

of the dermis, a dense layer of large and abundant (125–650 μ diameter) nerve fascicles clusters together, likely the large terminal ramifications of the pudendal nerve (Figure 1E), and numerous genital corpuscles are seen (Figure 1F). The nerve fascicles likely connect to the free nerve endings in the dermal papillae of the clitoris and the corpuscles. Genital corpuscles are involved in the sexual pleasure response of the human clitoris⁵ and glans penis⁸, and their presence suggests a similar function in the dolphin.

The tunica albuginea that surrounds the spongy tissue and cavernosum is rich in collagen (Figure 1E) and short abundant elastin fibers (Orcein stain; Figure S1E). The tunica maintains the structural integrity of the erectile tissue and prevents bulging under pressure, suggesting enlargement of the erectile tissue. In lateral sections, the tunica fully divides the cavernosum from the spongy tissue. More medially, the two erectile tissues are continuous and both are surrounded by tunica. The spongy tissue has abundant vascular spaces lined with endothelium, small blood vessels, and adipose cells with a ‘spongy’ aspect (Figure 1E). The corpus cavernosum has large lacunae, densely packed collagen, less adipose tissue, and some smooth muscle fibers (Figure S1C). Clitoral arteries are often near nerves (Figure 1G), which function in orgasm in humans⁹.

Our anatomical examination of the clitoris of the common bottlenose dolphin reveals a complex organ with many similarities to the clitoris of other species known to have sexual pleasure, including humans^{4,5}. Our study suggests that female dolphins likely experience pleasure when the clitoris is stimulated during copulation, homosexual behavior, and masturbation. Understanding the phylogenetic history of sexual pleasure may elucidate the role of female orgasm. Our study is a novel approach to test the functionality of the clitoris of non-model animals when neurobehavioral examination is not feasible.

SUPPLEMENTAL INFORMATION

Supplemental information includes one figure, one table, inclusion and diversity statement, and experimental procedures, and can be found with this article online at <https://doi.org/10.1016/j.cub.2021.11.020>.

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DECLARATION OF INTERESTS

The authors declare no competing interests.

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Unexpectedly deep diving in an albatross

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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 becoming 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 (19 m) and for much longer (52 s) than previously thought — three times the maxima previously recorded for this species (6 m and 15 s), 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 underwater 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. These measurements yielded 436 valid dives below 1 m depth over 80 bird-days. 88 dives (20%) were deeper than the deepest dive reliably recorded previously for this species (6 m)⁴, 30 (6.8%) were to at least 10 m, and the deepest dive recorded was 19.12 m (Figure 1A). Dive durations (Figure 1B) were commensurately long, with 139 (31.9%) dives longer than 15 s, and the longest lasting 52 s — more than three times longer than previously recorded reliably for this species⁴, and more than 2.5 times longer than any albatross (19 s 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 1 m depth, 19 birds (68%) to at least 6 m, and 14 (50%) diving to at least 10 m. Individual mean maximum depth was 10.0 m (range, 2.3 m–9.1 m). Similarly, most birds tracked (76%) showed maximum submergence times longer than the maximum previously recorded for this species (15 s), with the mean maximum dive duration 30.7 s (range, 7–52 s). Neither was diving restricted by sex or age. Excluding two birds that did not record dives below 1 m (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

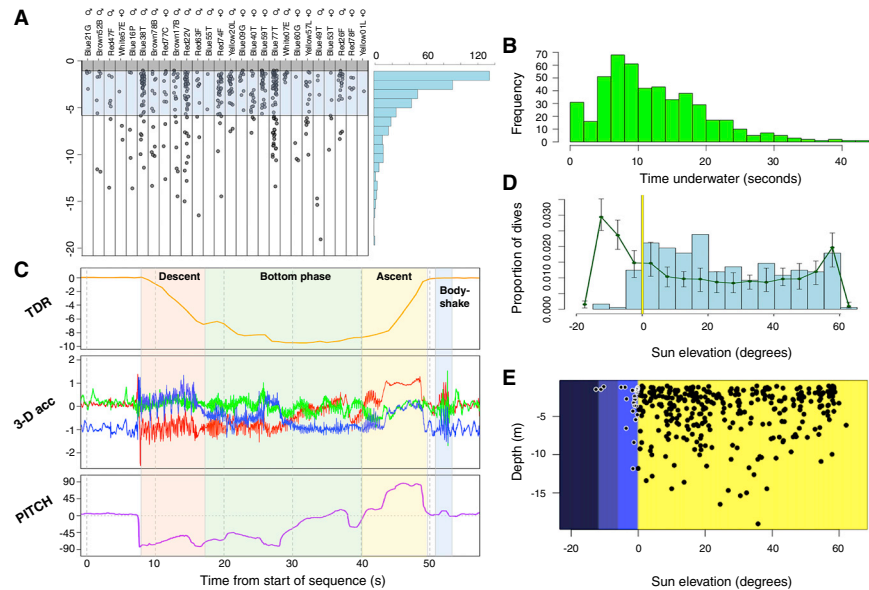


Figure 1. Depth distribution, durations, structure, and diel pattern of albatross dives.

(A) Recorded dives below 1 m for individually known albatrosses (N = 28) with blue shading to 6 m (previous maximum), and dive frequency histogram by depth on the right. (B) Frequency histogram of durations. (C) Example 38 s dive to 9.5 m 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 within 20 s 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).

from an aerial plunge, underwater propulsion, or both. While 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 Supplemental information). Active underwater propulsion drives the entire descent — either with a pulsing movement at about 1 Hz, 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 in 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 38 s dive to 9.5 m, the bird spends around 20 s 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 while 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 to 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 11.8 m), with only shallow dives (max 1.5 m) 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.

SUPPLEMENTAL INFORMATION

The supplemental information contains two supplemental figures, supplemental experimental procedures, and supplemental references, and can be found with this article online at <https://doi.org/10.1016/j.cub.2021.11.036>.

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AUTHOR CONTRIBUTIONS

T.G., L.M. and 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. and O.P. wrote the manuscript with assistance from P.C. and L.M.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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Letter

Ratios can be misleading for detecting selection

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Using ratios of non-synonymous to synonymous mutations is a common approach to standardize the variable of a trait (a numerator) to a predictor variable (a denominator). Yet, interpretations of ratios are not straightforward and are often non-intuitive^{1–4}. Still, simple ratios of non-synonymous to synonymous mutations are widely used in evolutionary biology and population genetics⁴. In a recent paper in *Current Biology*, Leroy *et al.*⁵ reported marked differences between island and continental bird species in nucleotide diversity at non-synonymous (π_N), presumably neutral, and at synonymous (π_S), presumably weakly deleterious, sites. They concluded that the strong inverse relationship between π_N/π_S and estimated effective population size (N_e) documents a lower adaptive potential of island species and their disability to effectively remove weakly deleterious mutations. Here we show that the inverse relationship between π_N/π_S and N_e can also emerge by the non-zero intercept (additive term) in the linear relationship between π_N and π_S . The linear relationship is not expected under the nearly neutral theory of evolution, as it means the proportional change in π_N with a change in π_S . We warn that conclusions based on analyses of ratios in population genetics can be misleading and suggest replacing them by other computational approaches.

Leroy *et al.*⁵ analysed genomes of 14 insular and 11 continental species/populations of songbird. They documented that insular species have generally much smaller N_e and on average 40% higher π_N/π_S ratios, reflecting a strong inverse relationship between π_N/π_S and N_e . They interpreted these results as support for accumulation of non-synonymous mutations in the insular populations predicted by the nearly neutral theory of evolution. But, is the negative

