





Estimating the extinction date of the thylacine with mixed certainty data

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Abstract: *The thylacine (Thylacinus cynocephalus), one of Australia's most characteristic megafauna, was the largest marsupial carnivore until hunting, and potentially disease, drove it to extinction in 1936. Although thylacines were restricted to Tasmania for 2 millennia prior to their extinction, recent so-called plausible sightings on the Cape York Peninsula in northern Queensland have emerged, leading some to speculate the species may have persisted undetected. We compiled a data set that included physical evidence, expert-validated sightings, and unconfirmed sightings up to the present day and implemented a range of extinction models (focusing on a Bayesian approach that incorporates all 3 types of data by modeling valid and invalid sightings as independent processes) to evaluate the likelihood of the thylacine's persistence. Although the last captive individual died in September 1936, our results suggested that the most likely extinction date would be 1940. Our other extinction models estimated the thylacine's extinction date between 1936 and 1943, and the most optimistic scenario indicated that the species did not persist beyond 1956. The search for the thylacine, much like similar efforts to rediscover other recently extinct charismatic taxa, 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 millennia. The search for the thylacine may become a rallying point for conservation and wildlife biology and could indirectly help fund and support critical research in understudied areas such as Cape York. However, our results suggest that attempts to rediscover the thylacine will be unsuccessful and that the continued survival of the thylacine is entirely implausible based on most current mathematical theories of extinction.*

Keywords: sighting record, Tasmania, Tasmanian tiger

Estimación de la Fecha de Extinción del Tilacino con Datos Mixtos de Certidumbre

Resumen: *El tilacino (Thylacinus cynocephalus), una de las especies de megafauna más características de Australia, era el carnívoro marsupial más grande hasta que la caza, y potencialmente las enfermedades, lo llevó a la extinción en 1936. Aunque los tilacinos estuvieron restringidos a Tasmania durante dos milenios previos a su extinción, recientemente han emergido presuntos avistamientos plausibles en la península de Cape York al norte de Queensland, lo que ha llevado a algunos a especular que la especie pudo haber persistido sin ser detectada. Recopilamos un conjunto de datos que incluyó evidencia física, avistamientos validados por expertos, y avistamientos sin confirmación hasta el día de hoy, e implementamos una gama de modelos de extinción (enfocados en la estrategia bayesiana que incorpora los tres tipos de datos al modelar avistamientos válidos e inválidos como procesos independientes) para evaluar la probabilidad de la persistencia del tilacino. Aunque el último individuo cautivo murió en septiembre de 1936, nuestros resultados sugirieron que la fecha más probable de extinción habría sido en 1940. Nuestros otros modelos de extinción estimaron la fecha de extinción del tilacino entre 1936 y 1943, y el escenario más optimista indicó que la especie no persistió más allá de 1956. Es probable que la búsqueda del tilacino, como muchos esfuerzos similares para*

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redescubrir a otros taxones carismáticos recientemente extintos, sea infructífera, especialmente debido a que la persistencia en Tasmania no habría sido garantía de que la especie pudiera reaparecer en regiones que no habían sido ocupadas durante milenios. La búsqueda del tilacino podría convertirse en un punto de reunión para la biología de la conservación y de la vida silvestre y podría ayudar indirectamente a financiar y a apoyar investigaciones críticas en áreas que no han sido estudiadas suficientemente, como Cape York. Sin embargo, nuestros resultados sugieren que los intentos por redescubrir al tilacino no serán exitosos y que la supervivencia continuada del tilacino es completamente implausible con base en las teorías matemáticas de extinción más recientes.

Palabras Clave: registro de avistamientos, Tasmania, tigre de Tasmania

摘要: 澳洲最具代表性的动物群之一的袋狼 (*Thylacinus cynocephalus*) 曾是当地最大型的有袋类食肉动物, 然而捕猎及可能的疾病导致它在 1936 年灭绝。尽管袋狼在灭绝前两千年内仅在塔斯马尼亚岛有分布, 但近期在昆士兰北部的约克角半岛出现了所谓的疑似目击记录, 这使人推测这个物种可能在没有被人类发现的情况下存活至今。我们收集了实物证据、专家证实的目击记录以及至今为止未确认的目击数据构建数据集, 用一系列灭绝模型 (重点关注一种贝叶斯方法, 该方法把已证实和未证实的目击记录作为独立过程建模, 并整合所有三种类型的数据) 评估了袋狼存活的可能性。虽然最后一只圈养个体死于 1936 年 9 月, 但我们的结果表明袋狼最有可能的灭绝时间是 1940 年。其它灭绝模型估计袋狼的灭绝时间在 1936–1943 年, 在最乐观的情况下这个物种的存活也不超过 1956 年。搜寻袋狼, 就像试图重新发现其它近期灭绝的神秘类群一样, 很可能是徒劳的, 特别是考虑到袋狼在塔斯马尼亚岛的存活也不能保证这个物种能重新出现在它几千年内都没有占据的地区。而对袋狼的搜寻或能号召人们关注保护和野生动植物的生物学, 并间接地为在研究不足的地区 (如约克角) 的关键研究带来资金和支持。然而, 我们的结果还是表明重新发现袋狼的努力不会成功, 基于现有大多数的灭绝数学理论, 袋狼的持续幸存是完全不可信的。【翻译: 胡怡思; 审校: 魏辅文】

关键词: 袋狼, 塔斯马尼亚岛, 目击记录

Introduction

The history of conservation biology has included a few exceptional errors, in which experts have pronounced a species extinct only for it to be later rediscovered. Perhaps, most famous are Lazarus taxa known originally from the fossil record (e.g., the coelacanth [*Latimeria* sp.] and dawn redwood [*Metasequoia* sp.]), but even recently declared species extinctions can also sometimes be overturned. Hope of rediscovering a supposedly extinct species can inspire volumes of peer-reviewed research, and sometimes a single controversial sighting (e.g., Fitzpatrick et al. 2005) 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 (National Audubon Society 2016). Similarly, in Queensland, Australia, 2 unconfirmed sightings in early 2017 have inspired a new search for the thylacine (*Thylacinus cynocephalus*).

The thylacine, or Tasmanian tiger, has been presumed extinct since the last captive specimen died on 7 September 1936 (Sleightholme & Campbell 2016). Thylacines are believed to have gone extinct on the Australian mainland 2 millennia ago, thereafter persisting only as Tasmanian endemics (Paddle 2002). State-sponsored eradication in Tasmania between 1886 and 1909 caused a devastating population crash (Sleightholme & Campbell 2016). This eradication campaign, combined with prey declines, could have been sufficient extinction pressure (Prowse

et al. 2013), but other research strongly suggests that a disease similar to canine distemper could have helped drive the species to extinction (De Castro & Bolker 2005; Paddle 2012). Although the mechanism has been a topic of debate, the extinction status of the thylacine has been essentially unchallenged in peer-reviewed literature. Despite this, sightings have continued throughout Tasmania and mainland Australia, often gathering national and international media attention. In January 2017, 2 unconfirmed “detailed and plausible” sightings in the Cape York Peninsula in northern Queensland sparked renewed interest in the thylacine’s persistence, particularly in the Australian mainland. Researchers currently intend to investigate those sightings with camera traps later this year (James Cook University 2017).

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 from 1933 to 1935; only 1 model (using temporally subsetted data) suggests the species might be extant (Fisher & Blomberg 2012). A subsequent study suggested that based on search effort, thylacine’s body size, and former density, they would have been rediscovered by 1983 if they were still extant (Lee et al. 2017b). These methods exclude sightings data, but recently developed Bayesian models differentiate between the processes of verified and unverified sightings explicitly, allowing researchers to include uncertain sightings in models as a separate class of data (Solow & Beet 2014). We applied those

models (and several other extinction date estimators) to thylacine sightings and asked: What is the probability that the species might be rediscovered?

Methods

Most of the sightings in our data set are from Sleightholme and Campbell’s (2016) appendix (covering 1937–1980), which includes 1167 post-1900 sightings classified as a capture, kill, or sighting and Smith et al.’s (1981) summary of 243 sightings from 1936 to 1980. Additional sightings were compiled from Heberle (2004), records on public websites maintained by interested citizen groups (www.tasmanian-tiger.com, www.thylacineresearchunit.org, and www.thylacineawarenessgroup.com), and online news stories from 2007 to 2016. We scored records as 1, physical evidence (e.g., from bounty records, museum specimens, or confirmed captures); 2, confirmed sighting (sightings agreed as valid by experts); or 3, unconfirmed sighting (sightings not considered valid by experts) (Fig. 1). For each year from 1900 to 1939, we used the sighting of the highest evidentiary quality; captures or killed individuals were physical evidence ($n = 101$) (Supporting Information). Our assembled data set spanned from 1900 to 2016 and included the last confirmed specimen collected in 1937. Thirty-six of the years included confirmed sightings. There was only 1 instance of an expert sighting without physical evidence (1932). The remaining sightings in the data set were unconfirmed sightings. Although this reduction to 1 record per year was required by only some models, we aimed for data consistency across methods. Because there were also likely unreported unconfirmed sightings, we also ran models based on the assumption that an unconfirmed sighting occurred annually from 1938 (the 1st year with no verified sightings or specimens) to 2016, which produced a marginally higher chance of persistence but

without changing the overall conclusions (Supporting Information).

For all analyses, we considered the species across its historical range (i.e., mainland Australia and Tasmania) and included valid sightings from Tasmania alongside highly questionable sightings from mainland Australia, despite the species’ supposed extirpation 2 millennia earlier on the continent. We considered this the only optimistic modeling scenario for the thylacine’s persistence in which recent high-profile sightings could be valid, even if it represents one of the most biologically implausible scenarios. In Supporting Information, we present an analysis in which we used only confirmed sightings from Tasmania, which could be considered a more realistic analysis of the probability that the thylacine persisted on Tasmania alone (although this would fail to explain the most controversial recent sightings throughout mainland Australia) (Supporting Information).

Bayesian Extinction Estimators

Methods to estimate extinction dates from time series data have been popular in conservation biology since the 1990s, but the majority fail to account for the variability in quality and certainty of most sighting records (Boakes et al. 2015). However, several Bayesian methods have been developed recently that incorporate variable sighting quality, including unconfirmed sightings, in estimation of extinction date. These methods rely on the assumption that the probability a species is extinct (an event E), based on a time series of sightings $t = (t_1, \dots, t_n)$, is expressed by Bayes’ theorem:

$$P(E|t) = \frac{P(t|E)}{p(t)} P(E) = \frac{P(t|E)P(E)}{p(t|E)p(E) + p(t|\bar{E})(1 - p(E))} \quad (1)$$

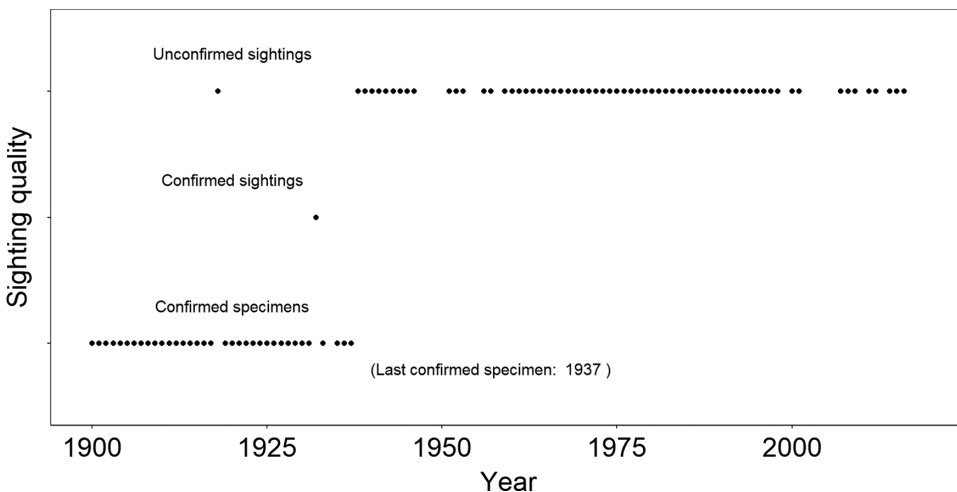


Figure 1. Thylacine sighting data (confirmed specimens, absolute and certain form of evidence; confirmed sightings, expert-verified sightings of intermediate level of certainty; unconfirmed sightings, controversial sightings or indirect evidence based on scat or tracks, weakest source of evidence).

and where \bar{E} is the scenario that the species is not extinct within the period in question. The prior probability of extinction $P(E)$ can often be hard to define, although it is sometimes uninformatively set to 0.5 for explicit estimation of $P(E|t)$. However, the Bayes factor can be used as a test of support for E where

$$B(t) = \frac{p(t|E)}{p(t|\bar{E})} \tag{2}$$

(although it can be formatted in reverse in some studies, as in the case of Lee et al. [2014], given the probability that a species persists). The relationship between the Bayes factor and the probability of the species' extinction is given as

$$P(E|t) = \frac{1}{\left(1 + \frac{1-P(E)}{P(E)B(t)}\right)} \tag{3}$$

Consequently, with an uninformative prior,

$$P(E|t) = \frac{B(t)}{B(t) + 1}, \tag{4}$$

and given a sufficiently large Bayes factor, the probability of persistence is

$$P(\bar{E}|t) = \frac{1}{B(t) + 1} \approx \frac{1}{B(t)}. \tag{5}$$

A handful of extinction-date estimation methods have been developed using Bayesian frameworks that allow estimation of the Bayes factor and thereby support hypothesis testing. The set of models on which we focused were first developed by Solow et al. (2012), who proposed a method in which all sightings leading up to a date t_L (the date of the last certain sighting) were certain and those after t_L were uncertain. Valid and invalid sightings were generated by stationary Poisson processes with different rates, but certain and uncertain sightings had the same rate (Solow et al. 2012). A more recent revision (Solow & Beet 2014) proposes 2 major modifications. In the first modification (model 1), the same assumptions are made as in the original method, except that uncertain sightings are permitted before t_L . The second modification (model 2, which we used) differs more notably in that it also treats certain and uncertain sightings as independent Poisson processes. This model is recommended for cases in which certain and uncertain sightings “differ qualitatively,” as in our study. For example, we note that blurry photographic or video evidence and crowdsourced sighting records from citizen groups are unique issues for later, uncertain thylacine sightings. Therefore, this model is more appropriate than model 1 (or the model from Solow and Beet 2012) for our study.

In Solow and Beet's (2014) model 2, although 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 unconfirmed. The

sighting data set 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 , whereas invalid sightings occur at rate Θ , meaning that valid sightings occur at proportion

$$\Omega = \frac{\Lambda}{\Lambda + \Theta}. \tag{6}$$

Confirmed sightings occur, at an independently determined rate, which divides the data set of sightings t into confirmed sightings t_c and unconfirmed sightings t_u . The likelihood of the data conditional on τ_E is given as

$$p(t|\tau_E) = p(t_c|\tau_E)p(t_u|\tau_E). \tag{7}$$

These 2 values are calculated using n_c (the number of confirmed sightings, all before τ_E) and n_u (the number of unconfirmed sightings), where $n_u(\tau_E)$ are the subset recorded before τ_E , and ω acts as a dummy variable replacing Ω :

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

$$p(t_u|\tau_E) = \int_0^1 \left[\omega^{-n_u} (1 - \omega)^{n_u - n_u(\tau_E)} \left(\tau_E + \frac{1 - \omega}{\omega} T \right)^{-n_u} \right] d\omega. \tag{8}$$

Likelihood $p(t|\tau_E)$ is calculated as the product of those 2 terms.

The posterior probability that the species became extinct in the interval $(0, T)$, which we denoted as an event E (with alternate hypothesis \bar{E}), is given for a prior $p(\tau_E)$ as

$$p(t|E) = p(t|\tau_E)p(\tau_E). \tag{9}$$

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

$$B(t) = \frac{p(t|E)}{p(t|\bar{E})}, \tag{10}$$

and expresses the relative support for the hypothesis that extinction happened in the interval $[0, T)$. The most subjectivity in the method is therefore introduced in selecting the prior τ_E . Solow and Beet (2014) suggest 3 possibilities: a linear or exponential decline after the last confirmed sighting or a uniform (uninformative) prior. We elected to use the uniform prior in all the models because it makes the least constrained assumption about the species' likely extinction status.

In addition to the models developed by Solow and Beet (2014), we also included another Bayesian model (Lee et al. 2014) that builds on similar foundational work (Solow 1993; Solow et al. 2012). Like Solow and Beet's (2014) model 2, the model from Lee et al. (2014) treats confirmed and unconfirmed sightings as separate processes, and Lee et al. (2014) make slightly different recommendations regarding how to select a prior

probability that a given sighting is valid, but the overall intention of the model is largely the same. The approach in Lee et al. (2014) is also implemented stochastically with an Monte Carlo Markov Chain (MCMC) approach in BUGS, whereas Solow and Beet's (2014) model calculates likelihoods explicitly. We implemented the model from Lee et al. (2014) with some of the simplest possible assumptions: the false positive rate for confirmed sightings is 0, whereas the false positive rate for unconfirmed sightings samples from a large uniform distribution. That method can also be implemented more flexibly by assigning different priors to different categories of evidence, as Lee et al. (2014) suggest. However, rather than use somewhat arbitrarily chosen priors to differentiate among our uncertain reports (a refinement with limited benefits, per a recent study [Lee et al. 2017a]), we simply divided our data into confirmed and unconfirmed sightings. Other Bayesian models existed, but we chose to include the 2 appropriate recently developed Bayesian methods with available code (Boakes et al. 2015).

Other Extinction Estimators

For the sake of completeness, we also included several other widely used non-Bayesian estimators with varying levels of complexity (Rivadeneira et al. 2009; Boakes et al. 2015) that could be readily calculated with the R package sExtinct (Clements 2013a). Were we to include every unconfirmed, controversial sighting up to 2016 and to treat these as valid sightings (because these models make no such distinction), all methods would indicate that the species is unequivocally extant. Consequently, we limited the implementation of other methods to 2 practical applications and examined how results changed by either including only confirmed, uncontroversial specimens or both confirmed specimens and confirmed sightings (Supporting Information).

Among the methods we included, Robson and Whitlock (1964) suggested a nonparametric method based on the last 2 sightings (with an associated P value):

$$\tau_E = t_n + (t_n - t_{n-1}), \quad (11)$$

$$p = \frac{t_n - t_{n-1}}{T - t_{n-1}}. \quad (12)$$

This produced the latest thylacine τ_E (Supporting Information), as expected, given that the method can be prone to severe overestimation. Burgman et al. (1995) used the length of the period of observation, the number of years with and without records, and the length of the longest consecutive set of years with records to derive a combinatoric probability of unobserved presence. Similarly, Strauss and Sadler (1989) developed a Bayesian method focused on the discrepancy between the observed interval of sightings (between the first and last sighting) and the true range of a species in the fossil

record. Setting a precedent on which more current methods are based, Solow (1993) in his original method assumes that sightings are a stationary Poisson process, in which the probability of persistence is

$$p(\tau_E) = \left(\frac{t_n}{\tau_E}\right)^n. \quad (13)$$

However, a subsequent formulation makes the more accurate assumption that sightings follow a truncated exponential distribution, declining until extinction (Solow 2005). Finally, the optimal linear estimator (OLE) method (Roberts & Solow 2003) is the most robust nonparametric extinction estimator (Clements et al. 2013) and is based on a subset of the last s sightings of k total,

$$\tau_E = \sum_{i=1}^s w_i t_{k-i+1}; \quad w = (\mathbf{b}' \Lambda^{-1} \mathbf{b})^{-1} \Lambda^{-1} \mathbf{b}, \quad (14)$$

where \mathbf{b} is a vector of s 1s, and Λ is a square matrix of dimension s with typical element

$$\Lambda_{ij} = \frac{\Gamma(2\hat{v} + i)\Gamma(\hat{v} + j)}{\Gamma(\hat{v} + i)\Gamma(j)}, \quad (15)$$

$$\hat{v} = \frac{1}{s-1} \sum_{i=1}^{s-2} \ln \frac{t_k - t_{k-s+1}}{t_k - t_{s+1}}. \quad (16)$$

Results

Based on model 2 from Solow and Beet (2014), the most likely value for τ_E was 1940; the posterior likelihood declined rapidly thereafter (Fig. 2). The probability the thylacine is extant was extremely low (Bayes factor = 6.08912×10^{13} ; equivalently, an odds ratio of 1 in 60.9 trillion). Using Lee et al.'s (2014) method, the probability of persistence was estimated to be zero by 1940. All of the non-Bayesian estimating models agreed with these findings. Using only confirmed specimens provided an OLE estimated extinction date of 1938 (95% CI 1937–1943). Adding confirmed sightings did not change the estimated extinction date or confidence interval. Robson and Whitlock's (1964) method gave τ_E as 1956, the latest estimate (Table 1 & Supporting Information).

Discussion

Based on the results of our Solow and Beet's (2014) model 2, it remains plausible that the thylacine's extinction could have occurred up to a decade later than believed. But for thylacines to appear in 2017, especially where they are believed to have been absent for 2 millennia, is highly implausible. The 2 sightings from Cape York described as "detailed" and "plausible" (Hunt 2017) may

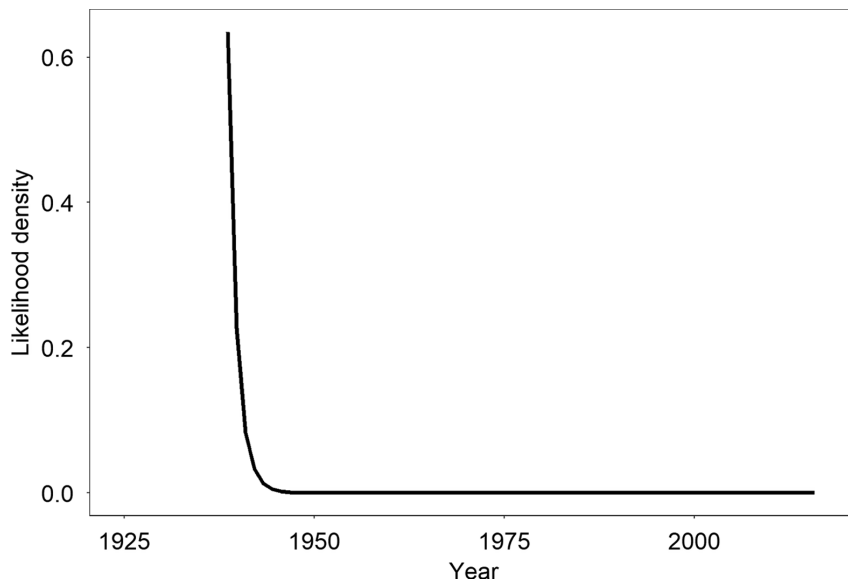


Figure 2. The posterior probability of a given thylacine extinction date (τ_E) scaled by the area under the entire likelihood curve. In Solow and Beet's (2014) model, specimen-based records are treated separately and as certain observations; consequently, evaluation begins in 1937, the year of the last certain sighting (i.e., extinction prior to that date is not considered).

Table 1. Main estimates for thylacine extinction dates.

| Model ^a | Explicit inclusion of uncertainty? | τ_E |
|------------------------------------|------------------------------------|----------|
| Roberts and Solow (2003) | no | 1938 |
| Solow and Beet (2014) ^b | yes | 1940 |
| Lee et al. (2014) | yes | 1940 |
| Strauss and Sadler (1989) | no | 1940 |
| Solow (1993) | no | 1941 |
| Solow (2005) | no | 1942 |
| Burgman et al. (1995) | no | 1945 |
| Robson and Whitlock (1964) | no | 1956 |

^aParametric estimates, except the optimal linear estimator, are calculated with a cutoff of $\alpha < 0.05$.

^bGiven by the year with the highest posterior likelihood.

^cGiven by the posterior probability reaching zero.

be so from a strictly zoological perspective, but from a modeling standpoint, they fit neatly into a pattern of ongoing, false sightings that follow nearly any high-profile extinction. However, models can be wrong, and new data may overturn a century of common knowledge in what could be one of the most surprising rediscoveries in conservation history.

The hope of rediscovering extinct species is one of the most powerful emotional forces in conservation and can bring attention to threatened species and ecosystems while igniting public interest (and funding) (Clements 2013b). The search for the thylacine may reap those benefits, and the proposed 2017 search has already gathered significant attention from journalists and on social media. Moreover, the data that will be collected during the search for the thylacine in Cape York may be invaluable for other conservation studies. But the ongoing search for extinct species, in the broader sense, likely diverts critical funds required desperately for the conservation of nearly extinct species. About 7% of some invertebrate groups

may already have gone extinct, at which rate 98% of all extinctions would be entirely undetected (Régnier et al. 2015). Globally, 36% of mammal species are threatened with extinction (classified as vulnerable, endangered or critically endangered by the International Union for Conservation of Nature), including 27% of native Australian mammals (IUCN 2016), and limited resources can be better spent reversing those declines than chasing the ghosts of extinction past.

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Supporting Information

The results of supplemental extinction models (Appendices S1–S3) and our data set of thylacine sightings (Appendix S4) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Supporting Information

Literature Cited

Boakes EH, Rout TM, Collen B. 2015. Inferring species extinction: the use of sighting records. *Methods in Ecology and Evolution* 6:678–687.

- Burgman MA, Grimson RC, Ferson S. 1995. Inferring threat from scientific collections. *Conservation Biology* **9**:923–928.
- Clements C. 2013a. sExtinct: calculates the historic date of extinction given a series of sighting events. R package version 1.1. R Foundation for Statistical Computing, Vienna.
- Clements CF. 2013b. Public interest in the extinction of a species may lead to an increase in donations to a large conservation charity. *Biodiversity and Conservation* **22**:2695–2699.
- Clements CF, Worsfold NT, Warren PH, Collen B, Clark N, Blackburn TM, Petchey OL. 2013. Experimentally testing the accuracy of an extinction estimator: Solow's optimal linear estimation model. *Journal of Animal Ecology* **82**:345–354.
- De Castro F, Bolker B. 2005. Mechanisms of disease-induced extinction. *Ecology Letters* **8**:117–126.
- Fisher DO, Blomberg SP. 2012. Inferring extinction of mammals from sighting records, threats, and biological traits. *Conservation Biology* **26**:57–67.
- Fitzpatrick JW, et al. 2005. Ivory-billed Woodpecker (*Campepibilus principalis*) persists in continental North America. *Science* **308**:1460–1462.
- Heberle G. 2004. Reports of alleged thylacine sightings in Western Australia. *Conservation Science Western Australia* **5**:1–5.
- Hunt E. 2017. 'Sightings' of extinct Tasmanian tiger prompt search in Queensland. *The Guardian*. Available from <https://www.theguardian.com/environment/2017/mar/28/tasmanian-tiger-sighting-search-thylacine-queensland-australia> (accessed March 2017).
- IUCN (International Union for Conservation of Nature). 2016. The IUCN red list of threatened species. Version 2016-3. IUCN, Gland, Switzerland. Available from <http://www.iucnredlist.org> (accessed March 2017).
- James Cook University. 2017. Press release: FNQ search for the Tasmanian tiger. James Cook University, Douglas, Queensland. Available from <https://www.jcu.edu.au/news/releases/2017/march/fnq-search-for-the-tasmanian-tiger> (accessed March 2017).
- Lee TE, Bowman C, Roberts DL. 2017a. Are extinction opinions extinct? *PeerJ* **5**:e3663.
- Lee TE, Fisher DO, Blomberg SP, Wintle BA. 2017b. Extinct or still out there? Disentangling influences on extinction and rediscovery helps to clarify the fate of species on the edge. *Global Change Biology* **23**:621–634.
- Lee TE, McCarthy MA, Wintle BA, Bode M, Roberts DL, Burgman MA. 2014. Inferring extinctions from sighting records of variable reliability. *Journal of Applied Ecology* **51**:251–258.
- National Audubon Society. 2016. April 11. The quest for the Ivory-Billed Woodpecker heads to Cuba. National Audubon Society, New York. Available from <http://www.audubon.org/news/the-quest-ivory-billed-woodpecker-heads-cuba> (accessed March 2017).
- Paddle R. 2002. *The last Tasmanian tiger: the history and extinction of the thylacine*. Cambridge University Press, Cambridge, United Kingdom.
- Paddle R. 2012. The thylacine's last straw: epidemic disease in a recent mammalian extinction. *Australian Zoologist* **36**:75–92.
- Prowse TA, Johnson CN, Lacy RC, Bradshaw CJ, Pollak JP, Watts MJ, Brook BW. 2013. No need for disease: testing extinction hypotheses for the thylacine using multi-species metamodels. *Journal of Animal Ecology* **82**:355–364.
- Régnier C, Achaz G, Lambert A, Cowie RH, Bouchet P, Fontaine B. 2015. Mass extinction in poorly known taxa. *Proceedings of the National Academy of Sciences* **112**:7761–7766.
- Rivadeneira MM, Hunt G, Roy K. 2009. The use of sighting records to infer species extinctions: an evaluation of different methods. *Ecology* **90**:1291–1300.
- Roberts DL, Solow AR. 2003. Flightless birds: When did the dodo become extinct? *Nature* **426**:245.
- Robson D, Whitlock J. 1964. Estimation of a truncation point. *Biometrika* **51**:33–39.
- Sleightholme SR, Campbell CR. 2016. A retrospective assessment of 20th century thylacine populations. *Australian Zoologist* **38**:102–129.
- Smith SJ, et al. 1981. *The Tasmanian tiger, 1980: a report on an investigation of the current status of thylacine *Thylacinus cynocephalus*, funded by the World Wildlife Fund Australia*. National Parks and Wildlife Service, Hobart, Tasmania.
- Solow A, Smith W, Burgman M, Rout T, Wintle B, Roberts D. 2012. Uncertain sightings and the extinction of the Ivory-Billed Woodpecker. *Conservation Biology* **26**:180–184.
- Solow AR. 1993. Inferring extinction from sighting data. *Ecology* **74**:962–964.
- Solow AR. 2005. Inferring extinction from a sighting record. *Mathematical Biosciences* **195**:47–55.
- Solow AR, Beet AR. 2014. On uncertain sightings and inference about extinction. *Conservation Biology* **28**:1119–1123.
- Strauss D, Sadler PM. 1989. Classical confidence intervals and Bayesian probability estimates for ends of local taxon ranges. *Mathematical Geology* **21**:411–427.

