

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

Authors

Colin J. Carlson*

cjcarlson@berkeley.edu

Department of Environmental Science, Policy, and Management, University of California, Berkeley; 130 Mulford Hall, Berkeley, CA 94720, U.S.A.

*Corresponding author

Alexander L. Bond

ardenna.research@gmail.com

Ardenna Research, Potton, Sandy, Bedfordshire, SG19 2QA United Kingdom

Kevin R. Burgio

kevin.burgio@uconn.edu

Department of Ecology and Evolutionary Biology, University of Connecticut; 75 N. Eagleville Rd. U-3043, Storrs, CT 06269, U.S.A.

Running title: The thylacine is (still) extinct

Word Count: 1210

Additional:

Number of Tables: 0

Number of Figures: 2

Number of References: 18

1 **Summary**

2
3 The thylacine, or Tasmanian tiger, was one of Australia’s most characteristic megafauna, and
4 was the largest marsupial carnivore until hunting, and potentially disease, drove them to
5 extinction in 1936¹⁻³. Current knowledge suggests the thylacine became extinct on mainland
6 Australia two millennia prior to its eradication on Tasmania, but recent “plausible” sightings on
7 the Cape York Peninsula have emerged, leading some to speculate the species may have escaped
8 extinction mostly undetected⁴. Here we show that sighting evidence indicates the continued
9 survival of the thylacine would be entirely implausible based on current mathematical theories of
10 extinction. We present a sightings dataset including physical evidence, expert-validated
11 sightings, and unconfirmed sightings leading up to the present day, and use a Bayesian
12 framework that takes all three types of data into account, by modelling them as independent
13 processes, to evaluate the likelihood of the thylacine’s persistence⁵. Although the last captive
14 thylacine died in 1936, our model suggests the most likely extinction date would be 1940, or at
15 the latest the 1950s. We validated this result by analysing our dataset with other frequently used
16 extinction estimator methods, all of which confirm that the thylacine’s extinction likely fell
17 within the interval of 1936-1943. Even the most optimistic scenario suggests the species did not
18 persist beyond the 1960s. The search for the thylacine, much like similar efforts to “rediscover”
19 the Ivory-Billed Woodpecker and other recently extinct charismatic species⁶, is likely to be
20 fruitless—especially given that persistence on Tasmania would have been no guarantee the
21 species could reappear in regions that had been unoccupied for centuries. The search for the
22 Tasmanian tiger may become a rallying point for conservation and wildlife biology in the
23 coming years, and could indirectly help fund and support critical research in understudied areas
24 like Cape York⁷. However, our results suggest that attempts to rediscover the thylacine will
25 likely be unsuccessful.

26 **Estimating the extinction date of the thylacine accounting for unconfirmed sightings**

27
28 The history of conservation biology has included a few exceptional errors, in which experts have
29 pronounced a species extinct only to be later disproven by its reappearance. Perhaps most
30 famous are “Lazarus” taxa known originally from the fossil record, like the coelacanth
31 (*Latimeria* sp.) or the dawn redwood (*Metasequoia* sp.); but recent extinctions can also
32 sometimes be overturned, like that of the Bermuda petrel (*Pterodroma cahow*). Just this year, the
33 rarest dog in the world, the New Guinea highland wild dog (*Canis lupus dingo*), was
34 rediscovered after an absence beginning in 1976 (with at least two unconfirmed sightings
35 including unconfirmed evidence in the interim). Hope of rediscovering an “extinct” species can
36 inspire volumes of peer-reviewed research, and sometimes a single controversial sighting⁶ can be
37 enough to reignite controversy and justify seemingly-endless field investigation, as in the
38 ongoing search for the Ivory-Billed Woodpecker (*Campephilus principalis*) despite all odds.⁸ In
39 Queensland, a similar story is beginning, as two recent unconfirmed sightings have inspired a
40 new search for the thylacine (*Thylacinus cynocephalus*).

41
42 The thylacine, also frequently called the Tasmanian tiger or marsupial wolf, has been presumed
43 extinct since the last captive specimen died on September 7, 1936.¹ Thylacines are believed to
44 have gone extinct on the Australian mainland roughly two millennia ago, persisting as
45 Tasmanian island endemics⁹. State-sponsored eradication in Tasmania began in 1886 and
46 continued until 1909, driving a devastating population crash.¹ Theoretical models indicate that
47 the eradication campaign, in combination with prey declines, could have been sufficient
48 extinction pressure²; but other research strongly suggests a disease similar to canine distemper
49 could have helped drive the species to extinction^{3,10}. While its mechanism has been a topic of
50 speculation, the status of the thylacine’s extinction has been essentially unchallenged in peer-
51 reviewed literature. However, sightings have continued until as recently as late 2016 throughout
52 Tasmania and mainland Australia, often gathering international media attention. Recently, two
53 unconfirmed “detailed and plausible” sightings in the Cape York Peninsula of northern
54 Queensland have sparked renewed interest in the thylacine’s persistence, particularly in the
55 Australian mainland; researchers currently intend to investigate those sightings with a camera
56 trap study beginning in Cape York later this year.⁴

57
58 Is there empirical support for this most recent search? Extinction date (τ_E) estimators have been a
59 key part of parallel debates about the Ivory-billed Woodpecker; what little work has been done
60 on the thylacine places τ_E in 1933-1935, with only one model (using temporally-subsetted data)
61 suggesting the species might be extant.¹¹ These methods are sensitive to inaccurate data and false
62 sightings, but more recently developed Bayesian models differentiate between the processes of
63 accurate and false sightings explicitly, and allow researchers to include uncertain sightings in
64 models as a separate class of data.⁵ Here, we apply those models (and several other frequently
65 used extinction date estimators) to 20th and 21st century thylacine sightings, and ask: what is the
66 probability that the species might be rediscovered?

67
68 Our study considers the only optimistic modeling scenario for the thylacine’s persistence, and
69 includes valid sightings from Tasmania alongside highly questionable sightings from Australia,
70 despite the species’ eradication two millennia earlier on the continent. (That scenario, in itself, is
71 fairly implausible; in the supplement, we present an analysis using only confirmed sightings

72 from Tasmania, which could be considered a more realistic analysis of the probability the
73 thylacine could have persisted in Tasmania alone). We used the sightings and specimens from
74 Sleightholme & Campbell (2016) (1900-1982)¹, sightings from Heberle (2004) (1939-1998)¹²,
75 and records detailed on public websites of interested citizen groups (www.tasmanian-tiger.com,
76 www.thylacineresearchunit.org, and www.thylacineawarenessgroup.com) supplemented by web
77 searches for news media stories from 2007-2016. For each year between 1900 and 2016, we
78 recorded the maximum level of certainty of records. Records were scored as confirmed
79 specimens (e.g., from bounty records, museum specimens, or confirmed captures), confirmed
80 sightings (sightings agreed as valid by experts), and unconfirmed sightings (sightings not
81 considered valid by experts; **Figure 1**). Because there are also likely unreported unconfirmed
82 sightings, we also ran models assuming that an unconfirmed sighting occurred in every year
83 from 1940-2016 (**Supplementary Information**). For all analyses, we considered the species
84 across its historical range (i.e., mainland Australia and Tasmania). All R code and more detailed
85 data is available in the S.I.

86
87 The Bayesian model we use, which explicitly differentiates sightings by certainty, suggests a
88 negligible probability that the thylacine might have persisted later than the 1940s, with 1940 as
89 the most likely value of τ_E , and the posterior likelihood declining rapidly thereafter (**Figure 2**).
90 Including unconfirmed sightings for years with no data did not change the probability
91 distribution (**see S.I.**). Other, non-Bayesian estimators all strongly agreed with these findings.
92 The optimal linear estimator (OLE) is considered the most robust of those tools¹³, and has been
93 applied to other high-profile extinctions like that of the dodo (*Raphus cucullatus*).¹⁴ Using only
94 confirmed specimens provides an OLE extinction date of 1939 (95% confidence interval: 1937-
95 1943); adding confirmed sightings did not change the estimated extinction date or confidence
96 interval. Most other commonly used extinction estimators concur with these findings, with
97 Robson & Whitlock's method¹⁵ (producing by far the latest estimate) approaching the 1960s (**see**
98 **S.I.**).

99
100 In our assessment, there is only an extremely low probability that the thylacine could be extant
101 (Bayes factor = 6.21524×10^{13} , or a probability of 1 in 1.6 trillion). Based on the results of our
102 primary model, it remains fairly plausible that the thylacine's extinction could have occurred up
103 to a decade later than believed. But for thylacines to appear in 2017, especially in an area where
104 they are believed to have been absent for two millennia, is highly implausible. The two sightings
105 from Cape York describe as "detailed" and "plausible" may be so, from a strictly zoological
106 perspective; but from a modeling standpoint, they fit neatly into a pattern of ongoing, false
107 sightings that follows nearly any high-profile extinction. Models can be wrong, and new data
108 may overturn a century of common knowledge in what could be one of the most surprising re-
109 discoveries in conservation history. But if the story of the Ivory-Billed Woodpecker offers any
110 parallels, camera trap evidence is more likely to produce blurry evidence that might match the
111 profile of a thylacine and sustain ongoing controversy, while producing little change in the state
112 of scientific consensus.

113
114 The hope to rediscover extinct species is one of the most powerful emotional forces in
115 conservation biology, and can bring attention to threatened species and ecosystems while
116 igniting public interest (and funding) in science⁷. The search for the thylacine may reap those
117 benefits, and the proposed 2017 search has already gathered significant attention from journalists

118 and social media. Moreover, the camera trap data that will be collected during the search for the
119 thylacine in Cape York will undoubtedly be valuable for many other conservation studies. But
120 the ongoing search for extinct species, in the broader scheme, likely drains critical funds that the
121 conservation of near-extinction species desperately requires. One estimate suggests 7% of some
122 invertebrate groups may already have gone extinct—at which rate, 98% of extinctions would be
123 going entirely undetected¹⁶. Globally, 36% of mammal species are threatened with extinction
124 (classified as Vulnerable, Endangered or Critically Endangered), including 27% of native
125 Australian mammals¹⁷, and often limited resources can be better spent reversing those declines,
126 than chasing the ghosts of extinction past.

127
128 **Supplementary Information** is linked to the online version of the paper at
129 www.nature.com/nature.

130
131 **Acknowledgements.** We thank A. Beet for the original Matlab code used in Solow & Beet
132 (2014), and A. Butler (Biomathematics and Statistics Scotland) for translating the Matlab code
133 into R. We thank L. Bartlett for helpful criticism and feedback.

134
135 **Author Contributions.** C.J.C. designed the study; A.L.B assembled the dataset. All authors
136 developed code, analyzed the data, and wrote the manuscript.

137
138 **Author Information.** Reprints and permissions information is available at
139 www.nature.com/reprints. The authors declare no competing financial interests. Correspondence
140 and requests for materials should be addressed to cjcarlson@berkeley.edu.

141
142
143
144
145
146
147
148
149
150
151
152
153
154
155
156
157
158
159
160
161
162
163
164
165
166
167
168
169
170
171
172
173
174
175
176
177
178

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) appendix¹, 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 & Beet⁵ 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

$$p(t|E) = p(t|\tau_E)p(\tau_E)$$

179

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

182

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

183

184 *Other Extinction Estimators*

185

186 We also include several other non-Bayesian estimators, readily derived using the R package
 187 ‘sExtinct’ v1.1.¹⁸ Were we to include every unconfirmed, controversial sighting continuing up to
 188 2016, all methods indicate that the species would likely be extinct. Consequently, we limit the
 189 implementation of other methods to two practical applications, examining how results change by
 190 either including (a) only confirmed, uncontroversial specimens and (b) both confirmed
 191 specimens and confirmed sightings (**Figure S1**).

192

193 Among the methods that we include, Robson and Whitlock¹⁵ suggested a nonparametric method
 194 based only on the last two sightings:

195

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

196

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

201

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

202

203 Where b is a vector of s 1’s and

204

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

205

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

207

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

208

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

209

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

212

213 *Sensitivity Analysis*

214

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

221

222 *Data Availability*

223

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

228

229 **References.**

230

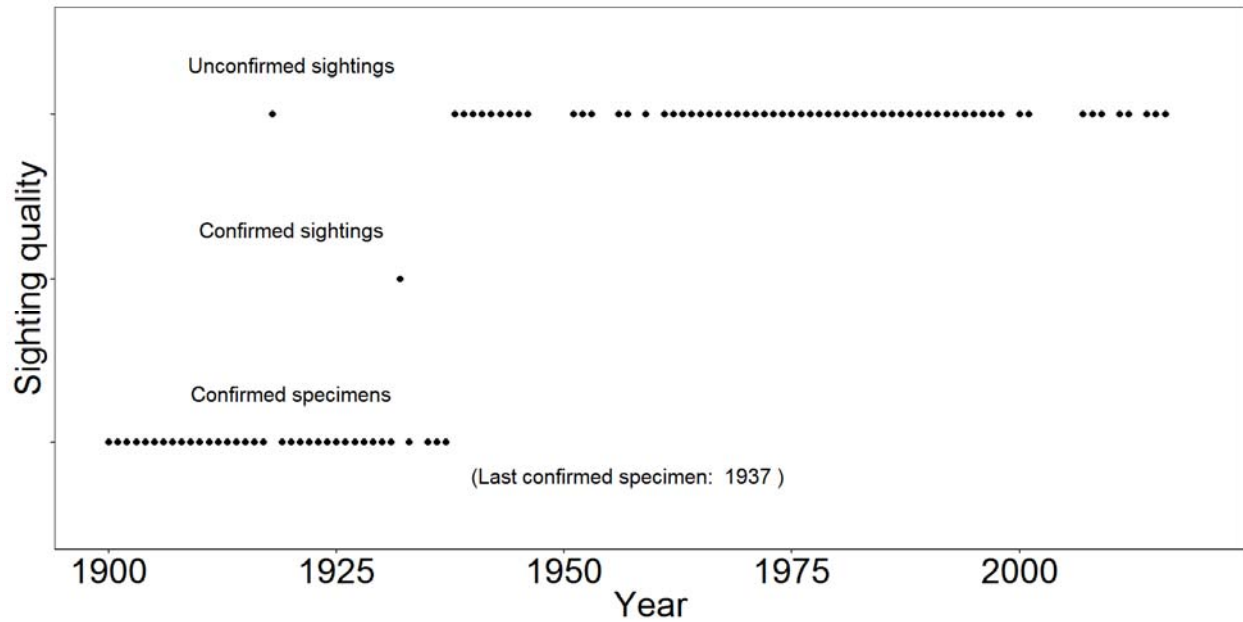
- 231 1. Sleightholme, S. R. & Campbell, C. R. A retrospective assessment of 20th century thylacine
232 populations. *Aust. Zool.* **38**, 102–129 (2016).
- 233 2. Prowse, T. A. *et al.* No need for disease: testing extinction hypotheses for the thylacine using
234 multi-species metamodels. *J. Anim. Ecol.* **82**, 355–364 (2013).
- 235 3. Paddle, R. The thylacine’s last straw: epidemic disease in a recent mammalian extinction.
236 *Aust. Zool.* **36**, 75–92 (2012).
- 237 4. James Cook University. Press release: FNQ search for the Tasmanian Tiger.
238 <https://www.jcu.edu.au/news/releases/2017/march/fnq-search-for-the-tasmanian-tiger>
- 239 5. Solow, A. R. & Beet, A. R. On uncertain sightings and inference about extinction. *Conserv.*
240 *Biol.* **28**, 1119–1123 (2014).
- 241 6. Fitzpatrick, J. W. *et al.* Ivory-billed Woodpecker (*Campephilus principalis*) persists in
242 continental North America. *Science* **308**, 1460–1462 (2005).
- 243 7. Clements, C. F. Public interest in the extinction of a species may lead to an increase in
244 donations to a large conservation charity. *Biodivers. Conserv.* **22**, 2695–2699 (2013).
- 245 8. Audubon Society. The quest for the Ivory-Billed Woodpecker heads to Cuba. (2016).
246 <http://www.audubon.org/news/the-quest-ivory-billed-woodpecker-heads-cuba>
- 247 9. Paddle, R. *The last Tasmanian tiger: the history and extinction of the thylacine*. (Cambridge
248 University Press, 2002).
- 249 10. De Castro, F. & Bolker, B. Mechanisms of disease-induced extinction. *Ecol. Lett.* **8**, 117–126
250 (2005).
- 251 11. Fisher, D. O. & Blomberg, S. P. Inferring extinction of mammals from sighting records,
252 threats, and biological traits. *Conserv. Biol.* **26**, 57–67 (2012).
- 253 12. Heberle, G. Reports of alleged thylacine sightings in Western Australia. *Conserv. Sci. West.*
254 *Aust.* **5**, 1–5 (2004).
- 255 13. Clements, C. F. *et al.* Experimentally testing the accuracy of an extinction estimator: Solow’s
256 optimal linear estimation model. *J. Anim. Ecol.* **82**, 345–354 (2013).

- 257 14. Roberts, D. L. & Solow, A. R. Flightless birds: When did the dodo become extinct? *Nature*
258 **426**, 245–245 (2003).
- 259 15. Robson, D. & Whitlock, J. Estimation of a truncation point. *Biometrika* **51**, 33–39 (1964).
- 260 16. Régnier, C. *et al.* Mass extinction in poorly known taxa. *Proc. Natl. Acad. Sci.* **112**, 7761–
261 7766 (2015).
- 262 17. IUCN. The IUCN Red List of Threatened Species. Version 2016-3. (2016).
- 263 18. Clements, C. sExtinct: Calculates the historic date of extinction given a series of sighting
264 events. R package version 1.1. (2013).
- 265

266
267
268
269
270
271
272
273

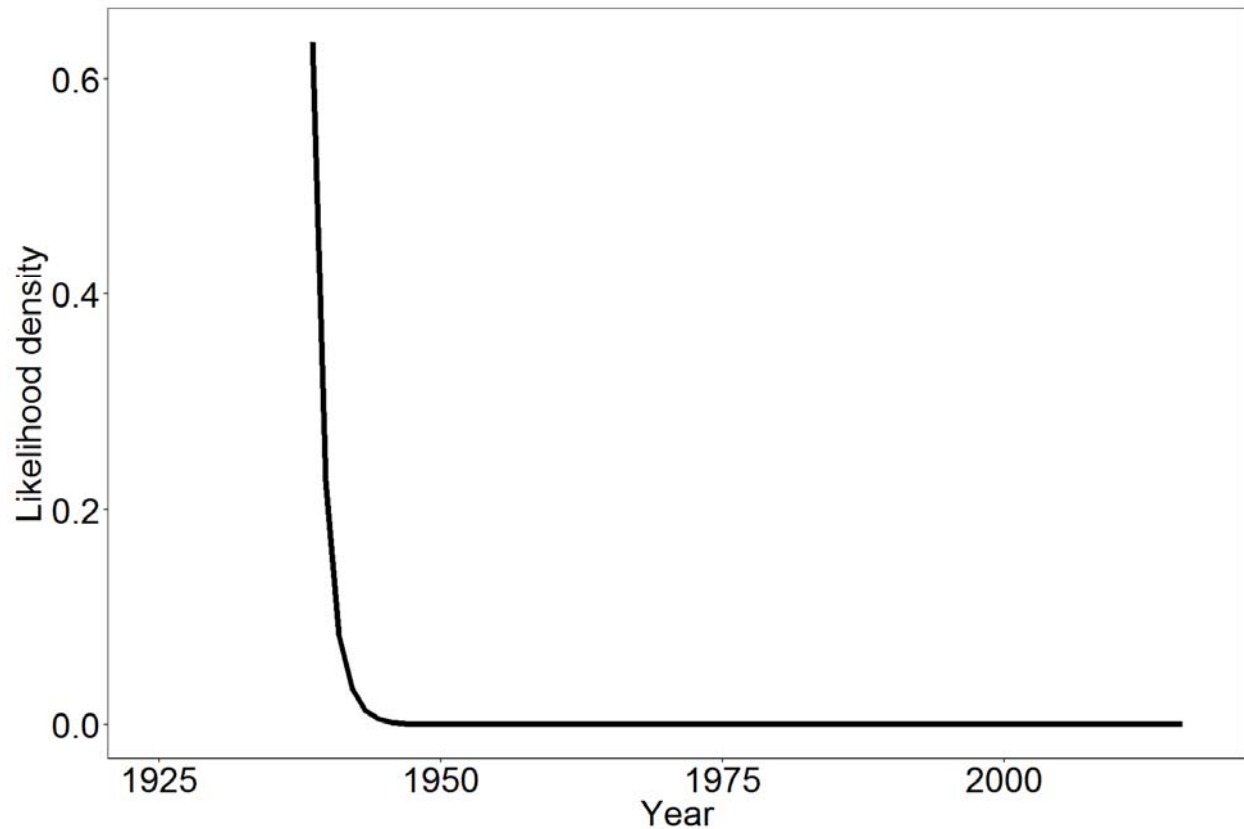
Figures

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**.



274
275
276

277 **Figure 2. The likelihood of thylacine persistence over time.** The figure presents the posterior
278 probability of a given extinction date τ_E scaled by the area under the entire likelihood curve. In
279 Solow & Beet's model, specimen-based records are treated separately and as certain
280 observations (see **Methods**); consequently evaluation begins in 1937, the year of the last certain
281 sighting (i.e., extinction prior to that date is not considered).
282



284