Letter

Genetically based demographic reconstructions require careful consideration of generation time

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Generation time (G), generally defined as the mean age at which individuals reproduce in a population, is a critical component of genetically based demographic reconstructions using coalescent models. In their recent study in *Current Biology*, Robinson *et al*.[1] present such a reconstruction with implications for understanding historical population sizes of Andean condors (*Vultur gryphus*), California condors (*Gymnogyps californianus*) and turkey vultures (*Cathartes aura*). However, here we argue that incorrect generation time estimates call into question their finding that the now critically endangered California condor once outnumbered the turkey vulture — currently the most abundant and widespread vulture in the Americas. Robinson *et al*.[1] use a G for condors of 10 years — less than half the true value, which we estimate to be ~25 years (Table S1). This shorter generation time inflates their historical effective population size (N_e) estimates, and their use of the same G for species with different life histories makes their relative abundance comparisons flawed. Here, we re-evaluate the findings of Robinson *et al*.[1] to highlight the importance of carefully estimating G in demographic reconstructions, especially for species of conservation concern.

Genetically based demographic reconstructions use genetic diversity patterns in contemporary individuals, along with an estimated mutation rate, to infer past N_e over time[2]. Mutation rates for these reconstructions are frequently derived from sequence divergence and estimated divergence times among taxa, yielding mutations per year, which is then converted to a per-generation mutation rate. For a fixed per-year mutation rate, increasing G linearly decreases N_e estimates but does not affect the overall shape of estimated N_e trends[2,3]. Therefore, misspecifications of G are especially problematic when comparing past population trajectories among species or when absolute historical N_e informs current conservation decisions.

Despite its importance, G is often not carefully defined or estimated when used in genetically based demographic reconstructions. There are several ways to define G[4,5], the most common being the mean age of parents at reproduction. In demographic reconstructions, authors sometimes estimate G as the age at first breeding, F, or twice the age at first breeding (Supplemental information), but we cannot find any published work validating these rules of thumb, which are not robust across species with different maturation, reproductive senescence or mortality rates. G can only be equal to age at first breeding for semelparous species, and thus this approach is inappropriate for most vertebrates. For birds, the ratio of G to F ranges from 1.1 to 6.7 ($\bar{X}$ = 2.5; Supplemental information) and for New World vultures (Cathartidae) from 1.7 to 5.3 ($\bar{X}$ = 2.8)[6]. Direct estimates of G rely on age-specific reproduction and survival[4], but G can be estimated with validated proxies using mean F and either adult mortality, M, or lifespan, L[6]. Although estimates of F, M and L are frequently unavailable, recently published analyses based on actual or model-derived estimates of these parameters report proxy-based G for all birds[6] and mammals[7]. We note that these recent analyses rely on current demographic rates, in which survival, and thus G, is likely to be lower than it would be in the absence of anthropogenic threats.

Robinson *et al*.[1] apply the same G to three cathartid vultures — Andean condors, California condors and turkey vultures — highlighting results for a G of 10 years, but also reporting results for G of five and 15 years. All three G values are substantial underestimates for both condor species, while five years is even below their mean age of first breeding (F, Table 1). Using readily available demographic data and validated proxies, we estimate G at 25 and 26 years for California and Andean condors, respectively, and at seven years for turkey vultures (Table 1). Robinson *et al.*[1] justify equal G, stating that even if G differs now, over evolutionary time it should be the same. However, the condor species diverged ~7 to 14 MYA from a common ancestor with turkey vultures[1] and almost certainly had demographic rates that precluded an equivalent G for the time interval of the reconstruction by Robinson *et al*.[1] California and Andean condors inherently have extremely low reproductive and mortality rates and are among the largest and most long-lived birds, while turkey vultures weigh <25% of the condor species, have higher reproductive and mortality rates, and a markedly shorter lifespan (Table 1).

Because the analyses of Robinson *et al*.[1] are based on estimated per-year mutation rates, their estimated N_e values scale linearly with G[2,3]. After rescaling with more plausible G values (Table 1), estimated California condor N_e never exceeds that of turkey vultures. Indeed, using our G values, the estimated turkey vulture N_e 10,000 years ago was 6 and 23 times higher than that of Andean and California condors, respectively, consistent with the turkey vulture's larger ancestral range and broader ecological niche.

California condors have suffered a severe population and genetic bottleneck[8], and population estimates prior to their declines are unavailable; therefore, estimating their historical N_e through demographic reconstructions may provide useful context when establishing conservation targets. Unfortunately, by assigning the same G to these three cathartids and implicitly assuming they have similar life histories, Robinson *et al*.[1] erroneously concluded that California condors were more numerous than turkey vultures 0.2–1 million years ago, an ecological comparison that could sharply alter recovery goals. Our rescaling indicates that California

Table 1. Corrected estimates of generation time (G) and historical effective population size (N_e).

Species	Age at first breeding, F^a	Clutch size	Breeding interval	Adult survival, S^b	Life span, L^c	Mass (kg)	Current population size (1000s)	G	G source	N_e (1000s)	
										10 KYA	0.2–1 MYA
California condor, *Gymnogyps californianus*	7	1	1–2	0.95	60	8.5	0.5	10	Robinson *et al.*[1]	0.5	35.0
								25	This study[d]	0.2	14.0
Andean condor, *Vultur gryphus*	10[e]	1	1.5–2	0.94	60	11	6.7	10	Robinson *et al.*[1]	2.0	10.0
								26	This study[d]	0.8	3.8
Turkey vulture, *Cathartes aura*	3[e]	2 (range 1–3)	1	0.79	17	2	13000	10	Robinson *et al.*[1]	3.0	17.0
								7	This study[d]	4.6	26.2

Life history traits for three cathartid vultures highlighted in *Robinson et al.*[1] and our corrected G and N_e estimates based on these traits. Ages and breeding intervals are given in years. See Table S1 for additional G estimates and expanded notes and references, including sources for demographic data.
[a]Estimated mean age of first breeding or age at which half the population has initiated breeding.
[b]Reported contemporary adult survival rates. Survival rates in the absence of modern anthropogenic threats are likely higher.
[c]Life span, defined as maximum longevity, is unknown for all three species but estimated to be greater than or equal to the values given, based on limited records.
[d]Mean of relative lifespan proxy and adult mortality proxy based on F, S, and L values reported in this table. Relative lifespan proxy defined as $G = F + z(L - F)$. z scales reproductive lifespan ($L - F$) to account for reproductive senescence. z was set to 0.236 for turkey vultures and 0.317 for condors based on[6]. Adult mortality proxy defined as $G = F - 1 + [1/(1 - S)]$. See Table S1 for additional details and sources.
[e]Age at first breeding for Andean condors is unknown, but captive birds have been reported to breed at age 8. Age at first breeding is unknown for turkey vultures, but breeding behavior has been observed in two-year olds.

condors were never more numerous than turkey vultures and their populations 10,000 years ago were likely <5% that of turkey vultures, and ~25% that of Andean condors.

The use of genetically based demographic reconstructions, such as the Markovian coalescent methods used by Robinson *et al.*[1], can be valuable for inferring population histories of endangered species but require numerous assumptions and parameter estimates that can directly and seriously influence results[9]. We focus here on G, yet cross-species comparisons must also carefully consider specification of a mutation rate and other assumptions of coalescent models that may be violated, potentially confounding the interpretations of historical N_e. We urge particular caution when applying these methods to species of conservation concern, where biased estimates could contribute to inefficient management or the establishment of unrealistic conservation goals.

SUPPLEMENTAL INFORMATION

Supplemental information includes one figure and one table and can be found with this article online at https://doi.org/10.1016/j.cub.2022.03.048.

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AUTHOR CONTRIBUTIONS

V.J.B., M.E.F., and S.K. conceived of the manuscript; V.J.B., M.E.F., J.D., D.F.D., and S.K. wrote the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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