

1 **Title: The macroecology and evolution of avian competence for *Borrelia burgdorferi***

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9 **Acknowledgments**

10 We thank BirdLife International for providing avian distribution data, Tao Huang for assistance  
11 with data processing, and JP Schmidt for technical advice on BRTs. We also thank Ellen  
12 Ketterson, members of the Ketterson lab, and two anonymous reviewers for feedback on this  
13 manuscript. DJB was supported by an appointment to the Intelligence Community Postdoctoral  
14 Research Fellowship Program, administered by Oak Ridge Institute for Science and Education  
15 through an interagency agreement between the U.S. Department of Energy and the Office of the  
16 Director of National Intelligence. BAH was supported by the National Science Foundation  
17 Ecology and Evolution of Infectious Diseases program (DEB-1717282 and DEB-1619072).

18

19 **Running head:** Avian competence for *Bbsl*

20 **Keywords:** machine learning; boosted regression tree; birds; transmission; tick-borne disease;  
21 Lyme borreliosis; phylogenetics

22

23

24 **Abstract**

25 **Aim:** Predicting novel reservoirs of zoonotic pathogens would be improved by identifying inter-  
26 specific drivers of host competence, the ability to transmit pathogens to new hosts or vectors.  
27 Tick-borne pathogens can provide a useful model system, as larvae become infected only when  
28 feeding on a competent host during their first bloodmeal. For tick-borne diseases, competence  
29 has been best studied for *Borrelia burgdorferi* sensu lato (*Bbsl*), which causes Lyme borreliosis.  
30 Major reservoirs include several small mammal species, but birds may play an underrecognized  
31 role in human risk given their ability to disperse infected ticks across large spatial scales. Here,  
32 we provide a global synthesis of the ecological and evolutionary factors that determine the ability  
33 of bird species to infect larval ticks with *Bbsl*.

34 **Location:** Global

35 **Time period:** 1983 to 2019

36 **Major taxa studied:** Birds

37 **Methods:** We compiled a dataset of *Bbsl* competence across 183 bird species and applied meta-  
38 analysis, phylogenetic factorization, and boosted regression trees to describe spatial and temporal  
39 patterns in competence, characterize its phylogenetic distribution across birds, reconstruct its  
40 evolution, and evaluate the trait profiles associated with competent avian species.

41 **Results:** Half of sampled bird species show evidence of competence for *Bbsl*. Competence  
42 displays moderate phylogenetic signal, has evolved multiple times across bird species, and is  
43 pronounced in the genus *Turdus*. Trait-based analyses distinguished competent birds with 80%  
44 accuracy and show that such species have low baseline corticosterone, exist on both ends of the  
45 pace-of-life continuum, breed and winter at high latitudes, and have broad migratory movements

46 into their breeding range. We use these trait profiles to predict various likely but unsampled  
47 competent species, including novel concentrations of avian reservoirs within the Neotropics.  
48 **Main conclusion:** Our results can generate new hypotheses for how birds contribute to the  
49 dynamics of tick-borne pathogens and help prioritize surveillance of likely but unsampled  
50 competent birds. Our findings further emphasize that birds display underrecognized variation in  
51 their contributions to enzootic cycles of *Bbsl* and the broader need to better consider competence  
52 in ecological and predictive studies of multi-host pathogens.

## 53 **Introduction**

54 As most emerging infectious diseases originate in animals (Jones *et al.*, 2008), diverse efforts  
55 have aimed to predict reservoir hosts and arthropod vectors of zoonotic pathogens (Morse *et al.*,  
56 2012; Babayan *et al.*, 2018). Because such predictions can guide surveillance and interventions,  
57 they are necessary steps toward a preemptive approach to minimizing pathogen spillover risks  
58 (Han & Drake, 2016; Becker *et al.*, 2019c). For example, PCR and serological data on Nipah  
59 virus from bats were leveraged to prioritize field sampling targets across India in response to a  
60 novel human outbreak (Plowright *et al.*, 2019a), and similar approaches have been applied to  
61 identify hosts of filoviruses, rodent zoonoses, and Zika virus (Han *et al.*, 2015, 2016, 2019).  
62 However, PCR and serological data better reflect host exposure rather than competence, the  
63 ability of a host to transmit a pathogen to a new host or vector (Gervasi *et al.*, 2015). Greater  
64 attention to competence could thus improve reservoir host predictions (Becker *et al.*, 2020b).

65 Host competence is an individual-level and continuous trait encompassing infection  
66 processes that occur within the host following exposure: susceptibility to infection, pathogen  
67 development, and pathogen survival until transmission (Merrill & Johnson, 2020). This  
68 individual heterogeneity mediates intra- and inter-specific variation in competence, which can  
69 produce species with disproportionate contributions to pathogen transmission (VanderWaal &  
70 Ezenwa, 2016). For example, American robins (*Turdus migratorius*) are on average more  
71 competent for West Nile virus than other bird species, infecting up to 71% of mosquito vectors  
72 despite low relative abundance in avian communities (Kilpatrick *et al.*, 2006). Similarly,  
73 transmission of many helminths is dominated by single host species among small mammals  
74 (Streicker *et al.*, 2013). Identifying the broader ecological or evolutionary drivers of competence  
75 could identify how different species contribute to pathogen transmission (Downs *et al.*, 2019).

76           Competence can be difficult to quantify, as infection status of the donor and recipient  
77 host must be known or directional transmission events must be inferred (Archie *et al.*, 2009;  
78 Martin *et al.*, 2016). However, many tick-borne diseases facilitate quantifying competence, as  
79 tick larvae hatch free of some pathogens and only become infected with their first bloodmeal  
80 (Richter *et al.*, 2011). Fed larvae are often collected from wild hosts and tested for infection to  
81 establish host-to-vector transmission; however, such data can only approximate competence.  
82 Instead, xenodiagnostic experiments provide ideal evidence, as uninfected larvae are fed on  
83 infected hosts, often allowed to molt (assuring transstadial transmission), and then tested for  
84 pathogen presence to infer competence (i.e., proportion of infected ticks) (Brunner *et al.*, 2008).

85           In this context, inter-specific variation in competence has been best studied for *Borrelia*  
86 *burgdorferi* sensu lato (*Bbsl*), which causes Lyme borreliosis. *Bbsl* is transmitted to humans by  
87 nymphal and adult *Ixodes* ticks (Hofhuis *et al.*, 2017; Eisen, 2020) and has infection foci across  
88 the northern hemisphere and parts of Latin America (Kurtenbach *et al.*, 2006; Ivanova *et al.*,  
89 2014). Lyme borreliosis is the most common vector-borne disease in the United States (i.e.,  
90 Lyme disease; (Schwartz, 2017), where fast-lived rodent species, specifically white-footed mice  
91 (*Peromyscus leucopus*) and eastern chipmunks (*Tamias striatus*), infect high proportions of  
92 larvae and are the most competent mammals (LoGiudice *et al.*, 2003; Huang *et al.*, 2013; Ostfeld  
93 *et al.*, 2014). By infecting most naïve vectors, these species contribute disproportionately to the  
94 production of infectious nymphs and to human risk (Mather *et al.*, 1996; Ostfeld *et al.*, 2006).

95           In contrast to mammals, birds likely play an underrecognized role in the global ecology  
96 of *Bbsl*, given that the capacity for flight and long-distance migration can allow avian hosts to  
97 disperse infected ticks across continents (Smith Jr *et al.*, 1996; Ishiguro *et al.*, 2005; Dubska *et*  
98 *al.*, 2009; Norte *et al.*, 2020). Migratory birds transport 50–175 million ticks across Canada each

99 spring (Ogden *et al.*, 2008), and the physiological stress of migration itself may help drive  
100 reactivation of latent *Bbsl* infection (Gylfe *et al.*, 2000). Individual studies have suggested some  
101 birds have important contributions to enzootic maintenance of *Bbsl* (Brinkerhoff *et al.*, 2011;  
102 Mysterud *et al.*, 2019). For example, birds dominate transmission of *B. garinii* and *B. valaisiana*  
103 to larvae across Europe (Hanincová *et al.*, 2003; Comstedt *et al.*, 2006) and contribute to  
104 enzootic cycles of the primarily rodent genospecies, *B. afzelli* (Franke *et al.*, 2010). In North  
105 America, *Bb* sensu stricto infects both rodents and birds; however, as with mammals, birds  
106 seemingly display interspecific variation in competence. For example, American robins infect up  
107 to 90% of naïve larvae (Richter *et al.*, 2000), whereas gray catbirds (*Dumetella carolinensis*) and  
108 veeries (*Catharus fuscescens*) infect fewer larvae and thus have lower competence (Anderson *et*  
109 *al.*, 1986; Mather *et al.*, 1989; Ginsberg *et al.*, 2005). High tick burdens of some bird species,  
110 such as ground foragers, may allow birds to contribute more to *Bbsl* transmission than some  
111 rodents (Wright *et al.*, 2000; Loss *et al.*, 2016). Many birds capable of infecting larvae are also  
112 common in suburban and urban habitats (Battaly & Fish, 1993; Hamer *et al.*, 2012), which could  
113 increase human exposure to infectious nymphs (Mead *et al.*, 2018). Yet despite opportunities for  
114 birds to play key roles in the global distribution of *Bbsl* and Lyme borreliosis risk, inter-specific  
115 drivers of reservoir competence across bird species have not yet been systematically identified.

116         Given the potential for birds to play important roles in the dynamics of *Bbsl*, we here  
117 compile a comprehensive, global dataset on avian competence and assess its ecological and  
118 evolutionary drivers. We first describe spatial and temporal patterns in competence, characterize  
119 its phylogenetic distribution across birds, and reconstruct its evolution. We then use a flexible  
120 machine learning algorithm to evaluate the trait profiles of competent avian species and predict  
121 unsampled reservoirs. For the latter, such data science approaches circumvent many issues

122 associated with traditional hypothesis testing (e.g., a large number of predictors, complex  
123 interactions, non-randomly missing covariates) and can uncover new and surprising patterns in  
124 data, thereby developing testable hypotheses (Hochachka *et al.*, 2007). Our work therefore aimed  
125 to identify the ecological and evolutionary drivers of avian competence while also generating  
126 predictions of likely novel *Bbsl* reservoirs and directions for future studies of tick-borne disease.

127

## 128 **Methods**

### 129 *Competence data*

130 To collate data on avian competence for *Bbsl*, we searched Web of Science, PubMed, and CAB  
131 Abstracts with the following string: ("reservoir competence" OR "host competence" OR  
132 prevalence) AND (bird\* OR Aves) AND (larva\* OR tick\* OR arthropod\*) AND ("Lyme  
133 disease" OR *Borrelia* OR "*B. burgdorferi*"). Using a systematic protocol (Fig. S1), we only  
134 included xenodiagnostic experiments and field studies that tested engorged larvae for *Bbsl*. We  
135 caution that the latter ignores both transstadial transmission and infection in the host. Although  
136 transstadial transmission is well established for *Bbsl* in *Ixodes* ticks (Burgdorfer & Gage, 1986),  
137 the absence of *Bbsl* in engorged larvae could simply result from lack of infection in the wild host  
138 rather than poor competence (Brunner *et al.*, 2008). Field-based measures thus only approximate  
139 competence, and failure to detect *Bbsl* in fed larvae requires either testing hosts or experimental  
140 validation; however, species to target for both approaches can be prioritized by the predictive  
141 methods employed here. From our systematic search, we excluded studies that only tested larvae  
142 for non-*Bbsl* *Borrelia* (e.g., *B. lonestari*), only tested nymph or adult ticks, pooled ticks by life  
143 stage, only tested wild birds themselves (e.g., blood), or pooled competence across bird species.

144 We identified 102 studies for inclusion, from which we recorded the sampling country  
145 and coordinates (or used centroids of reported regions), sampling months and years, bird and tick  
146 species, number of sampled and *Bbsl*-positive larvae, *Bbsl* genospecies, and assessment type  
147 (experimental trial or testing attached larvae). These studies encompassed 183 bird species for  
148 which engorged larval ticks have been tested for *Bbsl*. Each record ( $n=1069$ ) was a test of a bird–  
149 tick–*Bbsl* association over space and time, and most studies contributed multiple lines of data  
150 (88/102). Most data were from *Ixodes* ticks (90.11%, mostly *I. ricinus* and *I. scapularis*), with  
151 the remainder unstated (1.24%) or from *Haemaphysalis* (4.85%), *Hyalomma* (3.71%), or  
152 *Amblyomma* (0.10%). Whereas tick genera other than *Ixodes* are unlikely *Bbsl* vectors (Breuner  
153 *et al.*, 2020), we retained these records as they still indicate transmission from competent birds.

154

#### 155 *Meta-analysis of larval infection prevalence*

156 We used a phylogenetic meta-analysis to quantify heterogeneity in competence, the prevalence  
157 of *Bbsl* in bird-fed larvae ( $n=964$ , Fig. S2; some studies only reported presence of infected  
158 larvae). We obtained a phylogeny of our 183 bird species from the Open Tree of Life with the  
159 *rotl* package in R and used the *ape* package to calculate branch lengths (Paradis *et al.*, 2004;  
160 Michonneau *et al.*, 2016). We then used the *metafor* package to estimate logit-transformed  
161 proportions and sampling variances (Viechtbauer, 2010). We used restricted maximum  
162 likelihood to fit a random-effects model (REM), which included a species-level random effect  
163 (the covariance structure used the phylogenetic correlation matrix), observation nested in a  
164 study-level random effect, and weighting by sampling variances to account for sample size.  
165 Estimates of variance components were used to derive  $I^2$ , the contribution of true heterogeneity

166 to total variance in competence, and to partition variance attributed to each random effect. For  
167 avian species, we also calculated phylogenetic heritability ( $H^2$ ) (Nakagawa & Santos, 2012).

168 To assess spatial and temporal variation in competence, we fit mixed-effects models  
169 (MEMs) with the same random effects to the data describing *Bbsl* prevalence in engorged larvae  
170 from only wild birds ( $n=922$ ). Covariates included geographic region ( $n=922$ ), latitude ( $n=778$ ),  
171 year ( $n=917$ ), and season ( $n=654$ ). As many studies pooled data over time, we used the sampling  
172 year or the mid-point sampling year. We coded season as binary covariates (winter, spring,  
173 summer, fall;  $n=10$  records were from the southern hemisphere), as studies often reported data  
174 per season or pooled across seasons. Given the differences in sample size between predictors, we  
175 used Akaike information criterion (AICc) to compare two sets of MEMs (Burnham & Anderson,  
176 2002): (i) space and year and (ii) space and season. Comparisons included an intercept-only  
177 model, and we derived a pseudo- $R^2$  as the proportional reduction in the summed variance  
178 components per MEM compared with that of an equivalent REM (López-López *et al.*, 2014).

179

### 180 *Phylogenetic analyses*

181 We next aggregated tick-*Bbsl* data per avian species to assess phylogenetic patterns in  
182 competence as a simplified, binary trait. Using the *caper* package, we calculated the  $D$  statistic,  
183 where 1 indicates a phylogenetically random trait distribution and 0 indicates phylogenetic  
184 clustering under a Brownian motion model of evolution (Fritz & Purvis, 2010). Significant  
185 departure from either model was quantified using a randomization test. However, because traits  
186 such as competence may also arise under a punctuated equilibrium model of evolution, we next  
187 used a graph-partitioning algorithm, phylogenetic factorization, to flexibly identify clades with  
188 significantly different propensity to be competent at various taxonomic depths. We used the

189 *taxize* package to obtain a taxonomy from the NCBI database (Chamberlain & Szöcs, 2013) and  
190 used the *phylofactor* package to partition competence as a Bernoulli-distributed response in a  
191 generalized linear model (Washburne *et al.*, 2019). To account for variable study effort, we used  
192 the *rwos* package to quantify the number of citations per species in Web of Science and used the  
193 square-root transformed values as weights (Han *et al.*, 2016; Plowright *et al.*, 2019a). We  
194 determined the number of significant phylogenetic factors (clades) using a Holm's sequentially  
195 rejective 5% cutoff for the family-wise error rate. Lastly, to assess whether phylogenetic patterns  
196 in competence could stem from study effort alone, we performed a secondary analysis to  
197 partition Web of Science citation counts for each avian species as a quasi-Poisson response.

198         To investigate the evolution of competence across bird species, we used the *ape*  
199 package and maximum likelihood to reconstruct the ancestral character state (Paradis *et al.*,  
200 2004). We compared an equal-rate and an all-rates-different model of evolution with AIC  
201 (Schluter *et al.*, 1997) and used the most competitive model to perform stochastic character  
202 mapping with Markov chain Monte Carlo ( $n=1000$ ) using the *phytools* package (Revell, 2012).  
203 We displayed mean posterior probabilities of competence across our sampled avian phylogeny.

204

#### 205 *Trait-based analyses*

206 We compiled avian traits from EltonTraits (Wilman *et al.*, 2014), the Amniote Life History  
207 database (Myhrvold *et al.*, 2015), International Union for the Conservation of Nature (Baillie *et*  
208 *al.*, 2004), and HormoneBase (Vitousek *et al.*, 2018). Traits included diet composition and  
209 breadth, foraging strata, life history (e.g., maximum lifespan, clutch size, fledging age, clutches  
210 per year), morphology (e.g., adult mass, hatching weight), maximum elevation, global population  
211 trend, and physiology (i.e., baseline corticosterone; CORT). Using distribution maps from

212 BirdLife International and the Handbook of the Birds of the World (BirdLife International &  
213 NatureServe, 2014), we derived total range size, latitude of the centroids of breeding and non-  
214 breeding ranges, and mean migration distance (greater circle distance between these centroids).  
215 We also quantified migratory dispersion, the extent to which species inhabit larger (positive) or  
216 smaller (negative) areas in the non-breeding season relative to breeding range size, and made  
217 binary covariates for migratory strategy (resident, full migrant, partial migrant) (Gilroy *et al.*,  
218 2016). For resident species, migration distance and dispersion were set to zero. To represent  
219 avian taxonomy, we included binary covariates for each family and any clades identified by  
220 phylogenetic factorization; we also included a binary covariate for the Passeriformes (166/183  
221 species). We also derived evolutionary isolation with the *picante* package (Kembel *et al.*, 2010).  
222 We again used Web of Science citation counts per species to approximate study effort. We  
223 transformed continuous predictors that spanned orders of magnitude and excluded those with  
224 high homogeneity or missing values for over 80% of birds. We compiled features for our 183  
225 sampled birds and additional unsampled avian species to predict likely but undetected competent  
226 hosts. We limited these out-of-sample species to only the 39 families included in our dataset  
227 (4508 bird species). Feature definitions, transformations, and coverage are provided in Table S1.

228         To identify trait profiles of competent birds and to predict likely novel *Bbsl* reservoirs,  
229 we used boosted regression trees (BRTs) to fit a predictive model relating binary competence to  
230 a predictor matrix of avian traits (Elith *et al.*, 2008). BRTs were trained to maximize  
231 classification accuracy by learning patterns of features that best distinguish competent and non-  
232 competent species. BRTs generate recursive binary splits for randomly sampled predictors, and  
233 successive trees are built using residuals of the prior best-performing tree as the new response.  
234 Boosting generates an ensemble of linked trees, where each achieves increasingly more accurate

235 classification. Prior to analysis, we randomly split our data into training (90%) and test (10%)  
236 datasets while preserving the proportion of positive labels. Models were then trained with the  
237 *gbm* package (Ridgeway, 2006), with a maximum of 30000 trees, a learning rate of 0.0001, and  
238 an interaction depth of three (Elith *et al.*, 2008). BRTs used a Bernoulli error distribution and 10-  
239 fold cross-validation, and we used the *ROCR* and *hmeasure* packages to quantify three measures  
240 of classification accuracy: area under the receiver operator curve (AUC), sensitivity, and  
241 specificity (Sing *et al.*, 2005). As BRT results can depend on random splits between training and  
242 test data, we used five partitions to generate a model ensemble (Evans *et al.*, 2017). To diagnose  
243 if trait profiles of competent birds are driven by study effort, we ran a secondary BRT ensemble  
244 that modeled Web of Science citation counts as a Poisson response (Plowright *et al.*, 2019a).

245         After assessing accuracy of our BRTs against test data, we applied our model ensemble  
246 to the full trait dataset of 4691 avian species (183 sampled and 4508 unsampled species) to  
247 generate mean probabilities of competence. This allowed us to differentiate predictions that  
248 signal false negatives (i.e., sampled species without evidence of competence) and those denoting  
249 undetected reservoirs (i.e., unsampled species). To assess phylogenetic signal in predictions, we  
250 estimated Pagel's  $\lambda$  in the logit-transformed probabilities with the *caper* package (Orme, 2013)  
251 and applied phylogenetic factorization to identify clades of particularly likely competent birds.  
252 Lastly, to guide surveillance of these false negatives and undetected competent reservoirs, we  
253 mapped the distributions of species with mean predicted probabilities of over 50% and 60%.

254

## 255 **Results**

256 *Avian competence on a global scale*

257 Half of all sampled bird species were competent for *Bbsl* (91/183). Only nine bird species had  
258 experimental evidence of competence (i.e., xenodiagnosis), and all 91 competent species (with  
259 the exception of *Gallus gallus*) had larvae from wild birds test positive (Fig. S2). For records  
260 reporting *Bbsl* genospecies from bird-fed larvae, our global data were dominated by *B. garinii*  
261 (31%), *B. valaisiana* (20%), *Bbss* (16%), and *B. afzelii* (15%), representing data biases toward  
262 Europe (59%) and North America (37%); 3% of data were from Eastern Asia, whereas 1% were  
263 from South America (Fig. 1A). However, these 91 competent bird species were broadly  
264 distributed across the Americas, Africa, Asia, and Oceania throughout their annual cycles.

265 We observed significant heterogeneity in bird-fed larvae *Bbsl* prevalence ( $I^2=0.76$ ,  
266  $Q_{963}=2970$ ,  $p<0.0001$ ). Avian species accounted for more of this variation ( $I^2_{species}=0.31$ ) than  
267 study ( $I^2_{study}=0.19$ ) or individual record ( $I^2_{observation}=0.26$ ), resulting in moderate phylogenetic  
268 signal ( $H^2=0.40$ ). Given the stronger effect of avian phylogeny, we found no effect of study-level  
269 predictors such as space (Fig. 1B) or year (Fig. 1C) on the proportion of larvae infected by wild  
270 birds (Table S2). Seasons were also mostly uninformative (Table S3), but prevalence in bird-  
271 infected larvae was weakly lower during summer (Akaike weight=0.44,  $R^2=0.01$ ; Fig. 1D).

272

### 273 *Evolutionary patterns in competence*

274 We next considered competence as an intrinsic binary trait per species. We estimated  
275 intermediate phylogenetic signal in the ability of birds to transmit *Bbsl* to larvae ( $D=0.78$ ),  
276 indicating significant phylogenetic clustering between randomness ( $p<0.001$ ) and a Brownian  
277 motion model of evolution ( $p<0.001$ ). After controlling for study effort, phylogenetic  
278 factorization identified one clade, the genus *Turdus*, as having a significantly greater likelihood

279 of including competent species when compared to other avian taxa (Fig. 2). In particular, all but  
280 one sampled member of this clade displayed the ability to infect larval ticks with *Bbsl* (92%).

281 Our secondary analysis identified seven taxa as having significantly different Web of  
282 Science citation counts (Fig. S3), five of which were heavily studied species: *Gallus gallus*  
283 (4139), *Parus major* (3736), *Sturnus vulgaris* (2509), *Passer domesticus* (2162), and *Ficedula*  
284 *hypoleuca* (1500). Disproportionately studied taxa also included the Phasianidae ( $x^2=609$ ) and a  
285 subclade of the Icteridae (genera *Quiscalus*, *Molothrus*, and *Agelaius*;  $x^2=545$ ). Taxonomic  
286 patterns in Web of Science citation counts did not overlap with taxonomic patterns in avian  
287 competence, suggesting that the latter were not driven by variable study effort (Fig. S3).

288 The evolution of avian competence was best described by an equal-rate model ( $w_i=0.73$ ).  
289 Stochastic character mapping suggested equal transitions from non-competent to competent and  
290 from competent to non-competent (Fig. 2), with the ancestral state being equivocal. Competence  
291 was gained within the Turdidae as well as the Mimidae, Passerellidae, and Troglodytidae, with  
292 both gains and losses within the Parulidae. We also observed a clear loss of competence within  
293 the majority of the Carduelinae as well as within the Corvidae, Picidae, and Strigidae (Fig. 2).

294

### 295 *Trait profiles of competent birds*

296 Our BRT models distinguished competent from non-competent birds with moderate accuracy  
297 ( $\overline{AUC}=0.80 \pm 0.05$  SE;  $\overline{sensitivity}=0.71 \pm 0.08$  SE;  $\overline{specificity}=0.64 \pm 0.05$  SE; Fig. 3A).

298 Some top features for describing *Bbsl*-competent species included physiology (i.e., baseline  
299 CORT), life history (i.e., fledging age, maximum lifespan, birth and fledging weight, egg mass,  
300 incubation time, clutch size), migration (dispersion, distance), geography (breeding and non-  
301 breeding latitude, maximum elevation, geographic range size), evolutionary isolation, and study

302 effort. BRTs identified our phylofactorization clade (i.e., the *Turdus* genus) alongside the  
303 Turdidae family and passerines more generally as the only taxonomic features with non-trivial  
304 importance (i.e., <1%), and foraging traits were generally uninformative (Fig. 3B, Table S4).

305 Physiologically, *Bbsl*-competent birds have lower baseline concentrations of CORT, the  
306 main avian glucocorticoid (Fig. 4). Competent species were also described by either extreme of  
307 the pace-of-life continuum. On the one hand, competent birds have shorter incubation times and  
308 young that are smaller and fledge earlier than non-competent counterparts. On the other hand,  
309 competent birds also had longer lifespans, smaller clutches, and larger eggs and body size.  
310 Geographically, competent birds tend to breed and winter at higher latitudes, have broader  
311 distributions, and occupy lower elevations, and their populations are stable or increasing. Species  
312 with negative migratory dispersion were more likely to be competent, indicating such hosts have  
313 larger breeding ranges and greater diversity of migratory movements from their wintering to  
314 breeding grounds. Competence was less strongly related to mean migratory distance, with  
315 intermediate-distance migrants being most likely to transmit *Bbsl* to larvae. Members of the  
316 genus *Turdus*, the family Turdidae, and the Passeriformes as a whole were all more likely to be  
317 competent. Additionally, although foraging traits generally had low relative importance,  
318 competent birds were more likely to be granivorous and ground-foraging species. Lastly, well-  
319 studied species were also more likely to be competent. However, our secondary BRTs showed  
320 that citations were not predictable by these same traits ( $\overline{AUC}=0.50 \pm 0$  SE), suggesting that the  
321 trait profile of a competent bird is not confounded by the ecological traits of well-studied hosts.

322 Applying our BRT ensemble to trait and taxonomic data across the 39 sampled avian  
323 families revealed at least 21 undiscovered species that could be prioritized for *Bbsl* surveillance  
324 based on feature similarity to known competent reservoirs (Fig. 5A). We observed strong

325 phylogenetic signal in mean predicted probabilities ( $\lambda=0.94$ ), indicating the influential traits  
326 revealed by our BRTs are likely driven by clades with high potential for competence (Fig. 5B).  
327 Phylogenetic factorization found nine such clades with distinct model predictions (Table S5).

328 The geography of likely high-probability reservoirs revealed potential hotspots of  
329 competent birds across their breeding (Fig. 5C), non-breeding (Fig. 5D), and resident (Fig. 5E)  
330 ranges. Our BRTs suggested at least one likely false negative, the Indigo bunting (*Passerina*  
331 *cyanea*; Sonenshine *et al.*, 1995; Kinsey *et al.*, 2000; Schneider *et al.*, 2015). Likely but  
332 unsampled competent reservoirs included the American goldfinch (*Spinus tristis*), Harris's  
333 sparrow (*Zonotrichia querula*), Abert's towhee (*Melospiza aberti*), yellow-headed blackbird  
334 (*Xanthocephalus xanthocephalus*), western meadowlark (*Sturnella neglecta*), northern  
335 mockingbird (*Mimus polyglottos*), Brewer's blackbird (*Euphagus cyanocephalus*), and vesper  
336 sparrow (*Pooecetes gramineus*) in North America; Townsend's warbler (*Setophaga townsendi*),  
337 scarlet tanager (*Piranga olivacea*), eastern bluebird (*Sialia sialis*), Louisiana waterthrush  
338 (*Parkesia motacilla*), red-eyed vireo (*Vireo olivaceus*), grasshopper sparrow (*Ammodramus*  
339 *savannarum*), Acadian flycatcher (*Empidonax vireescens*), and clay-colored thrush (*Turdus grayi*)  
340 across the Americas; the corn bunting (*Emberiza calandra*) across Eurasia; the horned lark  
341 (*Eremophila alpestris*) across the northern hemisphere; and the thick-billed murre (*Uria lomvia*)  
342 and rhinoceros auklet (*Cerorhinca monocerata*) across pelagic zones. Species with probabilities  
343 above 50% (96<sup>th</sup> percentile of predictions) are included in Table S6 and shown in Figure S4; this  
344 cutoff found another three likely false negatives and 74 likely but unsampled competent species.

345

## 346 **Discussion**

347 Competence is increasingly recognized to govern infectious disease dynamics, especially in  
348 multi-host communities (Ostfeld *et al.*, 2014; Gervasi *et al.*, 2015). Efforts to predict new  
349 reservoirs of zoonotic pathogens would be improved by identifying the ecological or  
350 evolutionary drivers of this trait (Becker *et al.*, 2020b). We here applied such an approach to  
351 Lyme borreliosis, a model system to study competence for a tick-borne disease. Whereas inter-  
352 specific variation in competence has been characterized for mammals (LoGiudice *et al.*, 2003;  
353 Huang *et al.*, 2013; Ostfeld *et al.*, 2014), this trait has been understudied across birds, despite  
354 their ability to disperse infected ticks across large spatial scales and mounting evidence of  
355 competence across avian species (Richter *et al.*, 2000; Ginsberg *et al.*, 2005; Norte *et al.*, 2013).  
356 We here demonstrate that *Bbsl* competence can be predicted by the ecological and evolutionary  
357 characteristics of birds. Our phylogenetic analyses show that competence has evolved multiple  
358 times and is pronounced in the genus *Turdus*. Trait-based analyses distinguished competent  
359 avian hosts with 80% accuracy and emphasized that such species have low baseline CORT,  
360 occur on either extreme of the pace-of-life continuum, breed and winter at high latitudes and low  
361 elevations, and have diverse migratory movements into their breeding range. These patterns can  
362 be used to generate testable hypotheses for future studies, and predictions using these trait  
363 profiles can help prioritize surveillance of false negatives and likely but unsampled competent  
364 avian species. More broadly, these results emphasize birds display underrecognized intra- and  
365 interspecific variation in their contributions to the enzootic cycles of this zoonotic pathogen.

366         Although pathogen transmission inherently occurs from individuals, variation in  
367 competence can arise across broader biological scales (Gervasi *et al.*, 2015; VanderWaal &  
368 Ezenwa, 2016). Our meta-analysis identified high heterogeneity in *Bbsl* prevalence from bird-fed  
369 larvae that was better explained by within-study heterogeneity and bird phylogeny than study-

370 level variation and broad spatial or temporal covariates. Greater within- than between-study  
371 heterogeneity suggests a greater role for fine-scale environmental covariates, such as local  
372 densities of ticks or alternative hosts, in shaping vector feeding behavior and infection  
373 prevalence in avian hosts that in turn affect prevalence in bird-fed larvae (Kilpatrick *et al.*, 2017).  
374 Additionally, moderate contributions of avian phylogeny in our meta-analysis was mirrored by  
375 intermediate phylogenetic signal in our species-level analysis. Together, these analyses suggest  
376 that while intraspecific variation in host competence occurs over space and time (Norte *et al.*,  
377 2020), the ability to transmit *Bbsl* can also be considered an intrinsic trait of avian species.

378         Moderate phylogenetic signal in competence was reflected in numerous gains and losses  
379 of this trait across the avian phylogeny, suggesting competence has evolved multiple times to  
380 form clades of highly competent birds. Phylogenetic factorization identified one of these clades,  
381 the genus *Turdus*, as being especially competent, even after accounting for variable study effort.  
382 Our BRTs also identified this genus, and the family Turdidae, as having high likelihood of  
383 competence. Of the 12 sampled *Turdus* species, all but one (*T. obscurus*) had fed larvae test  
384 positive for *Bbsl* (Ishiguro *et al.*, 2000), and two (*T. migratorius* and *T. merula*) have  
385 experimentally infected larvae (Richter *et al.*, 2000; Norte *et al.*, 2013). Given the larger *Turdus*  
386 and Turdidae clades, these results suggest unsampled thrushes could also be competent *Bbsl*  
387 reservoirs. Thrushes are globally distributed and display diverse migratory strategies, with  
388 resident, migratory, and partial migratory species. However, most European *Turdus* are complete  
389 or partial migrants (Ashmole, 1962), and photoperiod manipulations suggest migration of at least  
390 one species (*T. iliacus*) can reactivate latent *Bbsl* infection (Gylfe *et al.*, 2000). Comparative  
391 studies across thrushes that vary in geography and migratory strategy could elucidate the  
392 generality of this pattern and the broader inter-specific drivers of competence in this taxon.

393 Our BRTs identified CORT as the top predictor of competence, for which competent  
394 birds were more likely to have lower baseline concentrations. Although persistently elevated  
395 CORT can be immunosuppressive and amplify competence (Gervasi *et al.*, 2017), baseline  
396 concentrations have mostly metabolic functions that allow animals to meet energetic demands  
397 and respond to adverse conditions (Sapolsky *et al.*, 2000). Low baseline CORT could be linked  
398 to competence by its association with breeding latitude. Birds tend to have lower baseline CORT  
399 at high latitudes, which could facilitate continued breeding in suboptimal habitats (Wingfield &  
400 Sapolsky, 2003). This is compatible with our finding that competent species also generally breed  
401 at high latitudes. Birds breeding further from the equator show stronger tradeoffs between arms  
402 of the immune system, such that high-latitude hosts mount weaker adaptive responses (Ardia,  
403 2007). Because robust *Bbsl*-specific antibody titers limit transmission to naïve ticks (Kurtenbach  
404 *et al.*, 1994), birds breeding at high latitudes could display weaker antibody defenses that  
405 increase competence. Sampling competent birds across latitudinal gradients could characterize  
406 such immunity tradeoffs and test if these restrict bird–tick transmission (Becker *et al.*, 2019a).

407 Our trait-based analyses also suggested that competent birds occur on either extreme of  
408 the pace-of-life continuum (Stearns, 1983). This possibly contrasts with work on mammals,  
409 where fast-lived species (i.e., rapid development and high fecundity at the expense of longevity)  
410 are more competent than their slow-lived counterparts (LoGiudice *et al.*, 2003; Huang *et al.*,  
411 2013; Ostfeld *et al.*, 2014). Although many of the top traits predicting competence in birds also  
412 reflect fast pace-of-life (e.g., short incubation times, young that are small and fledge early),  
413 competent birds were also characterized by long lifespans, large eggs, and small clutches more  
414 consistent with a slow life history. This pattern could arise from two competing signals in the  
415 data, such that both particularly fast- (e.g., many passerines) and slow-lived species (e.g., the

416 Alcidae and Phasianidae) display evidence of competence. Future tests of pace-of-life variation  
417 and competence within orders such as the Passeriformes or Charadriiformes could minimize  
418 confounding effects of taxonomy and assess if such patterns have an immunological basis, as  
419 suggested for mammalian competence (Previtali *et al.*, 2012; Albery & Becker, 2020).

420 Our BRTs identified several other important predictors related to bird geography and  
421 annual cycles, including low elevation, large distributions, and negative migratory dispersion.  
422 Rather than indicating physiological processes that facilitate bird–tick transmission, greater  
423 likelihood of competence in species at low elevations and with large geographic ranges may  
424 indicate greater exposure to questing nymphs that would cause infection in birds. Similarly,  
425 positive associations between competence and both breeding and wintering latitude could stem  
426 from optimal overlap with tick species (Hahn *et al.*, 2016; Hvidsten *et al.*, 2020). Although  
427 foraging traits were largely uninformative, positive associations between ground foraging and  
428 competence likely also reflect greater tick exposure (Loss *et al.*, 2016). However, migratory  
429 traits could better reflect within-host processes of competence itself. Negative migratory  
430 dispersion indicates birds with more diverse movements from their wintering to breeding  
431 grounds (Gilroy *et al.*, 2016). These more diverse migrations demand large energy expenditures  
432 that can impair immunity (Owen & Moore, 2008) and cause latent *Bbsl* infections to reactivate  
433 (Gylfe *et al.*, 2000). This mechanism could facilitate competent birds arriving at their breeding  
434 grounds primed to infect larval ticks. The generally positive association between migratory  
435 distance and competence also supports the idea that longer biannual migration, in being more  
436 costly, could promote relapse. Future work could test this hypothesis by sampling competent  
437 birds across their annual cycles (Marra *et al.*, 2015) and linking such data with mathematical  
438 models to understand when migratory relapse most increases risk (Becker *et al.*, 2020a).

439 Our analyses also inform surveillance of specific bird species for their contribution to  
440 enzootic cycles of *Bbsl* and other tick-borne pathogens. Phylogenetic factorization and our BRTs  
441 suggested unsampled *Turdus* thrushes are especially likely to be competent. Some thrushes such  
442 as *T. grayi* are known to be parasitized by ticks (Miller *et al.*, 2016), whereas others such as *T.*  
443 *torquatus* and *T. nigriceps* have had engorged nymphs test positive for *Bbsl* (Hasle *et al.*, 2011;  
444 Saracho Bottero *et al.*, 2017). Our BRT predictions displayed high phylogenetic signal,  
445 identifying clades of especially competent birds, such as the genus *Zonotrichia* as well as the  
446 families Alcidae, Mimidae, and Parulidae (Table S5). Some unsampled species in these clades  
447 have had blood or nymphs test positive for *Bbsl*, such as *Parkesia motacilla* (Anderson &  
448 Magnarelli, 1984). We suggest members of these clades be prioritized for spatiotemporal  
449 sampling to identify when and where they are likely to infect ticks (Plowright *et al.*, 2019b).

450 To test these model predictions, we encourage more definitive assessments of  
451 competence. Because most of our data included approximations of competence from *Bbsl* in  
452 engorged larvae on wild birds, xenodiagnostic experiments could be prioritized for unsampled  
453 avian species with high probabilities of being competent to establish bird–tick transmission  
454 (Ginsberg *et al.*, 2005; Norte *et al.*, 2013). As an alternative approach, field surveys could  
455 instead assess *Bbsl* infection in not only engorged larvae but also hosts themselves to test  
456 whether absence of the pathogen in ticks is due to poor competence or an uninfected host  
457 (Newman *et al.*, 2015). These increasing data on host competence would also facilitate future  
458 analytic efforts. Because *Bbsl* includes genospecies that vary in host specificity (e.g., *Bbss*  
459 infects both rodents and birds, whereas *B. garinii* and *B. valaisiana* are more specialized on the  
460 latter), better considering such coevolutionary relationships could improve model performance  
461 (Kurtenbach *et al.*, 2006; O’Keeffe *et al.*, 2020). We pooled *Bbsl* across genospecies due to the

462 relatively small sample of bird species, but models applied to taxonomic subsets of data may  
463 generate distinct predictions by reducing noise from hosts infected with other *Bbsl* genospecies.

464       Lastly, environmental change could play an important role in shaping how known and  
465 likely competent birds contribute to *Bbsl* dynamics. Breeding ranges of many birds are shifting  
466 north with climate change (Hitch & Leberg, 2007), which could synchronize bird and tick  
467 phenologies (Ostfeld & Brunner, 2015). Alternatively, warmer temperatures could facilitate  
468 residency, as observed for competent birds such as *Turdus merula* (Vliet *et al.*, 2009). If such  
469 species become resident where ticks are abundant, sedentary behavior could increase vector  
470 exposure and amplify bird–tick transmission. Similarly, several *Bbsl*-competent birds (e.g.,  
471 *Sylvia atricapilla*, *Junco hyemalis*) and unsampled but likely reservoirs (e.g., *Spinus tristis*) have  
472 shortened migration or become resident in cities (Yeh & Price, 2004; Plummer *et al.*, 2015;  
473 Bonnet-Lebrun *et al.*, 2020). This urban residency could increase or decrease competence  
474 depending on factors such as food availability and artificial light at night (Becker *et al.*, 2019b;  
475 Kernbach *et al.*, 2019). Combining sampling of known or likely competent birds across urban–  
476 rural gradients or their historic and recent range with mathematical models could forecast how  
477 environmental change will alter bird distributions, competence, and contribution to *Bbsl* risk.

478       In conclusion, we demonstrate that host ability to transmit pathogens to new hosts or  
479 vectors can be predicted by the ecological and evolutionary characteristics of bird species in the  
480 Lyme borreliosis system. By combining flexible phylogenetic and trait-based analyses, our work  
481 generates testable hypotheses for future comparative and theoretical studies of tick-borne disease  
482 alongside predictions that can inform bird surveillance efforts for not only *Bbsl* but also similar  
483 pathogens (e.g., *Anaplasma*, *Ehrlichia*) in the context of environmental change. Moving forward,

484 greater attention to the factors that shape competence within and between species could improve  
485 our ability to predict and manage reservoir hosts for zoonotic pathogens more broadly.

486

487 **Data availability**

488 Data and R code to reproduce the primary analyses are available in Dryad Digital Depository  
489 (Becker & Han, 2020):

490 [https://datadryad.org/stash/share/4shvYd0\\_1CUkjEFhO5g1yc95sSLUfq3zbrd79\\_1J-0Q](https://datadryad.org/stash/share/4shvYd0_1CUkjEFhO5g1yc95sSLUfq3zbrd79_1J-0Q).

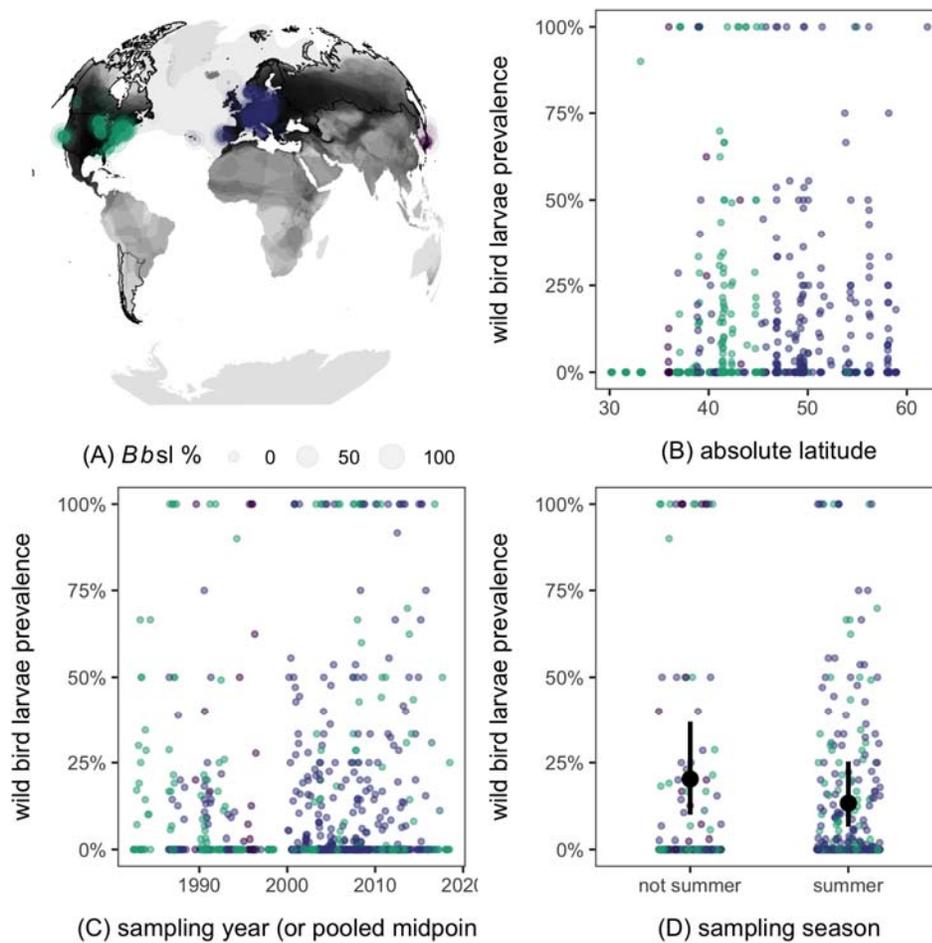
491

492 **Competing interests**

493 We declare no competing interests.

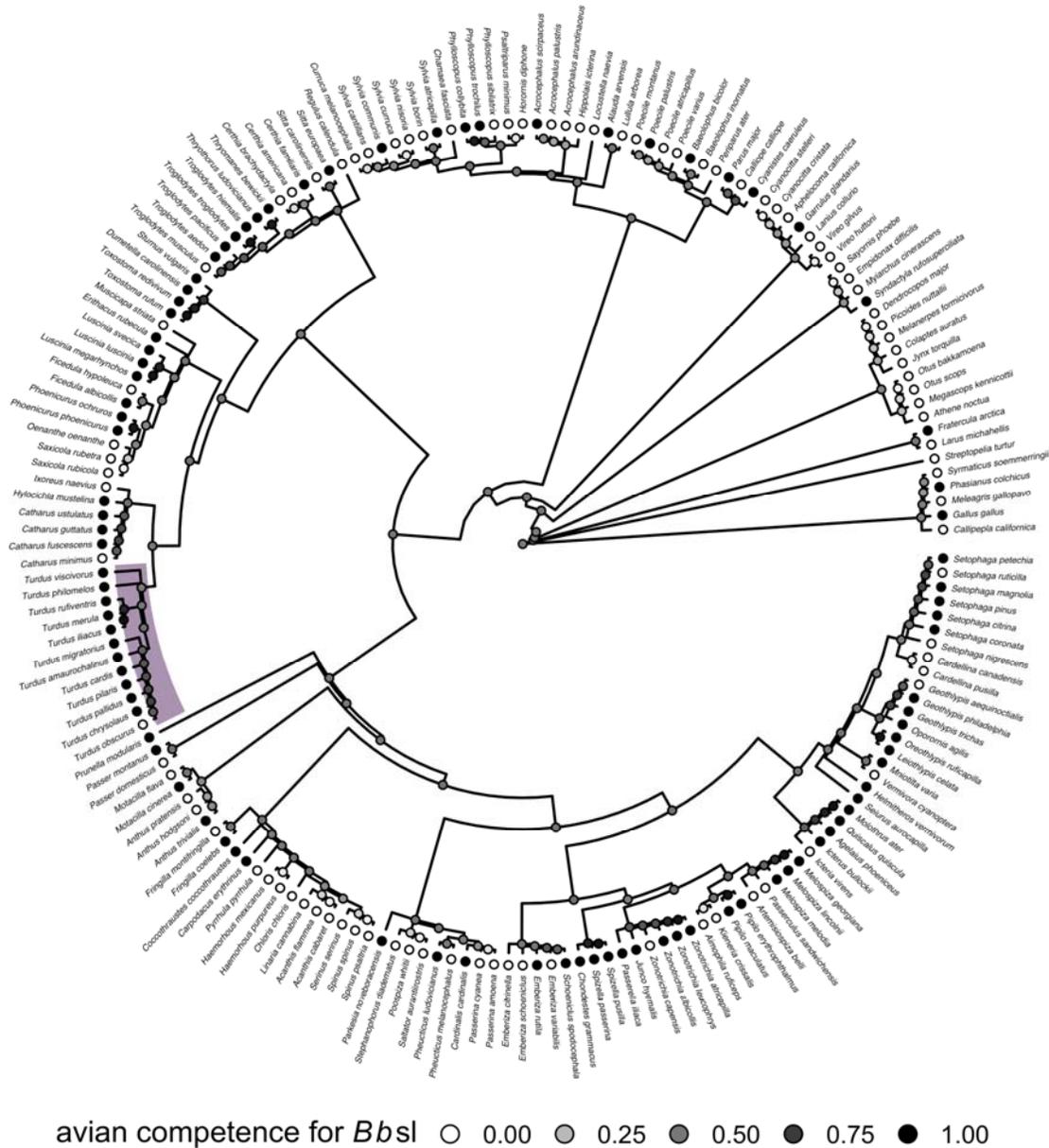
494 **Figure legends**

495 Figure 1. Global distribution of *Bbsl* prevalence in tick larvae sampled from wild birds. (A)  
496 Sampled countries are shown in black border with spatiotemporal bird–tick–*Bbsl* prevalences,  
497 which are sized by magnitude and colored by georegion. Shapefiles of the 91 competent species  
498 are derived from BirdLife International and Handbook of the Birds of the World and are overlaid  
499 in black (BirdLife International & NatureServe, 2014). Larval infection prevalence is plotted by  
500 absolute latitude (B), year (C), and season (D), with each point representing a bird–tick–*Bbsl*  
501 association; points are colored by region and jittered to reduce overlap. Black points and lines  
502 (D) display predicted means and 95% confidence intervals from the top MEM (Table S3).



503

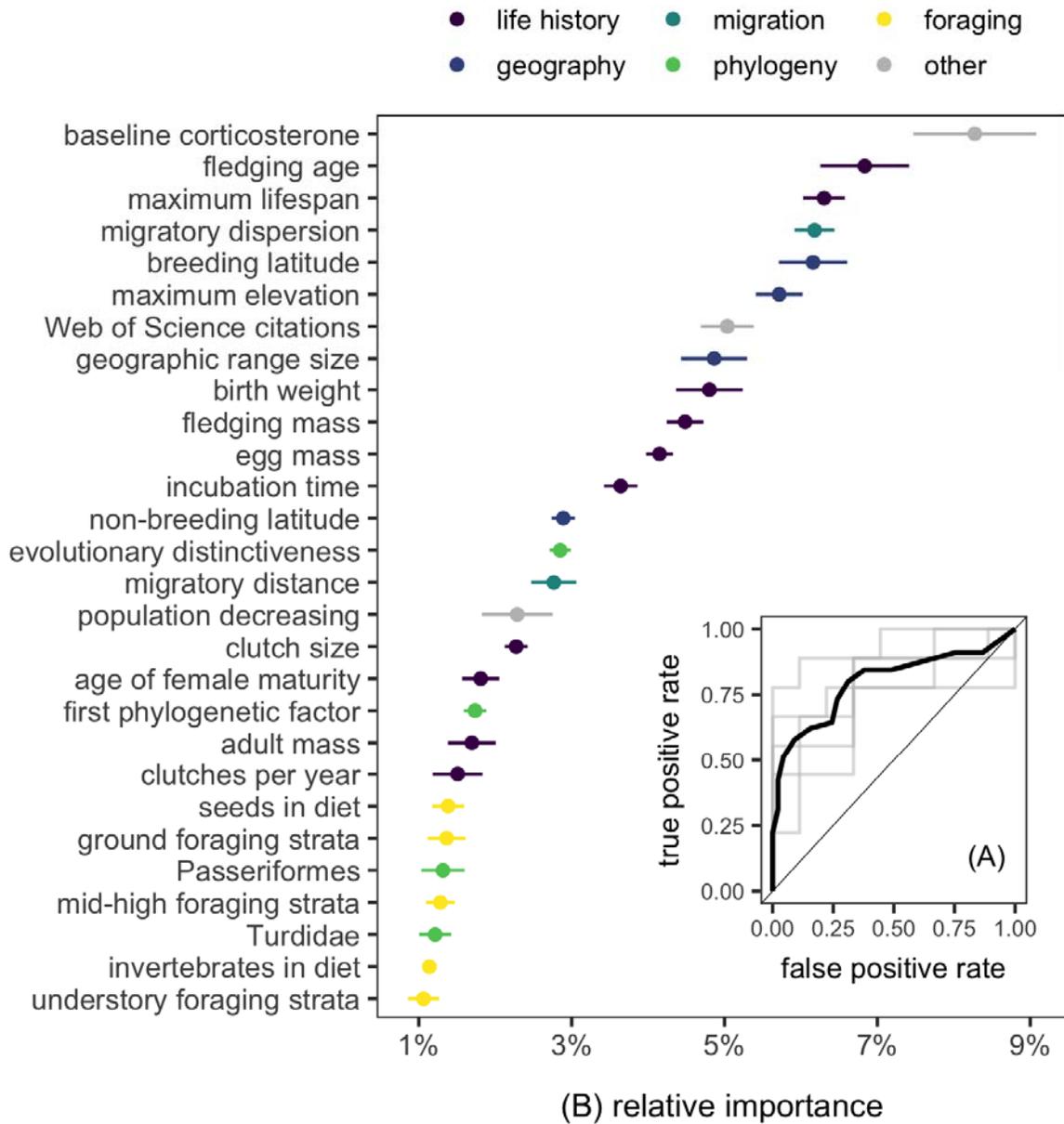
504 Figure 2. Phylogenetic patterns in avian competence for *Bbsl*. The avian phylogeny displays  
 505 observed species binary competence, and highlighted clades are those with significantly different  
 506 competence from the paraphyletic remainder using phylogenetic factorization. Nodes show the  
 507 mean posterior probabilities of being competent estimated from stochastic character mapping.



508

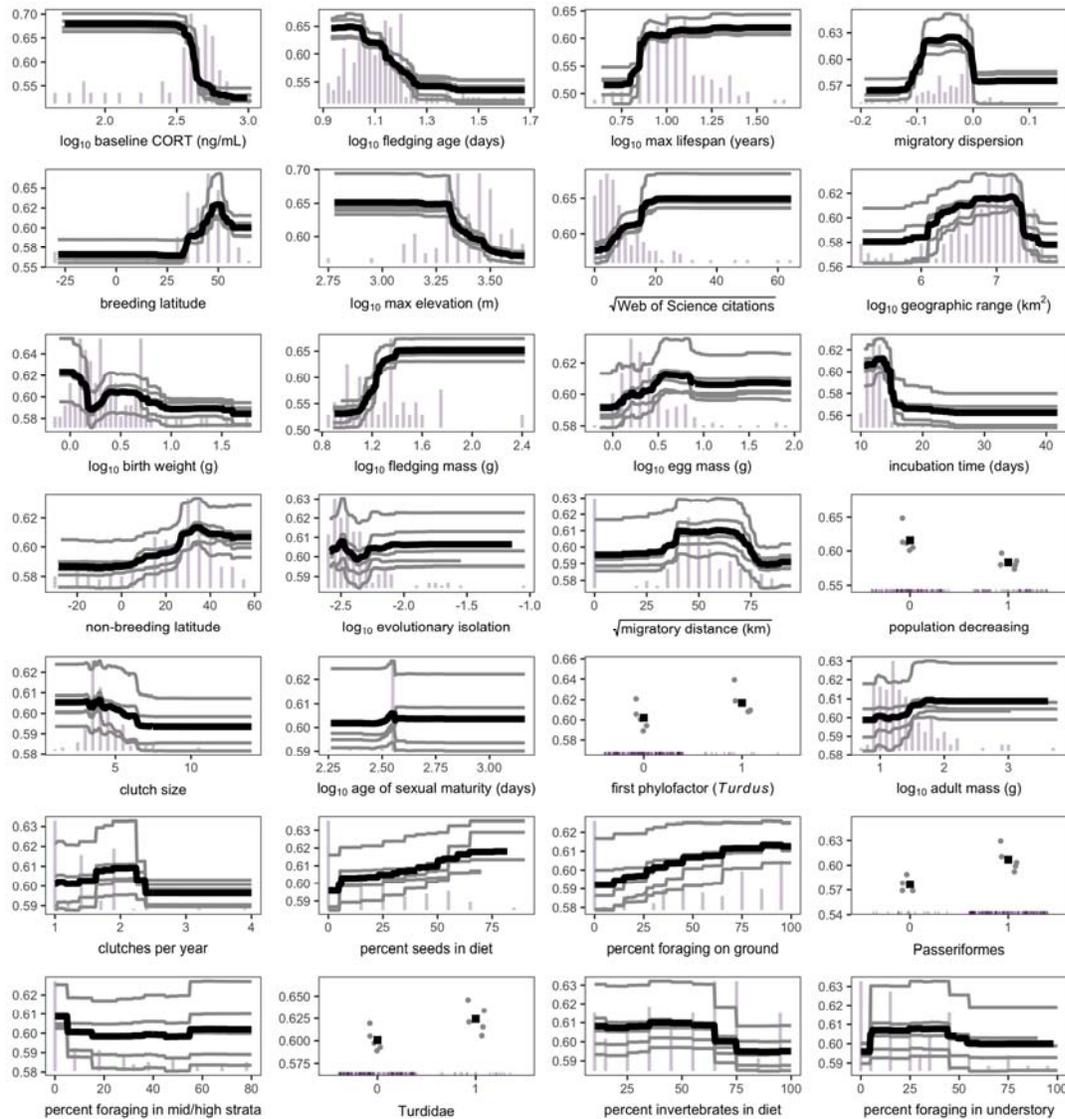
509

510 Figure 3. BRT performance in identifying traits predictive of avian competence for *Bbsl* and  
 511 their relative importance across five random partitions of training and test datasets. (A) Accuracy  
 512 is shown by the receiver operator curves obtained from 10-fold cross-validation on test data.  
 513 Grey lines show curves from each partition, whereas the black line displays the mean.  
 514 Relative importance per feature is shown as the mean and standard error across training and test  
 515 data partitions. Only features with mean importance greater than 1% are shown (Table S4).



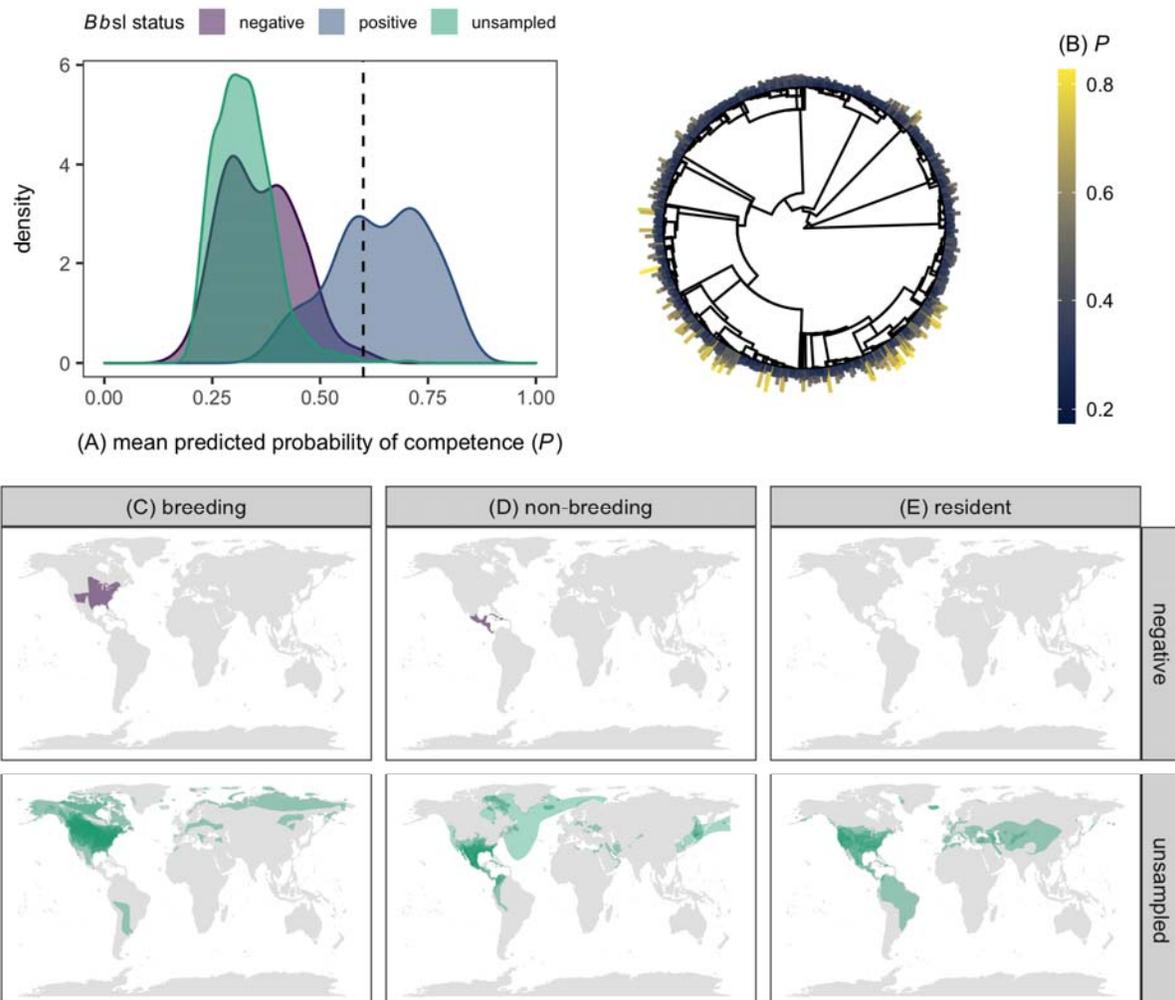
516

517 Figure 4. Trait profile of a *Bbsl*-competent avian species. Partial dependence plots of the top  
 518 predictors across BRTs applied to five random partitions of training and test data are shown  
 519 ordered by relative importance (>1%). Grey lines or point show the marginal effect of a given  
 520 variable for predicting *Bbsl* competence from each random data partition, whereas the black lines  
 521 or squares display the average marginal effect. Histograms and rug plots display the distribution  
 522 of continuous and categorical predictor variables, respectively, across the 183 sampled birds.



523

524 Figure 5. Distribution of the mean predicted probabilities of *Bbsl* competence across the 39  
525 sampled avian families. (A) Density plots show predictions for currently negative, positive, and  
526 unsampled species, and these propensity scores are also shown across the avian phylogeny (B).  
527 Distributions of species within a mean probability of over 60% are shown by their breeding (C),  
528 non-breeding (D), and resident ranges (E). Shapefiles are from BirdLife International and the  
529 Handbook of the Birds of the World (BirdLife International & NatureServe, 2014). Figure S4  
530 displays these geographic distributions with a less conservative prediction cutoff of 50%.



531

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850 **Supporting information**

851 Additional supporting information may be found online in the Supporting Information section.

852

853 **Biosketch**

854 Daniel Becker studies the ecology and evolution of infectious disease, with particular interests in

855 how anthropogenic factors affect infection dynamics in reservoir hosts and how competence data

856 can improve predicting reservoirs of zoonotic pathogens. Barbara Han is a disease ecologist at

857 the Cary Institute of Ecosystem Studies, where she applies machine learning and other modeling

858 in the predictive analytics of zoonotic risk.