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LETTER

Physiological tipping points in the relationship between foraging success and lifetime fitness of a long-lived mammal

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Abstract

Although anthropogenic change is often gradual, the impacts on animal populations may be precipitous if physiological processes create tipping points between energy gain, reproduction or survival. We use 25 years of behavioural, diet and demographic data from elephant seals to characterise their relationships with lifetime fitness. Survival and reproduction increased with mass gain during long foraging trips preceding the pupping seasons, and there was a threshold where individuals that gained an additional 4.8% of their body mass (26 kg, from 206 to 232 kg) increased lifetime reproductive success three-fold (from 1.8 to 4.9 pups). This was due to a two-fold increase in pupping probability (30% to 76%) and a 7% increase in reproductive lifespan (6.0 to 6.4 years). The sharp threshold between mass gain and reproduction may explain reproductive failure observed in many species and demonstrates how small, gradual reductions in prey from anthropogenic disturbance could have profound implications for animal populations.

KEYWORDS

foraging behaviour, life history theory, lifetime reproductive success, *Mirounga angustirostris*, movement ecology, northern elephant seal, open ocean ecology, phenotypic variability, pluck or luck, vital rates

INTRODUCTION

Gradual changes in temperature, carbon dioxide and precipitation are occurring worldwide. Many management and conservation efforts assume that biological responses will be gradual such that monitoring efforts will produce actionable early warning signs. However, some ecological and evolutionary processes including climate states (Dakos et al., 2008), population collapse (Pershing et al., 2015), species recoveries (Veraart et al., 2012) and social dynamics (Centola et al., 2018) exhibit sharp threshold relationships including a critical tipping point beyond which an unexpected and large change takes place that is not easily reversible (Scheffer, 2010). It is unknown whether physiological tipping points exist in the relationships between lifetime fitness, behavioural strategies and foraging success in long-lived organisms, which are thought to be buffered against stochastic environmental change. This uncertainty is due to the difficulty and cost of repeatedly sampling long-lived species through their entire lifespans. Therefore, it is critical to understand whether the fitness consequences of anthropogenic change on long-lived organisms will be gradual, or whether precipitous population declines could occur after a tipping point has been reached.

Roxanne S. Beltran and Keith M. Hernandez contributed equally to this work.

In many populations, lifetime reproductive success is highly variable, with a small number of individuals contributing disproportionately to population growth rates (Cabana & Kramer, 1991; Clutton-Brock, 1988; Tatarenkov et al., 2008). Some studies suggest that the majority of variation in lifetime reproductive success is due to chance, whereas a minor fraction is due to variation in quality (Broekman et al., 2020; Tuljapurkar et al., 2020), but environmental conditions also play an important role (Jenouvrier et al., 2019). Studies of lifetime reproductive success rarely examine individual behavioural strategies or foraging success. Understanding the shape of the relationship between energy gain and lifetime reproductive success can also elucidate the selective pressures on wild animals, which balance trade-offs between starvation and predation to survive and reproduce (Lima & Dill, 1990).

Behavioural strategies that increase the probability of reproduction may reduce lifespans, or vice versa, resulting in a trade-off. Alternatively, some strategies may increase both survival and reproduction without incurring tradeoff costs. For example, superior physiological capacities may enable movement strategies, such as farther migrations, enabling animals to exploit more profitable prey patches and avoid predators (Moxley et al., 2020). A third possibility is that behavioural strategies do not influence any metric of lifetime fitness, which is likely if starvation and/or predation are highly stochastic (Sinclair & Pech, 1996). Using a long-term data set, we examine the relative importance of behavioural strategies and foraging success for explaining intraspecific variation in reproduction and survival, including the directionality and sharpness of the relationships.

Links between foraging success and lifetime fitness ought to be strongest in capital breeders, in which stored energy reserves are critical for reproduction (Costa & Maresh, 2022). Northern elephant seals (*Mirounga angustirostris*) separate feeding from breeding in both space and time. They undergo long-distance migrations from the foraging areas, where they accumulate energy, to the breeding grounds, where they fast for prolonged periods (Costa et al., 1986). Despite genetic similarities between individuals due to a historic population bottleneck, behavioural strategies, including migration routes and timing, are highly variable across individuals (Abadía-Cardoso et al., 2017) and, thus, provide a potential mechanism for adaptation. For example, individual prey preferences could drive variability in energy intake; mesopelagic fishes, such as lanternfishes (Family *Myctophidae*) tend to be more energy dense and easier to capture than the squid species elephant seals consume (Goetsch et al., 2018). Consuming energy-rich prey may be worth the costs of travelling to specific prey patches and continuous foraging (Adachi et al., 2021; Robinson et al., 2012). However, foraging success may come at the cost of survival if profitable prey is located in areas with higher predation risk by white sharks (*Carcharodon carcharias*) and killer whales (*Orcinus orca*), as suggested by a male–female comparative analysis (Le Boeuf et al., 2000). Additionally, superior physiological capacity may confer a fitness advantage by increasing diving depth and/or duration (Costa, 1991). This may allow individuals to access more energetically beneficial prey resources (Naito et al., 2013) and avoid shallow water predators (Beltran et al., 2021). Yet the degree to which individual variability in these traits, alone or synergistically, influences female elephant seal survival, reproduction or both, has not been explored.

Our goal was to examine the shape of the relationship between behaviour, diet and lifetime fitness of elephant seals. We measured female elephant seal survival, reproduction and the number of pups produced as a proxy for lifetime reproductive success. We evaluated the contributions of diet (e.g. more frequent consumption of fishes that have high energy density), migratory routes (e.g. foraging in offshore regions), physiological capacity (e.g. diving deeper), life history phenology (e.g. stronger temporal overlap with prey species) and foraging success (e.g. higher mass gain). We hypothesized that mass gain would increase with foraging depth (Robinson et al., 2012), distance from the coast, fish in the diet (Naito et al., 2013) and an earlier departure from the colony. We also predicted that the probability of pupping would increase with mass gain because elephant seals are capital breeders. We did not make an a priori prediction about the effect of mass gain on survival because increasing foraging reduces starvation risk but could also increase predation risk (Brown, 1999); the relative importance of starvation versus predation to mortality of elephant seals and other marine mammals is not known.

METHODS

Animal handling and data methods

We studied adult female elephant seals instrumented with biologgers on at least one long (post-moult) foraging trip as a part of the long-term research program at Año Nuevo Reserve (Robinson et al., 2012). Elephant seals were flipper-tagged with unique alpha-numeric codes approximately 1 month after birth and observed each year until the end of their lives. The colony was searched approximately daily between December and June each year to resight flipper-tagged individuals and quantify annual survival. High resight effort during the breeding season allowed us to determine the presence of pups associated with tagged females annually. Lifespan was calculated as the number of years an animal was observed between birth and death. Because mortality is impossible to observe at sea, and elephant seals have high site fidelity and sighting probabilities, we used the year of last observation as the year of death. Lifetime reproductive success was the number of pups an individual female produced over her lifespan, as described by Le Boeuf et al. (2019). Our analysis focuses on 63 females we tracked for a foraging trip between 2004 and 2015 using biologgers. We obtained data from 75 trips: two animals tracked three times each, eight animals tracked twice, and 53 animals tracked once. The demographic data on annual survival and reproductive success span 25 years (1994–2018) between the birth years and last observed years of all study seals.

We chemically immobilised individuals to weigh, sample and attach tracking instruments (Argos or GPS and time-depth recorders) at the end of the moult haul-out and again to weigh, sample and recover tracking instruments at the beginning of the breeding haul-out. Details of animal handling and data processing are provided by Robinson et al. (2012). We calculated the distance between the coast and each processed latitude–longitude position using the function *distm()* within the R package 'geosphere' on the coastline from the function *map()* within the package 'maps.' We calculated mass gain as the difference between arrival and departure mass after correcting for time spent fasting ashore (Robinson et al., 2012). Of the 75 biologging records, 9 were from seals that did not produce a pup and therefore had varying return dates (four returned early, two returned during the normal breeding season and three returned after the breeding season). None of the 9 non-reproductive seals produced pups at other colonies. Including foraging trip duration, age and departure body mass as co-variates did not influence the relationship between reproductive success and mass gain.

To determine diet, we collected full-depth blubber biopsies from adult female elephant seals ($n = 30$) after their return from the foraging trip using a 6 mm biopsy punch. Quantitative fatty acid signature analysis (QFASA) models were run on a fatty acid profile from the metabolically active inner blubber and a range of potential prey species (homogenized whole) to determine the proportion of fish in the diet of each seal. Additional details regarding elephant seal sampling, prey library preparation and selection of prey for QFASA models are provided in Goetsch et al. (2018).

Statistical analyses

We conducted all statistical analyses in R v. 4.2.1. We examined the influence of four behavioural strategies on one measure of foraging success and the influence of all five of those metrics on survival and pupping success: median distance from the coast (hereafter, Distance), mean diving depth (Depth, which integrates across nocturnal and diurnal behaviour across all dive types), departure day-of-year (Date), the proportion of fish in the diet (Diet) and mass gain (MassGain). All metrics were measured during the longer of two annual foraging trips that immediately precedes pupping. We quantified the repeatability of each metric for individuals with multiple measurements ($n = 10$ seals) using the intra-class correlation coefficient from the *ICCest()* function in the R package 'ICC' (Wolak et al., 2012). Then, we averaged the behavioural metric for individuals we tracked more than once for survival analyses. Finally, we examined the relationship between the foraging success metric, MassGain, the four behavioural strategies, Distance, Depth, Date and Diet, and the simple pairwise correlations among all five variables.

We also fitted a generalised linear model with a binomial distribution with pupping success as the response variable and the five metrics described above as predictors: MassGain, Distance, Depth, Date and Diet. Additionally, we examined the impact of the same five predictors on survival by fitting a Cox proportional hazards model using the *coxph()* function from the R package 'survival'. The endpoint was the age at death (with no right censoring because all animals had died), and left truncation using the age at tracking (median: 8 years; range: 4–13 years), as animals were only included in the analysis if they were tracked. We fit models with and without diet for survival and pupping analyses because we only had diet data for a subset of the animals (48%; 30 of 63). We examined survival models with either Distance or Depth removed because these variables were moderately correlated ($r = 0.36$; $n = 63$; $p = 0.002$), and we wanted to understand their contribution. We compared models with subsets of variables using Akaike's Information Criterion (AIC). We report coefficients for the model with all four predictors (MassGain, Distance, Depth, and Date) even though some subset models have higher support by AIC because dropping variable biases remaining coefficients and p values (Whittingham et al., 2006). We use one-tailed p values for analyses that address the *a priori* hypotheses described above. We also explored principal component analysis (with the *prcomp()* function in R) for combining the four behavioural strategy metrics into orthogonal axes and correlated these axes with MassGain.

We estimated the impact of mass gain on lifetime fitness metrics using the fitted models for reproductive success and survival, which were both correlated with mass gain. Specifically, we calculated lifetime reproductive success (total pup production) and reproductive lifespan (lifespan minus two to account for recruitment to the breeding population at age three (Reiter & Le Boeuf, 1991)). We examined the relationship between lifetime reproductive success and lifespan using a generalised linear model with a quasi-Poisson distribution using the *glm()* function.

Finally, we investigated how elephant seal lifespans compare to other species based on their body mass. We extended the analysis of Healy et al. (2014) by adding body mass and lifespan information for male and female elephant seals separately, owing to the high degree of sexual dimorphism and differences in life histories. Specifically, we supplemented the figure with female body mass (504 kg; (Costa et al., 1986)), male body mass (1573 kg; (Le Boeuf et al., 2000)), female lifespan (23 years; (Le Boeuf et al., 2019)) and male lifespan (15 years; (Condit et al., 2014)).

RESULTS

There was substantial variation among females in behavioural strategies and outcomes (Figure 1), and four of the five metrics had moderate to excellent repeatability within individuals (ICC values MassGain = 0.58, Distance = 0.93, Depth = 0.46, Date = 0.69, Diet = 0.53; Wolak et al., 2012). There were significant positive correlations among some of the behavioural strategies, including Diet and Distance, Depth and Distance, Diet and Depth and Diet and Date (Figure 1). These correlations made it challenging to determine the unique contribution of each behavioural strategy to survival and reproduction. MassGain was positively correlated with Depth, but not significantly correlated with other variables (Figure 1). None of the principal component axes was as strongly correlated with MassGain as Depth.

There was a strong relationship between the probability of pupping and MassGain during the foraging trip but no significant relationship with individual behavioural strategies (Figure S1). The probability of pupping increased with MassGain after reaching a threshold of 205 kg, below which animals never pupped. Animals

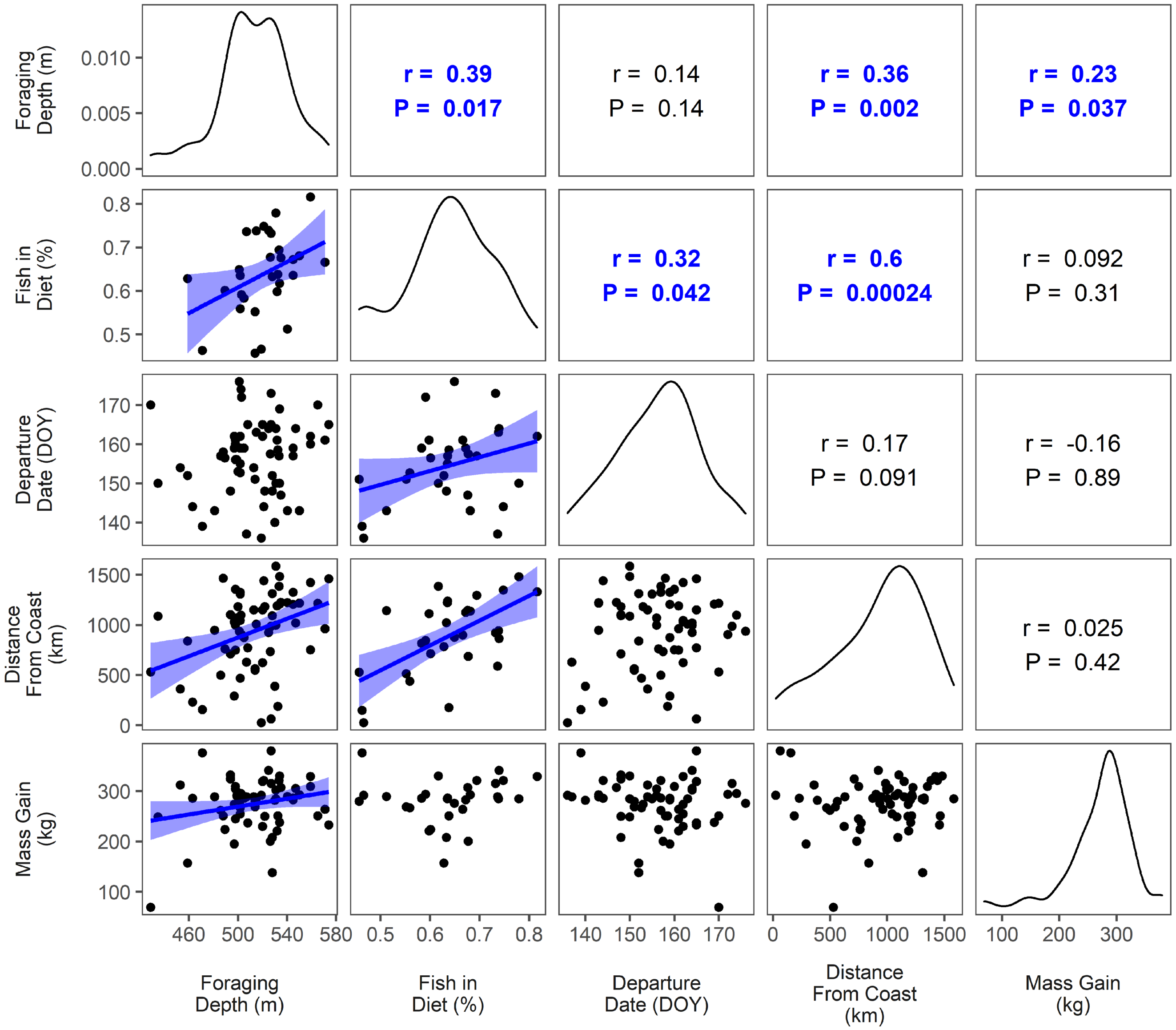

FIGURE 1 Mass gain is positively correlated with mean foraging depth, and diet and distance from the coast are positively correlated. Probability density plots of behavioural strategies (diagonal panels), correlations and p values of behavioural strategies (upper panels) and relationships between behavioural strategies (bottom panels). Blue colour indicates statistically significant relationships, and the shaded band around the linear model is a pointwise 95% confidence interval on the fitted values.

gaining more than 260 kg almost always pupped (Figure 2). For seals with repeated measurements and tracks, pupping failure always occurred after lower mass gain than when pupping was successful (Figure 2).

The annual survival of instrumented seals was approximately 80% until age 13. Half of the seals tracked at age 4 survived until age 7, and very few seals reached age 15. The lifetime reproductive success of instrumented seals ranged from 1 to 16 pups (median = 7). There was a very strong relationship between lifetime reproductive success and lifespan ($r = 0.87$, $N = 63$, $p < 0.0001$) because a relatively high fraction of instrumented females (79%) had pupped each year. Model comparison indicated that annual survival increased with MassGain (Figure 2), but relationships with Date, Depth and Distance were weaker or difficult to disentangle due to collinearity (Figure 1; Table S1, S2). Seals that gained 323 kg (the 90th percentile) had 6.4% higher survival than seals that gained 223 kg (the 10th percentile) (89.0% vs. 82.6%, respectively, for 8-year-old seals). The effect was even larger for older seals (above age 14), which had markedly lower survival, even for high rates of mass gain during the foraging trip, providing evidence of senescence (Figure 2).

The combined effects of MassGain on survival and reproduction resulted in a threshold relationship between lifetime reproductive success and MassGain (Figure 3). Increasing mass gain from 100 kg to 200 kg increased the reproductive lifespan of seals from 4.9 to 6.0 years. However, lifetime reproductive success for females that had a low mass gain (100 kg: 0.0; 200 kg: 1.3) was also low, as females gaining less than 200 kg during the foraging trip rarely pupped (Figure 2). In contrast, a 100 kg increase in mass gain from 200 to 300 kg increased lifetime reproductive success more than six-fold (from 1.3 to 7.5 pups). These females successfully produced pups every year and had a 25% increase in reproductive lifespan (6.0 to 7.5 years). Seals gaining 281 kg (the median mass gain) had a mean reproductive lifespan of 7.2 years and a lifetime reproductive success of 7.1 pups because they nearly always produced pups successfully (Figure 2). Further increases in mass gain increased lifetime reproductive success solely through increases in survival and reproductive lifespan (Figure 3).

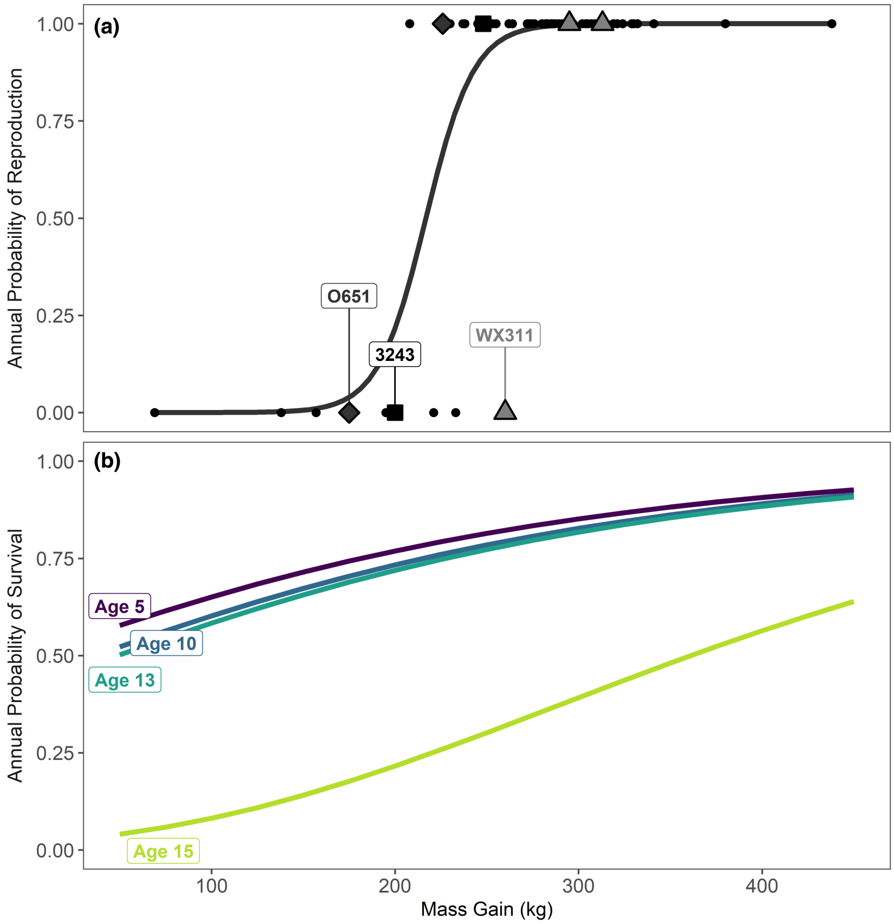

FIGURE 2 The relationships between mass gain and annual probability of producing a pup (a) or surviving (b). Seals with repeated measurements of mass gain and pupping success (seals O651, 3243, WX311) are shown in the upper panel as diamonds, squares and triangles, whereas all other seals are shown as circles. In (a), the line shows a generalised linear model fit of reproductive success (producing a pup) as a function of mass gain using a binomial distribution and a logit link (Intercept = -16.74 ± 6.06, $z = -2.76$, $p = 0.0058$; MassGain = 0.077 ± 0.026, $z = 2.97$, one-tailed $p = 0.0015$).

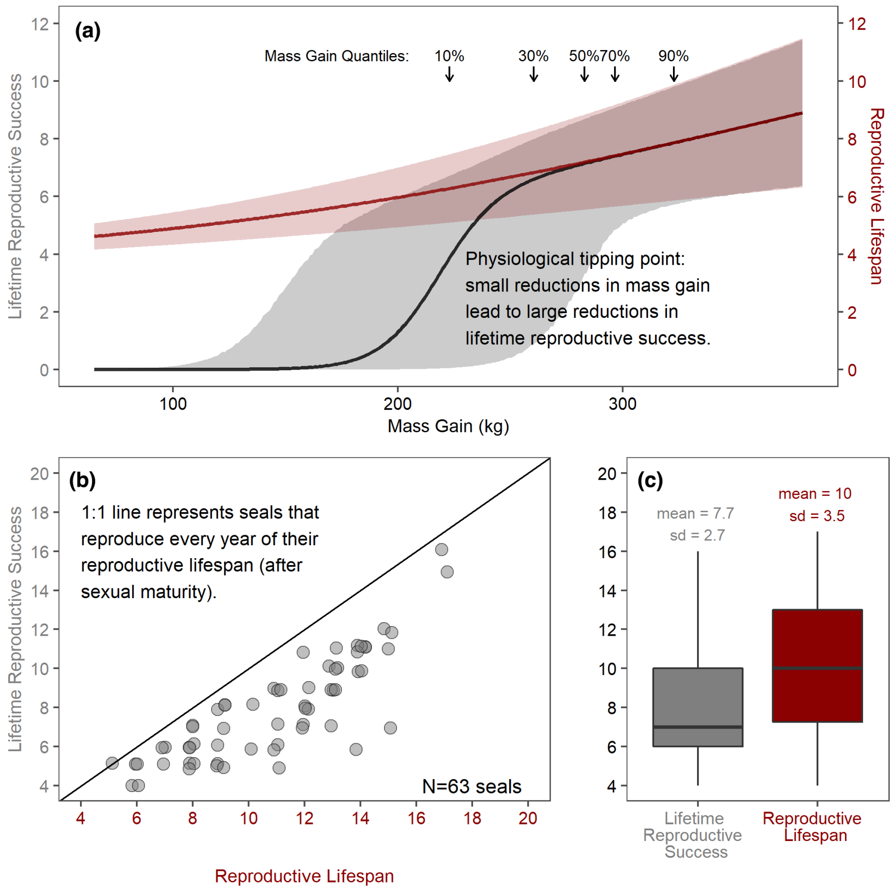

FIGURE 3 A physiological tipping point mediates the relationship between mass gain and lifetime fitness metrics in female elephant seals. (a) Combining annual predictions for survival and reproductive success demonstrates clear lifetime fitness benefits of mass gain, including increased reproductive lifespan (lifespan minus 2 to account for the age of recruitment to the breeding population) and increased lifetime reproductive success (total pup production). The shaded bands around the mean are pointwise 95% confidence intervals on the fitted values. Arrows indicate the 10th, 30th, 50th, 70th and 90th quantiles of mass gain. Where the lines converge, the probability of reproduction each year equals one such that all additional increases in lifetime reproductive success are due to increased longevity. To the left of this convergence point, the probability of reproduction is less than one. (b) Jittered scatterplot of lifetime reproductive success versus reproductive lifespan, with a 1:1 reference line assuming recruitment at age 3. (c) Distributions of lifetime reproductive success and reproductive lifespan for $N = 63$ seals we tracked through a foraging trip using biologgers. Each boxplot shows five summary statistics: the median, the lower and upper hinges (first and third quartiles, respectively) and the lower and upper whiskers (extending from each hinge to 1.5 times the interquartile range).

In other words, there is both a large fitness benefit of (1) gaining more mass to increase pupping probability up to the threshold where seals almost always reproduce and (2) an additional gradual fitness benefit of gaining more mass as these seals live longer and have more chances to reproduce. Finally, elephant seals have shorter lifespans than predicted based on their body mass, with males falling well below the trend for mammals and birds (Healy et al., 2014; Laws, 1956) (Figure S2).

DISCUSSION

Although variation in lifetime reproductive success among individuals strongly influences population dynamics and evolution, the drivers of this variation are not well understood (Tuljapurkar et al., 2020). We combined demography with movement data to link behavioural strategies and foraging success with lifetime reproductive success in a long-lived mammal. We discovered that both survival and reproduction, and consequently, lifetime reproductive success, were strongly influenced by mass gain, which in turn increased with foraging depth (Figure 4). Because behavioural strategies were highly repeatable, measurements from a single year could be used to explain lifetime variation in fitness across individuals. The influence of mass gain on reproductive success is expected for capital breeders like elephant seals (Costa & Maresh, 2022), but the precise relationship between mass gain and pupping, specifically, the sharp threshold we observed, illustrates the connection in exquisite detail. In contrast, the positive relationship between mass gain and survival was not expected because foraging can increase predation risk (Brown, 1999), resulting in a trade-off between reproduction and survival (Dobson & Jouventin, 2010). The combined influences of mass gain

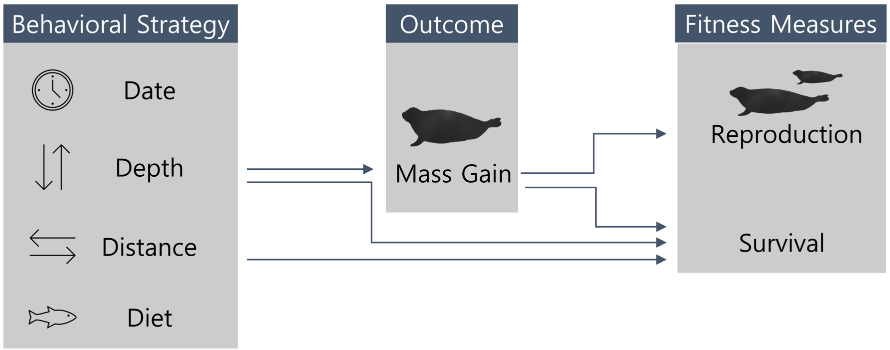

FIGURE 4 Conceptual model of behavioural strategies affecting fitness via mass gain. Diving depth and foraging distance from the coast were both positively correlated with survival. Mass gain, which was related to diving depth, was positively correlated with both reproduction and survival.

on survival and reproduction highlight the importance of behavioural strategies influencing foraging success.

We discovered a strong relationship between mass gain and pup production, which provides a mechanistic explanation for reproductive failure in long-lived vertebrates (Ropert-Coudert et al., 2015). This is especially relevant for capital breeding species, such as seals, whales and seabirds that rely on stored energy reserves for parental care (Jönsson, 1997). When sufficient energetic stores cannot be accumulated, such as during poor foraging years, females may skip breeding opportunities rather than invest in smaller offspring with a lower probability of survival (Desprez et al., 2018). Low foraging success could, in principle, affect reproduction in subsequent years, but the strong relationship we observed for mass gain and reproduction in the same year suggests that lagged effects are small in comparison. On the other hand, favourable conditions can facilitate increased energy partitioning to offspring (McMahon et al., 2017) which benefits offspring survival and recruitment (Oosthuizen et al., 2018). Long-lived animals are expected to maximize lifetime fitness by occasionally skipping a reproductive event because multiple years of future reproduction are contingent upon current survival (Griffen, 2018). Indeed, intermittent reproduction is common in long-lived mammals and birds (Badger et al., 2020; Chambert et al., 2013). In the case of northern elephant seals, it is unclear which portion of the reproductive cycle (breeding, delayed blastocyst implantation, or gestation) is negatively impacted by limited mass gain, or how skipping an annual reproductive event carries over to future behaviour, body mass or survival. One possibility is that skipping a reproductive event can benefit the survival rates of individuals, as in Weddell seals *Leptonychotes weddellii* (Hadley et al., 2007). Another possibility is that high-quality individuals breed early and often, with limited or absent impacts on survival, as in southern elephant seals *Mirounga leonina* (Oosthuizen et al., 2019, 2021). Future studies should evaluate the causes and consequences of intermittent reproduction including body condition and carry-over effects from other life history events.

Regardless of the physiological mechanisms underlying reproductive failure, the shape of the mass gain–reproduction relationship is important for both demography and evolution. However, it is often difficult to precisely characterise due to the challenge of measuring both mass gain and reproductive success in wide-ranging animals. Our results show that this relationship may have a steep threshold, such that small changes in foraging success can lead to dramatic decreases in pup production at the population level. Mass gain had the narrowest distribution of any behavioural trait we measured, suggesting strong selection via consistent reproductive success and survival (Figure 1). Although our metric of reproductive fitness did not account for offspring quality (e.g. pup survival, recruitment or reproductive frequency), the strong positive links between mass gain, offspring size (Le Boeuf & Crocker, 2005) and offspring survival (Le Boeuf et al., 2019) in elephant seals indicate that the relationship between mass gain and the number of offspring that reproduce is even steeper than with the probability of pupping.

Although mass gain is expected to increase the probability of reproduction, the relationship between mass gain and survival is less certain because behavioural strategies can impact the likelihood of both starvation (i.e. prey capture) and predation (i.e. predator avoidance) depending on whether predators and prey overlap in space and time. We found that mass gain substantially increased survival, but in contrast with the sharp threshold we observed with reproduction, the relationship was gradual, possibly due to the importance of ecological luck ([Snyder & Ellner, 2018], Figure 2). Predation can be highly stochastic because it varies with multiple interacting factors that are difficult to measure, even on land (Suraci et al., 2022). Marine vertebrates predominantly die at sea, where information on the three-dimensional distribution of predators and direct observations of predator–prey interactions are lacking (Hussey et al., 2015).

The strongest predictor of mass gain was foraging depth, likely due to the deep distribution of elephant seal prey, which emphasizes the importance of physiological capacities in air-breathing vertebrates (Braun et al., 2022). Deeper diving seals migrated farther from the coast and had fish-rich diets compared to shallower diving seals (Figure 1). Therefore, it appears that some seals were able to take advantage of productive oceanographic features in the open ocean, such as eddies, that promote foraging activity (Robinson et al., 2012), feeding success (Adachi et al., 2021) and deep, profitable prey patches (Green et al., 2020). Deeper diving may also help elephant seals avoid predators, which may be especially difficult in the open ocean where spatial refuges are rare (Beltran et al., 2021). This could explain why elephant seals have far shorter lifespans than expected, given their body size, compared to other mammals and birds (Figure S2). The shallower diving and more coastal foraging range of males (Kienle et al., 2022) may explain why males fall further below the mass-specific expectation of vertebrate lifespans relative to females ([Healy et al., 2014], Figure S2).

We found no trade-off between reproduction and survival, indicating that predator and prey abundance are not correlated, and no risk–reward trade-off exists for adult female elephant seals. It appears that superior diving ability allows elephant seals to avoid predators and capture more prey by diving deeper where prey is more abundant (Beltran et al., 2021). Tracking individuals over time to determine whether predation or starvation drives mortality can provide valuable insight into selective pressures shaping behavioural strategies over evolutionary time, as most (87%) of the variation in lifetime reproductive success was due to differences in lifespan. Our integrated framework (Figure 4) for investigating links between reproductive output, lifespan and behavioural strategies could be adapted to other taxa through long-term monitoring programs (Schradin & Hayes, 2017), which are disproportionately valuable given their cost (Abrahms et al., 2022; Hughes et al., 2017).

A key limitation of our findings is that this study was restricted to adult females. Elephant seals, like many large marine vertebrates (Hazen et al., 2012), have extremely high juvenile mortality (~50% per year (Condit et al., 2014)). As a result, most individuals die young (the average elephant seal lifespan is ~2 years (Condit et al., 2014)), and only a small number of seals survive to the age of first reproduction. Fewer live long and produce many pups (maximum lifespan ~23 years old (Le Boeuf et al., 2019)). Our sample of reproductive females is likely biased towards high-quality (or lucky (Snyder & Ellner, 2018)) individuals. The behavioural strategies affecting the survival of young animals to the age of first reproduction could have critical cascading impacts on population dynamics and should be a focus of future research (Snyder et al., 2021). Likewise, our understanding of foraging behaviour and lifetime fitness in adult male elephant seals is extremely limited, but there is some evidence that deep diving may come at the cost of physiological stress and shorter lifespans (McIntyre et al., 2010). Much remains to be learned about the adaptive benefits of three-dimensional movement ecology and its physiological underpinnings.

Understanding how foraging success and behavioural strategies influence lifetime fitness is a pre-requisite to managing and conserving wildlife across the globe. Increases in anthropogenic disturbances, including climate change, overharvesting (Estes, 1998), pollution (Savoca et al., 2021) and urbanisation may be gradual, but the fitness consequences could be precipitous if lifetime reproductive success has a sharp threshold relationship with foraging success. For example, lower feeding success due to proposed fishing in the mesopelagic zone (St. John et al. 2016) could have profound implications for population persistence if predators are pushed past physiological tipping points ([Scheffer, 2010], Figure 3). Our results demonstrate that critical thresholds may occur in nature (but see Hillebrand et al. (2020)), especially for animals already constrained by their dietary niches (Adachi et al., 2021), energetic requirements (Goldbogen et al., 2019), thermal performances (Grady et al., 2019), geographic ranges (Pagano et al., 2018), or requirements for vital activities including sleep (Rattenborg et al., 2016). Critical habitats and sensitive seasons that confer high lifetime fitness must be identified and strategically protected (Hindell et al., 2020).

AUTHOR CONTRIBUTIONS

Study design: Roxanne S. Beltran, Daniel P. Costa, A. Marm Kilpatrick and Keith M. Hernandez; Data collection: Patrick W. Robinson, Richard Condit, Daniel E. Crocker, Daniel P. Costa and Chandra Goetsch; Data analysis: Richard Condit, A. Marm Kilpatrick, Roxanne S. Beltran, Keith M. Hernandez, Daniel E. Crocker, Chandra Goetsch and Patrick W. Robinson; Manuscript drafting: Roxanne S. Beltran, Keith M. Hernandez and A. Marm Kilpatrick. Funding and supervision: Daniel P. Costa, Roxanne S. Beltran and A. Marm Kilpatrick. All authors edited the manuscript.

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ETHICS STATEMENT

Approval for elephant seal handling and sampling was approved by the University of California Santa Cruz Institutional Animal Care and Use Committee and following guidelines set forth by the ethics committee of the Society for Marine Mammalogy and the Canadian Council for Animal Care. Fieldwork was carried out under the National Marine Fisheries Service permits #786-1463, 87-143, 14636, 14535, and 19108. Prey sampling on the *T/S Oshoro-maru* was conducted under the United States Department of State, Bureau of Ocean and International Environment and Scientific Affairs permit U2012-013.

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DATA AVAILABILITY STATEMENT

The data file and code are available on Dryad (https://doi.org/10.7291/D1T685).

PEER REVIEW

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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