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Supplementary Materials for

Lightscapes of fear: How mesopredators balance starvation and predation in the open ocean

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Supplemental Information

Risk of daylight

We used ambient light across time and 3-dimensional space as a proxy for predation risk. This is not without precedent. Indeed, light level is commonly used as a proxy for predation risk with regards to marine predators (60). The vertical risk landscape is not well understood, but killer whales are limited in depth by their diving physiology (61) and white sharks are limited by light and temperature requirements (62). Previous studies have shown that seals change their behavior to avoid predators (63), often diving deeper as they approach coastal areas where shark presence is high (35). Exposure experiments have shown that marine mammals respond to predator vocalizations by extending both the depth and duration of dives (20, 64). Similarly, in response to predation risk pinnipeds move under cover of darkness (65), likely because the frequency of white shark attacks on seals is highest after sunrise when sharks have a visual acuity advantage over seals (66). In the open ocean, rapid light-dark cycles between the ocean surface and depth represent a similar dynamic to light-dark cycles during day-night and the resulting behavioral decisions by pinnipeds to transit from and return to haul-out sites.

While transient killer whales can use biosonar, they preferentially remain quiet to not alert their marine mammal prey, which have highly sensitive hearing (67). Sharks are known to silhouette their prey using surface light (68). This suggests that visual cues are important for both confirmed predators of elephant seals, killer whales and white sharks, and that light represents a good metric of relative risk. We note that sharks have multiple sensory modalities including lateral lines and hearing that play a role in prey detection and capture, although the degree to which these modalities are used and for which distances remain uncertain.

Supplemental Table 1. Model fit for the circular mixed-effects models to predict the timing of rest. The variables Daylength, Lipid, Latitude and Longitude are centered such that a value of 0 represents the average. Four indicators of model fit were used to choose between the competing models: two versions of the deviance information criterion (DIC and DIC_{alt}) and two versions of the Watanabe-Akaike information criterion (WAIC and WAIC₂). The best model is shown in bold.

Model	DIC	DIC _{alt}	WAIC	WAIC ₂
~Date*(Lipid + Daylength) + Latitude + Longitude	102018	102104	102064	102066
~Date*Daylength + Lipid + Latitude + Longitude	102082	102255	102155	102156
~Date*(Lipid + Daylength)	102151	102233	102200	102201
~Date*Lipid + Daylength + Latitude + Longitude	102178	102302	102225	102226
~Date*Daylength + Lipid	102186	102298	102254	102255
~Date + Daylength + Lipid + Latitude + Longitude	102208	102284	102251	102252
~Date + Daylength + Lipid	102278	102446	102361	102362
~Date*Lipid + Daylength	102327	102366	102358	102359
~Date	102783	102815	102802	102803

Supplemental Table 2. Coefficient estimates (fixed-effects) in degrees for the best fitting circular mixed-effects model. SD = standard deviation, HPD = highest posterior density interval given as [lower bound upper bound]. An asterisk (*) indicates that an HPD interval does not contain 0. The parameter Date represents days since departure and the parameter Lipid represents percent lipid. The coefficient estimates represent the average effect for each predictor (over the entire range of the predictor) and the circular mean of the drift time for the intercept. This coefficient is referred to as AS in Cremers, Mulder and Klugkist (57).

Coefficients	Posterior mode ± SD	95% HPD Interval
Intercept	13.84 ± 2.06	[10.15 18.06] *
Date	-0.12 ± 0.05	[-0.13 -0.10] *
Daylength	19.62 ± 1.93	[15.97 23.47] *
Lipid	-83.77 ± 6.50	[-98.38 -72.56] *
Latitude	0.98 ± 2.44	[0.42 2.75] *
Longitude	-1.68 ± 118.58	[-35.83 49.60]
Date * Lipid	0.02 ± 0.04	[0.02 0.11] *
Date*Daylength	1.13 ± 0.10	[0.94 1.33] *

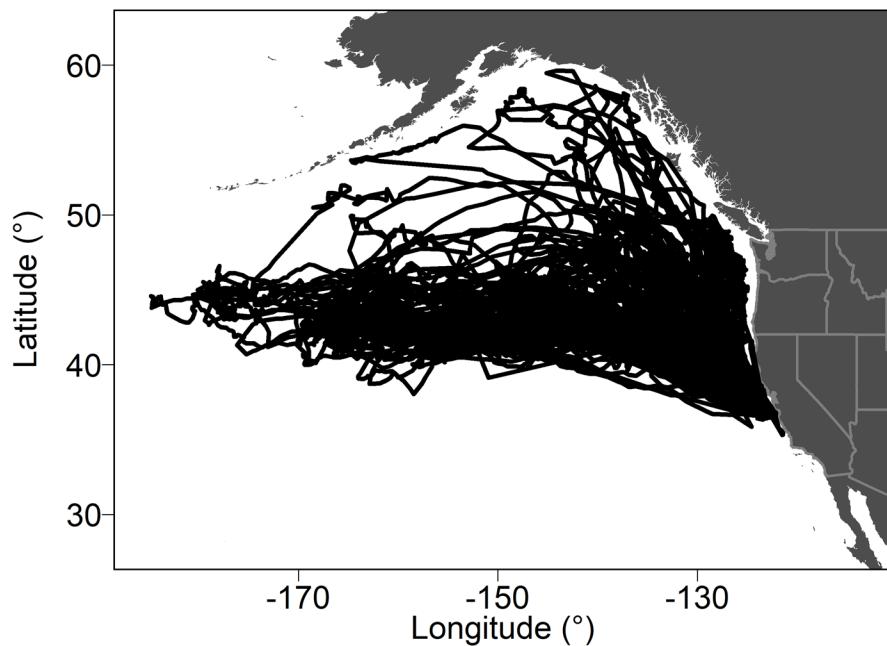


Fig. S1. Paths taken by elephant seals during the foraging migration. Individuals depart the beach at Año Nuevo, California and forage throughout the Northeast Pacific Ocean before returning to Año Nuevo to breed.

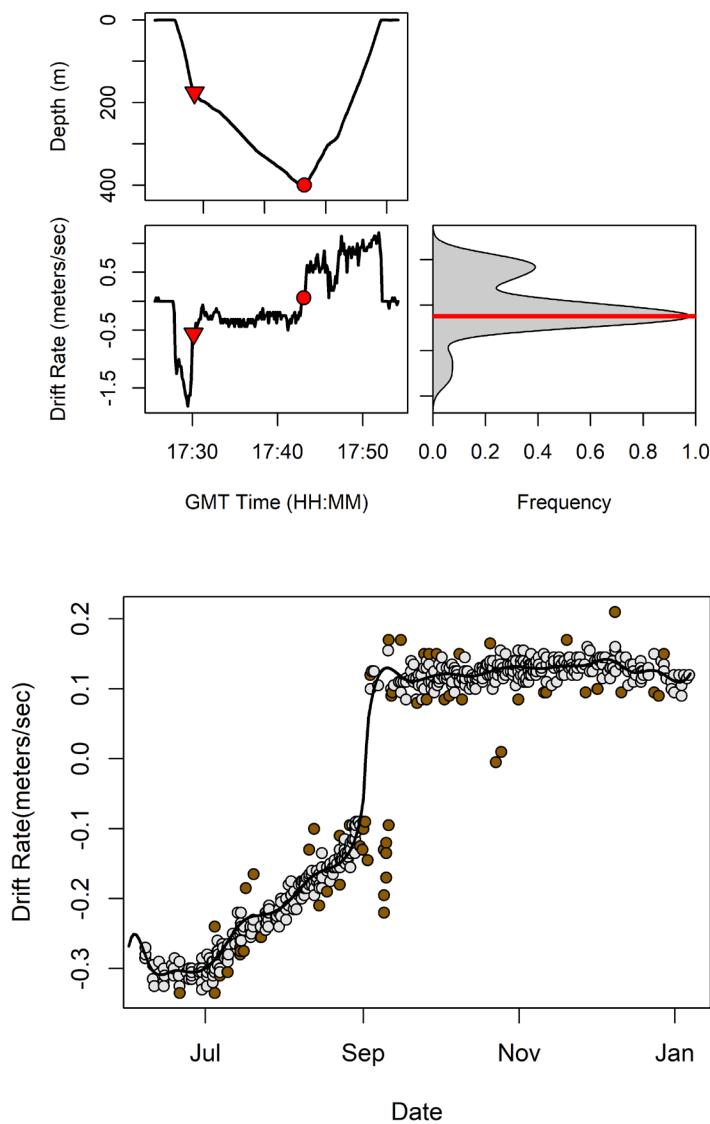


Fig. S2. Identification of the drift phase from the raw time-depth record (top left panel) based on change in depth over change in time (bottom left panel) for a single dive. A kernel density of the drift rate shows a dominant peak representing the average drift rate (in this case -0.24 meters/second, red line in bottom right panel). The custom algorithm identifies consecutive time points in which drift rate falls within 0.38 meters/second of the dominant drift rate (in this case -0.62 to +0.13 meters per second, red triangle and red circle, respectively in left plots). We then

used a cubic spline to calculate the dominant drift rate each day (lower panel, black line) and excluded drift segments that fell outside ± 0.03 meters/sec of the daily dominant drift rate (gold points).

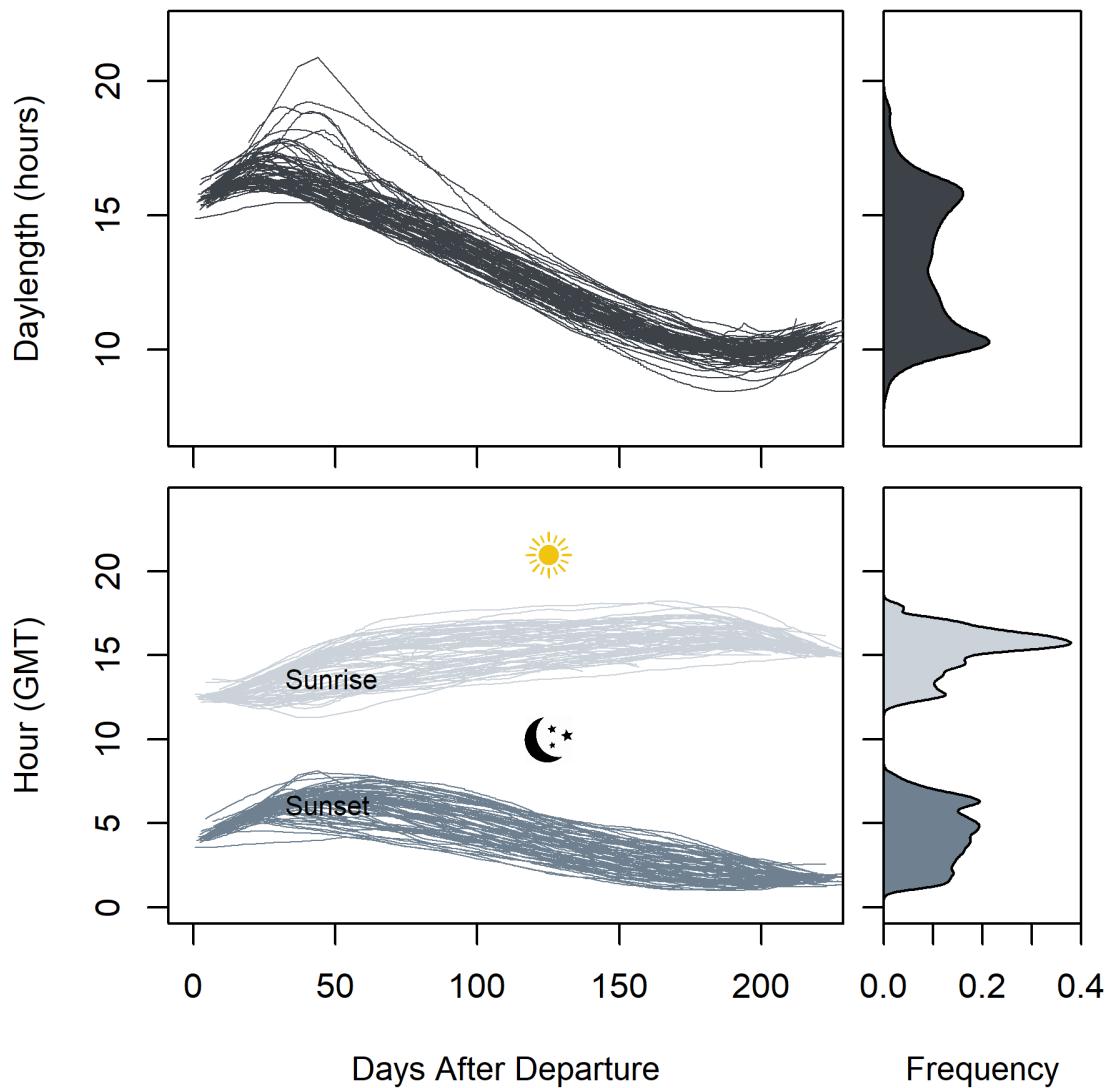


Fig. S3. For 71 instrumented elephant seals, daylength gets shorter (top left panel) as sunset becomes earlier and sunrise becomes later (bottom left panel). Sun and moon icons represent daytime and nighttime, respectively.

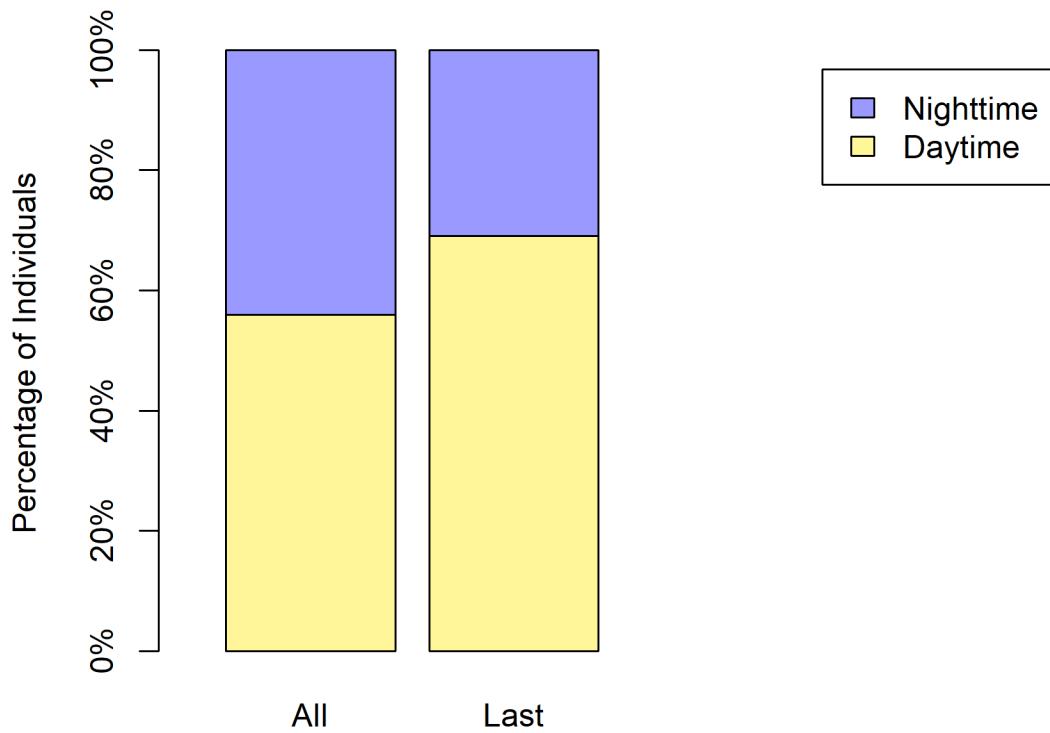


Fig. S4. Daily timing of Argos satellite tag transmissions for elephant seals that presumably died at sea between 2004 and 2018 (N=41,767 transmissions from N=42 seals). Daylight was associated with a higher risk for seals because 69% of last Argos satellite transmissions (N=29 of 42) occurred during the daytime whereas 56% of all transmissions (N=23,371 of 41,767) occurred during the daytime. As compared to all transmissions, last transmissions (indicating death at sea) were slightly more likely to occur during daytime as compared to nighttime ($\chi^2=2.9182, p=0.087$). Seals with last transmissions were never again seen at the colony and thus, last transmissions indicate mortality rather than instrument failure.

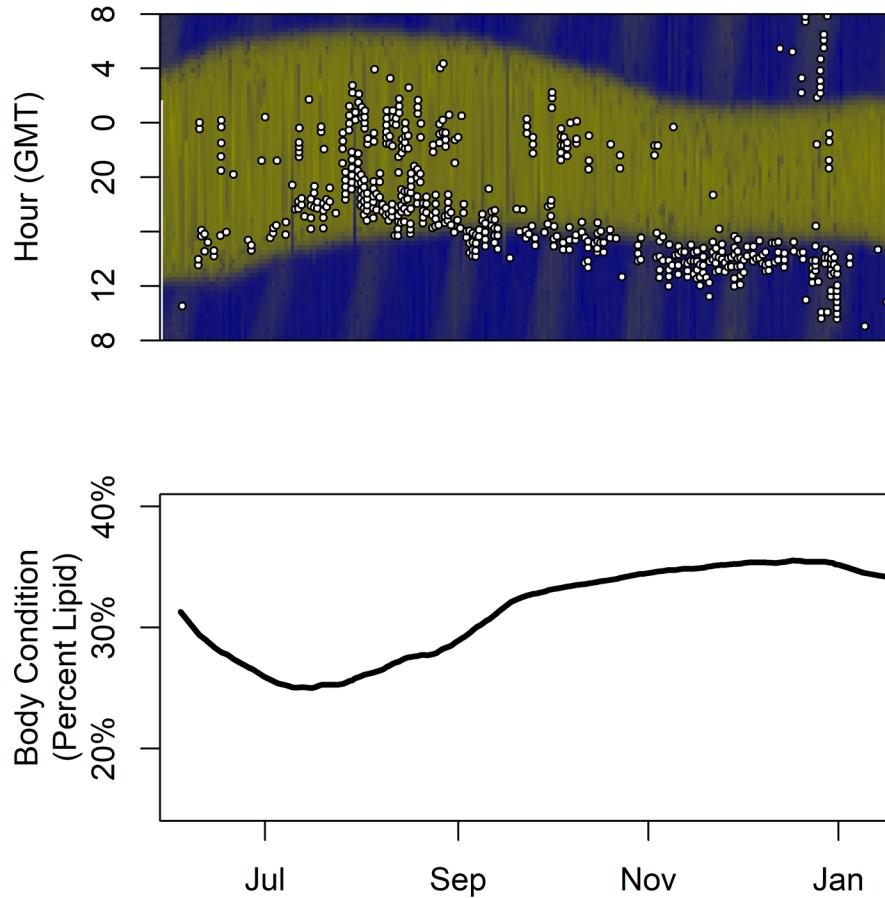


Fig. S5. Drift timing (upper panel) and body condition (lower panel) across the migration for one seal (#2004018). Upper panel shows drift dives (white dots) overlaid on a time-series of light level data collected by the seal. Blue represents nighttime and yellow represents daytime. Throughout the oceanic foraging migration, drift dives occur progressively earlier as daylength and body condition increase.

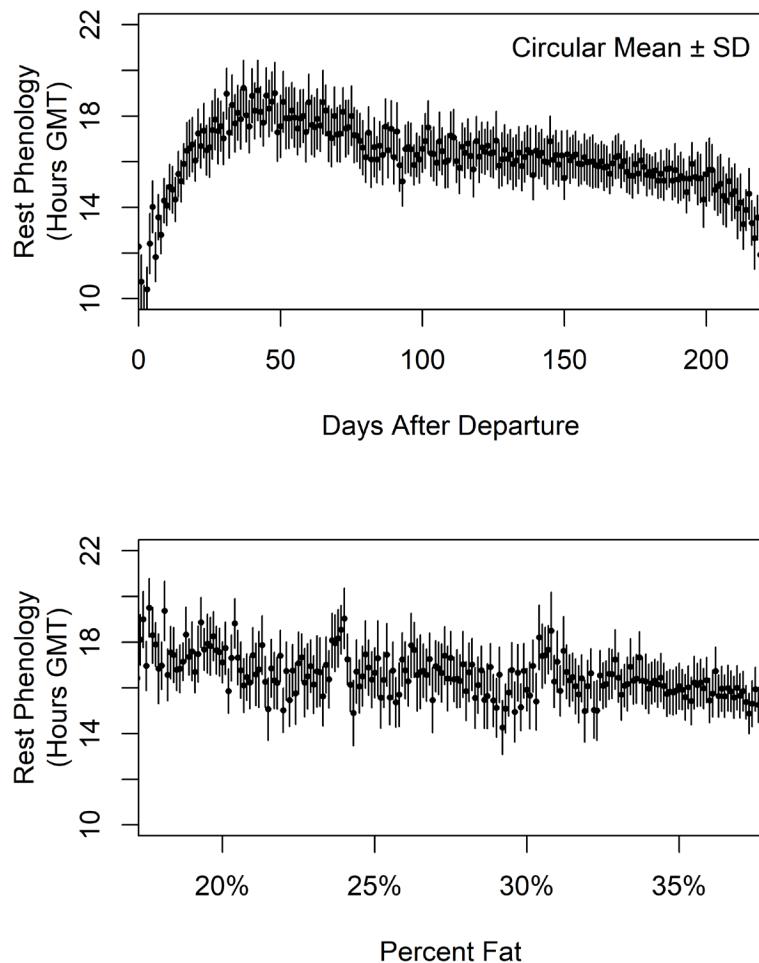


Fig. S6. Rest phenology (in relation to Greenwich Mean Time) as a function of time (upper panel) and body condition (lower panel). Elephant seal rest timing is strongly related to percent fat such that seals in poorer body condition early in the foraging migration rest slightly earlier in the day.

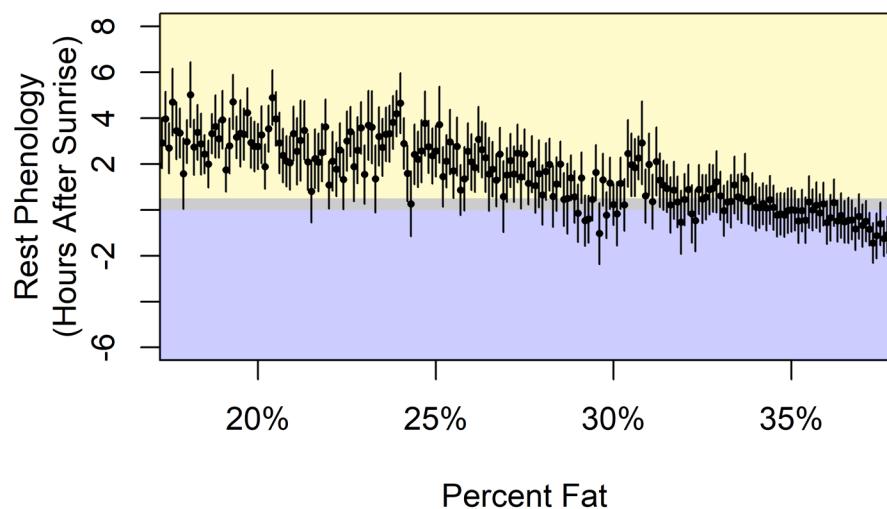


Fig. S7. Rest phenology (in relation to sunrise timing) as a function of body condition. Seals in poorer body condition (early in the foraging migration) rest considerably later in the day.

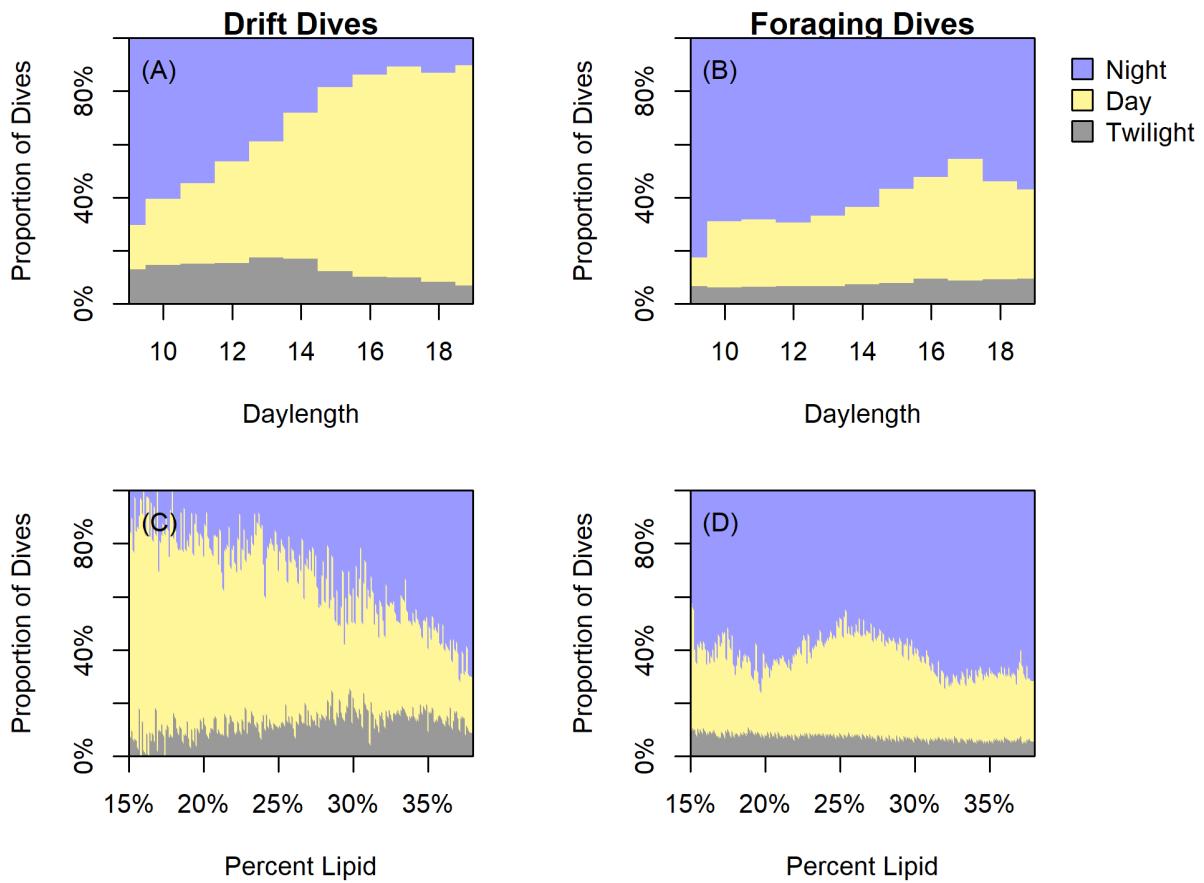


Fig. S8. The influence of daylength (upper panels) and body condition (lower panels) on the scheduling of drift dives (left panels) and foraging dives (right panels). Elephant seals drift more often during the day when they are **(A)** in locations and seasons with longer daylength and **(C)** in poorer body condition. In comparison, elephant seal foraging dives are less strongly impacted by **(B)** daylength and **(D)** body condition.

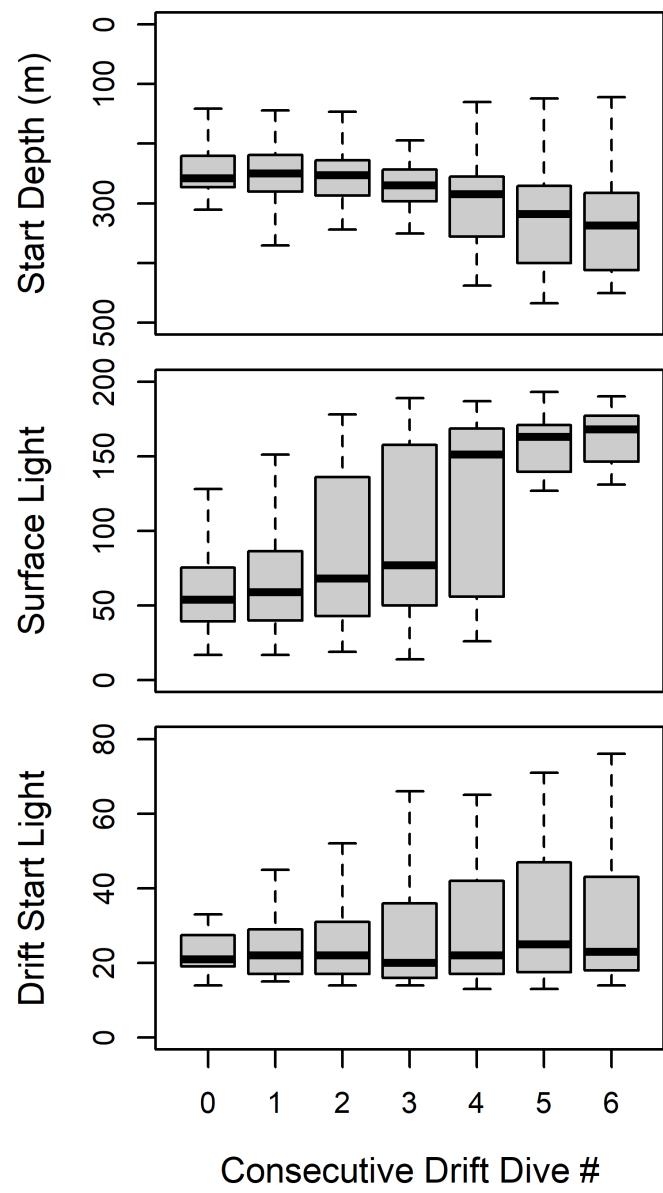


Fig. S9. Each day, consecutive drift (resting) dives get progressively deeper as the sun starts to rise, resulting in only marginally higher ambient light levels during the start of the drift phase. Data are from one seal (#2005036).

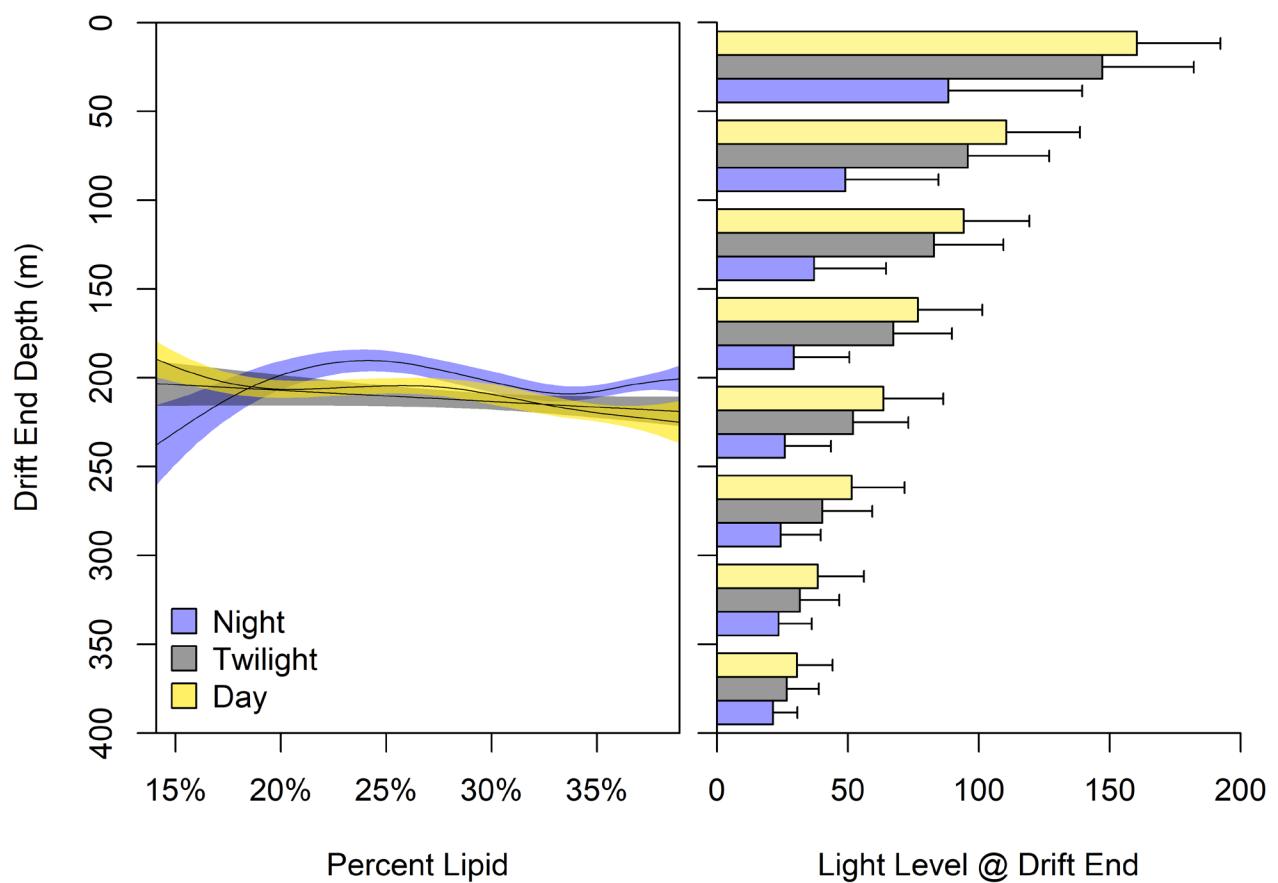


Fig. S10. Regardless of body condition and time of day, seals end their resting drift segments around the same depth and light level.

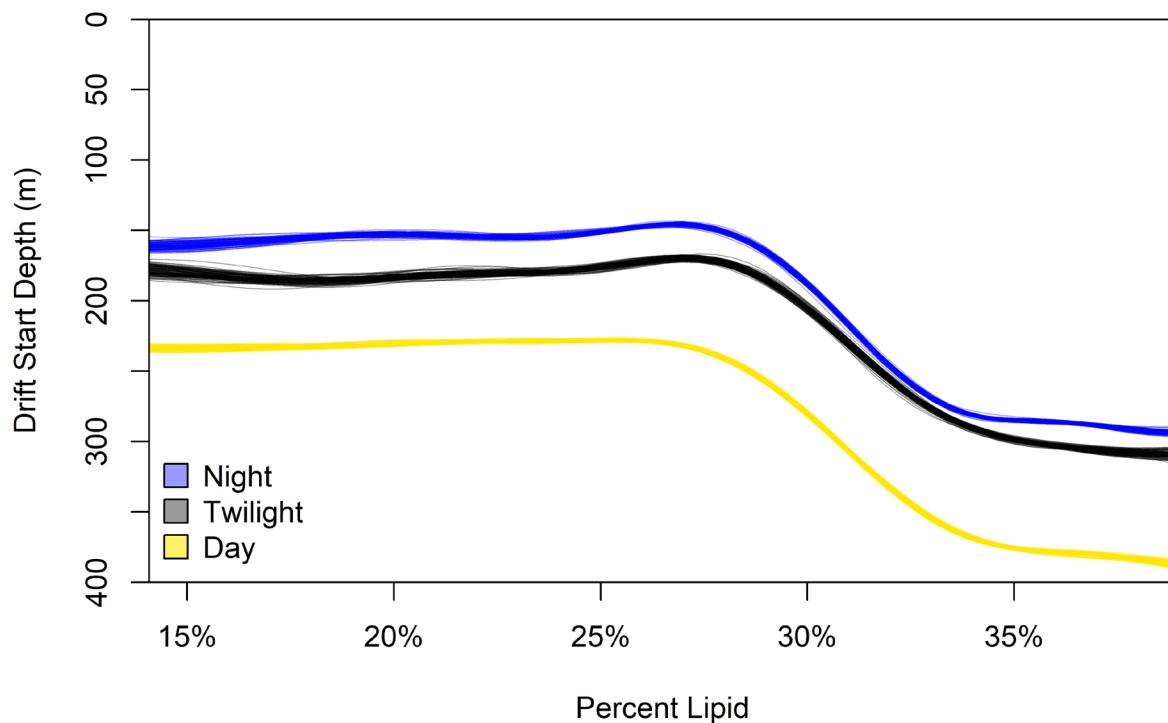


Fig. S11. The relationship between body condition and depth of the drift start did not change when incorporating uncertainty into the body condition values. Each line represents a single re-sample ($N=100$ re-samples) for night, twilight, or day.

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