# Black-swan events in animal populations

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# Black-swan events in animal populations

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**Black swans are improbable events that nonetheless occur—often with profound consequences. Such events drive important transitions in social systems (e.g., banking collapses) and physical systems (e.g., earthquakes), and yet it remains unclear the extent to which ecological population numbers buffer or suffer from such extremes. Here, we estimate the prevalence and direction of black-swan events (heavy-tailed process noise) in 609 animal populations after accounting for population dynamics (productivity, density dependence, and typical stochasticity). We find strong evidence for black-swan events in ~4% of populations. These events occur most frequently for birds (7%), mammals (5%), and insects (3%) and are not explained by any life-history covariates but tend to be driven by external perturbations such as climate, severe winters, predators, parasites, or the combined effect of multiple factors. Black-swan events manifest primarily as population die-offs and crashes (86%) rather than unexpected increases, and ignoring heavy-tailed process noise leads to an underestimate in the magnitude of population crashes. We suggest modelers consider heavy-tailed, downward-skewed probability distributions, such as the skewed Student $t$ used here, when making forecasts of population abundance. Our results demonstrate the importance of both modeling heavy-tailed downward events in populations, and developing conservation strategies that are robust to ecological surprises.**

mass mortality | ecological surprises | population dynamics | die-offs | ecological risk

**M**ajor surprises (black-swan events) happen more often than expected in financial, social, and natural systems (1–5). Massive unpredictable market swings are responsible for the majority of financial gains and losses (3), fatalities from the largest wars dwarf those from all others (6), and the frequency of the most damaging earthquakes has exceeded past expectations (5). In ecological systems, background rates of global extinction are punctuated by mass extinction (7), evolution is characterized by long periods of stasis interrupted by bursts of speciation (8), and billions of animals can die at once in mass mortality events (9).

Indeed, such die-offs may be the most important element affecting population persistence (10) and their importance is likely to increase given projected increases in the frequency and magnitude of climate-related extremes (11). However, the overwhelming majority of population model-fitting and risk-forecasting assumes that deviations from model predictions can be represented by a normal distribution [on a log scale (e.g., refs. 12 and 13)]. If black swans occur, however, a normal distribution would underestimate the probability of extreme events occurring (3).

Whereas there are many reports of black-swan events, only a flexible comparative approach consistently applied to a large number of time series can yield insights into the frequency, strength, and correlates of such events. We are unaware of such a comparative analysis. Previous comparative analyses fitting heavy-tailed distributions (distributions with higher probabilities of extreme events than the normal distribution) to time series have not accounted for an underlying population dynamics model (14–17). Alternatively, most examples of population die-offs come from identifying sudden changes in abundance that

exceed a chosen threshold of decline (9, 18–20). However, this approach does not distinguish events from expected dynamics. For instance, the range of natural variability can differ dramatically across taxa.

Here, we develop an approach to estimate the frequency and magnitude of black-swan dynamics across time series of 609 populations from a wide array of taxonomic groups—including many birds, mammals, insects, and fishes (*SI Appendix*, Table S1). We identify characteristics of time series or life-history traits associated with the detection of black-swan events and verify known causes. We develop a framework for identifying heavy-tailed (black-swan) process noise in population dynamics. We test whether the largest stochastic jumps in log abundance from one time step to the next are more extreme than typically seen with a normal distribution. Our framework allows for a range of population dynamic models, can incorporate observation uncertainty and skewness in process noise, and can be readily applied to abundance time series.

We fit population dynamics models in which the process noise is drawn from a Student $t$ distribution. By estimating the degrees of freedom parameter, $\nu$, we can estimate the extent to which the process deviations have heavy tails and are therefore diagnostic of black-swan events (Fig. 1). Lower values of $\nu$ result in heavy-tailed distributions. For example, an event four SDs below the mean is expected to happen once every 35 y with a $t$ distribution at $\nu = 2$ compared with once every 32,000 y with a normal distribution. As $\nu$ approaches infinity, the $t$ distribution approaches the normal distribution (Fig. 1).

## Significance

**Black swans—statistically improbable events with profound consequences—happen more often than expected in financial, social, and natural systems. Our work demonstrates the rare but systematic presence of black-swan events in animal populations around the world (mostly birds, mammals, and insects). These events are predominantly downward, implying that unexpected population crashes occur more frequently than increases. Black-swan events are not driven by life history (e.g., lifespan) but by external causes such as extreme winters and disease. Ignoring the presence of downward black swans may severely underestimate extinction risk in animal populations, particularly under a changing climate, where such extreme events are expected to increase in frequency and magnitude.**

**Fig. 1.** Illustration of population dynamic models that allow for heavy tails. (*A* and *B*) Probability density for the Student *t* distribution with scale parameter of 1 and different values of $\nu$. Small values of $\nu$ create heavy tails, whereas as $\nu$ approaches infinity, the distribution approaches the normal distribution. (*C*–*E*) Simulated population dynamics from a Gompertz model with process noise drawn from Student *t* distributions with three values of $\nu$. Colored dots in *C* and *D* represent jumps with less than a 1 in 1,000 chance of occurring in a normal distribution. (*F*–*H*) Estimates of $\nu$ from models fit to the times series in *C*–*E*. Shown are posterior samples (histograms), median and interquartile range of the posterior (IQR) (dots and line segments), and the exponential prior on $\nu$ (dashed lines). Color shading in *F*–*H* illustrates the approximate region of heavy tails.

## Results

We detected black-swan dynamics most frequently for birds (7%), mammals (5%), and insects (3%) but almost never in fishes (Fig. 2). Black-swan events were taxonomically widespread, occurring in 38% of taxonomic orders. Accounting for time-series length and partially pooling inference across taxonomic class and order with a hierarchical model, we found stronger evidence for black swans in insect populations than these statistics suggest—two of five orders with the highest median probability of heavy tails were insect orders (Fig. 3*A*).

The majority of our heavy-tailed estimates were robust to alternative population models, observation error, and choice of Bayesian priors (*SI Appendix*). Our conclusions were not systematically altered when we included autocorrelation in the residuals, modeled population growth rates with or without density dependence, or modeled the population dynamics as Ricker-logistic instead of Gompertz (*SI Appendix*, Fig. S1). Similarly, introducing moderate observation error (coefficient of variation = 0.2) only slightly decreased the estimated prevalence of black-swan events (*SI Appendix*, Fig. S1), and the strength of the prior on $\nu$ had little influence on estimates of black-swan dynamics (*SI Appendix*, Fig. S2). Finally, our simulation testing shows that, if anything, our models underpredict the true magnitude and probability of heavy-tailed events—especially given that the time series are relatively short, with a median of only 26 y in our analysis (*SI Appendix*, Fig. S3 and S4).

For model fits to the population data, the probability of detecting black-swan dynamics was positively related to time-series length and negatively related to magnitude of process noise but not clearly related to population growth rate, density dependence, or maximum lifespan (Fig. 3*B* and *SI Appendix*, Fig. S5). Longer time-series length was the strongest covariate of observing black-swan dynamics: there is a 1.5-times greater probability of detecting a black-swan event in populations with 60 time steps than in one with 30 time steps (*SI Appendix*, Fig. S5).

The majority of black-swan events (86%) were downward (die-offs) rather than upward (unexpectedly rapid abundance increases). Of the black-swan events with published explanations (*SI Appendix*, Table S2), the majority involved a combination of factors. For example, a synchronization of environmental- and predation-mediated population cycles is thought to have caused a downward black-swan event for a water vole (*Arvicola amphibius*) population (21). Other black swans were the result of a sequence of extreme climate events on their own. For instance, severe winters in 1929, 1940–1942, and 1962–1963 were associated with black-swan downswings in gray herons (*Ardea cinerea*) in the United Kingdom (22) (Fig. 4*C*). Our analysis finds that the last event was a combination of two heavy-tailed events in a row and that the population took three times longer to recover than predicted (22). Downward black swans were sometimes followed by upward black swans. For example, during a period of population crowding and nest shortages, a population of European shag cormorants (*Phalacrocorax aristotelis*) on the Farne Islands, United Kingdom, declined suddenly following a red tide event in 1968 (23). This population decline freed up quality nest sites for first-time breeders, productivity increased, and the population experienced a rapid upswing in abundance (23).

Given the prevalence of downward events, we refit our heavy-tailed models to measure the degree of skewness $\gamma$ of the process noise using a skew-*t* distribution (Fig. 4*A*) and used these models to make near-term risk forecasts. Aggregated across populations with strong evidence of heavy tails (median $\nu < 10$), 86% of the $\gamma$ probability density was below 1, indicating strong evidence of downwardly skewed process noise (Fig. 4*B* and *SI Appendix*, Fig. S6). In contrast, populations that did not have heavy tails (median $\nu \geq 70$) had little evidence of skewed process noise (Fig. 4*B*; 89% of 95% credible intervals overlapped 1). Projecting these heavy-tailed populations forward 5 y revealed that assuming standard normal process noise underestimated risk (99% lower credible interval of abundance) by 1.2– to 1.9-fold (interquartile range; Fig. 4*C* and *SI Appendix*, Fig. S7).

## Discussion

We systematically evaluated the prevalence of black-swan events in hundreds of animal populations. We find strong evidence for the occurrence of black-swan events in animal populations. Black-swan population crashes are substantially more frequent than black-swan population increases and are usually driven by external events such as weather and disease. Thus, our analysis provides strong evidence for downward-skewed heavy-tailed events in abundance time series of higher taxa, and ignoring these events will tend to underestimate the risk of population declines. Next, we consider (*i*) the possible mechanisms underlying black-swan events,
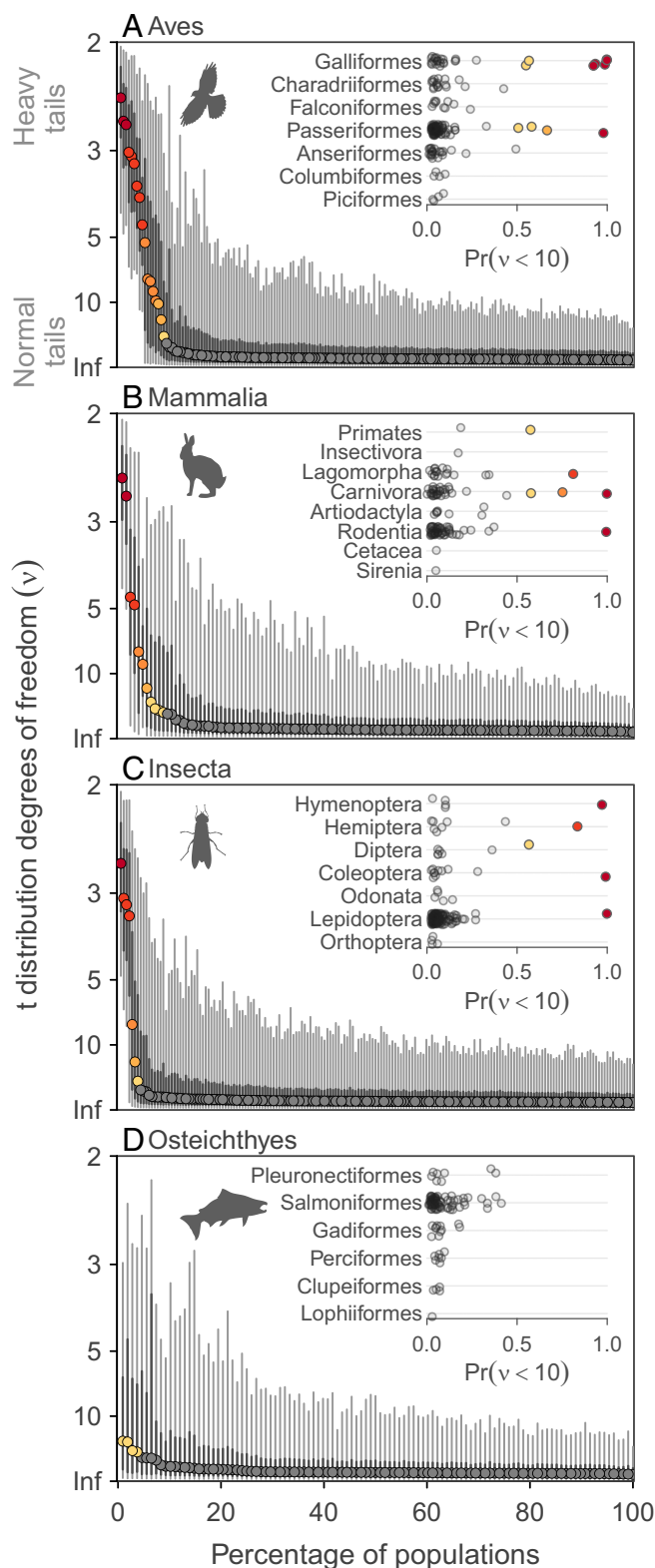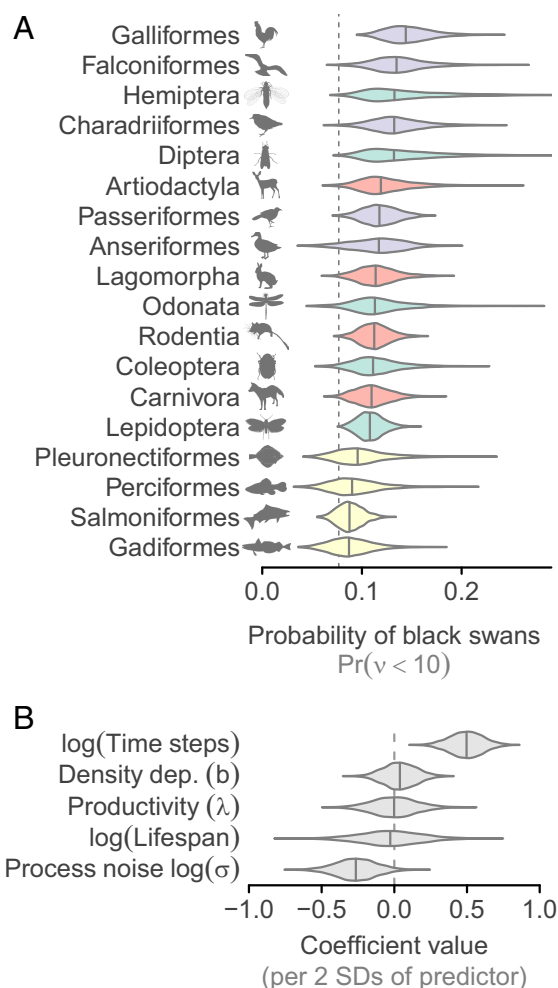
**Fig. 2.** Estimates of population dynamic heavy-tailedness for populations of birds, mammals, insects, and fishes. (*A–D*) Small values of $\nu$ suggest heavy-tailed black-swan dynamics. Vertical points and line segments represent posterior medians and 50%/90% credible intervals for individual populations. Inset plots show probability that $\nu < 10$ for populations arranged by taxonomic order and sorted by decreasing mean Pr($\nu < 10$). Taxonomic orders with three or fewer populations in *A* are omitted for space. Red to yellow points highlight populations with a high to moderately high probability of heavy-tailed dynamics. Silhouettes in *A–C* from phylopic.org; credits in *SI Appendix*.

(*ii*) caveats to our findings, (*iii*) the consequences of our findings for making risk forecasts, and (*iv*) for managing natural resources.

There are many possible causes of black-swan events, including unmodeled intrinsic properties of populations or extrinsic forces acting on populations. For example, we could have observed black-swan dynamics if we missed an underlying mixture of processes, because a mixture of normal distributions with different variances can generate a $t$ distribution with heavy tails (24). In ecology, these processes could arise through an aggregation of populations across space, population diversity (25), or an intrinsic change in population variability through time (26). Extrinsic ecological forces could also cause black-swan dynamics (27) including extreme climate events (11, 28, 29), predation from (or competition with) other species experiencing black-swan events, or sharp changes in human pressures such as fishing or habitat destruction. Alternatively, the synchrony of multiple extrinsic forces could give rise to black-swan dynamics through synergistic interactions (30) or a rare alignment of nonsynergistic forces (31). The prevalence of population die-offs rather than unexpected increases is likely due to biology: there is no limit to how fast a population can decline due to a catastrophe, but population increases are constrained by the maximum biological rate of increase for a given set of demographic traits (e.g., population birth rate, mortality, and age at maturity).

There are a number of caveats when considering the generality of our results. First, the Global Population Dynamics Database (GPDD) [Version 2 (2010); Natural Environment Research Council Centre for Population Biology, Imperial College London] that we used represents a taxonomically and geographically biased sample of populations—the longer time series we focused on are dominated by commercially and recreationally important species and a disproportionate number of populations are located in the United Kingdom. Although we would expect to find qualitatively similar evidence for black swans in other large taxonomic or geographic samples of populations, the common forces driving those black swans would likely differ. Second, some apparent black-swan events could be recording mistakes, although conversely, some extreme observations may have been discarded or altered if they were erroneously suspected of being recording mistakes. Indeed, we discarded three of the populations that our method initially identified as heavy-tailed because they turned out to be data-entry errors (*SI Appendix*). Third, the temporal scales of observation and population dynamics vary considerably across populations in the GPDD, and these likely influence the detection of heavy tails. For example, if we make frequent observations relative to generation time (e.g., for many large-bodied mammals), we will average across generations and perhaps miss black-swan events. Conversely, if we census populations infrequently relative to generation time (e.g., many insects in the GPDD), the recorded data may average across extreme and less-extreme events and also dampen black-swan dynamics. Finally, our models assume that the fitted parameters (e.g., productivity and density dependence) do not vary over time. Allowing for time-varying parameters could be an important development for understanding the dynamics of longer time series.

Given our results, we suggest modelers should routinely consider representing population dynamic process noise with a heavy-tailed, and possibly downward-skewed, distribution, especially when making forecasts to evaluate risk. However, what heavy-tailed distribution should one pick and how heavy-tailed should it be? This is an open research question. The exact shape of the tails has proven important in the field of dispersal biology (32, 33). Answers for the field of population dynamics might come from simulation analyses exploring the implications of tail shapes and from comparing the relative fit of heavy-tailed population models to time series with suspected mass mortality events

**Fig. 3.** Standardized probabilities and covariates of heavy-tailed dynamics. (*A*) Taxonomic-order-level posterior densities of $\Pr(\nu < 10)$ after accounting for time-series length in a hierarchical model. The dotted vertical line in *A* indicates the median expected $\Pr(\nu < 10)$ from the prior distribution. The color shading refers to taxonomic class (yellow: fishes; green: insects; purple: birds; and red: mammals). Estimates are standardized at the geometric mean of time-series length across all of the data (~27 time steps) and shown for orders with $\geq 5$ populations. (*B*) Posterior densities for potential covariates of $\Pr(\nu < 10)$. In both *A* and *B*, short vertical line segments within the density polygons indicate medians. All silhouettes (except Salmoniformes) from phylopic.org; credits in *SI Appendix*.

[e.g., the $t$ distribution compared with a mixture of two normal distributions (34)]. Nevertheless, our proposed $t$ (or the skew $t$) distribution is a simple and elegant solution that can be easily substituted for the normal distribution. Furthermore, if the degrees of freedom parameter ($\nu$) is fixed, it requires estimating no more parameters than the normal distribution. Barring a better estimate, we suggest using $\nu = 5$ and a skewness parameter ($\gamma$) of 0.7 (Fig. 4*A*) if a modeler wishes to allow for downward heavy-tailed events. These are midrange values from the populations identified as heavy-tailed here. Above $\nu = 10$, the $t$ distribution closely resembles the normal distribution, and compared with the normal distribution, $\nu = 5$ allows for an event three SDs below the mean to happen once every 66 y instead of once every 740 y. Adopting heavy-tailed process noise by default follows the intuition that our models are usually reasonable but occasionally very wrong.

In light of our findings, we suggest that natural resource management can learn from disciplines that focus on heavy tails. For example, earthquake preparedness and response is focused on black-swan events. Similarly to ecological black swans, we can rarely predict the specific timing of large earthquakes. However, earthquake preparedness involves spatial planning based on forecast probabilities to focus early detection efforts and develop disaster-response plans (35). The presence of ecological black swans also suggests that we develop management policy that is robust to heavy tails and encourages general resilience (36). For instance, setting target population abundances far back from critical limits may buffer against black-swan events (37), and maintaining genetic, phenotypic, and behavioral diversity may allow some components of populations to persist when others are affected by disease or extreme environmental forces (25). Finally, surprising, or counterintuitive, ecological dynamics offer a tremendous opportunity to learn about ecological systems, evaluate when models break down, and adjust future management policy (38, 39).

Rare catastrophes can have a profound influence on population persistence (10). In recent decades, ecology has moved toward focusing on aspects of variance in addition to mean responses (40). Our results suggest that an added focus on ecological extremes represents the next frontier, particularly in the face of increased climate extremes (11, 28, 40). Financial analysts are concerned with the shape of downward tails in financial returns because these directly impact estimates of risk—the probability of a market crash occurring. Similarly, ecologists should focus more on estimating and predicting downward tails of population abundance, because these may increase true extinction risk.

## Materials and Methods

**Data.** We selected abundance time series from the GPDD, which contains nearly 5,000 time series of abundance from ~1,000 species and ~100 taxonomic orders. We filtered the data (*SI Appendix*) to remove populations



**Fig. 4.** Heavy-tailed process noise tends to be downward skewed and ignoring this tendency can underestimate risk. (*A*) Illustrations of Student $t$ distributions with three levels of skewness ($\gamma$) and heavy-tails ($\nu$). (*B*) Posterior density of the skewness parameters aggregated across populations grouped into heavy-tailed ($\hat{\nu} < 10$), slightly heavy-tailed ($10 \leq \hat{\nu} \leq 70$), and normal-tailed populations ($\hat{\nu} > 70$). Approximate midvalues from *B* are illustrated in *A*. (*C*) Example time series of heavy-tailed populations with different levels of skewness. Red dots highlight likely heavy-tailed events. Forecasts (gray regions) show median (solid lines) and lower 99% credible intervals (dotted lines) of abundance. Black and red lines indicate forecasts from Gompertz models with lognormal and skew-$t$ process noise, respectively.

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from less reliable data sources, and those without sufficient data for our models, and then interpolated remaining missing values (sensu ref. 12). Our interpolation affected only ~1% of the final data points (*SI Appendix*, Table S1) and none of the data points that were later considered black-swan events. Our final dataset contained 609 populations across 39 taxonomic orders and 7 taxonomic classes, with a median of 26 time steps (range, 20–117) (*SI Appendix*, Table S1).

**Modeling Framework.** We fit heavy-tailed Gompertz population dynamics models to data from the GPDD. The Gompertz model represents population growth as a linear function in log space (here and throughout we use log to refer to the natural logarithm). If $x_t$ represents the log abundance ($N$) at time $t$, then

$$x_t = \lambda + bx_{t-1} + \epsilon_t,$$ [1]

$$\epsilon_t \sim \text{Student } t(\nu, 0, \sigma).$$ [2]

The parameter $\lambda$ represents the expected growth rate if $N_t = 1$. The model is density-independent if $b = 1$, maximally density-dependent if $b = 0$, and inversely density-dependent if $b < 0$. Usually, the process noise $\epsilon_t$ is modeled as normally distributed, but we allow it to be drawn from a Student $t$ distribution with scale parameter $\sigma$ and degrees of freedom $\nu$. We can then estimate the degree to which the process deviations have heavy tails (i.e., heavier tails than the lognormal distribution) and are therefore evidence of black-swan events (Fig. 1A and B).

We chose the $t$ distribution for a number of reasons. Pragmatically, the $t$ distribution requires the estimation of only one additional parameter over the normal distribution and reverts to the normal distribution if evidence of heavy-tailed process deviations is absent. Furthermore, the $t$ distribution arises from a mixture of normal distributions with the same mean and different variances (24), which mimics the underlying basis for black-swan events. There are a wide range of mechanistic processes that could give rise to extreme events in population dynamics, such as extreme climate events (11, 28, 29) or sudden changes in predation from other species. Although evaluating these various hypotheses would be important for diagnosing the underlying causes of extreme events and to develop predictive models, it would be impossible to tease out each of these underlying causes from population trend data alone. Instead, we seek a simple flexible phenomenological model that can be applied across the widest possible range of population time series to provide a comparative overview of the prevalence of black-swan events.

One alternative approach would involve fitting the generalized extreme value (GEV) distribution, which represents the limit distribution of a series of maxima or minima. Although the GEV is well-suited for environmental variables [e.g., sedimentation rates or wind speeds (31, 41)], the GEV requires maxima per time block. Therefore, the GEV requires longer or higher frequency time series than typically available for wild animal population abundance. Furthermore, to our knowledge, the GEV cannot be easily integrated into population dynamics models.

For the Gompertz model, we chose weakly informative priors for all parameters (*SI Appendix*, Fig. S8). For the degrees of freedom parameter $\nu$, we chose an exponential prior with a rate parameter of 0.01 truncated at values above 2—a slightly less informative prior than suggested by ref. 42. We truncated the distribution at 2 because below 2, there can be issues with computational stability. This prior gives only a 7.7% probability that $\nu < 10$ but constrains the sampling sufficiently to avoid $\nu$ drifting toward infinity. In any case, for $\nu > 20$, the $t$ distribution is almost indistinguishable from the normal distribution (Fig. 1). Based on the shape of the $t$ distribution, we chose the probability that $\nu < 10$, Pr($\nu < 10$), to define the probability of heavy-tailed (black-swan) dynamics. When categorizing a population as heavy-tailed, we applied a 0.5 probability threshold. The data must therefore alter the posterior so that more than 50% of the posterior probability has $\nu < 10$ for a population to be declared heavy-tailed. If the data are uninformative about heavy tails (e.g., Fig. 1E and H), and the population model is otherwise a reasonable representation of the dynamics, the posterior for $\nu$ will approximately match the prior (prior median = 71, mean = 102), and a metric of Pr($\nu < 10$) > 0.5 will not flag any populations as heavy-tailed.

We fit our models with Stan 2.14.1 (43–45) and R 3.3.1 (46). We began with four chains and 2,000 iterations, discarding the first 1,000 as warmup. If $\hat{R}$ (the potential scale reduction factor—a measure of chain convergence) was greater than 1.05 for any parameter, or if the minimum effective sample size, $n_{\text{eff}}$ (a measure of the effective number of uncorrelated samples), for any parameter was less than 200, we doubled both the total iterations and warmup period and sampled from the model again. In the majority of cases our minimum thresholds were greatly exceeded. We continued this

procedure up to 8,000 iterations, by which point all chains had sufficiently converged.

**Alternative Models and Simulation Testing.** We fit alternative population models to test if four key phenomena systematically changed our conclusions. Autocorrelation has been suggested as a reason for increased observed variability of abundance time series through time, which could create apparent heavy tails (47); therefore, we fit a model that included serial correlation in the residuals. Additionally, previous work has modeled abundance or growth rates without accounting for density dependence (16, 17); therefore, we fit a simpler model in which we assumed density independence. This model is equivalent to a random walk with drift on log abundance and therefore does not assume that the time series is stationary. Third, observation error could bias parameter estimates (13) or mask our ability to detect heavy tails (34); therefore, we fit a model where we allowed for a fixed quantity of observation error (0.2 SD on a log scale). Fourth, the Gompertz model assumes that population growth rate declines linearly with log abundance. Therefore, we also fit an alternative model, the Ricker logistic model, which assumes that population growth rate declines linearly with abundance (*SI Appendix*).

We investigated the sensitivity of our results to weaker and stronger priors (exponential rate parameter = 0.005, 0.02) and alternative priors (*SI Appendix*, Fig. S8). Furthermore, we used simulated data to test how easily we could detect $\nu$ given different sample sizes and to ensure we could recover unbiased parameter estimates from the Gompertz model (*SI Appendix*).

**Covariates of Heavy-Tailed Dynamics.** We fit a hierarchical beta regression model to the predicted probability of heavy tails, Pr($\nu < 10$), to investigate potential covariates of heavy-tailed dynamics. We obtained maximum lifespan and body-size data from ref. 12 for species from 568 of the 609 populations. Beta regression is useful when response data are on a continuous scale between 0 and 1 (48). The model was as follows:

$$\Pr(\nu_i < 10) \sim \text{Beta}(A_i, B_i)$$
$$\mu_i = \text{logit}^{-1}(\alpha + \alpha_{j[i]}^{\text{class}} + \alpha_{k[i]}^{\text{order}} + \alpha_{l[i]}^{\text{species}} + \mathbf{X}_i\beta),$$
$$\text{for } i = 1, \dots, 568$$
$$A_i = \phi_{\text{disp}}\mu_i$$
$$B_i = \phi_{\text{disp}}(1 - \mu_i)$$
$$\alpha_j^{\text{class}} \sim \text{Normal}(0, \sigma_{\alpha\,\text{class}}^2), \text{for } j = 1, \dots, 6$$
$$\alpha_k^{\text{order}} \sim \text{Normal}(0, \sigma_{\alpha\,\text{order}}^2), \text{for } k = 1, \dots, 37$$
$$\alpha_l^{\text{species}} \sim \text{Normal}(0, \sigma_{\alpha\,\text{species}}^2), \text{for } l = 1, \dots, 259,$$

where $A$ and $B$ represent the beta distribution shape parameters; $\mu_i$ represents the predicted value for population $i$, class $j$, order $k$, and species $l$; $\phi_{\text{disp}}$ represents the dispersion parameter; and $\mathbf{X}_i$ represents a vector of predictors (such as lifespan) for population $i$ with associated $\beta$ coefficients. The intercepts are allowed to vary from the overall intercept $\alpha$ by taxonomic class ($\alpha_j^{\text{class}}$), taxonomic order ($\alpha_k^{\text{order}}$), and species ($\alpha_l^{\text{species}}$) with SDs $\sigma_{\alpha\,\text{class}}$, $\sigma_{\alpha\,\text{order}}$, and $\sigma_{\alpha\,\text{species}}$. Where possible, we also allowed for error distributions around the predictors by incorporating the SD of the posterior samples for the Gompertz parameters $\lambda$, $b$, and $\log \sigma$ around the mean point value as normal distributions (not shown in the above equation).

We log-transformed $\sigma$, time-series length, and lifespan to make the relationship approximately linear on the logit-transformed response scale; this transformation matches the way the predictors are visually presented in *SI Appendix*, Fig. S5. All input variables were standardized by subtracting their mean and dividing by two SDs to make their coefficients comparable in magnitude (49). We excluded body length as a covariate because it was highly correlated with lifespan, and lifespan exhibited more overlap across taxonomy than body length. Lifespan is also more directly related to time and potential mechanisms driving black-swan dynamics.

We incorporated weakly informative priors into our model: Cauchy(0,10) on the global intercept $\alpha$, half-Cauchy(0, 2.5) on all SD parameters, half-Cauchy(0,10) on the dispersion parameter $\phi_{\text{disp}}$, and Cauchy(0, 2.5) on all other parameters (50, 51). We fit our model with 2,000 total iterations per chain, 1,000 warmup iterations, and four chains. We checked for chain convergence visually and with the same criteria as before ($\hat{R} < 1.05$ and $n_{\text{eff}} > 200$ for all parameters). Furthermore, we checked our model against a similar maximum likelihood model fit with the glmmADMB R package (52) without uncertainty around the predictors.

To derive taxonomic-order-level estimates of the probability of heavy tails accounting for time-series length (Fig. 3A), we fit a separate hierarchical model with the same structure but with only log time-series length as a

predictor—in this case, we did not want to control for intrinsic population characteristics such as density dependence. Because our predictors were centered by subtracting their mean value, we obtained order-level estimates of the probability of heavy tails at mean log time-series length by adding the posteriors for $\alpha$, $\alpha_j^{class}$, and $\alpha_k^{order}$.

**Skewed Student $t$ Forecasts.** To evaluate the apparent skewness of heavy-tailed process noise, we fit Gompertz models with skewed Student $t$ distributed process noise (42). This distribution adds one parameter to the Student $t$ distribution, $\gamma$, which controls the skewness. The distribution is symmetrical if $\gamma = 1$, left-skewed if $0 < \gamma < 1$, and right-skewed if $1 < \gamma < \infty$. We placed a weakly informative prior of Cauchy(0, 2.5) on $\log \gamma$. We aggregated 5,000 randomly selected posterior samples from the $\gamma$ parameter of each model at three levels of evidence for heavy tails: heavy-tailed, median $\nu < 10$; slightly heavy-tailed, $10 \leq$ median $\nu \leq 70$; and normal-tailed, median $\nu > 70$ (Fig. 4).

To generate 5-y forecasts of abundance, we combined the posterior parameter samples from the skewed $t$ Gompertz models with stochastically generated process noise. We compared these forecasts to those generated by a standard Gompertz model with normally distributed process noise fit to the same data. We calculated the ratio of the lower 99% quantile credible interval between the two model projections for all populations in which $Pr(\nu < 10) > 0.5$. To ensure the results had stabilized in the tails of the forecast posterior, we increased the number of posterior samples in Stan. We ran four chains of 20,000 iterations and discarded the first 10,000 as warmup. We then generated 5 sets of future stochastic process deviations for each sample for a total of 200,000 forecast samples per population.

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