

Unexpectedly deep diving in an albatross

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eTOC Blurb

Albatross are surprisingly deep divers, suggesting an unforeseen behavioural flexibility that could influence bycatch risk in human fisheries, a key factor in many species' decline. Using miniature biologging technologies Guilford et al recorded Black-browed albatross diving self-propelled to 19m (52s), more than twice previous reliable records.

Albatrosses are the iconic aerial wanderers of the oceans, supremely adapted for long-distance dynamic soaring flight. Perhaps because of this they are considered poorly adapted for diving¹, in contrast to many smaller shearwater and petrel relatives, despite having amphibious eyes², and an *a priori* mass advantage for oxygen storage tolerance³. Modern biologging studies have largely confirmed this view^{4,5}, casting doubt on earlier observations using capillary tube maximum depth gauges¹ which may exaggerate depths, and emphasising albatrosses' reliance on near-surface feeding. Nevertheless, uncertainty about albatross diving remains an important knowledge gap since bycatch in human fisheries (e.g. birds become hooked when diving for longline bait fish) is thought to be driving many population declines in this most threatened group of birds⁶. Here we show, using miniature electronic depth loggers (TDRs), that black-browed albatross, *Thalassarche melanophris*, can dive to much greater depths (19m) and for much longer (52s) than previously thought: three times the maxima previously recorded for this species (6m & 15s), and more than twice the maxima reliably recorded previously for any albatross (from 113.7 bird-days of tracking^{4,5,7}). Further evidence that diving may be a significant behavioural adaptation in some albatrosses comes from co-deployed 3-axis accelerometers showing that these deeper dives, which occur in most individuals we tracked, involve active under-water propulsion without detectable initial assistance from momentum, sometimes with bottom phases typical of active prey pursuit. Furthermore, we find (from co-deployed GPS) that diving occurs primarily in the distal portions of long-distance foraging trips, with deeper dives occurring exclusively during daylight or civil twilight confirming the importance of visual guidance.

Leg-mounted TDRs, and back-mounted GPS, were deployed during single foraging trips and successfully retrieved from 28 black-browed albatrosses of known sex and age breeding at

New Island, western Falklands, during late incubation and early brood guard, yielding 436 valid dives below 1m depth over 80 bird-days. 88 dives (20%) were deeper than the deepest dive reliably recorded previously for this species (6m)⁴, 30 (6.8%) were to at least 10m, and the deepest dive recorded 19.12m (Figure 1A). Dive durations (Figure 1B) were commensurately long, with 139 (31.9%) dives longer than 15 seconds, and the longest lasting 52s, more than three times longer than previously recorded reliably for this species⁴, and more than 2.5 times longer than any albatross (19s for a shy albatross⁷).

Figure 1A shows that diving was not restricted to just a small number of specialist individuals, with all but two birds (93%) diving to at least 1m depth, 19 birds (68%) to at least 6m, and 14 (50%) diving to at least 10m. Individual mean maximum depth was 10.0m (range, 2.3m - 19.1m). Similarly, most birds tracked (76%) showed maximum submergence times longer than the maximum previously recorded for this species (15s), with the mean maximum dive duration 30.7 seconds (range, 7 - 52sec). Neither was diving restricted by sex or age. Excluding two birds that did not record dives below 1m (one of each sex), male (N=15) and female (N=11) albatrosses had similar mean dive depths (4.2 ± 3.39 m for males; 3.8 ± 2.54 m for females), and dive depths did not vary with age (none of our age and sex models improved fit over the null model: Δ AIC: sex*age: 9.06; sex + age: 5.71; age: 4.91; sex: 0.83).

Many dives have active bottom phases with small depth changes characteristic of prey pursuit⁸. Concurrent data from back-mounted accelerometers for 9 birds (98 dives) show that these dives are complex behavioural manoeuvres. Seabirds can achieve depth through momentum from an aerial plunge, underwater propulsion, or both. Whilst some plunge diving has been suggested for shy albatross⁷, our data suggest surface duck diving or very limited aerial momentum, with slow descents (mean $0.6 \text{ m}\cdot\text{s}^{-1}$, max $1.2 \text{ m}\cdot\text{s}^{-1}$) which were no faster nearer the surface (see S1). Active under-water propulsion drives the entire descent, either with a pulsing movement at about 1Hz suggesting wing-propelled surges perhaps combined with balancing foot propulsion as the bird pitches vertically head-down (Figure 1C), or with faster oscillations, shallower pitch and slower descent indicating foot propulsion alone (see example Figure S1E). Ascent may be started with rapid oscillating inputs, suggesting foot propulsion, but completed using buoyancy alone (indicated by the smooth trace) as the bird pitches head-up and accelerates to the surface. In the Figure 1C example, a 38s dive to 9.5m, the bird spends around 20s in a bottom phase mainly pitched head-down, or partially so, with small changes in depth and variable motion indicative of active foraging or hunting (further examples in Figure S1).

Our findings show that whilst most foraging probably occurs near the surface, as found elsewhere^{4,5}, deeper diving could be ubiquitous in this population and must be considered a significant foraging strategy in this species' behavioural repertoire. Black-browed albatross are known to feed on a range of live prey⁹, including jellyfish, crustaceans, cephalopods, and fish, and also scavenge around human fishing operations where they are vulnerable to bycatch¹⁰. Currently the costs and benefits of deeper dives and their specific predatory function remain unknown, as is whether they are a unique adaptation of this population or the result of previously unforeseen behavioural flexibility since they have not been detected elsewhere⁴. In the Falklands, we have watched aggregations of black-browed albatrosses diving from the sea surface (far from any vessels), suggesting that diving can be used to

pursue shoaling prey. GPS data show that dives occur primarily in the distal portions of foraging trips, indicating that birds are commuting to areas where diving for prey may be necessary (Figure S2). Furthermore, analysis in relation to actual sun-elevation angle for every dive suggests restriction by available light, with far fewer than expected from birds' known positions occurring outside daylight or civil twilight (Figure 1D). Similarly, deep diving only starts during civil twilight (max 11.8m), with only shallow dives (max 1.5m) occurring when it is darker, and most deep diving occurring when the sun is relatively high (Figure 1E). The discovery of unexpectedly deep diving in this albatross population suggests that bycatch risk may extend much deeper in fishing operations such as pelagic longlining than previously thought, but its restriction to daylight hours confirms that night setting could still be part of effective mitigation¹⁰.

Declaration of Interests

The authors declare no competing interests.

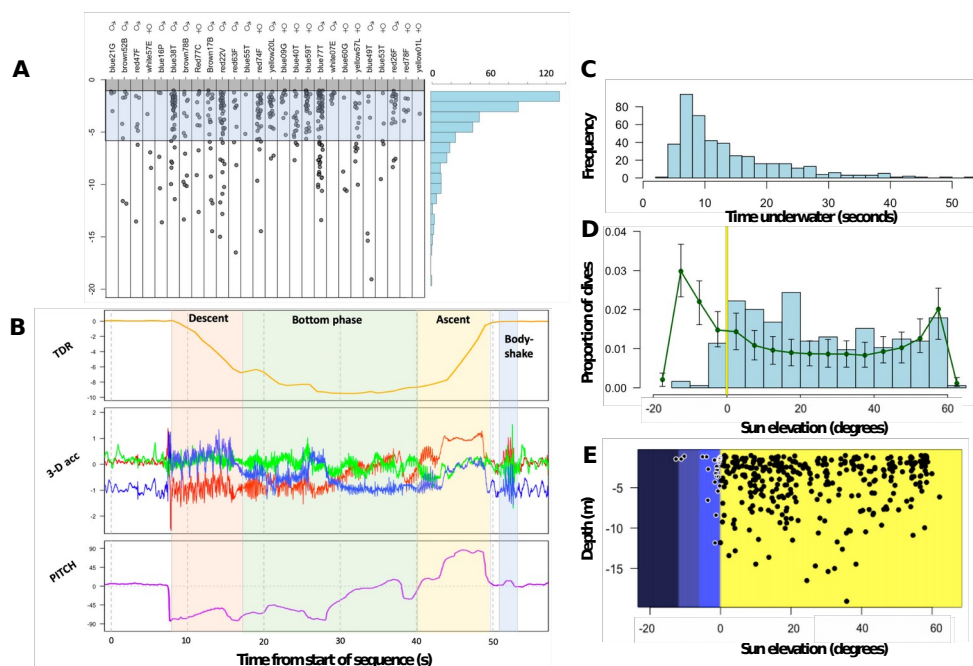
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Figure 1. Depth distribution, durations, structure, and diel pattern of albatross dives



(A) Recorded dives below 1m for individually known albatross (N=28) with blue shading to 6m (previous maximum), and dive frequency histogram by depth on the right.

(B) Frequency histogram of durations.

(C) Example 38s dive to 9.5m by female blue53T showing depth profile in metres (top panel), 3-axis raw acceleration profile in g (middle panel; red = surge, blue = heave, green = sway), and derived body pitch profile in degrees from horizontal (bottom panel). Distinct dive phases are shown by shading (descent = pink, bottom phase = green, ascent = yellow, body-shake at surface = blue).

(D) Proportions of dives (N=369) by sun elevation angle, derived from closest GPS location to each dive (within 1 hour, with all but three fixes were within 20s of the dive), and TDR time. Dark green line shows mean and range of randomly expected dive proportions derived from all tracked positions, with yellow vertical line indicating sunrise/sunset.

(E) Individual dives with depths (in metres) by sun elevation angle (in degrees above horizon), showing the daylight phases of Astronomical twilight (dark blue), Nautical twilight (mid blue), Civil twilight (light blue), and daylight (yellow).

Supplementary Information: Unexpectedly deep diving in an albatross

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Figure S1. Depth, acceleration, and pitch profiles of example albatross dives. Six additional example dives illustrating variation in depth, duration (below 1m), and dive shape, from four separate individuals (male and female). Details are otherwise the same as in main text Figure 1. Note that scales vary between examples.

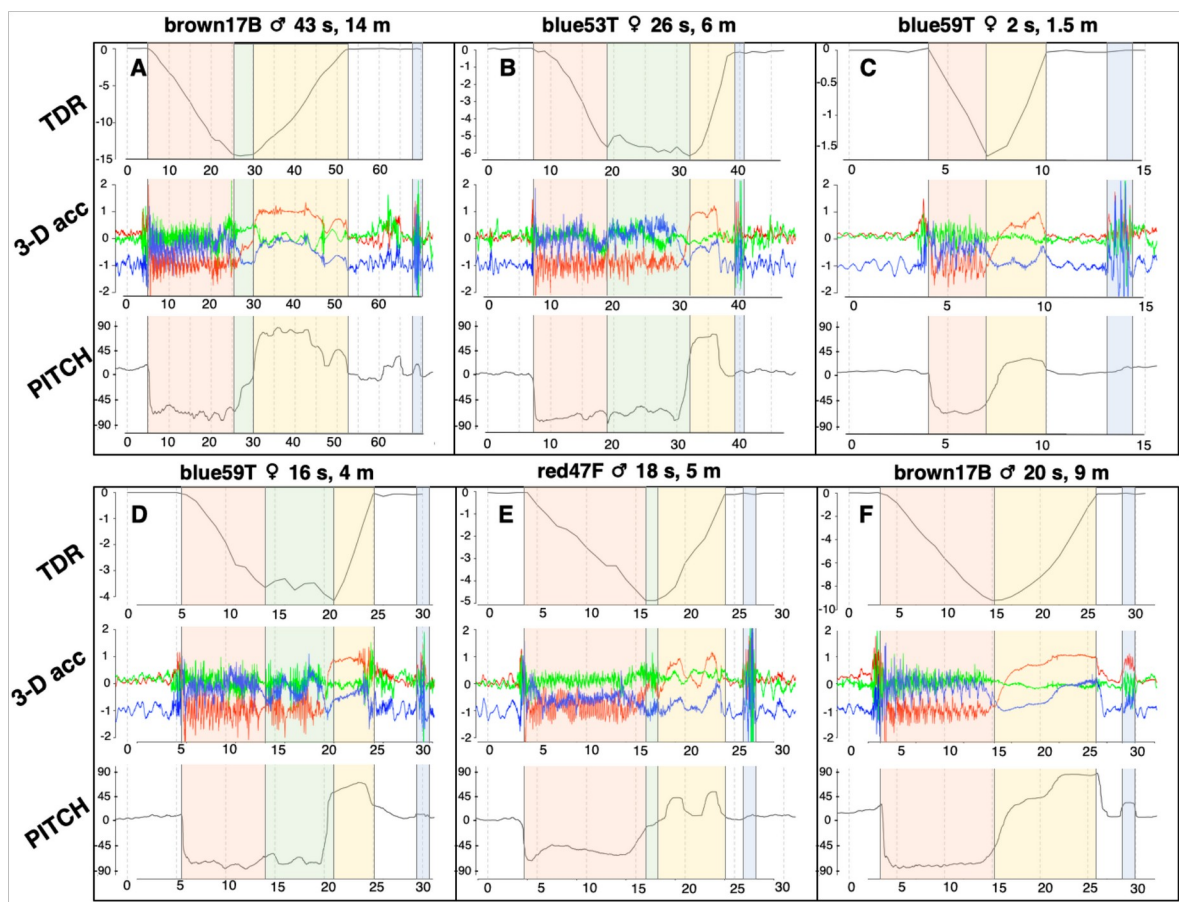
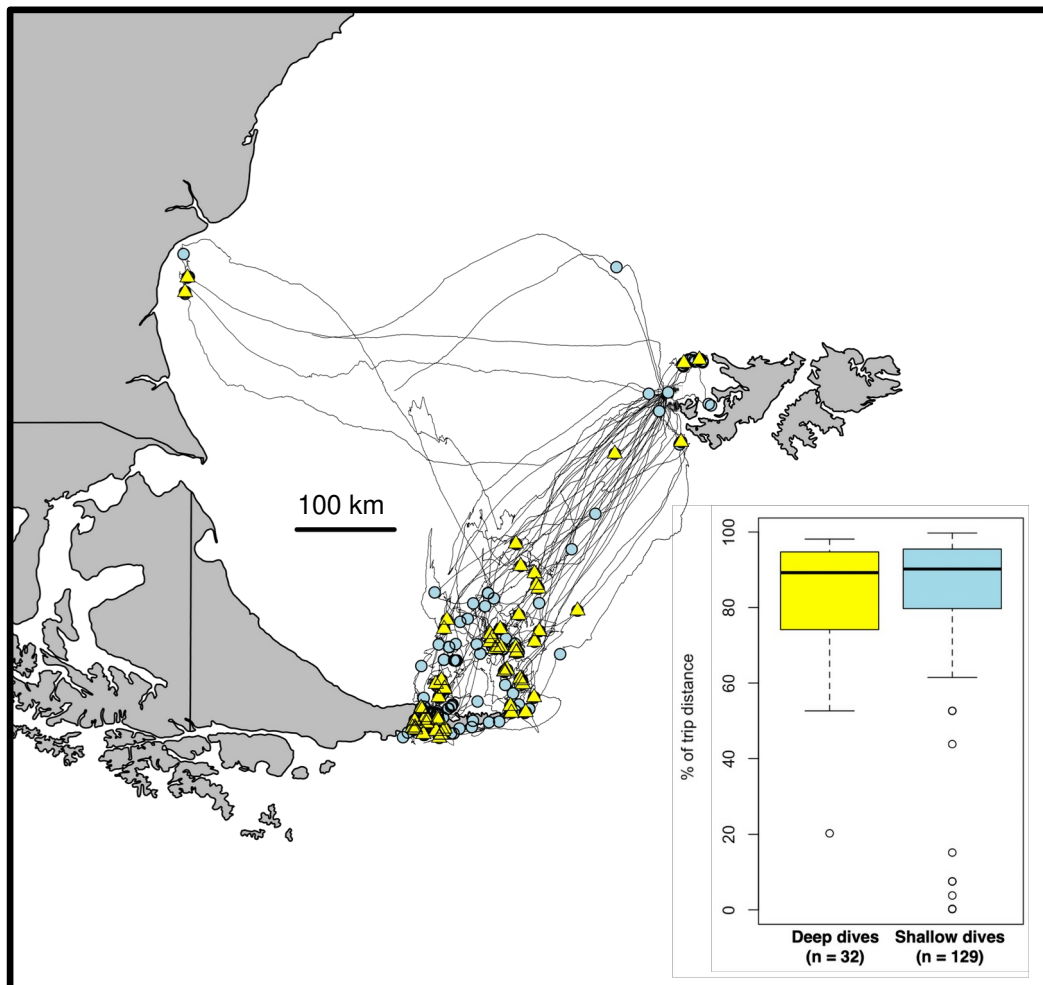


Figure S2. Albatross dive locations. Map of the Falkland Islands and the southern tip of South America with the New Island colony as a red dot, showing individual GPS tracks and positions of 369 accurately locatable dives. Blue points represent shallow dives (1-6m deep), yellow triangles represent deep dives (>6m deep). Inset shows a box plot (median, IQR, 1.5x IQR) of dive distance from the colony expressed as a % of the distance to the furthest point on each foraging trip (with dives on incompletely recorded trips excluded because maximum trip range could not be calculated), indicating that dives of both kinds are found predominantly near the distal ends of foraging trips.



Supplemental Experimental Procedures

Biologging methods

In the larger study of which this is a part, 56 black-browed albatross individually marked with numbered plastic leg rings and of known sex and age were instrumented with various combinations of logging devices at New Island in the western Falkland islands (Sub-colony C, coordinates: $51^{\circ} 43' S$, $61^{\circ} 18' W^{S1}$), between 11/12/2017 and 31/01/2018. For deployment, birds were taken by hand at the nest during late incubation or brood guard, usually in the minutes following changeover with their returning partner. For retrieval, birds were taken directly off their nest immediately before changeover, sometimes after the changeover, and on a few occasions when there was no partner present (in such cases the egg or chick was removed temporarily and given insulated protection). Instruments used in the current study were attached using TESA marine cloth tape to dorsal mantle feathers following sealing in heat-shrink plastic tubing (GPS, Accelerometers), or to a leg ring (TDR). TDRs (CEFAS G5) with a nominal depth resolution of 4cm were configured to record at 1Hz. GPS (modified Mobile Action IgotU) were configured to record at either 1Hz or 0.2Hz. Accelerometers (Axivity AX3) were configured to record at 100 Hz in orthogonal 3 axes, with a $\pm 4G$ range, and deployed so that the surge axis faced tail-to-head by eye, and the device was approximately flat to the bird's dorsal plane (so that the heave axis was approximately dorsal-ventral). The combined mass of deployments reported here was $<40g$ ($<1.5\%$ of body mass). Following biologging deployments, all 56 birds returned to their nests, all instruments were successfully retrieved (although some had malfunctioned or were flooded), and all birds continued with their breeding attempt successfully at the time the study finished. No individual was tracked more than once. Black-browed albatross can be stressed by weighing procedures, so birds were not weighed, but these results suggest that any disturbance from deployments and handling was minimal. The current study involved 29 deployments in which GPS and TDR were combined, of which 9 also carried an accelerometer. One TDR failed and 28 complete 1Hz depth traces were retrieved successfully.

Quantitative methods

Data processing. To adjust for TDR drift we subtracted each 1Hz record from the rolling median over a 10-minute moving window. For the purposes of this study, and for consistency (Bentley *et al.*, 2021), we classified an apparent immersion event as a putative dive only if it registered below a threshold 1.0 m depth. Activity very near the surface is in principle hard to distinguish from noise, and because TDRs were placed on the leg they could not readily identify dip foraging where the entire body was not substantially submerged. Putative dives were then visually inspected and filtered for spurious readings (spikes of a single reading below 1m, or events containing unrealistic descent or ascent rates of $>2m.s^{-1}$), presumably caused by the bird pecking at the device or some other movement resulting in high impact on the device. 436 valid dives were thus identified across 26 of the 28 birds (2 birds showed no valid dives). We chose 6m as the threshold beyond which dives were classified as deep dives, on the basis that this was the deepest dive previously recorded for this species. For calculating dive durations, dives were considered to start and end at the surface.

The locations of dives were determined by identifying the GPS fix that was closest in time to each dive. Because GPS devices sometimes depleted their battery before the bird returned to the colony, for analyses requiring location we took only dives that occurred within an hour of the last GPS fix (N=369). Of these, all but three fixes occurred within 20 seconds of the start of the dive.

Sun elevation. Because local time does not reflect light level differences particularly well across different latitudes and at different longitudes within a time zone, we used local sun elevation to investigate whether deep diving by albatrosses was limited by ambient light. We used the GPS location of each dive and each dive's start time to determine apparent sun elevation angle, accounting for refraction through Earth's atmosphere, using the "solarpos" function in the "maptools" R package⁵².

Acceleration and pitch. Acceleration data were initially visualised and analysed in Open Movement software, with subsequent analyses undertaken in R⁵³. Since static (posture) and dynamic acceleration (movement) involve acceleration signals that necessarily occur over different time scales, we parsed the acceleration signal for posture by computing a rolling median acceleration over a frame window of 2 seconds⁵⁴ using the "zoo" package in R⁵⁵. From static acceleration, pitch was then calculated as:

$$180 \times \frac{\tan^{-1}\left(\frac{x}{\sqrt{y^2 + z^2}}\right)}{\pi}$$

Where x, y, and z are acceleration in the forwards-backwards (surge), side to side (sway) and vertical axes (heave), respectively.

For the 98 dives for which we had both accelerometry and TDR traces, we investigated whether our data streams were consistent with dives being duck dives from the surface or plunge dives from the air. From the TDR traces, we could see that descent rates are slow (max ~1.2m.s⁻¹), and descent speed between the first two fully submerged points in the dive was not higher nearer the surface as would be expected from plunge diving (linear model increase in descent rate per metre increase in depth of descent rate of 0.039 +/- 0.094, t = 0.416, p = 0.68). Further, we examined the accelerometry traces for evidence of plunge diving. Plunge dives should involve a pitch forward and some freefall before a rapid deceleration upon entry to the water. We looked for this pitch forward in the static acceleration, and then for freefall and deceleration in the surge axis dynamic acceleration. While sometimes there was a small (-2 g) spike signalling deceleration in the surge axis, this was associated with the beginning of pitch change, and upon further examination, was attributable to an artefact. This artefact was caused by 'leakage' from static acceleration to dynamic acceleration when the 2-second moving window failed to capture, as static acceleration, rapid changes in the birds' pitch. This hypothesis was further corroborated since the sum of the 3 static acceleration axes, which should always be 1 g, had spikes where the sum was commensurately lower than 1 g during initial stages of pitching.

Statistics. To compute a null expectation for dive frequencies with different sun elevation angles, we randomly chose n locations in each individual albatross' GPS trajectory where a

dive could have occurred, where n was the number of qualifying dives (dives that were associated with a GPS fix) recorded by that bird. This was done for all birds, and the number of dives that, given these random GPS locations, fell in each sun elevation bin, were counted. This was repeated 999 times and the mean and 95% confidence intervals given (95% confidence intervals comprise the 2.5th and 97.5th percentile of the 999 samples for each elevation angle bin). This allowed us to see whether more or fewer dives occurred at different solar elevations compared chance expectation ($\alpha = 0.05$).

Supplemental References

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Author Contributions

T.G, L.M. & P.C. Designed the study, conducted the field trials and performed initial data analyses. L.M. Conducted the data handling. O.P. Conducted the main analyses and constructed the figures. T.G. & O.P. Wrote the manuscript with assistance from P.C. & L.M.