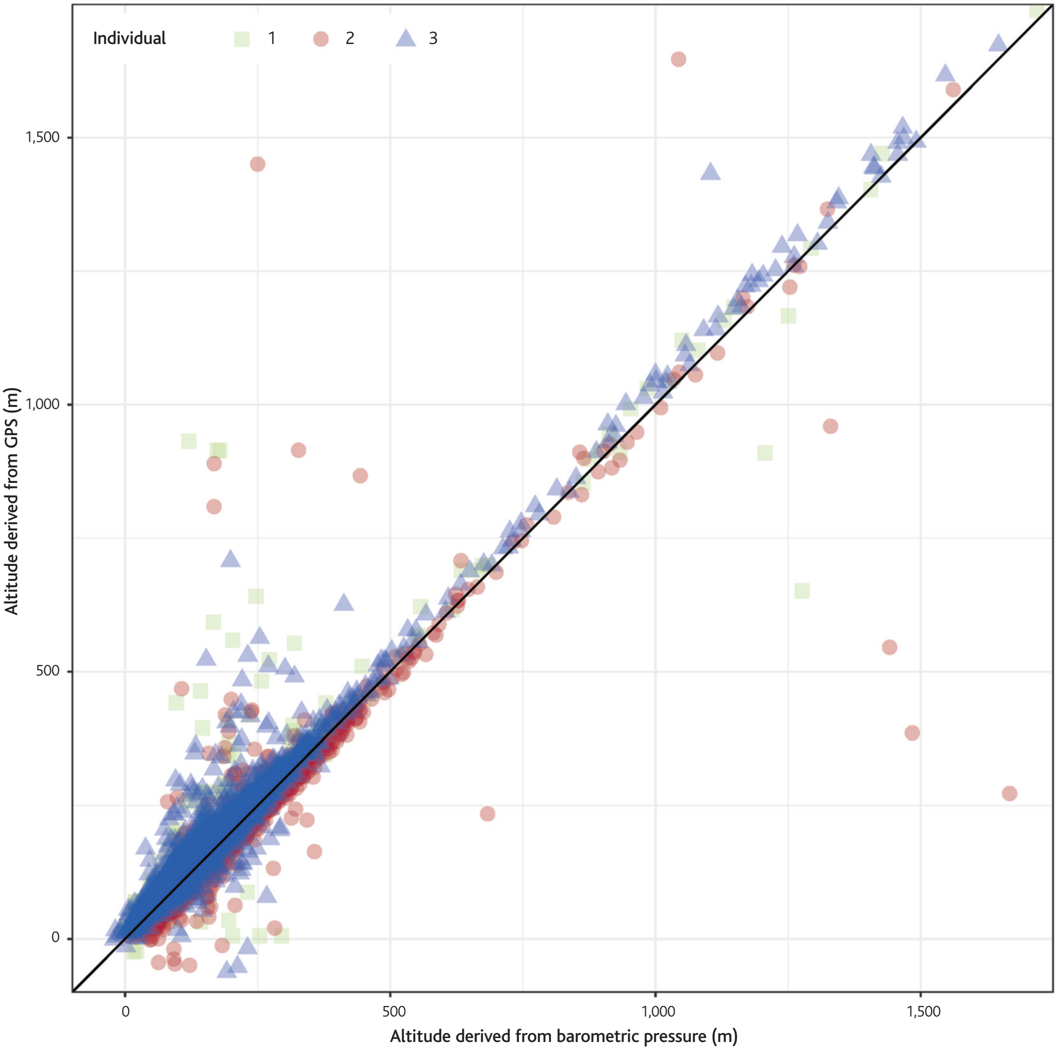
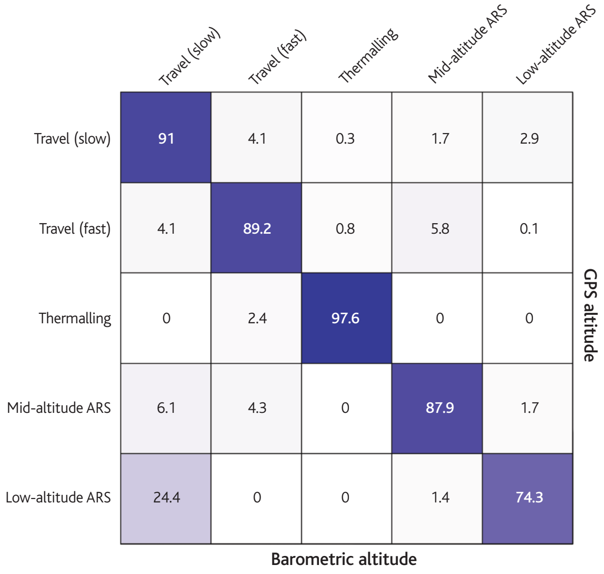


Figure 6. Comparison of altitude measures derived from barometric pressure loggers (higher accuracy) and GPS loggers (lower accuracy) for three sections of foraging trips made by Ascension Frigatebirds *Fregata aquila*. The black line shows y = x.



	Travel (slow)	Travel (fast)	Thermalling	Mid-altitude ARS	Low-altitude ARS
Travel (slow)	91	4.1	0.3	1.7	2.9
Travel (fast)	4.1	89.2	0.8	5.8	0.1
Thermalling	0	2.4	97.6	0	0
Mid-altitude ARS	6.1	4.3	0	87.9	1.7
Low-altitude ARS	24.4	0	0	1.4	74.3

Figure 7. Confusion matrix showing state assignment discrepancies in 3D hidden Markov models fit using GPS triangulation and barometric pressure-derived altitudes for Ascension Frigatebird *Fregata aquila* foraging trips. Values along the diagonal represent the percentage of locations that are classified consistently between the barometric pressure- and GPS-derived altitude (ARS = area-restricted search). The matrix is read row-wise and shows the percentage of state assignments in the pressure model that are 'misclassified' in the GPS model.

Discussion

We present the first 3D tracks of the Ascension Frigatebird (n = 3 females) and reveal the considerable altitudinal range occupied by this species. Tagged individuals periodically reached flight heights in excess of 1,000 m during extended foraging trips that ranged up to 677 km from their breeding colony. The mean maximum recorded altitude of 1,785 m (maximum 1,871 m) is similar to the 1,764 ± 620 m (maximum 2,867 m) reported for the Great Frigatebird *F. minor* in the Mozambique Channel (Weimerskirch *et al.* 2004), but somewhat less than the record of 4,600 m for Great Frigatebirds tracked from Galápagos (Rattenborg *et al.* 2016). However, although tracks were punctuated by periods of high-altitude flight, birds spent the largest proportion of their time travelling at 100–200 m, which may allow them to maintain visual contact with the ocean to detect potential foraging opportunities.

As shown in Magnificent Frigatebirds (Austin *et al*. 2019), hidden Markov models using 2D movement parameters derived from GPS coordinates (step length and turning angle) were able to distinguish between broad behavioural modes in Ascension Frigatebirds, interpreted as 'search' (59.6% of locations), 'fast travel' and 'slow travel'. However, due to the large vertical range occupied by this species, our results suggest that they provide an overly simplified representation of Ascension Frigatebird behaviour and are limited in their ability to provide an effective means of identifying hotspots of putative foraging (i.e. prey capture) that must occur at low-altitudes. The 2D model placed 95 locations in the state interpreted as 'search' that were above the maximum flight height of 'search' states from the 3D model (344 m), likely because high-altitude thermalling can resemble searching when measured in 2D (Figures 3–5). Furthermore, 2D models classified more low-altitude locations as 'travel' than 3D models, but some of these locations may represent foraging as frigatebirds prefer to travel at higher altitudes, particularly while sleeping (Rattenborg *et al.* 2016). By incorporating altitude into HMMs we were able to refine and further partition 'travel' and 'search' states to be more informative and representative of frigatebird behaviour (see McClintock *et al.* 2017). This included identifying periods of 'soaring/thermalling' behaviour, a defining characteristic of frigatebird flight, and separating mid- and low-altitude search, the latter of which is expected to

Ascension Frigatebirds
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encompass the vast majority of surface-orientated foraging and prey capture. Consequently, the low-altitude ARS class allows us to narrow down foraging hotspots from the 59.6% of locations classed as 'search' by the 2D model to the 12.2% classed as 'low-altitude search' by the 3D model. While searching could begin at high altitudes, we are often interested in locating areas where search may lead to prey capture, which must occur at low altitudes. This may mirror the hierarchical spatial scales at which foraging pelagic seabirds have been shown to operate in according to prey distribution and patchiness (Fauchald *et al*. 2000). The ability to discriminate between these behavioural modes is an important step that will allow for more detailed study of the underlying environmental factors that may trigger them.

Incorporating vertical data has the potential to dramatically improve behavioural inferences in seabird tracking studies, but its use has often been limited by the cost or additional weight of standalone altimeters or combined loggers. Many GPS tags record altitude data, although this is often considered to be error-prone and unreliable (Dussault *et al*. 2019), however, the scale of the errors had not been assessed in relation to frigatebird behaviour. At stable elevations, we found that the altitude data recorded by GPS loggers were more likely to exhibit large errors than the corresponding barometric altimeter data, with a maximum error of 675 m compared to only 23 m (Table 3). At sea, we also found more erroneous negative altitudes in the GPS data (29 compared to 11), down to a minimum of -53 m (compared to -22 m). Despite this, GPS altitude still provided sufficient information to inform behavioural models (Figure 3–5; Figure 7). Indeed, there was a strong correlation between altitude derived from the two methods (Figure 6), and overall state assignment accuracy was high between 3D HMMs fit using each data stream (Figure 7). It may also be possible to further improve GPS data by identifying a limit to possible rates of changes in altitude in order to filter anomalous records. The additional high altitude thermalling/soaring bouts labelled by the GPS altitude but not the barometric altitude (Figures 3–5) could be corrected by filtering or smoothing (De Monte *et al*. 2012). Future studies of Ascension Frigatebirds could therefore require only a single GPS logger to generate useable tracks for analysis in three dimensions. Our results are important because reducing logger weight and drag are key goals in biologging (Vandenabeele *et al*. 2011; Bodey *et al*. 2018; Kay *et al*. 2019).

Logger weight limited our study to individuals over 1,220 g with large loggers and 1,110 g with small loggers. This prevented us from tagging more than five individuals, with only three deployments returning data. This is a small sample, but all three showed a similar range of altitudes, maximum altitudes, and number of high-altitude flights per day (Figures 3–5). Additionally, they performed long trips; we recorded 5,169 locations over 18.3 days including 21 high altitude flights. However, our samples contain only large females (the heavier sex) as many females and all males were too light to be tagged with both loggers. Our study only tracked incubating females, and so we cannot confirm that they occupy similar altitudes to males or females during other breeding stages. Studies of flight altitude for other frigatebird species used either only females (Rattenborg *et al.* 2016; Weimerskirch *et al.* 2016) or did not report the sex (De Monte *et al.* 2012) or the effect of sex (Weimerskirch *et al.* 2004; Sachs & Weimerskirch 2018). Moreover, other studies only tagged during a single breeding stage (Rattenborg *et al.* 2016) or did not compare breeding stages (Weimerskirch *et al.* 2016; Sachs & Weimerskirch 2018). In 2D, male Ascension Frigatebirds had longer trip durations, total distances and maximum distances reached from the colony, but sex accounted for less variation than season (hot/cool) or breeding stage (incubation/chick-rearing; Oppel *et al.* 2017). While our sample is limited, we cannot think of a reason why individual, sex or breeding stage would impact the relationship between barometric and GPS altitudes, and if a larger sample provided by GPS altitude shows that other groups occupy a different altitudinal range, a group-specific model could be produced.

Improving our ability to identify important geographical areas or environmental features for foraging is key to conserving wide-ranging seabirds (BirdLife International 2010). Vertical data is particularly important for studies of frigatebird foraging ecology because they do not dive, meaning that feeding attempts cannot be identified using wet/dry sensors or dive depth loggers that can provide this information for many other species (e.g. Paredes *et al.* 2014; Cox *et al.* 2016). A better understanding of frigatebird foraging behaviour could also be useful for interpreting the behaviour of the other four frigatebird species, including the critically endangered Christmas Island Frigatebird (Hennicke *et al.* 2015; BirdLife International 2018b). Furthermore, covariates could inform our understanding of the causes of particular state changes, such as wind speed and direction (Amélineau *et al.* 2014; Weimerskirch *et al.* 2000). Many other studies of birds make use of GPS loggers, but do not include the altitude data in behavioural models and may be able to improve classification by incorporating these data. However, models would have to be validated before applying to species that do not have such a large altitude range. A similar approach could be applied for many species as HMMs can make use of a variety of additional data streams, including immersion, dive depth, acceleration and environmental covariates (Dean *et al.* 2013; McClintock *et al.* 2017; McClintock & Michelot 2018). In general, we advocate for more studies to incorporate different data streams and for more studies that use multiple measures of the same variables to assess relative error.

In conclusion, Ascension Frigatebird foraging behaviour is better described when altitude is considered alongside speed and turning angle, both in terms of providing foraging hotspots at multiple scales and reducing potential misclassifications. Furthermore, we show that while altitude measured by barometric pressure is less prone to large errors, GPS altitude is almost as informative for frigatebird foraging trips. Overall, we present an example of how additional data streams can be used in behavioural classification models and how potentially poor-quality data can be validated by comparing multiple measures of the same variable.

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