Impacts of changing rainfall regime on the demography of tropical birds

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Biodiversity in tropical regions is particularly high and may be highly sensitive to climate change[1,2]. Unfortunately, a lack of long-term data hampers understanding of how tropical species, especially animals, may react to projected environmental changes. The amount and timing of rainfall is key to the function of tropical ecosystems and, although specific model predictions differ[3,4], there is general agreement that rainfall regimes will change over large areas of the tropics[5,6]. Here, we estimate associations between dry season length (DSL) and the population biology of 20 bird species sampled in central Panama over a 33-year period. Longer dry seasons decreased the population growth rates and viability of nearly one-third of the species sampled. Simulations with modest increases in DSL suggest that consistently longer dry seasons will change the structure of tropical bird communities. Such change may occur even without direct loss of habitat—a finding with fundamental implications for conservation planning. Systematic changes in rainfall regime may threaten some populations and communities of tropical animals even in large tracts of protected habitat. These findings suggest the need for collaboration between climate scientists and conservation biologists to identify areas where rainfall regimes will be able to plausibly maintain wildlife populations.

The resilience of wildlife populations to climate change will be determined by their ability to cope with novel physical and ecological conditions[7,8]. Species with wide physiological tolerances or behavioural plasticity will probably persist or even thrive in altered environments; others will undergo changes in their distribution, adapt *in situ*, or experience widespread extirpation and possible extinction[9,10]. Species and biological systems at tropical latitudes may be especially vulnerable to environmental changes; tropical organisms are thought to be less resilient than temperate-zone species owing to their evolutionary histories in environments that are comparatively aseasonal and predictable[2,11]. Even moderate changes in conditions might exert novel challenges that cannot be modulated through behavioural or physiological responses[11]. Given that few studies on climate change have focused on the tropics[12], we know little about what to expect where biodiversity is greatest and potentially the most sensitive to pending climate change.

The most significant direct effects of climate change on terrestrial systems in the tropics may result from changes in rainfall regime[13–15]. Whereas future trends in precipitation outside of the tropics are also expected to be influential[16,17], the biology of tropical systems is especially sensitive to the amount and timing of annual rainfall. Studies of plants indicate that both annual rainfall and the timing of rain govern the productivity, physiognomy, and diversity of

tropical forests[18,19]. For example, in years with otherwise average total rainfall, prolonged dry seasons leading to more intense short-term drought can result in significant changes in flower, fruit and seed production[20]. Longer droughts (that is, >2 years) in the Neotropics and Palaeotropics have led to changes in the structure and floristic composition of tropical forests owing to the selective mortality of tree species[14].

How altered precipitation regimes will affect tropical animal populations and communities is uncertain[21]. Efforts to date have focused on potential changes in geographic distributions and vulnerability of populations based on present ranges, estimates of global population sizes, and species' associations with bioclimatic variables[9,21]. Although these population models are helpful and have found that rainfall alters species occupancy and distribution, understanding associations between vital demographic rates and environmental conditions is crucial for predicting the viability of tropical species in a changing world[22]. Few long-term population studies have characterized demographic changes in tropical species in response to different environmental conditions and this hampers efforts to predict changes in tropical populations and inform conservation policy.

Here, we report the first analyses of associations between rainfall regime and the demography of a multispecies sample of Neotropical forest birds. Using capture–mark–recapture data from a 33-year field study, we estimated annual rates of population growth (lambda, λ) for a suite of 20 species characteristic of the forest understorey in the moist lowlands of central Panama. Lambda combines annual adult survival and recruitment of offspring into the adult population and is an essential measure for understanding the ecology and viability of populations[22]. To assess how avian demography co-varies with annual variation in rainfall regime, we examined the length of the preceding dry season (DSL), which will probably increase in many tropical regions[6], including Panama. DSL directly influences the phenology and duration of avian reproductive activity (commonly beginning with the onset of rains), the availability of essential resources for birds[23], and the distribution of tropical tree species[18]. We also explored differential sensitivity among species to variation in DSL by assessing traits such as body mass and feeding behaviour. Finally, we modelled the effect of a future increase in DSL on the relative abundances of species and understorey community structure by taking our field-based estimates and simulating the effects of increased seasonal drought over the next 50 years.

Estimates of λ, averaged over the entire sampling period, were close to 1.0 for all 20 focal species (Supplementary Table 1), and we found no evidence of trends during the sampling period; this is expected for established populations that are not subject to

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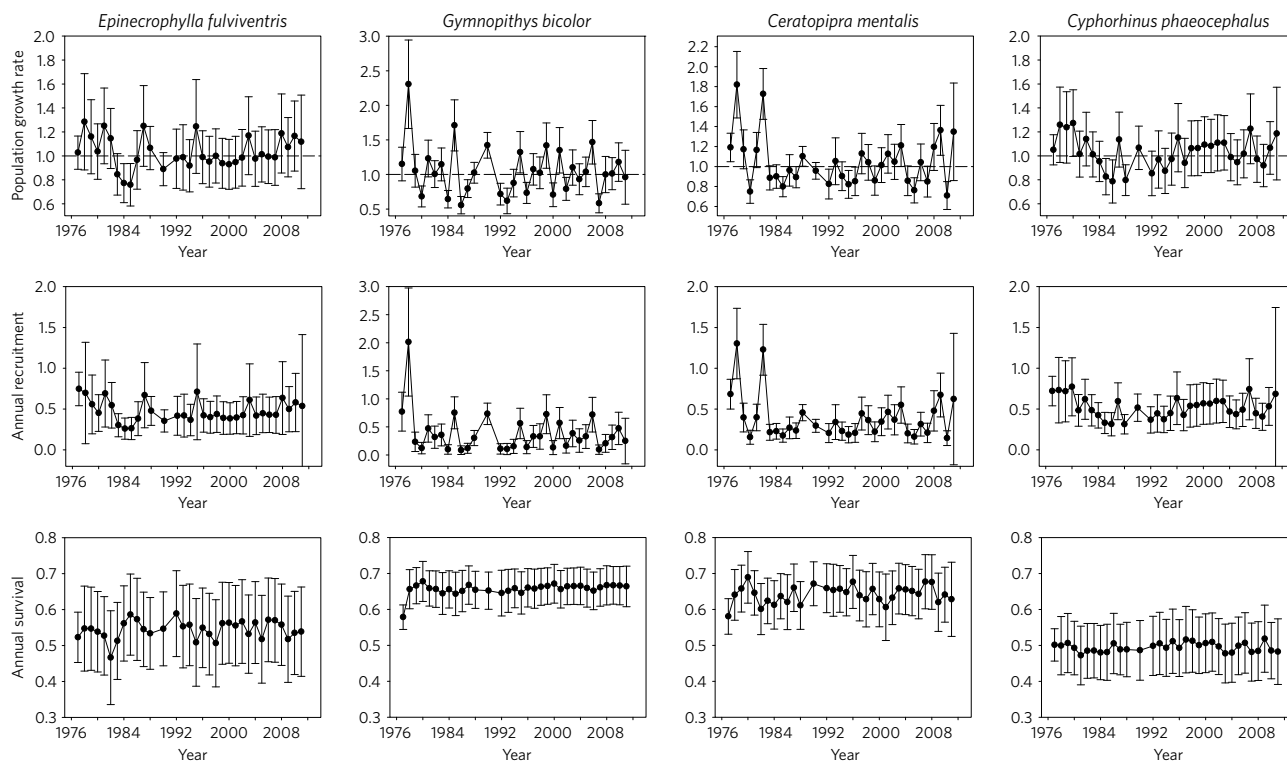
Figure 1 | Patterns of temporal variation in demographic parameters from 1977 through 2011 for species representing each of four species groups based on general foraging behaviour and diet. *Epinecrophylla fulviventris* for above-ground insectivore, *Gymnopithys bicolour* for ant-following insectivore, *Ceratopipra mentalis* for frugivore/granivore, and *Cyphorhinus phaeocephalus* for ground insectivore. Shown are median values and 95% credible intervals for parameter estimates based on posterior distributions of capture–mark–recapture data modelled with Bayesian Markov chain Monte Carlo analyses.

major environmental perturbation. Although the average values of λ indicated that the focal populations were stable over decadal periods, temporal variation was evident in species such as *Gymnopithys bicolor* (an ant-following insectivore) in which λ ranged from 0.55 to 2.3 with a coefficient of variation of 34% over the 33-year sampling period. In contrast, population growth rates of *Terenotriccus erythrurus*, a small flycatcher that forages in the forest understorey, varied little (CV = 1.5%). Overall, λ varied substantially over time (that is, CV > 15%) in one-fourth of the focal species (Supplementary Table 1). The magnitude of variation in recruitment over time was commonly more than that found in annual survival rates (Fig. 1 and Supplementary Table 1). For example, estimated annual survival in *Ceratopipra mentalis*, a frugivore, ranged from 0.58 to 0.70 with a coefficient of variation of 4% over 33 years whereas per capita recruitment ranged from 0.14 to 1.3 with a coefficient of variation of 70%.

Dry seasons in central Panama typically go from late December through April and often extend during severe El Niño/Southern Oscillation events, which occurred twice during the study (1983 and 1998). DSL in central Panama did not trend longer or shorter during the sampling period but did vary from 98 to 179 d (Fig. 2, average = 136 d, s.d. = 21.1), and provided a basis for assessing associations between variation in the intensity of seasonal drought and interannual variation in demography of the focal species. We considered the possibly confounding effect of temperature but found no relationship between DSL and average daily temperature and average daily maximum or minimum temperatures (Supplementary Fig. 1).

Estimated impacts of the duration of the preceding dry season on population growth were negative for 15 of the 20 species considered (Fig. 3a). Bayesian credible intervals (95%) for the effect of DSL on λ did not include 0 for six species, thus providing strong evidence that extended seasonal drought exerts negative effects on the population
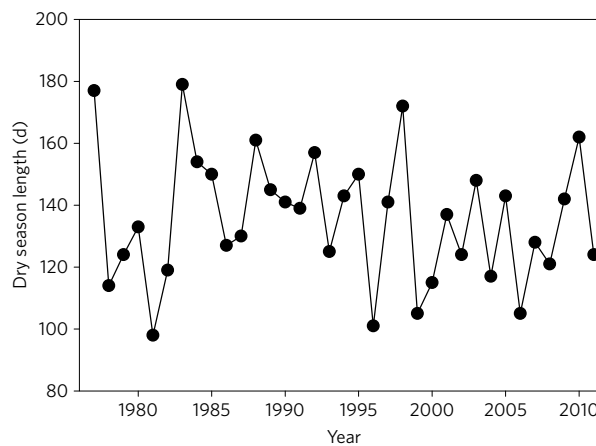

Figure 2 | Length of dry season (DSL) in central Panama (1977–2011).

viability of nearly one-third of the species we sampled. Growth rates in one species, *Sclerurus guatemalensis*, did appear to increase with longer dry seasons but the 95% credible interval around the estimated regression slope did not intersect 0.

Longer dry seasons influenced annual apparent survival rate and annual per capita recruitment differently (Fig. 3b,c). Only one species (*Terenotriccus erythrurus*) exhibited significantly lower adult survival rates following longer dry seasons, but evidence for the effect of DSL on annual recruitment into the sampled populations was more compelling. The estimated regression coefficients were negative in 15 species, of which 4 had 95% credible intervals that did not include 0.

The impact of DSL on populations of the focal species was not substantially influenced by body mass (estimated
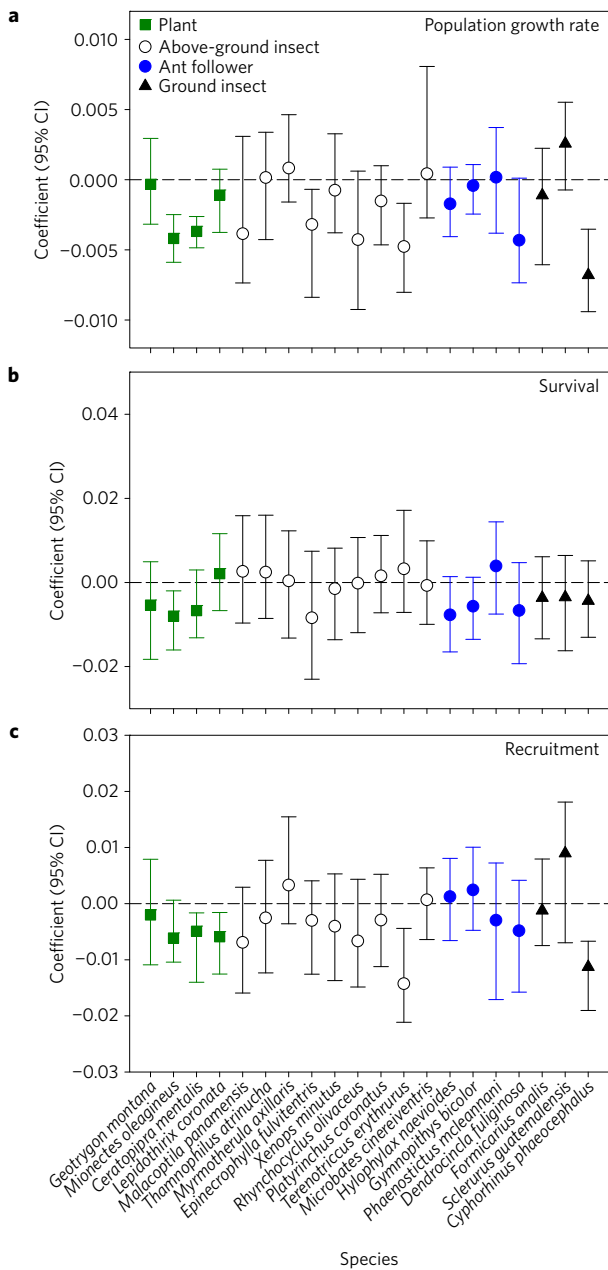
Figure 3 | Estimated regression (beta) coefficients characterizing associations between length of previous dry season and estimated demographic parameters. Each coefficient is a median value with 95% credible interval based on posterior distributions modelled with Bayesian Markov chain Monte Carlo analyses. **a**, Coefficients for population growth rates or λ. **b**, Coefficients for annual survival rates. **c**, Coefficients for annual rates of recruitment into sampled populations.
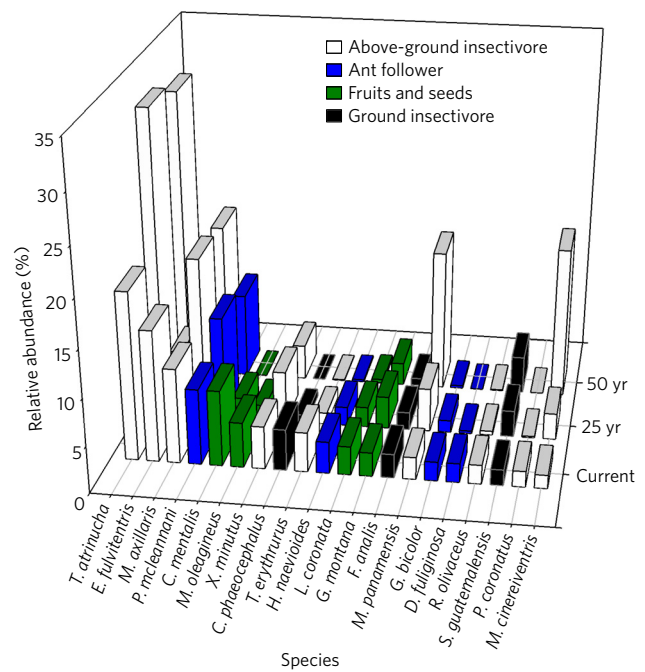

Figure 4 | Results of stochastic simulations depicting changes in relative abundances (percentage of total) of 20 species over 25 and 50 years subsequent to 10% increase in length of dry season. Species are ordered by rank abundance with current numbers based on field censuses of birds where mark–recapture sampling was conducted[31].

coefficient $= 0.00003$, s.e. $= 0.001$, $t = 1.4$, d.f. $= 7$, $p = 0.21$) and phylogenetic or taxonomic relationships had little effect (see Supplementary Table 2 and Supplementary Figs 2 and 3). We found more compelling evidence for the effect of feeding guild as the effect size for the fruit- and seeding-eating guild indicated a significant negative association between DSL and λ (estimated coefficient $= -0.0038$, s.e. $= 0.001$, $t = -3.84$, d.f. $= 8$, $p = 0.005$, see Supplementary Table 2 for complete results).

Stochastic simulations suggest that even modest changes in DSL could quickly result in what has been termed 'community disassembly'[24]. We simulated the effects of a 10% increase in average DSL over a 50-year period, which is within one standard deviation of the average DSL during the sampling period and plausible by current estimates[3]. Our simulations did not include constraints in population growth such as density dependence or interspecific competition nor did they allow for the possibility of recolonization following a local extirpation.

Longer DSL simulated over 50 years shifted the relative abundances of 15 of the 20 focal species (Fig. 4). Among the species whose relative abundances changed noticeably, four became locally extirpated and five increased. We note that in real biological systems other species could move into the community; therefore, although changes in community structure seem plausible, species richness may not necessarily decrease. Species that consume fruits and seeds and certain insectivores that forage on the forest floor were the most prone to simulated decreases. Insectivores that forage above the ground tended to increase.

Conjecture about the sensitivity of tropical species and their ability to cope with environmental change was initially framed in a biogeographic framework whereby topographic features such as mountain passes presented barriers to dispersal[2]. Today, the implications of this hypothesis are far more extensive and motivate serious concern about the ability of tropical species to cope with climate change. Similar analyses for other species and tropical regions are certainly needed to assess the generality of our results. Nonetheless, results here are derived from what we believe to be the longest-term population study of birds in the mainland Neotropics. Our results augment recent evidence that precipitation strongly influences the distribution of tropical endotherms[9]. Clearly, the demography and viability of tropical bird populations can be highly reactive to the changes in rainfall regime that are predicted throughout large portions of the Neotropics and Palaeotropics.

Shifting precipitation patterns might alter habitat suitability for tropical species independently of habitat loss or habitat fragmentation. This suggests that preserving large tracts of forest may not be sufficient to conserve many tropical bird species. Our focal species are relatively common in the lowland forests of central

Panama, are not generally recognized as species of concern by conservation organizations, and we sampled in a large tract of land (25,000 ha). Yet, we still saw declines in their populations in response to longer dry seasons. If more intense seasonal drought poses a potential threat for many of these focal species, the challenge of altered rainfall regimes for rare or declining species may be more drastic. Although the effects of climate change may be even more profound in fragmented habitat[25], our results indicate that tropical biota are negatively impacted by climate change even in the context of large, conserved tracts of forest. Changes in local avifaunas would probably place added stress on tropical forests as birds and other animal species provide key ecosystem services such as seed dispersal and protection from herbivorous insects[26,27].

The predicted impact of climate change on biodiversity is often evaluated with species distribution models constructed under different climate scenarios[28]. The extent and location of regions where conditions are expected to be suitable for focal species informs estimates of extinction risk and can help to identify priority areas for conservation[21]. Plausible changes in DSL have been reported for the Neotropics and Palaeotropics[29] and our study emphasizes the use of this information for predicting the future status of tropical species.

Models predicting the locations of 'precipitation refugia' have been established for the arid regions of Australia[30]; our analyses emphasize the value of similar efforts for the moist tropics. Certain tropical regions are likely to experience drying trends and others may get wetter[4]. Close communication between biologists and climate modellers and far more information on the demography and ecology of resident animal species will greatly improve predictions concerning future changes in wildlife populations. The direct effects of changes in temperature also merit investigation. Although there is much to learn, our results provide new evidence that tropical rainforests may function and sound dramatically different in coming decades.

Methods

Methods, including statements of data availability and any associated accession codes and references, are available in the online version of this paper.

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Author contributions

J.D.B. designed the project, conducted fieldwork, and contributed to the comparative analyses; C.E.T. conducted field sampling; T.J.B. contributed the demographic analyses and designed the simulations; M.S. and N.D.S. contributed the comparative analyses; J.D.B., T.J.B. and C.E.T. wrote the paper. All authors provided intellectual input, and read and approved the manuscript.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to J.D.B.

Competing financial interests

The authors declare no competing financial interests.

Methods

Field sampling and study sites. Field sampling was conducted from 1977 to 2011 in central Panama in moist lowland forest that varies in age from 60 to about 400 years old within Parque Nacional Soberania, a park comprising about 25,000 ha. Rainfall in the region is highly seasonal with about 90% of the annual rainfall (mean = 2,600 mm) occurring in the wet season (typically from late April to early January). Capture–mark–recapture sampling (CMR) was carried out with mist nets at two sites. Net lines on each consisted of 20–22, 36-mm mesh nets. Nets were open from dawn to dusk, for a total of about 600 net hours over 2.5 to 3 days per line per sampling period. Sampling generally occurred once in the dry and wet seasons of each year. First-capture birds were banded and released during 65 different occasions between 1977 and 2011, with intervals between capture occasions ranging from 44 to 863 days (mean = 195, s.d. = 130).

Estimation of demographic parameters and modeling effects of DSL. We focused on 20 species with 124 to 1,111 unique individuals captured. Effective sample size, based on the total number of captures, ranged from 196 to 1,582. Parameter estimates for other species with smaller sample sizes were not feasible. The focal species included species in nine families, four general categories of feeding behaviour or diet (frugivores/granivores, ant-following insectivores, ground insectivores, above-ground insectivores) and average body masses that ranged from 8 to 128 g. We estimated demographic parameters using CMR methods[32], specifically focusing on apparent annual survival, per capita recruitment, and population growth rate (λ). Apparent survival for open populations is the sum of true survival and permanent emigration for the focal population. With open populations, temporal variation in recruitment combines annual differences in the number of young birds produced locally by resident breeding pairs, survival of those juveniles to adulthood, and the number of individuals moving in and out of the focal populations. The estimated population growth rate is based on individuals that were present in the population on a previous occasion and survived as well as new individuals that have entered the population that were not previously present. Thus, this is an estimate of realized population growth rate rather than a projected value based on constituent demographic rates. We used two different parameterizations of our CMR models, one that simultaneously estimates survival and per capita recruitment, and one that simultaneously estimates survival and λ—both accounting for capture probability[32].

The presence of transient individuals is known to complicate the estimation of demographic rates when using CMR approaches[33]. Previous work in our study system demonstrated that the presence of transient individuals leads to negatively biased estimates of apparent survival when transients are not accounted for[34]. We confirmed that transience was a potential issue in our data using goodness of fit tests within the program U-CARE[35]. Consequently, we used a finite mixture approach to model heterogeneity in capture probability[36], including two groups to account for the presence of transients within the data set as well as individuals that stay within the population. Using finite mixture versions of Cormack–Jolly–Seber models[37], we confirmed that our approach gave comparable results to modelling heterogeneity in apparent survival or using a time-since-marking approach that estimates survival during the first interval as different from all subsequent intervals.

We examined the influence of DSL on each demographic parameter by using the length of the preceding dry season as a covariate for each of the 64 intervals. Rather than fitting separate parameters for all 64 separate intervals, we grouped intervals into roughly 1-year intervals where possible, resulting in 33 different estimates for each parameter. For each species, we ran two separate models, one with the per capita recruitment parameterization of the model, and one with the realized population growth parameterization of the model. For each model, we included preceding dry season length as an occasion-specific covariate on capture probability, apparent survival, and either per capita recruitment or realized population growth; that is, depending on the parameterization used[38]. We fit all models in Program MARK using a Bayesian Markov chain Monte Carlo approach[39]. Prior to running models, we examined the adequacy of default MARK options of 1,000 burn-in samples and 10,000 samples to keep for the posterior distribution. We conducted preliminary runs using the gibbsit option[40], confirming the adequacy of 1,000 burn-in samples and the need for >10,000 posterior samples. Along with the gibbsit results, preliminary runs with 3 chains of 30,000 posterior samples suggested adequate convergence based on chain mixing and $\hat{R} < 1.2$ (ref. 41). On the basis of the above results, we chose to retain the defaults of 4,000 tuning samples and 1,000 burn-in samples, but increased our number of posterior samples to 100,000; we inspected trace plots of the final runs to confirm the adequacy of our selected values for burn-in and posterior samples using the coda package in R[42]. We based our inferences on the medians and 95% credible intervals from the posterior distribution.

Simulations. To investigate the potential future effects of increased DSL, we conducted simulations based on the data-based responses of each species to DSL between 1977 and 2011. We conducted two sets of simulations for each species, one based on the observed DSL between 1977 and 2011 (mean = 136.1, s.d. = 21.1),

and another based on a 10% increase in DSL and variability (mean = 149.7, s.d. = 23.2). Each simulation run included 50 years, and involved randomly selecting a dry season length for each year from a normal distribution with specified mean and standard deviation (that is, normal or 10% longer), and randomly selecting a combination of estimated intercept and coefficient for the effect of preceding dry season length on realized population growth rate for each year from the estimated posterior distribution. The value for population growth rate for each yearly time step was calculated on the basis of the exponentiated linear combination of randomly selected intercept and the product of dry season length and coefficient; this value was multiplied by the population size from the previous yearly time step to get the new value for population size (rounded down to prevent fractions of individuals). We chose starting values for population size of each species based on ref. 31. This 50-year simulation was repeated 1,000 times for each species for both the normal and 10% drier scenarios. Simulations were conducted in R[43] (see Supplementary Information for details on field sampling, demographic analyses, and comparative methods).

Comparative analyses. We constructed a phylogeny using gene sequences for three mitochondrial and four nuclear loci available for the study species on Genbank (Supplementary Fig. 3). We aligned sequences in ClustalX V2.0[44], checked them by eye, and concatenated them with SequenceMatrix[45], coding gaps resulting from uneven sequence lengths and missing loci as missing data. Three species had only single loci available (*Malacoptila panamensis*, *Microbates cinereiventris* and *Cyphorhinus phaeocephalus*), so three closely related species with more sequence data (*Nystalus maculatus*, *Polioptila caerulea* and *Troglodytes aedon*, respectively) were added to the data set to strengthen the placement of the data-deficient species in the tree. *Anas platyrhynchos* was used as an outgroup. We used model selection in TOPALi v2.5[46] using PhyML[47] to identify the most appropriate model of molecular evolution. We then estimated the phylogeny using maximum likelihood with the program RAxML[48] as implemented in raxmlGUI[49]. We assigned the most appropriate model (GTR + gamma), assigned each locus to a separate partition, and performed rapid bootstrapping with 1,000 pseudoreplicates. For analysis we used the best-scoring tree, the topology of which is largely consistent with recent phylogenetic reconstructions[50–52].

We attempted to test for phylogenetic signal among traits using a number of different methods included in the phytools[53], ape[54], and nlme[55] packages implemented in program R. However, this proved problematic as data sets of such limited size lack power and estimates of phylogenetic signal can therefore be inaccurate[56]. This is especially true if phylogenetic signal is low (Pagel's λ approaching 0)[57]. Our data set contains only 20 species; therefore, the tree does not provide enough information about the relationships among taxa. Consequently, our estimates of λ spanned the entire range of possible values (from 0 to 1) or in some cases maximum likelihood models did not converge (Supplementary Fig. 4). Given this result, we expect that phylogenetic signal is indeed quite low within the data set. We therefore did not employ techniques for phylogenetic correction, as use of phylogenetically independent contrasts without proper assessment of phylogenetic signal can be inappropriate or misleading[53]. As an alternative, we simply included taxonomic family in our comparative analyses.

We modelled the influence of body size and general feeding behaviour on associations between rainfall and demography with linear mixed models and restricted maximum likelihood as the estimation procedure. Using the estimated beta coefficients for λ and DSL (weighted by the reciprocal of their variance) as the dependent variable, we included body size and feeding behaviour as fixed effects and family as a random factor.

Data availability. The data that support the findings of this study are available from the corresponding author on request.

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