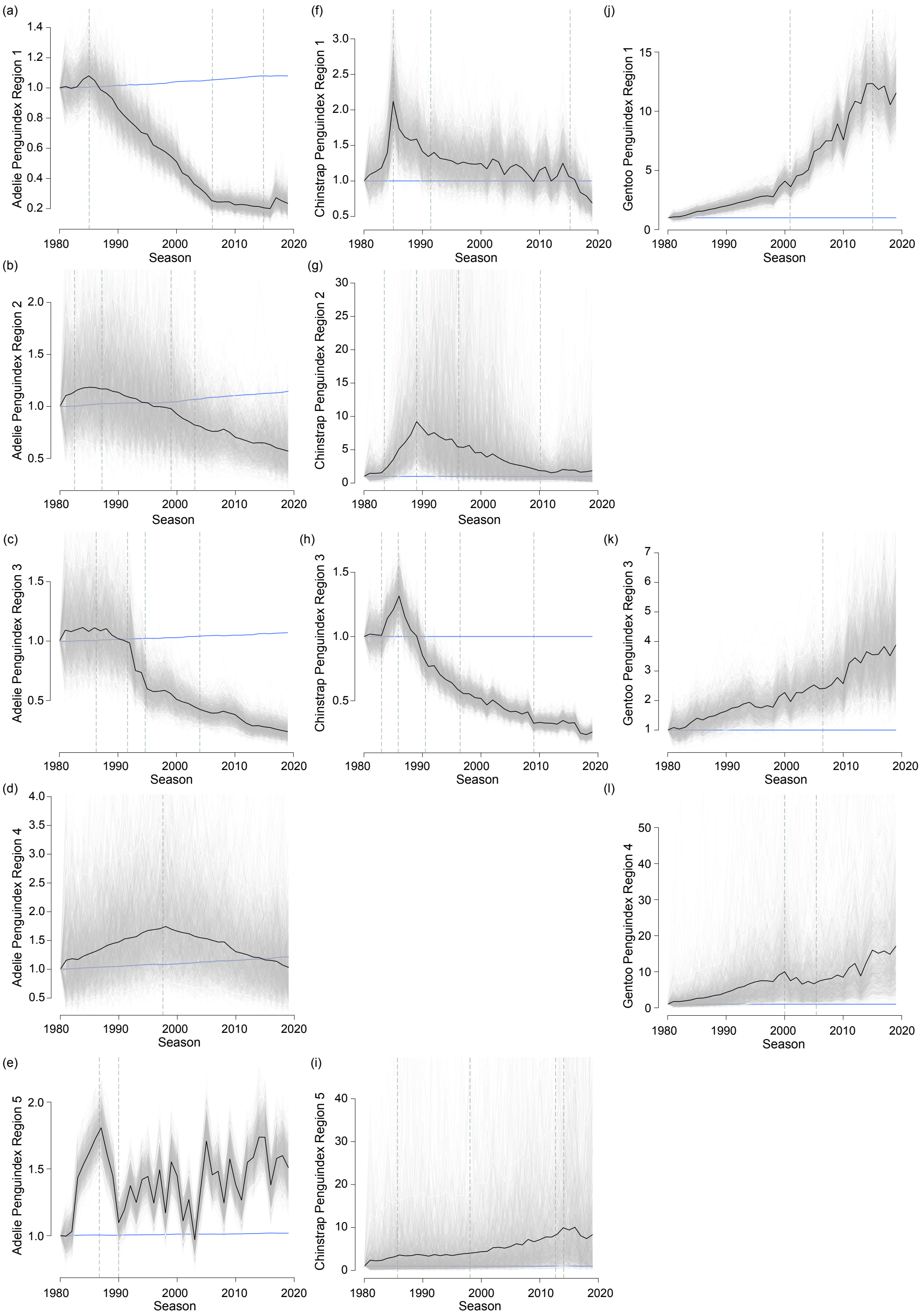

FIGURE 6.3: Region-level Penguindex for Regions 1-5 for (a-e) Adélie, (f-i) Chinstrap, and (j-l) Gentoo penguin populations from 1980-2019. Each black line denotes the mean, the white lines the 95% credible intervals, and the gray lines each iteration. Each blue line denotes the null model index. Identified change points are reported in Appendix S2: Table S1.

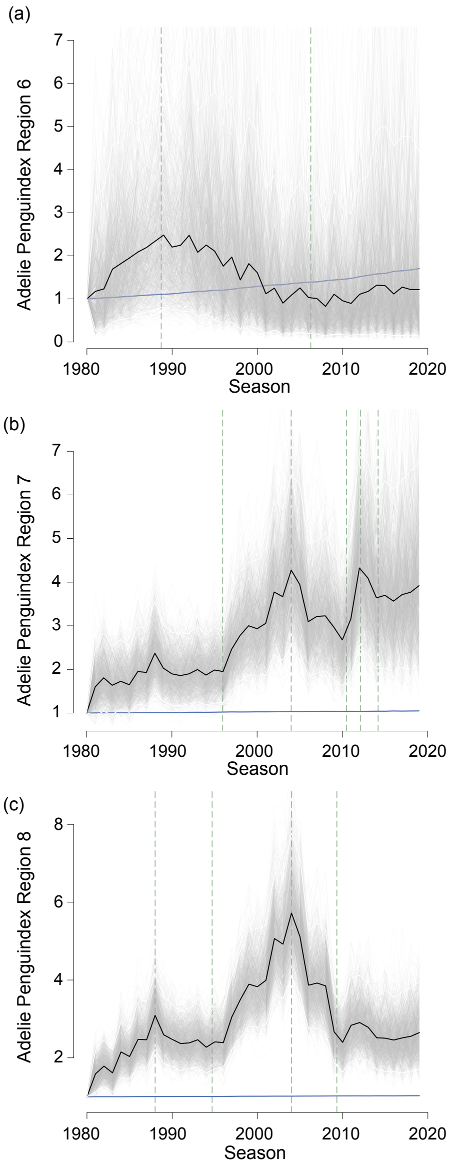

FIGURE 6.4: Region-level Penguindex for Regions 6-8 for Adélie penguin populations from 1980-2019. (Chinstrap and Gentoo penguin populations were not present in Regions 6-8.) Each black line denotes the mean, the white lines the 95% credible intervals, and the gray lines each iteration. Each blue line denotes the null model index. Identified change points are reported in Appendix S2: Table S1.

initial period of growth. Most of this decline occurred between 1992-1995 (1992 index 0.985, 95% CI 0.662-1.413; 1995 index 0.598, 95% CI 0.409-0.853), while recent declines have been slower. The average Adélie population on the Central- and Northwest AP (14 populations; Region 1, Figure 6.3a) declined by 75.7% (95% CI = 67.3-82.3%) of baseline by 2007 following a small amount of initial growth. In later years, Adélie populations on the Central- and Northwest AP were more stable on average (2019 index 0.235, 95% CI = 0.149-0.358; null model index 1.079).

For Adélie populations on the Southwestern AP (9 populations; Region 2, Figure 6.3b), two short periods of initial growth—first rapid until 1983 (1983 index 1.159, 95% CI 0.670-01.861) and then slow between 1983-1987 (1987 index 1.170, 95% CI 0.628-1.976)—were followed by three longer periods of slow decline—1987-1999 (1999 index 0.978, 95% CI 0.485-1.759), 1999-2003 (2003 index 0.822, 95% CI 0.455-1.320), and 2003-2019 (2019 index 0.570, 95% CI = 0.299-1.023; null model index 1.145). On the Northeastern AP (7 populations; Region 4, Figure 6.3d), Adélie populations increased steadily until 1998, by 74.4% (95% CI = 19.3% decrease - 254.2% increase) on average. Between 1998 and 2019, however, these Adélie penguin populations decreased just as steadily (2019 index 1.034, 95% CI = 0.382-2.219; null model index 1.064). The Bellingshausen Sea (Region 6, Figure 6.4a) had only one Adélie penguin population and contributed little to the global Adélie Penguindex.

Regional Chinstrap trends

The majority of Chinstrap breeding populations were located in Elephant Island, the South Orkney Islands, and the South Shetland Islands (60 populations; Region 3, Figure 6.3h). On average, these populations declined by 74.4% (95% CI = 81.0-66.7%) between 1980-2019. Prior to 1986, however, these populations increased on average by 31.5% (95% CI = 7.8-59.1%). After 1986, these populations declined at various rates until 2009 (2009 index 0.324, 95% CI = 0.256-0.411), after which populations remained relatively stable until 2019 (2019 index 0.256, 95% CI = 0.256-0.411). On average, Chinstrap populations on the Central- and Northwestern AP (31 populations; Region 1, Figure 6.3f) declined by only 30.9% (95% CI = 0.6-52.8%). Compared to Elephant Island, the South Orkney Islands, and the South Shetland Islands, Chinstrap populations on the Central- and Northwestern AP displayed a much steeper period of growth prior to 1985, more than doubling the 1980 baseline on average (1985 index 2.12, 95% CI = 1.41-3.00). Chinstrap populations in this region declined after this initial period of growth, first quickly until 1991 (1991 index 0.768, 95% CI = 0.612-0.961) and then slowly from 1991-2005 (2005 index 1.193, 95% CI = 0.786-1.754). The Southwestern AP (Region 2, Figure 6.3g) and Ross Sea (Region 5, Figure 6.3i) each had two or fewer Chinstrap penguin populations and contributed little to the global Chinstrap Penguindex. Null models for all regional-level Chinstrap indices were stable at 1.0.

Regional Gentoo trends

Gentoo penguin populations on the Central- and Northwestern AP (39 populations; Region 1, Figure 6.3j) increased on average over 10-fold (2019 index 11.529, 95% CI = 8.362-15.482). Initial growth was slow until 2001 (2001 index 3.622, 95% CI = 2.584-4.983), then steeper between 2001 and 2015 (2015 index 12.343, 95% CI 9.090-16.094). The growth of these populations, however, stalled between 2015-2019. Growth was relatively steady for Gentoo breeding populations on Elephant, South Orkney, and South Shetland Islands (Region 3, Figure 6.3k), with the average population increasing by 287.6% (95% CI = 195.2-664.2%) by 2019. On the Northeastern AP (Region 4, Figure 6.3l), Gentoo penguin populations increased 17-fold on average (2019 index 17.050, 95% CI = 3.094-51.692). With only 4 Gentoo penguin populations, this region contributed relatively little to the global Gentoo Penguindex. Null models for all three regional-level Gentoo penguin indices were stable at 1.0.

6.4 Discussion

To our knowledge, this is the first comprehensive examination of genus-wide trends for *Pygoscelis* penguins across the whole of the Antarctic. Our results identify key eras of global change for the average pygoscelid breeding population. While the dominant approach to Antarctic monitoring strategies has been to model overall population abundance [39, 53], the LPI framework used here instead aims to measure average trends in populations. Since region-level Penguindex calculations equally weight all populations within a region regardless of their size, our index is different from one calculated by aggregating populations at larger scales. Thus the trends described here by a region-level Penguindex are not commensurate with the trends observed for the total abundance of that species across the region (i.e., as in [39], Fig 2). For example, a region-level Penguindex for a species can be interpreted as describing the average percentage increase or decrease in any given population's abundance within that region, enabling trends in all populations to be reflected in the index rather than being dominated by the largest population. We see the Penguindex and the LPI framework as a complement to ongoing efforts to model aggregated abundance across the Antarctic.

6.4.1 Stark differences in individual species trends

Over the last four decades, our time series suggest an average decline of 21% within Chinstrap penguin populations across the Antarctic. While data is sparse, studies up to the 1990s found many Chinstrap populations to be increasing [73, 106, 185], with evidence of this growth dating back to the mid 1950s [52]. For example, [52] note a five-fold increase at North Point (S. Orkney Islands) between 1958 and 1978. However, more recent studies have established global declines in Chinstrap populations [143, 169, 194, 210]. Our global Chinstrap Penguindex quantifies both this initial period of Chinstrap population growth and its subsequent crash.

In stark contrast to the grim global trend of Chinstrap populations, however, Gentoo penguin populations have skyrocketed, with our global Gentoo Penguindex suggesting that the average population more than doubled between 1980 and 2019. In fact, an analysis of the public LPR database [139] reveals that the growth observed for Gentoo penguins is in the top 89th percentile for species undergoing population growth (see Appendix S1: Section S3). The regional trends observed here also align with previous studies showing that Gentoo populations along the Western AP have experienced the most rapid growth [95].

Compared to the overwhelming decline of Chinstrap populations and staggering growth of Gentoo populations, Adélie penguin populations across the Antarctic have experienced little change on average over the 40 years considered here. Even within an initial era of growth identified between 1980-1986, the average Adélie population never grew to more than 5.8% of the 1980 baseline, and went on to decline back to this baseline by 2019. Regional Adélie trends differ markedly, with declines in Adélie populations across the AP and sub-Antarctic islands being offset by increases in populations in the Ross Sea and Eastern Antarctica. These trends are similar to those identified by the first (and only) global Adélie penguin census, conducted in 2014 [141].

6.4.2 Notable eras of population change may be linked to warming

While Adélie populations on the Western AP and sub-Antarctic islands (Elephant, South Orkney, and South Shetland Islands) decreased drastically between 1980-2019, each constituent region was identified as having a recent distinct era of change in which declines slowed significantly. These eras each started roughly between 2003-2006 and extended until the end of our study period (2019). This recent leveling of decline among Adélie populations is perhaps related to the shift between a long period of steady warming to a recent period of cooling (beginning circa 1999) identified by Turner et al. [226, 229], with a lag roughly consistent with the time necessary for a shift in either reproductive success or juvenile survival to affect breeding abundance [218]. Adélie penguins have a tight-knit coupling to Antarctic sea ice [16, 73, 237] that has been the subject of considerable research over the last 40 years, though the relative roles of climate and Antarctic krill fishing as drivers of Adélie trends on the Peninsula remain subject to debate. Our findings are consistent with, though not conclusive of, climatically-driven forcings playing a key role in the observed and much discussed declines of Adélie penguins in this region.

While, on average, the 2019 abundance of Adélie populations on the Northeastern AP was nearly identical to the 1980 abundance, our data suggest that these populations were not stable over the 40 year time series considered here [27]. We identified a clear era of growth between 1980-1998 followed by an era of decline (1998-2019). Thus the period of warming across the AP prior to 1999 [226, 229] was correlated with growth of Adélie populations on the Northeastern AP, in contrast to the decline seen on the Western AP and sub-Antarctic islands. Additionally, the period of cooling observed across the AP after 1999 was met with declines in these Northeastern AP populations. These trends may indicate that the sea ice concentration in the Weddell Sea was unfavorably high at the start of our time series in 1980, and that the warming period prior to 1999 benefited Adélies until the region began to cool again.

Our species-level index for Gentoo penguins also suggests a recent period of relative stagnation in the growth of the average population, with a distinct period of stability identified between 2015-2019. While we have been unable to identify any promising potential environmental drivers for this halt in growth of Gentoo populations, it is clear that recent years have marked a new era for this species.

6.4.3 Global *Pygoscelis* trends are dominated by different species over time

Species-level pygoscelid penguin trends were equally weighted to obtain the global *Pygoscelis* Penguindex. Four distinct eras of global pygoscelid trends were identified, beginning with a period of growth across Antarctica for all species (1980-1986). Between 1986 and 1996, growth in the average Gentoo population was balanced with the decline in the average Adélie and Chinstrap populations, resulting in virtually complete stagnation in the global *Pygoscelis* Penguindex across this era. For the next two decades, from 1996-2015, growth in Gentoo populations outweighed the declines in Adélie and Chinstrap populations, as illustrated by a steadily rising global *Pygoscelis* Penguindex. As discussed above, recent years have seen a halt of growth in Gentoo penguin populations. This change point was identified in the global pygoscelid index as well, with the recent era between 2015-2019 demonstrating a global decline in the Penguindex as stable Gentoo populations were eclipsed by continuing, albeit gradual, declines in Adélie and Chinstrap populations.

While changes in the global Penguindex are driven by different species through time, it is important to note that both Adélie and Chinstrap penguins outnumber Gentoo penguins almost ten-fold across the Antarctic [95, 141, 210]. Thus the Penguindex provides information that is complementary, but not equivalent, to changes in overall penguin abundance. Instead, the Penguindex reflects average population change on a percentage basis by treating species trends equally regardless of the species population size, as described above.

6.4.4 Benefits of state-space models and the Penguindex approach

State-space models (SSMs) similar to the one employed here are valuable in their ability to synthesize data collected by different methods or with different precision by incorporating observation error into their estimation of trends [39, 114, 129, 174]. Here, the use of our hierarchical Bayesian SSMs also allowed for a more informed modeling approach than is provided by a generalized additive model (GAM) like the one employed by the LPI for interpolation [47, 159]. In the traditional LPI framework, a GAM not only interpolates missing data but also smooths time series, reducing interannual variation and affecting the resulting index. As *Pygoscelis* penguin time series display considerable interannual fluctuations [39, 218, 240], preserving this variability is important to understanding their dynamics and producing an accurate index of pygoscelid biodiversity. As an aggregation of species population trends, the traditional LPI can mask variation in the underlying data. By maintaining empirical interannual variation with the use of our SSMs and including species-specific indices to aid interpretation, the reflection of different species trends in the Penguindex can help to illustrate underlying environmental changes happening in the Antarctic. SSMs also allow for the incorporation of covariates or spatial autocorrelation to improve interpolation of missing data, which stand as future improvements to the Penguindex and the underlying SSMs.

The traditional LPI framework has several other shortcomings that we mitigate in the formulation of the Penguindex. First, the LPI is sensitive to random fluctuations in underlying population time series [32], leading to shifting a counterfactual rather than a fixed baseline set at 1980. The null models utilized in the Penguindex address this issue by allowing for a null expectation of the index that is robust to large population fluctuations. While most null model indices are fairly static, some (particularly for Adélies in Regions 1-3, see Figure 6.3) demonstrate an increasing counterfactual rather than a constant standard equal to the 1980 index. Additionally, the use of the geometric mean in the standard LPI means it is often sensitive to extremes. While the aggregation of the Penguindex does not weight population time series based on their size, and thus may still be sensitive to the influence of small populations, our region-level indices, showing underlying regional trends, and use of credible intervals, illustrating the variation in each index, aid in the determination of global and species-wide trends.

6.4.5 Updating the LPI for Antarctica and expanding the Penguindex

Pygoscelis penguins and the Southern Ocean ecosystem are extremely underrepresented in the database underlying the LPI and the biennial LPR. Though MAPPPD has identified 271 Adélie, 358 Chinstrap, and 109 Gentoo penguin breeding populations across the Antarctic, the Living Planet database currently includes only 76 Adélie, 18 Chinstrap, and 66 Gentoo time series. Through our analysis we have aggregated and adapted all MAPPPD pygoscelid penguin abundance observations into the format required for integration into the LPI [159] (see Appendix S1: Section S4). The inclusion of all MAPPPD *Pygoscelis* time series will drastically increase the data coverage for these Antarctic sentinels and our work provides a starting point for more comprehensive Antarctic coverage in the LPI.

Here we have started with the three Antarctic penguin species with the greatest data coverage. Ongoing efforts to track Emperor penguins using satellite imagery will greatly expand data availability for this species of conservation concern, and we consider the incorporation of these data into the Penguindex—and, further, the LPI—as a top priority. In addition, King and Macaroni penguins were recently added to MAPPPD. While these two species have relatively few populations in this region and the time series are particularly short and/or sparse, we expect that the Penguindex can be expanded to include them in the near future. Finally, penguins are only one small component of Antarctic biodiversity. As time series are collated for other species of long-standing research interest (e.g., pack-ice seals, petrels, fur seals, whales; [26, 28, 82, 195]), their full incorporation into the LPI will allow for a straight-forward assessment of biodiversity trends by a wide range of stakeholders.

Bibliography

[1] LM Abia, O Angulo, and JC López-Marcos. “Age-structured population models and their numerical solution”. In: *Ecological modelling* 188.1 (2005), pp. 112–136.

[2] Soohan Ahn, Joseph HT Kim, and Vaidyanathan Ramaswami. “A new class of models for heavy tailed distributions in finance and insurance risk”. In: *Insurance: Mathematics and Economics* 51.1 (2012), pp. 43–52. DOI: `https://doi.org/10.1016/j.insmatheco.2012.02.002`.

[3] Farshid S Ahrestani, Mark Hebblewhite, and Eric Post. “The importance of observation versus process error in analyses of global ungulate populations”. In: *Scientific Reports* 3.1 (2013), p. 3125. DOI: `https://doi.org/10.1038/srep03125`.

[4] David Ainley. *The Adélie penguin: bellwether of climate change*. Columbia University Press, 2002. DOI: `https://doi.org/10.1093/condor/105.4.835`.

[5] David Ainley et al. “Antarctic penguin response to habitat change as Earth’s troposphere reaches 2 C above preindustrial levels”. In: *Ecological Monographs* 80.1 (2010), pp. 49–66. DOI: `10.1890/08-2289.1`.

[6] David G Ainley, Nadav Nur, and Eric J Woehler. “Factors affecting the distribution and size of pygoscelid penguin colonies in the Antarctic”. In: *The Auk* 112.1 (1995), pp. 171–182.

[7] David G Ainley, Edmund F O’Connor, and Robert J Boekelheide. “The marine ecology of birds in the Ross Sea, Antarctica”. In: *Ornithological monographs* 32 (1984), pp. iii–97.

[8] R.E.A. Almond et al., eds. *Living Planet Report 2022 – Building a Nature Positive Society*. WWF, 2022.

[9] Rosamund EA Almond, Monique Grooten, and T Peterson. *Living Planet Report 2020-Bending the curve of biodiversity loss*. World Wildlife Fund, 2020.

[10] Benjamin M Althouse et al. “Superspreading events in the transmission dynamics of SARS-CoV-2: Opportunities for interventions and control”. In: *PLoS biology* 18.11 (2020), e3000897.

[11] Sean C Anderson et al. “Black-swan events in animal populations”. In: *Proceedings of the National Academy of Sciences* 114.12 (2017), pp. 3252–3257. DOI: `https://doi.org/10.1073/pnas.1611525114`.

[12] Muhammad Arif et al. “Modelling insurance losses with a new family of heavy-tailed distributions”. In: *Computers, Materials & Continua* 66.1 (2021), pp. 537–550.

[13] Barry C Arnold and Robert J Beaver. “The skew-Cauchy distribution”. In: *Statistics & probability letters* 49.3 (2000), pp. 285–290.

[14] Marie Auger-Méthé et al. “A guide to state–space modeling of ecological time series”. In: *Ecological Monographs* 91.4 (2021), e01470.

[15] William M. Balch. “The Ecology, Biogeochemistry, and Optical Properties of Coccolithophores”. In: *Annual Review of Marine Science* 10.1 (2018), pp. 71–98. DOI: https://doi.org/10.1146/annurev-marine-121916-063319.

[16] Tosca Ballerini et al. “Nonlinear effects of winter sea ice on the survival probabilities of Adélie penguins”. In: *Oecologia* 161.2 (2009), pp. 253–265. DOI: https://doi.org/10.1007/s00442-009-1387-9.

[17] Yinon M Bar-On, Rob Phillips, and Ron Milo. “The biomass distribution on Earth”. In: *Proceedings of the National Academy of Sciences of the United States of America* 115.25 (2018), pp. 6506–6511. DOI: https://doi.org/10.1073/pnas.1711842115.

[18] Donald R Barr and E Todd Sherrill. “Mean and variance of truncated normal distributions”. In: *The American Statistician* 53.4 (1999), pp. 357–361. DOI: 10.1080/00031305.1999.10474490.

[19] Norman C Beaulieu, Adnan A Abu-Dayya, and Peter J McLane. “Estimating the distribution of a sum of independent lognormal random variables”. In: *IEEE Transactions on Communications* 43.12 (1995), pp. 2869–2873. DOI: https://doi.org/10.1109/26.477480.

[20] Suchandan Bemal and Arga Chandrashekar Anil. “Picophytoplankton Synechococcus as food for nauplii of Amphibalanus amphitrite and Artemia salina”. In: *Hydrobiologia* 835.1 (2019), pp. 21–36. DOI: https://doi.org/10.1007/s10750-019-3923-x.

[21] Steve Bennett. “Log-logistic regression models for survival data”. In: *Journal of the Royal Statistical Society: Series C (Applied Statistics)* 32.2 (1983), pp. 165–171. DOI: https://doi.org/10.2307/2347295.

[22] Paul Arthur Berkman et al. “Science diplomacy”. In: *Antarctica, Science and the Governance of International Spaces* (2011). DOI: 10.1080/2154896X.2011.626645.

[23] Ottar N Bjørnstad and Bryan T Grenfell. “Noisy clockwork: time series analysis of population fluctuations in animals”. In: *Science* 293.5530 (2001), pp. 638–643. DOI: https://doi.org/10.1126/science.1062226.

[24] Caitlin E Black. “A comprehensive review of the phenology of Pygoscelis penguins”. In: *Polar Biology* 39 (2016), pp. 405–432.

[25] P Dee Boersma. “Penguins as marine sentinels”. In: *Bioscience* 58.7 (2008), pp. 597–607.

[26] A Borowicz et al. “Aerial-trained deep learning networks for surveying cetaceans from satellite imagery”. In: *PloS One* 14.10 (2019), e0212532. DOI: https://doi.org/10.1371/journal.pone.0212532.

[27] Alex Borowicz et al. “Multi-modal survey of Adélie penguin mega-colonies reveals the Danger Islands as a seabird hotspot”. In: *Scientific Reports* 8.1 (2018), pp. 1–9. DOI: 10.1038/s41598-018-22313-w.

[28] PL Boveng et al. “Population growth of Antarctic fur seals: limitation by a top predator, the leopard seal?” In: *Ecology* 79.8 (1998), pp. 2863–2877. DOI: https://doi.org/10.1890/0012-9658(1998)079[2863:PGOAFS]2.0.CO;2.

[29] Mark S Boyce. “Population viability analysis”. In: *Annual Review of Ecology and Systematics* 23.1 (1992), pp. 481–497. DOI: https://doi.org/10.1146/annurev.es.23.110192.002405.

[30] Kenneth P Burnham and David R Anderson. “Multimodel inference: understanding AIC and BIC in model selection”. In: *Sociological Methods & Research* 33.2 (2004), pp. 261–304. DOI: https://doi.org/10.1177/0049124104268644.

[31] Falko T Buschke. “Neutral theory reveals the challenge of bending the curve for the post-2020 Global Biodiversity Framework”. In: *Ecology and Evolution* 11.20 (2021), pp. 13678–13683. DOI: 10.1002/ece3.8097.

[32] Falko T Buschke et al. “Random population fluctuations bias the Living Planet Index”. In: *Nature Ecology & Evolution* 5.8 (2021), pp. 1145–1152. DOI: https://doi.org/10.1038/s41559-021-01494-0.

[33] Stuart HM Butchart et al. “Global biodiversity: indicators of recent declines”. In: *Science* 328.5982 (2010), pp. 1164–1168.

[34] Catherine Calder et al. “Incorporating multiple sources of stochasticity into dynamic population models”. In: *Ecology* 84.6 (2003), pp. 1395–1402. DOI: https://doi.org/10.1890/0012-9658(2003)084[1395:IMSOSI]2.0.CO;2.

[35] Corey T Callaghan, Shinichi Nakagawa, and William K Cornwell. “Global abundance estimates for 9,700 bird species”. In: *Proceedings of the National Academy of Sciences of the United States of America* 118.21 (2021). DOI: https://doi.org/10.1073/pnas.2023170118.

[36] Corey T Callaghan, Shinichi Nakagawa, and William K Cornwell. “Reply to Robinson et al.: Data integration will form the basis of future abundance estimates”. In: *Proceedings of the National Academy of Sciences* 119.10 (2022), e2117920119. DOI: https://doi.org/10.1073/pnas.2117920119.

[37] Hal Caswell. *Matrix population models*. Vol. 1. Sinauer Sunderland, 2000. DOI: https://doi.org/10.2307/2532473.

[38] Christian Che-Castaldo and Heather J Lynch. “Antarctic Penguin Biogeography Project: Database of abundance and distribution for the Adélie, chinstrap, gentoo, emperor, macaroni, and king penguin south of 60 S”. In Review.

[39] Christian Che-Castaldo et al. “Pan-Antarctic analysis aggregating spatial estimates of Adélie penguin abundance reveals robust dynamics despite stochastic noise”. In: *Nature Communications* 8.1 (2017), pp. 1–8. DOI: doi={10.1038/s41467-017-00890-0}.

[40] Xintong Chen et al. “Lagged response of Adélie penguin (Pygoscelis adeliae) abundance to environmental variability in the Ross Sea, Antarctica”. In: *Polar Biology* 43.11 (2020), pp. 1769–1781. DOI: https://doi.org/10.1007/s00300-020-02743-x.

[41] Xu Chen and Chang Guisong. “Exact distribution of the convolution of negative binomial random variables”. In: *Communications in Statistics-Theory and Methods* 46.6 (2017), pp. 2851–2856. DOI: https://doi.org/10.1080/03610926.2015.1053931.

[42] SL Chown et al. “Antarctica and the strategic plan for biodiversity”. In: *PLoS Biology* 15.3 (2017), e2001656. DOI: https://doi.org/10.1371/journal.pbio.2001656.

[43] James S Clark and Ottar N Bjørnstad. “Population time series: process variability, observation errors, missing values, lags, and hidden states”. In: *Ecology* 85.11 (2004), pp. 3140–3150. DOI: https://doi.org/10.1890/03-0520.

[44] T.J. Clark and Angela D. Luis. “Nonlinear population dynamics are ubiquitous in animals”. In: *Nature Ecology & Evolution* 4 (2020), pp. 75–81. DOI: https://doi.org/10.1038/s41559-019-1052-6.

[45] Andrea Clausen and Klemens Pütz. “Winter diet and foraging range of gentoo penguins (Pygoscelis papua) from Kidney Cove, Falkland Islands”. In: *Polar Biology* 26.1 (2003), pp. 32–40.

[46] Barry R Cobb, R Rumi, and Antonio Salmerón. “Approximating the distribution of a sum of log-normal random variables”. In: *Statistics and Computing* 16.3 (2012), pp. 293–308.

[47] BEN Collen et al. "Monitoring change in vertebrate abundance: the Living Planet Index". In: *Conservation Biology* 23.2 (2009), pp. 317–327. DOI: 10.1111/j.1523-1739.2008.01117.x.

[48] Matthew J Colloff et al. "Long-term ecological trends of flow-dependent ecosystems in a major regulated river basin". In: *Marine and Freshwater Research* 66.11 (2015), pp. 957–969. DOI: https://doi.org/10.1038/s41467-017-00890-0.

[49] Commission for the Conservation of Antarctic Marine Living Resources. *CCAMLR Ecosystem Monitoring Program (CEMP)*. https://www.ccamlr.org/en/science/ccamlr-ecosystem-monitoring-program-cemp. Accessed: 08-04-2022. 2013.

[50] Convention on Biological Diversity, ed. *Global Biodiversity Outlook 5*. 2020.

[51] Convention on Biological Diversity, ed. *Kunming-Montreal Global Biodiversity Framework*. CBD/COP/15/L.25, 2022.

[52] John P Croxall and ED Kirkwood. *The distribution of penguins on the Antarctic Peninsula and islands of the Scotia Sea*. British Antarctic Survey, 1979.

[53] JP Croxall, PN Trathan, and EJ Murphy. "Environmental change and Antarctic seabird populations". In: *Science* 297.5586 (2002), pp. 1510–1514. DOI: 10.1126/science.1071987.

[54] Sarah Cubaynes et al. "To breed or not to breed: a seabird's response to extreme climatic events". In: *Biology Letters* 7.2 (2011), pp. 303–306. DOI: https://doi.org/10.1098/rsbl.2010.0778.

[55] Jose J Cuervo and Anders P Møller. "Colonial, more widely distributed and less abundant bird species undergo wider population fluctuations independent of their population trend". In: *PloS One* 12.3 (2017). DOI: https://doi.org/10.1371/journal.pone.0173220.

[56] Alison C Cullen and H Christopher Frey. *Probabilistic techniques in exposure assessment: a handbook for dealing with variability and uncertainty in models and inputs*. Springer Science & Business Media, 1999.

[57] Jessica Currie et al. "Assessing the representation of species included within the Canadian Living Planet Index". In: *FACETS* (2022). DOI: 10.1139/facets-2022-0063.

[58] G Danabasoglu et al. "The Community Earth System Model version 2 (CESM2)". en. In: *Journal of Advances in Modeling Earth Systems* 12.2 (Feb. 2020). ISSN: 1942-2466. DOI: https://doi.org/10.1029/2019MS001916.

[59] Gergana N Daskalova, Isla H Myers-Smith, and John L Godlee. "Rare and common vertebrates span a wide spectrum of population trends". In: *Nature*

Communications 11.1 (2020), pp. 1–13. DOI: https://doi.org/10.1038/s41467-020-17779-0.

[60] Steven Delean, Barry W Brook, and Corey JA Bradshaw. “Ecologically realistic estimates of maximum population growth using informed Bayesian priors”. In: *Methods in Ecology and Evolution* 4.1 (2013), pp. 34–44. DOI: https://doi.org/10.1111/j.2041-210x.2012.00252.x.

[61] Marie Laure Delignette-Muller, Christophe Dutang, et al. “fitdistrplus: An R package for fitting distributions”. In: *Journal of Statistical Software* 64.4 (2015), pp. 1–34. DOI: 10.18637/jss.v064.i04.

[62] Brian Dennis and GP Patil. “Applications in ecology”. In: *Lognormal distributions*. Ed. by Edwin L. Crow and Kunio Shimizu. Routledge, 1988, pp. 303–330. DOI: https://doi.org/10.1201/9780203748664-12.

[63] Daniel Dufresne. “The log-normal approximation in financial and other computations”. In: *Advances in Applied Probability* 36.3 (2004), pp. 747–773. DOI: https://doi.org/10.1017/s0001867800013094.

[64] Katie M Dugger et al. “Effects of flipper bands on foraging behavior and survival of Adélie penguins (Pygoscelis adeliae)”. In: *The Auk* 123.3 (2006), pp. 858–869. DOI: https://doi.org/10.1093/auk/123.3.858.

[65] Katie M Dugger et al. “Survival differences and the effect of environmental instability on breeding dispersal in an Adélie penguin meta-population”. In: *Proceedings of the National Academy of Sciences* 107.27 (2010), pp. 12375–12380. DOI: https://doi.org/10.1073/pnas.1000623107.

[66] Christophe Dutang, Vincent Goulet, Mathieu Pigeon, et al. “actuar: An R package for actuarial science”. In: *Journal of Statistical software* 25.7 (2008), pp. 1–37.

[67] Lawrence Fenton. “The sum of log-normal probability distributions in scatter transmission systems”. In: *IRE Transactions on Communications Systems* 8.1 (1960), pp. 57–67. DOI: https://doi.org/10.1109/tcom.1960.1097606.

[68] Samuel B Fey et al. “Recent shifts in the occurrence, cause, and magnitude of animal mass mortality events”. In: *Proceedings of the National Academy of Sciences* 112.4 (2015), pp. 1083–1088. DOI: https://doi.org/10.1073/pnas.1414894112.

[69] Peter R Fisk. “The graduation of income distributions”. In: *Econometrica: Journal of the Econometric Society* (1961), pp. 171–185. DOI: https://doi.org/10.2307/1909287.

[70] Jaume Forcada et al. “Contrasting population changes in sympatric penguin species in association with climate warming”. In: *Global Change Biology* 12.3 (2006), pp. 411–423. DOI: https://doi.org/10.1111/j.1365-2486.2006.01108.x.

[71] James Foster, Michael Bevis, and William Raymond. “Precipitable water and the lognormal distribution”. In: *Journal of Geophysical Research: Atmospheres* 111 (2006), p. D15102. DOI: https://doi.org/10.1029/2005JD006731.

[72] John A Fowbert and Ronald I Lewis Smith. “Rapid population increases in native vascular plants in the Argentine Islands, Antarctic Peninsula”. In: *Arctic and Alpine Research* 26.3 (1994), pp. 290–296. DOI: 10.2307/1551941.

[73] William R Fraser et al. “Increases in Antarctic penguin populations: reduced competition with whales or a loss of sea ice due to environmental warming?” In: *Polar Biology* 11.8 (1992), pp. 525–531. DOI: 10.1007/BF00237945.

[74] Edward Furman. “On the convolution of the negative binomial random variables”. In: *Statistics & probability letters* 77.2 (2007), pp. 169–172. DOI: https://doi.org/10.1016/j.spl.2006.06.007.

[75] Thomas Galewski et al. “Long-term trends in the abundance of Mediterranean wetland vertebrates: from global recovery to localized declines”. In: *Biological Conservation* 144.5 (2011), pp. 1392–1399. DOI: 10.1016/j.biocon.2010.10.030.

[76] Alison P Galvani and Robert M May. “Dimensions of superspreading”. In: *Nature* 438.7066 (2005), pp. 293–295. DOI: https://doi.org/10.1038/438293a.

[77] R. J. Geider, H. L. MacIntyre, and T. M. Kana. “Dynamic model of phytoplankton growth and acclimation: responses of the balanced growth rate and the chlorophyll a:carbon ratio to light, nutrient-limitation and temperature”. In: *Marine Ecology Progress Series* 148 (1997), pp. 187–200. DOI: https://doi.org/10.3354/meps148187.

[78] Andrew Gelman and Jennifer Hill. *Data analysis using regression and multilevel / hierarchical models*. Cambridge university press, 2006. DOI: https://doi.org/10.1017/cbo9780511790942.

[79] Andrew Gelman and Donald B Rubin. “Inference from iterative simulation using multiple sequences”. In: *Statistical Science* (1992), pp. 457–472. DOI: 10.1214/ss/1177011136.

[80] Andrew Gelman et al. *Bayesian data analysis*. CRC Press, 2013. DOI: https://doi.org/10.1201/9780429258411.

[81] Yolanda M Gómez, Heleno Bolfarine, and Héctor W Gómez. “Gumbel distribution with heavy tails and applications to environmental data”. In: *Mathematics and Computers in Simulation* 157 (2019), pp. 115–129.

[82] BC Gonçalves, M Wethington, and HJ Lynch. “SealNet 2.0: Human-Level Fully-Automated Pack-Ice Seal Detection in Very-High-Resolution Satellite Imagery

with CNN Model Ensembles". In: *Remote Sensing* 14.22 (2022), p. 5655. DOI: https://doi.org/10.3390/rs14225655.

[83] Dominique Gravel, Frédéric Guichard, and Michael E Hochberg. "Species coexistence in a variable world". In: *Ecology Letters* 14.8 (2011), pp. 828–839. DOI: https://doi.org/10.1111/j.1461-0248.2011.01643.x.

[84] Rameshwar D Gupta and Debasis Kundu. "Generalized logistic distributions". In: *Journal of Applied Statistical Science* 18.1 (2010), p. 51.

[85] Jessica Gurevitch et al. "Landscape demography: Population change and its drivers across spatial scales". In: *The Quarterly Review of Biology* 91.4 (2016), pp. 459–485. DOI: https://doi.org/10.1086/689560.

[86] Karen L Haberman, Robin M Ross, and Langdon B Quetin. "Diet of the Antarctic krill (Euphausia superba Dana): II. Selective grazing in mixed phytoplankton assemblages". In: *Journal of Experimental Marine Biology and Ecology* 283.1 (2003), pp. 97–113. ISSN: 0022-0981. DOI: https://doi.org/10.1016/S0022-0981(02)00467-7.

[87] John Halley and Pablo Inchausti. "Lognormality in ecological time series". In: *Oikos* 99.3 (2002), pp. 518–530. DOI: https://doi.org/10.1034/j.1600-0706.2002.11962.x.

[88] Nikolaus Hansen et al. "When do heavy-tail distributions help?" In: *Parallel Problem Solving from Nature*. Springer. 2006, pp. 62–71.

[89] Per Juel Hansen, Peter Koefoed Bjørnsen, and Benni Winding Hansen. "Zooplankton grazing and growth: Scaling within the 2-2,-μm body size range". In: *Limnology and Oceanography* 42.4 (1997), pp. 687–704. DOI: https://doi.org/10.4319/lo.1997.42.4.0687.

[90] I. Hanski. "Metapopulation dynamics". In: *Nature* 396 (1998), pp. 41–49. DOI: https://doi.org/10.1038/23876.

[91] Ilkka Hanski et al. *Metapopulation ecology*. Oxford University Press, 1999.

[92] Philip J Harrison, Ilkka Hanski, and Otso Ovaskainen. "Bayesian state-space modeling of metapopulation dynamics in the Glanville fritillary butterfly". In: *Ecological Monographs* 81.4 (2011), pp. 581–598.

[93] Fengzhi He et al. "The global decline of freshwater megafauna". In: *Global Change Biology* 25.11 (2019), pp. 3883–3892. DOI: 10.1111/gcb.14753.

[94] Norbert Henze. "A probabilistic representation of the'skew-normal'distribution". In: *Scandinavian journal of statistics* (1986), pp. 271–275.

[95] Rachael Herman et al. "Update on the global abundance and distribution of breeding Gentoo Penguins (Pygoscelis papua)". In: *Polar Biology* 43.12 (2020), pp. 1947–1956. DOI: 10.1007/s00300-020-02759-3.

[96] Ray Hilborn and Marc Mangel. "The Ecological Detective". In: Princeton University Press, 1997, pp. 73–76, 242–244.

[97] Jefferson T Hinke, Susan G Trivelpiece, and Wayne Z Trivelpiece. "Adélie penguin (Pygoscelis adeliae) survival rates and their relationship to environmental indices in the South Shetland Islands, Antarctica". In: *Polar Biology* 37.12 (2014), pp. 1797–1809. DOI: `https://doi.org/10.1007/s00300-014-1562-2`.

[98] Jefferson T Hinke, Susan G Trivelpiece, and Wayne Z Trivelpiece. "Variable vital rates and the risk of population declines in Adélie penguins from the Antarctic Peninsula region". In: *Ecosphere* 8.1 (2017), e01666. DOI: `https://doi.org/10.1002/ecs2.1666`.

[99] Cang Hui, Gordon A Fox, and Jessica Gurevitch. "Scale-dependent portfolio effects explain growth inflation and volatility reduction in landscape demography". In: *Proceedings of the National Academy of Sciences* 114.47 (2017), pp. 12507–12511. DOI: `https://doi.org/10.1073/pnas.1704213114`.

[100] Jean-Yves Humbert et al. "A better way to estimate population trends". In: *Oikos* 118.12 (2009), pp. 1940–1946. DOI: `https://doi.org/10.1111/j.1600-0706.2009.17839.x`.

[101] Grant RW Humphries et al. "Predicting the future is hard and other lessons from a population time series data science competition". In: *Ecological Informatics* 48 (2018), pp. 1–11. DOI: `https://doi.org/10.1016/j.ecoinf.2018.07.004`.

[102] GRW Humphries et al. "Mapping application for penguin populations and projected dynamics (MAPPPD): data and tools for dynamic management and decision support". In: *Polar Record* 53.2 (2017), pp. 160–166. DOI: `10.1017/S0032247417000055`.

[103] Marat Ibragimov, Rustam Ibragimov, and Johan Walden. *Heavy-tailed distributions and robustness in economics and finance*. Vol. 214. Springer, 2015. DOI: `https://doi.org/10.1007/978-3-319-16877-7`.

[104] David A Iles et al. "Sea ice predicts long-term trends in Adélie penguin population growth, but not annual fluctuations: results from a range-wide multiscale analysis". In: *Global Change Biology* 26 (2020), pp. 3788–3798. DOI: `https://doi.org/10.1111/gcb.15085`.

[105] Xabier Irigoien et al. "Copepod hatching success in marine ecosystems with high diatom concentrations". In: *Nature* 419.6905 (2002), pp. 387–389. DOI: `https://doi.org/10.1038/nature01055`.

[106] Bolesław Jabłoński. "Distribution, numbers and breeding preferences of penguins in the region of the Admiralty Bay (King George Island, South Shetland Islands) in the season 1979/1980". In: *Polish Polar Research* 5.1-2 (1984).

[107] Stephanie Jenouvrier, Christophe Barbraud, and Henri Weimerskirch. "Effects of climate variability on the temporal population dynamics of southern fulmars". In: *Journal of Animal Ecology* 72.4 (2003), pp. 576–587. DOI: `https://doi.org/10.1046/j.1365-2656.2003.00727.x`.

[108] Stephanie Jenouvrier, Christophe Barbraud, and Henri Weimerskirch. "Long-term contrasted responses to climate of two Antarctic seabird species". In: *Ecology* 86.11 (2005), pp. 2889–2903. DOI: `https://doi.org/10.1890/05-0514`.

[109] Stéphanie Jenouvrier et al. "Climate change and functional traits affect population dynamics of a long-lived seabird". In: *Journal of Animal Ecology* 87.4 (2018), pp. 906–920. DOI: `https://doi.org/10.1111/1365-2656.12827`.

[110] M Chris Jones and MJ1959820 Faddy. "A skew extension of the t-distribution, with applications". In: *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* 65.1 (2003), pp. 159–174.

[111] Mariana A Juáres et al. "Adélie penguin population changes at Stranger Point: 19 years of monitoring". In: *Antarctic Science* 27.5 (2015), pp. 455–461. DOI: `https://doi.org/10.1017/S0954102015000152`.

[112] Matthew Kay. "ggdist: Visualizations of distributions and uncertainty". In: *R package version* 2.1 (2021).

[113] Benjamin Kedem and Long S Chiu. "On the lognormality of rain rate". In: *Proceedings of the National Academy of Sciences of the United States of America* 84.4 (1987), pp. 901–905. DOI: `https://doi.org/10.1073/pnas.84.4.901`.

[114] Holly K Kindsvater et al. "Overcoming the data crisis in biodiversity conservation". In: *Trends in Ecology & Evolution* 33.9 (2018), pp. 676–688. DOI: `10.1016/j.tree.2018.06.004`.

[115] Andrew G Klein et al. "The historical development of McMurdo station, Antarctica, an environmental perspective". In: *Polar Geography* 31.3-4 (2008), pp. 119–144.

[116] Shinya Kobayashi et al. "The JRA-55 Reanalysis: General Specifications and Basic Characteristics". In: *Journal of the Meteorological Society of Japan. Ser. II* 93.1 (2015), pp. 5–48. DOI: `https://doi.org/10.2151/jmsj.2015-001`.

[117] Arthur L Koch. "The logarithm in biology 1. Mechanisms generating the lognormal distribution exactly". In: *Journal of theoretical biology* 12.2 (1966), pp. 276–290.

[118] Gabrielle Koerich et al. "Forecasting the future of life in Antarctica". In: *Trends in Ecology & Evolution* (2022).

[119] Mark Kot. *Elements of mathematical ecology*. Cambridge University Press, 2001.

[120] K. M. Krumhardt et al. "Coccolithophore Growth and Calcification in an Acidified Ocean: Insights From Community Earth System Model Simulations". In: *Journal of Advances in Modeling Earth Systems* 11.5 (2019), pp. 1418–1437. DOI: `https://doi.org/10.1029/2018MS001483`.

[121] John Kruschke. "Doing Bayesian data analysis: A tutorial with R, JAGS, and Stan". In: (2014).

[122] William E Kunin. "Extrapolating species abundance across spatial scales". In: *Science* 281.5382 (1998), pp. 1513–1515. DOI: `10.1126/science.281.5382.1513`.

[123] R Kwok and JC Comiso. "Southern Ocean climate and sea ice anomalies associated with the Southern Oscillation". In: *Journal of Climate* 15.5 (2002), pp. 487–501. DOI: 10.1175/1520-0442(2002)015<0487:SOCASI>2.0.CO;2.

[124] M.A. LaRue, S. Stapleton, and M. Anderson. "Feasibility of using high-resolution satellite imagery to assess wildlife vertebrate populations". In: *Conservation Biology* 31 (2016), pp. 213–220. DOI: `https://doi.org/10.1111/cobi.12809`.

[125] S.E.H Ledger et al. *Wildlife Comeback in Europe: Opportunities and challenges for species recovery*. Final report to Rewilding Europe by the Zoological Society of London, BirdLife International, the European Census Council, 2022.

[126] Sophie EH Ledger et al. "Past, present, and future of the Living Planet Index". In: *bioRxiv* (2022). DOI: `10.1101/2022.06.20.496803`.

[127] Jasmine R Lee et al. "Climate change drives expansion of Antarctic ice-free habitat". In: *Nature* 547.7661 (2017), pp. 49–54.

[128] Erich L Lehmann. "'Student' and small-sample theory". In: *Selected works of EL Lehmann*. Springer, 2012, pp. 1001–1008. DOI: `https://doi.org/10.1007/978-1-4614-1412-4\_83`.

[129] Brian Leung et al. "Clustered versus catastrophic global vertebrate declines". In: *Nature* 588.7837 (2020), pp. 267–271. DOI: `10.1038/s41586-020-2920-6`.

[130] Dyani Lewis. "Superspreading drives the COVID pandemic–and could help to tame it." In: *Nature* 590.7847 (2021), pp. 544–547.

[131] Eckhard Limpert, Werner A Stahel, and Markus Abbt. "Log-normal distributions across the sciences: Keys and clues: On the charms of statistics, and how mechanical models resembling gambling machines offer a link to a handy way to characterize log-normal distributions, which can provide deeper insight into variability and probability—Normal or log-normal: That is the question". In: *BioScience* 51.5 (2001), pp. 341–352. DOI: `https://doi.org/10.1641/0006-3568(2001)051[0341:LNDATS]2.0.CO;2`.

[132] David B Lindenmayer et al. “Conservation conundrums and the challenges of managing unexplained declines of multiple species”. In: *Biological Conservation* 221 (2018), pp. 279–292. DOI: `https://doi.org/10.1016/j.biocon.2018.03.007`.

[133] Haoqi Liu, Weide Li, and Guanghui Lv. “How nonrandom habitat loss affects nature reserve planning strategies”. In: *Ecological Modelling* 397 (2019), pp. 39–46. DOI: `https://doi.org/10.1016/j.ecolmodel.2018.12.014`.

[134] James O Lloyd-Smith et al. “Superspreading and the effect of individual variation on disease emergence”. In: *Nature* 438.7066 (2005), pp. 355–359. DOI: `https://doi.org/10.1038/nature04153`.

[135] Chi-Fai Lo. “The sum and difference of two lognormal random variables”. In: *Journal of Applied Mathematics* 2012 (2012), p. 838397. DOI: `https://doi.org/10.2139/ssrn.2064829`.

[136] Jonathan Loh et al. “The Living Planet Index: Using species population time series to track trends in biodiversity”. In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 360.1454 (2005), pp. 289–295. DOI: `10.1098/rstb.2004.1584`.

[137] Matthew C. Long et al. “Simulations With the Marine Biogeochemistry Library (MARBL)”. In: *Journal of Advances in Modeling Earth Systems* 13.12 (2021), e2021MS002647. DOI: `https://doi.org/10.1029/2021MS002647`.

[138] JS Lopes and Mark A Beaumont. “ABC: a useful Bayesian tool for the analysis of population data”. In: *Infection, Genetics and Evolution* 10.6 (2010), pp. 825–832. DOI: `https://doi.org/10.1016/j.meegid.2009.10.010`.

[139] LPI 2022. *Living Planet Index database*. www.livingplanetindex.org/. 2022.

[140] David Lunn et al. *The BUGS book: A practical introduction to Bayesian analysis*. CRC Press, 2012. DOI: `https://doi.org/10.1201/b13613`.

[141] H.J. Lynch and M.A. LaRue. “First global census of the Adélie penguin”. In: *The Auk* 131.4 (2014), pp. 457–466. DOI: `https://doi.org/10.1642/AUK-14-31.1`.

[142] H.J. Lynch and M.R. Schwaller. “Mapping the abundance and distribution of Adélie penguins using Landsat-7: First steps towards an integrated multi-sensor pipeline for tracking populations at the continental scale”. In: *PLoS ONE* 9.11 (2014), e113301. DOI: `https://doi.org/10.1371/journal.pone.0113301`.

[143] H.J. Lynch et al. “Spatially integrated assessment reveals widespread changes in penguin populations on the Antarctic Peninsula”. In: *Ecology* 93.6 (2012), pp. 1367–1377. DOI: `https://doi.org/10.1890/11-1588.1`.

[144] Phil O'B Lyver. *Landcare Research Adélie census data*. Dataset. 1983.

[145] Phil O'B Lyver et al. "Trends in the breeding population of Adélie penguins in the Ross Sea, 1981–2012: a coincidence of climate and resource extraction effects". In: *PLoS One* 9.3 (2014), e91188. DOI: https://doi.org/10.1371/journal.pone.0091188.

[146] Robert MacArthur. "On the relative abundance of species". In: *The American Naturalist* 94.874 (1960), pp. 25–36. DOI: https://doi.org/10.1086/282106.

[147] Robert H MacArthur. "On the relative abundance of bird species". In: *Proceedings of the National Academy of Sciences* 43.3 (1957), pp. 293–295.

[148] Anne E Magurran and Peter A Henderson. "Explaining the excess of rare species in natural species abundance distributions". In: *Nature* 422.6933 (2003), pp. 714–716. DOI: https://doi.org/10.1038/nature01547.

[149] Marc Mangel and Charles Tier. "Four facts every conservation biologists should know about persistence". In: *Ecology* 75.3 (1994), pp. 607–614. DOI: https://doi.org/10.2307/1941719.

[150] Valentina Marconi et al. "Population declines among Canadian vertebrates: But data of different quality show diverging trends". In: *Ecological Indicators* 130 (2021), p. 108022. DOI: 10.1016/j.ecolind.2021.108022.

[151] Robert A Massom et al. "Extreme anomalous atmospheric circulation in the West Antarctic Peninsula region in austral spring and summer 2001/02, and its profound impact on sea ice and biota". In: *Journal of Climate* 19.15 (2006), pp. 3544–3571. DOI: https://doi.org/10.1175/JCLI3805.1.

[152] Jason Matthiopoulos et al. "State-space modelling reveals proximate causes of harbour seal population declines". In: *Oecologia* 174 (2014), pp. 151–162.

[153] Mark N Maunder and James T Thorson. "Modeling temporal variation in recruitment in fisheries stock assessment: A review of theory and practice". In: *Fisheries Research* 217 (2019), pp. 71–86. DOI: https://doi.org/10.1016/j.fishres.2018.12.014.

[154] Robert M May and Roy M Anderson. "Transmission dynamics of HIV infection". In: *Nature* 326.6109 (1987), pp. 137–142. DOI: https://doi.org/10.1038/326137a0.

[155] Michael A McCarthy. *Bayesian methods for ecology*. Cambridge University Press, 2007.

[156] James McClintock, Hugh Ducklow, and William Fraser. "Ecological Responses to Climate Change on the Antarctic Peninsula: The Peninsula is an icy world

that's warming faster than anywhere else on Earth, threatening a rich but delicate biological community". In: *American Scientist* 96.4 (2008), pp. 302–310.

[157] James B McDonald, Jeff Sorensen, and Patrick A Turley. "Skewness and kurtosis properties of income distribution models". In: *Review of Income and Wealth* 59.2 (2013), pp. 360–374. DOI: https://doi.org/10.1111/j.1475-4991.2011.00478.x.

[158] Brian J McGill et al. "Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework". In: *Ecology Letters* 10.10 (2007), pp. 995–1015. DOI: https://doi.org/10.1111/j.1461-0248.2007.01094.x.

[159] Louise McRae, Stefanie Deinet, and Robin Freeman. "The diversity-weighted Living Planet Index: controlling for taxonomic bias in a global biodiversity indicator". In: *PloS One* 12.1 (2017), e0169156. DOI: 10.1371/journal.pone.0169156.

[160] Louise McRae et al. "The Arctic Species Trend Index: Using vertebrate population trends to monitor the health of a rapidly changing ecosystem". In: *Biodiversity* 13.3-4 (2012), pp. 144–156. DOI: 10.1080/14888386.2012.705085.

[161] Beatriz Vaz de Melo Mendes and Hedibert Freitas Lopes. "Data driven estimates for mixtures". In: *Computational statistics & data analysis* 47.3 (2004), pp. 583–598.

[162] RD Methot. "User manual for stock synthesis". In: *NOAA Fisheries, Seattle, USA* (2009).

[163] Richard D Methot Jr and Ian G Taylor. "Adjusting for bias due to variability of estimated recruitments in fishery assessment models". In: *Canadian Journal of Fisheries and Aquatic Sciences* 68.10 (2011), pp. 1744–1760. DOI: https://doi.org/10.1139/f2011-092.

[164] D Miller and NM Slicer. "CCAMLR and Antarctic conservation: the leader to follow?" In: *Governance of Marine Fisheries and Biodiversity Conservation: Interaction and Coevolution* (2014), pp. 253–270. DOI: 10.1002/9781118392607.ch18.

[165] Jeffrey E Moore and Jay Barlow. "Bayesian state-space model of fin whale abundance trends from a 1991–2008 time series of line-transect surveys in the California Current". In: *Journal of Applied Ecology* 48.5 (2011), pp. 1195–1205. DOI: https://doi.org/10.1111/j.1365-2664.2011.02018.x.

[166] Vito MR Muggeo. "Estimating regression models with unknown break-points". In: *Statistics in Medicine* 22.19 (2003), pp. 3055–3071. DOI: 10.1002/sim.1545.

[167] Vito MR Muggeo and Maintainer Vito MR Muggeo. "Package 'segmented'". In: *Biometrika* 58.525-534 (2017), p. 516.

[168] Dennis L Murray and Brett K Sandercock. *Population ecology in practice*. John Wiley & Sons, 2020, pp. 79–80.

[169] Ron Naveen et al. "First direct, site-wide penguin survey at Deception Island, Antarctica, suggests significant declines in breeding chinstrap penguins". In: *Polar Biology* 35.12 (2012), pp. 1879–1888. DOI: 10.1007/s00300-012-1230-3.

[170] JC Nejstgaard, I Gismervik, and PT Solberg. "Feeding and reproduction by Calanus finmarchicus, and microzooplankton grazing during mesocosm blooms of diatoms and the coccolithophore Emiliania huxleyi". In: *Marine Ecology Progress Series* 147 (1997), pp. 197–217. DOI: https://doi.org/10.3354/meps147197.

[171] Roger M Nisbet and William Gurney. *Modelling fluctuating populations*. John Wiley & Sons, 1982, pp. 176–178.

[172] Steffen Oppel et al. "Population status and trend of the Critically Endangered Montserrat Oriole". In: *Bird Conservation International* 24.2 (2014), pp. 252–261. DOI: https://doi.org/10.1017/s0959270913000373.

[173] Otso Ovaskainen. "Long-term persistence of species and the SLOSS problem". In: *Journal of Theoretical Biology* 218.4 (2002), pp. 419–433. DOI: https://doi.org/10.1006/jtbi.2002.3089.

[174] Nathan Pacoureau et al. "Half a century of global decline in oceanic sharks and rays". In: *Nature* 589.7843 (2021), pp. 567–571. DOI: 10.1038/s41586-020-03173-9.

[175] Claire L Parkinson. "Trends in the length of the Southern Ocean sea-ice season, 1979–99". In: *Annals of Glaciology* 34 (2002), pp. 435–440. DOI: 10.3189/172756402781817482.

[176] M Plummer. "rjags: Bayesian graphical models using MCMC, v. 4-10". In: *The Comprehensive R Archive Network* (2013).

[177] Martyn Plummer. *JAGS Version 4-10 user manual*. 2019.

[178] Pedro Puig and Jordi Valero. "Characterization of count data distributions involving additivity and binomial subsampling". In: *Bernoulli* (2007), pp. 544–555. DOI: 10.3150/07-BEJ6021.

[179] R Core Team R. *R: A language and environment for statistical computing. R version 4.0.2*. 2020.

[180] R Core Team R. *R: A language and environment for statistical computing. R version 4.1.2*. 2021.

[181] Jonathan R Rhodes and Niclas Jonzén. "Monitoring temporal trends in spatially structured populations: how should sampling effort be allocated between

space and time?” In: *Ecography* 34.6 (2011), pp. 1040–1048. DOI: https://doi.org/10.1111/j.1600-0587.2011.06370.x.

[182] David C Roberts and Donald L Turcotte. “Fractality and self-organized criticality of wars”. In: *Fractals* 6.04 (1998), pp. 351–357. DOI: https://doi.org/10.1142/S0218348X98000407.

[183] Orin J Robinson et al. “Extreme uncertainty and unquantifiable bias do not inform population sizes”. In: *Proceedings of the National Academy of Sciences of the United States of America* 119.10 (2022), e2113862119. DOI: https://doi.org/10.1073/pnas.2113862119.

[184] Robert A Robinson, Stephen R Baillie, and Ruth King. “Population processes in European blackbirds Turdus merula: a state–space approach”. In: *Journal of Ornithology* 152 (2012), pp. 419–433.

[185] DM Rootes. “The status of birds at Signy Island, South Orkney Islands”. In: *British Antarctic Survey Bulletin* 80 (1988), pp. 87–119.

[186] Yan Ropert-Coudert et al. “The retrospective analysis of Antarctic tracking data project”. In: *Scientific Data* 7.1 (2020), p. 94.

[187] Christian Roy, Eliot JB McIntire, and Steven G Cumming. “Assessing the spatial variability of density dependence in waterfowl populations”. In: *Ecography* 39.10 (2016), pp. 942–953. DOI: https://doi.org/10.1111/ecog.01534.

[188] Joellen L Russell et al. “The Southern Hemisphere westerlies in a warming world: Propping open the door to the deep ocean”. In: *Journal of Climate* 19.24 (2006), pp. 6382–6390. DOI: 10.1175/JCLI3984.1.

[189] Grace K Saba et al. “Winter and spring controls on the summer food web of the coastal West Antarctic Peninsula”. In: *Nature Communications* 5.1 (2014), pp. 1–8. DOI: https://doi.org/10.1038/ncomms5318.

[190] Bernt-Erik Sæther et al. “Geographical gradients in the population dynamics of North American prairie ducks”. In: *Journal of Animal Ecology* 77.5 (2008), pp. 869–882. DOI: https://doi.org/10.1111/j.1365-2656.2008.01424.x.

[191] Bernt-Erik Sæther et al. “Life-history variation predicts the effects of demographic stochasticity on avian population dynamics”. In: *The American Naturalist* 164.6 (2004), pp. 793–802. DOI: https://doi.org/10.1086/425371.

[192] Anwesha Saha et al. “Tracking global population trends: Population time-series data and a living planet index for reptiles”. In: *Journal of Herpetology* 52.3 (2018), pp. 259–268. DOI: 10.1670/17-076.

[193] Martin Sander et al. “Decline of the breeding population of Pygoscelis antarctica and Pygoscelis adeliae on Penguin Island, South Shetland, Antarctica”. In:

Polar Biology 30.5 (2007), pp. 651–654. DOI: `https://doi.org/10.1007/s00300-006-0218-2`.

[194] Martin Sander et al. "Recent decrease in chinstrap penguin (Pygoscelis antarctica) populations at two of Admiralty Bay's islets on King George Island, South Shetland Islands, Antarctica". In: *Polar Biology* 30.5 (2007), pp. 659–661. DOI: `10.1007/s00300-007-0259-1`.

[195] Mathew R Schwaller et al. "A continent-wide search for Antarctic petrel breeding sites with satellite remote sensing". In: *Remote Sensing of Environment* 210 (2018), pp. 444–451. DOI: `https://doi.org/10.1016/j.rse.2018.02.071`.

[196] Tucker Scully. "The development of the antarctic treaty system". In: *Science diplomacy: Antarctica, science, and the governance of international spaces* (2011).

[197] Nathaniel E Seavy et al. "Postcatastrophe population dynamics and density dependence of an endemic island duck". In: *The Journal of Wildlife Management* 73.3 (2009), pp. 414–418. DOI: `https://doi.org/10.2193/2007-420`.

[198] Bilgecan Şen et al. "Spatio-temporal transferability of population dynamics: A case study with the Adélie penguins". In Review.

[199] Zhuang Shen et al. "Superspreading SARS events, Beijing, 2003". In: *Emerging Infectious Diseases* 10.2 (2004), p. 256. DOI: `10.3201/eid1002.030732`.

[200] Richard B Sherley et al. "The conservation status and population decline of the African penguin deconstructed in space and time". In: *Ecology and Evolution* 10.15 (2020), pp. 8506–8516. DOI: `https://doi.org/10.1002/ece3.6554`.

[201] Victor Smetacek et al. "Mesoscale distribution of dominant diatom species relative to the hydrographical field along the Antarctic Polar Front". In: *Deep Sea Research Part II: Topical Studies in Oceanography* 49.18 (2002), pp. 3835–3848. ISSN: 0967-0645. DOI: `https://doi.org/10.1016/S0967-0645(02)00113-3`.

[202] Raymond C Smith et al. "The Palmer LTER: A long-term ecological research program at Palmer Station, Antarctica". In: *Oceanography* 8.3 (1995), pp. 77–86.

[203] Nicholas Socci, Daniel Lee, and H Sebastian Seung. "The rectified Gaussian distribution". In: *Advances in neural information processing systems* 10 (1997).

[204] Tony Soper. *Antarctica: a guide to the wildlife*. Bradt travel guides, 2018.

[205] Didier Sornette. "Dragon-kings, black swans and the prediction of crises". In: *International Journal of Terraspace Science and Engineering* (2009). DOI: `https://doi.org/10.48550/arXiv.0907.4290`.

[206] Didier Sornette. "Predictability of catastrophic events: Material rupture, earthquakes, turbulence, financial crashes, and human birth". In: *Proceedings of the*

National Academy of Sciences 99.suppl 1 (2002), pp. 2522–2529. DOI: https://doi.org/10.1073/pnas.022581999.

[207] Leif Christian Stige et al. "Density-and size-dependent mortality in fish early life stages". In: *Fish and Fisheries* 20.5 (2019), pp. 962–976. DOI: https://doi.org/10.1111/faf.12391.

[208] Dietmar Straile. "Gross growth efficiencies of protozoan and metazoan zooplankton and their dependence on food concentration, predator-prey weight ratio, and taxonomic group". In: *Limnology and Oceanography* 42.6 (1997), pp. 1375–1385. DOI: https://doi.org/10.4319/lo.1997.42.6.1375.

[209] Arco J van Strien et al. "Modest recovery of biodiversity in a western European country: The Living Planet Index for the Netherlands". In: *Biological Conservation* 200 (2016), pp. 44–50. DOI: 10.1016/j.biocon.2016.05.031.

[210] Noah Strycker et al. "A global population assessment of the Chinstrap penguin (Pygoscelis antarctica)". In: *Scientific Reports* 10.1 (2020), pp. 1–11. DOI: 10.1038/s41598-020-76479-3.

[211] Sam Subbey et al. "Modelling and forecasting stock–recruitment: current and future perspectives". In: *ICES Journal of Marine Science* 71.8 (2014), pp. 2307–2322. DOI: https://doi.org/10.1093/icesjms/fsu148.

[212] Fernando G Taboada and Ricardo Anadón. "Determining the causes behind the collapse of a small pelagic fishery using Bayesian population modeling". In: *Ecological Applications* 26.3 (2016), pp. 886–898. DOI: https://doi.org/10.1890/15-0006.1.

[213] Pandu R Tadikamalla. "A look at the Burr and related distributions". In: *International Statistical Review* (1980), pp. 337–344. DOI: https://doi.org/10.2307/1402945.

[214] Nassim Nicholas Taleb. *The black swan: The impact of the highly improbable*. Vol. 2. Random House, 2007.

[215] Emma J Talis, Christian Che-Castaldo, and Heather J Lynch. "Difficulties in summing log-normal distributions for abundance and potential solutions". In: *Plos One* 18.1 (2023), e0280351. DOI: https://doi.org/10.1371/journal.pone.0280351.

[216] Emma J Talis et al. "Data from: Variability, Skipped Breeding, and Heavy-tailed Dynamics in an Antarctic Seabird". In: *Zenodo* (2022). DOI: https://doi.org/10.5281/zenodo.7191370.

[217] Emma J Talis et al. "Penguindex: A biodiversity indicator for *Pygoscelis* species penguins identifies key eras of population change". In Review.

[218] Emma J Talis et al. “Variability, skipped breeding and heavy-tailed dynamics in an Antarctic seabird”. In: *Journal of Animal Ecology* 91.12 (2022), pp. 2437–2450. DOI: 10.1111/1365-2656.13827.

[219] Aleks Terauds and Jasmine R Lee. “Antarctic biogeography revisited: updating the Antarctic Conservation Biogeographic Regions”. In: *Diversity and Distributions* 22.8 (2016), pp. 836–840. DOI: https://doi.org/10.1111/ddi.12453.

[220] James T Thorson and Kasper Kristensen. “Implementing a generic method for bias correction in statistical models using random effects, with spatial and population dynamics examples”. In: *Fisheries Research* 175 (2016), pp. 66–74. DOI: https://doi.org/10.1016/j.fishres.2015.11.016.

[221] Megan Tierney et al. “Evaluating and using stable-isotope analysis to infer diet composition and foraging ecology of Adélie penguins Pygoscelis adeliae”. In: *Marine Ecology Progress Series* 355 (2008), pp. 297–307.

[222] Ram C Tiwari et al. “Bayesian model selection for join point regression with application to age-adjusted cancer rates”. In: *Journal of the Royal Statistical Society: Series C (Applied Statistics)* 54.5 (2005), pp. 919–939. DOI: 10.1111/j.1467-9876.2005.00518.x.

[223] Phil N Trathan and Grant Ballard. “Adélie penguin: (Pygoscelis adeliae)”. In: *Penguins: Natural History and Conservation* (2013), pp. 37–57.

[224] Geoffrey N Tuck et al. “Modelling the impact of fishery by-catches on albatross populations”. In: *Journal of Applied Ecology* 38.6 (2001), pp. 1182–1196. DOI: https://doi.org/10.1046/j.0021-8901.2001.00661.x.

[225] Peter Turchin. “Does population ecology have general laws?” In: *Oikos* 94.1 (2001), pp. 17–26.

[226] John Turner et al. “Absence of 21st century warming on Antarctic Peninsula consistent with natural variability”. In: *Nature* 535.7612 (2016), pp. 411–415. DOI: 10.1038/nature18645.

[227] John Turner et al. “Antarctic climate change and the environment: an update”. In: *Polar Record* 50.3 (2014), pp. 237–259. DOI: 10.1017/S0032247413000296.

[228] John Turner et al. “Antarctic climate change during the last 50 years”. In: *International Journal of Climatology* 25.3 (2005), pp. 279–294. DOI: 10.1002/joc.1130.

[229] John Turner et al. “Antarctic temperature variability and change from station data”. In: *International Journal of Climatology* 40.6 (2020), pp. 2986–3007. DOI: 10.1002/joc.6378.

[230] Jean-Christophe Vié et al. "The IUCN Red List: a key conservation tool". In: *Wildlife in a changing world–An analysis of the 2008 IUCN Red List of Threatened Species* (2009), p. 1.

[231] David Vose. *Quantitative risk analysis: a guide to Monte Carlo simulation modelling*. John Wiley & Sons, 1996.

[232] Wei-Lei Wang et al. "Convergent estimates of marine nitrogen fixation". In: *Nature* 566.7743 (2019), pp. 205–211. DOI: https://doi.org/10.1038/s41586-019-0911-2.

[233] Sally E Wayte. "Management implications of including a climate-induced recruitment shift in the stock assessment for jackass morwong (Nemadactylus macropterus) in south-eastern Australia". In: *Fisheries Research* 142 (2013), pp. 47–55. DOI: https://doi.org/10.1016/j.fishres.2012.07.009.

[234] Henri Weimerskirch et al. "Changes in wind pattern alter albatross distribution and life-history traits". In: *Science* 335.6065 (2012), pp. 211–214. DOI: 10.1126/science.1210270.

[235] Harold E. Welch. "Relationships between Assimiliation Efficiencies and Growth Efficiencies for Aquatic Consumers". In: *Ecology* 49.4 (1968), pp. 755–759. ISSN: 00129658, 19399170. DOI: https://doi.org/10.2307/1935541.

[236] J Westveer et al. *A Deep Dive into the Living Planet Index: A Technical Report*. 2022.

[237] PR Wilson et al. "Adélie penguin population change in the pacific sector of Antarctica: relation to sea-ice extent and the Antarctic Circumpolar Current". In: *Marine Ecology Progress Series* 213 (2001), pp. 301–309. DOI: 10.3354/meps213301.

[238] Thomas W Yee. "The VGAM package". In: *R News* 8.2 (2008), pp. 28–39.

[239] Casey Youngflesh and Heather J Lynch. "Black-swan events: Population crashes or temporary emigration?" In: *Proceedings of the National Academy of Sciences* 114.43 (2017), E8953–E8954. DOI: https://doi.org/10.1073/pnas.1713621114.

[240] Casey Youngflesh et al. "Circumpolar analysis of the Adélie Penguin reveals the importance of environmental variability in phenological mismatch". In: *Ecology* 98.4 (2017), pp. 940–951. DOI: https://doi.org/10.1002/ecy.1749.

[241] H Jay Zwally et al. "Variability of Antarctic sea ice 1979–1998". In: *Journal of Geophysical Research: Oceans* 107.C5 (2002), pp. 9–1. DOI: 10.1029/2000JC000733.

Appendix A

Difficulties in summing log-normal distributions for abundance and potential solutions

A.1 Supplementary Methods

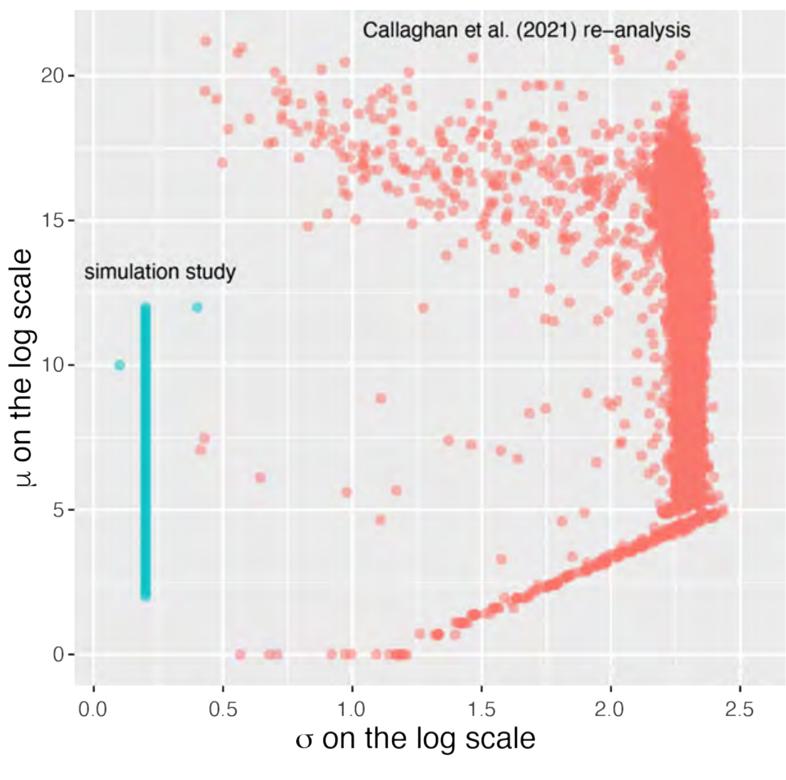

FIGURE A.1: Parameter values used in the simulation study and global bird abundance study. Log-normal parameter values μ and σ used in both the simulation study and the re-analysis of Callaghan et al.'s global bird abundance data.

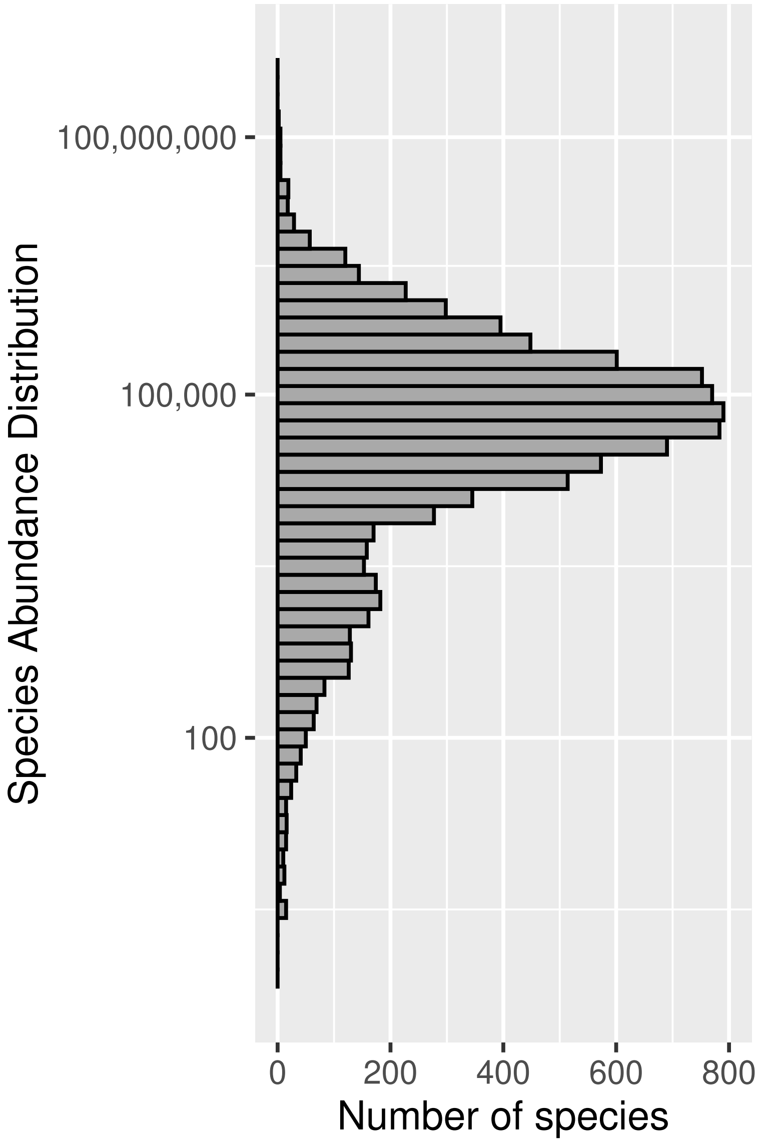

FIGURE A.2: Reconstructed global species abundance distribution for global bird abundance. The global species abundance distribution, calculated using the median of each species' simulated abundance distribution (each a log-normal distribution) for the re-analysis of the global bird abundance data. A constant 1 is added for species predicted to have zero abundance. Reproduction of Fig 2A in Callaghan et al. (shown on the same scale, $\log_{10}$).

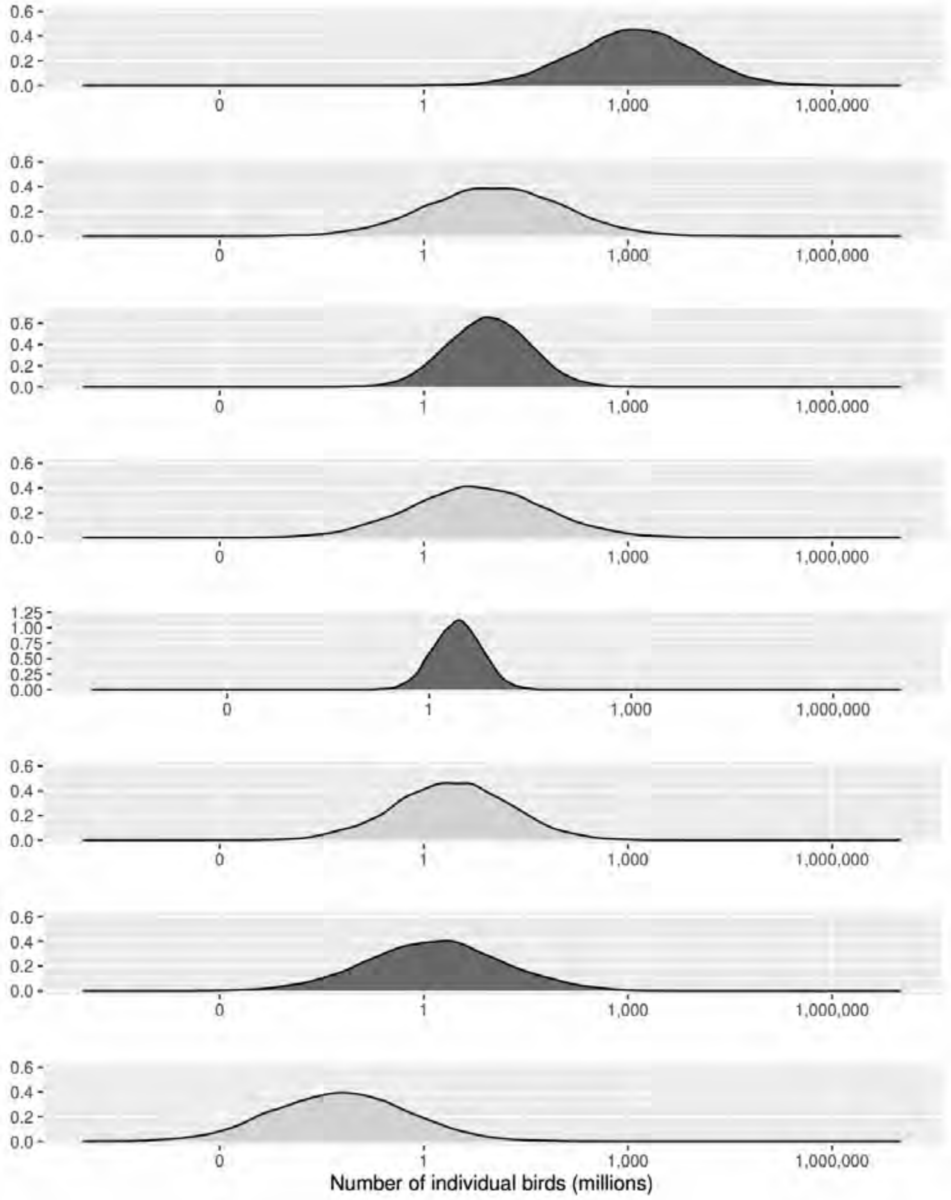

FIGURE A.3: Examples of reconstructed species' simulated abundance distributions for global bird abundance study. Species shown, from top to bottom: Ring-billed Gull; Green Heron; Northern Wheatear; Ashy Prinia; Osprey; Acorn Woodpecker; Yellow-tailed Black-Cockatoo; and Midget Flowerpecker. Reproduction of Fig 2B in Callaghan et al. (shown on the same scale, $\log_{10}$, in millions).

A.2 Derivation of linearity of difference in global abundance estimates

Consider $n = \{10, 100, 1000\}$ i.i.d. log-normally distributed populations $N_1, N_2, ..., N_n$ each satisfying $\log(N_{i_t}) \sim N(\mu, \sigma^2)$. Let the D be equal to the logged-difference between the median of the posterior for the aggregate sum of populations and the sum of the individual population medians. Then

$$D = \log(M - S), \tag{A.1}$$

where M is the median of the posterior for $N = N_1 + N_2 + ... + N_n$, the aggregate sum of populations and S is the sum of the individual medians of each population.

The sum of n i.i.d. log-normal random variables N has no closed form probability density function. However, the Fenton-Wilkinson (FW) approximation produces a commonly used estimate for the PDF of N [67]. According to the FW approximation [46], N can be approximated by a log-normal PDF with parameters μ_N and σ_N^2 such that

$$\sigma_N^2 = \frac{\log(e^{\sigma^2 - 1})}{n} + 1, \tag{A.2}$$

$$\mu_N = \log(ne^{\mu}) + \frac{1}{2}(\sigma^2 - \sigma_N^2). \tag{A.3}$$

Thus the median of N is given approximated by

$$M = \text{med}(N) \approx \frac{\log(ne^{\mu}) + \frac{1}{2}(\sigma^2 - \sigma_N^2)}{e^{\sigma_N^2/2}} \tag{A.4}$$

$$= \frac{\log(ne^{\mu}) + \frac{1}{2}(\sigma^2 - (\frac{1}{n}\log(e^{\sigma^2 - 1}) + 1))}{e^{(\frac{1}{n}\log(e^{\sigma^2} - 1) + 1)/2}} \tag{A.5}$$

$$= \frac{\log(n) + \log(e^{\mu}) + \frac{1}{2}(\sigma^2 - (\frac{1}{n}\log(e^{\sigma^2 - 1}) + 1))}{e^{(\frac{1}{n}\log(e^{\sigma^2} - 1) + 1)/2}} \tag{A.6}$$

$$= \frac{\log(n) + \mu + \frac{1}{2}(\sigma^2 - (\frac{1}{n}\log(e^{\sigma^2 - 1}) + 1))}{e^{(\frac{1}{n}\log(e^{\sigma^2} - 1) + 1)/2}} \tag{A.7}$$

$$= \frac{\mu}{e^{(\frac{1}{n}\log(e^{\sigma^2} - 1) + 1)/2}} + \frac{\log(n) + \frac{1}{2}(\sigma^2 - (\frac{1}{n}\log(e^{\sigma^2 - 1}) + 1))}{e^{(\frac{1}{n}\log(e^{\sigma^2} - 1) + 1)/2}}. \tag{A.8}$$

Setting $a = \log(n) + \frac{1}{2}(\sigma^2 - (\frac{1}{n}\log(e^{\sigma^2 - 1}) + 1))$ and $b = e^{(\frac{1}{n}\log(e^{\sigma^2} - 1) + 1)/2}$, A.8 reduces to

$$M \approx \frac{1}{b}\mu + \frac{a}{b}. \tag{A.9}$$

Since the median of each log-normally distributed population N_i is equal to e^{μ}, the value of S can be found easily:

$$\begin{aligned} S &= \sum_{i=1}^{n} \text{med}(N_i) \\ &= \sum_{i=1}^{n} e^{\mu} \\ &= ne^{\mu}. \end{aligned} \tag{A.10}$$

Thus A.1 becomes

$$D = \log\left(\frac{1}{b}\,\mu + \frac{a}{b} - ne^{\mu}\right). \tag{A.11}$$

Differentiating with respect to μ yields

$$\frac{dD}{d\mu} = \frac{\frac{1}{b} - ne^{\mu}}{\frac{\mu}{b} + \frac{a}{b} - ne^{\mu}} \tag{A.12}$$

$$\approx 1, \tag{A.13}$$

since the e^{μ} terms dominate all others in A.12 for sufficiently large values of μ.

A.3 How Bayesians interpret the tail of the skewed distributions

For simplicity, we limited our manuscript's discussion on the mechanics of summing distributions for population abundance. However, it is also worth reflecting on our interpretation of the posterior distribution and, specifically, on the interpretation of the log-normal distribution's long right tail. One interpretation of this long right tail is that such abundances are infrequent and thus including them in the aggregate sum (at the appropriately small probability) is appropriate. A more Bayesian interpretation would be that such tail events are not infrequent but are instead *unlikely to be true* (in the "degree-of-belief" sense), in which case they should *not* be included in the aggregate total. While extreme outcomes (i.e. those in the right tail of the distribution) are by nature rare, the probability of drawing at least one extremely large abundance when summing across posteriors can be quite high, and eventually inevitable (as illustrated in Fig 1C in the main text), meaning the aggregate abundance will almost certainly include at least one very large draw, and thus will be larger than anticipated by the central tendencies of the individual populations. The interpretation of the Bayesian posterior in this context deserves discussion but falls outside the scope of our manuscript, which was written for an audience of conservation practitioners.

A.4 Summing negative binomial distributions

Consider a collection of $n = \{10, 100, 1000\}$ independent and identically negative binomially-distributed populations of animals, each with an abundance that is modeled as $N_{i,t} \sim NB(\mu, k)$ where μ is the mean of abundance, varying between 2,000 and 160,000, and k is the overdispersion ("size") parameter, fixed at 4. (The overdispersion parameter measures the amount of clustering, or aggregation, or heterogeneity in the data: a smaller k means more heterogeneity; when $k = 0$, the NB distribution is equivalent to the Possion distribution.) Each population consists of $m = 1000$ negative binomially-distributed draws. If an estimate for the total abundance across all of these populations (the "regional" abundance) is sought, then the distribution of interest, that of the regional abundance, is thus the sum of many log-normal distributions. We first consider the choice of summary statistic for a single negative binomial distribution, and then consider the differences between methods of summing across multiple distributions. Similar to that of the log-normal distribution, the mean of a negative binomial random variable is pulled toward the extreme values of the distribution's long right tail and, as a result, the mean is always larger than the median (Fig A.4).

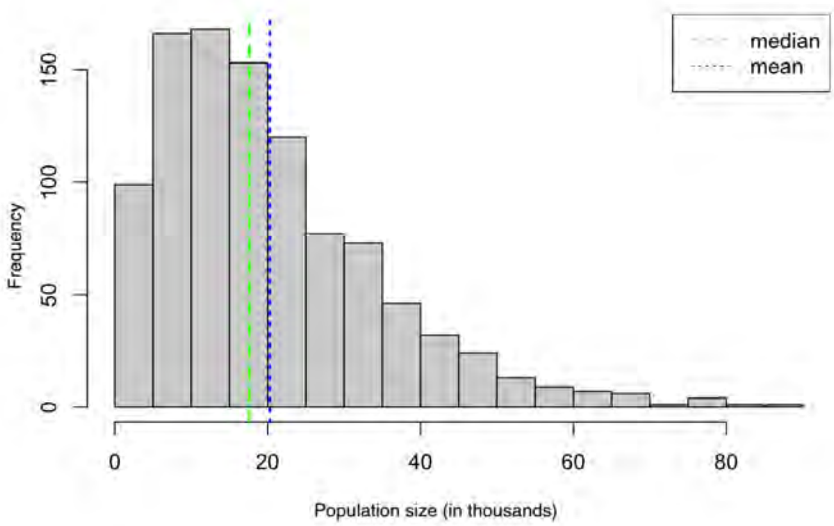

FIGURE A.4: Negative binomial distribution for abundance with $\mu = 20,000$ and $k = 2$.

We now consider summing across multiple populations whose abundances are described each by a negative binomial distribution. Unlike the case of the log-normal distribution, the probability generating function of the sum of n negative binomial random variables is known in closed form. The sum $S = X_1 + X_2 + ... + X_n$ where each X_i follows the negative binomial distribution has been shown to be a mixture binomial random variable [41, 74]. However, we show in Fig A.5 that sums of negative

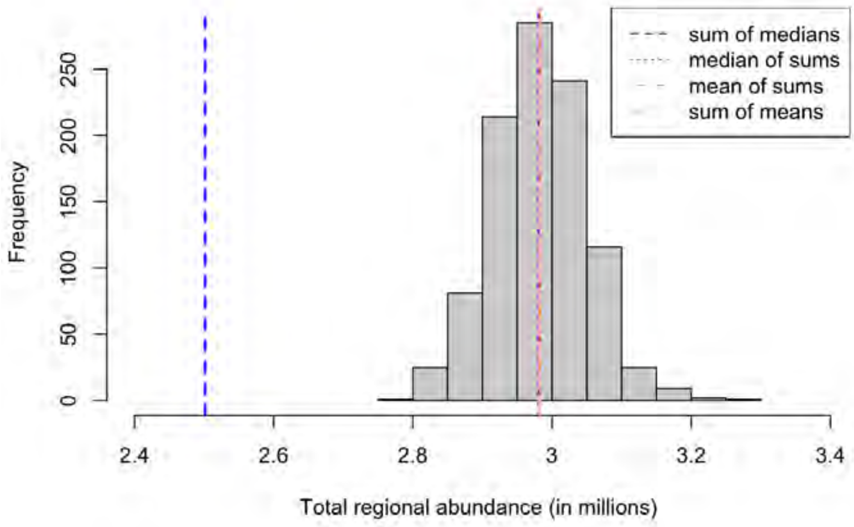

FIGURE A.5: The distribution of $m = 1000$ sums of NB-distributed abundance samples across $n = 1000$ independent populations. Each NB-distributed population has mean abundance $\mu = 4000$ and overdispersion parameter $k = 2$. The values of the sum of the medians, median of sums, and mean of sums (which is equal to the sum of the means) are shown.

binomial random variables behave similarly to those of log-normal random variables when the median is used as the measure of central tendency. If the median is used as a point estimate of abundance, it follows that either the median of the sums or the sum of the medians represents the best estimate of the aggregate abundance. However, since the median of sums is not the sum of medians, these two methods give different estimates for total abundance across the region, with the latter approach (sum-then-summarize, giving the median of the sums) yielding a significantly larger estimate of total abundance than former (summarize-then-sum, giving the sum of the medians), as shown in Fig A.6. This phenomenon is similar to that described for the log-normal distribution.

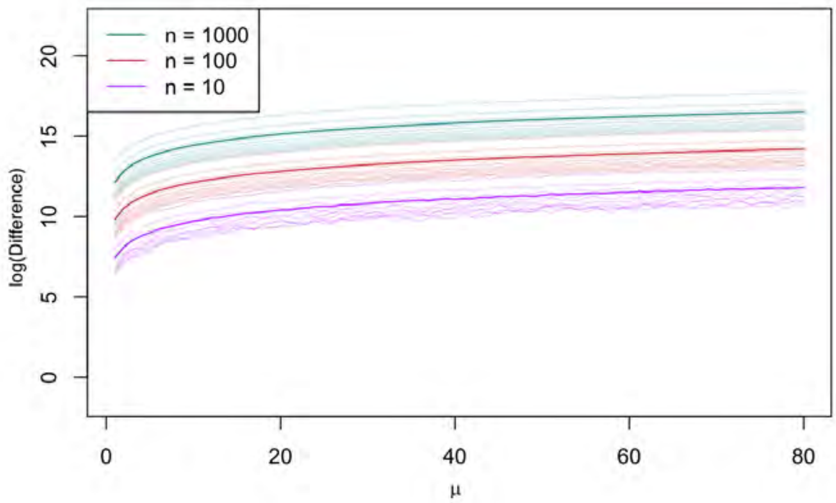

FIGURE A.6: The logged difference in global abundance estimates for $n = \{10, 100, 1000\}$ i.i.d. negative binomial-distributed populations is plotted against the mean abundance μ. Solid lines represent the mean of each set of 10 ensembles. For each simulation, we draw $m = 1000$ samples for each population and calculate the difference between the median of the sample-wise aggregated regional population and the sum of the empirical population medians.

Appendix B

Heavy-tailed distributions in animal population modeling

B.1 Heavy-tailed distributions for Adélie penguin abundance

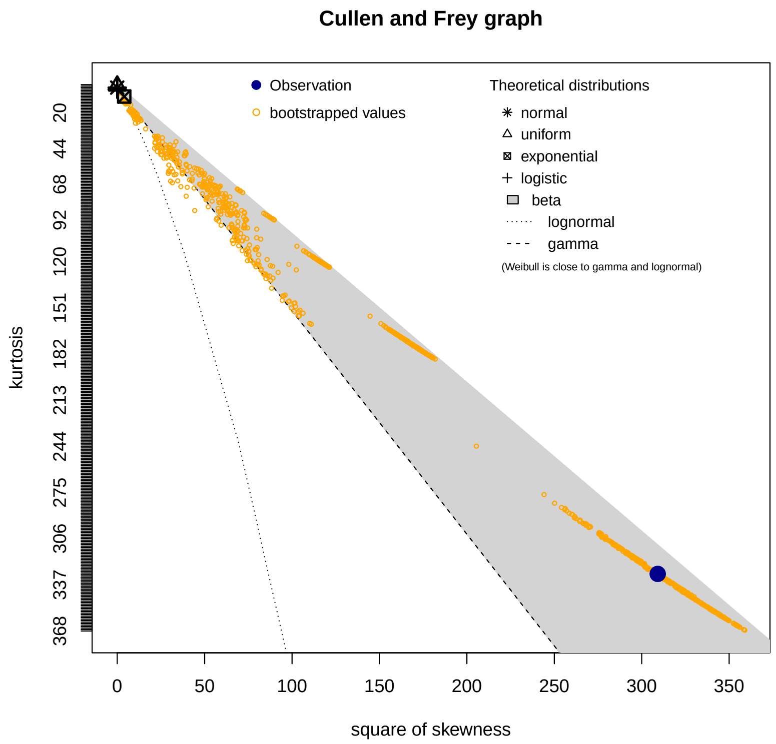

FIGURE B.1: Skewness-kurtosis plot for empirical Adélie abundance data on the linear scale ($\frac{N_{t+1}}{N_t}$), including values for 1000 bootstrap samples. Values are also given for several common distributions.

Distribution	Parameter	Estimate	Standard error
Normal	`mean`	0.015	0.020
	`sd`	0.309	0.014
Student's t †	`mu`	-0.001	0.011
	`sigma`	0.175	0.012
	`df`	2.542	0.401
Logistic	`location`	0.002	0.013
	`scale`	0.154	0.007
Cauchy	`location`	-0.001	0.010
	`scale`	0.126	0.009
Gumbel *	`mu`	-0.120	0.015
	`sigma`	0.278	0.010

TABLE B.1: Estimates and standard errors for each parameter for the distributions in Table 3.2 fitted to empirical Adélie penguin abundance between 1970-2019 ($\log(\frac{N_{t+1}}{N_t})$). †The nonstandard Student's t distribution, with mean μ, standard deviation σ, and degrees of freedom ν, is fit here (it is defined for use in R by the `ggdist` package [112]). *The Gumbel distribution is defined for use in R by the `VGAM` package [238]. All other distributions are defined in Base R.

Distribution	Parameter	Estimate	Standard error
Log-normal	`meanlog`	0.012	0.018
	`sdlog`	0.289	0.013
Gamma	`shape`	10.192	0.897
	`rate`	9.580	0.864
Weibull	`shape`	2.276	0.082
	`scale`	1.189	0.035
Log-logistic **	`shape`	6.514	0.288
	`scale`	1.002	0.013
Burr **	`shape1`	0.560	0.071
	`shape2`	8.376	0.603
	`rate`	1.113	0.027

TABLE B.2: Estimates and standard errors for each parameter for the distributions in Table 3.1 fitted to empirical Adélie penguin abundance between 1970-2019 ($\frac{N_{t+1}}{N_t}$). **The log-logistic and Burr distributions are defined for use in R by the `actuar` package [66]. All other distributions are defined in Base R.

B.2 Fitting heavy-tailed distributions in JAGS

B.2.1 Table 3.4 Supplementary Results

Distribution	Parameter	MLE Estimate	MLE Standard Error
Logistic	$\mu = 1$	0.99	0.99
	$s = 2$	1.96	0.77
Student's t (Standard)	$\nu = 5$	5.08	5.15
Student's t	$\mu = 1$	0.98	0.98
	$\sigma = 0.5$	0.51	0.51
	$\nu = 5$	5.07	5.24
Gamma	$\alpha = 5$	4.92	4.92
	$\beta = 2$	1.93	1.93
Weibull	$k = 1.5$	1.52	1.52
	$\lambda = 1$	0.99	1.00

TABLE B.3: Estimates and standard errors for each parameter using MLE (using the `fitdistrplus` package in R [61]), as compared to true parameter values, for the distributions in Table 3.4.

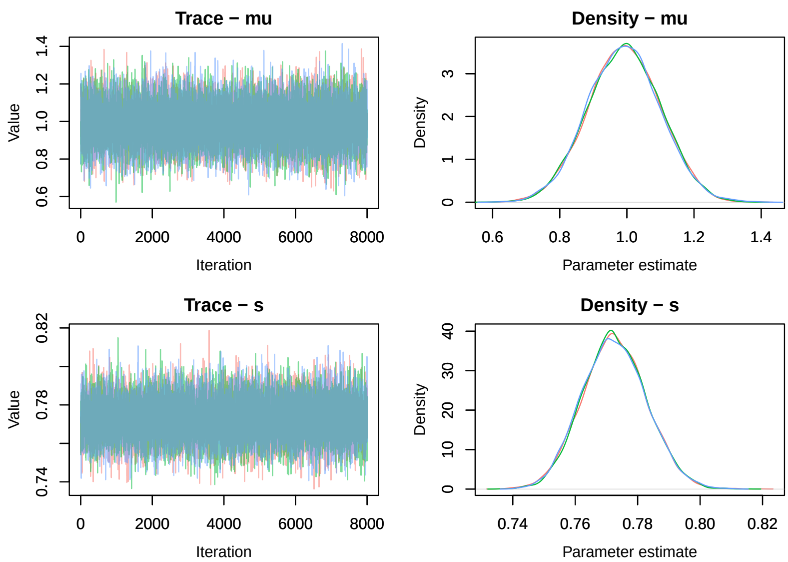

FIGURE B.2: Trace plots and posterior distributions for the JAGS built-in logistic distribution model (see Table 3.4).

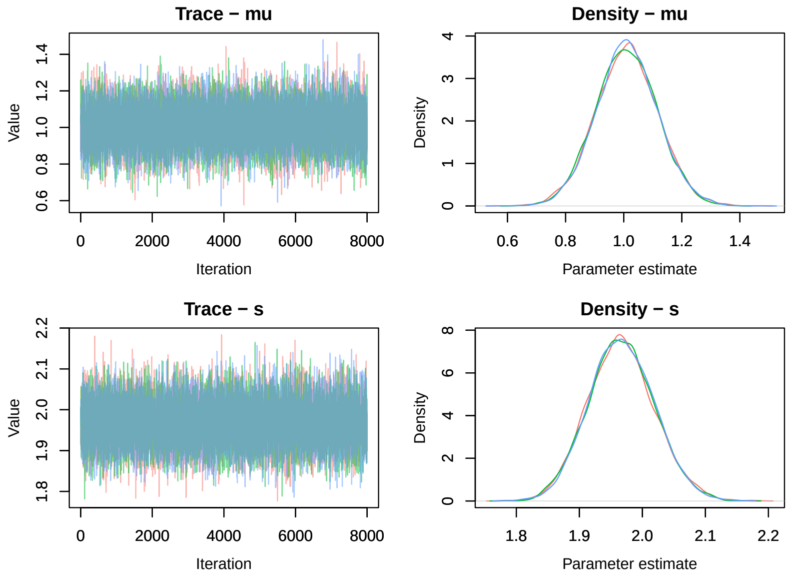

FIGURE B.3: Trace plots and posterior distributions for the JAGS logistic distribution model using the zeros trick (see Table 3.4).

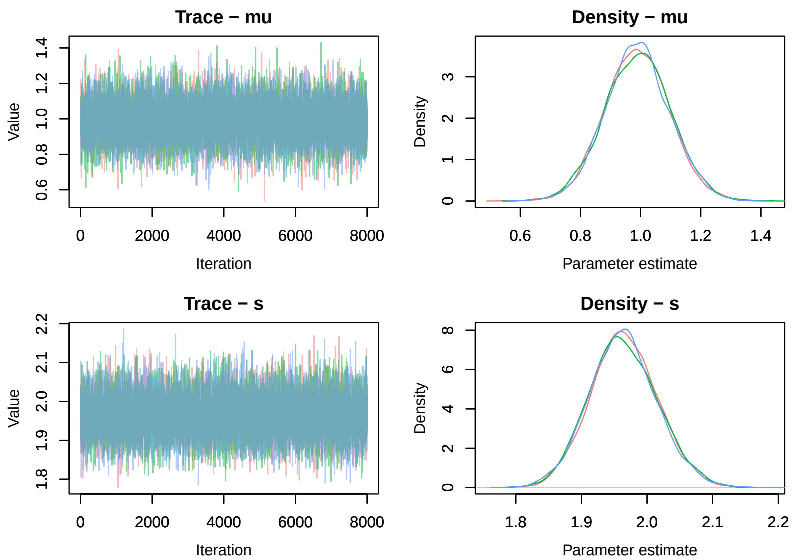

FIGURE B.4: Trace plots and posterior distributions for the JAGS logistic distribution model using the ones trick (see Table 3.4).

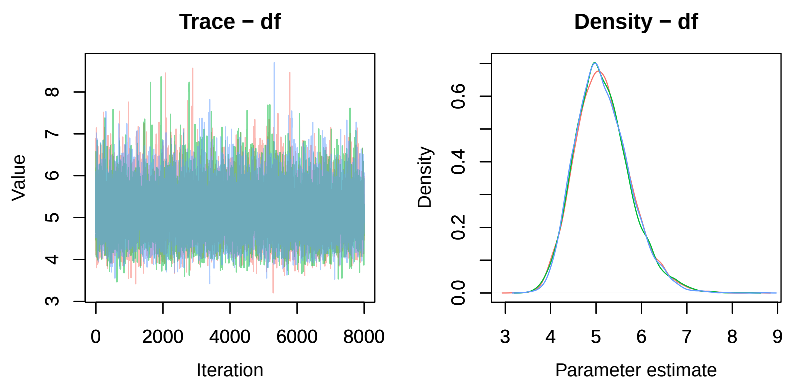

FIGURE B.5: Trace plots and posterior distributions for the JAGS built-in Student's t distribution model (see Table 3.4). Data simulated using a standard Student's t distribution (defined in Base R).

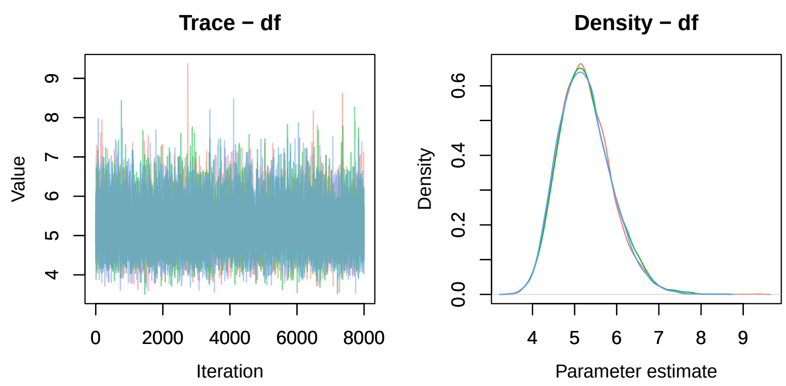

FIGURE B.6: Trace plots and posterior distributions for the JAGS Student's t distribution model using the zeros trick (see Table 3.4). Data simulated using a standard Student's t distribution (defined in Base R).

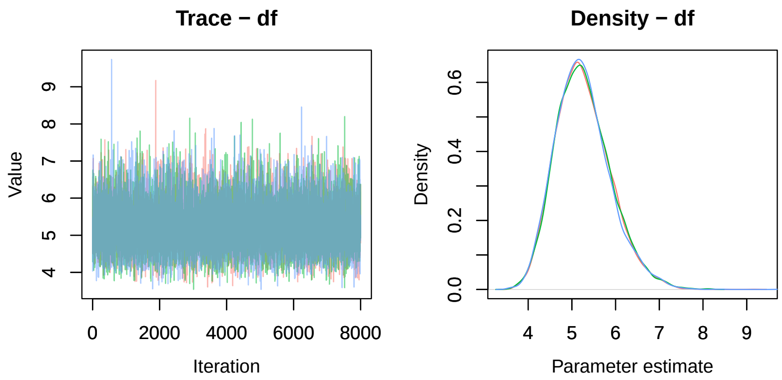

FIGURE B.7: Trace plots and posterior distributions for the JAGS Student's t distribution model using the ones trick (see Table 3.4). Data simulated using a standard Student's t distribution (defined in Base R).

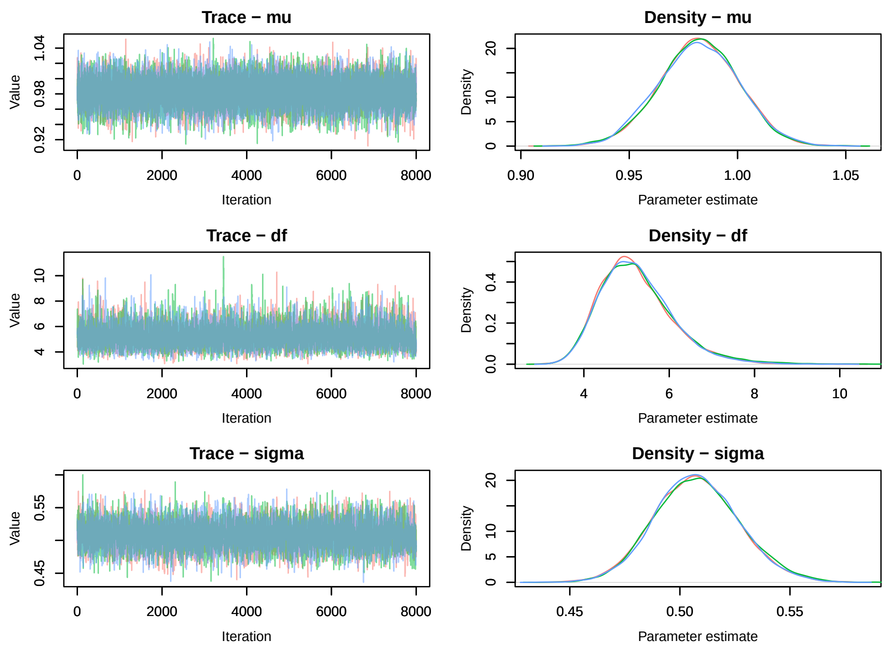

FIGURE B.8: Trace plots and posterior distributions for the JAGS built-in Student's t distribution model (see Table 3.4). Data simulated using a nonstandard Student's t distribution (defined in the R package `ggdist` [112]).

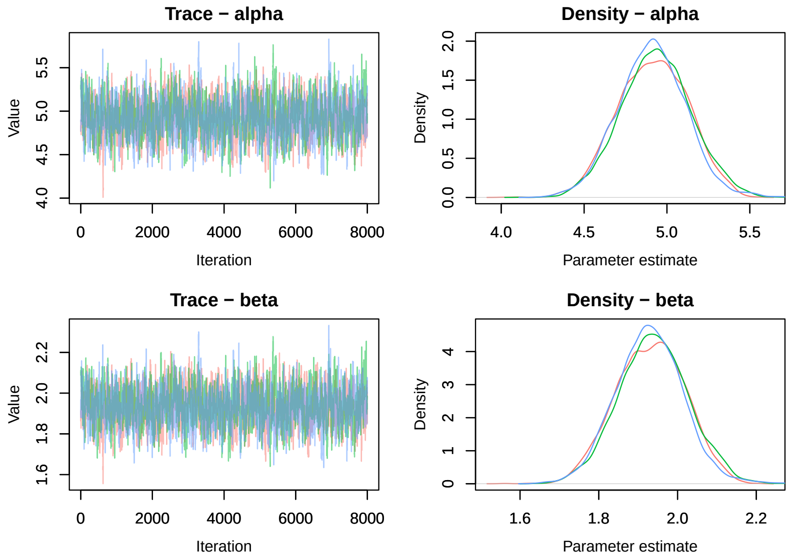

FIGURE B.9: Trace plots and posterior distributions for the JAGS built-in Gamma distribution model (see Table 3.4).

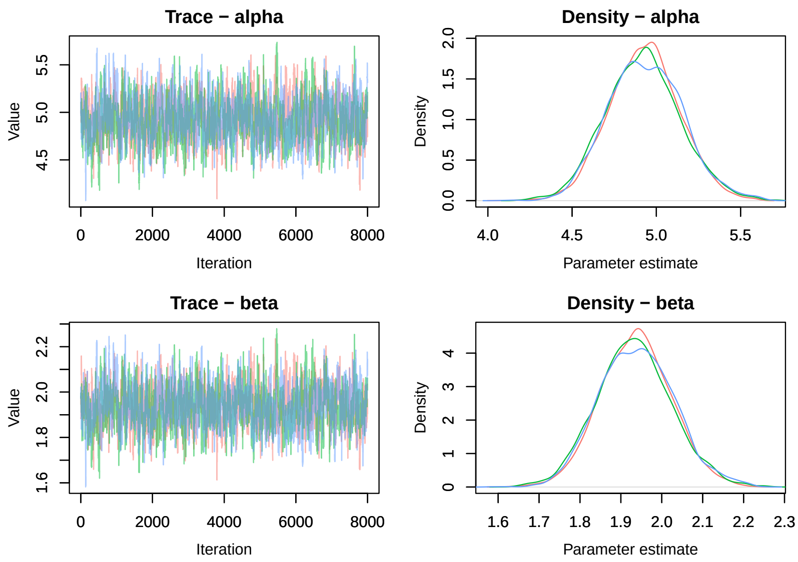

FIGURE B.10: Trace plots and posterior distributions for the JAGS Gamma distribution model using the zeros trick (see Table 3.4).

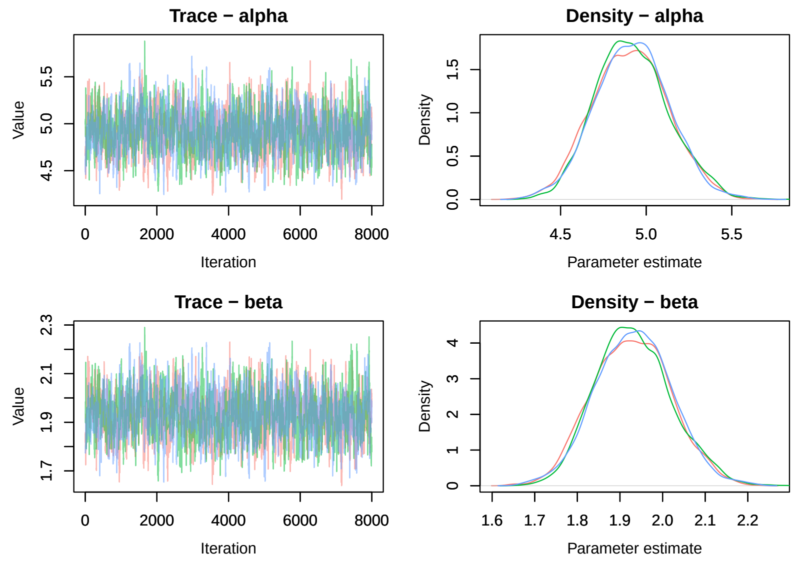

FIGURE B.11: Trace plots and posterior distributions for the JAGS Gamma distribution model using the ones trick (see Table 3.4).

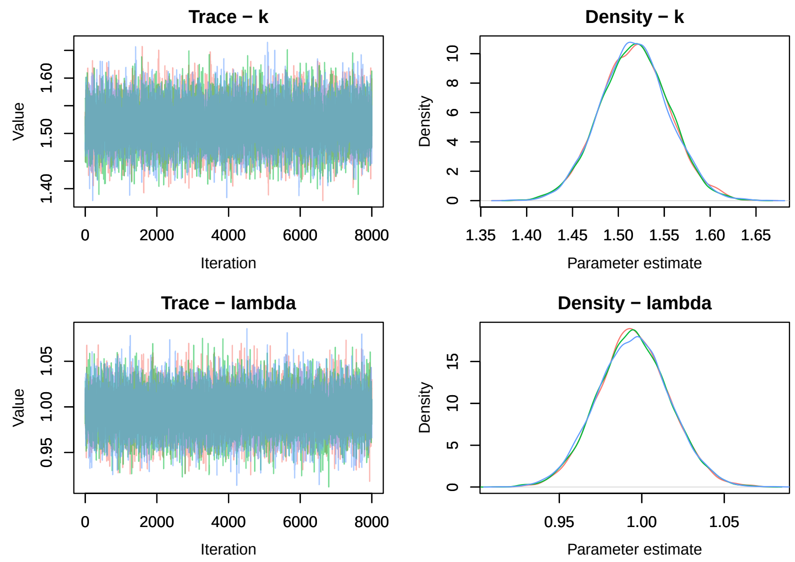

FIGURE B.12: Trace plots and posterior distributions for the JAGS built-in Weibull distribution model (see Table 3.4).

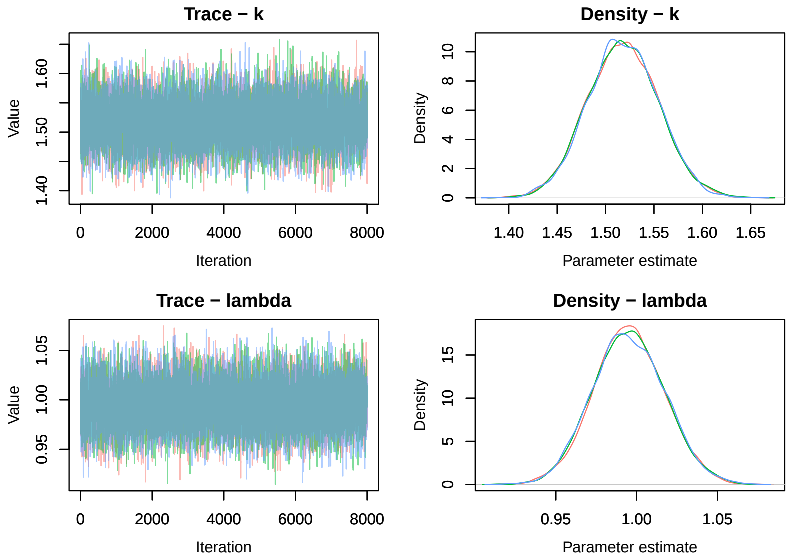

FIGURE B.13: Trace plots and posterior distributions for the JAGS Weibull distribution model using the zeros trick (see Table 3.4).

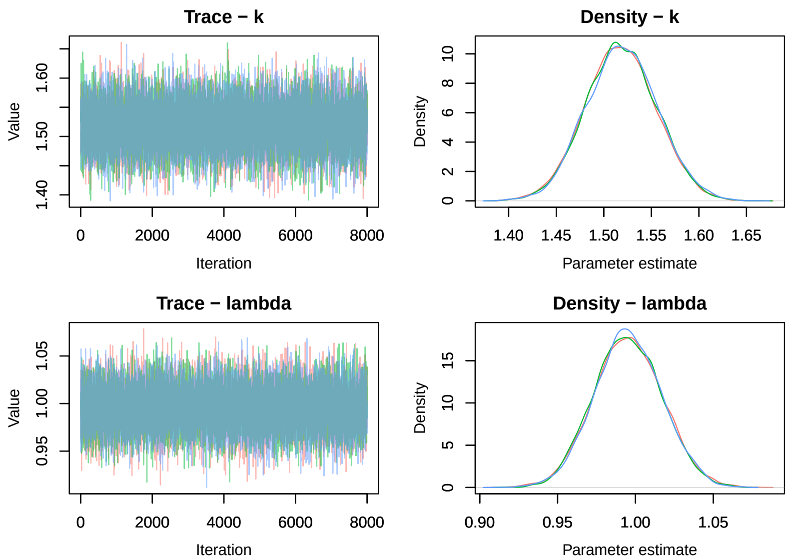

FIGURE B.14: Trace plots and posterior distributions for the JAGS Weibull distribution model using the ones trick (see Table 3.4).

B.2.2 Table 3.5 Supplementary Results

N	Parameter	MLE Estimate	MLE Standard Error
1000	$k = 1.5$	1.52	0.037
	$\lambda = 1$	0.99	0.022
500	$k = 1.5$	1.53	0.053
	$\lambda = 1$	0.98	0.030
100	$k = 1.5$	1.41	0.111
	$\lambda = 1$	0.92	0.069
50	$k = 1.5$	1.60	0.169
	$\lambda = 1$	0.98	0.092

TABLE B.4: Estimates and standard errors for each parameter using MLE (using the `fitdistrplus` package in R [61]), as compared to true parameter values, for the fitted Weibull distributions in Table 3.5.

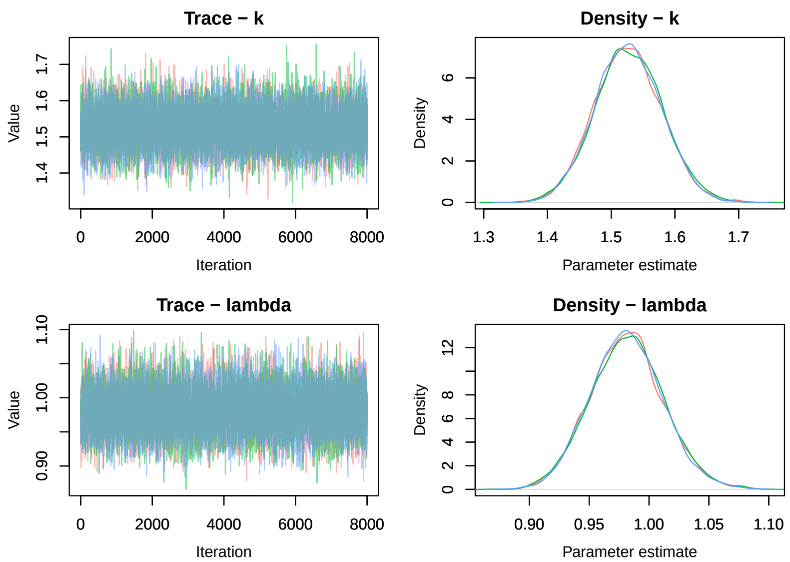

FIGURE B.15: Trace plots and posterior distributions for the JAGS built-in Weibull distribution model, fitting a dataset of size $N = 500$ (see Table 3.5).

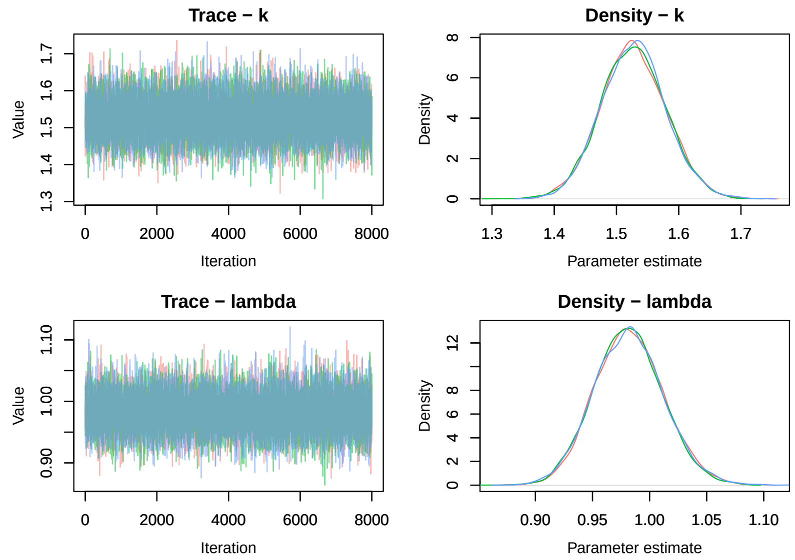

FIGURE B.16: Trace plots and posterior distributions for the JAGS Weibull distribution model using the zeros trick, fitting a dataset of size $N = 500$ (see Table 3.5).

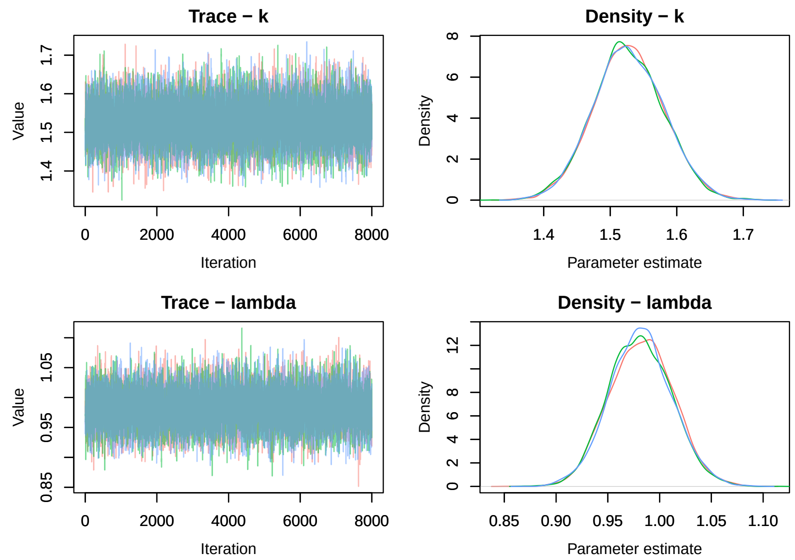

FIGURE B.17: Trace plots and posterior distributions for the JAGS Weibull distribution model using the ones trick, fitting a dataset of size $N = 500$ (see Table 3.5).

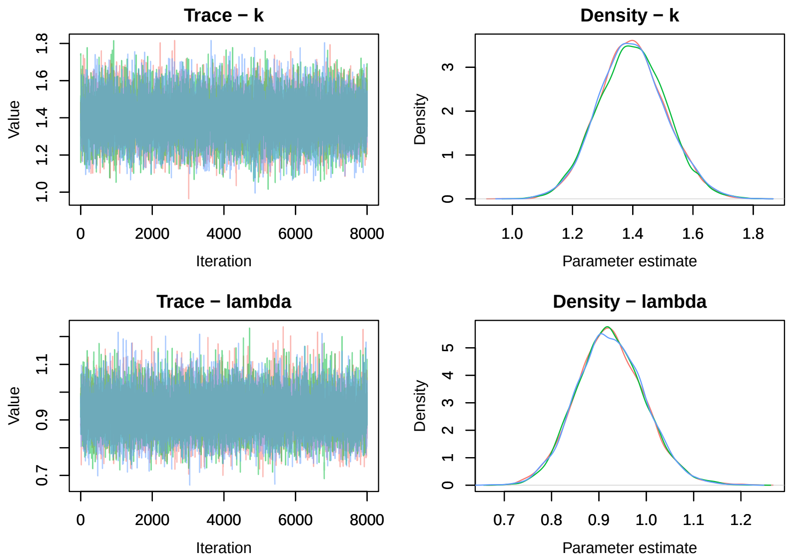

FIGURE B.18: Trace plots and posterior distributions for the JAGS built-in Weibull distribution model, fitting a dataset of size $N = 100$ (see Table 3.5).

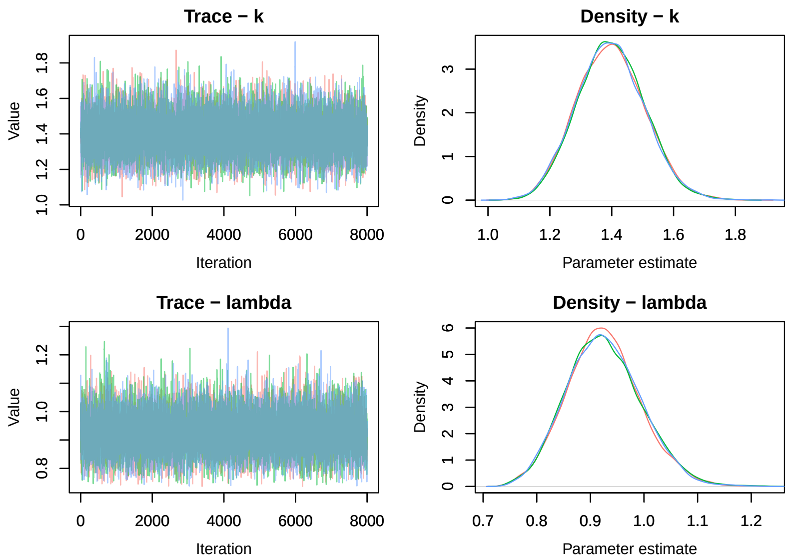

FIGURE B.19: Trace plots and posterior distributions for the JAGS Weibull distribution model using the zeros trick, fitting a dataset of size $N = 100$ (see Table 3.5).

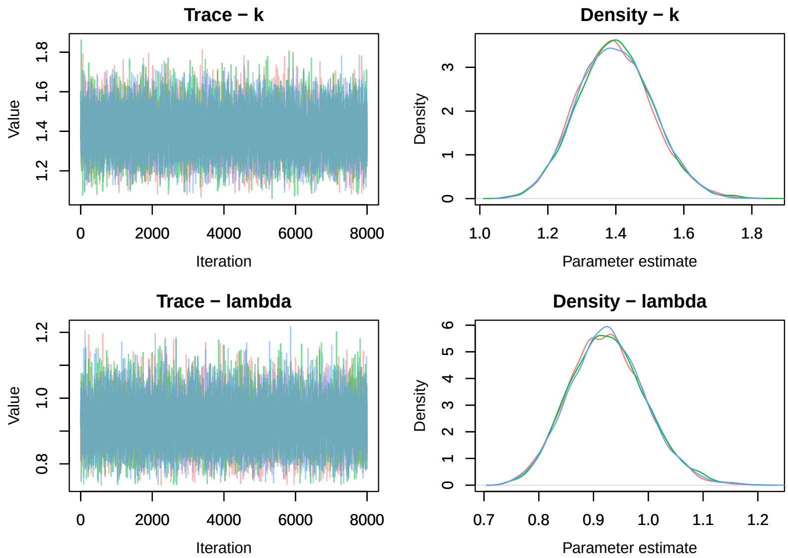

FIGURE B.20: Trace plots and posterior distributions for the JAGS Weibull distribution model using the ones trick, fitting a dataset of size $N = 100$ (see Table 3.5).

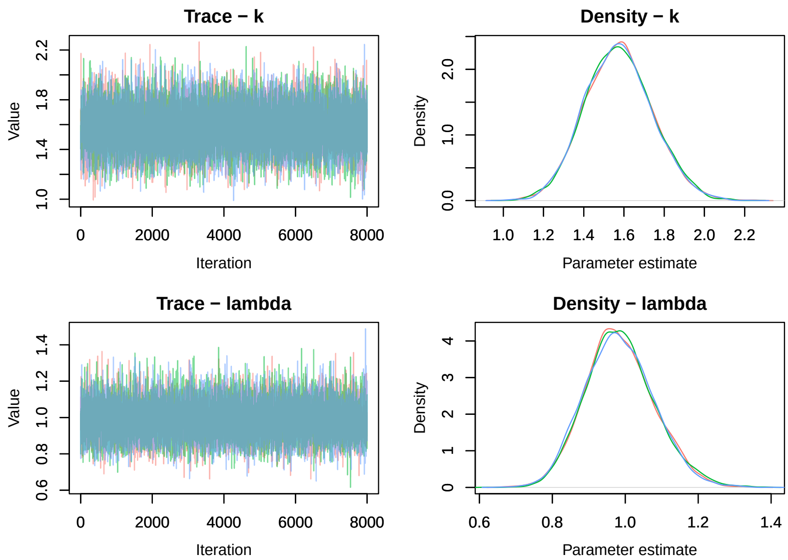

FIGURE B.21: Trace plots and posterior distributions for the JAGS built-in Weibull distribution model, fitting a dataset of size $N = 50$ (see Table 3.5).

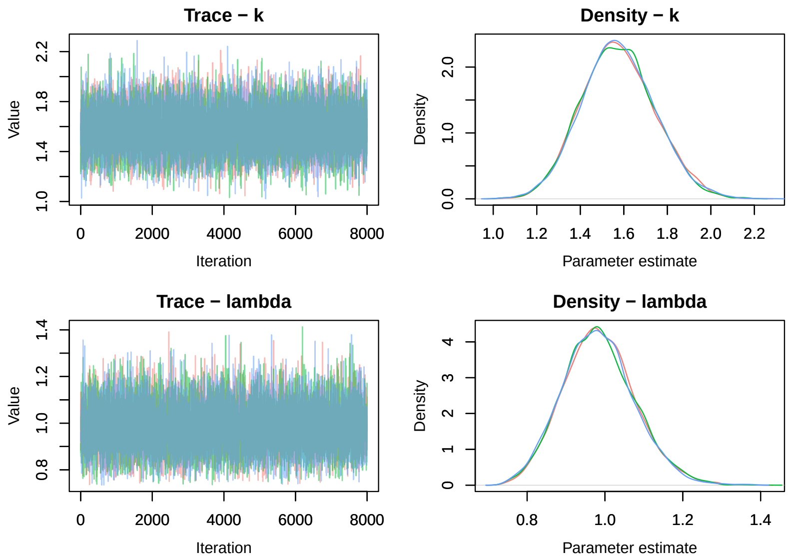

FIGURE B.22: Trace plots and posterior distributions for the JAGS Weibull distribution model using the zeros trick, fitting a dataset of size $N = 50$ (see Table 3.5).

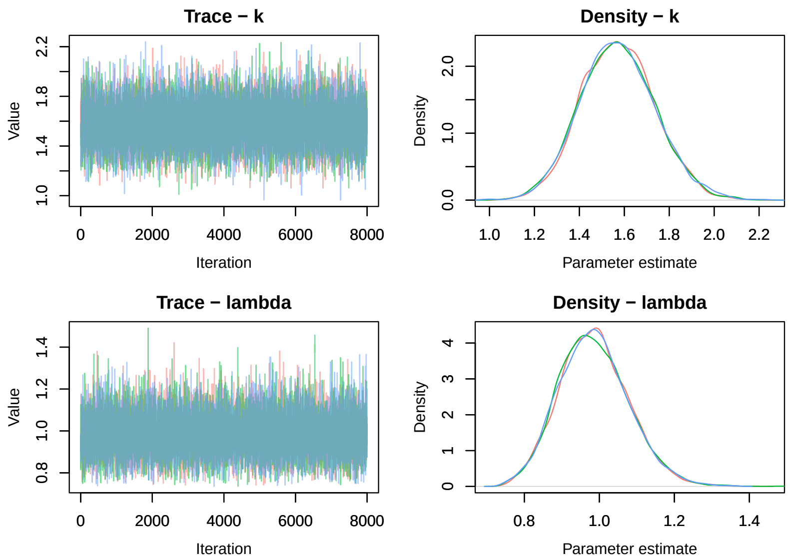

FIGURE B.23: Trace plots and posterior distributions for the JAGS Weibull distribution model using the ones trick, fitting a dataset of size $N = 50$ (see Table 3.5).

Appendix C

Variability, skipped breeding, and heavy-tailed dynamics in an Antarctic seabird

C.1 Approximate Bayesian computation

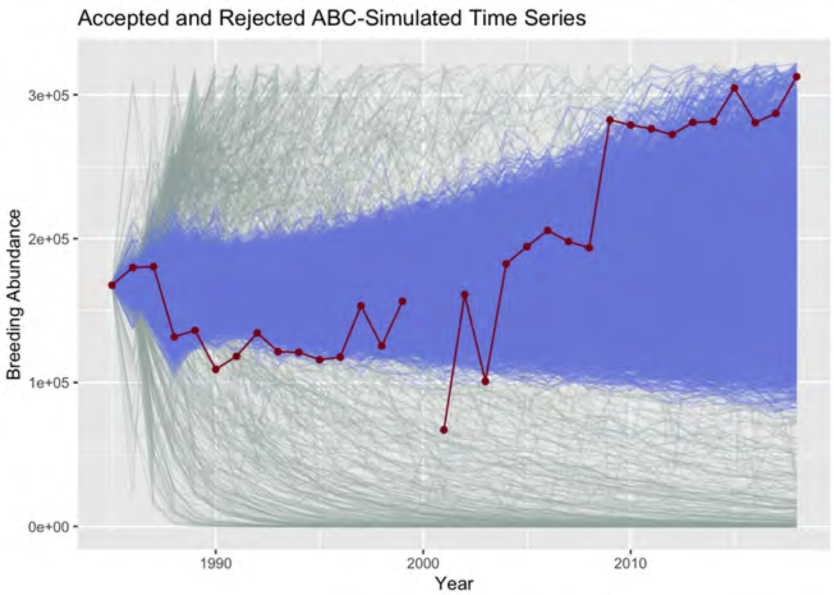

FIGURE C.1: ABC-simulated time series shown with the observed time series for Cape Crozier from 1985 to 2018. Simulated time series are accepted (shown in blue) or rejected (shown in faint gray) based on mean absolute percentage error from observed time series.

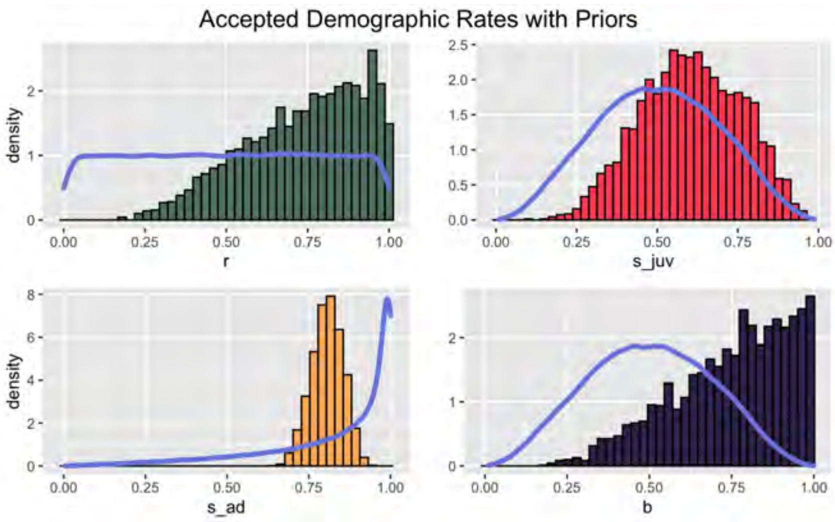

FIGURE C.2: Histograms of accepted values for demographic parameters in the ABC parameter estimation, shown with their priors (blue).

C.2 Bayesian population model

C.2.1 Model description

We used a Bayesian state-space model to estimate annual Adélie nest abundances for all 271 known Adélie breeding sites from 1970 – 2020. We model the intrinsic rate of growth r_i for the i_{th} site as only the region-specific mean $\gamma_{R[i]}$. Regions are dictated by the Antarctic Conservation Biogeographic Regions, as determined by [219]. We purposefully avoided additional covariates as to create a simplistic default model whose predictive ability could be compared to that of more biologically nuanced process models.

C.2.2 Antarctic Conservation Biogeographic Regions

Adélie penguin colony sites were grouped into the following ACBRs [219] (listed here with the number of sites and number of total site/year observations in each):

1. North-east Antarctic Peninsula (6 sites, 12 total observations)
2. South Orkney Islands (22 sites, 73 total observations)
3. Northwest Antarctic Peninsula (80 sites, 481 total observations)
4. Central South Antarctic Peninsula (2 sites, 4 total observations)
5. Enderby Land (27 sites, 192 total observations)
6. Dronning Maud Land (0 sites)
7. East Antarctica (32 sites, 58 total observations)

8. North Victoria Land (28 sites, 217 total observations)
9. South Victoria Land (10 sites, 199 total observations)
10. Transantarctic Mountains (0 sites)
11. Ellsworth Mountains (0 sites)
12. Marie Byrd Land (7 sites, 10 total observations)
13. Adélie Land (13 sites, 40 total observations)
14. Ellsworth Land (7 sites, 9 total observations)
15. South Antarctic Peninsula (1 site, 1 observation)
16. Prince Charles Mountains (26 sites, 55 total observations)

Observation errors

Counts were provided by the observer(s) as the nest or chick count y along with an associated accuracy score (which we convert to measurement error) such that y represented a draw from a distribution:

$$[y|lz, \sigma_o^2], \tag{C.1}$$

centered on the "true", or latent, count lz whose dispersion was controlled by σ_o^2, which represented the uncertainty in the count due to measurement imprecision. The accuracy scores were selected from a 4 point scale that penguin census counters traditionally use to represent count precision [52]. The precision for the 5th category was determined from highly uncertain nest abundance estimates derived from satellite imagery [141]. Table C.1 shows the reported accuracy categories and their confidence intervals.

Reported accuracy	Reported 95% confidence interval
1	(95, 105)
2	(90, 110)
3	(75, 125)
4	(50, 150)
5	(20, 500)

TABLE C.1: Reported accuracy categories and their confidence intervals. For each category, if 100 nests was the true count then the 95% confidence intervals for each accuracy category's distribution was defined as described here.

We used the log-normal distribution to model the observation process, as all counts must be positive. However, the confidence intervals (with the exception of category 5) were symmetric around the true count and did not correspond to the skewed credible intervals generated by the log-normal distribution. To compute the appropriate scale parameters for each accuracy category, we defined a function that output the squared deviations between the upper and lower confidence interval (Table C.1) and the 0.975 and 0.025 quantiles from the cumulative density function for a log-normal distribution whose median was 100. We then used the optim function to select the scale parameter σ_o that minimized the sums of squares for each accuracy category.

Abundance process models

Nest abundance

For the purpose of clarity we build our nest abundance model in a series of steps, first modeling abundance on the arithmetic scale using the log-normal distribution. We then introduce a term to shift these distributions to the left as a corrective for biases that result when summing log-normal distributions, a step we explain more fully below. Finally, we re-express this model using logged abundance modeled normally and briefly discuss its equivalence to modeling abundance log-normally. Adopting the bracket notation from [78] for assigning group membership (for example, $R[35] = 2$ means that the 35^{th} unit in the data ($i = 35$) is from region 2), we start by modeling "true" (hereafter latent) nest abundance $z_{i,t}$ at the i_{th} breeding site located in region $R[i]$ in the t_{th} season as:

$$\log(z_{i,t}) \sim \text{student-t}(\mu_{i,t} = \log(z_{i,t-1}e^{r_i}), \sigma^2_{R[i]}, \nu_{R[i]}), \tag{C.2}$$

where the mean of the Student's t distribution, $\mu_{i,t}$, is a deterministic model for discrete exponential growth, such that nest abundance $z_{i,t}$ is the product of nest abundance in the previous season $z_{i,t-1}$ at the site and the intrinsic rate of growth, r_i. We model the intrinsic growth rate as just the regional mean $\gamma_{R[i]}$ (without site effects or seasonal effects):

$$r_i = \gamma_{R[i]}, \tag{C.3}$$

where gamma is modeled hierarchically as:

$$\gamma_{R[i]} \sim \text{normal}(0, \sigma^2_{region}) \tag{C.4}$$

In Equation C.2, $\sigma^2_{R[i]}$ represents process error, or the variation in logged latent nest abundance due to unmodeled biotic or abiotic processes not captured by the simple growth model embedded as the distribution's median.

Chick abundance

We modeled the latent chick abundance $zc_{i,t}$ at the i_{th} breeding site in the t_{th} season as:

$$zc_{i,t} \sim \text{binomial}(N_{i,t}, \alpha_{i,t}) \tag{C.5}$$

$$N_{i,t} = 2 \times \text{round}(e^{lz_{i,t}}) \tag{C.6}$$

$$\alpha_{i,t} \sim \text{beta}(a = 1.875, b = 1.125). \tag{C.7}$$

Pygoscelid penguins typically produce one chick per nest (the maximum number of chicks per nest is two), although breeding success can fluctuate considerably between sites and seasons. We use the well-informed priors $\mu = 0.5$, $\sigma^2 = 0.0625$ for $\alpha_{i,t}$, the proportion of chicks produced at the i_{th} site in the t_{th} season, to reflect observed variation in breeding success due to environmental and demographic stochasticity. Note that, when moment-matched, these priors result in a and b in Equation C.7.

Initial season abundance

We modeled the logged latent nest abundance at the i_{th} site (for the first season nest abundance was recorded, $t = I_i$) as:

$$lz_{i,t-1} \sim \text{normal}(lz_{i,t} - \gamma_{R[i]}, \sigma^2_{R[i]}) \tag{C.8}$$

This method of hindcasting was possible because the exponential growth function can be inverted, making hindcasting nest abundances functionally no different than forecasting nest abundances into the future or in seasons of missing data within a site's time series. For sites whose first season of data was 1970, hindcasting was unnecessary.

Observation process models

We modeled the logged observed nest counts y_{n_s} and chick counts y_{c_s} recorded at the i_{th} breeding site in the t_{th} season as:

$$y_{n_{i,t}} \sim \text{normal}(lz_{i,t}, \sigma^2_{n_{i,t}}) \tag{C.9}$$

$$y_{c_{i,t}} \sim \text{normal}(lz_{i,t}, \sigma^2_{c_{i,t}}) \tag{C.10}$$

where $\sigma^2_{n_{i,t}}$ and $\sigma^2_{c_{i,t}}$ are the observation errors in the recorded nest and chick count, respectively. These errors are computed from the accuracy ratings reported by the observer, the details of which are outlined in Section C.2.1. Here we model observations being drawn from a log-normal distribution whose median is $lz_{i,t}$, as over- and under-counts are equally likely. Note that sites can have both nest and chick counts in the same season.

C.2.3 Results

	mean	sd	95%_HPDL	95%_HPDU	Rhat	n.eff
	<dbl>	<dbl>	<dbl>	<dbl>	<dbl>	<dbl>
gamma[1]	-0.008	0.014	-0.037	0.021	1.01	4018
gamma[2]	-0.018	0.010	-0.039	0.002	1.01	1134
gamma[3]	-0.028	0.006	-0.040	-0.017	1.00	3525
gamma[4]	-0.332	1.569	-4.574	2.754	1.37	2802
gamma[5]	0.034	0.013	0.008	0.061	1.00	6626
gamma[6]	0.006	2.763	-5.226	5.411	1.00	7681
gamma[7]	0.010	0.011	-0.011	0.031	1.00	1594
gamma[8]	0.014	0.008	-0.001	0.030	1.00	7196
gamma[9]	0.015	0.016	-0.016	0.047	1.00	7500
gamma[10]	0.024	2.770	-5.567	5.202	1.00	7715
gamma[11]	0.027	2.755	-5.080	5.593	1.00	7500
gamma[12]	-0.006	0.088	-0.179	0.174	1.00	6851
gamma[13]	0.026	0.013	-0.001	0.049	1.00	3393
gamma[14]	-0.109	0.149	-0.425	0.193	1.00	5065
gamma[15]	-0.040	2.762	-5.377	5.487	1.00	7500
gamma[16]	0.008	0.017	-0.027	0.039	1.01	663
sigma[1]	0.078	0.066	0.007	0.220	1.02	108
sigma[2]	0.099	0.071	0.010	0.253	1.03	53
sigma[3]	0.145	0.014	0.118	0.172	1.00	898
sigma[4]	0.380	0.285	0.000	0.916	1.30	752
sigma[5]	0.210	0.031	0.146	0.270	1.00	1318
sigma[6]	0.504	0.288	0.054	1.000	1.00	7312
sigma[7]	0.181	0.057	0.064	0.293	1.01	152
sigma[8]	0.193	0.018	0.156	0.226	1.00	1748
sigma[9]	0.237	0.019	0.200	0.275	1.00	6001
sigma[10]	0.502	0.289	0.045	0.992	1.00	7781
sigma[11]	0.503	0.288	0.005	0.951	1.00	7500
sigma[12]	0.656	0.194	0.336	0.999	1.00	722
sigma[13]	0.176	0.050	0.083	0.279	1.04	271
sigma[14]	0.562	0.243	0.174	0.996	1.00	904
sigma[15]	0.500	0.292	0.034	0.984	1.00	7144
sigma[16]	0.084	0.029	0.036	0.147	1.01	994
nu[1]	30.634	20.728	1.518	71.652	1.00	7236
nu[2]	4.954	8.763	0.685	26.178	1.02	67
nu[3]	3.096	0.542	2.152	4.173	1.00	1390
nu[4]	20.042	21.935	0.105	63.240	1.73	5755
nu[5]	25.314	20.557	1.661	66.455	1.00	3360
nu[6]	28.323	21.353	0.051	69.676	1.00	7500
nu[7]	28.549	20.993	1.507	68.679	1.00	2584
nu[8]	20.858	17.118	2.769	56.903	1.00	3138
nu[9]	26.468	18.856	2.904	64.523	1.00	6984
nu[10]	28.192	21.240	0.054	69.847	1.00	7846
nu[11]	27.446	21.208	0.052	68.200	1.00	7468
nu[12]	29.186	20.962	1.068	70.054	1.00	5258
nu[13]	30.226	20.671	1.499	69.973	1.00	4779
nu[14]	28.564	20.992	0.448	69.295	1.00	5379
nu[15]	28.093	21.008	0.051	68.991	1.00	7500
nu[16]	27.153	20.534	0.628	68.154	1.00	4563

FIGURE C.3: Model summary tables for mean growth rate (γ_{R_i}), standard deviation (σ_{R_i}), and degrees of freedom (ν_{R_i}) of the Student's t distribution for abundance for ACBR R_i.