

RESEARCH PAPER

Global Ecology
and BiogeographyA Journal of
Macroecology

WILEY

The macroecology and evolution of avian competence for *Borrelia burgdorferi*

Daniel J. Becker^{1,2}  | Barbara A. Han³ 

¹Department of Biology, Indiana University, Bloomington, IN, USA

²Center for the Ecology of Infectious Disease, University of Georgia, Athens, GA, USA

³Cary Institute of Ecosystem Studies, Millbrook, NY, USA

Correspondence

Daniel J. Becker, Department of Biology, Indiana University, 1001 East Third Street, Bloomington, IN, 47405 USA.
Email: danbeck@iu.edu

Funding information

National Science Foundation, Grant/Award Number: DEB-1619072 and DEB-1717282; Intelligence Community Postdoctoral Research Fellowship Program

Editor: Pauline Kamath

Abstract

Aim: Prediction of novel reservoirs of zoonotic pathogens would be improved by the identification of interspecific drivers of host competence (i.e., the ability to transmit pathogens to new hosts or vectors). Tick-borne pathogens can provide a useful model system, because larvae become infected only when feeding on a competent host during their first blood meal. For tick-borne diseases, competence has been studied best for *Borrelia burgdorferi* sensu lato (*Bbsl*), which causes Lyme borreliosis. Major reservoirs include several small mammal species, but birds might play an under-recognized role in human risk given their ability to disperse infected ticks across large spatial scales. Here, we provide a global synthesis of the ecological and evolutionary factors that determine the ability of bird species to infect larval ticks with *Bbsl*.

Location: Global.

Time period: 1983–2019.

Major taxa studied: Birds.

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

Results: Half of the sampled bird species show evidence of competence for *Bbsl*. Competence displays moderate phylogenetic signal, has evolved multiple times across bird species and is pronounced in the genus *Turdus*. Trait-based analyses distinguished competent birds with 80% accuracy and showed that such species have low baseline corticosterone, exist on both ends of the pace-of-life continuum, breed and winter at high latitudes and have broad migratory movements into their breeding range. We used these trait profiles to predict various likely but unsampled competent species, including novel concentrations of avian reservoirs within the Neotropics.

Main conclusion: Our results can generate new hypotheses for how birds contribute to the dynamics of tick-borne pathogens and help to prioritize surveillance of likely but unsampled competent birds. Our findings also emphasize that birds display under-recognized variation in their contributions to enzootic cycles of *Bbsl* and the broader need to consider competence in ecological and predictive studies of multi-host pathogens.

KEYWORDS

birds, boosted regression tree, Lyme borreliosis, machine learning, phylogenetics, tick-borne disease, transmission

1 | INTRODUCTION

Given that most emerging infectious diseases originate in animals (Jones et al., 2008), diverse efforts have aimed to predict reservoir hosts and arthropod vectors of zoonotic pathogens (Babayan et al., 2018; Morse et al., 2012). Given that such predictions can guide surveillance and interventions, they are necessary steps towards a pre-emptive approach to minimizing pathogen spillover risks (Becker, Washburne, et al., 2019; Han & Drake, 2016). For example, polymerase chain reaction (PCR) and serological data on Nipah virus from bats were leveraged to prioritize field sampling targets across India in response to a novel human outbreak (Plowright, Becker, Crowley, et al., 2019), and similar approaches have been applied to identify hosts of filoviruses, rodent zoonoses and Zika virus (Han et al., 2015, 2016, 2019). However, PCR and serological data better reflect host exposure rather than competence (i.e., the ability of a host to transmit a pathogen to a new host or vector) (Gervasi et al., 2015). Greater attention to competence could thus improve reservoir host predictions (Becker, Seifert, et al., 2020).

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

Competence can be difficult to quantify, because the infection status of the donor and recipient host must be known, or directional transmission events must be inferred (Archie et al., 2009; Martin et al., 2016). However, many tick-borne diseases facilitate the quantification of competence, because tick larvae hatch free of some pathogens and become infected only with their first blood meal (Richter et al., 2011). Fed larvae are often collected from wild hosts and tested for infection to establish host-to-vector transmission; however, such data can only approximate competence. Instead, xenodiagnostic experiments provide ideal evidence, because uninfected larvae are fed on infected hosts, often allowed to moult (assuring transstadial transmission), and then tested for pathogen presence

to infer competence (i.e., the proportion of infected ticks; Brunner et al., 2008).

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

In contrast to mammals, birds are likely to play an under-recognized role in the global ecology of *Bbsl*, given that the capacity for flight and long-distance migration can allow avian hosts to disperse infected ticks across continents (Smith Jr et al., 1996; Ishiguro et al., 2005; Dubska et al., 2009; Norte et al., 2020). Migratory birds transport 50–175 million ticks across Canada each spring (Ogden et al., 2008), and the physiological stress of migration itself might help to drive reactivation of latent *Bbsl* infection (Gylfe et al., 2000). Individual studies have suggested that some birds have important contributions to enzootic maintenance of *Bbsl* (Brinkerhoff et al., 2011; Myserud et al., 2019). For example, birds dominate transmission of *Borrelia garinii* and *Borrelia valaisiana* to larvae across Europe (Comstedt et al., 2006; Hanincová et al., 2003) and contribute to enzootic cycles of the primarily rodent genospecies, *Borrelia afzelli* (Franke et al., 2010). In North America, *Borrelia burgdorferi* sensu stricto (*Bbss*) infects both rodents and birds; however, as with mammals, birds seem to display interspecific variation in competence. For example, American robins infect $\leq 90\%$ of naïve larvae (Richter et al., 2000), whereas gray catbirds (*Dumetella carolinensis*) and veeries (*Catharus fuscescens*) infect fewer larvae and thus have lower competence (Anderson et al., 1986; Ginsberg et al., 2005; Mather et al., 1989). High tick burdens of some bird species, such as ground foragers, might allow birds to contribute more to *Bbsl* transmission than some rodents (Loss et al., 2016; Wright et al., 2000). Many birds capable of infecting larvae are also common in suburban and urban habitats (Battaly & Fish, 1993; Hamer et al., 2012), which could increase human exposure to infectious nymphs (Mead et al., 2018). Nevertheless, despite opportunities for birds to play key roles in the global distribution of *Bbsl* and Lyme borreliosis risk, interspecific drivers of reservoir competence across bird species have not yet been identified systematically.

Given the potential for birds to play important roles in the dynamics of *Bbsl*, we here compile a comprehensive, global dataset on avian competence and assess its ecological and evolutionary drivers. We first describe spatial and temporal patterns in competence, characterize its phylogenetic distribution across birds and reconstruct its evolution. We then use a flexible machine learning algorithm to evaluate the trait profiles of competent avian species and predict unsampled reservoirs. For the latter, such data science approaches circumvent many issues associated with traditional hypothesis testing (e.g., a large number of predictors, complex interactions, non-randomly missing covariates) and can uncover new and surprising patterns in data, thereby developing testable hypotheses (Hochachka et al., 2007). Our work, therefore, aimed to identify the ecological and evolutionary drivers of avian competence while also generating predictions of likely new *Bbsl* reservoirs and directions for future studies of tick-borne disease.

2 | METHODS

2.1 | Competence data

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

We identified 102 studies for inclusion, from which we recorded the sampling country and coordinates (or used centroids of reported regions), sampling months and years, bird and tick species, number of sampled and *Bbsl*-positive larvae, *Bbsl* genospecies and assessment type (experimental trial or testing attached larvae). These studies encompassed 183 bird species for which engorged larval ticks have been tested for *Bbsl*. Each record ($n = 1,069$) was a test of a bird-tick-*Bbsl* association over space and time, and most studies (88/102) contributed multiple lines of data. Most data were from *Ixodes* ticks (90.11%, primarily *I. ricinus*

and *I. scapularis*), with the remainder unstated (1.24%) or from *Haemaphysalis* (4.85%), *Hyalomma* (3.71%) or *Amblyomma* (0.10%). Although tick genera other than *Ixodes* are unlikely to be *Bbsl* vectors (Breuner et al., 2020), we retained these records because they still indicate transmission from competent birds.

2.2 | Meta-analysis of larval infection prevalence

We used a phylogenetic meta-analysis to quantify heterogeneity in competence, the prevalence of *Bbsl* in bird-fed larvae ($n = 964$; Supporting Information Figure S2; some studies reported only presence of infected larvae). We obtained a phylogeny of our 183 bird species from the Open Tree of Life with the *rotl* package in R and used the *ape* package to calculate branch lengths (Michonneau et al., 2016; Paradis et al., 2004). We then used the *metafor* package to estimate logit-transformed proportions and sampling variances (Viechtbauer, 2010). We used restricted maximum likelihood to fit a random-effects model (REM), which included a species-level random effect (the covariance structure used the phylogenetic correlation matrix), observation nested in a study-level random effect, and weighting by sampling variances to account for sample size. Estimates of variance components were used to derive I^2 , the contribution of true heterogeneity to total variance in competence, and to partition variance attributed to each random effect. For avian species, we also calculated phylogenetic heritability (H^2 ; Nakagawa & Santos, 2012).

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

2.3 | Phylogenetic analyses

We next aggregated tick-*Bbsl* data per avian species to assess phylogenetic patterns in competence as a simplified, binary trait. Using the *caper* package, we calculated the D statistic, where one indicates a phylogenetically random trait distribution and zero indicates phylogenetic clustering under a Brownian motion model of evolution

(Fritz & Purvis, 2010). Significant departure from either model was quantified using a randomization test. However, because traits such as competence might also arise under a punctuated equilibrium model of evolution, we next used a graph-partitioning algorithm, phylogenetic factorization, to identify flexibly clades with significantly different propensity to be competent at various taxonomic depths. We used the *taxize* package to obtain a taxonomy from the National Center for Biotechnology Information (NCBI) database (Chamberlain & Szöcs, 2013) and used the *phylofactor* package to partition competence as a Bernoulli-distributed response in a generalized linear model (Washburne et al., 2019). To account for variable study effort, we used the *rwos* package to quantify the number of citations per species in Web of Science and used the square root-transformed values as weights (Han et al., 2016; Plowright, Becker, Crowley, et al., 2019). We determined the number of significant phylogenetic factors (clades) using Holm's sequentially rejective 5% cut-off for the family-wise error rate. Lastly, to assess whether phylogenetic patterns in competence could stem from study effort alone, we performed a secondary analysis to partition Web of Science citation counts for each avian species as a quasi-Poisson response.

To investigate the evolution of competence across bird species, we used the *ape* package and maximum likelihood to reconstruct the ancestral character state (Paradis et al., 2004). We compared an equal-rate and an all-rates-different model of evolution with Akaike information criterion (AIC; Schluter et al., 1997) and used the most competitive model to perform stochastic character mapping with Markov chain Monte Carlo ($n = 1,000$) using the *phytools* package (Revell, 2012). We displayed mean posterior probabilities of competence across our sampled avian phylogeny.

2.4 | Trait-based analyses

We compiled avian traits from EltonTraits (Wilman et al., 2014), the Amniote Life History database (Myhrvold et al., 2015), the International Union for the Conservation of Nature (Baillie et al., 2004) and HormoneBase (Vitousek et al., 2018). Traits included diet composition and breadth, foraging strata, life history (e.g., maximum life span, clutch size, fledging age and number of clutches per year), morphology (e.g., adult mass and hatching weight), maximum elevation, global population trend and physiology [i.e., baseline corticosterone (CORT)]. Using avian distribution maps (BirdLife International & Handbook of the Birds of the World, 2017), we derived the total range size, latitude of the centroids of breeding and non-breeding ranges, and mean migration distance (greater circle distance between these centroids). We also quantified migratory dispersion, the extent to which species inhabit larger (positive) or smaller (negative) areas in the non-breeding season relative to breeding range size, and made binary covariates for migratory strategy (resident, full migrant or partial migrant; Gilroy et al., 2016). For resident species, migration distance and dispersion were set to zero. To represent avian

taxonomy, we included binary covariates for each family and any clades identified by phylogenetic factorization; we also included a binary covariate for the Passeriformes (166 of 183 species). We also derived evolutionary isolation with the *picante* package (Kembel et al., 2010). We again used Web of Science citation counts per species to approximate study effort. We transformed continuous predictors that spanned orders of magnitude and excluded those with high homogeneity or missing values for > 80% of birds. We compiled features for our 183 sampled birds and additional unsampled avian species to predict likely but undetected competent hosts. We limited these out-of-sample species to only the 39 families included in our dataset (4,508 bird species). Feature definitions, transformations and coverage are provided in the Supporting Information (Table S1).

To identify trait profiles of competent birds and to predict likely novel Bbsl reservoirs, we used boosted regression trees (BRTs) to fit a predictive model relating binary competence to a predictor matrix of avian traits (Elith et al., 2008). The BRTs were trained to maximize classification accuracy by learning patterns of features that best distinguish competent and non-competent species. BRTs generate recursive binary splits for randomly sampled predictors, and successive trees are built using residuals of the prior best-performing tree as the new response. Boosting generates an ensemble of linked trees, where each achieves increasingly more accurate classification. Before analysis, we randomly split our data into training (90%) and test (10%) datasets while preserving the proportion of positive labels. Models were then trained with the *gbm* package (Ridgeway, 2006), with a maximum of 30,000 trees, a learning rate of 0.0001 and an interaction depth of three (Elith et al., 2008). The BRTs used a Bernoulli error distribution and 10-fold cross-validation, and we used the *ROCR* and *hmeasure* packages to quantify three measures of classification accuracy: area under the receiver operating characteristic curve (AUC), sensitivity and specificity (Sing et al., 2005). Given that BRT results can depend on random splits between training and test data, we used five partitions to generate a model ensemble (Evans et al., 2017). To diagnose whether trait profiles of competent birds are driven by study effort, we ran a secondary BRT ensemble that modelled Web of Science citation counts as a Poisson response (Plowright, Becker, Crowley, et al., 2019).

After assessing the accuracy of our BRTs against test data, we applied our model ensemble to the full trait dataset of 4,691 avian species (183 sampled and 4,508 unsampled species) to generate mean probabilities of competence. This allowed us to differentiate predictions that signal false negatives (i.e., sampled species without evidence of competence) and those denoting undetected reservoirs (i.e., unsampled species). To assess phylogenetic signal in predictions, we estimated Pagel's λ in the logit-transformed probabilities with the *caper* package (Orme, 2013) and applied phylogenetic factorization to identify clades of particularly likely competent birds. Lastly, to guide surveillance of these false negatives and undetected competent reservoirs, we mapped the distributions of species with mean predicted probabilities of > 50 and > 60%.

3 | RESULTS

3.1 | Avian competence on a global scale

Half of all sampled bird species were competent for *Bbsl* (91 of 183). Only nine bird species had experimental evidence of competence (i.e., xenodiagnosis), and all 91 competent species (with the exception of *Gallus gallus*) had larvae from wild birds test positive (Supporting Information Figure S2). For records reporting *Bbsl* genospecies from bird-fed larvae, our global data were dominated by *B. garinii* (31%), *B. valaisiana* (20%), *Bbss* (16%) and *B. afzelii* (15%), representing data biases towards Europe (59%) and North America (37%); 3% of data were from Eastern Asia, whereas 1% were from South America (Figure 1a). However, these 91 competent bird species were broadly

distributed across the Americas, Africa, Asia and Oceania throughout their annual cycles.

We observed significant heterogeneity in *Bbsl* prevalence in bird-fed larvae ($I^2 = .76$, $Q_{963} = 2,970$, $p < .0001$). Avian species accounted for more of this variation ($I^2_{\text{species}} = .31$) than study ($I^2_{\text{study}} = .19$) or individual record ($I^2_{\text{observation}} = .26$), resulting in moderate phylogenetic signal ($H^2 = .40$). Given the stronger effect of avian phylogeny, we found no effect of study-level predictors, such as space (Figure 1b) or year (Figure 1c), on the proportion of larvae infected by wild birds (Supporting Information Table S2). Seasons were also mostly uninformative (Supporting Information Table S3), but the prevalence in bird-infected larvae was weakly lower during summer (Akaike weight [w_i] = .44, $R^2 = .01$; Figure 1d).

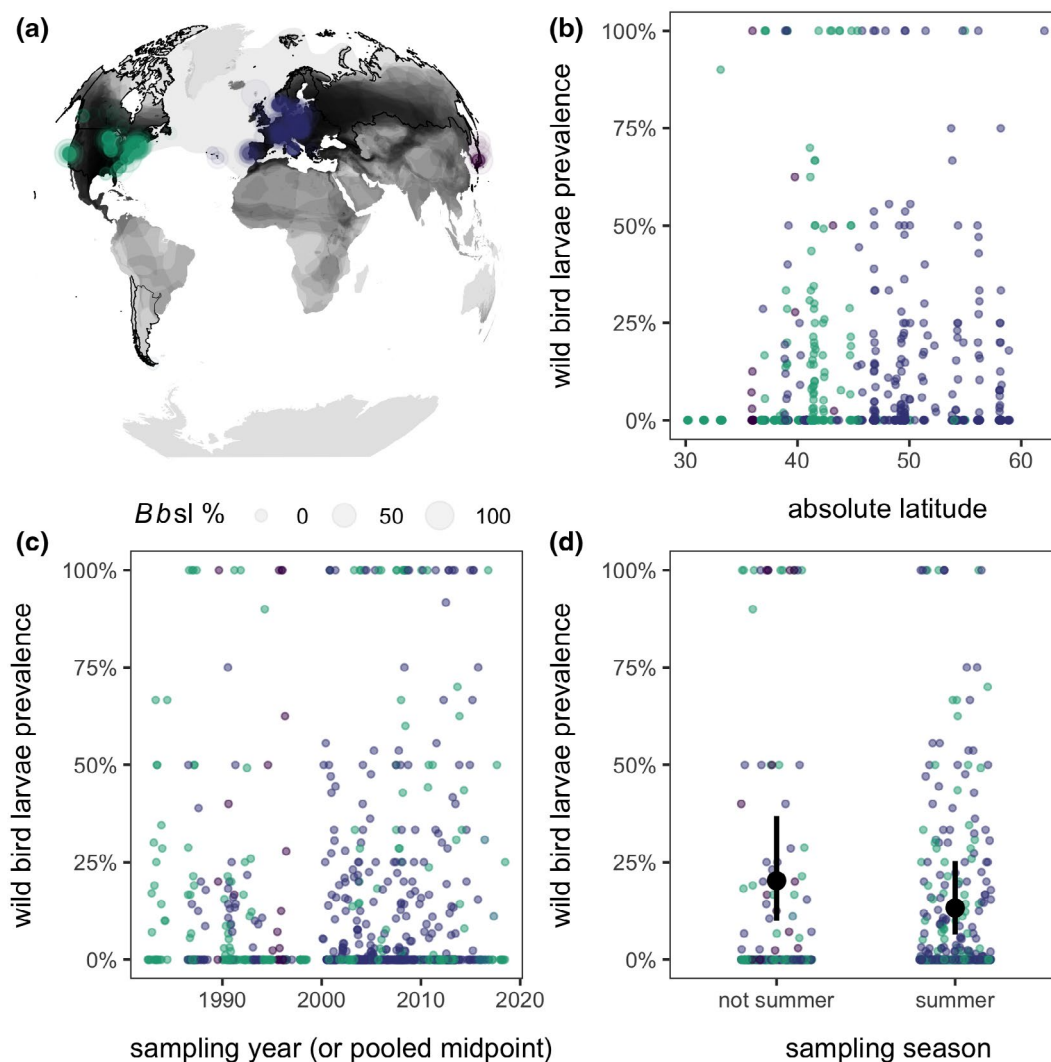


FIGURE 1 Global distribution of *Borrelia burgdorferi* sensu lato (*Bbsl*) prevalence in tick larvae sampled from wild birds. (a) Sampled countries are shown with a black border, with spatio-temporal bird-tick-*Bbsl* prevalences, which are sized by magnitude and coloured by georegion. Shapefiles of the 91 competent species are overlaid in black (BirdLife International & Handbook of the Birds of the World, 2017). (b–d) Larval infection prevalence is plotted by absolute latitude (b), year (c) and season (d), with each point representing a bird-tick-*Bbsl* association; points are coloured by region and jittered to reduce overlap. Black points and lines in (d) display predicted means and 95% confidence intervals from the top mixed-effect model (Supporting Information Table S3) [Colour figure can be viewed at wileyonlinelibrary.com]

3.2 | Evolutionary patterns in competence

We next considered competence as an intrinsic binary trait per species. We estimated intermediate phylogenetic signal in the ability of birds to transmit *Bbsl* to larvae ($D = 0.78$), indicating significant phylogenetic clustering between randomness ($p < .001$) and a Brownian

motion model of evolution ($p < .001$). After controlling for study effort, phylogenetic factorization identified one clade, the genus *Turdus*, as having a significantly greater likelihood of including competent species when compared with other avian taxa (Figure 2). In particular, all but one sampled member of this clade displayed the ability to infect larval ticks with *Bbsl* (92%).

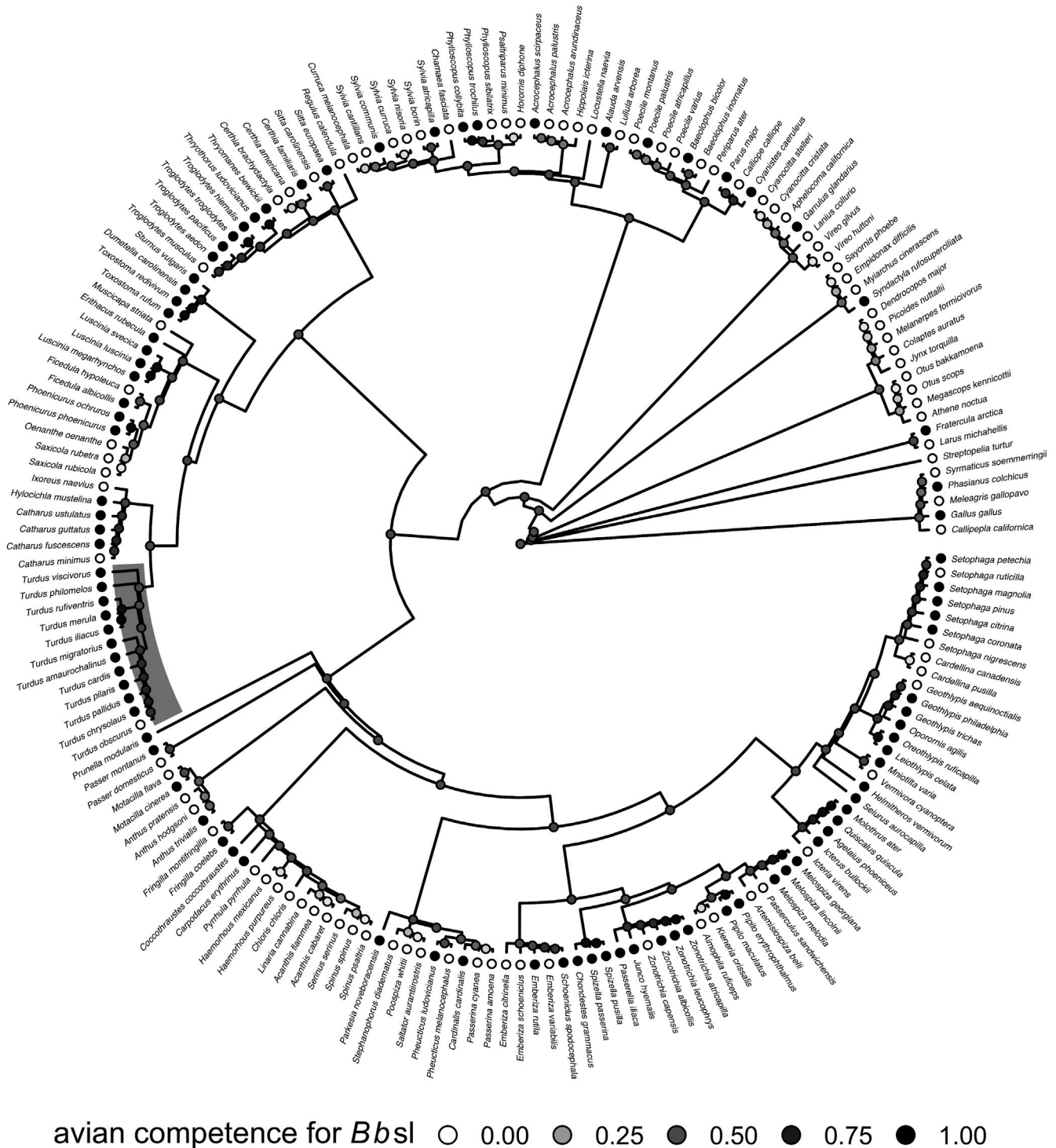


FIGURE 2 Phylogenetic patterns in avian competence for *Borrelia burgdorferi* sensu lato (*Bbsl*). The avian phylogeny displays observed species binary competence, and highlighted clades are those with significantly different competence from the paraphyletic remainder using phylogenetic factorization. Nodes show the mean posterior probabilities of being competent estimated from stochastic character mapping

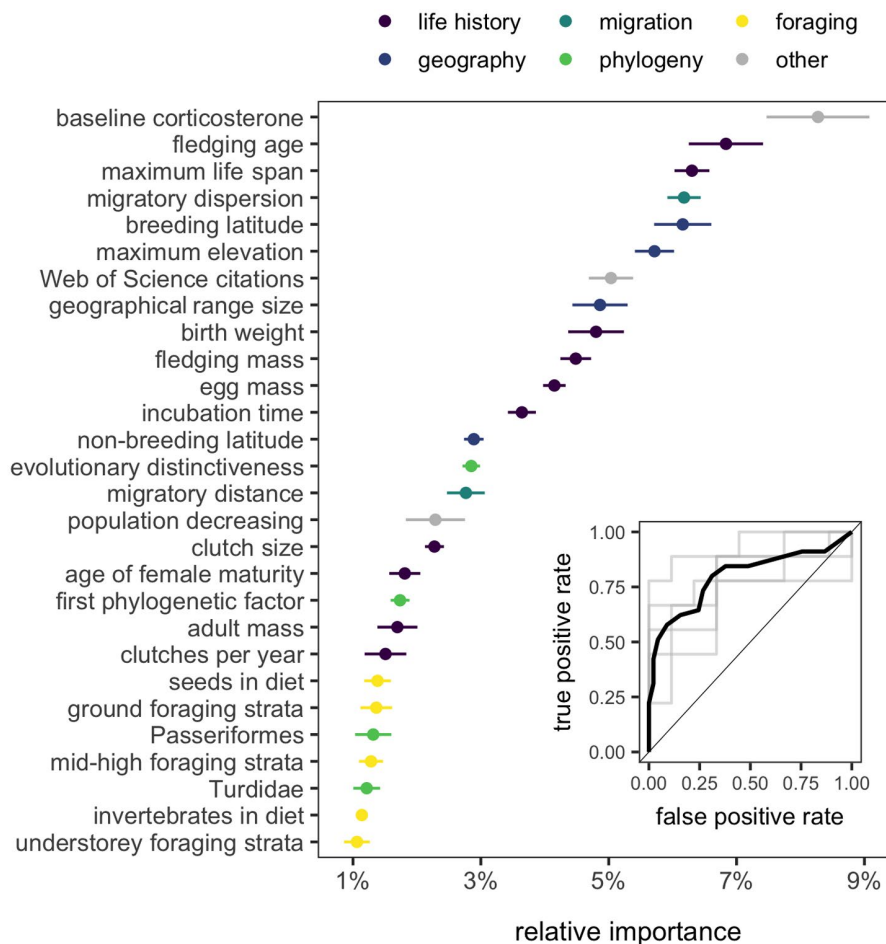


FIGURE 3 Boosted regression tree performance in identifying traits predictive of avian competence for *Borrelia burgdorferi sensu lato* (*Bbsl*) and their relative importance across five random partitions of training and test datasets. The relative importance per feature is shown as the mean and standard error across training and test data partitions. Only features with mean importance > 1% are shown (Supporting Information Table S4). The inset shows accuracy through the receiver operating characteristic curves obtained from 10-fold cross-validation on test data. Grey lines show curves from each partition, and the black line displays the mean [Colour figure can be viewed at wileyonlinelibrary.com]

Our secondary analysis identified seven taxa as having significantly different Web of Science citation counts (Supporting Information Figure S3), five of which were heavily studied species: *Gallus gallus* (4,139), *Parus major* (3,736), *Sturnus vulgaris* (2,509), *Passer domesticus* (2,162) and *Ficedula hypoleuca* (1,500). Disproportionately studied taxa also included the Phasianidae (\bar{x} = 609) and a subclade of the Icteridae (genera *Quiscalus*, *Molothrus* and *Agelaius*; \bar{x} = 545). Taxonomic patterns in Web of Science citation counts did not overlap with taxonomic patterns in avian competence, suggesting that the latter were not driven by variable study effort (Supporting Information Figure S3).

The evolution of avian competence was best described by an equal-rate model (w_i = .73). Stochastic character mapping suggested equal transitions from non-competent to competent and from competent to non-competent (Figure 2), with the ancestral state being equivocal. Competence was gained within the Turdidae, Mimidae, Passerellidae and Troglodytidae, with both gains and losses within the Parulidae. We also observed a clear loss of competence within the majority of the Carduelinae and within the Corvidae, Picidae and Strigidae (Figure 2).

3.3 | Trait profiles of competent birds

Our BRT models distinguished competent from non-competent birds with moderate accuracy (AUC = .80 \pm 0.05 SE; sensitivity = .71 \pm 0.08

SE; specificity = .64 \pm 0.05 SE; Figure 3). Some top features for describing *Bbsl*-competent species included physiology (i.e., baseline CORT), life history (i.e., fledging age, maximum life span, birth and fledging weight, egg mass, incubation time and clutch size), migration (dispersion and distance), geography (breeding and non-breeding latitude, maximum elevation and geographical range size), evolutionary isolation and study effort. The BRTs identified our phylofactorization clade (i.e., the *Turdus* genus) alongside the Turdidae family and passerines more generally as the only taxonomic features with non-trivial importance (i.e., < 1%), and foraging traits were generally uninformative (Figure 3; Supporting Information Table S4).

Physiologically, *Bbsl*-competent birds had lower baseline concentrations of CORT, the main avian glucocorticoid (Figure 4). Competent species were also described by either extreme of the pace-of-life continuum. On the one hand, competent birds had shorter incubation times and young that were smaller and fledged earlier than non-competent counterparts. On the other hand, competent birds also had longer life spans, smaller clutches and larger eggs and body size. Geographically, competent birds tended to breed and winter at higher latitudes, had broader distributions and occupied lower elevations, and their populations were stable or increasing. Species with negative migratory dispersion were more likely to be competent, indicating that such hosts had larger breeding ranges and greater diversity of migratory movements from their wintering to breeding grounds.

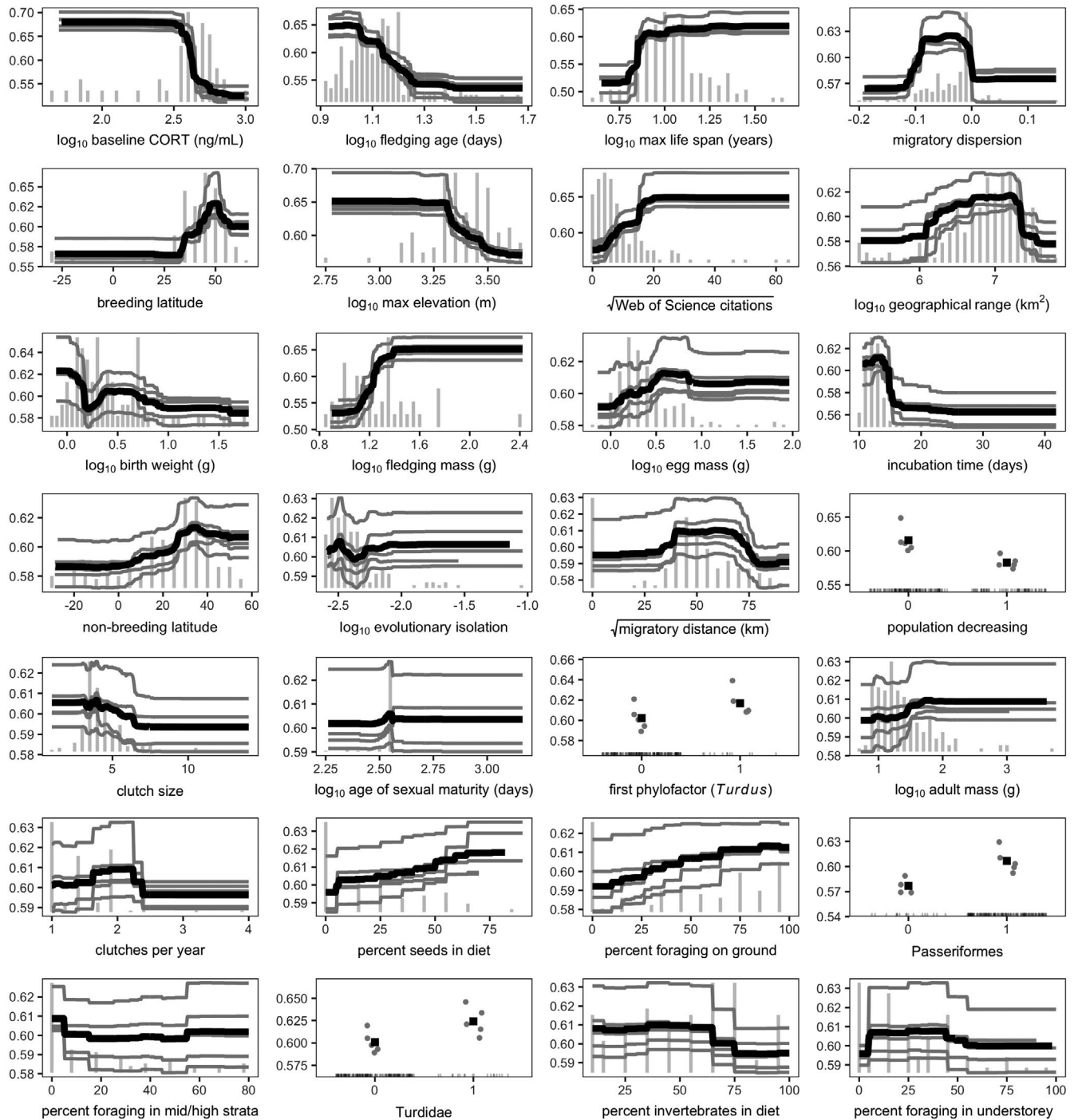


FIGURE 4 Trait profile of a *Borrelia burgdorferi sensu lato* (*Bbsl*)-competent avian species. Partial dependence plots of the top predictors across boosted regression trees applied to five random partitions of training and test data are shown ordered by relative importance ($> 1\%$). Grey lines or points show the marginal effect of a given variable for prediction of *Bbsl* competence from each random data partition, whereas the black lines or squares display the average marginal effect. Histograms and rug plots display the distribution of continuous and categorical predictor variables, respectively, across the 183 sampled bird species

Competence was less strongly related to mean migratory distance, with intermediate-distance migrants being most likely to transmit *Bbsl* to larvae. Members of the genus *Turdus*, the family Turdidae and the Passeriformes as a whole were all more likely to be competent. Additionally, although foraging traits generally had low relative importance, competent birds were more likely to be granivorous and ground-foraging species. Lastly, well-studied species were also more

likely to be competent. However, our secondary BRTs showed that citations were not predictable by these same traits ($AUC = .50 \pm 0.05$ SE), suggesting that the trait profile of a competent bird was not confounded by the ecological traits of well-studied hosts.

Application of our BRT ensemble to trait and taxonomic data across the 39 sampled avian families revealed ≥ 21 undiscovered species that could be prioritized for *Bbsl* surveillance based on

similarity of features to known competent reservoirs (Figure 5a). We observed strong phylogenetic signal in mean predicted probabilities ($\lambda = .94$), indicating that the influential traits revealed by our BRTs are likely to be driven by clades with high potential for competence (Figure 5b). Phylogenetic factorization found nine such clades with distinct model predictions (Supporting Information Table S5).

The geography of likely high-probability reservoirs revealed potential hotspots of competent birds across their breeding (Figure 5c), non-breeding (Figure 5d) and resident (Figure 5e) ranges. Our BRTs suggested at least one likely false negative, the Indigo bunting (*Passerina cyanea*; Kinsey et al., 2000; Schneider et al., 2015; Sonenshine et al., 1995). Likely but unsampled competent reservoirs included the American goldfinch (*Spinus tristis*), Harris's

sparrow (*Zonotrichia querula*), Abert's towhee (*Melospiza aberti*), yellow-headed blackbird (*Xanthocephalus xanthocephalus*), western meadowlark (*Sturnella neglecta*), northern mockingbird (*Mimus polyglottos*), Brewer's blackbird (*Euphagus cyanocephalus*) and vesper sparrow (*Pooecetes gramineus*) in North America; Townsend's warbler (*Setophaga townsendi*), scarlet tanager (*Piranga olivacea*), eastern bluebird (*Sialia sialis*), Louisiana waterthrush (*Parkesia motacilla*), red-eyed vireo (*Vireo olivaceus*), grasshopper sparrow (*Ammodramus saviannarum*), Acadian flycatcher (*Empidonax virens*) and clay-colored thrush (*Turdus grayi*) across the Americas; the corn bunting (*Emberiza calandra*) across Eurasia; the horned lark (*Eremophila alpestris*) across the Northern Hemisphere; and the thick-billed murre (*Uria lomvia*) and rhinoceros auklet (*Cerorhinca monocerata*) across pelagic zones.

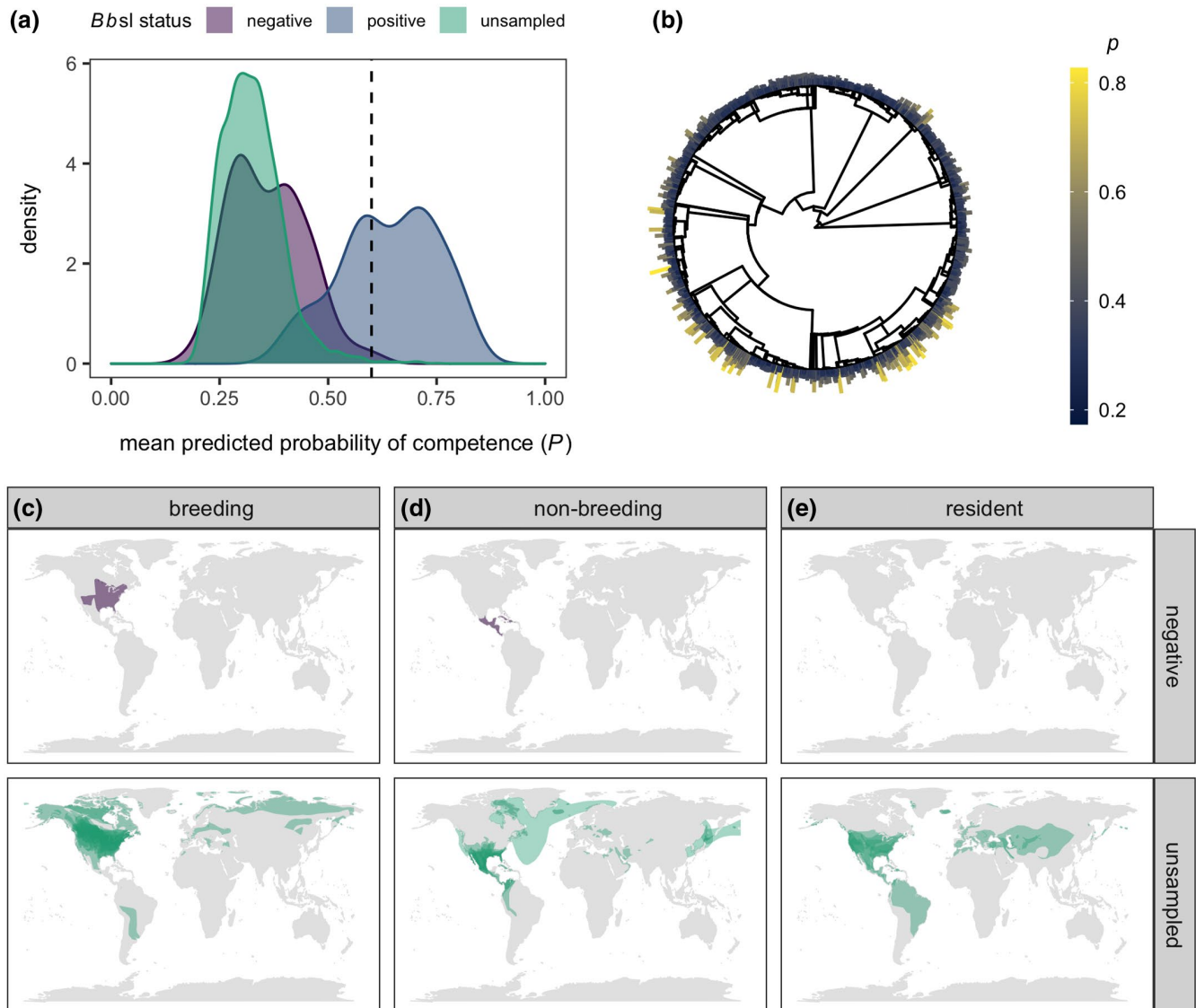


FIGURE 5 Distribution of the mean predicted probabilities of *Borrelia burgdorferi* sensu lato (*Bbsl*) competence across the 39 sampled avian families. (a) Density plots show predictions for currently negative, positive and unsampled species. (b) These propensity scores are also shown across the avian phylogeny. (c–e) Distributions of species within a mean probability of > 60% are shown by their breeding (c), non-breeding (d) and resident (e) ranges (BirdLife International & Handbook of the Birds of the World, 2017). The Supporting Information (Figure S4) displays these geographical distributions with a less conservative prediction cut-off of 50% [Colour figure can be viewed at wileyonlinelibrary.com]

Species with probabilities > 50% (96th percentile of predictions) are included in the Supporting Information (Table S6; Figure S4); this cut-off found another three likely false negatives and 74 likely but unsampled competent species.

4 | DISCUSSION

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

Although pathogen transmission inherently occurs from individuals, variation in competence can arise across broader biological scales (Gervasi et al., 2015; VanderWaal & Ezenwa, 2016). Our meta-analysis identified high heterogeneity in *Bbsl* prevalence from bird-fed larvae that was better explained by within-study heterogeneity and bird phylogeny than study-level variation and broad spatial or temporal covariates. Greater within- than between-study heterogeneity suggests a greater role for fine-scale environmental covariates, such as local densities of ticks or alternative hosts, in shaping vector feeding behaviour and infection prevalence in avian hosts that, in turn, affect the prevalence in bird-fed larvae (Kilpatrick et al., 2017). Additionally, the moderate contribution of avian phylogeny in our meta-analysis was mirrored by intermediate phylogenetic signal in our species-level analysis. Together, these analyses suggest that although intraspecific variation in host competence occurs over space and time (Norte et al., 2020), the ability to transmit *Bbsl* can also be considered an intrinsic trait of avian species.

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

Our BRTs identified CORT as the top predictor of competence, for which competent birds were more likely to have lower baseline concentrations. Although persistently elevated CORT can be immunosuppressive and amplify competence (Gervasi et al., 2017), baseline concentrations have mostly metabolic functions that allow animals to meet energetic demands and respond to adverse conditions (Sapolsky et al., 2000). Low baseline CORT could be linked to competence by its association with breeding latitude. Birds tend to have lower baseline CORT at high latitudes, which could facilitate continued breeding in suboptimal habitats (Wingfield & Sapolsky, 2003). This is compatible with our finding that competent species also generally breed at high latitudes. Birds breeding further from the equator show stronger trade-offs between arms of the immune system, such that high-latitude hosts mount weaker adaptive responses (Ardia, 2007). Given that robust *Bbsl*-specific antibody titres limit transmission to naïve ticks (Kurtenbach et al., 1994), birds breeding at high latitudes could display weaker antibody defenses that increase competence. Sampling competent birds across latitudinal gradients could characterize such immunity trade-offs and test whether these restrict bird-tick transmission (Becker, Albery, et al., 2020).

Our trait-based analyses also suggested that competent birds occur at either extreme of the pace-of-life continuum (Stearns, 1983). This possibly contrasts with work on mammals, where fast-lived species (i.e., rapid development and high fecundity at the expense of longevity) are more competent than their slow-lived counterparts (Huang et al., 2013; LoGiudice et al., 2003; Ostfeld et al., 2014). Although many of the top traits predicting competence in birds also reflect a fast pace of life (e.g., short incubation times, young that are small and fledge early), competent birds were also characterized by long life spans, large eggs and small clutches, more consistent with a

slow life history. This pattern could arise from two competing signals in the data, such that both particularly fast- (e.g., many passerines) and slow-lived species (e.g., the Alcidae and Phasianidae) display evidence of competence. Future tests of pace-of-life variation and competence within orders such as the Passeriformes or Charadriiformes could minimize confounding effects of taxonomy and assess whether such patterns have an immunological basis, as suggested for mammalian competence (Albery & Becker, 2020; Previtali et al., 2012).

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

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

To test these model predictions, we encourage more definitive assessments of competence. Given that most of our data included approximations of competence from *Bbsl* in engorged larvae on wild birds, xenodiagnostic experiments could be prioritized for unsampled avian species with high probabilities of being competent to establish bird-tick transmission (Ginsberg et al., 2005; Norte et al., 2013). As an alternative approach, field surveys could instead assess *Bbsl* infection not only in engorged larvae but also in the hosts themselves to test whether absence of the pathogen in ticks is attributable to poor competence or an uninfected host (Newman et al., 2015). These increasing data on host competence would also facilitate future analytical efforts. Given that *Bbsl* includes genospecies that vary in host specificity (e.g., *Bbss* infects both rodents and birds, whereas *B. garinii* and *B. valaisiana* are more specialized on the latter), better consideration of such co-evolutionary relationships could improve model performance (Kurtenbach et al., 2006; O'Keeffe et al., 2020). We pooled *Bbsl* across genospecies owing to the relatively small sample of bird species, but models applied to taxonomic subsets of data might generate distinct predictions by reducing noise from hosts infected with other *Bbsl* genospecies (Dallas & Becker 2020).

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

In conclusion, we demonstrate that host ability to transmit pathogens to new hosts or vectors can be predicted by the ecological and evolutionary characteristics of bird species in the Lyme borreliosis system. By combining flexible phylogenetic and trait-based analyses, our work generates testable hypotheses for future comparative and theoretical studies of tick-borne disease alongside predictions that can inform bird surveillance efforts, not only for *Bbsl* but also for similar pathogens (e.g., *Anaplasma* and *Ehrlichia*) in the context of environmental change. In future, greater attention to the factors that shape competence within and between species could improve our ability to predict and manage reservoir hosts for zoonotic pathogens more broadly.

ACKNOWLEDGMENTS

We thank BirdLife International for providing avian distribution data, Tao Huang for assistance with data processing and J. P. Schmidt for technical advice on BRTs. We also thank Ellen Ketterson, members of the Ketterson laboratory and two anonymous reviewers for feedback on this manuscript. D.J.B. was supported by an appointment to the Intelligence Community Postdoctoral Research Fellowship Program, administered by Oak Ridge Institute for Science and Education through an interagency agreement between the U.S. Department of Energy and the Office of the Director of National Intelligence. B.A.H. was supported by the National Science Foundation Ecology and Evolution of Infectious Diseases program (DEB-1717282 and DEB-1619072).

CONFLICT OF INTERESTS

The authors have declared no conflicts of interest for this article.

AUTHOR CONTRIBUTIONS

D.J.B. designed the study, collected data, performed the analyses and wrote the manuscript. B.A.H. contributed to data analysis and provided critical feedback on the manuscript.

DATA AVAILABILITY STATEMENT

Data and R code to reproduce the primary analyses are available in the Dryad Digital Depository: 10.5061/dryad.r7sqv9s88 (Becker & Han, 2020).

ORCID

Daniel J. Becker  <https://orcid.org/0000-0003-4315-8628>

Barbara A. Han  <https://orcid.org/0000-0002-9948-3078>

REFERENCES

- Albery, G. F., & Becker, D. J. (2020). Fast-lived hosts and zoonotic risk. *Trends in Parasitology*. <https://doi.org/10.1016/j.pt.2020.10.012>
- Anderson, J. F., Johnson, R. C., Magnarelli, L. A., & Hyde, F. W. (1986). Involvement of birds in the epidemiology of the Lyme disease agent *Borrelia burgdorferi*. *Infection and Immunity*, 51, 394–396. <https://doi.org/10.1128/IAI.51.2.394-396.1986>
- Anderson, J. F., & Magnarelli, L. A. (1984). Avian and mammalian hosts for spirochete-infected ticks and insects in a Lyme disease focus in Connecticut. *The Yale Journal of Biology and Medicine*, 57, 627–641.
- Archie, E. A., Luikart, G., & Ezenwa, V. O. (2009). Infecting epidemiology with genetics: A new frontier in disease ecology. *Trends in Ecology and Evolution*, 24, 21–30. <https://doi.org/10.1016/j.tree.2008.08.008>
- Ardia, D. R. (2007). The ability to mount multiple immune responses simultaneously varies across the range of the tree swallow. *Ecography*, 30, 23–30. <https://doi.org/10.1111/j.0906-7590.2007.04939.x>
- Ashmole, M. J. (1962). The migration of European thrushes: A comparative study based on ringing recoveries. *Ibis*, 104, 522–559. <https://doi.org/10.1111/j.1474-919X.1962.tb08684.x>
- Babayan, S. A., Orton, R. J., & Streicker, D. G. (2018). Predicting reservoir hosts and arthropod vectors from evolutionary signatures in RNA virus genomes. *Science*, 362, 577–580. <https://doi.org/10.1126/science.aap9072>
- Baillie, J., Hilton-Taylor, C., & Stuart, S. N. (2004). *IUCN Red List of Threatened Species. A Global Species Assessment*. IUCN. Retrieved from: <https://www.iucnredlist.org/resources/baillie2004>
- Battaly, G. R., & Fish, D. (1993). Relative importance of bird species as hosts for immature *Ixodes dammini* (Acari: Ixodidae) in a suburban residential landscape of southern New York State. *Journal of Medical Entomology*, 30, 740–747. <https://doi.org/10.1093/jmedent/30.4.740>
- Becker, D. J., Albery, G. F., Kessler, M. K., Lunn, T. J., Falvo, C. A., Cziráj, G. Á., Martin, L. B., & Plowright, R. K. (2020). Macroimmunology: The drivers and consequences of spatial patterns in wildlife immune defense. *Journal of Animal Ecology*, 89, 972–995.
- Becker, D. J., & Han, B. A. (2020). Data from: The macroecology and evolution of avian competence for *Borrelia burgdorferi*. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.r7sqv9s88>
- Becker, D. J., Ketterson, E. D., & Hall, R. J. (2020). Reactivation of latent infections with migration shapes population-level disease dynamics. *Proceedings of the Royal Society B: Biological Sciences*, 287, 20201829. <https://doi.org/10.1098/rspb.2020.1829>
- Becker, D. J., Schultz, E. M., Atwell, J. W., & Ketterson, E. D. (2019). Urban residency and leukocyte profiles in a traditionally migratory songbird. *Animal Migration*, 6, 49–59. <https://doi.org/10.1515/ami-2019-0002>
- Becker, D. J., Seifert, S. N., & Carlson, C. J. (2020). Beyond infection: Integrating competence into reservoir host prediction. *Trends in Ecology and Evolution*, 35, 1062–1065. <https://doi.org/10.1016/j.tree.2020.08.014>
- Becker, D. J., Washburne, A. D., Faust, C. L., Mordecai, E. A., & Plowright, R. K. (2019). The problem of scale in the prediction and management of pathogen spillover. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 374, 20190224. <https://doi.org/10.1098/rstb.2019.0224>
- BirdLife International & Handbook of the Birds of the World. (2017). *Bird species distribution maps of the world*. BirdLife International and Handbook of the Birds of the World. Retrieved from <http://datazone.birdlife.org/species/requestdis>
- Bonnet-Lebrun, A.-S., Manica, A., & Rodrigues, A. S. (2020). Effects of urbanization on bird migration. *Biological Conservation*, 244, 108423. <https://doi.org/10.1016/j.biocon.2020.108423>
- Breuner, N. E., Ford, S. L., Hojgaard, A., Osikowicz, L. M., Parise, C. M., Rosales Rizzo, M. F., Bai, Y., Levin, M. L., Eisen, R. J., & Eisen, L. (2020). Failure of the Asian longhorned tick, *Haemaphysalis longicornis*, to serve as an experimental vector of the Lyme disease spirochete, *Borrelia burgdorferi* sensu stricto. *Ticks and Tick-Borne Diseases*, 11, 101311. <https://doi.org/10.1016/j.ttbdis.2019.101311>
- Brinkerhoff, R. J., Folsom-O'Keefe, C. M., Tsao, K., & Diuk-Wasser, M. A. (2011). Do birds affect Lyme disease risk? Range expansion of the vector-borne pathogen *Borrelia burgdorferi*. *Frontiers in Ecology and the Environment*, 9, 103–110. <https://doi.org/10.1890/090062>
- Brunner, J. L., LoGiudice, K., & Ostfeld, R. S. (2008). Estimating reservoir competence of *Borrelia burgdorferi* hosts: Prevalence and infectivity, sensitivity, and specificity. *Journal of Medical Entomology*, 45, 139–147.
- Burgdorfer, W., & Gage, K. L. (1986). Susceptibility of the black-legged tick, *Ixodes scapularis*, to the Lyme disease spirochete, *Borrelia burgdorferi*. *Zentralblatt für Bakteriologie, Mikrobiologie und Hygiene. Series A: Medical Microbiology, Infectious Diseases, Virology, Parasitology*, 263, 15–20.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. Springer Science & Business Media.
- Chamberlain, S. A., & Szöcs, E. (2013). Taxize: Taxonomic search and retrieval in R. *F1000Research*, 2, 191. <https://doi.org/10.12688/f1000research.2-191.v2>
- Comstedt, P., Bergström, S., Olsen, B., Garpmo, U., Marjavaara, L., Mejlom, H., Barbour, A. G., & Bunikis, J. (2006). Migratory passerine birds as reservoirs of Lyme borreliosis in Europe. *Emerging Infectious Diseases*, 12, 1087–1095. <https://doi.org/10.3201/eid1207.060127>

- Dallas, T. A., & Becker, D. J. (2020). Taxonomic resolution affects host-parasite association model performance. *Parasitology*, 1–28. <https://doi.org/10.1017/s0031182020002371>
- Downs, C. J., Schoenle, L. A., Han, B. A., Harrison, J. F., & Martin, L. B. (2019). Scaling of host competence. *Trends in Parasitology*, 35, 182–192. <https://doi.org/10.1016/j.pt.2018.12.002>
- Dubska, L., Literak, I., Kocianova, E., Taragelova, V., & Sychra, O. (2009). Differential role of passerine birds in distribution of *Borrelia* spirochetes, based on data from ticks collected from birds during the post-breeding migration period in Central Europe. *Applied and Environmental Microbiology*, 75, 596–602. <https://doi.org/10.1128/AEM.01674-08>
- Eisen, L. (2020). Vector competence studies with hard ticks and *Borrelia burgdorferi* sensu lato spirochetes: A review. *Ticks and Tick-borne Diseases*, 11, 101359. <https://doi.org/10.1016/j.ttbdis.2019.101359>
- Elith, J., Leathwick, J. R., & Hastie, T. (2008). A working guide to boosted regression trees. *Journal of Animal Ecology*, 77, 802–813. <https://doi.org/10.1111/j.1365-2656.2008.01390.x>
- Evans, M. V., Dallas, T. A., Han, B. A., Murdock, C. C., & Drake, J. M. (2017). Data-driven identification of potential Zika virus vectors. *eLife*, 6, e22053. <https://doi.org/10.7554/eLife.22053>
- Franke, J., Moldenhauer, A., Hildebrandt, A., & Dorn, W. (2010). Are birds reservoir hosts for *Borrelia afzelii*? *Ticks and Tick-borne Diseases*, 1, 109–112. <https://doi.org/10.1016/j.ttbdis.2010.03.001>
- Fritz, S. A., & Purvis, A. (2010). Selectivity in mammalian extinction risk and threat types: A new measure of phylogenetic signal strength in binary traits. *Conservation Biology*, 24, 1042–1051. <https://doi.org/10.1111/j.1523-1739.2010.01455.x>
- Gervasi, S. S., Burgan, S. C., Hofmeister, E., Unnasch, T. R., & Martin, L. B. (2017). Stress hormones predict a host superspreader phenotype in the West Nile virus system. *Proceedings of the Royal Society B: Biological Sciences*, 284, 20171090.
- Gervasi, S. S., Civitello, D. J., Kilvitis, H. J., & Martin, L. B. (2015). The context of host competence: A role for plasticity in host-parasite dynamics. *Trends in Parasitology*, 31, 419–425. <https://doi.org/10.1016/j.pt.2015.05.002>
- Gilroy, J. J., Gill, J. A., Butchart, S. H., Jones, V. R., & Franco, A. M. (2016). Migratory diversity predicts population declines in birds. *Ecology Letters*, 19, 308–317. <https://doi.org/10.1111/ele.12569>
- Ginsberg, H. S., Buckley, P. A., Balmforth, M. G., Zhioua, E., Mitra, S., & Buckley, F. G. (2005). Reservoir competence of native North American birds for the Lyme disease spirochete, *Borrelia burgdorferi*. *Journal of Medical Entomology*, 42, 445–449.
- Gylfe, A., Bergström, S., Lundström, J., & Olsen, B. (2000). Reactivation of *Borrelia* infection in birds. *Nature*, 403, 724–725. <https://doi.org/10.1038/35001663>
- Hahn, M. B., Jarnevich, C. S., Monaghan, A. J., & Eisen, R. J. (2016). Modeling the geographic distribution of *Ixodes scapularis* and *Ixodes pacificus* (Acari: Ixodidae) in the contiguous United States. *Journal of Medical Entomology*, 53, 1176–1191.
- Hamer, S. A., Goldberg, T. L., Kitron, U. D., Brawn, J. D., Anderson, T. K., Loss, S. R., Walker, E. D., & Hamer, G. L. (2012). Wild birds and urban ecology of ticks and tick-borne pathogens, Chicago, Illinois, USA, 2005–2010. *Emerging Infectious Diseases*, 18, 1589–1595. <https://doi.org/10.3201/eid1810.120511>
- Han, B. A., & Drake, J. M. (2016). Future directions in analytics for infectious disease intelligence. *EMBO Reports*, 17, 785–789. <https://doi.org/10.15252/embr.201642534>
- Han, B. A., Majumdar, S., Calmon, F. P., Glicksberg, B. S., Horesh, R., Kumar, A., Perer, A., von Marschall, E. B., Wei, D., Mojsilović, A., & Varshney, K. R. (2019). Confronting data sparsity to identify potential sources of Zika virus spillover infection among primates. *Epidemics*, 27, 59–65. <https://doi.org/10.1016/j.epidem.2019.01.005>
- Han, B. A., Schmidt, J. P., Alexander, L. W., Bowden, S. E., Hayman, D. T., & Drake, J. M. (2016). Undiscovered bat hosts of filoviruses. *PLoS Neglected Tropical Diseases*, 10, e0004815. <https://doi.org/10.1371/journal.pntd.0004815>
- Han, B. A., Schmidt, J. P., Bowden, S. E., & Drake, J. M. (2015). Rodent reservoirs of future zoonotic diseases. *Proceedings of the National Academy of Sciences USA*, 112, 7039–7044. <https://doi.org/10.1073/pnas.1501598112>
- Hanincová, K., Taragelová, V., Koci, J., Schäfer, S. M., Hails, R., Ullmann, A. J., Piesman, J., Labuda, M., & Kurtenbach, K. (2003). Association of *Borrelia garinii* and *B. valaisiana* with songbirds in Slovakia. *Applied and Environmental Microbiology*, 69, 2825–2830. <https://doi.org/10.1128/AEM.69.5.2825-2830.2003>
- Hasle, G., Bjune, G. A., Midthjell, L., Røed, K. H., & Leinaas, H. P. (2011). Transport of *Ixodes ricinus* infected with *Borrelia* species to Norway by northward-migrating passerine birds. *Ticks and Tick-borne Diseases*, 2, 37–43. <https://doi.org/10.1016/j.ttbdis.2010.10.004>
- Hitch, A. T., & Leberg, P. L. (2007). Breeding distributions of North American bird species moving north as a result of climate change. *Conservation Biology*, 21, 534–539. <https://doi.org/10.1111/j.1523-1739.2006.00609.x>
- Hochachka, W. M., Caruana, R., Fink, D., Munson, A. R. T., Riedewald, M., Sorokina, D., & Kelling, S. (2007). Data-mining discovery of pattern and process in ecological systems. *The Journal of Wildlife Management*, 71, 2427–2437. <https://doi.org/10.2193/2006-503>
- Hofhuis, A., van de Kasstele, J., Sprong, H., van den Wijngaard, C. C., Harms, M. G., Fonville, M., van Leeuwen, A. D., Simões, M., & van Pelt, W. (2017). Predicting the risk of Lyme borreliosis after a tick bite, using a structural equation model. *PLoS One*, 12, e0181807. <https://doi.org/10.1371/journal.pone.0181807>
- Huang, Z. Y. X., de Boer, W. F., van Langevelde, F., Olson, V., Blackburn, T. M., & Prins, H. H. T. (2013). Species' life-history traits explain interspecific variation in reservoir competence: A possible mechanism underlying the dilution effect. *PLoS One*, 8, e54341.
- Hvidsten, D., Frafjord, K., Gray, J. S., Henningsson, A. J., Jenkins, A., Kristiansen, B. E., Lager, M., Rognerud, B., Slåtsve, A. M., Stordal, F., Stuen, S., & Wilhelmsson, P. (2020). The distribution limit of the common tick, *Ixodes ricinus*, and some associated pathogens in north-western Europe. *Ticks and Tick-borne Diseases*, 11, 101388. <https://doi.org/10.1016/j.ttbdis.2020.101388>
- Ishiguro, F., Takada, N., & Masuzawa, T. (2005). Molecular evidence of the dispersal of Lyme disease *Borrelia* from the Asian continent to Japan via migratory birds. *Japanese Journal of Infectious Diseases*, 58, 184–186.
- Ishiguro, F., Takada, N., Masuzawa, T., & Fukui, T. (2000). Prevalence of Lyme disease *Borrelia* spp. in ticks from migratory birds on the Japanese mainland. *Applied and Environmental Microbiology*, 66, 982–986. <https://doi.org/10.1128/AEM.66.3.982-986.2000>
- Ivanova, L. B., Tomova, A., González-Acuña, D., Murúa, R., Moreno, C. X., Hernández, C., Cabello, J., Cabello, C., Daniels, T. J., Godfrey, H. P., & Cabello, F. C. (2014). *Borrelia chilensis*, a new member of the *Borrelia burgdorferi* sensu lato complex that extends the range of this genus-species in the Southern Hemisphere. *Environmental Microbiology*, 16, 1069–1080.
- Jones, K. E., Patel, N. G., Levy, M. A., Storeygard, A., Balk, D., Gittleman, J. L., & Daszak, P. (2008). Global trends in emerging infectious diseases. *Nature*, 451, 990–993. <https://doi.org/10.1038/nature06536>
- Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P., & Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26, 1463–1464. <https://doi.org/10.1093/bioinformatics/btq166>
- Kernbach, M. E., Newhouse, D. J., Miller, J. M., Hall, R. J., Gibbons, J., Oberstaller, J., Selechnik, D., Jiang, R. H. Y., Unnasch, T. R., Balakrishnan, C. N., & Martin, L. B. (2019). Light pollution increases West Nile virus competence of a ubiquitous passerine reservoir

- species. *Proceedings of the Royal Society B: Biological Sciences*, 286, 20191051. <https://doi.org/10.1098/rspb.2019.1051>
- Kilpatrick, A. M., Daszak, P., Jones, M. J., Marra, P. P., & Kramer, L. D. (2006). Host heterogeneity dominates West Nile virus transmission. *Proceedings of the Royal Society B: Biological Sciences*, 273(1599), 2327–2333.
- Kilpatrick, A. M., Dobson, A. D. M., Levi, T., Salkeld, D. J., Swei, A., Ginsberg, H. S., Kjemtrup, A., Padgett, K. A., Jensen, P. M., Fish, D., Ogden, N. H., & Diuk-Wasser, M. A. (2017). Lyme disease ecology in a changing world: Consensus, uncertainty and critical gaps for improving control. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372, 20160117.
- Kinsey, A. A., Durden, L. A., & Oliver, J. H. Jr. (2000). Tick infestations of birds in coastal Georgia and Alabama. *Journal of Parasitology*, 86, 251–254. [https://doi.org/10.1016/S0022-3395\(2000\)0086\[0251:TIOBIC\]2.0.CO;2](https://doi.org/10.1016/S0022-3395(2000)0086[0251:TIOBIC]2.0.CO;2)
- Kurtenbach, K., Dizij, A., Seitz, H. M., Margos, G., Moter, S. E., Kramer, M. D., Wallich, R., Schaible, U. E., & Simon, M. M. (1994). Differential immune responses to *Borrelia burgdorferi* in European wild rodent species influence spirochete transmission to *Ixodes ricinus* L. (Acari: Ixodidae). *Infection and Immunity*, 62, 5344–5352. <https://doi.org/10.1128/IAI.62.12.5344-5352.1994>
- Kurtenbach, K., Hanincová, K., Tsao, J. I., Margos, G., Fish, D., & Ogden, N. H. (2006). Fundamental processes in the evolutionary ecology of Lyme borreliosis. *Nature Reviews Microbiology*, 4, 660. <https://doi.org/10.1038/nrmicro1475>
- LoGiudice, K., Ostfeld, R. S., Schmidt, K. A., & Keesing, F. (2003). The ecology of infectious disease: Effects of host diversity and community composition on Lyme disease risk. *Proceedings of the National Academy of Sciences USA*, 100, 567–571. <https://doi.org/10.1073/pnas.0233733100>
- López-López, J. A., Marín-Martínez, F., Sánchez-Meca, J., Noortgate, W., & Viechtbauer, W. (2014). Estimation of the predictive power of the model in mixed-effects meta-regression: A simulation study. *British Journal of Mathematical and Statistical Psychology*, 67, 30–48. <https://doi.org/10.1111/bmsp.12002>
- Loss, S. R., Noden, B. H., Hamer, G. L., & Hamer, S. A. (2016). A quantitative synthesis of the role of birds in carrying ticks and tick-borne pathogens in North America. *Oecologia*, 182, 947–959. <https://doi.org/10.1007/s00442-016-3731-1>
- Marra, P. P., Cohen, E. B., Loss, S. R., Rutter, J. E., & Tonra, C. M. (2015). A call for full annual cycle research in animal ecology. *Biology Letters*, 11, 20150552. <https://doi.org/10.1098/rsbl.2015.0552>
- Martin, L. B., Burgan, S. C., Adelman, J. S., & Gervasi, S. S. (2016). Host competence: An organismal trait to integrate immunology and epidemiology. *Integrative and Comparative Biology*, 56, 1225–1237. <https://doi.org/10.1093/icb/icw064>
- Mather, T. N., Nicholson, M. C., Donnelly, E. F., & Matyas, B. T. (1996). Entomologic index for human risk of Lyme disease. *American Journal of Epidemiology*, 144, 1066–1069. <https://doi.org/10.1093/oxfordjournals.aje.a008879>
- Mather, T. N., Telford, S. R., MacLachlan, A. B., & Spielman, A. (1989). Incompetence of catbirds as reservoirs for the Lyme disease spirochete (*Borrelia burgdorferi*). *The Journal of Parasitology*, 75, 66–69. <https://doi.org/10.2307/3282938>
- Mead, P., Hook, S., Niesobecki, S., Ray, J., Meek, J., Delorey, M., Prue, C., & Hinckley, A. (2018). Risk factors for tick exposure in suburban settings in the Northeastern United States. *Ticks and Tick-borne Diseases*, 9, 319–324. <https://doi.org/10.1016/j.ttbdis.2017.11.006>
- Merrill, T. E. S., & Johnson, P. T. (2020). Towards a mechanistic understanding of competence: A missing link in diversity–disease research. *Parasitology*, 147, 1159–1170.
- Michonneau, F., Brown, J. W., & Winter, D. J. (2016) rotl: an R package to interact with the Open Tree of Life data. *Methods in Ecology and Evolution*, 7, 1476–1481.
- Miller, M. J., Esser, H. J., Loaiza, J. R., Herre, E. A., Aguilar, C., Quintero, D., Alvarez, E., & Bermingham, E. (2016). Molecular ecological insights into Neotropical bird-tick interactions. *PLoS One*, 11, e0155989. <https://doi.org/10.1371/journal.pone.0155989>
- Morse, S. S., Mazet, J. A., Woolhouse, M., Parrish, C. R., Carroll, D., Karesh, W. B., Zambrana-Torrel, C., Lipkin, W. I., & Daszak, P. (2012). Prediction and prevention of the next pandemic zoonosis. *The Lancet*, 380, 1956–1965. [https://doi.org/10.1016/S0140-6736\(12\)61684-5](https://doi.org/10.1016/S0140-6736(12)61684-5)
- Myhrvold, N. P., Baldridge, E., Chan, B., Sivam, D., Freeman, D. L., & Ernest, S. K. M. (2015). An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology*, 96, 3109. <https://doi.org/10.1890/15-0846R.1>
- Mysterud, A., Heylen, D. J., Matthysen, E., Garcia, A. L., Jore, S., & Viljugrein, H. (2019). Lyme neuroborreliosis and bird populations in northern Europe. *Proceedings of the Royal Society B: Biological Sciences*, 286, 20190759. <https://doi.org/10.1098/rspb.2019.0759>
- Nakagawa, S., & Santos, E. S. (2012). Methodological issues and advances in biological meta-analysis. *Evolutionary Ecology*, 26, 1253–1274. <https://doi.org/10.1007/s10682-012-9555-5>
- Newman, E. A., Eisen, L., Eisen, R. J., Fedorova, N., Hasty, J. M., Vaughn, C., & Lane, R. S. (2015). *Borrelia burgdorferi* sensu lato spirochetes in wild birds in northwestern California: Associations with ecological factors, bird behavior and tick infestation. *PLoS One*, 10, e0118146. <https://doi.org/10.1371/journal.pone.0118146>
- Norte, A. C., de Carvalho, I. L., Nuncio, M. S., Ramos, J. A., & Gern, L. (2013). Blackbirds *Turdus merula* as competent reservoirs for *Borrelia turdi* and *Borrelia valaisiana* in Portugal: Evidence from a xenodiagnostic experiment. *Environmental Microbiology Reports*, 5, 604–607.
- Norte, A. C., Margos, G., Becker, N. S., Albino Ramos, J., Nuncio, M. S., Fingerle, V., Araújo, P. M., Adamík, P., Alivizatos, H., Barba, E., Barrientos, R., Cauchard, L., Csörgő, T., Diakou, A., Dingemans, N. J., Doligez, B., Dubiec, A., Eeva, T., Flaisz, B., ... Lopes de Carvalho, I. (2020). Host dispersal shapes the population structure of a tick-borne bacterial pathogen. *Molecular Ecology*, 29, 485–501. <https://doi.org/10.1111/mec.15336>
- O’Keeffe, K. R., Oppler, Z. J., & Brisson, D. (2020). Evolutionary ecology of Lyme *Borrelia*. *Infection, Genetics and Evolution*, 85, 104570. <https://doi.org/10.1016/j.meegid.2020.104570>
- Ogden, N. H., Lindsay, L. R., Hanincová, K., Barker, I. K., Bigras-Poulin, M., Charron, D. F., Heagy, A., Francis, C. M., O’Callaghan, C. J., Schwartz, I., & Thompson, R. A. (2008). Role of migratory birds in introduction and range expansion of *Ixodes scapularis* ticks and of *Borrelia burgdorferi* and *Anaplasma phagocytophilum* in Canada. *Applied and Environmental Microbiology*, 74, 1780–1790. <https://doi.org/10.1128/AEM.01982-07>
- Orme, D. (2013). The caper package: comparative analysis of phylogenetics and evolution in R. R package version, 5. Retrieved from <https://cran.r-project.org/web/packages/caper/vignettes/caper.pdf>
- Ostfeld, R. S., & Brunner, J. L. (2015). Climate change and *Ixodes* tick-borne diseases of humans. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370, 20140051.
- Ostfeld, R. S., Canham, C. D., Oggenfuss, K., Winchcombe, R. J., & Keesing, F. (2006). Climate, deer, rodents, and acorns as determinants of variation in Lyme-disease risk. *PLoS Biology*, 4, e145. <https://doi.org/10.1371/journal.pbio.0040145>
- Ostfeld, R. S., Levi, T., Jolles, A. E., Martin, L. B., Hosseini, P. R., & Keesing, F. (2014). Life history and demographic drivers of reservoir competence for three tick-borne zoonotic pathogens. *PLoS One*, 9, e107387. <https://doi.org/10.1371/journal.pone.0107387>
- Owen, J. C., & Moore, F. R. (2008). Swainson’s thrushes in migratory disposition exhibit reduced immune function. *Journal of Ethology*, 26, 383–388. <https://doi.org/10.1007/s10164-008-0092-1>
- Paradis, E., Claude, J., & Strimmer, K. (2004). APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20, 289–290. <https://doi.org/10.1093/bioinformatics/btg412>

- Plowright, R. K., Becker, D. J., Crowley, D. E., Washburne, A. D., Huang, T., Nameer, P. O., Gurley, E. S., & Han, B. A. (2019). Prioritizing surveillance of Nipah virus in India. *PLoS Neglected Tropical Diseases*, 13, e0007393. <https://doi.org/10.1371/journal.pntd.0007393>
- Plowright, R. K., Becker, D. J., McCallum, H., & Manlove, K. R. (2019). Sampling to elucidate the dynamics of infections in reservoir hosts. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 374, 20180336.
- Plummer, K. E., Siriwardena, G. M., Conway, G. J., Risely, K., & Toms, M. P. (2015). Is supplementary feeding in gardens a driver of evolutionary change in a migratory bird species? *Global Change Biology*, 21, 4353–4363. <https://doi.org/10.1111/gcb.13070>
- Previtali, M. A., Ostfeld, R. S., Keesing, F., Jolles, A. E., Hanselmann, R., & Martin, L. B. (2012). Relationship between pace of life and immune responses in wild rodents. *Oikos*, 121, 1483–1492. <https://doi.org/10.1111/j.1600-0706.2012.020215.x>
- Revell, L. J. (2012). phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, 3, 217–223. <https://doi.org/10.1111/j.2041-210X.2011.00169.x>
- Richter, D., Debski, A., Hubalek, Z., & Matuschka, F.-R. (2011). Absence of Lyme disease spirochetes in larval *Ixodes ricinus* ticks. *Vector-Borne and Zoonotic Diseases*, 12, 21–27.
- Richter, D., Spielman, A., Komar, N., & Matuschka, F. R. (2000). Competence of American robins as reservoir hosts for Lyme disease spirochetes. *Emerging Infectious Diseases*, 6, 133–138. <https://doi.org/10.3201/eid0602.000205>
- Ridgeway, G. (2006). gbm: Generalized boosted regression models. R Package Version, 1. Retrieved from <https://pbil.univ-lyon1.fr/CRAN/web/packages/gbm/vignettes/gbm.pdf>
- Sapolsky, R. M., Romero, L. M., & Munck, A. U. (2000). How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocrine Reviews*, 21, 55–89.
- Saracho Bottero, M. N., Sebastian, P. S., Carvalho, L. A., Claps, L. G., Mastropaolo, M., Mangold, A. J., Venzal, J. M., & Nava, S. (2017). Presence of *Borrelia* in different populations of *Ixodes parvicinus* from northwestern Argentina. *Ticks and Tick-borne Diseases*, 8, 488–493. <https://doi.org/10.1016/j.ttbdis.2017.02.008>
- Schluter, D., Price, T., Mooers, A. Ø., & Ludwig, D. (1997). Likelihood of ancestor states in adaptive radiation. *Evolution*, 51, 1699–1711. <https://doi.org/10.1111/j.1558-5646.1997.tb05095.x>
- Schneider, S. C., Parker, C. M., Miller, J. R., Page Fredericks, L., & Allan, B. F. (2015). Assessing the contribution of songbirds to the movement of ticks and *Borrelia burgdorferi* in the midwestern United States during fall migration. *EcoHealth*, 12, 164–173. <https://doi.org/10.1007/s10393-014-0982-3>
- Schwartz, A. M., Hincley, A. F., Mead, P. S., Hook, S. A., & Kugeler, K. J. (2017). Surveillance for Lyme Disease—United States, 2008–2015. *Morbidity and Mortality Weekly Report (MMWR). Surveillance Summaries*, 66(22), 1–12.
- Sing, T., Sander, O., Beerenwinkel, N., & Lengauer, T. (2005). ROCr: Visualizing classifier performance in R. *Bioinformatics*, 21, 3940–3941. <https://doi.org/10.1093/bioinformatics/bti623>
- Smith, R. P. Jr, Rand, P. W., Lacombe, E. H., Morris, S. R., Holmes, D. W., & Caporale, D. A. (1996). Role of bird migration in the long-distance dispersal of *Ixodes dammini*, the vector of Lyme disease. *Journal of Infectious Diseases*, 174, 221–224. <https://doi.org/10.1093/infdis/174.1.221>
- Sonenshine, D. E., Ratzlaff, R. E., Troyer, J., Demmerle, S., Demmerle, E. R., Austin, W. E., Tan, S., Annis, B. A., & Jenkins, S. (1995). *Borrelia burgdorferi* in eastern Virginia: Comparison between a coastal and inland locality. *The American Journal of Tropical Medicine and Hygiene*, 53, 123–133. <https://doi.org/10.4269/ajtmh.1995.53.123>
- Stearns, S. C. (1983). The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos*, 173–187. <https://doi.org/10.2307/3544261>
- Streicker, D. G., Fenton, A., & Pedersen, A. B. (2013). Differential sources of host species heterogeneity influence the transmission and control of multihost parasites. *Ecology Letters*, 16, 975–984. <https://doi.org/10.1111/ele.12122>
- VanderWaal, K. L., & Ezenwa, V. O. (2016). Heterogeneity in pathogen transmission: Mechanisms and methodology. *Functional Ecology*, 30, 1606–1622. <https://doi.org/10.1111/1365-2435.12645>
- Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, 36, 1–48.
- Vitousek, M. N., Johnson, M. A., Donald, J. W., Francis, C. D., Fuxjager, M. J., Goymann, W., Hau, M., Husak, J. F., Kircher, B. K., Knapp, R., Martin, L. B., Miller, E. T., Schoenle, L. A., Uehling, J. J., & Williams, T. D. (2018). HormoneBase, a population-level database of steroid hormone levels across vertebrates. *Scientific Data*, 5, 180097. <https://doi.org/10.1038/sdata.2018.97>
- Vliet, J. V., Musters, C. J. M., & Keurs, W. J. T. (2009). Changes in migration behaviour of blackbirds *Turdus merula* from the Netherlands. *Bird Study*, 56, 276–281.
- Washburne, A. D., Silverman, J. D., Morton, J. T., Becker, D. J., Crowley, D., Mukherjee, S., David, L. A., & Plowright, R. K. (2019). Phylofactorization: A graph partitioning algorithm to identify phylogenetic scales of ecological data. *Ecological Monographs*, 89, e01353. <https://doi.org/10.1002/ecm.1353>
- Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M., & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, 95, 2027. <https://doi.org/10.1890/13-1917.1>
- Wingfield, J. C., & Sapolsky, R. M. (2003). Reproduction and resistance to stress: When and how. *Journal of Neuroendocrinology*, 15, 711–724. <https://doi.org/10.1046/j.1365-2826.2003.01033.x>
- Wright, S. A., Thompson, M. A., Miller, M. J., Knerl, K. M., Elms, S. L., Karpowicz, J. C., Young, J. F., & Kramer, V. L. (2000). Ecology of *Borrelia burgdorferi* in ticks (Acari: Ixodidae), rodents, and birds in the Sierra Nevada foothills, Placer County, California. *Journal of Medical Entomology*, 37, 909–918.
- Yeh, P. J., & Price, T. D. (2004). Adaptive phenotypic plasticity and the successful colonization of a novel environment. *The American Naturalist*, 164, 531–542. <https://doi.org/10.1086/423825>

BIOSKETCHES

Daniel J. Becker studies the ecology and evolution of infectious disease, with particular interest in how anthropogenic factors affect infection dynamics in wildlife and how competence data can improve reservoir host prediction. **Barbara A. Han** is a disease ecologist at the Cary Institute of Ecosystem Studies, where she applies machine learning and other modelling in the predictive analytics of zoonotic risk.

SUPPORTING INFORMATION

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

How to cite this article: Becker DJ, Han BA. The macroecology and evolution of avian competence for *Borrelia burgdorferi*. *Global Ecol Biogeogr*. 2021;30:710–724. <https://doi.org/10.1111/geb.13256>