M8802 was almost 11 g and that the hatchling mass was 4.7 g (table S4).

The relation of IEM to adult mass provides direct evidence of reproductive effort and shows that birds make a significantly greater investment in their young than do reptiles (28, 29). Pterosaurs are demonstrably reptilian in this respect, a conclusion that is consistent with other evidence regarding their reproductive biology. This includes the possibility that sexual maturity preceded somatic maturity (13, 14); parchment-like eggshells (7, 8, 16, 17); the burial of eggs (2, 16, 17, 30), facilitating the possibility of water uptake after oviposition (16, 17); and hatchlings with a postcranial anatomy that was similar in many of its proportions, but not size, to that of adults, hinting at locomotor precociality, including flight (2, 30). Some aspects of this reproductive strategy, such as burial of the egg, resulting in the development of the embryo at ambient temperatures, are incongruent with ideas regarding, for example, pterosaur physiology (17), which assumes that they achieved a degree of homeothermic endothermy comparable to that of birds or bats (1, 2, 5, 6, 18). On the other hand, and contrasting sharply with the high resource investment strategy of extant birds (31) and bats (32), the relatively small investment of resources by pterosaurs in their eggs and the likely absence of any need to care for the eggs, or the young, may have proved highly advantageous to their volant lifestyle and strong selection pressure for mass reduction and energy conservation.

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Changes in Climatic Water Balance Drive Downhill Shifts in Plant Species' Optimum Elevations

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Uphill shifts of species' distributions in response to historical warming are well documented, which leads to widespread expectations of continued uphill shifts under future warming. Conversely, downhill shifts are often considered anomalous and unrelated to climate change. By comparing the altitudinal distributions of 64 plant species between the 1930s and the present day within California, we show that climate changes have resulted in a significant downward shift in species' optimum elevations. This downhill shift is counter to what would be expected given 20th-century warming but is readily explained by species' niche tracking of regional changes in climatic water balance rather than temperature. Similar downhill shifts can be expected to occur where future climate change scenarios project increases in water availability that outpace evaporative demand.

Climatic warming during the 20th century has led to a variety of responses from biota (1), including changes in phenology for plants (2, 3) and animals (4, 5), and shifts in the geographic distributions of species poleward in latitude (6, 7) or uphill in elevation (8, 9). Because climate-change scenarios project warming during the 21st century (10), changes in the distributions of species are predicted to continue, with shifts toward higher elevations and latitudes projected for species that are able to track changes in temperature (11).

The assumption that temperature is the principal factor defining species' distributions ignores the fact that many species, including plants, are constrained by energy and water availability (12, 13). Consequently, considering changes in temperature alone may be inadequate for understanding distributional shifts of plant species. Consistent with this, there is ample evidence of stasis and even downhill shifts in species' distributions despite climatic warming (14–16). These seemingly inconsistent responses are attributed to changes in competitive interactions at range margins (17), human-induced landscape modification (14), lags in the effect of climatic warming (15), or idiosyncratic responses of individual species (18). As such, there has been limited progress in understanding the drivers of shifts in species' distributions and their associated mechanisms.

We sought to determine how the altitudinal distributions of vascular plant species in California, USA, have changed during the 20th century and whether changes, if any, could be attributed to changing climatic parameters. We defined our study area based on the availability of long-term climate station data and spatial coverage of vegetation survey data in both historical (1930–1935) and modern (2000–2005) time periods (19). This region includes approximately one-half of the state (177,000 km^2) and encompasses most of the major mountain ranges north of 35° latitude (Fig. 1). Mean annual temperatures in California increased by ~0.6°C during this time period, with warming occurring across the entire state (19). Changes in precipitation exhibited regional-

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scale variability, with increases across the northern portion of the state (19) that have resulted in a net decrease in the climatic water deficit (difference between potential evapotranspiration and precipitation) relative to the early 20th century (Fig. 2).

We quantified species' responses by analyzing shifts in species' optimum elevations, the elevation at which there is a maximum probability of occurrence within the species' altitudinal distribution (16). Using modern climate records and records from the early 20th century, we tested whether changes in optimum elevation were consistent with patterns of observed changes in climate (19). We quantified climatic water balance using climatic water deficit, a measure of the evaporative demand of a reference crop that is not met by precipitation and thus estimates drought at a site independent of that site's vegetation (12). Climate data from weather stations in our study area indicated a decrease in climatic water deficit of 100.0 mm [63.3 to 136.7 mm, 95% confidence interval (CI)] between the early and latter years of the 20th century (Fig. 2) and are consistent with a decreasing linear trend of 19.4 mm per decade from 1920 to 2005 (19) (Fig. 2 and fig. S1).

We used two temporally independent data sets of survey plots collected from the major mountain ranges of the state. The first data set comprised 13,746 survey plots sampled in the 1930s (19–21); the second was compiled from a variety of sources and comprised ~33,000 plots sampled from 2000 to 2005 (19). We conducted a subsampling procedure to remove potential sampling bias between the data sets (19), which left a balanced sample of 8747 plots in each period. We used interpolated climate surfaces representing 30-year monthly normals to extract climatic data from historical (1905–1935) and modern (1975–2005) plot locations (19, 22). We used logistic regression to estimate species' optimum elevations in each period, focusing on species with at least 50 occurrences that exhibited unimodal bell-shaped response functions in each period (16). Altitudinal shifts were measured as the difference in optimum elevation between periods.

We found significant downhill shifts in optimum elevations (mean difference = –88.2 m, t = –2.49, df = 63, P = 0.016), with a higher proportion of species shifting their distributions downhill [proportion (p) = 0.72, 95% CI = 0.59 to 0.82] than uphill (p = 0.28, 95% CI = 0.18 to 0.41) (Fig. 3). We found no changes in optimum climatic water deficit (mean difference = –11.1 mm, t = –0.20, df = 45, P = 0.843), with similar proportions shifting their distributions toward drier (p = 0.41, 95% CI = 0.27 to 0.57) and wetter conditions (p =

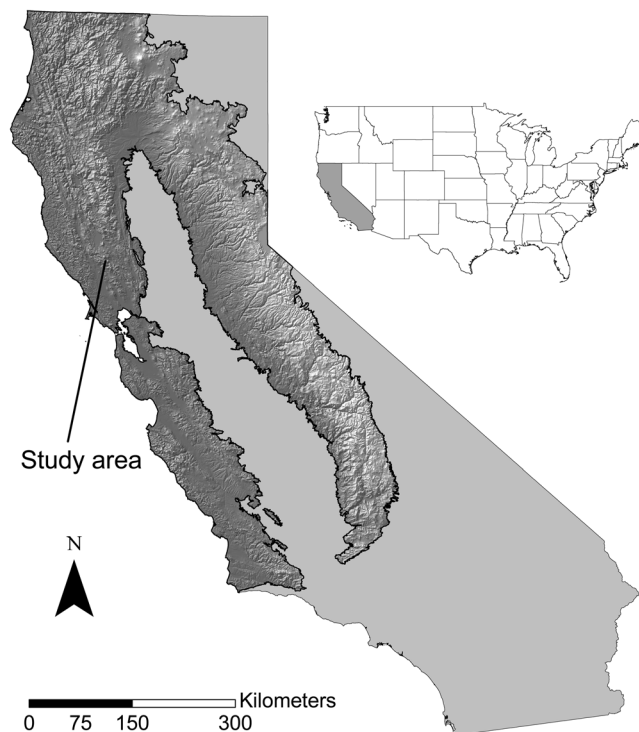**Fig. 1.** Portion of California used in study (~177,000 km²).

Study area

N

Kilometers
0   75   150   300

Fig. 2. Change in annual precipitation (**A**), potential evapotranspiration (**B**), and climatic water deficit (**C**) between historical (1920–1949) and modern (1976–2005) time periods at long-term meteorological stations in California, USA (study area outlined in black). Values expressed in mm and precipitation changes inverted for consistency with water deficit changes. Stations that exhibited statistically significant differences are shown by circles. Anomalies (red, positive; blue, negative) for mean annual temperature (**D**), potential evapotranspiration (**E**), annual precipitation (**F**), and climatic water deficit (**G**) were averaged across 33 climate stations from our study area. Solid curve represents a running mean of 11 years. Linear trend is indicated in each plot and is significant at the 90th percentile.
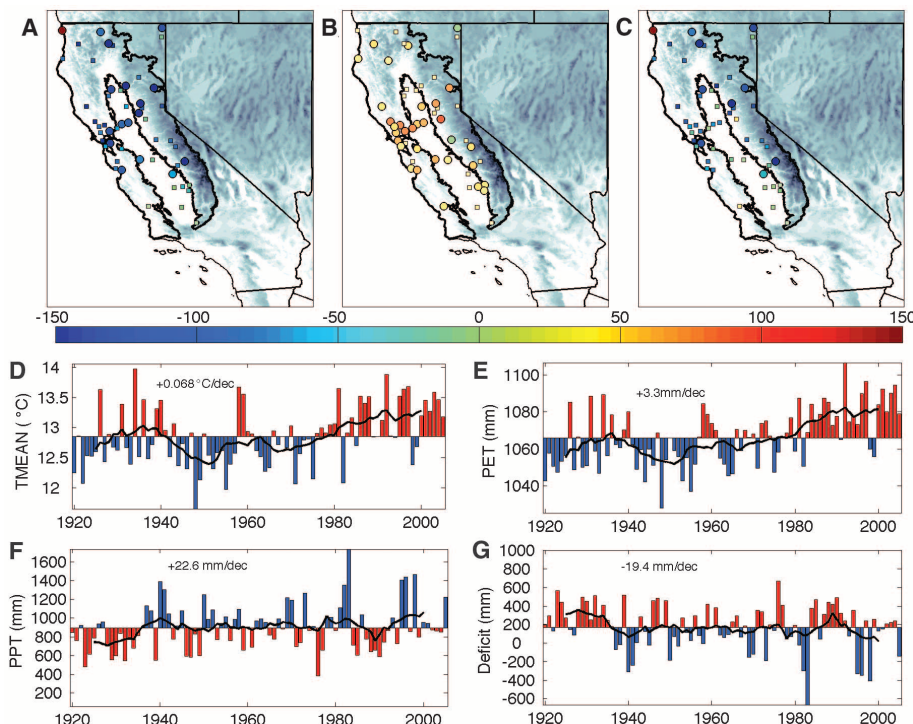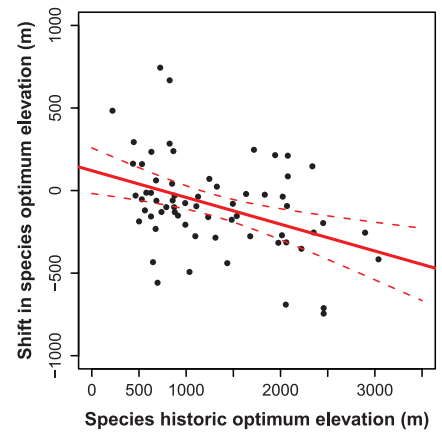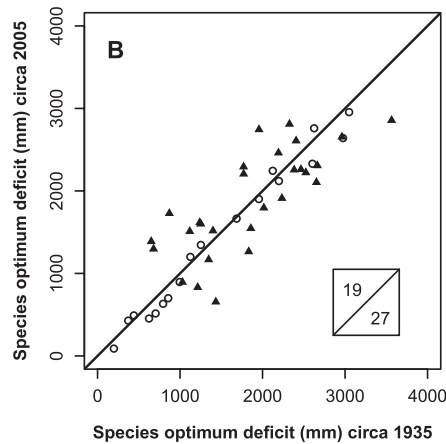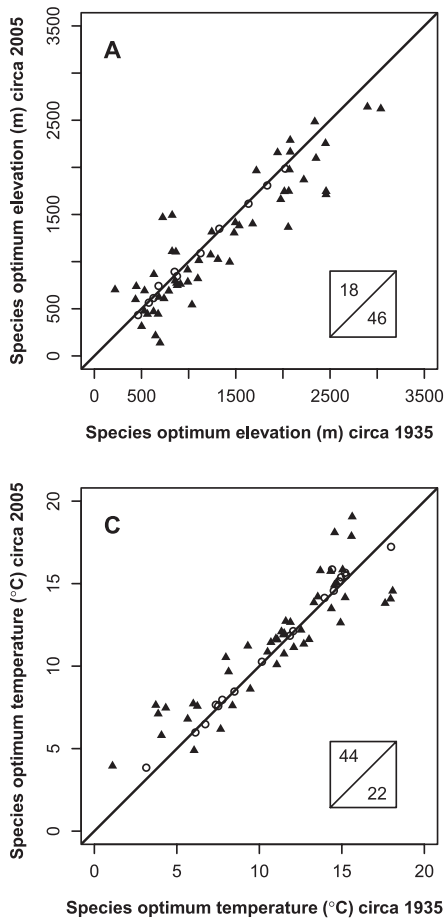
Fig. 3. Scatterplots of optimum elevation (**A**), climatic water deficit (**B**), and mean annual temperature (**C**) between historical (circa 1935) and modern (circa 2005) time periods. Each point represents a single species. Species below the diagonal represent species with decreasing optimums. Species with nonoverlapping 95% CIs around optimums between time periods are displayed as filled triangles (▲); species with overlapping 95% CIs are displayed as open circles (○). Insets represent number of species with increasing or decreasing optimums.

Fig. 4. Scatterplot of shift in optimum elevation (m) versus historical (circa 1935) altitudinal position (m) for plant species in California. Solid line represents linear regression model with 95% CI bands (as dashed lines).

0.59, 95% CI = 0.43 to 0.73) (Fig. 3). There was moderate evidence of increases in optimum temperatures experienced by species (mean difference = 0.37°C, $t = 1.87$, df = 65, $P = 0.067$), with a higher proportion of species shifting toward warmer conditions ($p = 0.67$, 95% CI = 0.54 to 0.78) than cooler conditions ($p = 0.33$, 95% CI = 0.22 to 0.46) (Fig. 3). Species traits were unrelated to shifts in optimums (Kruskal-Wallis tests, $P > 0.05$ for all comparisons) (19).

Plant species in our study area appear to be tracking their climatic niche by shifting their altitudinal distributions downhill in response to decreased climatic water deficit. These shifts represent niche tracking of changes in water availability rather than changes in temperature. Assuming constant temperature and precipitation lapse rates for our study area, we estimated that the observed historical changes in temperature and precipitation would result in a mean downward shift in optimum elevation of 85 m (95% CI - 64 to 106 m) (19), an interval that covers the observed change in mean optimum elevation (88.2 m downhill). The consistency of our results across a wide array of taxa (46 species from 17 families) (table S1) and broad geographic scale suggests that these are the effects of large-scale climatic drivers of species' distributions. One line of evidence to support this conclusion is that species with higher optimum elevations exhibited larger downhill shifts (linear model, $\beta_1 = -0.162$, $F =$

11.8, df = 62, $P = 0.001$) (Fig. 4). Regional changes in precipitation and temperature differentially alter the local climatic water balance across complex topography owing to the nonlinear relationship between temperature and vapor pressure deficit. Cooler and wetter sites at higher elevations would be expected to exhibit greater sensitivity to changes in precipitation, whereas warmer and drier sites at lower elevations would be expected to exhibit greater sensitivity to changes in temperature. Given the observed study area–wide increase in precipitation, we would thus expect downhill shifts to be more likely at wetter sites (higher elevations) (Fig. 4). Our results are also consistent with observational studies within the region showing an increase in the density of younger cohorts of tree species at lower elevations during the past century (18, 23). Further, we found no evidence of changes in the width of species' response curves between periods, which suggests that the observed shifts in elevation are occurring across their entire altitudinal distribution rather than at range margins (fig. S4). This, coupled with evidence of downhill shifts across the entire elevation gradient (Fig. 4), supports a widespread driver such as climate.

The assumption that plant species will move uphill to track increases in temperature does not account for coupled environmental constraints on their growth and persistence. We show that plant species in our study area are experiencing an in-

crease in their optimum temperature (0.36°C) due to both climatic warming and downhill shifts. For these organisms, the effects of warming on moisture balance are being offset by enhanced water availability. This combination of factors has likely increased net primary productivity in the region (24). Our findings highlight the importance of characterizing climatic water balance for understanding plant responses to climate change. Regional increases in climatic water balance have been identified elsewhere in the northern hemisphere (25), which suggests that downhill shifts by plant species may not be isolated to our study region. Most locations north of 45° latitude have experienced increased precipitation over the past century (10), and at continental scales, global climate models generally predict those locations to become wetter over the next century (10). If increases in precipitation outpace increases in evaporative demand in these regions, we can expect downhill shifts by species to occur.

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Raptor Nest Decorations Are a Reliable Threat Against Conspecifics

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Individual quality is often signaled by phenotypic flags, such as bright plumage patches in birds. Extended phenotype signals can similarly show quality, but in these cases the signals are external to the individual, often taking the form of objects scavenged from the environment. Through multiple manipulative experiments, we showed that objects used for nest decoration by a territorial raptor, the black kite (*Milvus migrans*), act as reliable threats to conspecifics, revealing the viability, territory quality, and conflict dominance of the signaler. Our results suggest that animal-built structures may serve as signaling devices much more frequently than currently recognized.

Animals transfer information through anatomical, physical, and behavioral traits, such as brightly colored body patches, extravagant ornaments, or size-revealing calls (*1–3*). Some species go to further extents by collecting objects to build external signaling structures or "extended phenotype signals" (*4*). Such external signals may involve higher cognitive abilities (*5*) and be subject to cultural transmission (*6*). Further, our ability to address questions about such signals are facilitated by the facts that (i) they are often flexible and less constrained than bodily traits (*4*) and (ii) their constituent materials may be readily available for experimental manipulation (*7, 8*). Despite the broader appeal, extended phenotype signals have been examined in only a handful of passerine bird and fish species, and these were almost exclusively structures built solely for mate attraction

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Fig. 1. Decoration of nests by black kites (*Milvus migrans*). (**A**) Highly decorated nest and (**B**) selection of materials by kites relative to their availability in the environment. Kites show a preference for white ($\chi^2 = 270.0$, $P < 0.0001$) plastic ($\chi^2 = 57.0$, $P < 0.0001$), whereas all other materials and colors are used at rates equal to (other materials $\chi^2 = 0.1$, $P = 0.76$) or less than (paper $\chi^2 = 68.1$, $P < 0.0001$; cryptic colors $\chi^2 = 77.2$, $P < 0.0001$; other colors $\chi^2 = 148.3$, $P < 0.0001$) their availability in the environment. [Photo credit: F. Sergio]