Crowdsourcing and phylogenetic modelling reveal parrot tool use is not rare

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Abstract

Putatively rare behaviours, such as tool use, are challenging to study because absence of evidence can arise either from a species' inability to produce the behaviour or from insufficient research effort. Here, we tackle this challenge by combining crowdsourcing and phylogenetic modelling to estimate actual rates of tool use in parrots. Crowdsourcing on a social media platform revealed novel instances of tool use in 17 parrot species, more than doubling the confirmed number of tool-using parrot species from 11 (3%) to 28 (7%). Phylogenetic modelling ranked additional species that are most likely to be unobserved tool users, suggesting that between 11% and 17% of extant parrot species may be tool users. These discoveries have implications for inferences about the evolutionary drivers and origins of tool use in parrots, revealing associations with relative brain size and feeding generalism and indicating several genera where tool use was likely an ancestral trait. Overall, our findings challenge the assumption that current sampling effort captures the full distribution of putatively rare animal behaviours. Combining our sampling and analysis methods offers a fruitful approach for investigating the distribution, drivers, and origins of other rare behaviours.

Keywords: tool use; technical intelligence; parrots; crowdsourcing; phylogenetic modelling

Significance Statement

Tool use has been identified in a number of non-human animal species, including 11 species of parrot. However, it is possible that the number of tool-using parrot species has been underestimated due to insufficient research effort. Here, we combine two approaches – crowdsourcing and phylogenetic modelling – to estimate actual rates of tool use in parrots. Crowdsourcing on a social media platform identified tool use in 17 novel parrot species, more than doubling the confirmed number of tool-using parrot species from 11 to 28. Moreover, phylogenetic modelling ranked additional species that are likely to be unobserved tool users. Our findings have implications for inferences about the evolutionary origins of technical intelligence in parrots.

1   **Introduction**

2   Our understanding of the evolution of animal behaviour is built on the assumption

3   that we have access to sufficient data (1–3). However, this is not always the case. Data on

4   behaviours that are rare, fleeting, or otherwise difficult to observe are likely to be patchy

5   and incomplete (4, 5). Among species for which such behaviours have not been observed, it

6   can be difficult to differentiate between cases in which the species is truly incapable of

7   producing the behaviour and cases in which the species is capable of producing the

8   behaviour but the behaviour has not yet been observed. Such a distinction can be critical

9   for drawing conclusions about the rarity and evolution of the behaviour in question.

10   Comparative work on the evolution of tool use is a paradigmatic example of this

11 issue. The initial discoveries of tool use in chimpanzees (6), birds (7), dolphins (8), and

12 octopuses (9) occurred decades after significant advances on other more easily measurable

13 aspects of their biology. Since then, scholars have proposed a clear operational definition of

14 tool use applicable to all species — the manipulation of an unattached object as an

15 extension of the animal's body to achieve a goal (10) — and have used the distribution of

16 species meeting this definition to make various claims about the evolutionary drivers of

17 tool use behaviours. For example, based on the observation that bird species with reported

18 tool use tended to have larger brains, researchers have identified higher relative brain size

19 as a likely precondition for tool using capabilities (11–13). These researchers argue that

20 larger brains are better able to integrate visual and somatosensory information when

21 innovating novel behaviours, such as tool use, in changing environments (14, 15). Similarly,

22 researchers have used existing reports of tool use in birds to debate the roles of generalist

23 versus specialist feeding strategies in driving the evolution of tool use, with some arguing

24 that feeding generalists require technical innovations to expand their dietary niche (14, 16,

25 17) and others arguing that feeding specialists require technical innovations for extractive

26 foraging of specific foods (18, 19).

27   However, before we can make claims of this kind, we need to know whether current

28   research effort in the literature is sufficient for robust conclusions to be drawn about the

29   evolution of tool use. In fact, evidence suggests that research effort is often systematically

30   biased towards particular taxonomic groups, parts of the world that are easy to access, and

31   species with life history traits that make them easier to study, such as larger distribution

32   ranges and population sizes (20). This is a crucial limitation because insufficient

33   observation may lead researchers to miss true instances of tool behaviours and thus draw

34   premature conclusions about the evolutionary drivers and origins of tool use. While

35   researchers have attempted to deal with this problem by controlling for the number of

36   scientific papers published on different species, previous work has not yet attempted to

37   quantify and explicitly model the relationship between actual tool-using behaviour and

38   what is reported in the scientific literature. If more tool-using species exist than previously

39   thought, this could have important implications for theories of the evolutionary drivers and

40   origins of tool use and for our understanding of how rare this behaviour actually is.

41   One potentially powerful method for quantifying actual rates of rare animal

42   behaviours is crowdsourcing (21). In a crowdsourcing study, researchers collect reports

43   from the general public and/or collate and analyse videos posted on social media

44   platforms. This citizen science approach has been widely used in ecology to monitor the

45   distributional patterns of species (22), but has also recently been used to uncover a variety

46   of rare animal behaviours, including interspecies play in dogs (21), novel problem-solving

47   behaviours in horses (23), and socially-learned foraging innovations in cockatoos (24, 25).

48   By casting the net wider than the scientific literature, the crowdsourcing method can

49   provide an indication of the tool-using species that the literature might be missing.

50   Even after using this crowdsourcing approach, some tool-users could *still* remain

51   unobserved. One principled framework for identifying these unobserved species is to specify

52   a causal model of the process that generates the observed data. We propose one such

53   causal model in Figure 1. In this model, we assume that the presence of tool use in the

54 scientific literature (or in crowdsourced reports) is caused by both unobserved tool use

55 capabilities and the number of published studies (or the number of crowdsourced reports)

56 for any given species. Tool users are more likely to be observed if they are well studied, but

57 understudied tool users may go undetected. Furthermore, based on existing theories of the

58 evolution of tool use (11–19), we propose that the unobserved tool use capabilities are

59 additionally caused by relative brain size, feeding strategy, and shared phylogenetic

60 ancestry. Expressing this causal model as a statistical model can suggest further species

61 which are likely to be unobserved tool-users and, simultaneously, test existing theories of

62 the evolutionary drivers of tool use without incorrectly assuming that absence of evidence
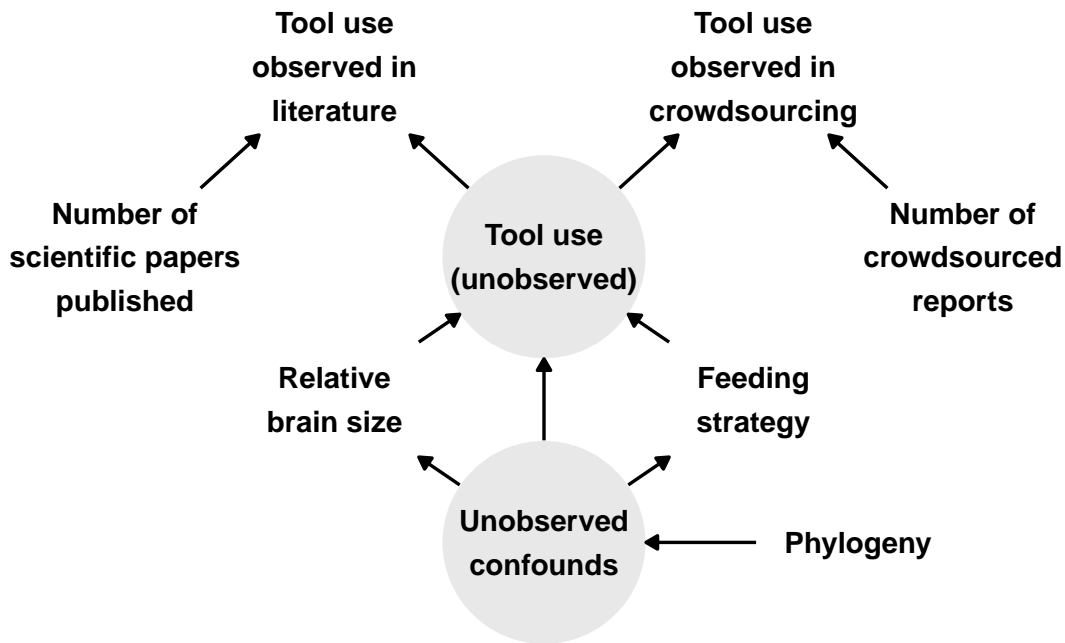
63 is evidence of absence.

Figure 1. Causal model of observed tool use. Directed acyclic graph of the causal relationships between observed tool use and other variables. Available scientific data on tool use is caused both by unobserved tool use presence and scientific research effort (i.e., number of publications). Available crowdsourced data on tool use is caused both by unobserved tool use presence and crowdsourcing effort (i.e., number of crowdsourced reports). According to theory, unobserved tool use presence should be caused by relative brain size (encephalisation quotient) and feeding strategy (generalist vs. specialist). These variables all share unobserved confounds generated by shared phylogenetic history. Grey circles indicate unobserved variables.

64 Here, we apply these crowdsourcing and phylogenetic modelling approaches to tool

65 use in the parrot order. We focus on tool use in parrots for a number of reasons. First, the

66 scientific literature suggests that only a small proportion of extant parrot species (11 out of

67 398; 3%) use tools (11, 26–38). Parrot tool use thus provides an ideal test case for

68 examining how robust sampling is in the scientific literature. Second, parrots are highly

69 popular as pets. Over 70% of all extant parrot species are bred in the aviculture industry

70 and kept as pets worldwide (39–45), enabling us to leverage the power of crowdsourcing on

71 a social media platform to search for evidence of tool use (21). Third, detailed data on

72 relative brain sizes (46–51), feeding strategies (52), and shared ancestry (53) exist for

73 parrots, allowing us to fit the statistical model implied by Figure 1 to the entire parrot

74 order.

75 We first present the results from our crowdsourcing survey, in which we collated

76 videos of tool use in parrots from an online video platform. This survey reveals a number

77 of previously unidentified tool-using parrot species, which we map onto the phylogeny of

78 the parrot order. We then describe our statistical model in more detail, and use it to (*i*)

79 rank further parrot species that are likely unobserved tool users and (*ii*) re-examine key

80 hypotheses regarding the evolutionary drivers and origins of tool use in parrots.

81 **Results**

82 **Crowdsourcing reveals tool use in additional parrot species**

83 We surveyed the social media platform YouTube for video evidence of tool use in

84 parrots (see Methods for detailed search criteria). In our search, we used the standard

85 criteria for identifying tool use in the literature, defining "true" tool use behaviour as the

86 manipulation of an unattached object as an extension of the animal's body to achieve a

87 goal (10), while "borderline" tool use involved the use of an object that was still attached

88 to a substrate (54).

In total, we found 116 videos of 104 individuals from 25 parrot species performing behaviours that met the definition of either true tool use (100 videos of 89 individuals from 22 species) or borderline tool use (16 videos of 16 individuals from 7 species). All videos featured pet parrots in captive settings. In 68 of these videos, owners did not appear to interact with the subjects. In 43 videos, there was potential human interaction, either from the owners being in close physical contact with the bird (e.g., bird perching on hand), talking to the bird, or handing it the tool (which occurred in only two videos). We could not establish the degree of human interaction in the remaining 5 videos, as sound had been removed or was substituted by music. None of the videos featured owners directly rewarding tool use behaviours with food. All borderline tool use cases were excluded from further analyses.

Of the 22 parrot species performing true tool use, 13 were represented in our video survey by two or more individuals over multiple independent observations. True tool use always involved the subject using an object for self-scratching (95 videos involved scratching the head and/or neck). The most common tool (53 videos) was a moulted feather. Human-made objects (e.g., pens, spoons, pieces of wood, cardboard) were also common.

According to YouTube video descriptions and owner comments, 45 of the individuals performing true tool use were males and 18 were females. No sex information was provided for the remaining 26 individuals. As owners provided no information on whether sex had been established through genetic testing, and sexual dimorphism in parrots is rare (55, 56), we could not typically ascertain if descriptions were accurate. It is unclear if the disproportionately large number of males in the sample is a consequence of owners more readily assuming their parrots are male when they have not been genetically tested, owners being more likely to own or film male parrots, or male parrots exhibiting more true tool use behaviours than female parrots.

Figure 2 maps the findings from the video survey onto a maximum clade credibility

phylogeny for the parrot order, plotted alongside species previously identified in the

scientific literature. Before the video survey, 11 parrot species (3%) had been identified as

tool users in the scientific literature. Across our video survey, we observed true tool use in

22 species, 5 of which overlapped with the scientific literature and 17 of which were novel

species. All of the species identified in the video survey were cockatoos (*Cacatuidae*), Old

World parrots (*Psittacinae*), or neotropical parrots (*Arinae*). The most common species in

our survey, accounting for 41 videos from 37 individuals, was the green-cheeked conure

(*Pyrrhura molinae*). In accordance with the scientific literature, the video survey found no

evidence of tool use in any species of Psittaculidae, despite this family containing some of

the most commonly kept pet species, including lovebirds, lorikeets, and Asian parakeet

species. Combining both the video survey and the scientific literature, we can thus identify

28 tool-using parrot species overall (7%), compared to the 11 previously reported.

The identification of new tool-using species in our video survey increases the extent

to which phylogeny can explain the distribution of tool use in the parrot order. We

estimated phylogenetic signal (Pagel's λ) of tool use using both the pre-video-survey and

post-video-survey data. Pagel's λ varies between 0 and 1, where 0 implies that the

distribution of a trait across species is unexplained by phylogenetic relatedness and 1

implies that the distribution of a trait across species is fully explained by phylogeny. Using

the evidence of tool use from the scientific literature alone (pre-video-survey data; 11

tool-using species), we estimated an average posterior Pagel's λ of 0.60 (95% credible

interval [0.00 0.90]; total $n = 174$ species). This estimate was moderate-to-strong, but

highly uncertain. In comparison, combining the evidence from both the literature and the

video survey (post-video-survey data; 28 tool-using species) resulted in a stronger and more

certain estimate of phylogenetic signal. With these data, we estimated Pagel's $\lambda = 0.65$

(95% CI [0.50 0.77]; total $n = 174$ species). Thus, the results of our video survey increase

the extent to which the distribution of tool use across parrot species can be explained by

shared phylogenetic ancestry. This suggests that we can potentially use phylogenetic
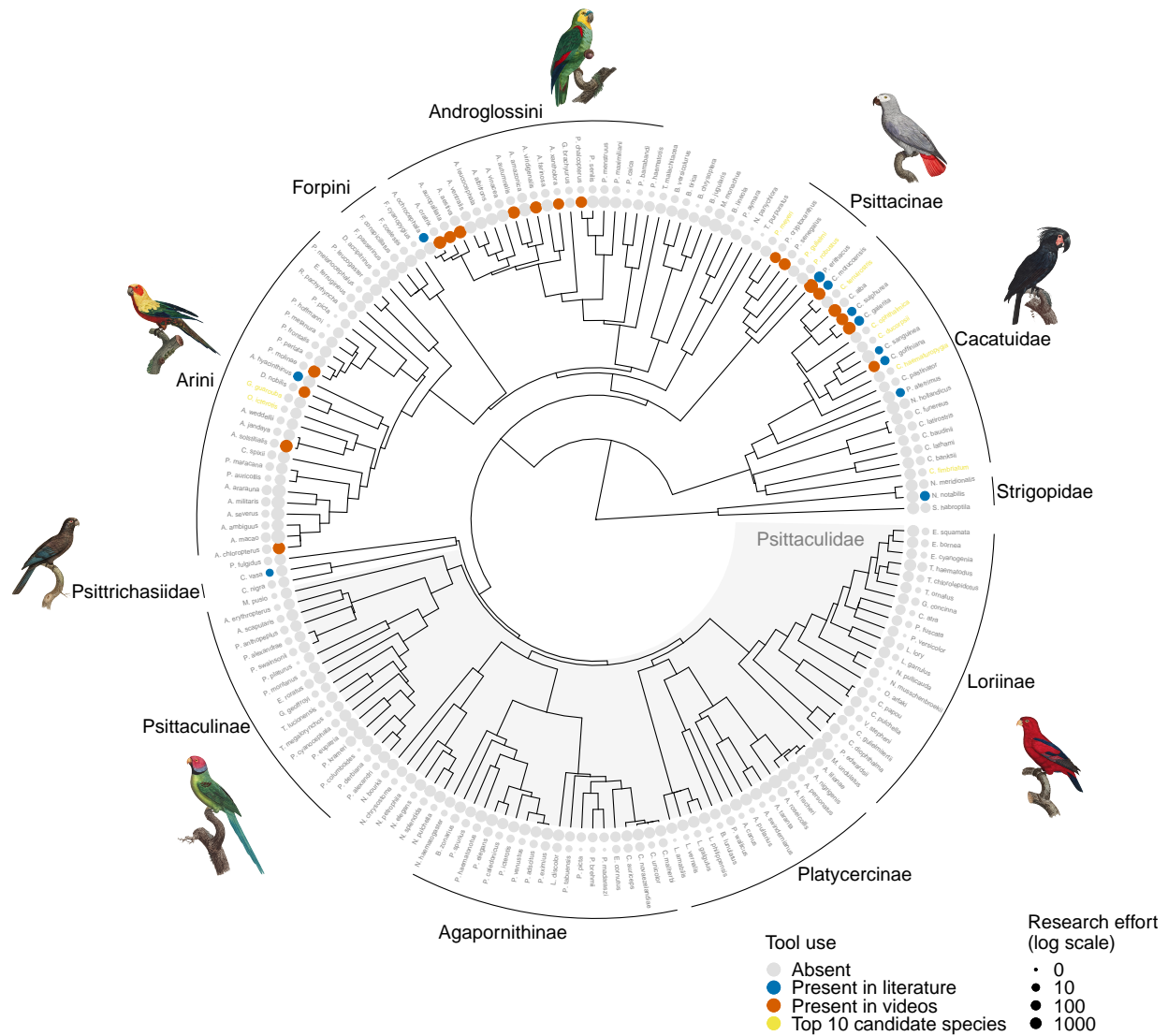
Figure 2. *Results of crowdsourcing video survey and phylogenetic survival cure modelling mapped onto a maximum clade credibility phylogeny of the parrot order.* Orange points in the inner ring indicate species observed in the video survey, with point size scaled by the number of videos for each species (note that three species observed only in the video survey are not present in the phylogeny due to a lack of genomic data: *Psittacara erythrogenys*, *Psittacus timneh*, and *Aratinga nenday*). Blue points in the outer ring indicate species observed in the scientific literature, with point size scaled by the number of papers published on each species. Yellow species names indicate the top ten most likely tool-using species from our phylogenetic survival cure model which were not observed in the scientific literature or the video survey. Total $n = 174$ species.

₁₄₂ information, along with other variables, to identify further tool-using parrot species that

₁₄₃ may remain undetected.

Phylogenetic survival cure modelling identifies further candidate tool users

₁₄₅   In addition to the 28 tool-using species identified in the literature and our video

₁₄₆ survey, we fitted a Bayesian phylogenetic survival cure model to rank further species that

₁₄₇ are likely to be undetected tool-users (i.e., tool-using species with no tool use reported in

₁₄₈ the literature or in crowdsourced videos).

₁₄₉   Survival cure models (57), also known as split population models (58), are used to

₁₅₀ analyse the time to some event of interest with the added assumption that a certain

₁₅₁ proportion of the population will never experience the event, no matter how long they are

₁₅₂ measured for. These models have been used to analyse a variety of right-censored

₁₅₃ outcomes, from cancer relapse (57) to criminal recidivism (58). The data are right-censored

₁₅₄ because some individuals will have experienced the event when they are measured (e.g.,

₁₅₅ disease onset, return to prison) while others will have not experienced the event. For those

₁₅₆ who have not experienced the event, this may be because (*i*) the event has not happened

₁₅₇ to them yet or (*ii*) the event will *never* happen to them. Survival cure models treat these

₁₅₈ two processes separately.

₁₅₉   Our tool use problem has the same features. We are modelling a time-to-event;

₁₆₀ specifically, the amount of "time" (i.e., observation opportunities measured as the number

₁₆₁ of published papers or crowdsourced videos) until tool use is identified. This is

₁₆₂ right-censored data because many species will not have had tool use identified when we

₁₆₃ measure them. Moreover, we can assume that a certain proportion of the population will

₁₆₄ never experience the event – that is, they are a non-tool-user and so we will never identify

₁₆₅ tool use no matter how long we measure them for.

₁₆₆   In our model, we infer the tool-using status of each species by allowing each species

167 to have their own probability of being a non-tool-user. Following our causal model (Figure

168 1), we predict these probabilities based on feeding strategy, encephalisation quotient, and

169 phylogenetic history (see Methods for full model). The model additionally takes research

170 effort into account by allowing that, among species for which tool use is unobserved, all else

171 being equal those with fewer published papers and fewer video search hits have a higher

172 probability of being undetected tool users (Supplementary Figure S1).

173   We found that this phylogenetic survival cure model was able to adequately

174 distinguish between species with and without evidence for tool use, with an

175 area-under-the-curve classification statistic of 0.95 (Supplementary Figure S2). To further

176 estimate the accuracy of the model's predictions, we also used a leave-one-species-out

177 approach with known tool users. For each of the 25 tool-using species that were

178 represented on the phylogeny and for which we had brain size and genomic data (we lacked

179 data for three tool-using species), we fitted the model to a modified dataset which set tool

180 use to be absent for the target species in both the scientific literature and the video survey.

181 Across 25 cross-validation models, 18 models (72%) continued to predict the target species

182 as having a median posterior probability of tool use that was within the range of all other

183 tool users. This classification rate was greater than the baseline classification rate of 26%

184 for species without evidence of tool use in the full model (38 of 149 species without

185 evidence of tool use had a median posterior probability of tool use that was within the

186 range of the tool-using species). Together, the area-under-the-curve statistic and the

187 leave-one-species-out approach suggest that the model is able to adequately classify known

188 tool users, with some error.

189   Figure 3 visualises the ranked posterior probabilities of tool use from the phylogenetic

190 survival cure model for all parrot species. As expected, the known tool users are ranked

191 towards the top of this list. However, several "tool use absent" species also rank highly on

192 the list, despite not being identified as tool users in the scientific literature or in our video

193 survey. In fact, according to the model, the most likely tool user is a species for which tool

194 use is unobserved in our data: the blue-eyed cockatoo (*Cacatua opthalmica*). This species

195 is endemic to Papua New Guinea and is relatively understudied, with only 6 published

196 papers and 596 video search hits, which is fewer than the model expects are necessary to

197 discover tool use when it is present (Figure 4). This species is also found in the *Cacatua*

198 genus, a clade containing several known tool users. This prediction makes sense given the

199 high phylogenetic signal for tool use reported by the model (Supplementary Figures S3 and

200 S4). Beyond the blue-eyed cockatoo, other highly ranked species without observed evidence

201 of tool use are the Meyer's parrot (*Poicephalus meyeri*), the golden parakeet (*Guaruba*

202 *guarouba*), the long-billed corella (*Cacatua tenuirostris*), the Solomons cockatoo (*Cacatua*

203 *ducorpsii*), the red-fronted parrot (*Poicephalus gulielmi*), the Cape parrot (*Poicephalus*

204 *robustus*), the yellow-eared parrot (*Ognorhynchus icterotis*), the red-vented cockatoo

205 (*Cacatua haematuropygia*), and the gang-gang cockatoo (*Callocephalon fimbriatum*). Figure

206 2 plots these species on the parrot phylogeny, using the top ten highest ranked species

207 without observed evidence of tool use as an arbitrary cutoff for visualisation purposes.

208   The posterior probabilities shown in Figure 3 are estimated with uncertainty, so it is

209 difficult to "identify" any particular species as an undetected tool user. Nevertheless,

210 taking the sum of all the posterior probabilities for the 149 species without observed

211 evidence of tool use, we can estimate that around 26 of those species are likely to be

212 undetected tool users (median sum of probabilities = 25.68, 95% CI [15.15 41.33]). When

213 combined with the species known to use tools, this implies that between 11% and 17% of

214 extant parrot species may be tool users.

215 **Implications for the evolutionary drivers and origins of tool use**

216   The predicted probabilities from our phylogenetic survival cure model have

217 implications for inferences about the evolutionary drivers and origins of tool use in the

218 parrot order. Regarding the drivers of tool use hypothesised in Figure 1, the phylogenetic

219 survival cure model revealed that encephalisation quotient strongly positively predicted the
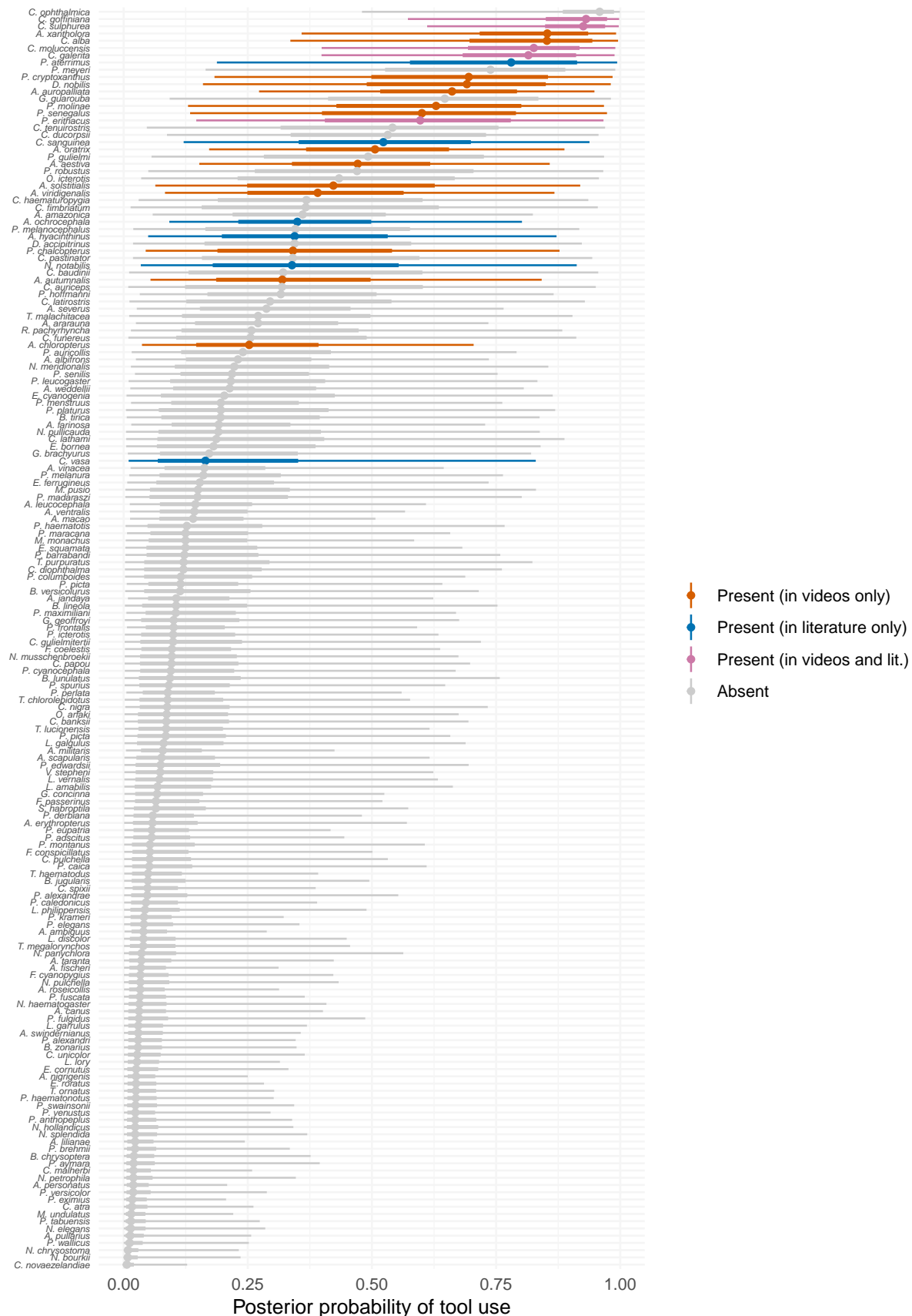
Figure 3. *Posterior predicted probabilities of tool use for each species from our phylogenetic survival cure model.* Points are posterior medians and lines are 50% and 95% credible intervals. Total $n = $ 174 species.
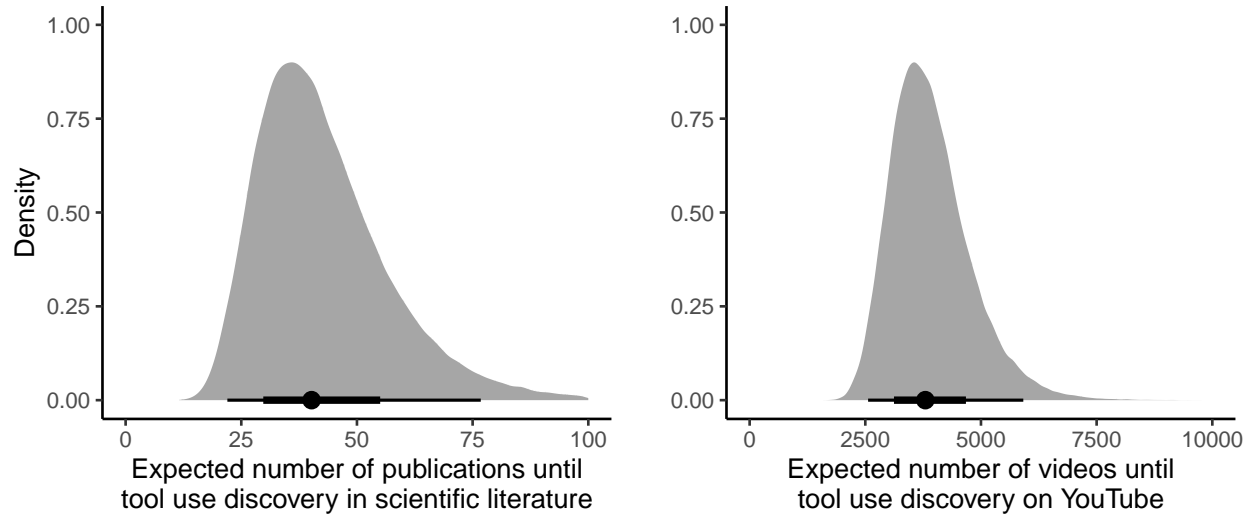
Figure 4. Expected number of published papers and videos until tool use discovery, according to the survival component of the phylogenetic survival cure model. Densities are full posterior distributions, points are posterior medians, and lines are 50% and 95% credible intervals.

probability of tool use (median posterior log odds slope = 1.12, 95% CI [0.39 2.00]; total n

= 174 species; Figure 5). This helps explain the ranking in Figure 3: the blue-eyed

cockatoo has the largest relative brain size in the dataset. We also found that feeding

generalist species were slightly more likely to be tool users, though the posterior difference

between generalists and specialists was quite uncertain (median posterior log odds

difference = 0.33, 95% CI [-1.13 1.76]; total n = 174 species). These results from the

survival cure model differed from the results of models fitted to pre-video-survey and

post-video-survey data without the survival cure component, which found no effect of

relative brain size and no difference between feeding strategies, respectively

(Supplementary Figure S5).

Regarding the origins of tool use, we fitted exploratory ancestral state reconstruction

models to the pre-video-survey data, the post-video-survey data, and the predicted

probabilities from the phylogenetic survival cure model. The discoveries from our video

survey and from our phylogenetic modelling increased the likelihood that tool use was

present in the most recent common ancestor for several parrot genera. These include the

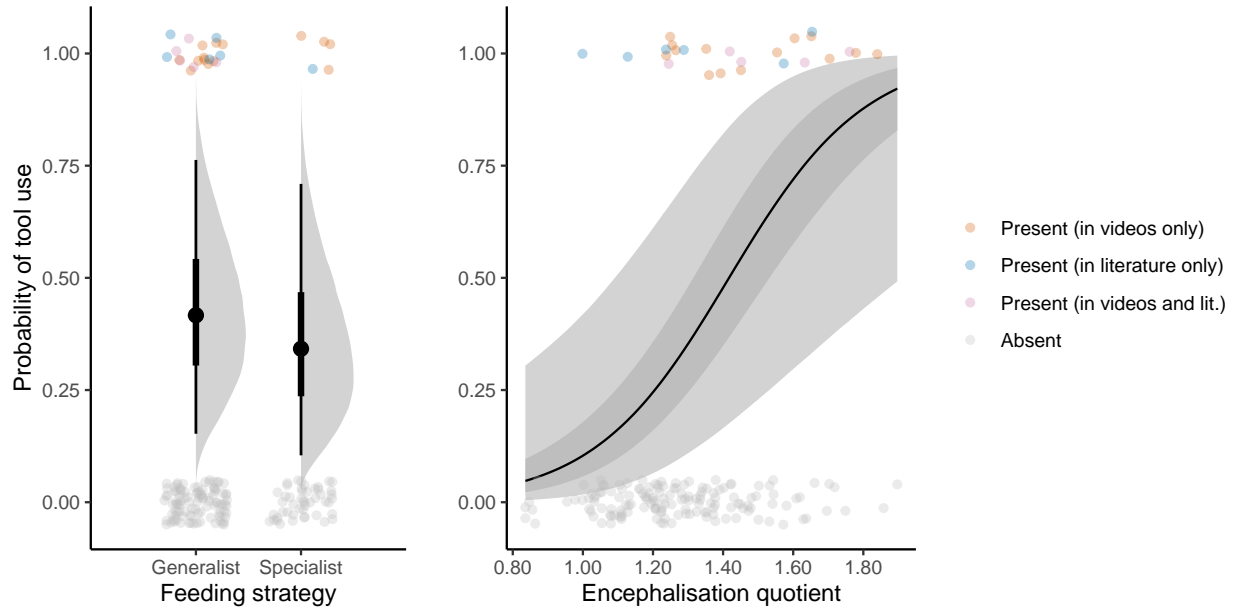amazon parrots native to the Americas (*Amazona*), the true white cockatoos and corellas

Figure 5. *Posterior predictions for the effects of feeding strategy and encephalisation quotient on the probability of tool use from the phylogenetic survival cure model.* In the left plot, points and lines represent posterior medians and 50% and 95% credible intervals, with densities representing full posterior distributions. In the right plot, the line and shaded areas represent the posterior median regression line with 50% and 95% credible intervals. In both plots, individual species are coloured according to the presence / absence of tool use in the video survey and the scientific literature. Total $n = 174$ species, generalist $n = 121$ species, specialist $n = 53$ species.

found in South East Asia and Australasia (*Cacatua*), the kea and the kākā from New

Zealand (*Nestor*), and the *Poicephalus* genus native to Africa (Table 1; Supplementary

Figures S6 - S8). These findings suggest that species from each of these genera may share

their tool use capabilities via common descent from their respective common ancestors,

rather than via independent evolution within each genus or behavioural innovation within

species.

Discussion

Since the earliest anecdotes of parrots using tools by Wallace in the 1880s (59) and

more systematic anecdotal reports in the 1970s (60), only 11 parrot species (3% of all

extant parrots) have been documented as tool users in the scientific literature. Our study

used crowdsourcing to identify 17 additional tool-using parrot species that are new to

Table 1

Estimated probabilities of tool use for most recent common ancestors of several parrot genera.
Probabilities estimated using exploratory ancestral state reconstruction models fitted to the
pre-video-survey data, post-video-survey data, and predicted probabilities from the phylogenetic
survival cure model. Total $n = 174$ species.

Genus	Pre-video-survey	Post-video-survey	Survival cure probabilities
Amazona	0.06, 95% CI [0.01 0.17]	0.21, 95% CI [0.04 0.66]	0.48, 95% CI [0.05 0.84]
Cacatua	0.08, 95% CI [0.03 0.20]	0.17, 95% CI [0.03 0.45]	0.81, 95% CI [0.23 0.99]
Nestor	0.11, 95% CI [0.05 0.29]	0.21, 95% CI [0.12 0.37]	0.53, 95% CI [0.29 0.66]
Poicephalus	0.06, 95% CI [0.02 0.11]	0.19, 95% CI [0.12 0.41]	0.72, 95% CI [0.16 0.90]

247 science, more than doubling the overall count to 28 species (7%). These species consisted

248 of cockatoos (*Cacatuidae*), Old World parrots (*Psittacinae*), and neotropical parrots

249 (*Arinae*). Beyond the crowdsourcing survey, the strong phylogenetic signal in our dataset

250 allowed us to use phylogenetic information, along with other variables, to infer the

251 unobserved probabilities of tool use across the parrot order. Our phylogenetic survival cure

252 model incorporated information on phylogenetic history, research effort, relative brain size,

253 and feeding specialisation to rank parrot species that were most likely to be undetected

254 tool users. The sum of probabilities from this model implied that between 15 and 41 of the

255 species without observed evidence of tool use are likely to be undetected tool users,

256 suggesting that the true proportion of tool users may be as high as 17%.

257   These findings have a number of important implications. First, our findings show

258 that current research effort in the scientific literature is insufficient to capture the real

259 world occurrence of parrot tool use. If the scientific literature had sampled the natural

260 world sufficiently, we would expect to see close correspondence between those species

261 reported as tool users in the literature and those species the public have filmed performing

262 tool use. Instead, we discovered a large discrepancy between these two data sources, both

263 in the prevalence of tool use and the species identified. This raises the possibility that

264 insufficient research effort is a general issue across the scientific literature, both for tool use

265 in other groups and for other rare behaviours.

266   Second, in terms of the evolution of tool use in parrots, our study challenges a key

267 assumption made in the literature to date: that only a minority of parrots are tool users

268 (30, 31, 34, 37, 38). The paucity of evidence for tool use across parrots in the literature

269 initially implied that the capacity for tool use may have evolved independently in different

270 parrot species. Our discovery of the widespread distribution of tool use across the parrot

271 phylogeny, along with the strong phylogenetic signal in this expanded dataset, challenges

272 this and suggests that, at least for some parrot clades, the capacity for tool use might be a

273 homologous trait that has been evolutionarily conserved. Our exploratory ancestral state

274 reconstruction analysis provides preliminary support for this hypothesis, revealing an

275 increased probability of tool use among the most recent common ancestors for the

276 *Amazona*, *Cacatua*, *Nestor*, and *Poicephalus* genera. Even at this preliminary stage, our

277 analysis therefore raises an alternative hypothesis for the observed tool use in *Cacatua* (30,

278 38) and *Nestor* (26–29, 31, 34), namely that tool behaviours have arisen due to the

279 common ancestor having the capacity to use tools, rather than from independent evolution

280 or behavioural innovation within species.

281   Third, our results support existing theories of the drivers of tool use. We found that

282 encephalisation was strongly positively related to the probability of tool use in our

283 phylogenetic model, supporting previous theories linking relative brain size to increased

284 tool innovation in birds (11–13) and primates (61). We acknowledge that encephalisation

285 quotient is not a perfect measure due to measurement error and challenges with

286 interpretation (3, 4). However, encephalisation quotient has much greater coverage across

287 the parrot phylogeny than more fine-grained measures like whole neuron count (62) and

288 there is no reason to think that measurement error would produce the consistent patterns

289 across our study and prior work. To understand the causal mechanisms responsible for

290 these relationships, we encourage further work on the specific neural correlates of technical

291 intelligence in parrots, e.g., (63). In our phylogenetic model, we also found that tool use

292 was somewhat more likely among feeding generalists compared to feeding specialists,

293 although this difference was uncertain. This trend supports previous suggestions that

294 increased cognitive abilities and technical innovation rates are required to expand a

295 generalist species' dietary niche (16, 18, 64). However, the trend contradicts theories

296 linking tool use to dietary specialisation, whereby species eating specific foods that require

297 extractive foraging have higher cognitive ability and are especially prone to using tools (18).

298   All instances of tool use in our crowdsourcing survey met the established criteria for

299 tool use in the literature: the manipulation of an unattached object as an extension of the

300 animal's body to achieve a goal (10). However, a striking feature of the dataset is that the

301 17 additional species identified in the video survey were exclusively observed using tools for

302 self-scratching. While parrots in the wild use tools to achieve a variety of goals, including

303 extractive foraging and preening (34, 38), parrots in captivity only require tools to achieve

304 the latter goal. Despite this difference in the type of tool use observed, self-scratching is

305 nonetheless a major category of animal tool use. Self-scratching also meets the definition

306 for a more complex type of embodied tool use known as 'tooling', the deliberate generation

307 of a mechanical interface by using an object to manipulate another target or surface (65).

308 This makes it difficult to dismiss self-scratching as unimportant: to do so would require a

309 redefinition of tool-use in non-human animals. Moreover, the fact that we found strong

310 phylogenetic clustering of self-scratching tool use from the video survey with other

311 examples of tool use from the literature supports a common underlying cognitive

312 mechanism. In line with this, some of the species of parrots that use tools for

313 self-scratching in captivity also use tools for other purposes in the wild (30, 31, 34, 38).

314   There was little evidence to suggest that the observations of self-scratching tool use

315 in the video survey were merely unintentional accidents or explicitly trained behaviours.

316 Individual parrots often used tools slowly and repetitively over long periods of time, even

317 across multiple different videos, suggesting that their behaviour was not random or

318 accidental (66). Parrots preferentially employed self-scratching tools on areas of their body

that were otherwise inaccessible, with 96% of all instances involving scratching of the head or neck, suggesting intentional tool use. For 60% of the species in the video survey, we found two or more videos of repetitive and sustained scratching by different individuals of the same species in separate households, suggesting that the manipulations were intentional and recurring events that did not represent unusual stereotypies of any single individual. Regarding the possibility of training or cueing from owners, over half of the videos contained no evidence of human interaction aside from filming the behaviour. Humans only handed parrots their tools in two of the videos, and none of the videos featured owners directly rewarding tool use behaviours with food. Finally, the high levels of phylogenetic signal in our data provide strong evidence that the observations from our video survey reflect biologically-endowed capacities for tool use rather than accidental or trained behaviours, which would likely appear uniformly across the phylogeny.

While missing data imputation is becoming more common in phylogenetic analyses (67), the important distinction between absence of evidence and evidence of absence has not been given as much attention. Our phylogenetic analysis provides one approach to this problem by distinguishing between true absences of tool use and absences of tool use due to a lack of research effort in the scientific literature or in crowdsourced videos. To achieve this, we explicitly modelled the measurement of the outcome variable along a research effort time series, such that species with lower research effort in the literature or in videos were likely to be censored. In line with our causal model, we also included relative brain size, feeding strategy, and phylogenetic history as predictors of unobserved tool use. We encourage researchers to test this model by directing future study efforts towards the parrot species with the highest probabilities of being undetected tool-users. Future work should also refine the causal model in Figure 1 to provide more certain estimates of tool use probabilities, either by including additional predictor variables or modelling further causes of measurement error in the taxonomic record, such as species abundance and geographic accessibility (20).

346   In conclusion, we have shown that the scientific literature has insufficiently captured

347 the full distribution of tool use in the parrot order. Our crowdsourcing survey more than

348 doubled the number of known tool using parrot species from 11 to 28, and our phylogenetic

349 model suggested that the true proportion of parrot tool users could be as high as 17% of all

350 species in this order. These discoveries have implications for theories of the evolutionary

351 drivers and origins of tool use in parrots. Beyond parrot tool use, the crowdsourcing and

352 phylogenetic methods used in this study have the potential to be applied to other rarely

353 observed behaviours, including tool use in other taxa (68), rhythmic entrainment in birds

354 (69–72), teasing behaviours in primates (73), and tactical deception across all animals

355 (74–76). We hope that these methods will continue to uncover a diverse array of ephemeral

356 behaviours that have as yet gone undetected in the scientific literature.

357   **Methods**

358 **Video searches and coding**

359   Our video search was conducted on YouTube in July 2020. Search terms included

360 "parrot using tool" and variants (e.g., "macaw using tool", "lorikeet using tool", "parakeet

361 using tool"), "tool use in parrot", "parrot tool use", "parrot scratching itself" (included

362 after we found several videos demonstrating self-care tool use in previous searches) and

363 equivalent terms (e.g., "parrot preening itself", "parrot grooming itself", "parrot

364 scratching"). For all species that did not display results including object manipulation or

365 scratching behaviours, we also searched the species' common name(s) + "tool use", as well

366 as the species' common name(s) + "scratching". We also searched for translations of the

367 terms "parrot tool use" and "parrot scratching" in languages for all countries where bird

368 ownership was reported as >5% (77), namely, Turkish, Czech, Polish, French, Italian,

369 Dutch, German, Russian, Spanish, Portuguese, and Mandarin.

370   When we found a relevant video, we also searched for similar content uploaded by the

same person/channel. For each YouTube search conducted, we watched all relevant videos until we reached five consecutive videos that did not feature any parrots. At this point, we ended that search and initiated the next search. In line with previous recommendations (21), we planned to exclude any videos that consisted of four or more shots edited together so as to ensure the behaviours being observed were not edited or manipulated, but none of the videos obtained qualified for exclusion.

All videos featuring parrots manipulating objects were investigated for potential tool use or borderline tool use. We defined tool use as the manipulation of an unattached object as an extension of the beak or foot to achieve a goal towards another object, individual, or oneself (10). Borderline tool use was similarly defined, except that it involved the use of an object that was still attached to a substrate (54). For example, if individuals used a fallen feather or stick for self-scratching this was defined as tool use, but using one's currently attached tail feathers or cage furnishings for the same purpose was defined as borderline tool use. Self-scratching had to involve slow and repeated movements of touching an object to one's body (or, in the case of borderline tool use, rubbing repetitively against an attached object (66)).

All relevant videos were coded for video length, species, tool use presence (yes/borderline), tool use type (e.g., scratching, feeding), the object being used (e.g., feather, stick), tool use target, human interaction (talking or handing object to parrot, holding parrot), and the number of shots within each video. Our complete dataset also includes the name for each video, link, subject name, sex (as declared by owner, as most parrot species are not sexually dimorphic), publishing date, and dates found and coded.

Data for parrot species

We collected data for 194 parrot species (Supplementary Figures S9 - S11). We gathered feeding strategy data as a dichotomous variable ("generalist" or "specialist") from

396 the EltonTraits ecological database (52). As per the database, specialists were defined as

397 species whose diet comprised at least 70% of a single food source. To calculate relative

398 brain size, we collated data from the literature for all known body mass (g) and brain mass

399 (g) values across parrots (46–51). For all species for which we obtained body and brain

400 mass data, we calculated the encephalisation quotient (EQ) using the following formula

401 (78): $BrainWeight/(0.12 * BodyWeight(\frac{2}{3}))$. We found body mass and brain mass data

402 for a total of 194 parrot species. This included all tool-using species in our video dataset,

403 with the exception of three species: *Diopsittaca nobilis*, *Psittacara erythrogenys*, and

404 *Coracopsis vasa*. For the latter, we used values for the closely related *Coracopsis nigra*.

405 The other two species were excluded from the final dataset.

406 For modelling purposes, we coded research effort in both the scientific literature and

407 the crowdsourced videos. For the scientific literature, we operationalised research effort as

408 the number of papers published for each species' Latin name up to and including the first

409 paper containing tool use for that species. If no tool use had been identified in the

410 scientific literature for a species, then we coded the total number of papers published to

411 date. We used the scientific database Scopus for coding the number of published papers.

412 For the crowdsourced videos, we coded research effort as the number of search hits for each

413 species on YouTube. If tool use had been identified on YouTube, we estimated the number

414 of search hits when the first video of tool use was published on YouTube, assuming linear

415 growth of search hits since the inception of YouTube. If tool use had not been identified,

416 we used the current number of search hits.

417 For phylogenetic data, we used the phylogenetic tool at www.birdtree.org (53) to

418 compile 1000 posterior draws of phylogenetic trees for 174 of the 194 parrot species for

419 which both EQ and genomic data exist. A single maximum clade credibility tree was

420 generated from these posterior draws for visualisation purposes. In our analyses, we

421 iterated over posterior draws of the phylogeny to account for phylogenetic uncertainty.

Phylogenetic signal

We used the *fitDiscrete* function in the *ape* R package (79) to calculate phylogenetic signal, for both the pre-survey and post-survey tool use data. We iterated the model over 100 posterior parrot phylogenies to incorporate phylogenetic uncertainty.

Causal model of tool use

To infer unobserved probabilities of tool use across parrots, we proposed a causal model of observed tool use (Figure 1). We assumed that observed tool use in the scientific literature and in the crowdsourced videos is caused by both the unobserved presence or absence of tool use and research effort, proxied by the number of papers published on a species and the number of videos published on a species. Tool users are more likely to be observed if they are well studied, but understudied tool users may go undetected. In addition, based on theory, we also assumed that unobserved tool use is caused by feeding strategy and relative brain size (11–14, 16–18). Finally, we assumed that shared phylogenetic history causes unobserved confounding and non-independence in unobserved tool use, feeding strategy, and relative brain size across the parrot phylogeny.

Bayesian phylogenetic survival cure model

Given our proposed causal model, we constructed a statistical model to impute unobserved probabilities of tool use and test existing theories of the evolution of tool use in parrots. To understand the model, suppose that we have the following observed variables for parrot species i. For the scientific literature, we declare $N_{\text{Lit},i}$ as the number of papers published before and up to tool use identification for species i (or, if tool use has not been identified, the total number of papers published for species i) and $T_{\text{Lit},i}$ as a binary variable stating whether (1) or not (0) tool use has yet been observed in the scientific literature for species i. For the crowdsourced videos, we declare $N_{\text{Vid},i}$ as the number of videos published

before and up to tool use identification for species i (or, if tool use has not been identified, the total number of videos published for species i) and $T_{\text{Vid},i}$ as a binary variable stating whether (1) or not (0) tool use has yet been observed in the crowdsourced videos for species i. Additionally, F_i and EQ_i are feeding strategy and encephalisation quotient values for species i and we have a phylogenetic distance matrix D that describes the patristic distances between all parrot species.

We assume that species i is a non-tool-user with some probability p_i. We also assume that tool use is identified in the scientific literature and the crowdsourced videos at constant rates λ_{Lit} and λ_{Vid} following exponential survival functions. Given these assumptions, we can then describe the different ways in which variables N_{Lit} and N_{Vid} can be distributed. Focusing on the scientific literature, if tool use has been observed ($T_{\text{Lit},i} = 1$), then the likelihood for $N_{\text{Lit},i}$ is:

$$\Pr(N_{\text{Lit},i} | T_{\text{Lit},i} = 1, p_i, \lambda_{\text{Lit}}) = (1 - p_i) \cdot \text{Exponential}(N_{\text{Lit},i} | \lambda_{\text{Lit}}) \tag{1}$$

On the other hand, if tool use has not yet been observed ($T_{\text{Lit},i} = 0$), there are two ways that the outcome variable could have been realised. First, the species could be a non-tool-user with probability p_i. Second, the species could be a tool-user with probability $(1 - p_i)$ that has been censored and has not had its tool use measured yet. Together, then, the likelihood for $N_{\text{Lit},i}$ is:

$$\Pr(N_{\text{Lit},i} | T_{\text{Lit},i} = 0, p_i, \lambda_{\text{Lit}}) = p_i + ((1 - p_i) \cdot \text{Exponential-CCDF}(N_{\text{Lit},i} | \lambda_{\text{Lit}})) \tag{2}$$

The Exponential-CCDF function allows for the censored nature of the data. The same data generating process is assumed to underlie the crowdsourced videos.

465   We define the mixture likelihood SurvivalCure as the distribution above, with

466 parameters p (the probability of being a non-tool-user) and λ (the rate of the exponential

467 distribution). We use an Ornstein-Uhlenbeck Gaussian process (80) to model phylogenetic

468 covariance. Below, we specify the full model with priors:

$$N_{\text{Lit},i} \sim \text{SurvivalCure}(\lambda_{\text{Lit},i}, p_i) \tag{3}$$

$$N_{\text{Vid},i} \sim \text{SurvivalCure}(\lambda_{\text{Vid},i}, p_i)$$

$$\lambda_{\text{Lit},i} = 1/\exp(\gamma_{\text{Lit}})$$

$$\lambda_{\text{Vid},i} = 1/\exp(\gamma_{\text{Vid}})$$

$$\text{logit}(p_i) = \alpha_{\text{FEEDING}[i]} + \beta \text{EQ}_i + k_{\text{SPECIES}[i]}$$

$$\begin{pmatrix} k_1 \\ k_2 \\ ... \\ k_n \end{pmatrix} \sim \text{MVNormal} \left(\begin{pmatrix} 0 \\ 0 \\ ... \\ 0 \end{pmatrix}, \mathbf{K} \right)$$

$$\mathbf{K_{ij}} = \eta^2 \exp(-\rho^2 D_{ij})$$

$$\gamma_{\text{Lit}}, \gamma_{\text{Vid}}, \alpha_{1,2}, \beta \sim \text{Normal}(0, 1)$$

$$\eta^2, \rho^2 \sim \text{Exponential}(0.5)$$

469   The priors for this model produce reasonable prior predictions of the probabilities of

470 tool use for each parrot species (Supplementary Figure S12), but a sensitivity analysis

471 revealed that the ranking and posterior probabilities reported in the main text were robust

472 to modifying these priors (Supplementary Figure S13). We estimated the posterior

473 distribution of this model using Hamiltonian Monte Carlo as implemented in Stan version

474 2.26.1 (81). We ran the model for 4000 samples, with 2000 warmup samples, and iterated

475 the model over 100 posterior parrot phylogenies to incorporate phylogenetic uncertainty.

⁴⁷⁶ R-hat values and effective sample sizes suggested that the model converged normally. Trace

⁴⁷⁷ plots are reported in Supplementary Figure S14. We report equal-tailed credible intervals

⁴⁷⁸ to describe the posterior distribution of this model in the main text.

⁴⁷⁹ To validate our method, we fitted the model to 100 simulated datasets with known

⁴⁸⁰ parameters. The model was able to successfully recover those parameters (Supplementary

⁴⁸¹ Figure S15). We also ran a leave-one-species-out exercise to ensure that we could

⁴⁸² accurately predict known tool users. We repeated this approach for each known tool user

⁴⁸³ by setting observed tool use to zero. Cross-validation results are reported in the main text.

⁴⁸⁴ **Ancestral state reconstruction**

⁴⁸⁵ To determine whether the identification of novel tool-using species has implications

⁴⁸⁶ for our understanding of the evolutionary origins of tool use in parrots, we fitted three

⁴⁸⁷ exploratory ancestral state reconstruction models. We used the *ancThresh* function from

⁴⁸⁸ the *phytools* R package (82), iterating the function over 100 posterior parrot phylogenies.

⁴⁸⁹ This function estimates discrete ancestral states by assuming the evolution of a latent

⁴⁹⁰ continuous variable following an Ornstein-Uhlenbeck process. We fitted this model to three

⁴⁹¹ different outcome variables: (*i*) presence vs. absence of tool use in scientific literature only,

⁴⁹² (*ii*) presence vs. absence of tool use in literature and/or videos, and (*iii*) the median

⁴⁹³ predicted probabilities of tool use from the phylogenetic survival cure model.

⁴⁹⁴ **Reproducibility**

⁴⁹⁵ All analyses were conducted in R v4.2.1. (83). Visualisations were produced using

⁴⁹⁶ the *ggtree*(84), *ggplot2* (85), and *cowplot* (86) packages. The manuscript was reproducibly

⁴⁹⁷ generated using the *targets* (87) and *papaja* (88) packages. Code to reproduce all analyses

⁴⁹⁸ and figures can be found here: https://github.com/ScottClaessens/phyloParrot

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Author Contributions

All authors contributed to the conceptualisation of the paper. A.P.M.B., X.J.N., and A.H.T. developed the video search methodology. S.C., D.W., and Q.A.D. developed the statistical models and analysed the data. All the authors wrote the manuscript and approved the final version for submission.

Competing Interests

The authors declare no competing interests.

Data Availability

All data used in this study are publicly available on GitHub:

https://github.com/ScottClaessens/phyloParrot

Code Availability

All code to reproduce the analyses in this study are publicly available on GitHub:

https://github.com/ScottClaessens/phyloParrot

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Supplementary Information

Crowdsourcing and phylogenetic modelling reveal parrot tool use is not rare

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Supplementary Figures
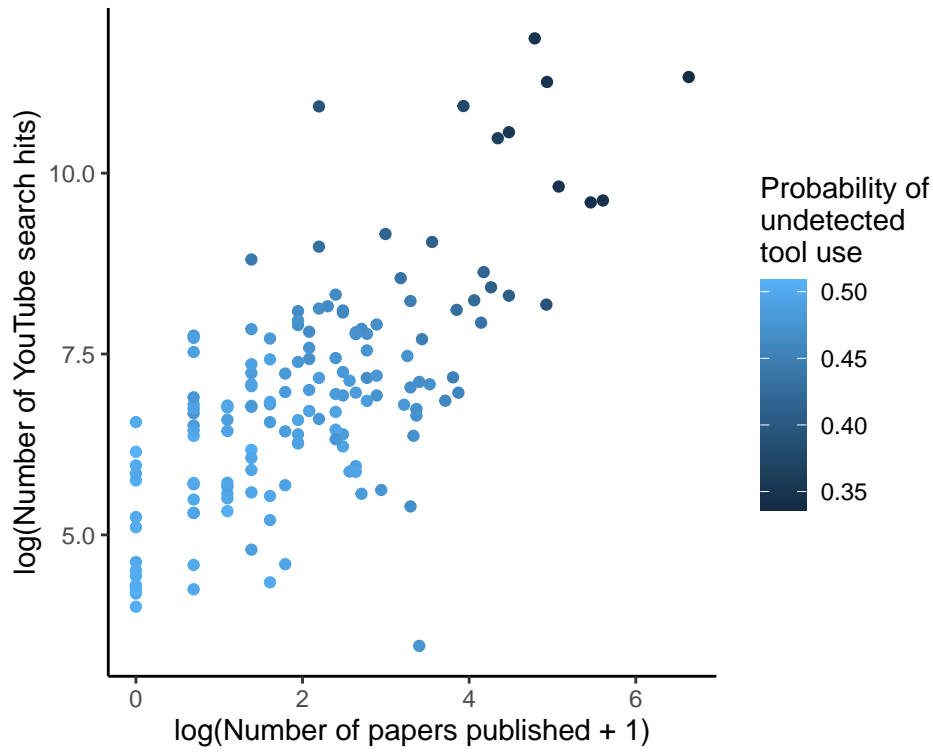
Figure S1. Median posterior probabilities of undetected tool use for each parrot species without observed evidence of tool use from reduced model. This reduced version of the phylogenetic survival cure model does not contain relative brain size or feeding strategy as predictors, nor does it contain any phylogenetic covariance. The only information included in the model is the number of papers published and the number of YouTube search hits for each species. Each point is a parrot species without observed evidence of tool use, and the colour of the points scales with the probability of undetected tool use. All else being equal, those species with fewer published papers and fewer YouTube search hits have a higher probability of being undetected tool users.
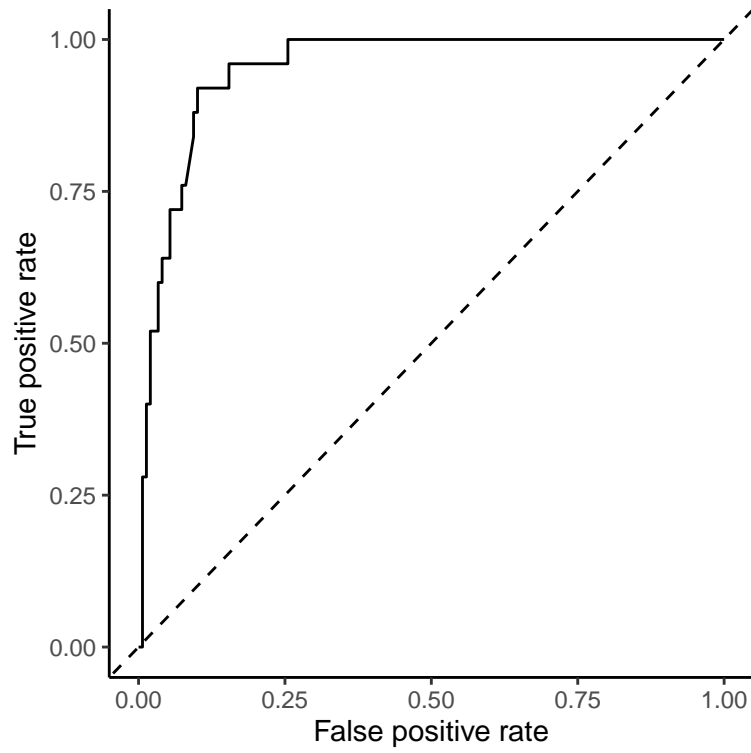
Figure S2. *Receiver operating characteristic (ROC) curve for the phylogenetic survival cure model.* The area-under-the-curve in this plot is 0.95, suggesting that the model is able to adequately classify observed tool users and non-tool users.
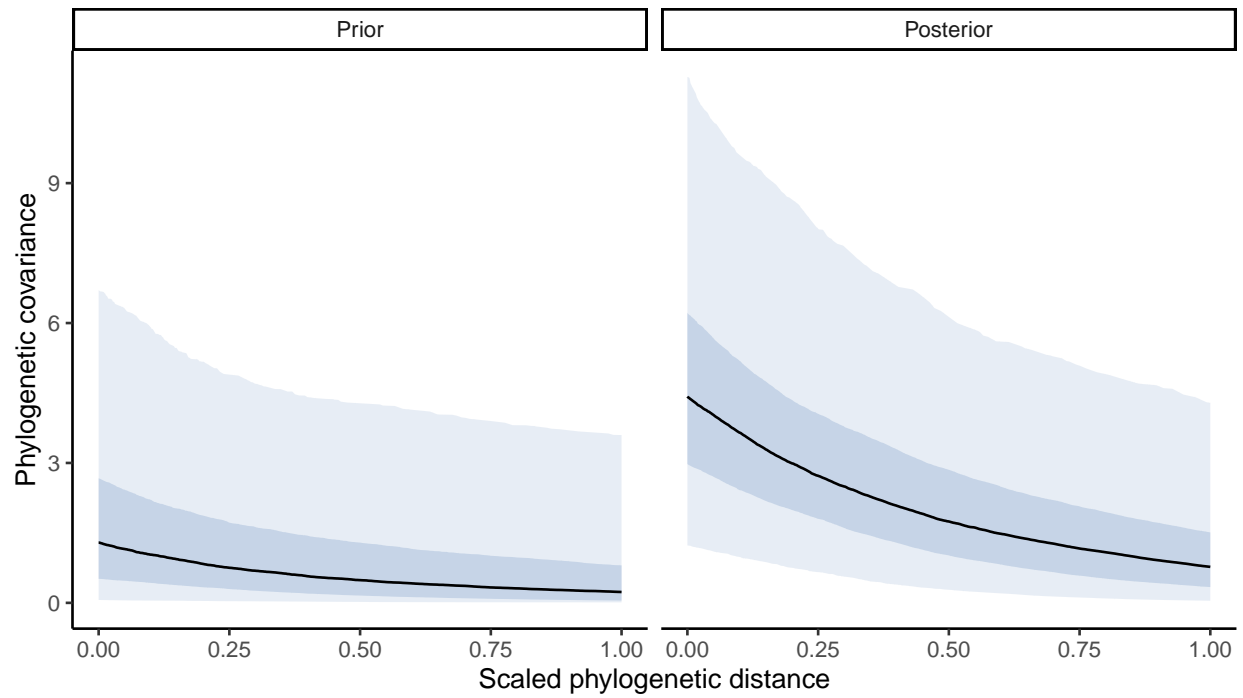
Figure S3. Prior and posterior phylogenetic covariance functions from the Bayesian survival cure model fitted to the full dataset. Lines are median posterior functions and shaded areas are 50% and 95% credible intervals.
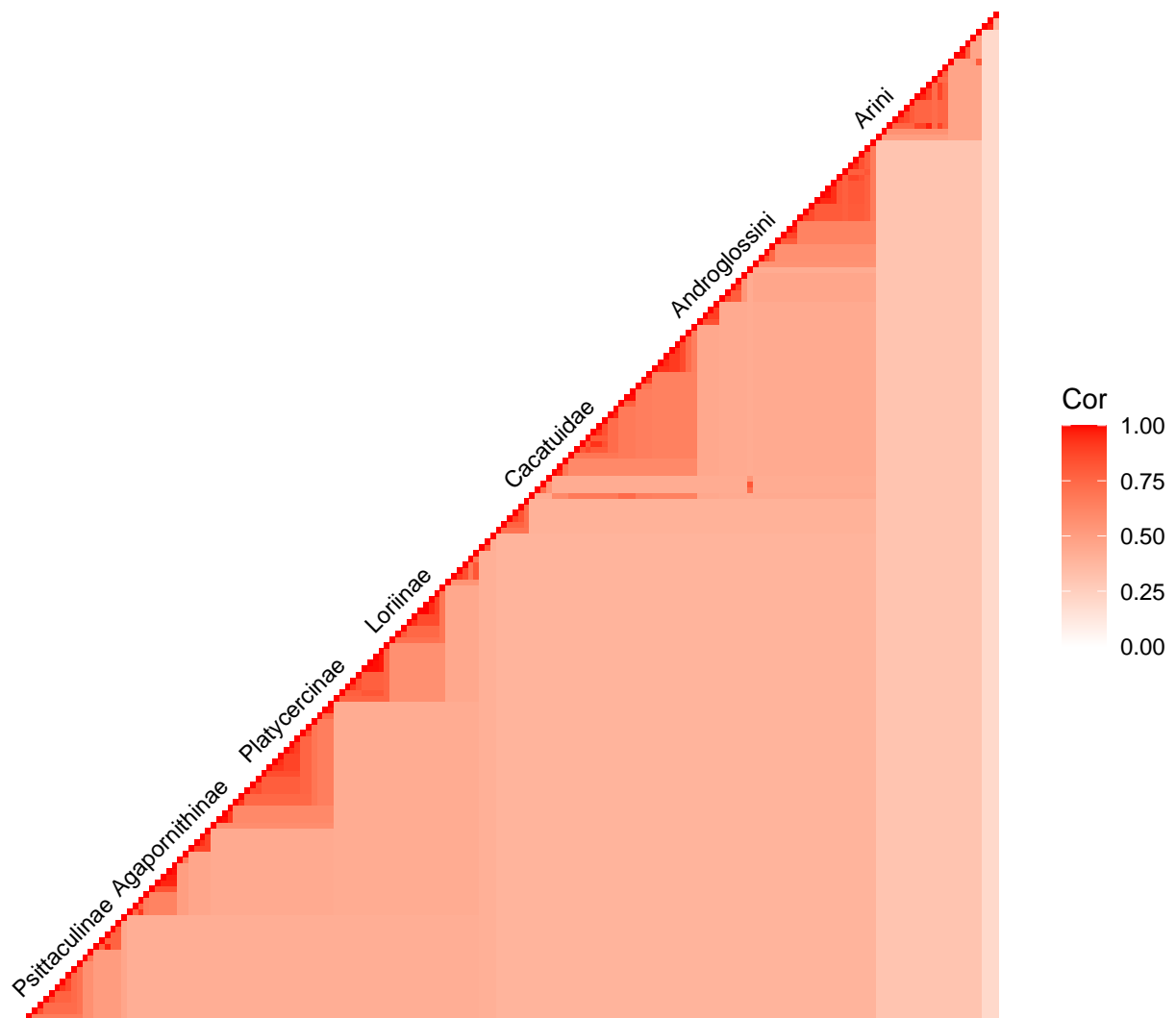
Figure S4. Between-species correlation matrix implied by the posterior phylogenetic covariance function from the Bayesian survival cure model. Correlations are median posterior estimates. Individual species names omitted for space reasons.
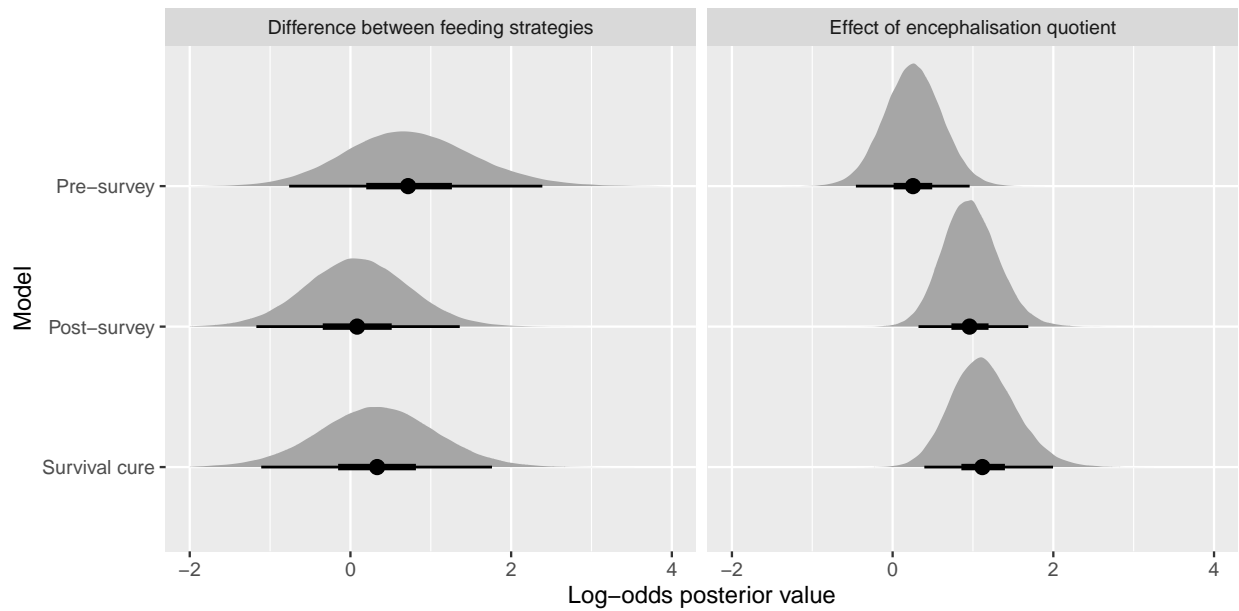
Figure S5. Comparing results between the survival cure model and models fitted to the pre-survey and post-survey data without any survival cure component. Densities are full posterior distributions from three separate models iterated over 100 posterior parrot phylogenies. Points represent posterior medians, and lines represent 50% and 95% credible intervals.
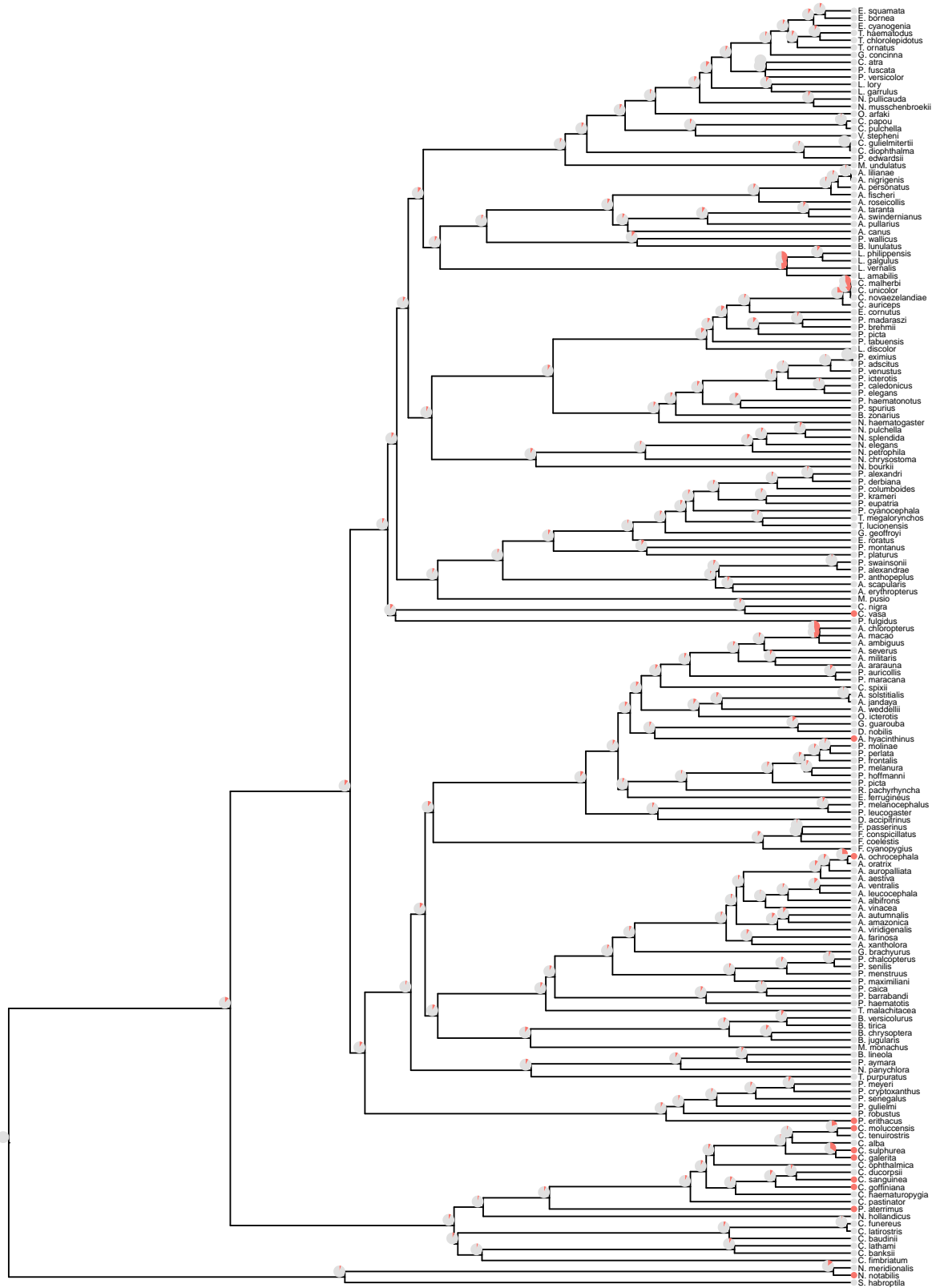
Figure S6. Results of exploratory ancestral state reconstruction analysis fitted to pre-video-survey data, represented on a maximum clade credibility tree. Tip nodes represent the presence (red) or absence (grey) of observed tool use in the scientific literature. Pie charts represent the posterior probability of tool use presence at each ancestral node.
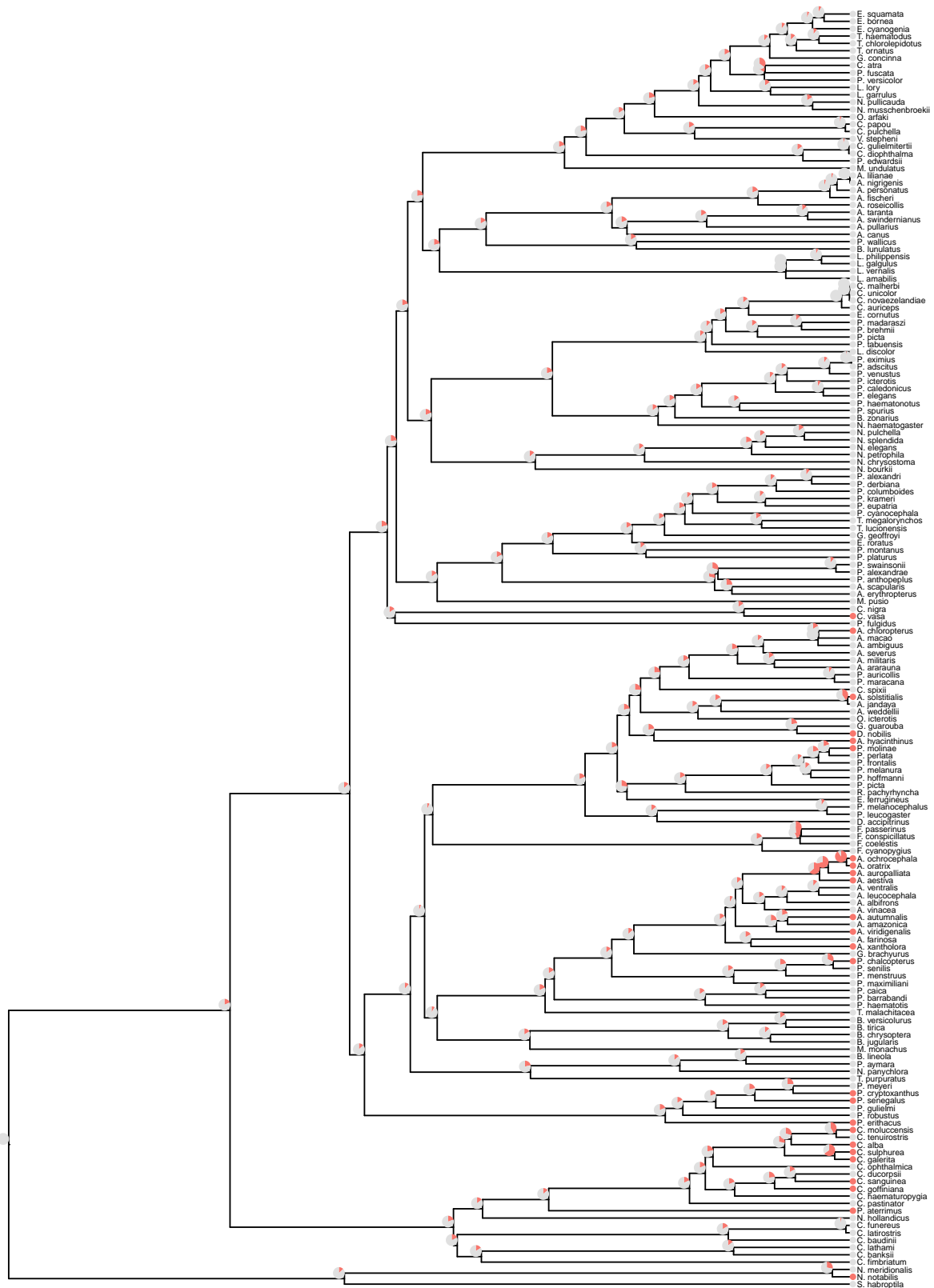
Figure S7. Results of exploratory ancestral state reconstruction analysis fitted to post-video-survey data, represented on a maximum clade credibility tree. Tip nodes represent the presence (red) or absence (grey) of observed tool use in the scientific literature and the video survey. Pie charts represent the posterior probability of tool use presence at each ancestral node.
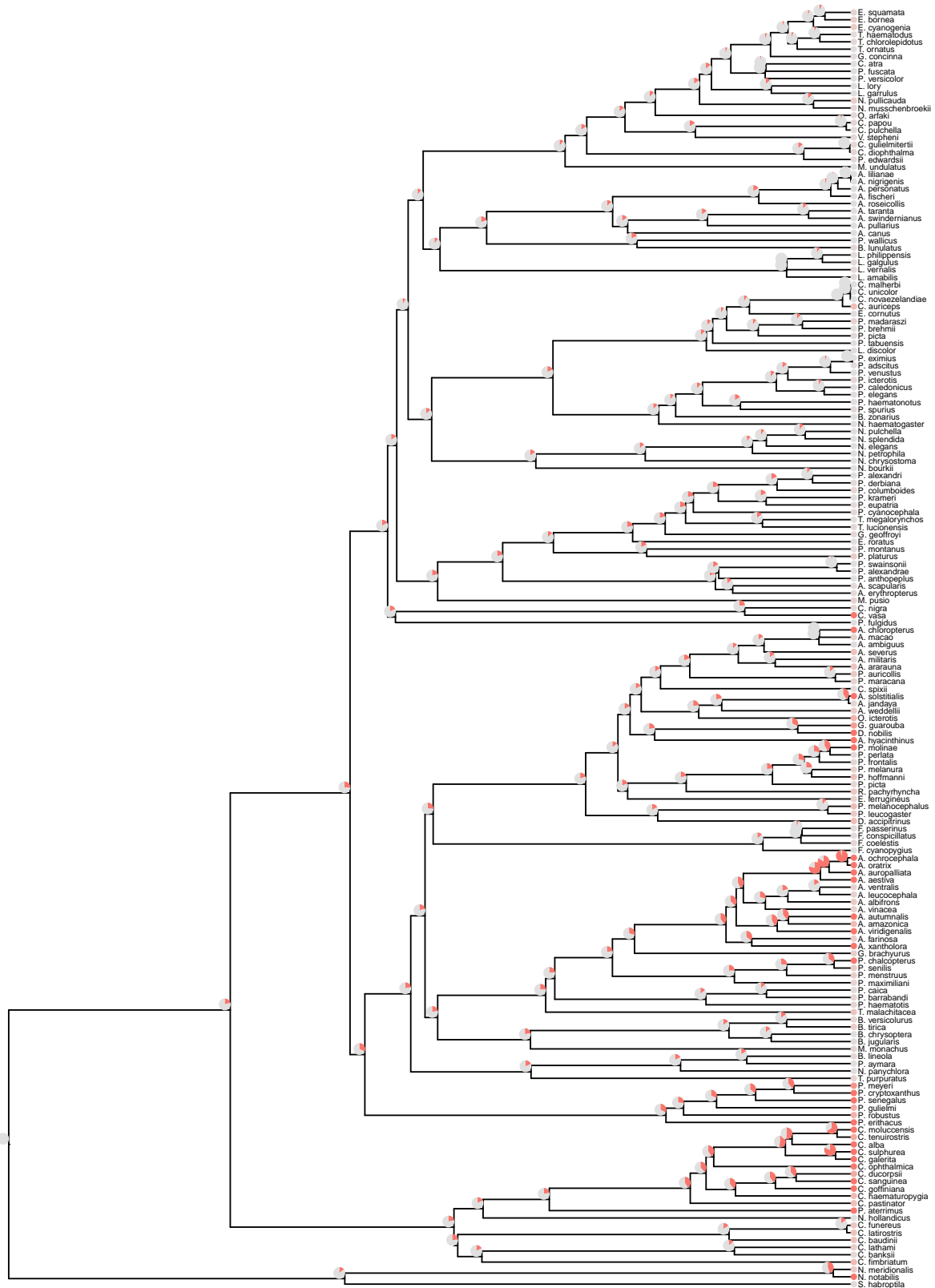
Figure S8. Results of exploratory ancestral state reconstruction analysis fitted to predicted probabilities from the phylogenetic survival cure model, represented on a maximum clade credibility tree. Tip nodes represent the median posterior predicted probabilities of tool use from the phylogenetic survival cure model, with more red indicating an increasing probability of tool use presence and more grey indicating a decreasing probability of tool use presence. Pie charts represent the posterior probability of tool use presence at each ancestral node.
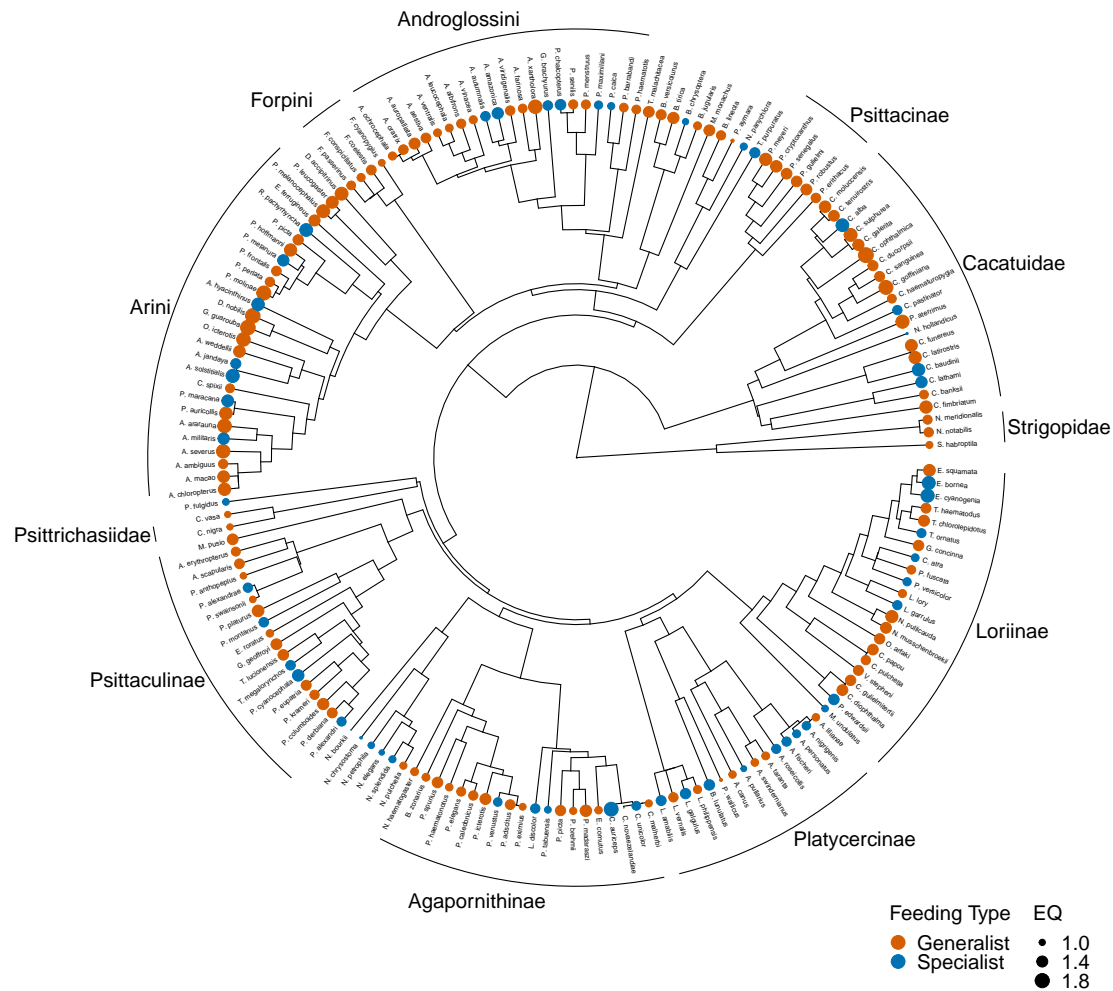
Figure S9. Data on encephalisation quotient and feeding strategy for all parrots, presented on a maximum clade credibility tree. Tip points are coloured according to feeding generalism (orange) and specialism (blue), and scaled according to encephalisation quotient (EQ).
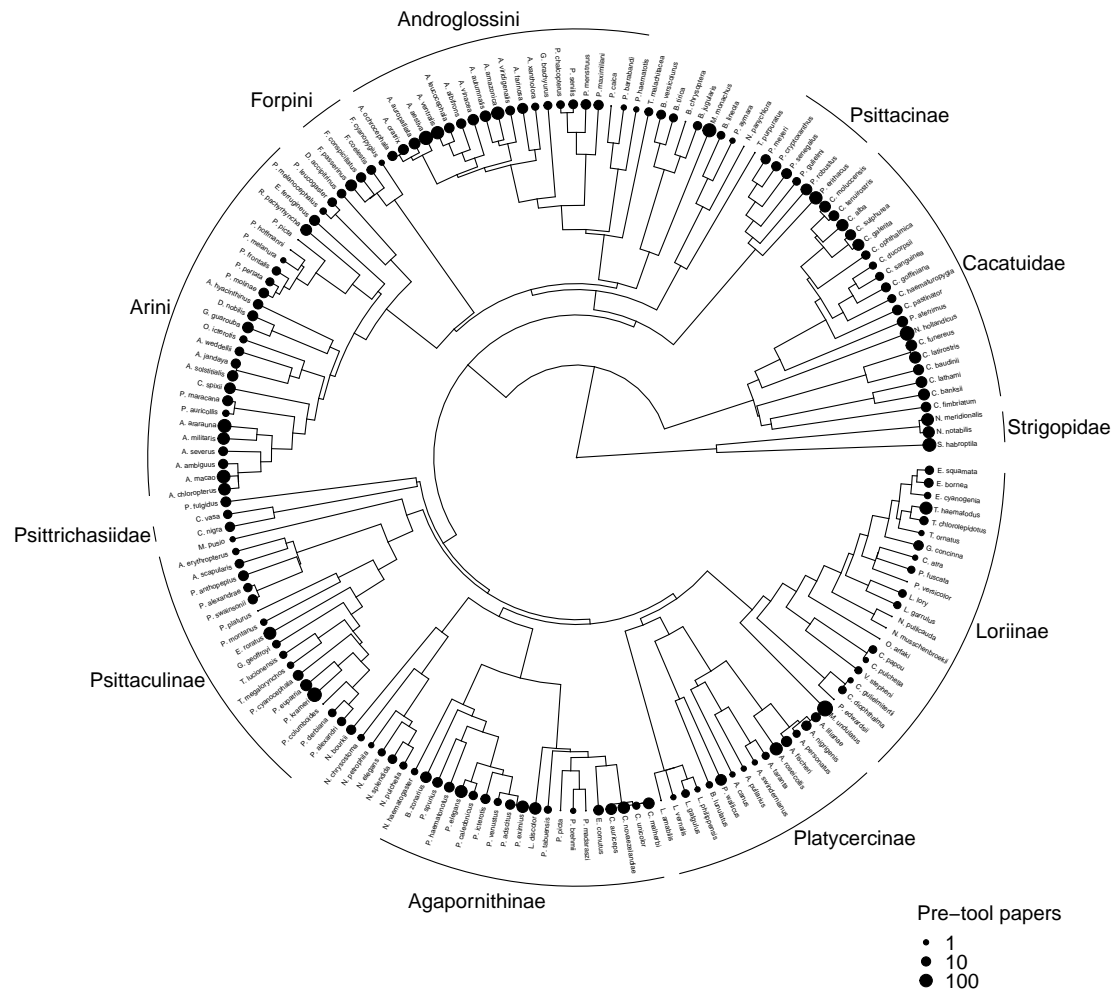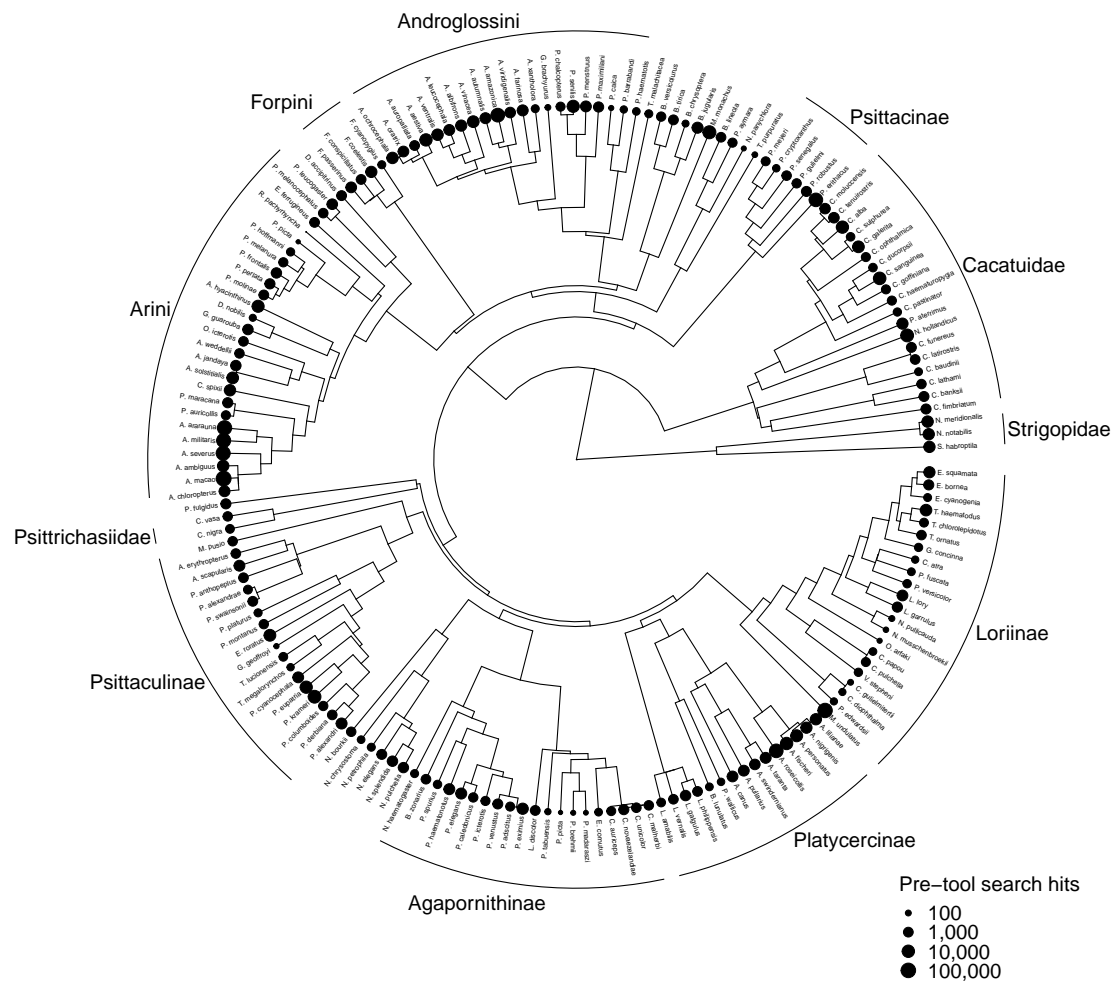
Figure S10. Data on number of scientific publications until tool use discovery for all parrots, presented on a maximum clade credibility tree. Tip points are scaled according to the number of published papers up until tool use discovery (or, if tool use has not been observed, the current number of published papers).

Figure S11. Data on number of video search hits until tool use discovery for all parrots, presented on a maximum clade credibility tree. Tip points are scaled according to the estimated number of video search hits up until tool use discovery (or, if tool use has not been observed, the current number of video search hits).
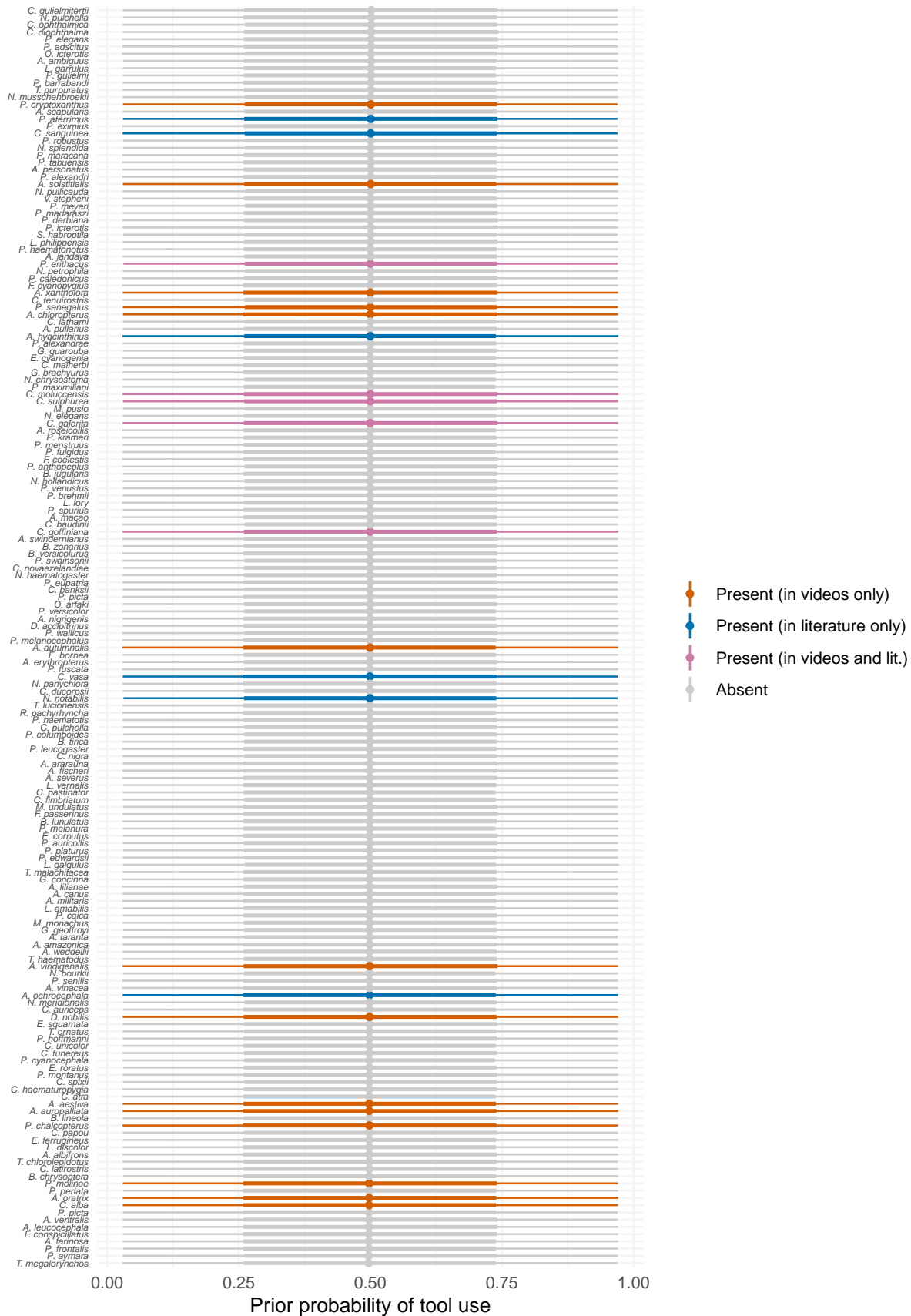
Figure S12. Prior predicted probabilities of tool use for each species from our phylogenetic survival cure model. Points are prior medians and lines are 50% and 95% credible intervals.
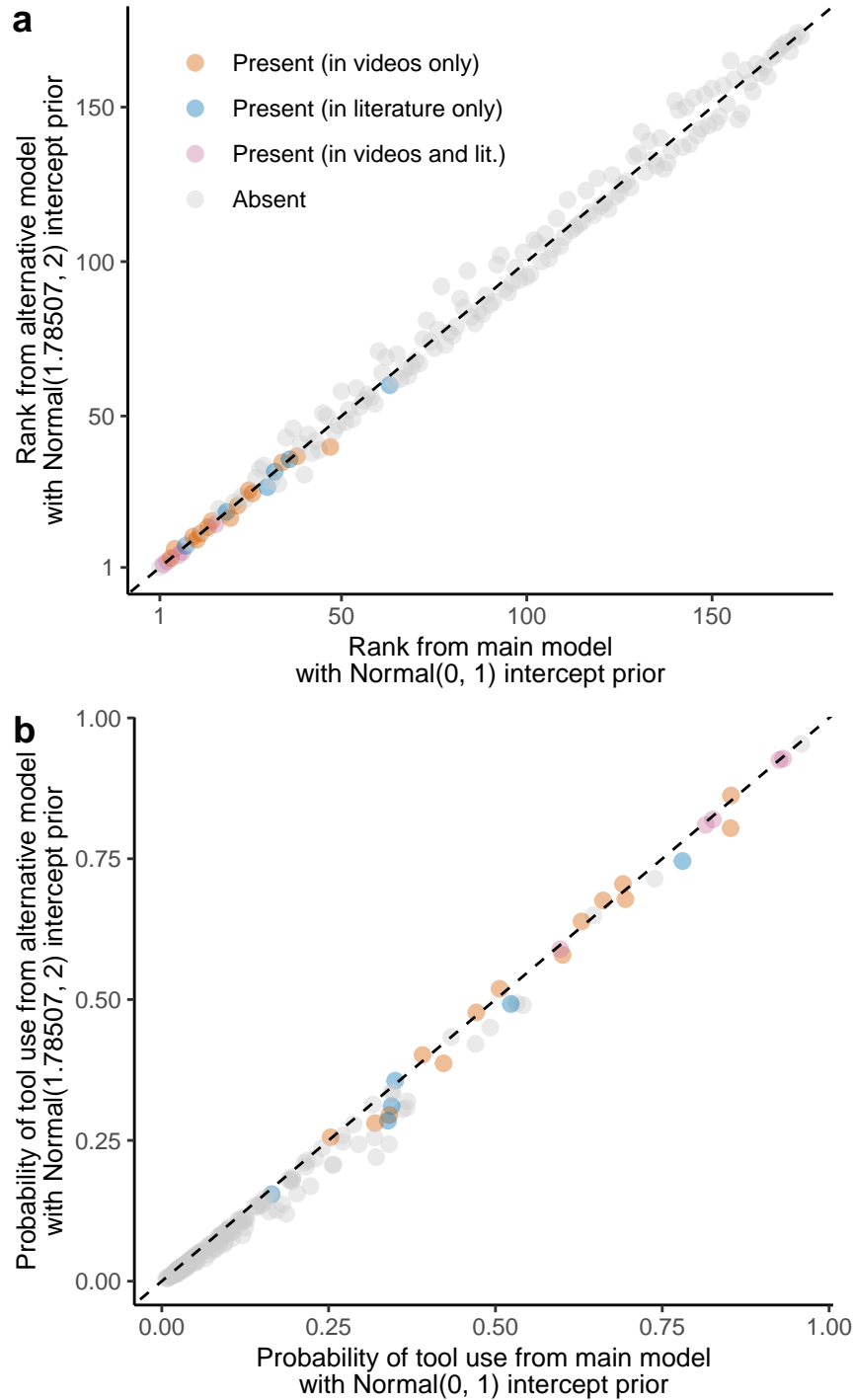
Figure S13. Results of sensitivity analysis. The phylogenetic survival cure model was fitted with either a standard Normal(0, 1) prior on the intercept or an alternative Normal(1.78507, 2) prior on the intercept. This latter prior is wider on the logit scale and roughly converts to a 0.86 prior probability of non-tool-use (or a 0.14 prior probability of tool-use, which is the proportion of tool users in the dataset). The sensitivity analysis showed that changing this intercept prior did not have a marked impact on (a) the posterior rankings of parrot species from 1st to 174th or (b) the median posterior probabilities of tool use for parrot species.
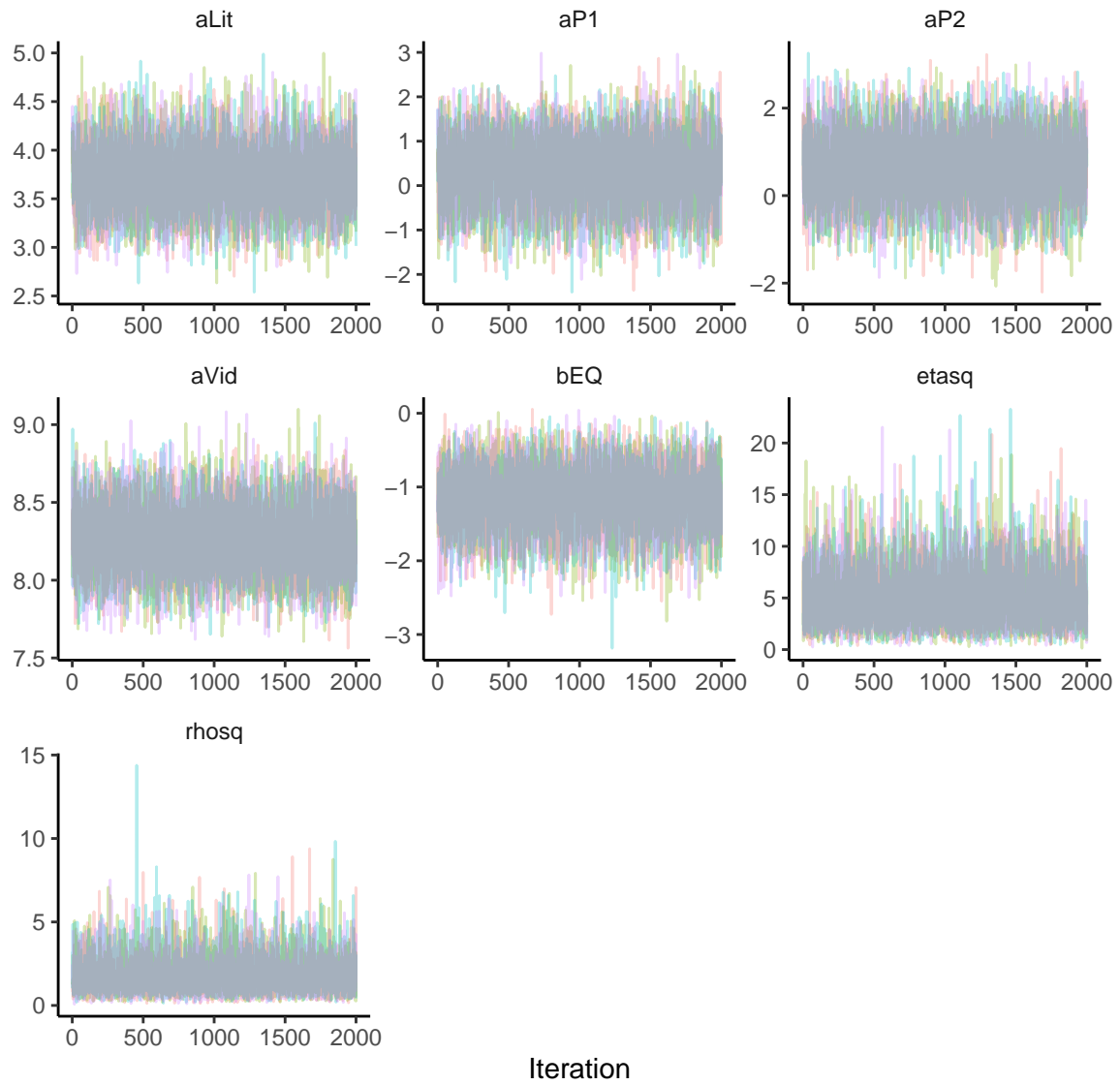
Figure S14. *Trace plots for the Bayesian phylogenetic survival cure model.* Only four chains are shown for ease of presentation.
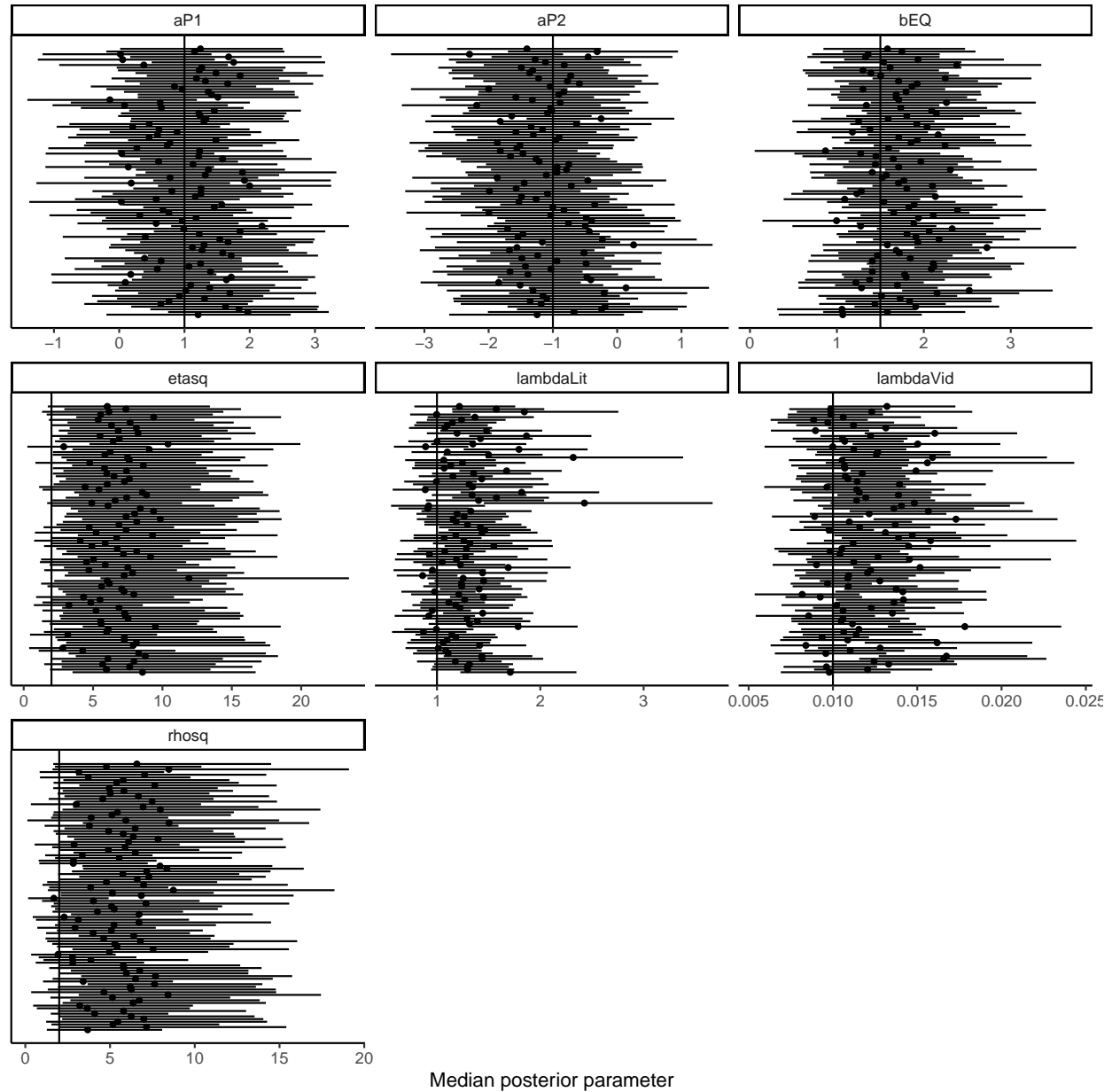
Figure S15. *Posterior estimates from Bayesian survival cure models fitted to 100 datasets simulated with known parameters.* Each dataset consisted of 100 species. Known parameters are presented as solid vertical lines, whereas points and horizontal lines represent posterior medians and 95% credible intervals. The models were successfully able to recapture the parameters from the simulated datasets.