

# Fostering public health and academic partnerships during and beyond a public health emergency: lessons learned from COVID19

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## Introduction

The COVID-19 pandemic severely strained local, state, and federal health agencies across the United States. Rapid and sometimes unexpected rises in disease transmission led to increased morbidity and mortality and associated shortages in health care staffing, testing capacity, and personal protective equipment. Modeling and advanced analytics that provided predictive information on the timing and magnitude of surges under various scenarios were urgently needed to inform public health response. However, in order to provide such insights, there were several challenges to overcome. First, prior to the COVID-19 pandemic, minimal infectious disease modeling existed at state, tribal, local, and territorial health departments. At the federal level, the Centers for Disease Control and Prevention (CDC) also had limited capacity until the formation of the Center for Forecasting and Outbreak Analytics (CFA) in late 2021; even then, its capacity for locally focused modeling outputs remained restricted. Second, early in the COVID-19 pandemic, government systems struggled to ingest, manage, and report the tremendous volume of COVID-19 data, while data access for infectious disease modelers remained a barrier. Despite significant funding efforts by CDC and other agencies in support of data modernization and forecasting, challenges persisted for many public health agencies, including the California Department of Public Health (CDPH).

The CDPH addressed the need for infectious disease modeling expertise in

Analytics Team that both leveraged existing CDPH staff and onboarded infectious disease modelers. The team was dedicated to synthesizing externally developed nowcasts, forecasts, and scenarios and producing internal modeling and analytical tools, with a major focus on the launch and development of the California COVID Assessment Tool (CalCAT, <https://calcat.cdph.ca.gov/>). The CalCAT compiles available nowcasts, forecasts, and scenario models for both internal situational awareness and to share with other public health agencies, health care systems, and the public. These modeling resources—especially those at the county scale—were extremely helpful for understanding near-future health care impacts and informing policy decisions in the face of substantial uncertainty about COVID-19 biology, epidemiology, and control measures by Virginia Polytechnic Institute and State University.

However, the CDPH Modeling and Advanced Analytics Team sometimes had insufficient staff for specific expertise to answer pressing policy questions in a short timeframe, especially when evidence in the literature was lacking. Specifically, there was a need for rapid, ad hoc modeling and expert assessment on fast-breaking topics such as the potential impact of emerging viral variants and waning immunity on transmission. Acquiring these resources within CDPH and other health jurisdictions would have required significant time and effort amidst many competing priorities during an ongoing public health emergency. In contrast, many academics were already well-positioned to digest rapidly

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multiple ways. First, CDPH engaged external public and private sector stakeholders and citizen scientists early on during the COVID-19 response to iteratively develop and synthesize

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This effort resulted in the formation of a Modeling and Advanced

The University of California Health-CDPH COVID Modeling

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evolving literature on variant properties and immunity and synthesize the implications for modeling transmission and hospital burden. Therefore, CDPH recognized that its response would benefit from closer academic collaborations, including with the I(Campus University of California (UC) system, a large state-based institution.

Consortium (<https://modelingconsortium.ucsf.edu/>), hereafter referred as

the "Modeling Consortium", was launched in early 2021 with the backing of top leadership of both institutions to facilitate collaboration between CDPH and UC scientists on COVID-19 through 4 major areas. First, the Modeling Consortium awarded several rapid grants and contracts to UC-based investigators, enabled by state and federal funding for the pandemic response. The CDPH leadership and staff scientists provided frequent input on project progress, resulting in deliverables that were directly relevant to CDPH for pressing policy questions, including tailored nowcasts, forecasts, and scenarios that were displayed on CalCAT, as well as more traditional academic publications.<sup>1-4</sup> Second, the Modeling Consortium provided UC investigators access to more granular data than publicly available for rapid analysis of research questions specifically relevant to California's COVID-19 situation. Although data sharing challenges persisted, this finer scale data access and ongoing alignment with CDPH and its counties may have benefited model performance. In a retrospective analysis of forecasting performance, two California-specific forecasting models run by UC partners (ie, COVID NearTerm and LEMMA) outperformed the CalCAT ensemble when forecasting COVID-19 hospital census at the county level.<sup>5-7</sup> Third, through mutual training opportunities, UC graduate students and postdoctoral researchers interacted more directly with public health practice, and CDPH employees gained access to academic courses and cutting-edge research to further their professional development. Finally, the Modeling Consortium hosted virtual seminars and targeted small-group meetings 1 to 2 times each month. Each seminar combined short-format presentations on a topic of urgent concern (eg, COVID-19 transmission in schools, masking effectiveness) followed by open discussion. These fora included dozens of scientists from across the UC system and a range of CDPH staff including the State Health Officer and State Epidemiologist who indicated that these meetings provided them with critical information to make urgent policy-related decisions and recommendations to state government leadership. The targeted small-group meetings included the CDPH Modeling Team and a core group of UC scientists who discussed the most urgent scientific questions that the CDPH Modeling Team was addressing. Three key examples that demonstrated the benefit of the Modeling Consortium were the prediction of hospital burden during emergence of the Delta and Omicron variants, discussion and synthesis of evidence around nonpharmaceutical interventions, and collaborative work on understanding COVID-19 transmission in K-12 schools.<sup>3,6</sup>

Several challenges to this collaboration were mitigated but not eliminated during the pandemic, and many lessons were learned from this joint effort (Table 1). It was challenging for CDPH to establish data use agreements (DUAs) quickly and to subsequently

available to academic investigators in a timely manner. Personnel from the State of California and the University of California, Berkeley, maintained data pipelines and context. Maintaining data pipelines requires resources not traditionally covered by grants and other funding mechanisms. Future efforts should include support for this necessary aspect of collaboration with contingencies for changes in data sharing depending on whether a statewide public health emergency declaration order is in effect. Health departments should also be encouraged to engage in robust and ongoing data governance practices, so that data sharing questions can be quickly evaluated and approved when needed. Another key challenge was that incentives in state government and academia were not initially aligned; cooperation depended on both academics and CDPH setting aside other activities to focus on California's COVID-19 response. Modeling Consortium academics set aside or delayed writing publications to focus on providing model forecasts that were displayed on CalCAT, updated daily, and could be adjusted in response to feedback from CDPH leadership. The mutual engagement and singular focus in the early pandemic years paid large dividends but were unsustainable at that level beyond the crisis phase of the pandemic.

The most important outcome of the Modeling Consortium was stronger collaborations—trust, partnerships, and networks—between state-based academic and government institutions that are both focused on serving the health and well-being of Californians. Funding academics to work directly with a state health department on locally important public health problems is

make that data one way to continue to increase collaborations and improve coordination across levels and sectors. However, the feasibility and sustainability of such an approach is not certain, as the COVID-19 pandemic response facilitated funding this type of collaboration in an unprecedented way. State, territorial, local, and tribal (STLT) governments are generally not in a position to provide such funding, but funding bodies should consider alternative mechanisms wherein STLTs can help shape grant priorities and deliverables rather than being more passive partners. Building internal capacity for modeling infectious diseases within CDPH was also a key feature in promoting crosssector communication and collaboration; the CDPH Modeling Team played a key role in translating requests from leadership to academic partners and synthesizing evidence from academic deliverables for leadership, thus amplifying the ability of partners to influence policy decisions and resource prioritization. Our experiences working together have demonstrated tangible benefits for both sides: academic trainees better understood and contributed to applied public health practice, and research was catalyzed to have real-world impact in the hands of practitioners and policymakers. Additionally, government workers were informed about cutting-edge research, while learning methodologies and approaches from academic colleagues. This training fostered workforce development and employment opportunities in public health that benefited CDPH and public health more broadly. Expanding academic incentives for this sort of public service and supporting publication of research for academic and public health scientists will support ongoing partnerships.

A key overall question is: what parts of the Modeling Consortium, and academic-public health modeling partnerships in general, should be preserved and fostered for work on current and emerging public health issues as well as pandemic preparedness going forward? CDPH occupies a unique and privileged position in having access to multiple world-class universities within the state of California. Since the number of public health jurisdictions greatly exceeds the number academic centers with expertise in infectious disease modeling, national and regional coordination will be necessary for optimizing the performance and impact of such collaborations. Some of this work is just beginning through national scenario modeling and forecasting hubs, as well as dedicated efforts such as the National Outbreak Analytics & Disease Modeling Network (Insight Net). More work is needed to make sure that such collaborations are benefiting jurisdictions across a range of capacities and experience in infectious disease modeling. As others have suggested, high-frequency, real-time outbreak analyses are well-suited tasks for in-house modeling teams.<sup>8</sup> Therefore, modeling pipelines and tools should be built in a

Table 1. Modeling consortium successes, challenges, and opportunities in preparedness and response activities.

	Preparedness	Response
Accomplished	Stronger trust, partnerships, and networks between academics and government staff	Collaboration on emerging topics
	Increased internal CDPH capacity for advanced modeling and analytics	Regularly scheduled seminars and targeted small-group meetings for exchange of ideas and information
	UC system academic training opportunities for CDPH staff	Funding of rapid grants and contracts for UC investigators with ongoing engagement with project deliverables from CDPH staff
	Applied public health training opportunities for academic trainees	Generation of tailored nowcasting/forecasting/scenario deliverables specific to California context Sharing more granular data for UC investigators via secure server
Needs improvement	Rapid deployment of data use agreements	Faster engagement in cryptic phase Engagement with broader interdisciplinary fields
	Health department personnel and capacity for data pipeline maintenance and provisioning	Better mechanisms for sharing data with academic collaborators in real time with and without a public health order in effect
	Incentives for public health service for academics	Sustainability of collaborative pandemic response

To support this approach, many Modeling Consortium investigators participated in the national modeling hubs, and the CDPH Modeling Team engaged in dialogs with researchers about tooling that could be used by other jurisdictions.

Pandemic and public health emergency preparedness are widely shared priorities across sectors and jurisdictions. The successes of the Modeling Consortium in California during the COVID-19 pandemic highlight the potential value of synchronized academic-government partnerships in the face of new public health threats. Increased internal public health capacity for modeling and analytics, more rapid data sharing frameworks, funding mechanisms to enable rapid support for academic efforts, and incentives to facilitate close coordination between academic and government institutions will enable a better evidence-based public health response in California and throughout the United States during the next public health emergency.

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### Conflict of interest

The authors declare no conflicts of interest.

### Disclaimer

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### References

1. Bayer D, Goldstein IH, Fintzi J, et al. Semi-parametric modeling of SARS-CoV-2 transmission using tests, cases, deaths, and seroprevalence data. *Ann Appl Stat.* 2024; 8(3):2307-2325. <https://doi.org/10.1214/24-AOASI882>
2. Goldstein IH, Wakefield J, Minin VM. Incorporating testing volume into estimation of effective reproduction number dynamics. *Journal of the Royal Statistical Society Series A: Statistics in Society.* 2024; 187(2):436-453. <https://doi.org/10.1093/rsssa/qnac128>
3. Head JR, Collender PA, Leen TM, et al. COVID-19 vaccination and incidence of pediatric SARS-CoV-2 infection and hospitalization. *JAMA Network Open.* 2024;7(4):e247822. <https://doi.org/10.1001/jamanetworkopen.2024.7822>
4. Oh DL, Kemper KE, Meltzer D, et al. Neighborhood-level COVID vaccination and booster disparities: a population-level analysis across California. *SSM Popul Health.* 2023;22:1-8. <https://doi.org/10.1016/j.ssmph.2023.101366>
5. White LA, McCrorie R, Crow D, et al. Assessing the accuracy of California county-level COVID-19 hospitalization forecasts to inform public policy decision making. *BMC Public Health.* 2023;23(1):782. <https://doi.org/10.1186/s12889-023-15649-0>
6. Sachdev DD, Petersen M, Havlir DV, et al. San Francisco's citywide COVID-19 response: strategies to reduce COVID-19 severity and health disparities, March 2020 through May 2022. *Public Health Rep.* 2023; 38(5):747-755. <https://doi.org/10.1177/00333549231181353>
7. Olshen AB, Garcia A, Kappahn KI, et al. COVIDNearTerm: a simple method to forecast COVID-19 hospitalizations. *J Clin Transl Sci.* 6(1):e59. <https://doi.org/10.1017/cts.2022.389>
8. Pung R, Kucharski AJ. Building in-house capabilities in health agencies and outsourcing to academia or industry: considerations for effective infectious disease modelling. *Epidemics.* 2024; 49: 1-4. <https://doi.org/10.1016/j.epidem.2024.100802>

mass of adult females; Beltran et al., 2022; Haley et al., 1994), male offspring are on average only 7%—8% heavier than females at the time of weaning (Le Boeuf et al., 2019). This difference in maternal allocation may be too small to be substantially influenced by maternal age. If elephant seals do adaptively modify offspring sex ratios, environmental conditions appear to be more influential than maternal age (Kretzmann et al., 1993; Lee & Sydeman, 2009).

Declining foraging efficiency with age is one mechanism for reproductive senescence (Lecomte et al., 2010). If older seals need additional foraging time to meet energy demands for maintenance and reproduction, then a greater portion of their annual cycle would need to be allocated to foraging trips. Since the breeding haul out is highly synchronous (Beltran et al., 2022), we hypothesized that older seals would reallocate time from the moulting haul out to foraging. However, the moulting haul out duration did not significantly change among females 11 years old and older. If seals skip breeding more often as they age, but are not altering their annual cycle, that suggests that the haul out durations are already as short as is physiologically possible. Skipped breeding may therefore become increasingly necessary with advanced age to reset seals' annual cycles.

## 5 | CONCLUSIONS

Northern elephant seals exhibit both fertility and maternal effect senescence. The rates of decline for these two processes (i.e. how rapidly fertility and offspring survival decline with maternal age) were not different from each other. Theory predicts maternal effect senescence should evolve to be more rapid than fertility senescence (Moorad & Nussey, 2015); similar analyses with larger sample sizes and more species are necessary to fully test this hypothesis. Furthermore, maternal effect senescence had a substantially larger impact on offspring production than fertility senescence. Although maternal effect senescence is relatively understudied, it appears to be highly prevalent, as it has been detected in 93% of studied populations (Ivimey-Cook & Moorad, 2020). Our results show that

~~population growth rates for age-structured populations may be~~ by Vi

overestimated if only fertility senescence is considered.

## AUTHOR CONTRIBUTIONS

Roxanne S. Beltran, Allison R. Payne and Patrick W. Robinson conceived the ideas and designed methodology; Allison R. Payne, Patrick W. Robinson, Cara M. O. Munro, Kelli Ong, Adrien Bastidas, Alegra O. Negrete, Brecken Theders, Bryn Stillwell, Danissa Coffey, Elijah Schweitzer, Elise Baugh, Jasmine Salazar, Keenan Chau-Pech, Mason

Rodrigues, Mimi Chavez, Savanna Wright, Sofia Rivas, R. Condit, Joanne Reiter, Daniel P. Costa and Roxanne S. Beltran collected the data; Allison R. Payne, Max F. Czapanskiy, A. Marm Kilpatrick and Roxanne S. Beltran analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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## CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to disclose.

## DATA AVAILABILITY STATEMENT

Data and code available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.pg4f4qr1> (Payne et al., 2024). Code is also available on GitHub (<https://github.com/allisongpayne/sealing>).

## ETHICAL APPROVAL

All research procedures were conducted under the National Marine Fisheries

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Animal care was authorized through the University of California, Santa

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## REFERENCES

Akaike, H. (1973). Information theory and an extension of the maximum likelihood principle. In B. N. Petrov & F. Caski (Eds.), *Proceedings of the second international symposium on information theory* (pp. 267—281). Akademiai Kiado.

Bates, D., Machler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed effects models using {lme4}. *Journal of Statistical Software*, 67(1), 1—48.

<https://doi.org/10.18637/jss.v067.i01.434> PAYNE et al.

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Beltran, R. S., Hernandez, K. M., Condit, R., Robinson, P. W., Crocker, D. E., Goetsch, C., Kilpatrick, A. M., & Costa, D. P. (2023). Physiological tipping points in the relationship between foraging success and lifetime fitness of a long-lived mammal. *Ecology Letters*, 26(5), 706—716.

<https://doi.org/10.1111/ele.14193>

Beltran, R. S., Hindell, M. A., & McMahon, C. R. (2022). The elephant seal: Linking phenotypic variation with behavior and fitness in a sexually dimorphic Phocid. In D. P. Costa & E. A. McHuron (Eds.), *Ethology and behavioral ecology of phocids* (pp. 401—440). Springer International Publishing. [https://doi.org/10.1007/978-3-030-88923-4\\_11](https://doi.org/10.1007/978-3-030-88923-4_11)

Beltran, R. S., Lozano, R. R., Morris, P. A., Robinson, P. W., Holser, R. R., Keates, T. R., Favilla, A. B., Kilpatrick, A. M., & Costa, D. P. (2024). Individual variation in life-history timing: Synchronous presence, asynchronous events and phenological compensation in a wild mammal. *Proceedings of the Royal Society B: Biological Sciences*, 291(2021), 20232335. <https://doi.org/10.1098/rspb.2023.2335>

Berman, M., Gaillard, J.-M., & Weimerskirch, H. (2009). Contrasted patterns of age-specific reproduction in long-lived seabirds. *Proceedings of the Royal Society B: Biological Sciences*, 276(1655), 375—382. <https://doi.org/10.1098/rspb.2008.0925>

Bouwhuis, S., Charmantier, A., Verhulst, S., & Sheldon, B. C. (2010). Transgenerational effects on ageing in a wild bird population. *Journal of Evolutionary Biology*, 23(3), 636—642. <https://doi.org/10.1111/j.1429-9101.2009.01929.x>

Condit, R., Beltran, R. S., Robinson, P. W., Crocker, D. E., & Costa, D. P. (2022). Birth timing after the long feeding migration in northern elephant seals. *Marine Mammal Science*, 38(3), 931—940.

Condit, R., Hatfield, B., Morris, P. A., & Costa, D. P. (2023). Quantifying dispersal between two colonies of northern elephant seals across 17 birth cohorts. *PLOS one*, 18(11), e0288921. <https://doi.org/10.1371/journal.pone.0288921>

Condit, R., Reiter, J., Morris, P. A., Berger, R., Allen, S. G., & Le Boeuf, B. J. (2014). Lifetime survival rates and senescence in northern elephant seals. *Marine Mammal Science*, 30(1), 122—138. <https://doi.org/10.1111/mms.12025>

Costa, D. P., Boeuf, B. J. L., Huntley, A. C., & Ortiz, C. L. (1986). The energetics of lactation in the Northern elephant seal, *Mirounga angustirostris*. *Journal of Zoology*, 209(1), 21—33. <https://doi.org/10.1111/j.1469-7998.1986.tb03563.x>

Descamps, S., Boutin, S., Berteaux, D., & Gaillard, J.-M. (2008). Age-specific variation in survival, reproductive success and offspring quality in red squirrels: Evidence of senescence. *Oikos*, 117(9), 1406—1416. <https://doi.org/10.1111/j.1365-2745.2007.13238.x>

Hoffman, C. L., Higham, J. P., Mas-Rivera, A., Ayala, J. E., & Maestripieri, D. (2015). <https://doi.org/10.1098/rspa.2015.0318>

Fay, R., Barbraud, C., Delord, K., & Weimerskirch, H. (2016). Paternal but not maternal age influences early-life performance of offspring in a long-lived seabird. *Proceedings of the Royal Society B: Biological Sciences*, 283(1828), 20152318. <https://doi.org/10.1098/rspb.2015.2318>

Hadley, G. L., Rotella, J. J., & Garrott, R. A. (2007). Influence of maternal characteristics and oceanographic conditions on survival and recruitment probabilities of Weddell seals. *Oikos*, 116(4), 601—613. <https://doi.org/10.1111/j.0030-1299.2007.15528.x>

(2010). Terminal investment and senescence in rhesus macaques (*Macaca mulatta*) on Cayo Santiago. *Behavioral Ecology*, 21(5), 972—978. <https://doi.org/10.1093/beheco/arp098>

Ivimey-Cook, E., & Moorad, J. (2020). The diversity of maternal-age effects upon pre-adult survival across animal species. *Proceedings of the Royal Society B: Biological Sciences*, 287(1932), 20200972. <https://doi.org/10.1098/rspb.2020.0972>

Jönsson, K. I. (1997). Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos*, 78(1), 57—66. <https://doi.org/10.2307/3545800>

Kienle, S. S., Friedlaender, A. S., Crocker, D. E., Mehta, R. S., & Costa, D. P. (2022). Trade-offs between foraging reward and mortality risk drive sex-specific foraging strategies in sexually dimorphic northern elephant seals. *Royal Society Open Science*, 9(1), 210522. <https://doi.org/10.1098/rsos.210522>

Kretzmann, M. B., Costa, D. P., & Le Boeuf, B. J. (1993). Maternal energy investment in elephant seal pups: Evidence for sexual equality? *The American Naturalist*, 141(3), 466—480. <https://doi.org/10.1086/285484>

Le Boeuf, B. J., Condit, R., & Reiter, J. (1989). Parental investment and the secondary sex ratio in northern elephant seals. *Behavioral Ecology and Sociobiology*, 25(2), 109—117. <https://doi.org/10.1007/BF00302927>

Le Boeuf, B. J., Condit, R., & Reiter, J. (2019). Lifetime reproductive success of northern elephant seals (*Mirounga angustirostris*). *Canadian Journal of Zoology*, 97(12), 1203—1217. <https://doi.org/10.1139/cjz-2019-0104>

Le Boeuf, B. J., Crocker, D. E., Costa, D. P., Blackwell, S. B., Webb, P. M., & Houser, D. S. (2000). Foraging ecology of northern elephant seals. *Ecological Monographs*, 70(3), 353—382. [https://doi.org/10.1890/0012-9615\(2000\)07010353:FEONESI2.0.CO;2](https://doi.org/10.1890/0012-9615(2000)07010353:FEONESI2.0.CO;2)

Le Boeuf, B. J., & Reiter, J. (1988). Lifetime reproductive success in northern elephant seals. In T. Clutton-Brock (Ed.), *Reproductive success* (pp. 344—362). University of Chicago Press.

Lecomte, V. J., Sorci, G., Cornet, S., Jaeger, A., Faivre, B., Arnoux, E., Gaillard, M., Trouvé, C., Besson, D., Chastel, O., & Weimerskirch, H. (2010). Patterns of aging in the long-lived wandering albatross. *Proceedings of the National Academy of Sciences of the United States of America*, 107(14), 6370—6375. Lee, D. E., & Sydeman, W. J. (2009). North Pacific climate mediates offspring sex perspectives in the wild. *Biological Reviews*, 92(4), 2182—2199. <https://doi.org/10.1111/j.1365-294X.2009.01654.x>

Emlen, J. M. 226 by Virginia Polytechnic Institute And State University, Wiley Online Library

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ratio in northern elephant seals. *Journal of Mammalogy*, 90(1), 1—8. <https://doi.org/10.1644/08-MAMM-A-130.1>

Lemattre, J.-F., & Gaillard, J.-M. (2017). Reproductive senescence: New

## 10.1111/j.0030-1299.2007.15528.x

Haley, M. P., Deutsch, C. J., & Le Boeuf, B. J. (1994). Size, dominance and copulatory success in male northern elephant seals, *Mirounga angustirostris*. *Animal Behaviour*, 48(6), 1249—1260. <https://doi.org/10.1006/anbe.1994.1361>

Hindle, A. G., Horning, M., Mellish, J.-A. E., & Lawler, J. M. (2009). Diving into old age: Muscular senescence in a large-bodied, long-lived mammal,

Weddell seal (*Leptonychotes weddellii*). *Journal of*

Experimental Biology, 212(6), 790—796. <https://doi.org/10.1242/jeb.025387>

LemaTre, J.- F., Ronget, V., & Gaillard, J.- M. (2020). Female reproductive senescence across mammals: A high diversity of patterns modulated by life history and mating traits. *Mechanisms of Ageing and Development*, 192, 111377. <https://doi.org/10.1016/j.mad.2020.111377>

Levine, M. E. (2013). Modeling the rate of senescence: Can estimated biological age predict mortality more accurately than chronological age? *The Journals of Gerontology: Series A*, 68(6), 667—674. <https://doi.org/10.1093/gerona/gls233>

Lowry, M. S., Condit, R., Hatfield, B., Allen, S. G., Berger, R., Morris, P. A., Le Boeuf, B. J., & Reiter, J. (2014). Abundance, distribution, and population growth of the northern elephant seal (*Mirounga angustirostris*) in the United States from 1991 to 2010. *Aquatic Mammals*, 40(1), 20—31.

Martin, J. G. A., & Festa- Bianchet, M. (2011). Age- independent and age-dependent decreases in reproduction of females. *Ecology Letters*, 14(6), 576—581. <https://doi.org/10.1111/j.1461-0248.2011.01621.x>

Moorad, J. A., & Nussey, D. H. (2015). Evolution of maternal effect senescence. *Proceedings of the National Academy of Sciences*, 113(2), 362—367. <https://doi.org/10.1073/pnas.1520494113>

Payne, A. R., Czapanskiy, M. F., Kilpatrick, A. M., Costa, D. P., & Beltran, R. S. (2024). Data from: Age and reproduction in northern elephant seals. Dryad Digital Repository. <https://doi.org/10.5061/dryad.pg4f4qrxf>

Reid, J. M., Bignal, E. M., Bignal, S., McCracken, D. I., Bogdanova, M. I., & Monaghan, P. (2010). Parent age, lifespan and offspring survival: Structured variation in life history in a wild population. *Journal of Animal Ecology*, 79(4), 851—862. <https://doi.org/10.1111/j.1365-2656.2010.01669.x>

Reiter, J., & Le Boeuf, B. J. (1991). Life history consequences of variation in age at primiparity in northern elephant seals. *Behavioral Ecology and Sociobiology*, 28(3), 153—160. <https://doi.org/10.1007/BFO0172166>

Reiter, J., Panken, K. J., & Le Boeuf, B. J. (1981). Female competition and reproductive success in northern elephant seals. *Animal Behaviour*, 29(3), 670—687. [https://doi.org/10.1016/S0003-3472\(81\)80002-4](https://doi.org/10.1016/S0003-3472(81)80002-4)

Reiter, J., Stinson, N. L., & Le Boeuf, B. J. (1978). Northern elephant seal development: The transition from weaning to nutritional independence. *Behavioral Ecology and Sociobiology*, 3(4), 337—367. <https://doi.org/10.1007/BF00303199>

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., Kuhn, C. E., Maresh, J. L., Maxwell, S. M., McDonald, B. I., Peterson, S. H., Simmons, S. E., Teutschel, N. M., Villegas- Amtmann, S., & Yoda, K. (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(5), e36728. <https://doi.org/10.1371/journal.pone.0036728>

Rödel, H. G., Von Hoist, D., & Kraus, C. (2009). Family legacies: Short- and longterm fitness consequences of early- life conditions in female European rabbits. *Journal of Animal Ecology*, 78(4), 789—797. <https://doi.org/10.1111/j.1365-2656.2009.01537.x>

Stephens, P. A., Boyd, I. L., McNamara, J. M., & Houston, A. I. (2009). Capital breeding and income breeding: Their meaning, measurement, and worth. <https://doi.org/10.1111/j.1365-2656.2009.01422.x>

Pol, M., & Verhulst, S. (2006). Age- dependent traits: A new statistical method for between- individual effects. *The American Naturalist*, 167(5), 766—773. <https://doi.org/10.1086/503331>

von Hardenberg, A., Bassano, B., Arranz, M. d. P. Z., & Bogliani, G. (2004). Horn growth but not asymmetry heralds the onset of senescence in male Alpine ibex (*Capra ibex*). *Journal of Zoology*, 263(4), 425—432. <https://doi.org/10.1017/S0952836904005485>

Williams, G. C., Maynard Smith, J., & Holliday, R. (1997). The question of adaptive sex ratio in outcrossed vertebrates. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 205(1161), 567—580. <https://doi.org/10.1098/rspb.1997.0085>

Zeno, R. L., Crocker, D. E., Hassrick, J. L., Allen, S. G., & Costa, D. P. (2008). Development of foraging behavior in juvenile northern elephant seals. *Journal of Zoology*, 274(2), 180—187. <https://doi.org/10.1111/j.1469-0795.2007.00446.x>

Experimental Biology, 212(6), 790—796. <https://doi.org/10.1242/jeb.025387>

Ecology, 90(8), 2057—2067. <https://doi.org/10.1890/08-1369.1>

Tompkins, E. M., & Anderson, D. J. (2019). Sex- specific patterns of senescence in Nazca boobies linked to mating system. *Journal of Animal Ecology*, 88(7), 986—1000. <https://doi.org/10.1111/1365-2656.12944>

Torres, R., Drummond, H., & Velando, A. (2011). Parental age and lifespan influence offspring recruitment: A long- term study in a seabird. *PLOS One*, 6(11), e27245. <https://doi.org/10.1371/journal.pone.0027245>

Trivers, R. L., & Willard, D. E. (1973). Natural selection of parental ability to vary the sex ratio of offspring. *Science*, 179(4068), 90—92. <https://doi.org/10.1126/science.179.4068.90>

Figure S2. Comparison of the coefficients (estimate and 95% CI) for age, among post- senescent animals, for HI (fertility senescence) and H2a (offspring survival) for the base model and models including selective appearance, selective disappearance, or both. Figure S3. The probability that an animal was observed decreased throughout the animal's lifetime. Table S1. Covariates for all models (fertility senescence, maternal- effect senescence, sex ratio, and phenology).

Table S2. Results for quadratic models.

Table S3. AIC comparisons of the quadratic and breakpoint models for the analyses with significant results (HI, fertility senescence and H2a, offspring survival). Both models have the same number of degrees of freedom. Table S4. AIC weights for threshold ages 6—14 for each hypothesis using the breakpoint model.

Table S5. Fitted model for HI (fertility senescence). Table S6. Fitted model for H2a (maternal effect senescence: offspring survival).

Table S7. Fitted model for H2b (maternal effect senescence: offspring recruitment).

Table S8. Fitted model for H3 (offspring sex ratio).

Table S9. Fitted model for H4 (phenology).

Table S10. Fitted models accounting for selective appearance, disappearance, and combined for hypotheses with significant results (HI and H2a).

Table S11. Fitted model for biological age.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article. Figure S1. Coefficients for analyses with different threshold age breakpoints on a log scale.