Title: Estimating the extinction date of the thylacine accounting for unconfirmed sightings

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Summary

The thylacine, or Tasmanian tiger, was one of Australia's most characteristic megafauna, and was the largest marsupial carnivore until hunting, and potentially disease, drove them to extinction in 1936[1–3]. Current knowledge suggests the thylacine became extinct on mainland Australia two millennia prior to its eradication on Tasmania, but recent "plausible" sightings on the Cape York Peninsula have emerged, leading some to speculate the species may have escaped extinction mostly undetected[4]. Here we show that sighting evidence indicates the continued survival of the thylacine would be entirely implausible based on current mathematical theories of extinction. We present a sightings dataset including physical evidence, expert-validated sightings, and unconfirmed sightings leading up to the present day, and use a Bayesian framework that takes all three types of data into account, by modelling them as independent processes, to evaluate the likelihood of the thylacine's persistence[5]. Although the last captive thylacine died in 1936, our model suggests the most likely extinction date would be 1940, or at the latest the 1950s. We validated this result by analysing our dataset with other frequently used extinction estimator methods, all of which confirm that the thylacine's extinction likely fell within the interval of 1936-1943. Even the most optimistic scenario suggests the species did not persist beyond the 1960s. The search for the thylacine, much like similar efforts to "rediscover" the Ivory-Billed Woodpecker and other recently extinct charismatic species[6], is likely to be fruitless—especially given that persistence on Tasmania would have been no guarantee the species could reappear in regions that had been unoccupied for centuries. The search for the Tasmanian tiger may become a rallying point for conservation and wildlife biology in the coming years, and could indirectly help fund and support critical research in understudied areas like Cape York[7]. However, our results suggest that attempts to rediscover the thylacine will likely be unsuccessful.

Estimating the extinction date of the thylacine accounting for unconfirmed sightings

The history of conservation biology has included a few exceptional errors, in which experts have pronounced a species extinct only to be later disproven by its reappearance. Perhaps most famous are "Lazarus" taxa known originally from the fossil record, like the coelacanth (*Latimeria* sp.) or the dawn redwood (*Metasequoia* sp.); but recent extinctions can also sometimes be overturned, like that of the Bermuda petrel (*Pterodroma cahow*). Just this year, the rarest dog in the world, the New Guinea highland wild dog (*Canis lupus dingo*), was rediscovered after an absence beginning in 1976 (with at least two unconfirmed sightings including unconfirmed evidence in the interim). Hope of rediscovering an "extinct" species can inspire volumes of peer-reviewed research, and sometimes a single controversial sighting[6] can be enough to reignite controversy and justify seemingly-endless field investigation, as in the ongoing search for the Ivory-Billed Woodpecker (*Campephilus principalis*) despite all odds.[8] In Queensland, a similar story is beginning, as two recent unconfirmed sightings have inspired a new search for the thylacine (*Thylacinus cynocephalus*).

The thylacine, also frequently called the Tasmanian tiger or marsupial wolf, has been presumed extinct since the last captive specimen died on September 7, 1936.[1] Thylacines are believed to have gone extinct on the Australian mainland roughly two millennia ago, persisting as Tasmanian island endemics[9]. State-sponsored eradication in Tasmania began in 1886 and continued until 1909, driving a devastating population crash.[1] Theoretical models indicate that the eradication campaign, in combination with prey declines, could have been sufficient extinction pressure[2]; but other research strongly suggests a disease similar to canine distemper could have helped drive the species to extinction[3,10]. While its mechanism has been a topic of speculation, the status of the thylacine's extinction has been essentially unchallenged in peer-reviewed literature. However, sightings have continued until as recently as late 2016 throughout Tasmania and mainland Australia, often gathering international media attention. Recently, two unconfirmed "detailed and plausible" sightings in the Cape York Peninsula of northern Queensland have sparked renewed interest in the thylacine's persistence, particularly in the Australian mainland; researchers currently intend to investigate those sightings with a camera trap study beginning in Cape York later this year.[4]

Is there empirical support for this most recent search? Extinction date (τ_E) estimators have been a key part of parallel debates about the Ivory-billed Woodpecker; what little work has been done on the thylacine places τ_E in 1933-1935, with only one model (using temporally-subsetted data) suggesting the species might be extant.[11] These methods are sensitive to inaccurate data and false sightings, but more recently developed Bayesian models differentiate between the processes of accurate and false sightings explicitly, and allow researchers to include uncertain sightings in models as a separate class of data.[5] Here, we apply those models (and several other frequently used extinction date estimators) to 20th and 21st century thylacine sightings, and ask: what is the probability that the species might be rediscovered?

Our study considers the only optimistic modeling scenario for the thylacine's persistence, and includes valid sightings from Tasmania alongside highly questionable sightings from Australia, despite the species' eradication two millennia earlier on the continent. (That scenario, in itself, is fairly implausible; in the supplement, we present an analysis using only confirmed sightings from Tasmania, which could be considered a more realistic analysis of the probability the thylacine could have persisted in Tasmania alone). We used the sightings and specimens from Sleightholme & Campbell (2016) (1900-1982)[1], sightings from Heberle (2004) (1939-1998)[12], and records detailed on public websites of interested citizen groups (www.tasmanian-tiger.com, www.thylacineresearchunit.org, and www.thylacineawarenessgroup.com) supplemented by web searches for news media stories from 2007-2016. For each year between 1900 and 2016, we recorded the maximum level of certainty of records. Records were scored as confirmed specimens (e.g., from bounty records, museum specimens, or confirmed captures), confirmed sightings (sightings agreed as valid by experts), and unconfirmed sightings (sightings not considered valid by experts; **Figure 1**). Because there are also likely unreported unconfirmed sightings, we also ran models assuming that an unconfirmed sighting occurred in every year from 1940-2016 (**Supplementary Information**). For all analyses, we considered the species across its historical range (i.e., mainland Australia and Tasmania). All R code and more detailed data is available in the S.I.

The Bayesian model we use, which explicitly differentiates sightings by certainty, suggests a negligible probability that the thylacine might have persisted later than the 1940s, with 1940 as the most likely value of τ_E, and the posterior likelihood declining rapidly thereafter (**Figure 2**). Including unconfirmed sightings for years with no data did not change the probability distribution (**see S.I.**). Other, non-Bayesian estimators all strongly agreed with these findings. The optimal linear estimator (OLE) is considered the most robust of those tools[13], and has been applied to other high-profile extinctions like that of the dodo (*Raphus cucullatus*).[14] Using only confirmed specimens provides an OLE extinction date of 1939 (95% confidence interval: 1937-1943); adding confirmed sightings did not change the estimated extinction date or confidence interval. Most other commonly used extinction estimators concur with these findings, with Robson & Whitlock's method[15] (producing by far the latest estimate) approaching the 1960s (**see S.I.**).

In our assessment, there is only an extremely low probability that the thylacine could be extant (Bayes factor = 6.21524×10^{13}, or a probability of 1 in 1.6 trillion). Based on the results of our primary model, it remains fairly plausible that the thylacine's extinction could have occurred up to a decade later than believed. But for thylacines to appear in 2017, especially in an area where they are believed to have been absent for two millennia, is highly implausible. The two sightings from Cape York describe as "detailed" and "plausible" may be so, from a strictly zoological perspective; but from a modeling standpoint, they fit neatly into a pattern of ongoing, false sightings that follows nearly any high-profile extinction. Models can be wrong, and new data may overturn a century of common knowledge in what could be one of the most surprising re-discoveries in conservation history. But if the story of the Ivory-Billed Woodpecker offers any parallels, camera trap evidence is more likely to produce blurry evidence that might match the profile of a thylacine and sustain ongoing controversy, while producing little change in the state of scientific consensus.

The hope to rediscover extinct species is one of the most powerful emotional forces in conservation biology, and can bring attention to threatened species and ecosystems while igniting public interest (and funding) in science[7]. The search for the thylacine may reap those benefits, and the proposed 2017 search has already gathered significant attention from journalists and social media. Moreover, the camera trap data that will be collected during the search for the thylacine in Cape York will undoubtedly be valuable for many other conservation studies. But the ongoing search for extinct species, in the broader scheme, likely drains critical funds that the conservation of near-extinction species desperately requires. One estimate suggests 7% of some invertebrate groups may already have gone extinct—at which rate, 98% of extinctions would be going entirely undetected[16]. Globally, 36% of mammal species are threatened with extinction (classified as Vulnerable, Endangered of Critically Endangered), including 27% of native Australian mammals[17], and often limited resources can be better spent reversing those declines, than chasing the ghosts of extinction past.

Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions. C.J.C. designed the study; A.L.B assembled the dataset. All authors developed code, analyzed the data, and wrote the manuscript.

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Methods.

Data Availability

Our study utilizes a compendium of sightings gathered from previous studies on the thylacine (**Table S1**). The majority are taken from Sleightholme & Campbell's (2016) appendix[1], which includes 1167 geo-referenced post-1900 sightings classified as a capture, kill, or sighting. For each year from 1900-1939, we used the sighting of the highest evidentiary quality, with captures or killed individuals being confirmed specimens. Additional sightings were taken from Heberle (2004)[12], and Internet searches for recent news media reports.

Bayesian Extinction Estimators

The primary model we employ in our paper is the latter of a pair developed by Solow & Beet[5] to address the independent process of accurate and inaccurate sightings. While the rate of valid sightings is likely to change leading up to an extinction event, after extinction that rate remains constant (at zero) and all sightings are presumed inaccurate. The sighting dataset t occurs over an interval $[0,T)$, where $0 \leq \tau_E < T$. During the interval $[0, \tau_E)$, valid sightings occur at rate Λ while invalid sightings occur at rate Θ, meaning that valid sightings occur at proportion

$$\Omega = \frac{\Lambda}{\Lambda + \Theta}$$

It is assumed further that certain sightings occur – at an independently determined rate – which divides the dataset of sightings t into certain sightings t_c and uncertain sightings t_u. The likelihood of the data conditional on τ_E is given as

$$p(t|\tau_E) = p(t_c|\tau_E)p(t_u|\tau_E)$$

These two values are calculated using n_c (the number of certain sightings, all before τ_E), and n_u (the number of uncertain sightings), where $n_u(\tau_E)$ are the subset recorded before τ_E, and ω acts as a dummy variable replacing Ω:

$$p(t_c|\tau_E) = \frac{(n_c - 1)!}{(\tau_E)^{n_c}}$$

$$p(t_u|\tau_E) = \int_0^1 \left[\omega^{-n_u}(1-\omega)^{n_u - n_u(\tau_E)}\left(\tau_E + \frac{1-\omega}{\omega}T\right)^{-n_u}\right] d\omega$$

In the main manuscript, we present that likelihood $p(t|\tau_E)$ calculated as the product of those two terms; however, the likelihood a species is presently extinct can be calculated a Bayes factor, which can be treated as the odds that the species went extinct in the interval $[0,T)$, which they denote as an event E (with alternate hypothesis $\bar{E}$). Based on some prior distribution set for $p(\tau_E)$, the posterior probability the species went extinct in the interval of observation is

$$p(t|E) = p(\mathrm{t}|\tau_E)p(\tau_E)$$

The alternate probability $p(t|\bar{E})$ can be calculated by evaluating the same expression given above for $p(\mathrm{t}|\tau_E)$ at $\tau_E = T$. The Bayes factor is subsequently given as

$$B(t) = \frac{p(t|E)}{p(t|\bar{E})}$$

Other Extinction Estimators

We also include several other non-Bayesian estimators, readily derived using the R package 'sExtinct' v1.1.[18] Were we to include every unconfirmed, controversial sighting continuing up to 2016, all methods indicate that the species would likely be extinct. Consequently, we limit the implementation of other methods to two practical applications, examining how results change by either including (a) only confirmed, uncontroversial specimens and (b) both confirmed specimens and confirmed sightings (**Figure S1**).

Among the methods that we include, Robson and Whitlock[15] suggested a nonparametric method based only on the last two sightings:

$$\tau_E = t_k + (t_k - t_{k-1})$$

In this study, that estimator consistently suggests the latest τ_E (see **Figure S1**). A more middle-of-the-road estimator, the optimal linear estimator (OLE) method is typically considered the most robust non-parametric extinction estimator.[14] Based on a subset of the last *s* sightings of *k* total:

$$\tau_E = \sum_{i=1}^{s} w_i t_{k-i+1}$$

Where *b* is a vector of *s* 1's and

$$w = (b'\Lambda^{-1}b)^{-1}\Lambda^{-1}b$$

such that Λ is a square matrix of dimension *s* with typical element

$$\Lambda_{\mathrm{ij}} = \frac{\Gamma(2\hat{v} + i)\Gamma(\hat{v} + j)}{\Gamma(\hat{v} + i)\Gamma(j)}$$

$$\hat{v} = \frac{1}{s-1}\sum_{i=1}^{s-2} \ln \frac{t_k - t_{k-s+1}}{t_k - t_{s+1}}$$

The results of these analyses, as well as three other (weaker) extinction estimators, are presented in **Figure S1**.

Sensitivity Analysis

As there is likely an unknown number of unreported unconfirmed sightings after 1940, we also considered a case where we assumed unconfirmed sightings occurred annually from 1940-2016 to ascertain the "best case" scenario in the absence of a confirmed sighting or specimen. The extinction date estimated using the Bayesian model was 1940 (Bayes factor: 4.53×10^{13}), an identical date as our original model, and with a certainty in the same order of magnitude (**Figure S2**).

Data Availability

All sighting data is available in **Table S1**. All scripts in R to implement both sExtinct and the Solow & Beet method are available as a supplemental file. The authors declare that all data supporting the findings of this study are available within the paper and its supplementary information files.

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Figures

Figure 1. Thylacine sighting data. Specimens are treated as an absolute, certain form of evidence, while expert-verified sightings are treated as an intermediate level of certainty. Controversial sightings, or indirect evidence based on scat or tracks, are classified as unconfirmed sightings, the weakest source of evidence. More detailed sighting data is available in **Table S1.**

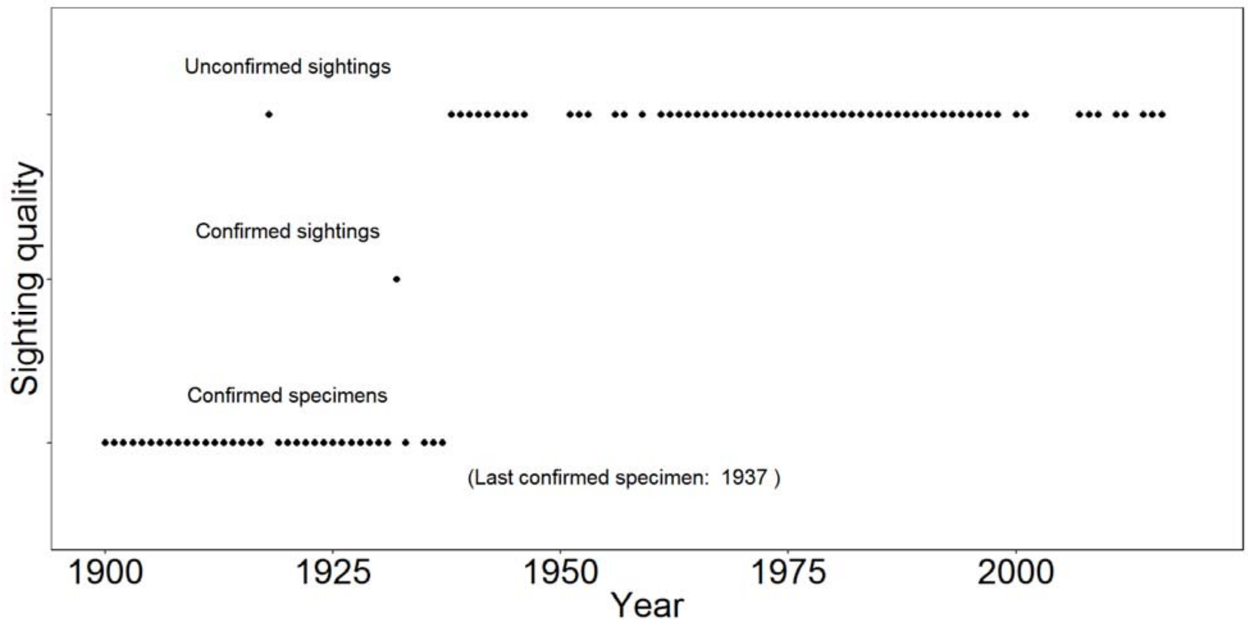

Figure 2. The likelihood of thylacine persistence over time. The figure presents the posterior probability of a given extinction date τ_E scaled by the area under the entire likelihood curve. In Solow & Beet's model, specimen-based records are treated separately and as certain observations (see **Methods**); consequently evaluation begins in 1937, the year of the last certain sighting (i.e., extinction prior to that date is not considered).