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Longer-lived tropical songbirds reduce breeding activity as they buffer impacts of drought

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Droughts are expected to increase in frequency and severity with climate change. Population impacts of such harsh environmental events are theorized to vary with life history strategies among species. However, existing demographic models generally do not consider behavioural plasticity that may modify the impact of harsh events. Here we show that tropical songbirds in the New and Old Worlds reduced reproduction during drought, with greater reductions in species with higher average long-term survival. Large reductions in reproduction by longer-lived species were associated with higher survival during drought than pre-drought years in Malaysia, whereas shorter-lived species maintained reproduction and survival decreased. Behavioural strategies of longer-lived, but not shorter-lived, species mitigated the effect of increasing drought frequency on long-term population growth. Behavioural plasticity can buffer the impact of climate change on populations of some species and differences in plasticity among species related to their life histories are critical for predicting population trajectories.

Understanding the demographic impact of droughts is critical since droughts are expected to increase in frequency and severity due to global climate change[1–3]. Theory and demographic models predict that long-lived species with high average survival and low annual fecundity are at greatest risk of population decline from harsh environmental events that increase adult mortality[4–8]. In contrast, populations of short-lived species with high fecundity are predicted to be more sensitive to impacts on reproduction[4–7]. Droughts are harsh events that can impact both adult survival and reproduction[9–15] and may thus impact populations of both short- and long-lived species. Studies of some individual species have found severe population declines related to drought[11–15]. However, the relative demographic consequences of drought among species with differing life histories have not been studied.

The demographic consequences of drought might differ among species with differing life history strategies due to variation in behavioural responses. Reducing reproductive effort during a drought may yield benefits to survival given the commonly assumed trade-off between survival and reproductive effort[16–18]. In particular, reduced reproduction might buffer effects of drought whereby survival does not change, or alternatively, only decreases slightly in drought versus non-drought years compared with maintaining reproduction (Fig. 1a). Longer-lived species might especially be expected to reduce reproduction in a drought year if it enhances chances of surviving to reproduce in future years when conditions are better[19–21]. A few studies of single species have observed reduced levels of reproduction during drought[9–13]. However, whether reduced reproduction enhanced survival during the drought is unknown and even the existence of survival–reproduction trade-offs in the wild has been debated[16–18]. Shorter-lived species already have a lower chance of surviving to the next year such that they may benefit from maintaining their levels of reproduction despite poor environmental conditions[19–21]. These predictions suggest that species may differ in their reproductive responses to drought related to their survival probabilities. Yet, it is not known whether species differ in the extent to which they reduce reproduction as a function of their life history strategies and whether reduced reproduction can mitigate survival impacts of drought.

We conducted detailed demographic studies of 38 species of tropical songbirds during droughts and non-droughts in rainforest on New and Old World continents (Fig. 1b,c and Extended Data Fig. 1). Tropical organisms are thought to be particularly sensitive to climate change due to the relatively low climatic variance they have experienced historically[22,23]. Apparent survival rates and reproductive strategies vary substantially among tropical songbird species, although many species show high average survival rates[24]. Tropical songbirds, therefore, provide a valuable group in which to study demographic responses to drought as a function of varying life histories. We worked in Venezuela from 2002 through 2008[25,26], where 2008 was a drought year, and in Malaysia from 2009 through 2018[25,26], where 2016 was a drought year (Fig. 1b,c). Level of reproduction was measured as the number of active nests found per species each year based on constant-effort sampling (same number of nest-searchers, area and time spent searching). For the species reported here, we found and monitored 2,929 nests in Venezuela and 5,127 nests in Malaysia, providing robust samples of reproductive activity. In addition, 2,793 adults in Venezuela and 3,550 adults in Malaysia were uniquely colour-banded and recaptured or resighted to estimate apparent adult survival probability[24,25]. We used phylogenetic generalized least squares for all cross-species analyses.

Levels of reproduction were reduced in drought years on average by 36.3 ± 5.36% among 20 species in Malaysia and 51.9 ± 5.66% among 18 species in Venezuela (Fig. 2a). Most tropical rainforest songbirds are sedentary residents that do not leave in harsh years, such that reduced reproduction in the drought year reflects individuals foregoing reproduction. For example, *Henicorhina leucophrys* in Venezuela has high apparent annual survival[24,25,27] and showed the largest decline in reproductive activity among all species (Fig. 2a). Like many tropical songbirds[28], *H. leucophrys* establish permanent territories and do not move, even in harsh years. They make nests for breeding and other nests as dormitories and both types of nest

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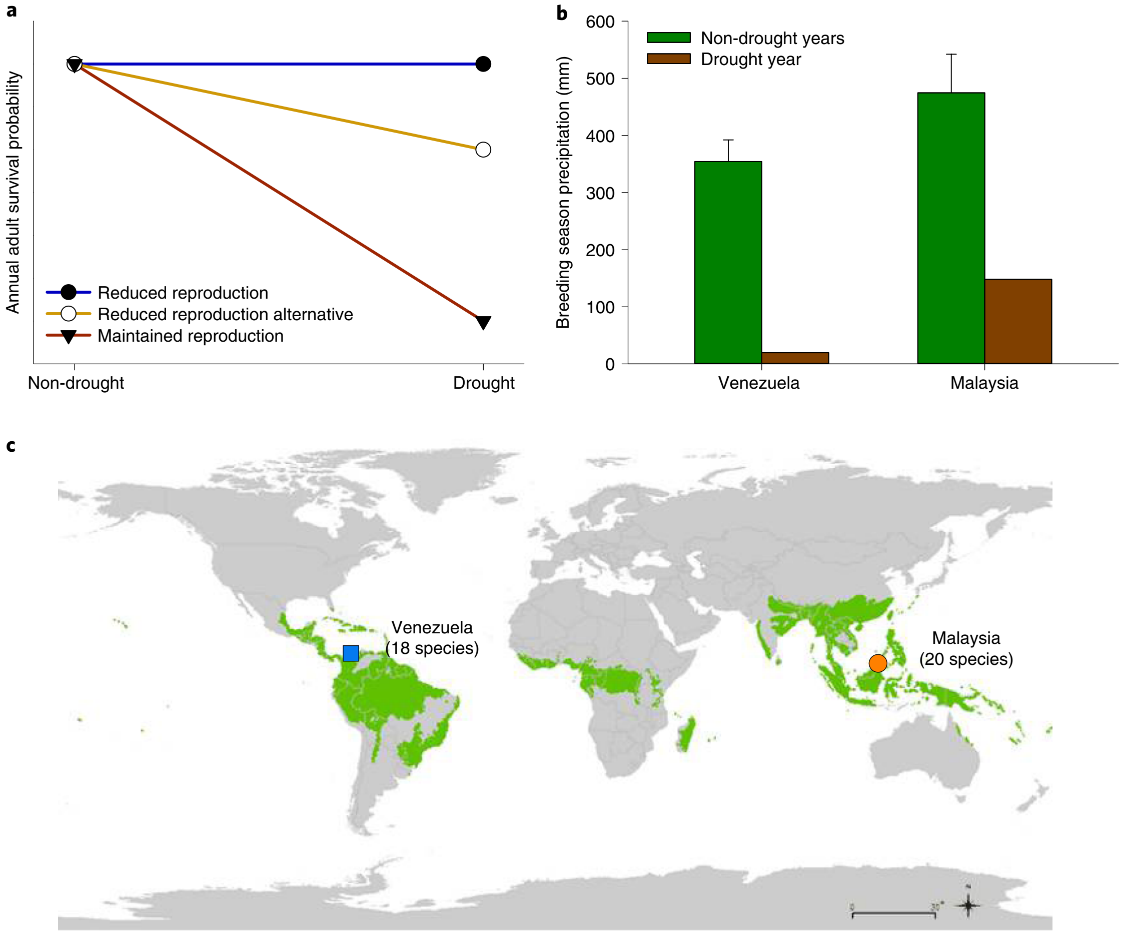


Fig. 1 | Possible demographic consequences of drought in tropical rainforest for songbirds. **a**, Conceptual schematic of potential responses of annual adult survival probability and reproduction to drought where: reproduction is reduced and adult survival is not impacted (closed circles, blue line); reproduction is reduced but adult survival still decreases (open circles, yellow line); or reproduction is maintained at normal levels with a large cost to adult survival (triangles, red line). **b**, Total precipitation (mm) during songbird breeding seasons in Venezuela and Malaysia study sites for non-drought versus drought years. Error bars, s.e.m. **c**, World map showing the global extent of tropical rainforest in green and location of the two study sites.

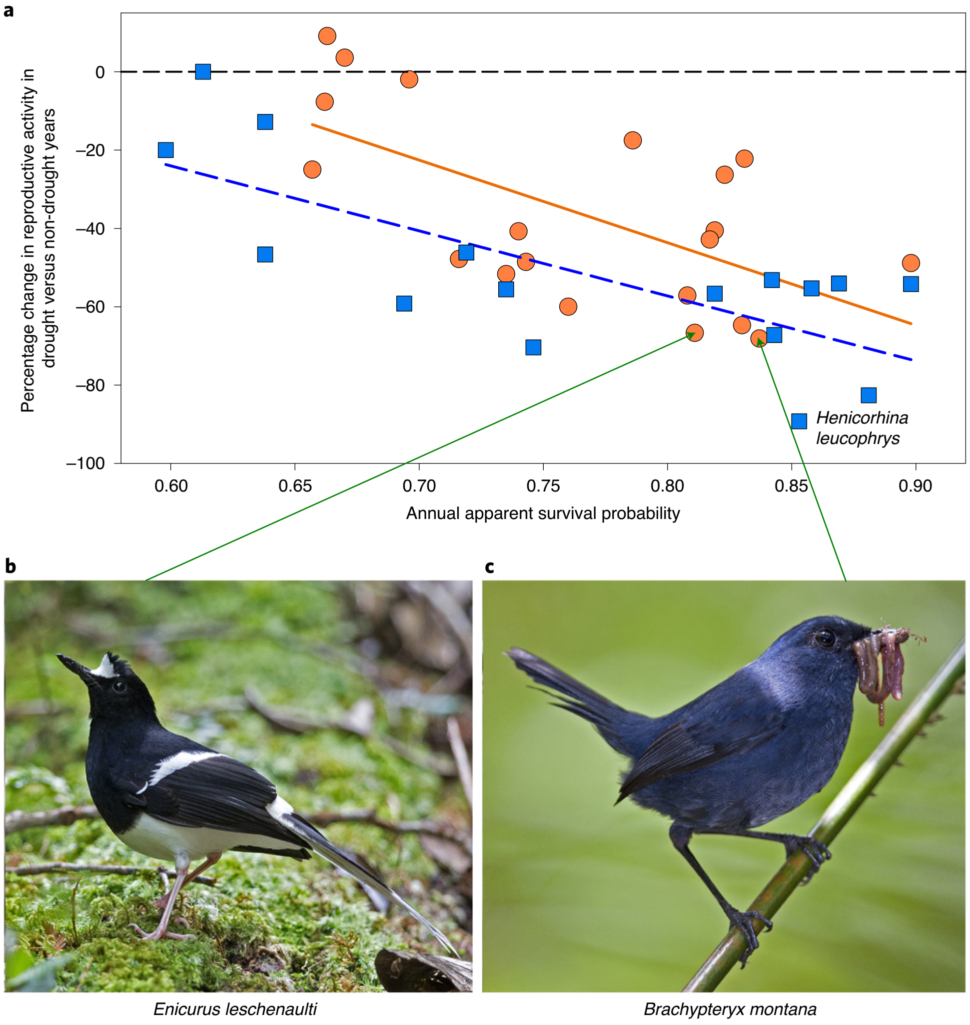
are relatively easy to find[27]. We sampled an average of 65 active breeding nests in the predrought years. In contrast, only seven nests with active breeding were observed in the drought year even though birds and active dormitory nests were readily observed. Thus, the reduction in numbers of breeding nests (Fig. 2a) reflected individuals skipping reproduction in the drought year.

Moreover, we captured, recaptured or resighted nearly identical numbers of unique individuals in predrought versus drought years at both sites, as expected for stable resident populations under standard-effort sampling[24–26]. For example, in Malaysia, we recaptured or resighted 812 versus 798 unique individuals that were banded in previous years in the predrought versus drought years, respectively. We also captured 628 and 646 new adults in the predrought and drought years, respectively. In other words, tropical residents were readily observed in drought years in similar numbers as in predrought years and the reduction in numbers of nests (Fig. 2a) reflected reduced reproduction in the drought year.

The extent of reductions in breeding during droughts differed between sites but was greater in species with higher annual survival in both Venezuela and Malaysia (Fig. 2a; survival, $t=-5.2$, $P<0.001$; site, $t=2.6$, $P=0.015$; $R^2=0.50$; $n=36$ species because survival could not be estimated for two species in Venezuela). Some of the largest declines in reproduction were by species with relatively high survival that relied on particularly wet microhabitats. For example, *Enicurus leschenaulti* in Malaysia and *Premnoplex brunnescens* in Venezuela both nest exclusively along streams and they reduced reproduction by 67% and 72%, respectively in the drought years (Fig. 2a,b). *Brachypteryx montana*, relies on wet, muddy areas and reduced reproduction by 68% (Fig. 2a,c). Overall, however, species with higher annual apparent survival showed greater reductions in reproduction in both New (Venezuela) and Old (Malaysia) World communities (Fig. 2a).

Drought did not impact offspring production in nests that were initiated. Clutch size did not differ in either site between drought and non-drought years, nor did the number of young fledged per successful nest (Extended Data Fig. 2). These results indicate that birds can breed successfully in droughts but many choose not to do so.

The drought occurred in the final year of study in Venezuela such that reproductive activity in the following year and survival costs during the drought could not be assessed. However, reproductive activity in Malaysia strongly recovered in the postdrought year (Fig. 3a), verifying that reductions in the drought reflected behavioural plasticity. Similarly, aquatic taxa skipped reproduction in a drought but returned to normal levels of reproduction following the drought, despite assumed drought impacts on energy reserves[10]. Yet whether reduced reproduction benefits survival during the drought is generally unknown.



Enicurus leschenaulti

Brachypteryx montana

Fig. 2 | Tropical songbirds reduce breeding activity in drought years on two continents. a, Reproductive activity decreased more in drought compared with non-drought years for tropical songbird species with higher annual apparent survival rates in Venezuela (blue squares) and Malaysia (orange circles). The horizontal dashed line reflects no change between non-drought and drought years. *Henicorhina leucophrys* of Venezuela showed the largest reduction in reproduction among all species on both continents, as described in the text. **b**,**c**, *Enicurus leschenaulti* (**b**) and *Brachypteryx montana* (**c**) depend on wet habitats and show very large declines in reproduction among Malaysian species. Photographs by T.E.M.

We estimated annual apparent survival probability in Malaysia from constant-effort capture–recapture–resight data[24–26] for the pre-drought and drought years. We expected survival to decrease for all species in the drought as commonly reported[9–15] but that survival impacts might be lessened for species that reduced reproduction. We were surprised to find that many species that reduced reproductive activity the most showed increased, rather than decreased, apparent survival during the drought compared with predrought years (Figs. 3b and 4). In contrast, species that maintained or only slightly reduced reproductive activity in the drought year experienced reduced apparent survival (Figs. 3b and 4), as commonly observed in droughts[9–15]. Costs of reproduction have been widely espoused but rarely observed in the wild in part because studies have focused within single species where variation in individual quality can obfuscate costs[16–18]. Furthermore, costs of reproduction might be expected to be minimal in long-lived tropical songbirds where fecundity is low as a mechanism to facilitate high survival[20]. Our observation that long-lived species increased survival while reducing reproduction, despite harsh environmental conditions imposed by drought, suggests that costs of reproduction may have important demographic consequences for tropical songbirds in the wild.

A few species, on the other hand, reduced reproduction and still experienced reduced apparent survival (Figs. 3b and 4). The most extreme examples were the species reliant on wet microhabitat. They showed large decreases in reproductive activity in the drought and also showed large decreases in apparent survival probability in the drought year (triangle symbols in Fig. 3). *Myophonus borneensis* extensively uses wet microhabitat, although does not rely exclusively on it[29] but its changes in reproductive activity and apparent survival in the drought were similar to the two wet-habitat species (Fig. 3b). Ultimately, reducing reproduction may generally yield benefits to survival and buffer the impacts of drought, except in species that rely on the wettest microhabitats and possibly in some of the shorter-lived species.

Previous demographic models suggested that impacts on survival have larger effects on population growth in longer-lived species, whereas population growth of shorter-lived species was more sensitive to impacts on reproduction[4,5]. Thus, the variation among species in behavioural adjustments of reproduction in response to drought documented here may benefit population growth by buffering the most sensitive vital rates. To test this idea, we simulated population growth and conducted elasticity

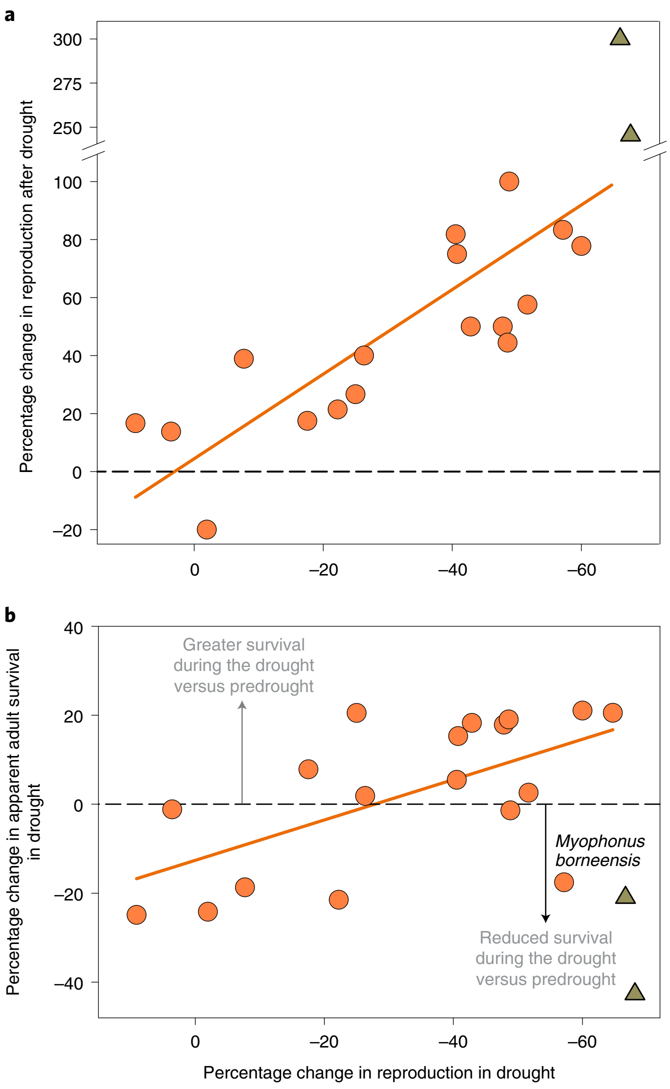


Fig. 3 | Relationships of reproductive activity and survival across Malaysian species. a, Species that reduced reproductive activity more during the drought year increased reproductive activity more in the following non-drought year. Triangle symbols represent the two species (*E. leschnaulti* and *B. montana*) that rely on the wettest habitat in Malaysia (Fig. 1). **b**, The relative change in adult survival in drought compared to predrought years increased in those species that reduced their reproductive activity the most in the drought year (survival, $t=2.9$, $P=0.009$; wet-habitat species, $t=-4.4$, $P<0.001$; $R^2=0.54$; $n=20$).

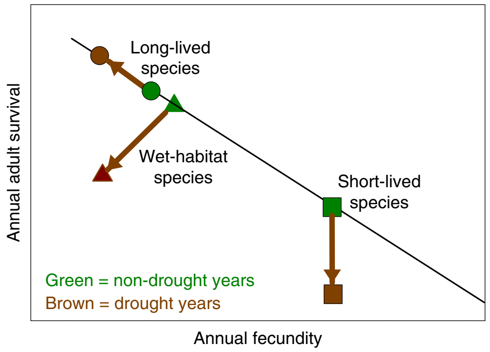


Fig. 4 | General demographic consequences of drought. Summary figure depicting overall changes in survival and reproduction for long-lived (circles), short-lived (squares) and wet-habitat (triangles) species. Arrows point to drought responses (brown) relative to non-drought (green) years. Long-lived species have low fecundity that is reduced during drought and associated with increased survival. Short-lived species have higher annual fecundity that is largely maintained during droughts but experience reduced survival. Species that depend on wet habitats, which in the Malaysia site were species with high average survival, suffered large survival costs of drought despite large reductions in reproductive activity.

analyses[30,31] for eight Malaysian species that typified long-lived ($n=3$ species), short-lived ($n=3$) and wet-microhabitat specialists ($n=2$). We modelled population growth during drought and non-drought years for each species using demographic data based on our long-term field study augmented with relevant data from the literature[32,33] and the actual occurrence of droughts associated with strong El Niño events from historic data (1864–2018)[34]. El Niño events cause drought across Southeast Asia including northern Borneo[35] and are indicated by low values of the Southern Oscillation Index (SOI). We created distributions of stage-specific survival and fecundity (accounting for survival to independence) based on 10 yr of field data and used them to parameterize 1,000 population matrices. Matrices were randomly drawn from this set 1,000 times for normal and severe drought years. We found that population growth of most species, both short- and long-lived, was more strongly affected by changes in adult survival than fecundity (Fig. 5a). Indeed, elasticity of adult survival broadly overlapped between short- and long-lived species (Fig. 5a).

Despite the benefit of increased survival (Fig. 5a), population growth was lower in drought years than in non-drought years for long-lived as well as short-lived species (Fig. 5b). In other words, the >50% decrease in reproduction in longer-lived species (Fig. 2a) was not fully compensated by the ~20% increase in survival (Fig. 3b) in drought years. However, impacts on population growth in drought years were smaller in longer-lived than shorter-lived species (Fig. 5b). The latter results reflected that reduced reproduction in longer-lived species was partially compensated by increased survival, whereas the decrease in survival during drought years for shorter-lived species (Fig. 3b) was not offset by any increases in reproduction (Fig. 2a). Not surprisingly, the impacts of drought on both reproduction and survival in wet-microhabitat specialists yielded the largest population impacts (Fig. 5b).

We examined the long-term population consequences of drought when using the opposing strategy for short- and long-lived species. In other words, we compared long-term population growth of long-lived species using our measured demographic rates for them in drought versus non-drought years versus if they used a short-lived species strategy of maintaining reproduction but suffering decreased survival. Similarly, we compared long-term population growth of short-lived species with their measured demographic rates versus a long-lived strategy of reduced reproduction and increased survival. We found that long-lived species had higher mean stochastic population growth with their strategy than the short-lived strategy of maintaining reproduction and suffering decreased survival (solid red bars in Fig. 5c). Conversely, short-lived species actually had higher mean stochastic population growth with the long-lived strategy if they reduce breeding effort and are able to obtain increased survival during drought years (solid blue bars in Fig. 5c). However, short-lived species may be unable to gain the same survival benefits from reducing breeding effort that we observed for long-lived species. Instead, individuals of shorter-lived species may gain no survival advantage from skipping reproduction because their lower survival rates may be set by environmental factors[36,37]. To test this possibility, we also modelled populations of the short-lived species under a hypothetical scenario where they reduced reproductive activity in drought years but still experienced the decreased

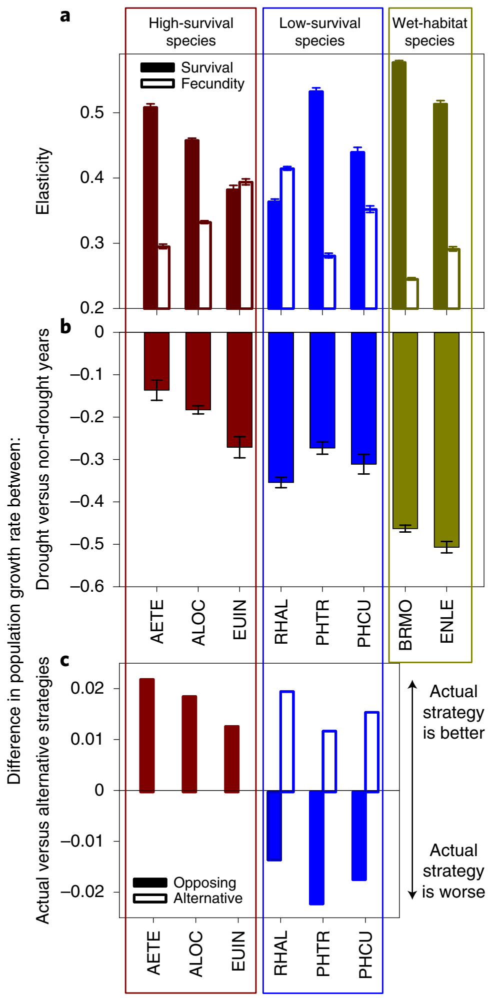


Fig. 5 | Population elasticity and simulated population growth under historic frequencies of drought. a, Population growth rates of long-lived (red), short-lived (blue) and wet-habitat (yellow) species were generally more sensitive to changes in adult survival (filled bars) than fecundity (open bars), except for one short-lived species (RHAL). **b**, Longer-lived species experienced relatively mild reductions in population growth during drought years compared to short-lived species and especially wet-habitat species. **c**, Differences in long-term stochastic population growth between the actual demographic strategy versus the opposing (filled bars) or a hypothetical strategy (open bars) with reduced reproductive activity but reduced survival under an assumption that survival is dictated by the environment. Error bars indicate s.e.m. AETE, *Aethopyga temminckii*; ALOC, *Alophoixus ochraceus*; EUIN, *Eumyias indigo*; RHAL, *Rhipidura albicollis*; PHTR, *Phylloscopus trivirgatus*; PHCU, *Phyllergates cuculatus*; BRMO, *Brachypteryx montana*; ENLE, *Enicurus leschenaulti*.

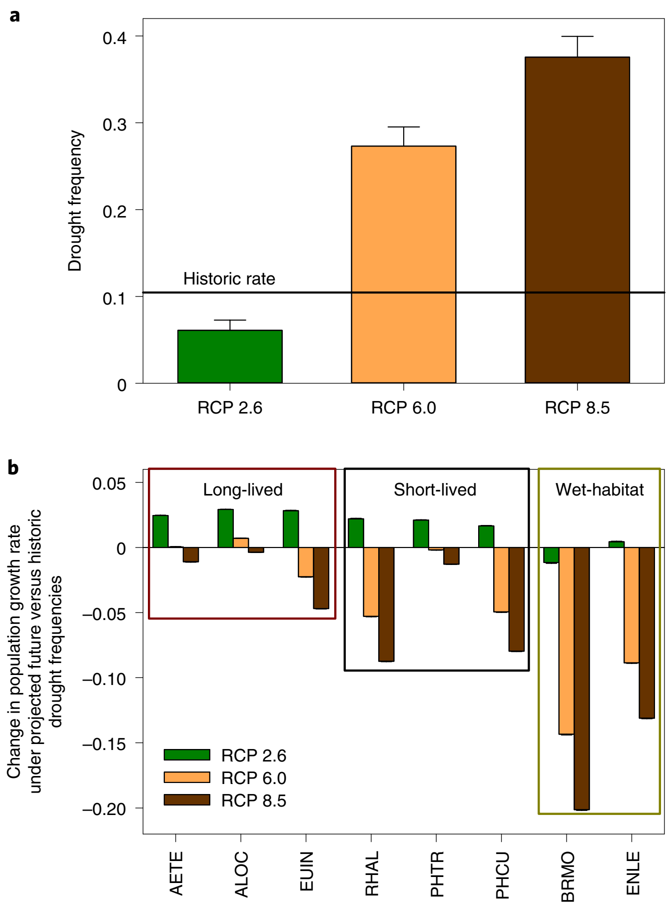


Fig. 6 | Drought frequency and simulated population growth under alternative climate change scenarios for the future. a, Frequency of droughts associated with severe El Niño events based on historic SOI data (horizontal line) and projected SOI values under three climate change scenarios for 2019–2100 depicting low (RCP 2.6), medium (RCP 6.0) and high (RCP 8.5) CO_2 concentrations. Error bars indicate s.e.m. **b**, Simulated long-term stochastic population growth was largely stable or increasing when based on scenarios with the lowest CO_2 concentrations but showed long-term declines under scenarios with higher CO_2 concentrations. AETE, *Aethopyga temminckii*; ALOC, *Alophoixus ochraceus*; EUIN, *Eumyias indigo*; RHAL, *Rhipidura albicollis*; PHTR, *Phylloscopus trivirgatus*; PHCU, *Phyllergates cuculatus*; BRMO, *Brachypteryx montana*; ENLE, *Enicurus leschenaulti*.

survival observed in drought years. Long-term stochastic population growth was much better under their actual strategy than under this hypothetical scenario (open blue bars in Fig. 5c). Ultimately, reducing reproduction during droughts may not help mitigate population declines from droughts in species with faster life histories but can buffer population trends of long-lived species. However, both long- and short-lived species may be acting with the best possible strategies for drought if short-lived species cannot obtain survival benefits from reduced reproduction.

We also examined the possible consequences of these strategies for long-term population growth in the future under alternative climate change projections. We used switching-Markov models to simulate annual El Niño events from 2019 to 2100 on the basis of temperature and SOI projections for low, medium and high atmospheric CO_2 concentrations on the basis of representative concentration pathways (RCP 2.6, RCP 6.0 and RCP 8.5 respectively)[34,38–40]. Overall, our projections generally matched results from previous studies predicting that lower future CO_2 concentrations would be associated with less drought[41]. Simulated frequency of severe droughts ($SOI < -1$) was relatively similar to the historic data under the low CO_2 concentration scenario but drought frequency was substantially greater under the projected medium and high CO_2 concentration scenarios (Fig. 6a).

To examine population responses to changes in drought frequency due to climate change, we simulated 1,000 populations under each of 1,000 projected future SOI series for each CO_2 concentration scenario. Projected mean stochastic population growth from 2019 to 2100 decreased with increasing CO_2 concentration scenarios for all species (Fig. 6b). However, long-lived species experienced smaller reductions in long-term stochastic population growth, while short-lived species (especially wet-habitat species) showed dramatic declines (Fig. 6b). Thus, even with substantially increased drought frequency, longer-lived species that reduced breeding during droughts and obtained enhanced survival were better able to buffer long-term population growth, while shorter-lived and wet-habitat specialist species suffered substantially reduced population growth.

Theory predicts that long-lived species are at greater risk of population vulnerability from harsh environmental events[4,5,7,8] but such theory and models have not taken into account possible behavioural adjustments that can minimize population impacts. The results here indicate that long-lived species can adjust reproduction to reduce long-term demographic impacts through survival benefits. Of course, we only show survival benefits in a single site and year and population impacts even for long-lived species may be much greater in more severe droughts than we experienced, such that studies of more years of drought of varying severity are needed[11]. Climate change is expected to drastically increase the frequency and severity of droughts globally[1–3] and unprecedented drought severity and frequency may impact populations of both long- and short-lived species regardless of adjustment to reproductive activity. Nonetheless, species in both Old and New World communities adjusted reproduction to drought in very similar responses as a function of their survival probabilities and that seemed to minimize long-term population impacts. The results here suggest that longer-lived tropical species may be more resilient to at least some forms of climate change than currently thought, although with an important caveat for wet-microhabitat specialists. Ultimately, the demographic consequences of behavioural adjustments to climate variation need to be better understood to be able to model projections of population vulnerability to climate change.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41558-020-0864-3.

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Methods

Study areas. We studied tropical passerine species on two continents with crews of nine field assistants each year: seven nest-searchers and two banders, plus a field supervisor. The field assistants were largely undergraduates and postgraduates previously trained on one of T.E.M.'s North American projects. The species that were studied in Venezuela (9° N) and Malaysia (6° N) represent a broad phylogenetic range among songbirds (Extended Data Fig. 1). Nests and adult mortality were studied for 7 yr (2002–2008) in primary forest in Yacambu National Park, Venezuela at elevations of 1,400–2,000 m and for 10 yr (2009–2018) in primary forest in Kinabalu Park, Malaysia at 1,400–1,950 m elevation[24–26] (Fig. 1a).

Rainfall. Rainfall data for the Yacambu site in Venezuela were obtained from Instituto Nacional de Metereología e Hidrología, Ministerio del Poder Popular para el Ecosocialismo, República Bolivariana de Venezuela (http://www.inameh.gob.ve, accessed December 2011). Data were obtained for all 7 years of the study. We report the total rainfall for 1 January to 1 May averaged for the 6 years before the drought year (2002–2007) versus the drought year itself (2008).

Rainfall for the Mount Kinabalu site in Malaysia was obtained for 2016 through 2018 from data collected using a HOBO Rain Gauge Datalogger RG3 (Onset Computer Corporation). The station was implemented at the beginning of February 2016. Consequently, we report rainfall from 1 February to 1 May for the drought year of 2016 versus the average of this period for 2017 and 2018. Rainfall data for prior years of the study were not available, so we assume the average of 2017 and 2018 reflects typical non-drought rainfall. This assumption was supported by the fact that the average in these 2 years (474.7 ± 67.48, where 67.48 is 1 s.e.m.) was nearly identical to rainfall for this February–May period reported for the same site in 8 years of non-drought (477.9 ± 79.84) in the late 1970s and early 1980s[42].

Reproductive measures. We used a standard-effort approach to assessing levels of reproduction, analogous to similar standard-effort approaches used for capture rates or point counts of abundances[43]. Reproductive activity was based on the number of nests that we found each year. Except for the first year at each study site, the nest-searching crew size, numbers of study plots and number of days searching for nests were the same every year, thereby providing standard-effort nest-sampling across years. Nonetheless, nest-finding has a learning curve in these tropical forests where the species have not been previously studied[44]. Because of this learning curve, we used reproductive activity in the 2 yr before the drought as our estimate of predrought activity because it represented the period that was most like the drought year in terms of nest-finding knowledge. Moreover, numbers of nests per species were highly correlated between the two predrought years in both Venezuela ($R = 0.90$, $P < 0.001$) and Malaysia ($R = 0.97$, $P < 0.001$), demonstrating the consistency of this standard-effort metric.

The number of nests ± s.e.m. per species for the predrought years in Malaysia averaged across all species was 30.7 ± 6.4 nests versus 20.1 ± 4.0 nests during the drought. In Venezuela, numbers of nests per species during the predrought years were 33.2 ± 6.0 versus 14.1 ± 2.6 during the drought. As documented for Malaysia in the text, this reduction in numbers of nests did not reflect birds leaving the area. Like Malaysia, we captured, recaptured and resighted similar numbers of birds in the predrought and drought years in Venezuela. In particular, in Venezuela we recaptured or resighted more previously banded unique individuals in the drought year (356) than in the predrought year (252), while capturing a similar number of new individuals in the drought (339) versus predrought (314) years. Numbers were lower in Venezuela than Malaysia because we did not band non-focal species or hummingbirds in Venezuela, with the latter being abundant. In contrast, we banded all captured birds in Malaysia. We captured similar numbers of unbanded individuals in the predrought (370) and drought (345) years in Venezuela. Unbanded birds would have increased the numbers of recaptures, resights and new individuals had they been banded. Nonetheless, as observed for Malaysia (see main text), observations of banded resident birds demonstrated that they remained on the site in the drought year.

We found almost exactly half of the nests during building and this percentage did not differ between the drought and non-drought years in Malaysia (paired *t*-test, $t = 0.6$, $P = 0.96$; 50.8 ± 4.7% versus 51.1 ± 2.5% of nests found during building in drought versus non-drought years, respectively), although slightly higher percentages of nests were found during building in drought than non-drought years in Venezuela (paired *t*-test, $t = 2.7$, $P = 0.015$; 51.3 ± 4.4% versus 44.9 ± 3.1% of nests found during building in drought versus non-drought years, respectively). We excluded the first year at each site in these analyses to reduce learning effects at the beginning of these studies. The large percentage of nests found during building in both locations and not declining during the drought demonstrates that our data were not strongly impacted by missing nests due to early failure in the drought.

Clutch size (number of eggs laid) and number of young that fledged were included from all years because these metrics did not rely on a learning skill. Clutch size was only counted for nests found during nest-building or egg-laying and observed to remain the same for 2 d after egg-laying to eliminate any possible inaccuracies from partial loss in nests found after incubation began[25]. Numbers of young fledged were only counted for nests where the exact number of young was observed within 2 d of when the young left the nest and fledglings were confirmed.

Adult survival. We assessed average annual apparent survival rates for each species in Venezuela (2001–2008) and Malaysia (2009–2018) and studied the effect of the 2016 drought on annual survival in Malaysia. We were unable to study the survival effects of the drought in Venezuela because it occurred in the final year of the study (2008). In Malaysia and Venezuela, 240 marked net sites in 20 subplots were distributed across nest-searching plots[24,26]. Each netting subplot consisted of 12 net sites, with nets 25–50 m apart. These netting subplots were deployed three times per breeding season, with 5–6 weeks between visits, from 2009 to 2018. Nets for a subplot were deployed for 6 h starting at dawn and moved to the next subplot each day. All unbanded birds that were captured were banded with numbered metal bands and unique combinations of three colour bands (two bands per leg). Colour bands were used for resighting by us and nest-searchers who visited each plot daily throughout the season. Resighting and recaptures were used in programme MARK[45] to estimate annual apparent adult survival probabilities (see Statistical analyses).

El Niño/Southern Oscillation simulations. We used Markov-switching autoregressive models to predict the occurrence of severe El Niño associated droughts at our field site[38]. We fit historic SOI data to a candidate set of models with two or three state regimes, a fixed effect term for mean global temperature[34] (GISS Surface Temperature Analysis v.4. https://data.giss.nasa.gov/gistemp/[39]) and between one and four autoregressive terms. We used Aikaike's Information Criterion corrected for a small sample size (AICc) to determine the model with two states and three autoregressive terms best fit the historic data. We then simulated 1,000 sequences of SOI values from 2019 until 2100 on the basis of global mean temperatures for 2015–2019 and projected global mean temperatures on the basis of IPCC climate projection models[40]. We predicted SOI under three CO_2 concentration scenarios depicting global CO_2 emissions peaking between 2010 and 2020 (RCP 2.6), peaking around 2080 (RCP 6.5) or continuing to rise through 2100 (RCP 85). For all SOI simulations, we considered years with $SOI < -1$ as severe drought years because they indicated a drought about as severe as the drought experienced in Malaysia in 2016, and considered all other years as normal years.

Population simulations. We used population matrix models to simulate stochastic population growth from 1866 to 2019 using historic SOI data and from 2019 to 2100 using simulated SOI data[30,34,39].

For each species, we created 1,000 population matrices based on juvenile and adult life stages. Demographic parameters were drawn from distributions based on field data[31]. Mean annual adult survival was drawn from a beta distribution with mean and variance based on apparent survival estimates and error (see above). Juvenile survival (from independence to 1 yr of age) is poorly studied in tropical songbirds and we lack robust estimates for our species. However, juvenile survival was more variable and consistently 24% lower than adult survival across 40 Amazonian species[32]. Thus, we modelled juvenile survival distributions for each species to be the same as adult survival distributions except the mean was 0.24 lower and the variance was 39% greater. We modelled mean annual fecundity for each species as the product of percentage of females breeding in a given year, mean clutch size, the number of breeding attempts per year, nest survival for each day of the nesting period and fledgling survival. We estimated mean nest survival rates using the logistic exposure method[46]. We modelled fledgling survival (ϕ_{Fldg}) on the basis of adult survival (ϕ_{Adult}) estimates following ref. [33]:

$$\arcsin\left(\sqrt{\phi_{\mathrm{Fldg}}}\right) = 0.249 + 0.692\ \arcsin\left(\sqrt{\phi_{\mathrm{Adult}}}\right)$$

We drew the proportion of females breeding in non-drought years from a normal distribution with mean of 0.95 and variance of 0.05. We assumed first-year fecundity was 90% of adult fecundity for all species.

We estimated how sensitive population size was to proportional (10%) changes in each demographic parameter for every population matrix simulated on the basis of normal years for each species[31].

For each species, we created another 1,000 population matrices for drought years. We drew parameters from the same distributions as above but multiplied fecundity and survival by a factor to reflect various responses to drought. For simulations based on historic temperature data, we modelled responses to drought years by (1) decreasing breeding activity by 57% and increasing annual adult survival by 19.65% (average response based on the longer-lived species) or (2) increasing breeding activity by 3.5% and decreasing annual adult survival by 24.5% (average response based on the shorter-lived species). We simulated the two wet-habitat species assuming they responded to drought years by decreasing breeding activity by 71.15% and decreasing annual adult survival by 31.8% (average response based on the two wet-habitat species). We also simulated short-lived species under a hypothetical scenario where they reduced reproduction by 57%

and survival by 24.5% during drought years compared to non-drought years. For simulations based on projected SOI data for 2019–2100, we modelled responses to drought years on the basis of the observed response to the 2016 drought for each species (Fig. 3b).

We simulated populations across all years of either historic or projected drought sequences drawing population matrices from the set of either normal or drought year matrices. All simulations started with 5,000 individual females in a stable age distribution based on the population matrix drawn for the first year. For every drought sequence, we calculated mean stochastic population growth as the geometric mean of percentage change in total population size each year. We also calculated the difference in population growth between normal and drought years for each simulation.

Statistical analyses. We used Cormack–Jolly–Seber models for live encounter data for open populations in programme MARK to estimate apparent annual adult survival[45,47]. Mean survival probability for each species was taken across all 7 yr of sampling in Venezuela and from 2009 to 2016 as previously reported[45,47]. We also estimated survival probability in drought versus non-drought time periods for each species in Malaysia. Given three sampling occasions each year (see above), we set time intervals as 0.125, 0.125 and 0.75 for actual netting intervals in each year. For each species, models were built with four time factors: all years pooled before the drought year in 2016, the drought year in 2016, the postdrought year in 2017 and the final year of 2018 (the 3,550 banded individuals were recaptured or resighted 9,946 times). Rigorous estimates of change in survival during the drought in 2016 were made possible by the continued capture–recapture–resighting during two postdrought years (2017 and 2018). Sex included two categories, male and female together, and an unknown category because many of our study species do not show sexual dimorphism and many individuals are not in breeding condition when captured. We excluded all first-year birds, as previously suggested by careful tests[24] but individuals of unknown sex may include older immatures that are transient, whereas identified sexes reflected breeding birds. Consequently, we focused survival estimates on individuals with identified sexes. We built four models, all of which included the four time periods because the goal was to examine apparent survival (ϕ) in the drought year compared with the previous non-drought years accounting for detection probability (p). The first model included the time periods (t), with all sex classes combined (.) [$\phi(t, .)\ p(t, .)$]. The second model allowed identified sexes (s) to differ from individuals of unknown sex [$\phi(t, s)\ p(t, s)$]. The third model separated first year of capture (a_1) from all subsequent years (a_2) in a time-since-marking approach[48], with sexes combined [$\phi(t+a, .)\ p(t+a, .)$]. The fourth model was the same as the third but included the two (known, unknown) sex classes [$\phi(t+a, s)\ p(t+a, s)$]. To examine whether survival in the drought year did not simply reflect stochastic annual variation and that these drought versus non-drought year model structures were appropriate, we also tested another set of the four models above but allowing survival to vary among all years. We used AIC, with adjustment for small sample sizes (AICc; ref. [45]) for model selection and used programme RELEASE[47] to test goodness-of-fit. We corrected for overdispersion ($\hat{c} > 1$) whenever it occurred on the basis of an adjusted $\hat{c}$ and model selection was based on quasi-AIC corrected for small sample size (QAICc)[49]. When the top model included the two sex classes, we reported changes in survival for the identified (not unknown) sexes among time periods. We found that our previous models based on drought versus non-drought years produced a top model in 19 of the 20 species in Malaysia, with a delta AIC for the best annual variation model averaging 13.5 ± 1.5 AIC units higher than the top drought versus non-drought model. The one exception was *Yuhina everetti*, where an annual variation model was the top model. Two other species (*Ficedula hyperythra* and *Brachypteryx montana*) had an annual variation model within 2 delta AIC units of the top model but a drought versus non-drought model was the top model in both cases indicating that a drought versus non-drought structure was an appropriate and reasonable structure, especially given that it produced a top model in 19 of the 20 species. Consequently, we report results based on the drought versus non-drought models.

We corrected for possible phylogenetic effects[50] in all analyses of reproductive activity and survival using the Caper[51] package in R v.3.5.0 for Windows on the basis of phylogenetic generalized least squares analyses based on two-tailed tests. Phylogenetic trees were obtained from www.birdtree.org[52] using the Hackett et al.[53] backbone and imported into programme Mesquite[54] where a majority rules consensus tree was constructed on the basis of 1,000 trees (Extended Data Fig. 1). This consensus tree was then used in phylogenetically controlled analyses that incorporated Pagel's lambda[55] to transform branch lengths and reduce overcorrection for phylogenetic effects[56].

We tested the relationships between the change in reproductive activity during the drought relative to annual apparent adult survival probabilities (Fig. 1c) using the phylogenetic generalized least squares approach described above with change in reproduction as the dependent variable, apparent adult survival probability as a covariate, site as a fixed factor, and their interaction. The interaction was not significant ($t = -0.7$, $P = 0.46$) so we removed it for the final model reported. We tested the relationship between the increase in reproductive activity in the year after the drought relative to the decrease in reproductive activity during the drought (Fig. 2a) using the phylogenetic generalized least squares approach with the increase in reproductive activity postdrought as the dependent variable, the decrease in reproductive activity in the drought year as an independent covariate, and a fixed factor dummy variable for the two wet-habitat species (blue diamonds). We tested the relationship between the change in apparent adult survival versus the change in reproductive activity during the drought using phylogenetic generalized least squares with the change in apparent adult survival during the drought as the dependent variable, the change in reproductive activity during the drought as an independent covariate and a fixed factor dummy variable for the two wet-habitat species (blue diamonds).

We used linear mixed-effects models based on programme LME4 (ref. [57]) to test whether clutch size and number of fledged young differed between drought and non-drought years. Data from all years were included. Species and year were treated as random factors and differences were tested for drought (no, yes) and site (Venezuela, Malaysia) as factors and their interaction. Interactions were not significant (clutch size analysis: $t = -0.45$, $P = 0.66$; fledgling analysis: $t = 0.12$, $P = 0.90$) and were dropped in the final model reported.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Life history data are available in Dryad (https://doi.org/10.5061/dryad.gf1vhhmm8). Source data are provided with this paper.

Code availability

R code for population models are available in Dryad (https://doi.org/10.5061/dryad.gf1vhhmm8).

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Author contributions

T.E.M. designed the study, analysed the field data and obtained funding. J.C.M. conducted all climate and demographic modelling. Both authors collected data and contributed to writing and revising the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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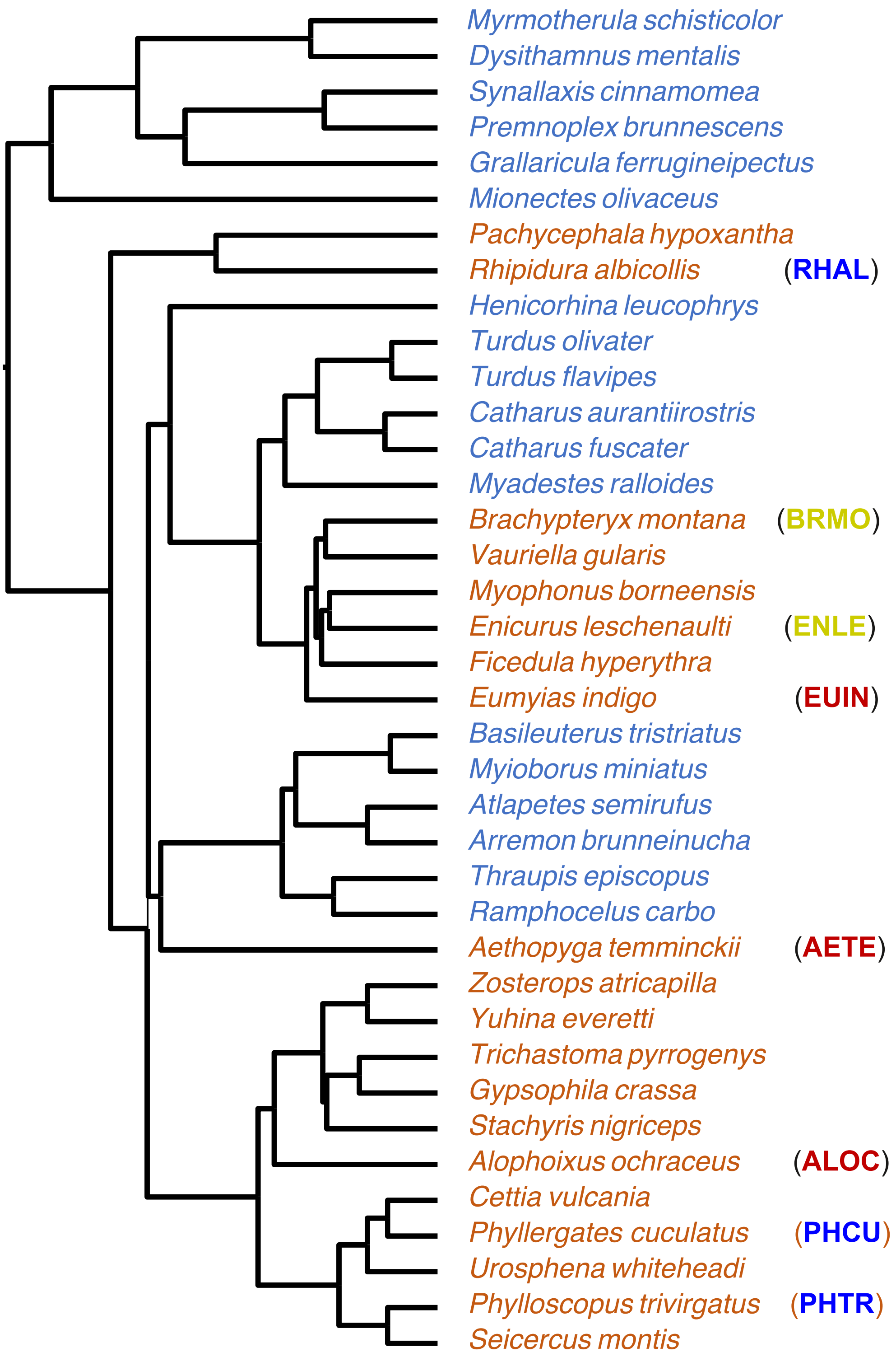
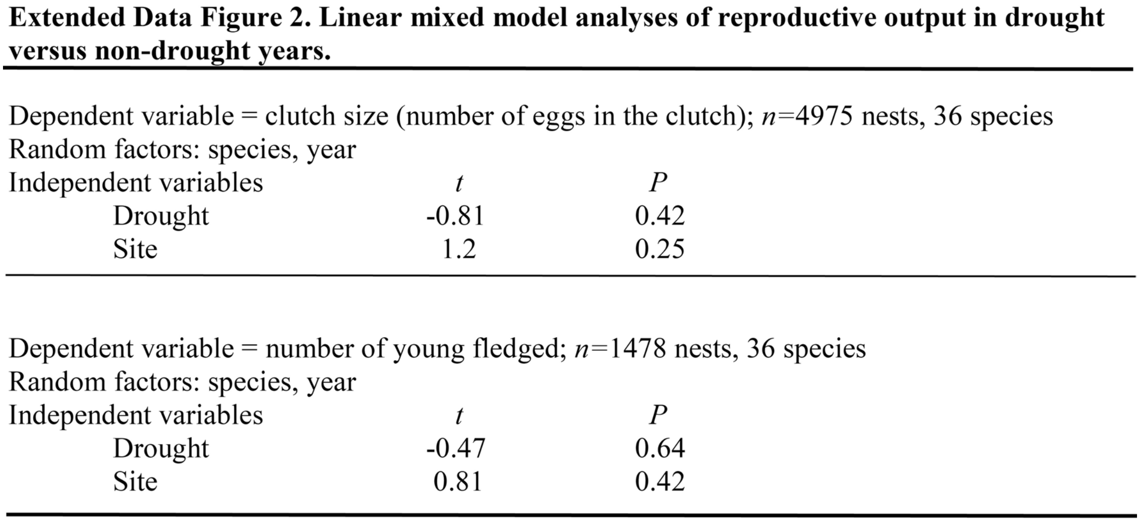


Extended Data Fig. 1 | Phylogenetic relationships of all study species from birdtree.org. Species from the Venezuela site are depicted blue and species from the Malaysia site are depicted in orange. Abbreviations based on scientific names in parentheses are the eight species used for population simulation analyses, and include long-lived in red, short-lived in blue, and wet-habitat species in yellow-green.



Extended Data Figure 2. Linear mixed model analyses of reproductive output in drought versus non-drought years.

Dependent variable = clutch size (number of eggs in the clutch); *n*=4975 nests, 36 species
Random factors: species, year

Independent variables	*t*	*P*
Drought	-0.81	0.42
Site	1.2	0.25

Dependent variable = number of young fledged; *n*=1478 nests, 36 species
Random factors: species, year

Independent variables	*t*	*P*
Drought	-0.47	0.64
Site	0.81	0.42

Extended Data Fig. 2 | Linear mixed model analyses of reproductive output in drought versus non-drought years. Differences in clutch size and number of young that fledged (left the nest) were compared between drought versus non-drought years, while including species and year as random factors.