

Correspondence

Elephant seals time their long-distance migrations using a map sense

Roxanne S. Beltran^{1,*}, Alexander L. Yuen¹, Richard Condit¹, Patrick W. Robinson¹, Max F. Czapanskiy², Daniel E. Crocker³, and Daniel P. Costa¹

Many marine animals migrate between foraging areas and reproductive sites, often timing the return migration with extreme precision. In theory, the decision to return should reflect energy acquisition at foraging areas, energetic costs associated with transit, and timing arrival for successful reproduction. For long-distance migrations to be successful, animals must integrate 'map' information to assess where they are relative to their reproductive site as well as 'calendar' information to know when to initiate the return migration given their distance from home¹. Elephant seals, *Mirounga angustirostris*, migrate thousands of kilometers from reproductive sites to open ocean foraging areas (Figure 1A), yet return within a narrow window of time to specific beaches². Each year, pregnant female elephant seals undertake a ~240-day, 10,000 km foraging migration across the Northeast Pacific Ocean before returning to their breeding beaches, where they give birth 5 days after arriving². We found that the seals' abilities to adjust the timing of their return migration is based on the perception of space and time, which further elucidates the mechanisms behind their astonishing navigational feats³.

A first step in understanding the navigational abilities required to complete the migration on time is determining whether elephant seals have a map sense (i.e. whether they strategically begin the inbound migration based on how far they need to travel). Using satellite tracking data collected from adult female seals (N = 126 tracks from N = 108 individuals, 2004–2015), we determined the date on which each seal started its return migration,

defined as the date after which daily displacements were consistently toward the breeding beach³ (Figures 1A and S1). Turnaround dates depended strongly on distance from the breeding beach, but were unrelated to body condition determined by vertical velocity during drift dives. Seals that foraged farther began their inbound migration

earlier. These data provide evidence that seals know their distance from the breeding beach and allocate extra time to get back if they have farther to travel. It also provides an understanding of how population-level reproductive synchrony is possible for migratory animals.

Elephant seals return to the same beaches year after year with minimal

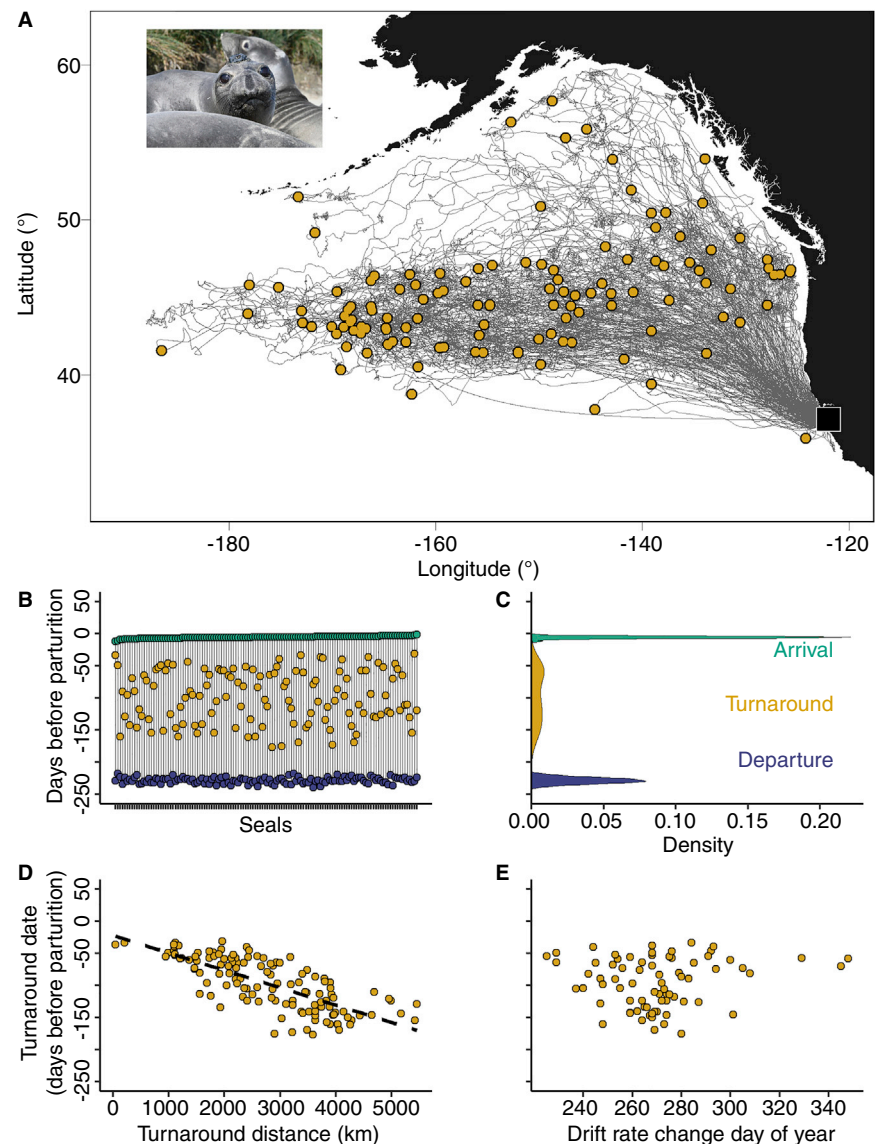


Figure 1. During 10,000 km roundtrip migrations, elephant seals schedule their return to the breeding beach based on their distance.

(A) Turnaround locations for each elephant seal in yellow overlaid onto the full migration tracks (grey lines). The breeding beach at Año Nuevo Reserve is a black square. (B,C) Departure and arrival dates are highly constrained across individuals, while turnaround dates are variable. (D) There is a strong correspondence between the distance and date at which seals began their return to the breeding beach such that closer seals turned around later. This staggered turnaround allowed for population-level synchrony for the breeding season. (E) There was no relationship between the day seals became positively buoyant and the day seals turned around, suggesting that the attainment of sufficient fat stores does not trigger the return to the breeding colony. (Photo by Daniel P. Costa under NMFS permit #23188.)

variation in migration arrival and departure date across individuals (Figure 1B). However, this consistency is not a result of group travel or active coordination because seals forage independently, and it is unknown which cue causes female elephant seals to begin their return migration months prior to giving birth at the breeding beach². The animals have vast distributions at sea, across longitudes and latitudes with dramatically different celestial cues and daylengths⁴ yet return to their beaches a few days before birth. Our objective was to determine the intrinsic and extrinsic factors that motivate foraging elephant seals to turn around and begin directed travel back to their breeding beaches. We predicted that the seals that traveled the farthest would initiate their return the earliest, to allow sufficient time for travel back to the breeding site. Alternatively, we hypothesized that seals would initiate their return after they attained sufficient energy stores for the return home and the subsequent reproductive event. Because elephant seals do not feed while nursing, they must derive all energy needed for lactation from fat reserves gained on the long foraging migration.

We calculated migration departure and arrival dates using satellite tags and time-depth recorders (Figure 1C)³. Distance from the Año Nuevo breeding beach was averaged every day for each seal and the first derivative of that distance calculated as the daily change, positive or negative (see Supplemental experimental procedures). The initiation of the return migration was defined as the last date on which the derivative fell above zero (i.e. the movement was directed toward the breeding beach until the end of the migration). After the migration, each seal was monitored so the birthdate of the pup could be determined. Using drift rate from time-depth recorders as a proxy for body condition, we identified the date at which each seal's buoyancy switched from negative (e.g. leaner) to positive (e.g. fatter) (Figure S1).

Pupping dates were January 20 ± 7 days, meaning that seals began their return migration ~98 days before giving birth (Figure 1B). Seals started their return migrations when they were $2,814 \pm 1,129$ km from the breeding beach (Figure 1A). Turnaround distance ($p < 0.0001$) but not buoyancy change date

($p = 0.60$) had significant partial effects in the full model ($R^2_{\text{conditional}} = 0.80$). Seals that did not travel as far had later turnaround dates than farther traveling seals (TurnaroundDate = $-0.027 \times \text{TurnaroundDistance} - 21.91$, Figure 1D).

Despite extensive research into how migratory animals pursue foraging patches in terrestrial⁵ and marine⁶ ecosystems, there has been substantial uncertainty in the when and why of movement decisions made by wild animals. We found that elephant seals show a great deal of variability in when and where they begin their multi-week return migration (Figure 1B) based on their real-time distance from the breeding beach. While the sensory basis of elephant seals' ability to assess their position (e.g. geomagnetic, celestial, acoustic, or olfactory) remains unknown, our data suggest that elephant seals have a map sense, which allows them to adjust their movement based on their current position relative to their destination⁷. This may help explain how elephant seals return to the breeding beach just before giving birth despite a maximum transit speed of ~150 km/day. Explaining movement decisions in this species can help us better understand the annual cycle⁸ and explore parallels with other long-distance migrants — including seabirds and whales — with implications for resource management, population connectivity, nutrient flow, species interactions, ecosystem control, and disease dynamics^{9,10}.

SUPPLEMENTAL INFORMATION

Supplemental information contains one figure, one table, experimental procedures and references, and can be found with this article online at <https://doi.org/10.1016/j.cub.2022.01.031>.

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AUTHOR CONTRIBUTIONS

R.S.B., A.L.Y., D.P.C., P.W.R. conceptualized the manuscript. All authors curated and analyzed the data. R.S.B. and A.L.Y. wrote the original draft. R.S.B. and M.F.C. created the data visualizations. All authors reviewed and edited the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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Supplemental information for: Elephant seals time their long-distance migrations using a map sense

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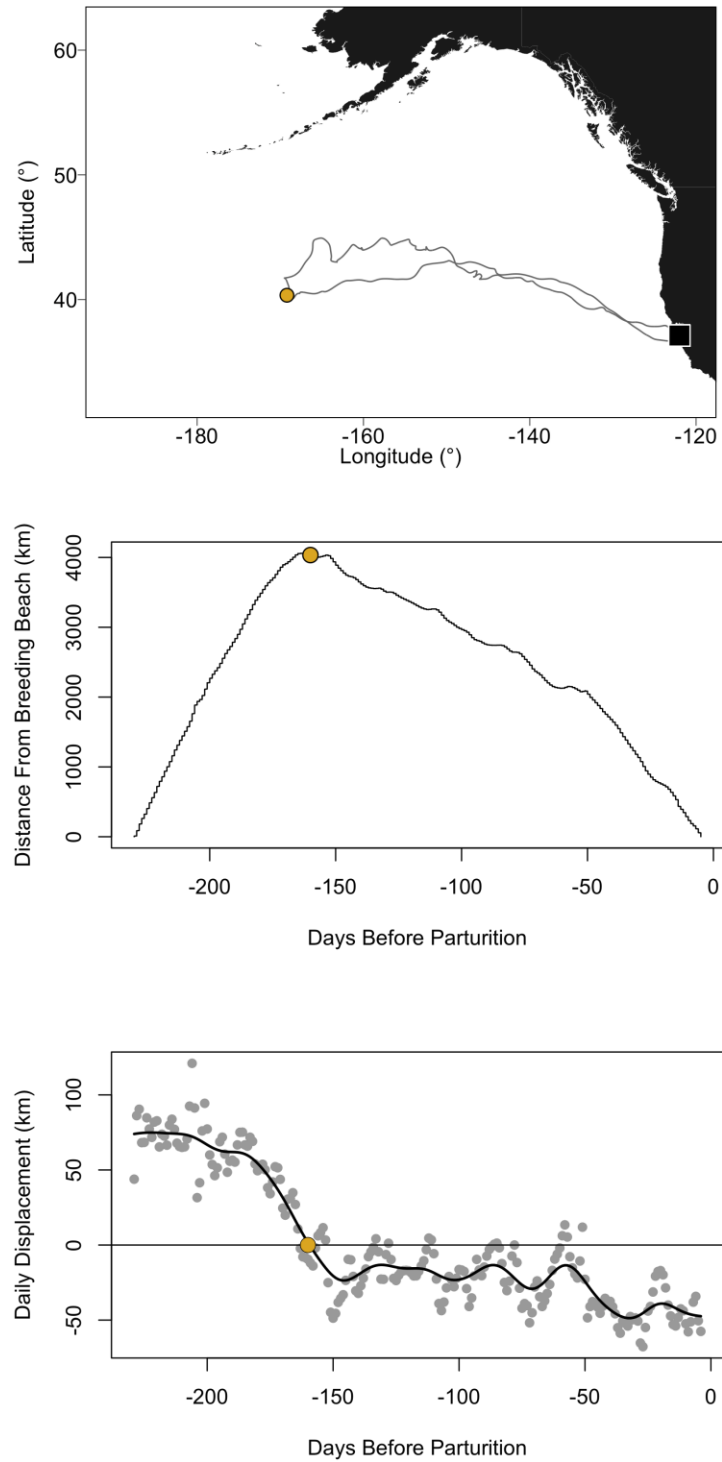


Figure S1: Metrics used to identify turnaround locations of migrating northern elephant seals. Tracking data (top), distance traveled from the breeding beach (middle), and daily displacement from the breeding beach (bottom) for a representative seal (#2007048). Gold points indicate turnaround locations in all panels.

- Session info

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- Packages

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```

Table S1: Computational environment. This analysis was generated on 2022-01-04 16:03:04 using the below computational environment and dependencies.

Supplemental Experimental Procedures

Animal handling methods, biollogger specifications, and calculation of arrival and departure dates are described in Robinson, *et al.*^{S1} Satellite tracking data were filtered and processed using the R package *crawl*^{S2, S3} to eliminate inaccurate location points and interpolate between locations. The resulting latitude and longitude estimates were used to calculate great circle distance (in kilometers) from the Año Nuevo breeding beach (37.1083°N, 122.3366°W) for each time-latitude-longitude point in the MATLAB function *distance()*. Across all seals, foraging trip timing (mean \pm SD day-of-year) was as follows: departure 157 ± 9 , turnaround 287 ± 40 , and arrival 15 ± 8 (Figure 1C). Therefore, outbound trip durations were 130 ± 41 days, and inbound trip durations were 93 ± 41 days. Turnaround dates were calculated using Gaussian kernels with standard deviation 6 hours using custom functions in R. Code and data for a subset of animals are available on Zenodo^{S4} (<https://doi.org/10.5281/zenodo.5777504>). Drift rate dates were calculated using a custom MATLAB code based on kernel density estimation of fine-scale changes in depth over time (drift rate, measured in meters/sec).^{S5} Dates are presented as day-of-year relative to parturition date, with negative numbers indicating dates before pupping. All analyses were carried out in R v4.0.2. A linear mixed-effects model of turnaround date (relative to pupping date) as a function of turnaround distance and buoyancy change date was run in the package *lme4*^{S6} after scaling and centering the continuous variables and including individual as a random effect.

Supplemental references

- S1. Robinson, P.W., Costa, D.P., Crocker, D.E., Gallo-Reynoso, J.P., Champagne, C.D., Fowler, M.A., Goetsch, C., Goetz, K.T., Hassrick, J.L., Hückstädt, L.A., et al. (2012). Foraging behavior and success of a mesopelagic predator in the Northeast Pacific Ocean: Insights from a data-rich species, the northern elephant seal. *PLoS ONE* 7, e36728.
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