Received: 23 February 2021 | Revised: 1 June 2021 | Accepted: 26 July 2021

DOI: 10.1002/eap.2523

ECOLOGICAL APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

ARTICLE

A trait-based framework for predicting foodborne pathogen risk from wild birds

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Abstract

Recent foodborne illness outbreaks have heightened pressures on growers to deter wildlife from farms, jeopardizing conservation efforts. However, it remains unclear which species, particularly birds, pose the greatest risk to food safety. Using >11,000 pathogen tests and 1565 bird surveys covering 139 bird species from across the western United States, we examined the importance of 11 traits in mediating wild bird risk to food safety. We tested whether traits associated with pathogen exposure (e.g., habitat associations, movement, and foraging strategy) and pace-of-life (clutch size and generation length) mediated foodborne pathogen prevalence and proclivities to enter farm fields and defecate on crops. *Campylobacter* spp. were the most prevalent enteric pathogen (8.0%), while *Salmonella* and Shiga-toxin producing *Escherichia coli* (STEC) were rare (0.46% and 0.22% prevalence, respectively). We found that several traits related to pathogen exposure predicted pathogen prevalence. Specifically, *Campylobacter* and STEC-associated virulence genes were more often detected in species associated with cattle feedlots and bird feeders, respectively. *Campylobacter* was also more prevalent in species that consumed plants and had longer generation lengths. We found that species associated with feedlots were more likely to enter fields and defecate on crops. Our results indicated that canopy-foraging insectivores were less likely to deposit foodborne pathogens on crops, suggesting growers may be able to promote pest-eating birds and birds of conservation concern (e.g., via nest boxes) without necessarily compromising food safety. As such, promoting insectivorous birds may represent a win-win-win for bird conservation, crop production, and food safety. Collectively, our results suggest that separating crop production from livestock farming may be the best way to lower food safety risks from birds. More broadly, our trait-based framework suggests a path forward for co-managing

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Funding information
Division of Behavioral and Cognitive Sciences, Grant/Award Number: CNH-1824871; National Institute of Food and Agriculture, Grant/Award Numbers: USDA-NIFA-BcENRE grant 2017-67019-26293, USDA-NIFA-OREI grant 2015-51300-24155

Handling Editor: Paul C. Cross

wildlife conservation and food safety risks in farmlands by providing a strategy for holistically evaluating the food safety risks of wild animals, including under-studied species.

KEYWORDS
Campylobacter spp., feedlot, food safety, *Salmonella* spp., Shiga-toxin producing *Escherichia coli*, species traits, wild birds

INTRODUCTION

Enteric pathogens cause millions of illnesses and hundreds of thousands of deaths worldwide each year (Havelaar et al., 2015). The three most important foodborne bacteria are *Salmonella* spp., *Escherichia coli*, and *Campylobacter* spp., which originate in human, livestock, or wildlife waste (Havelaar et al., 2015). Because wildlife have been implicated in several foodborne illness outbreaks (Angelo et al., 2017; Gardner et al., 2011; Langholz & Jay-Russel, 2013), growers of fresh produce face increasing market and regulatory pressure to prevent wildlife from entering their farms (Baur et al., 2016; Beretti & Stuart, 2008). Wild birds (hereafter, "birds"), in particular, are of great concern because they cannot be easily excluded (Olimpi et al., 2019; Parker et al., 2012; Rivadeneira et al., 2018). As a result, growers are often forced to turn to economically costly (e.g., bird netting or "noise makers") and ecologically costly measures (e.g., removal of natural vegetation) to prevent bird intrusion (Beretti & Stuart, 2008; Karp et al., 2015; Olimpi et al., 2019).

Nonetheless, it remains unclear whether bird intrusion and defecation in farm fields constitutes a meaningful food safety risk (Smith et al., 2020c). Only one outbreak has been attributed to birds: a campylobacteriosis outbreak traced to migrating Sandhill Crane (*Grus canadensis*) intrusion in pea fields in Alaska (Gardner et al., 2011). Moreover, prior efforts to quantify enteric pathogen prevalence in birds have largely focused on only a few nonnative and native synanthropic (i.e., human-associated) bird species. For example, Smith et al. (2020c) found that in only 5 of 431 (1.2%) North American breeding bird species examined were there sufficient data to precisely calculate *Salmonella* spp., pathogenic *E. coli*, and *Campylobacter* spp. prevalence, leaving great uncertainty around pathogen prevalence in the vast majority of North American birds.

The prevalence of pathogens in these commonly studied, synanthropic species is likely much higher than in other bird species that frequent farm fields, based on current limited evidence (Smith et al., 2020a, 2020c). One reason is that strong associations with human habitats may increase the exposure of synanthropic species to foodborne pathogens (Gibb et al., 2020; Karp et al., 2015; Smith et al., 2020a, 2020c). For example, birds may be exposed to pathogens in livestock operations or through contact with human wastewater or landfills (Butterfield et al., 1983; Hald et al., 2016). A second reason is that synanthropic species sometimes invest in rapid growth and reproduction, which may affect immune function (Lee, 2006; Ostfeld et al., 2014), and has been hypothesized to cause them to have high reservoir competence (i.e., the "ecoimmunological pace of life hypothesis"; Ostfeld et al., 2014). Correspondingly, prior analyses estimate much higher prevalence of pathogens across samples collected directly from a few, mostly synanthropic, bird species relative to feces from a broader diversity of bird species collected directly from farm fields (e.g., 27% vs. 13.1% for *Campylobacter* spp., 20% vs. 0% for pathogenic *E. coli*, and 6.4% vs. 0.2% for *Salmonella* spp.; Smith et al., 2020a, 2020c).

To cause foodborne illness, birds must not only carry a pathogen but also defecate in production areas (Smith et al., 2020a, 2020c). However, very few studies link estimates of pathogen prevalence among birds with their proclivities to enter and defecate in farm fields (but see Smith et al., 2020a). Smith et al. (2020c) found that only 3.3% of studies included in their meta-analysis reported data across the spillover cycle (i.e., from pathogen exposure to contact with food to transmission to humans or other hosts). As such, growers cannot reliably determine which bird species pose significant food safety risks and should be deterred from farm fields vs. species that are unlikely to spread pathogens. This is important because birds provide economically important ecosystem services to agriculture, such as pest control (Karp et al., 2013; Kross et al., 2012). Additionally, farms represent vital habitat for many species of conservation concern (Donald et al., 2001; Stanton et al., 2018), which is critical given that over 3 billion birds have been lost from North America alone over the past several decades (Rosenberg et al., 2019).

Ecologists often use functional traits to explain species' effects on ecosystems functions and extrapolate potential impacts of understudied species (McGill et al., 2006; Wood et al., 2015), yet this approach has not previously been applied to predicting food safety risks from wild birds. Species traits can also elucidate species' roles in pathogen transmission, as traits can influence species' exposure to pathogens as well as their immune system function (Daversa et al., 2017; Gibb et al., 2020; Ostfeld et al., 2014; Smith et al., 2020a, 2020c). For example, birds that use bird feeders are known to spread *Mycoplasma* and *Salmonella* spp. (CDC, 2021; Daoust et al., 2000; Hartup et al., 1992). Traits may also prove useful for understanding which species are most likely to enter and defecate in farm fields (Flynn et al., 2009; Newbold et al., 2013). For example, traits related to where species forage may predict the ability of birds to use crop fields: birds that usually forage on the ground or in herbaceous vegetation may also regularly forage in produce fields whereas canopy-foraging birds may behaviorally exclude themselves from fields (Flynn et al., 2009; Smith et al., 2020b). When traits facilitate both high pathogen prevalence and high crop contact, pathogens can "flow through" and spillover from reservoir hosts to recipient hosts (i.e., birds to humans; Figure 1; Gibb et al., 2020; Plowright et al., 2017; Smith et al., 2020c). By identifying traits associated with higher food safety risks, traits can be used to classify species as high-to-low risk along prevalence and crop contact axes, which sparse data have previously precluded (Figure 2).

Here, we couple data on foodborne pathogen prevalence in birds with point-count surveys to assess whether 11 species traits (Appendix S1: Table S1) exacerbate or mitigate food safety risks from birds (Figure 1). Then, we use our trait-based analyses to classify species as high-to-low risk along prevalence and crop contact axes (Figure 2). We organized our analyses around three overarching questions. First, what traits are associated with higher *Campylobacter* spp., *Salmonella* spp., and Shiga-toxin producing *E. coli* (STEC) prevalence in birds? Because STEC was so rare (0.22%), we also examined relationships between traits and carriage of STEC-associated virulence genes. We hypothesized that pathogens would occur more frequently in species with traits that increase pathogen exposure potential (e.g., regular use of livestock feedlots) and traits associated with a fast pace-of-life (e.g., larger clutch sizes; see Appendix S1: Table S1 for all hypotheses). Second, we asked which traits increase the probability that birds enter and then defecate

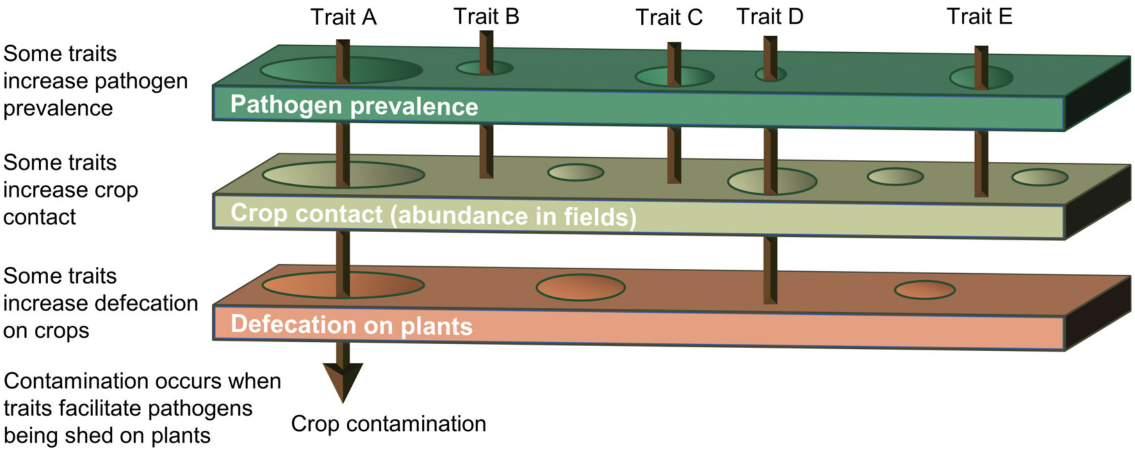

FIGURE 1 Conceptual diagram of how species traits (e.g., synanthropy and generation length) mediate food safety risks associated with wild birds. A bird host must have traits that facilitate pathogen acquisition and shedding (simplified as pathogen prevalence in the diagram) and traits that facilitate use of crop fields. Crop contamination and subsequent spillover can only occur if the trait facilitates both and species defecate in crops. Diagram modified from Plowright et al. (2017)

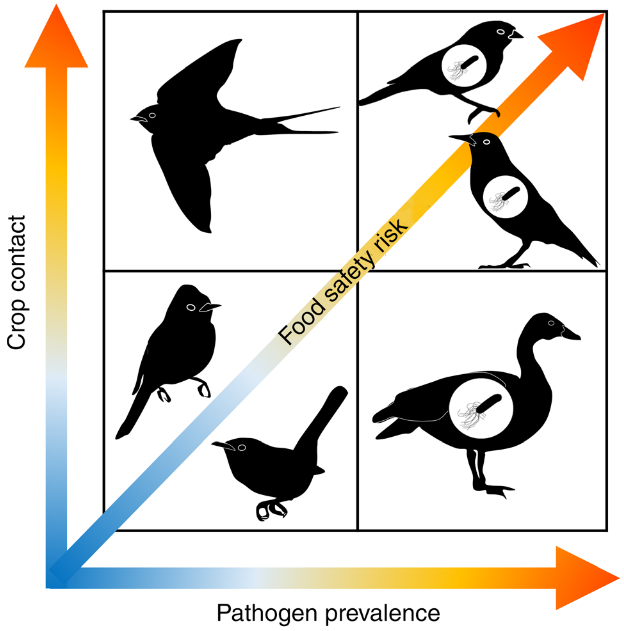

FIGURE 2 The risk that birds pose to food safety can be depicted along two axes: how frequently the pathogen is found in the species (x-axis) and how often birds contact crops (y-axis). Bird silhouettes represent types of birds hypothesized to fall into each quadrant

in crop fields? We predicted that crop contact and defecation rates would increase in species that forage in lower vegetation strata resembling crop fields (i.e., the ground or understory but not the canopy) and/or regularly occupy other anthropogenic habitats (e.g., feedlots; see Appendix S1: Table S2 for all hypotheses). Finally, using the best-supported models from questions 1 and 2 above, which species present the highest food safety risks?

METHODS

To answer our questions, we assembled the most comprehensive database to date on prevalence of *Campylobacter* spp., *Salmonella* spp., and STEC and carriage of STEC-associated virulence genes in birds from produce systems (i.e., farms that grow fruits and vegetables) across the western United States (Figure 3a; Appendix S1: Table S3). We then collected data on species' crop contact rates (i.e., relative abundance and densities in crop fields) from point-count surveys conducted across 350 sites in some of the same systems and fecal contact rates (Figure 3b; Appendix S1: Table S4; Smith et al. 2020a, 2020b, 2021). We compiled a database of species traits predicted to impact pathogen prevalence and/or crop contact (Appendix S1: Tables S1 and S2). We then used Akaike information criterion corrected for small sample sizes (AIC$_c$) to select models (Appendix S1: Table S5; Burnham & Anderson, 2002) to identify which traits were the most important in predicting pathogen prevalence and crop contact. Finally, we combined this information to predict pathogen prevalence and contact rates to classify species as high to low risk along prevalence and crop contact axes.

Data acquisition

We compiled enteric pathogen prevalence data from studies that tested for *Campylobacter* spp., *Salmonella* spp., and/or STEC: (1) in at least five species of free-ranging birds (e.g., no single species studies and no captive birds), (2) using feces and/or cloacal swabs (e.g., no necropsy studies), and (3) from samples collected on farms that grow produce in the United States. We omitted trace-back studies investigating particular outbreaks because they would inflate apparent prevalence (e.g., Gardner et al. [2011], who investigated a *Campylobacter* outbreak in Alaska). We began by searching the reference list of the recent meta-analysis of foodborne pathogen prevalence in North American breeding birds by Smith et al. (2020c) for suitable studies, then expanded their list to include several as-of-then unpublished studies and gray literature, ultimately yielding pathogen data from five studies (Figure 3a; see Appendix S1: Table S3 for included study meta-data). Three of the five studies are fully published (Navarro-Gonzalez et al., 2020; Rivadeneira et al., 2016; Smith et al., 2020a). One study was previously unpublished (Olimpi et al. sub-data in Smith et al., 2021). Finally, we used data from a Center for Produce Safety final grant report (Gordus et al., 2011) that is partially published in Cooley et al. (2007) and Gorski et al. (2011). Published studies focused on reporting pathogen prevalence and possible transmission across wildlife and in the environment (Cooley et al., 2007; Gorski et al., 2011), prevalence in a variety of bird species sampled across seasons (Navarro-Gonzalez et al., 2020), or identifying landscape/farm-level pathogen risk factors (Rivadeneira et al., 2016; Smith et al., 2020a).

Studies that tested for STEC were diverse in methodology (Appendix S1: Table S3). Three studies performed the necessary steps for bacterial culture, isolation, and identification, then confirmed presumptive colonies by PCR. In contrast, two studies directly tested feces for STEC-associated virulence genes by extracting DNA and then using PCR but did not culture for bacteria first. Due to diverse methodologies, we considered samples to be positive for STEC if *stx*1 and/or *stx*2 (Shiga-toxin producing genes) were detected. Because these genes were rarely detected (0.22% of samples), we conducted additional analyses on data from the PCR-only studies, counting

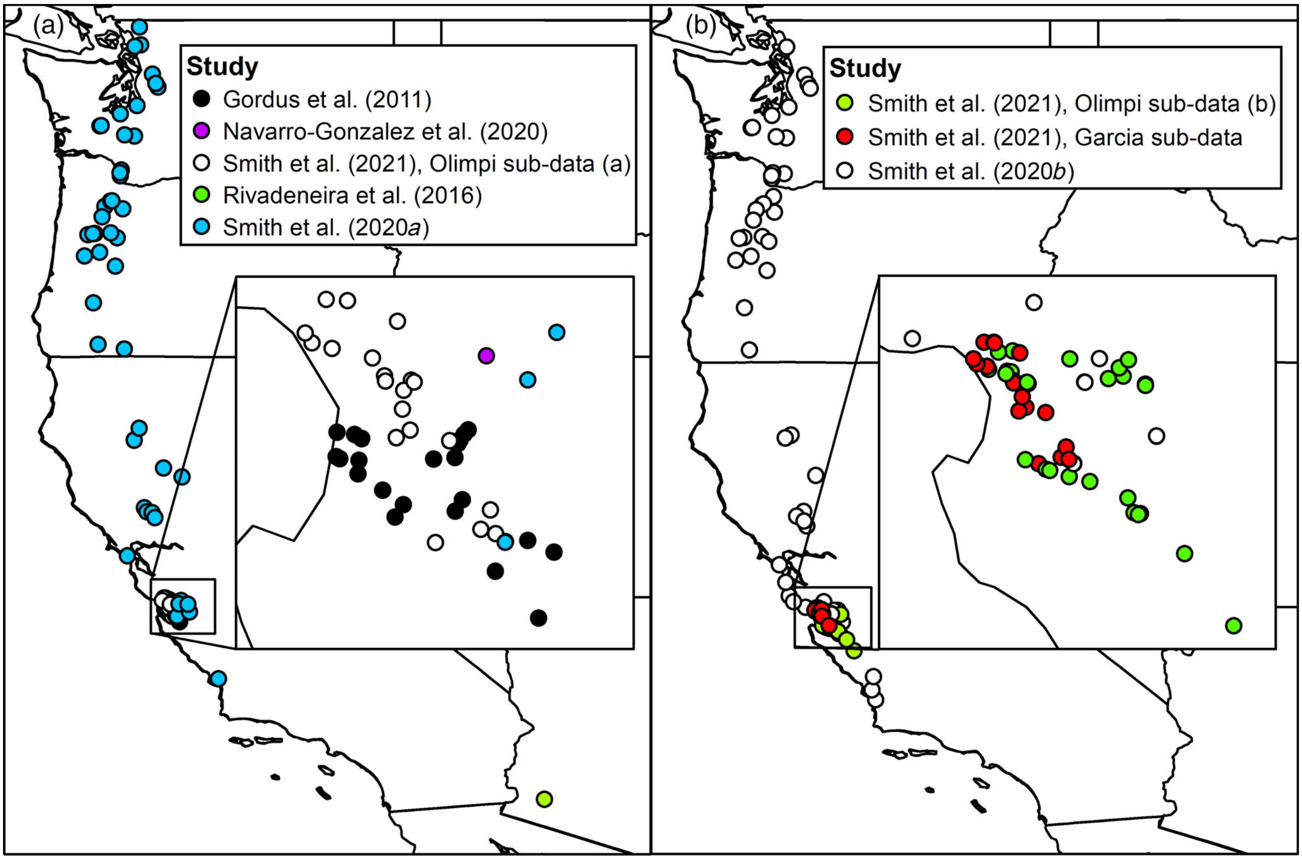

FIGURE 3 Map showing farm locations by study. (a) Studies included in pathogen database. (b) Studies included in point-count database

samples as positive if any proven or putative STEC-associated virulence gene(s) was/were detected (referred to as "STEC-associated virulence genes" for simplicity). The interest of this additional analysis resides in potential for horizontal transmission of virulence genes between *E. coli* strains (Bryan et al., 2015). Thus, from a broader public health perspective, it is important to know whether birds frequently carry *E. coli* possessing any virulence factor (sensu lato) typically found in STEC. We note that the bacteria referred to here as positive for STEC-associated virulence genes are not necessarily pathogenic to humans.

Second, we combined bird point-count data collected by the authors in three prior projects to estimate bird abundance in crop fields ("crop contact rates"; Figure 3b; see Appendix S1: Table S4 for included study meta-data. Briefly, Smith et al. (2020b, 2021) conducted 100-m radius, 10-minute point-count surveys during the breeding season twice per year over 2 yr on 52 highly diversified farms across the U.S. states of Washington, Oregon, and California. The other two projects (Olimpi et al. and Garcia et al. sub-data published in Smith et al., 2021) each conducted 50-m radius, 10-minute point-count surveys during the breeding season three times per year over 2 yr across 20 organic farms in the Central Coast of California. Five of their farms overlapped and were only counted once in analyses. We only used data from survey points conducted in crop fields, and birds were only counted as "contacts" if they were in fields (we included aerial foraging as contacts but excluded flyovers). We excluded tree fruit contacts because of the structural similarity to non-crop trees and due to the focus of included studies on leafy greens, brassicas, and strawberries.

Finally, to identify which species were most likely to defecate in crop fields, we leveraged a data set of 1215 fecal samples collected by Smith et al. (2020a) from brassica fields and food wash/packing areas across 37 farms in Washington, Oregon, and California, USA. These samples were subsequently attributed to bird species through COI gene testing. Smith et al. (2020a) determined the bird species responsible for defecating 463 of the 1215 (38.1%) fecal samples, which were traced back to 35 species (Appendix S1: Figure S1). Here, we examined traits that predicted the number of feces identified back to a bird species from the entire bird species pool ($n = 106$) observed while conducting point counts at the collection locations.

Although we sought studies on foodborne pathogen prevalence in birds from any farms that grow produce throughout the United States, we only found data collected from the West Coast that met our inclusion criteria (Figure 3). Briefly, studies in our analysis surveyed farms that spanned a gradient of types and diversity of crops grown, sizes, and landscape contexts. For example, Smith et al. (2020a, 2020b) surveyed highly diversified farms ranging from 0.38 to 272.2 ha that spanned a wide range of landscape contexts from 0% to 100% seminatural. Similarly, one of the previously unpublished studies (Olimpi et al. sub-data in Smith et al., 2021) surveyed farms ranging from 1.3 to 100.3 ha, spanning a wide range of landscape contexts from 0% to 85.4% seminatural. Farms ranged from highly diversified with many crop types to strawberry monocultures. The farm and regional contexts for included studies are described in full detail in Appendix S1: Tables S3 and S4.

Species traits

We took a barriers-to-spillover approach, meaning that we considered how species traits influence alignment of a series of hierarchical barriers that must align to enable transmission of foodborne pathogens from birds to crops (Figure 1; Plowright et al., 2017). Thus, we first generated a priori hypotheses about traits that might affect foodborne pathogen prevalence in birds (Appendix S1: Table S1). We then examined how the same traits we hypothesized would impact foodborne pathogen prevalence impacted the "downstream layers" of contact with crops and fecal deposition in fields (Figure 1). Our hypotheses broadly covered aspects of exposure/habitat preferences (diet guild, foraging strata, migratory strategy, sociality, high use of bird feeders, feedlot association, synanthropy, large daily movements [proxied by hand-wing index due to limited data available quantifying home range size or actual daily movement; Sheard et al., 2020]), pace of life (clutch size and generation length), and nonnative status (i.e., nonnative birds possess several traits that may increase reservoir competence; Altizer et al., 2011; Daversa et al., 2017; Ostfeld et al., 2014; Smith et al., 2020a, 2020c; Waldenstrom et al., 2002).

We first sought existing databases with relevant traits and were successful for diet guild, foraging strata, hand-wing index, and generation length (Barnagaud et al., 2017; Bird et al., 2020; De Graaf et al., 1985; Sheard et al., 2020; Smith et al., 2020b; Wilman et al., 2014). We did not find robust estimates for several traits of interest (migratory strategy in the study region, sociality/gregariousness, clutch size, bird feeder use, feedlot association, and synanthropy). For these traits, we generated novel databases from secondary and primary sources. We used Birds of the World Online (Billerman et al., 2020) to classify mean clutch size and migratory strategy for populations in our study region and sociality during the breeding season (i.e., when most produce is grown). We classified birds as highly associated with bird feeders if they were on one or more Project FeederWatch top 25 lists for Washington, Oregon, and California for 2016–2017 (https://feederwatch.org/pfw/top25).

To classify feedlot association (highly associated, somewhat associated, not associated), we conducted a literature review, searched Birds of the World Online (Billerman et al., 2020), and consulted eBird checklists (www.eBird.org). Because of discrepancies in data availability, methods, and reporting, we used the review to guide expert elicitation because we were unable to use specific numerical guidelines to classify species (see Appendix S1: Section S1 and Smith et al., 2021). To quantify synanthropy, we extracted citizen-science data from eBird and filtered checklists according to "best practices" (Strimas-Mackey et al., 2020). We used the 500-m resolution MODIS MCD12Q1 v006 land cover product to calculate the proportion of anthropogenic land cover within a 700-m radius of each checklist location (Friedl & Sulla-Menashe, 2015). We then used generalized additive models to quantify species' responses to anthropogenic land cover while accounting for nuisance variables and spatial autocorrelation (Wood, 2006). We first modeled the effect of each type of natural and anthropogenic habitat on occupancy and then used our model to identify the most preferred natural habitat type. The synanthropy index was calculated as the relative log-fold increase (or decrease) of occurrence probability in anthropogenic habitat vs. the natural habitat where the species was most abundant. Specifically, this quantity was calculated as the slope of a species' response to anthropogenic land covers minus the slope of their response to their most preferred "natural" land cover (see Appendix S1: Section S1 and Smith et al., 2021 for full details).

Our efforts resulted in 18 traits that we then narrowed down to 11 to represent key hypotheses. We selected traits that were least correlated with metrics representing other hypotheses by examining pairwise correlations. For example, mass, wing chord, and hand-wing index may all represent dispersal ability (Sheard et al., 2020; Sutherland et al., 2000), but mass is also highly correlated with generation length (Bird et al., 2020). Therefore, we only used hand-wing index and generation length since they were the least correlated with each other. Nevertheless, some traits remained correlated after our selection (the highest

Pearson's correlation for traits used in models was 0.48 between synanthropy and bird feeder association; Appendix S1: Figure S2).

Statistical analysis

We modeled pathogen prevalence (*Campylobacter* spp., *Salmonella* spp., and STEC) and carriage of STEC-associated virulence genes as a function of bird traits using generalized linear mixed-effects models (GLMMs) with a binomial error distribution and logit link function (glmmTMB package in R; Brooks et al., 2017). Additionally, we used GLMMs to examine the impact of species traits on (1) the total number of individuals detected in crops within each point using a negative binomial distribution to account for overdispersion and (2) the total number of environmental fecal samples attributed to each species via COI gene testing, again using a negative binomial distribution to account for overdispersion. We modeled (1) using both the relative abundance (i.e., number of individuals counted in crop fields) of species across all sites within each study as well as their relative abundances per survey point (see Appendix S1: Section S1).

We first determined the optimal random effects structure for each of the seven response variables described (Appendix S1: Table S5). To account for variation in methods between studies, we included "study" as a random effect in models using data from three or more studies and as a fixed effect in models using data from two studies. To account for multiple bird surveys on the same farm and multiple visits to each point-count location, we included point nested within farm in analyses of crop contact per survey point. Finally, to account for non-independence in phylogenetic relationships, we also included order, family, genus, and species as random effects. Including order, family, and genus, rather than a continuous measure of phylogenetic relatedness, allowed us to identify the taxonomic level of non-independence. Specifically, we constructed models with all combinations of order, family, genus, and species, and then used AIC to determine which taxonomic levels to include. Our final candidate model sets included a random effect of family for all response variables except *Campylobacter* spp. (genus only) and crop contact (both family and species).

After determining the optimal random effects structures, we constructed 44 candidate models that tested the relative importance of each of the 11 traits for the seven response variables (Appendix S1: Table S5). The 44 models included the null model, 11 models that tested a single trait, 16 additive models that tested one exposure and one pace of life trait, and 16 models that tested for an interaction between one exposure and one pace of life trait. All models that included hand-wing index also included an intercept for aerial foraging to account for the higher hand-wing index observed in species specialized in foraging in flight (Sheard et al., 2020). Continuous physiological traits were log transformed to reduce leverage of high values.

We then ranked models based on $\mathrm{AIC_c}$ and identified those that were most supported ($\Delta\mathrm{AIC_c} < 2.0$; Burnham & Anderson, 2002). We assessed if variables improved model fit using likelihood ratio tests for all models with weights >0.05. We assessed multicollinearity for candidate models using the performance package in R (Ludecke et al., 2020) and found it not to be an issue in our models ($\mathrm{VIF} < 5$). We used generalized Tukey HSD tests in the multcomp package in R (Hothorn et al., 2008) to examine differences in categorical predictor variables that had high support (were included in models with <2 $\Delta\mathrm{AIC_c}$) and improved model fit (likelihood ratio tests). We predicted pathogen prevalence and crop contact rates per species from the best-supported models using the predict() function in R, then model-averaged predictions. Finally, we reran models described above to determine if landscape context influenced conclusions, but our conclusions were qualitatively similar when including the percent seminatural habitat within 1000 m (see Appendix S1: Section S1 and Tables S6–S8 for full details). We found no evidence for spatial autocorrelation using Moran's *I*.

RESULTS

Foodborne pathogen prevalence

Our final data sets included 139 bird species (Appendix S1: Figure S1; $n = 94$ in pathogen database; $n = 130$ in point count database; $n = 35$ in environmental fecal sample database) from produce farms (Figure 3). We found an overall *Campylobacter* spp. prevalence of 8.0% ($n = 3023$ individuals, 80 species, 68 sites, and 2 studies). *Campylobacter coli*, *Campylobacter jejuni*, and *Campylobacter fetus* subsp. *fetus* were detected in 3.3%, 1.9%, and 1.4% of the samples, respectively. We found a very low overall prevalence of *Salmonella* spp. (0.46%; $n = 4093$ individuals, 93 species, 92 sites, and 5 studies) and STEC (0.22%; $n = 4693$ individuals, 94 species, 92 sites, and 5 studies). Both proven and putative STEC virulence genes were generally rarely detected: 0.22% for *eaeA* ($n = 3250$), 0.06% for *stx*1 ($n = 3250$), 0.06% for *stx2* ($n = 3250$), 0.65% for *hlyA* ($n = 3250$), and 8.8% for *saa* ($n = 3016$). Two studies reported testing for *stx*1 and *stx*2, among other genes above ($n = 1443$ samples) but did not report gene detection rates so are not included in the preceding gene carriage summaries.

Traits that predict pathogen prevalence

Campylobacter spp. prevalence

Species that primarily consume plants (i.e., herbivores, granivores, nectarivores, and frugivores) had higher *Campylobacter* spp. prevalence than omnivorous or insectivorous species (Figure 4a; Appendix S1: Tables S9 and S10). Species that were highly feedlot associated had higher *Campylobacter* spp. prevalence than species that were not feedlot associated or somewhat associated (Figure 4b; Appendix S1: Table S11). Finally, species with longer generation lengths had higher *Campylobacter* spp. prevalence (Figure 4c). Extrapolated *Campylobacter* spp. prevalence from our traits-based models ranged from 2.11% (Savannah Sparrow, *Passerculus sandwichensis*) to 54.0% (Cedar Waxwing, *Bombycilla cedrorum*). The next highest predicted *Campylobacter* spp. prevalence was for Canada Goose (46.7%; *Branta canadensis*) and Brown-headed Cowbird (44.0%; *Molothrus ater*).

Salmonella spp. prevalence

Resident species had higher *Salmonella* spp. prevalence than migratory species, but *Salmonella* spp. prevalence did not differ between partially migratory species (facultative migrants and species that migrate in part of the study region) and other groups (Figure 4d; Appendix S1: Tables S12 and S13). Additionally, species with smaller hand-wing indices (a proxy for lower daily movements and dispersal ability) had higher *Salmonella* spp. prevalence, though the effect was weak (Appendix S1: Figure S3). Extrapolated *Salmonella* spp. prevalence from our traits-based models ranged from 0.002% (Rufous Hummingbird, *Selasphorus rufus*) to 17.1% (Common Raven, *Corvus corax*). The next highest predicted *Salmonella* spp. prevalence was for Steller's Jay (6.91%; *Cyanocitta stelleri*) and California Scrub-Jay (5.15%; *Aphelocoma californica*).

STEC prevalence and carriage of STEC-associated virulence genes

The null model containing only random effects was the best predictor of STEC prevalence (Appendix S1: Table S14), likely because the *stx*1 and *stx*2 genes were so rarely detected in birds (0.22% prevalence). When examining samples with any STEC-associated virulence gene(s) (i.e., samples with one or more proven or putative virulence genes detected), large clutch sizes (Figure 4e) and high bird feeder association (Figure 4f) were associated with increased carriage (Appendix S1: Table S15). Extrapolated STEC-associated virulence gene prevalence from our traits-based models ranged from 1.10% (Horned Lark, *Eremophila alpestris*) to 24.4% (Black-capped Chickadee, *Poecile atricapillus*). The next highest predicted STEC-associated virulence gene prevalence was for Red-breasted Nuthatch (21.4%; *Sitta canadensis*) and Golden-crowned Sparrow (17.0%; *Zonotrichia atricapilla*).

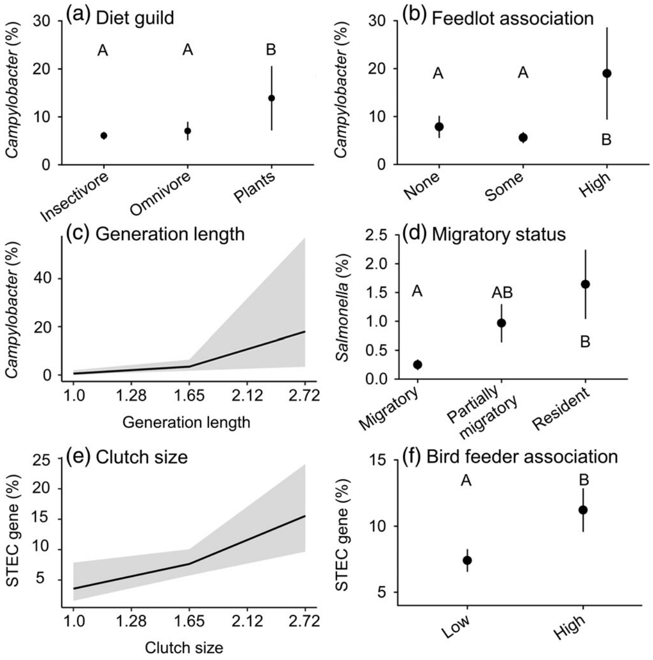

FIGURE 4 Effects of species traits on pathogen prevalence. (a–c) *Campylobacter* spp. prevalence is higher in species that (a) primarily consume plants (i.e., herbivores, nectarivores, frugivores, and granivores), (b) have high feedlot associations, and (c) have longer generation lengths. (d) *Salmonella* spp. prevalence is higher in resident species than in migratory species. (e, f) Carriage of Shiga-toxin producing *E. coli* (STEC) associated virulence genes (e) is higher in species with larger clutch sizes and (f) in species on the FeederWatch top 25 lists for one of the states in the study region (Washington, Oregon, and California). Different letters indicate significant differences between groups from Tukey HSD pairwise comparisons. (a, b, d, f) show means ±95% CI by group. (c, e) Gray area shows ±95% confidence intervals

Traits that predict crop contact

Crop contact from point count surveys

Our point count database included 18,955 individual birds from 130 species across three studies. Of these, we observed 6177 individuals from 77 species in crop fields, with Brewer's Blackbird (*Euphagus cyanocephalus*, $n = 1148$), Barn Swallow (*Hirundo rustica*, $n = 617$), and European Starling (*Sturnus vulgaris*, $n = 524$) being most abundant (Appendix S1: Figure S1). When examining relative abundance across sites (i.e., total potential contribution to pathogen load across the system), species with some or high feedlot association were more abundant in crop fields than species that were not associated with feedlots (Appendix S1: Tables S16 and S17, Figure S4). When examining birds per survey point (i.e., potential contribution to pathogen load in an average field), feedlot association was again an important predictor of greater bird densities in crops (Figure 5a; Appendix S1: Tables S18 and S19). Aerial, ground, and understory foragers were also found in greater densities in crops than bird species that primarily forage in upper vegetation strata (Figure 5b; Appendix S1: Table S20).

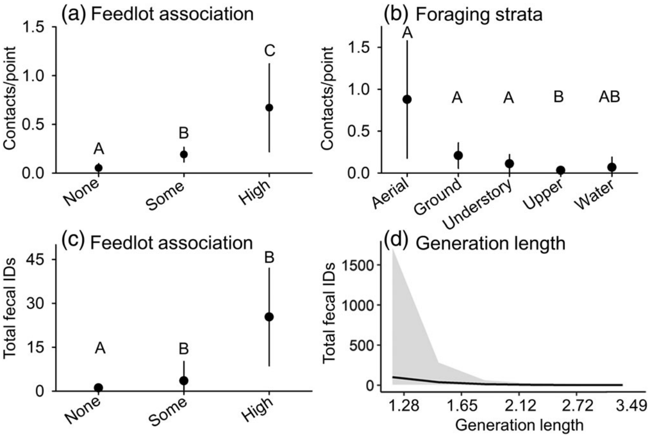

FIGURE 5 Effects of species traits on crop contact (number of individuals counted in crop fields) and defecation rates. (a, b) Crop contacts per survey are higher in species that (a) have some to high feedlot association and (b) primarily forage aerially, on the ground, and in the understory. Crop contacts are lowest in species that primarily forage in the upper strata. (c, d) Total feces in production areas linked to species identities through COI gene testing is higher in species with (c) some to high feedlot association and (d) shorter generation lengths. Total feces are the total traced back to a species across all farms. (a–c) Different letters above bars indicate significant differences between groups from Tukey HSD pairwise comparisons and show means ±95% CI by group. (d) Gray area shows ±95% confidence intervals

Traits that predict fecal abundance in production areas

White-crowned Sparrows (*Zonotrichia leucophrys*; $n = 90$), Song Sparrows (*Melospiza melodia*; $n = 70$), and House Sparrows (*Passer domesticus*, $n = 60$) were the most frequently identified species through COI gene testing of fecal samples collected from production areas (brassica fields and food wash/packing stations). Fecal samples were more often traced back to species that were highly or somewhat feedlot associated (Figure 5c; Appendix S1: Tables S21 and S22) and to species with shorter generation lengths (Figure 5d). The total number of contacts per species (in point count surveys from collection locations) was positively correlated with the number of feces traced back to that species through COI gene testing (Appendix S1: Figure S5; Pearson's $R^2 = 0.41$, $P = 0.0017$). However, deviations occurred wherein some species appeared to deposit feces in production areas infrequently (based on COI gene testing) despite often being observed to contact production areas during point-count surveys (e.g., Barn Swallows). In contrast, other species appeared to defecate at disproportionately high rates relative to their observed production area contacts in point-count surveys (e.g., White-crowned Sparrows).

Species likely to pose the greatest risk to food safety

To determine aggregate food safety risks associated with birds, we used our best-supported models to predict each species' prevalence of *Campylobacter* spp., prevalence of *Salmonella* spp., and carriage of STEC-associated virulence genes, as well as how often each species contacted crops (using the point count survey analysis; Figure 6; Appendix S1: Figures S6 and S7; Smith et al., 2021). In contrast to our hypotheses (Figure 2), no birds were predicted to have both high prevalence and high contact rates for any of the pathogens examined (i.e., top right quadrants of Figure 6). There were no significant correlations between a species' predicted prevalence of *Campylobacter* spp., prevalence of *Salmonella* spp., or carriage of STEC-associated virulence genes and its predicted crop contact rates (Appendix S1: Figure S8). For example, our models predicted that Cedar Waxwings (54%), Canada Geese (47%), Brown-headed Cowbirds (44%), Eurasian-Collared Doves (*Streptopelia decaocto*, 26%), and House Sparrows (20%) are likely to have the highest *Campylobacter* spp. prevalence (Figure 6a). In contrast, swallows (family Hirundinidae), native blackbirds (family Icteridae), and European Starlings were predicted to enter farm fields most commonly (Figure 6a). Nonetheless, species with high feedlot associations fell at the forefront of the contact-by-prevalence continuum (Figures 4b and 5a,c), suggesting high feedlot association is likely to carry the greatest food safety risks. On the other hand, many species commonly found around farms were predicted to rarely enter farm fields

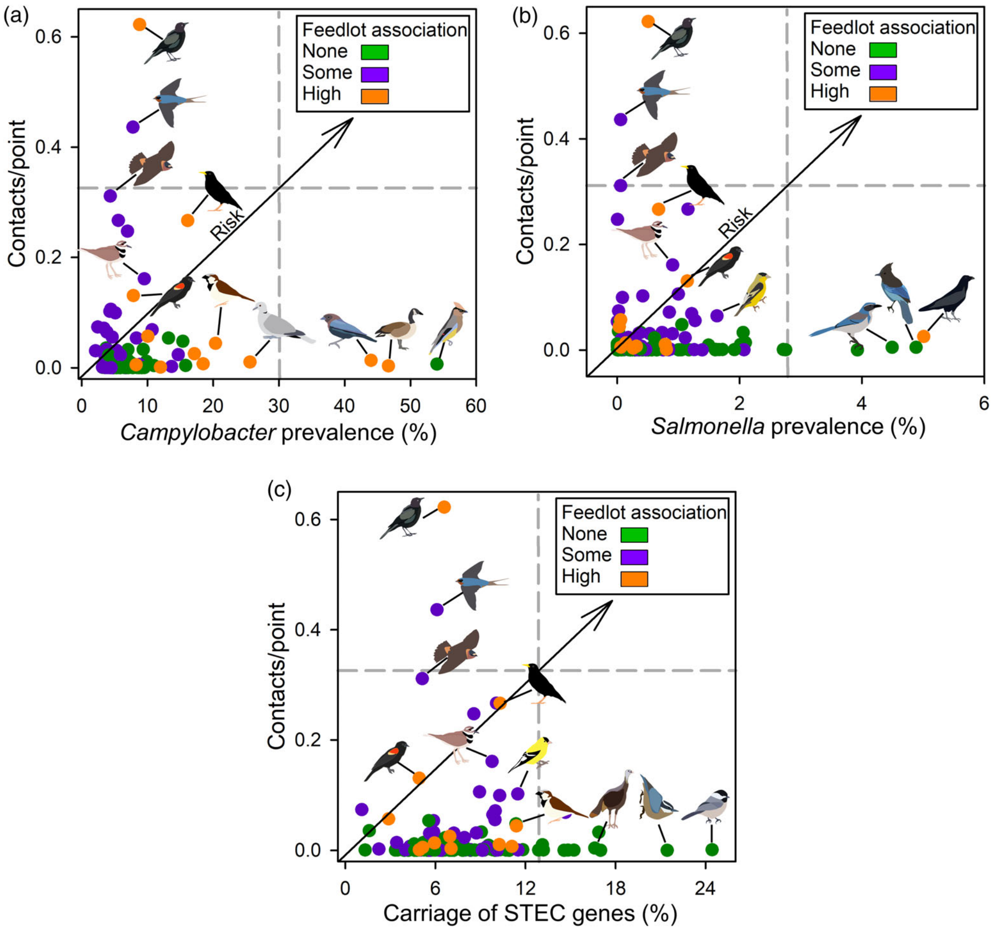

FIGURE 6 Predicted risk of species to food safety along foodborne pathogen prevalence axes (x) and crop contact axes (y). Color indicates feedlot association. The x-axis displays predicted (a) *Campylobacter* spp. prevalence, (b) *Salmonella* spp. prevalence, and (c) carriage of STEC-associated virulence genes. Birds displayed next to their point from top left to bottom right: (a) Brewer's Blackbird (*Euphagus cyanocephalus*), Barn Swallow (*Hirundo rustica*), Cliff Swallow (*Petrochelidon pyrrhonota*), European Starling (*Sturnus vulgaris*), Killdeer (*Charadrius vociferus*), Red-winged Blackbird (*Agelaius phoeniceus*), House Sparrow (*Passer domesticus*), Eurasian Collared-Dove (*Streptopelia decaocto*), Brown-headed Cowbird (*Molothrus ater*), Canada Goose (*Branta canadensis*), and Cedar Waxwing (*Bombycilla cedrorum*). (b) See (a) and also displays Lesser Goldfinch (*Spinus psaltria*), California Scrub-Jay (*Aphelocoma californica*), Steller's Jay (*Cyanocitta stelleri*), and Common Raven (*Corvus corax*). (c) See (a) and (b) and also shows American Goldfinch (*Spinus tristis*), Wild Turkey (*Meleagris gallopavo*), Red-breasted Nuthatch (*Sitta canadensis*), and Black-capped Chickadee (*Poecile atricapillus*). See Appendix S1: Figure S6 for a version with four-letter species codes

while also having low pathogen prevalence (e.g., Yellow Warbler, *Setophaga petechia*, and Northern Flicker, *Colaptes auratus*; Figure 6).

DISCUSSION

Our work demonstrates that traits mediate food safety risks and can be used to extrapolate risk across diverse bird species and farm bird communities, which expensive pathogen testing has previously precluded (Smith et al., 2020c). Overall, *Campylobacter* spp. were the most frequently detected enteric pathogen in birds (8.0%, $n = 3023$), whereas *Salmonella* spp. and STEC were rare (0.46% and 0.22%, respectively). Although Shiga-toxin producing genes (*stx*1 and/or *stx*2) were seldom detected in our meta-analysis, other STEC-associated virulence genes were more frequently detected, with *saa* being the most common (8.8%, $n = 3016$). In combination with Shiga toxins, other virulence factors contribute to pathogenesis, namely adhesins that enable the adherence and colonization of the human gut by STEC, typically *eae*, or in atypical strains, *saa* (Paton et al., 2001; Paton & Paton, 2002). Carriage of bacteria that harbor STEC-associated accessory virulence genes does not mean that birds are a direct, imminent risk to food safety. Still, horizontal gene transfer of virulence genes from bacteria carried by birds to human pathogens could contribute to the emergence of virulent strains, as is the case in other animal reservoirs (Karmali, 2018).

The low pathogen prevalences reported here contrast with some prior studies (Smith et al., 2020c). For example, Kirk et al. (2002) found a *Salmonella* spp. prevalence of 3.1% ($n = 451$) for House Sparrows and 3.2% ($n = 95$) for Brown-headed Cowbirds in California dairies. Similarly, Monaghan et al. (1985) estimated 9.6% ($n = 2021$) of Herring Gulls (*Larus argentatus*) carry *Salmonella* spp. in refuse sites. This suggests that the disproportionate focus of these prior studies on synanthropic bird species in urban or feedlot settings may have inflated the perception that birds are likely to cause STEC and *Salmonella* outbreaks when found on produce farms (Olimpi et al., 2019; Smith et al., 2020c).

Traits mediate pathogen prevalence and carriage of STEC-associated virulence genes

Exposure traits

Traits related to pathogen exposure were generally the most important mediators of pathogen prevalence and gene carriage. For example, we found higher prevalence of *Campylobacter* spp. and carriage of STEC-associated virulence genes in species associated with feedlots and bird feeders, respectively. Bird feeders have been implicated in transmission of other pathogens in the past. For example, fecal material on bird feeders may transmit *Salmonella* spp. between songbirds and cause mass mortality events, especially during harsh winters, as seen in a recent large-scale outbreak (CDC, 2021; Daoust et al., 2000). Additionally, our finding that feedlot association increases *Campylobacter* spp. prevalence is unsurprising given that multiple studies have noted that food safety risks increase in proximity to livestock (Hald et al., 2016; Karp et al., 2015; Smith et al., 2020a). It thus seems likely that birds may acquire pathogens from livestock feedlots and then carry them, potentially over long distances, into produce fields (Billerman et al., 2020; Rivadeneira et al., 2016; Smith et al., 2020a).

The few studies that have related functional traits to food safety risks in birds have tended to compare foraging guilds and have had mixed results. For example, prior studies suggest that *Campylobacter* spp. prevalence may be higher in omnivores, ground foragers, opportunistic feeders, carnivores, and/or arboreal/herbaceous insectivores (Hald et al., 2016; Smith et al., 2020c; Waldenstrom et al., 2002). Leveraging a database that encompasses many more species than prior primary studies, distributed across diverse guilds but collected in similar environments, we found *Campylobacter* spp. prevalence was lower in insectivores than in plant-eating species. We hypothesize this result may reflect a combination of traits related to pathogen exposure that are correlated with diet. For example, birds that primarily consumed plants constituted a higher proportion than average of species with high feedlot association (21% vs. 17%), high bird feeder use (58% vs. 26%), and preference for synanthropic habitats (synanthropic index >1; 42% vs. 17%).

Unlike *Campylobacter* spp., movement traits most strongly influenced *Salmonella* spp., with more sedentary species exhibiting higher prevalence (i.e., residents with lower hand-wing indices). *Salmonella* spp., in contrast to *Campylobacter* spp. that are generally considered commensal, are known to cause mass mortality events in small passerines (Daoust et al., 2000; Hall & Saito, 2008; Smith et al., 2020c). Thus, infected individuals may be culled during stressful seasonal movements (Altizer et al., 2011). Additionally, "migratory escape" may occur during migration wherein individuals leave behind environments with high pathogen loads (Altizer et al., 2011). Alternatively, prior work has shown that migratory birds mount greater immune defenses than resident species (Moller & Erritzoe, 1998), potentially cascading into lower *Salmonella* spp. prevalence.

Pace-of-life traits

While exposure traits appear to mediate pathogen prevalence, the impact of pace-of-life traits was less clear. In contrast to the predicted relationship between generation length and pathogen prevalence in the "ecoimmunological pace-of-life hypothesis" (Ostfeld et al., 2014), we found that species with longer generation lengths had higher *Campylobacter* spp. prevalence. However, clutch size was positively correlated with carriage of STEC-associated virulence genes, aligning with the pace-of-life hypothesis, while no pace-of-life traits were related to *Salmonella* spp. prevalence. Altogether, there was weak and inconsistent support for the "ecoimmunological pace-of-life hypothesis," in line with mixed support in the literature (Nwaogu et al., 2018; Tieleman, 2018).

An alternative explanation for the positive relationship between generation length and *Campylobacter* spp. prevalence is that individuals from species with longer generation lengths may be older, on average, and may have had more time to be exposed to pathogens, allowing for pathogen "accumulation." Indeed, *Campylobacter* spp. are generally considered wild bird commensals and could accumulate (Smith et al., 2020c). However, it remains unclear whether individuals infected with

Campylobacter spp., or other foodborne pathogens, maintain infections for substantial lengths of time (Smith et al., 2020c). One study that may shed light on this issue recaptured European Starlings from 1 to 364 d apart and found that ~40% of birds tested positive for *Campylobacter* spp. on only one occasion. For those that tested positive both times, ~84% of *C. jejuni* isolates were of a different genotype between surveys, suggesting rapid turnover and re-colonization (Colles et al., 2009). Another study that observed shedding in captive Herring Gulls failed to detect *Campylobacter* spp. after week 4 of a 58-week trial (Glunder et al., 1992). Therefore, it is unclear whether pathogens really do accumulate in species with longer generation lengths, or whether other factors covarying with generation length (e.g., mass and diet guild; Bird et al., 2020) may be at play.

Traits mediate crop contact

We found that species associated with feedlots and those that forage in lower vegetation strata were most likely to contact crops. These results are intuitive as species preadapted to exploit feedlots may also be able to exploit crop fields, and upper-strata foragers may be unlikely to venture out of the treetops into low-growing crops. Simply entering farm fields, however, does not necessarily mean that a species will contaminate the crops by defecating. Indeed, while feedlot-associated species were both more likely to enter and defecate in farm fields, feces in brassica fields and food wash/packing structures were also more likely to be attributed to species with shorter generation lengths. One explanation is that species with shorter-generation lengths in our system tend to be small-bodied species like Savannah Sparrow and Song Sparrow (*Melospiza melodia*) that actively forage among crops (Smith et al., 2020a). While few studies have compared fecal outputs per unit time during different activities, Canada Geese are known to have higher defecation rates while feeding compared to loafing (Feare et al., 1999). Moreover, birds actively foraging on plants likely have higher fecal output rates than birds foraging in flight or flying over crops (Guillemette, 1994). These observations may explain why aerial insectivores were often observed foraging over crops, yet few feces were traced back to them.

Managing risk in the field

Our results suggest that, although prevalence of enteric pathogens is often low in birds, feedlot-associated species present higher risks because they are more likely to shed *Campylobacter* spp., enter farm fields, and defecate on high-risk products. Because birds have been observed moving between livestock operations and farm fields (Rivadeneira et al., 2016), growers could consider planting high-risk produce as far away as possible from livestock areas (Karp et al., 2015). Unfortunately, however, many of the livestock-associated species studied here move great distances on a daily basis (Billerman et al., 2020), so this might be difficult in practice. Growers may also benefit from focusing monitoring and deterrence efforts in areas near livestock, including measures such as installing raptor perches and nest boxes or using sound cannons (Olimpi et al., 2020; Rivadeneira et al., 2018; Shave et al., 2018). The efficacy of most bird deterrence mechanisms are thought to be low or are untested, but using a combination of methods and rotating their use may help reduce fecal contamination on crops (Olimpi et al., 2020).

More optimistically, however, our results suggest that co-managing fresh produce fields for food safety and economic benefits from birds may be possible. Insectivorous birds often consume damaging crop pests and improve crop yields (Boesing et al., 2017; Karp et al., 2013). Our study suggests that these insect-eating species are also less likely to carry *Campylobacter* spp. One strategy for promoting insectivorous birds (as well as farmland biodiversity overall) is restoring or maintaining non-crop vegetation around farms (Gonthier et al., 2019). Importantly, farms with more surrounding non-crop habitat may be less likely to host birds that shed *Campylobacter* spp. in fields (Smith et al., 2020a) and removing habitat may increase STEC prevalence on crops (Karp et al., 2015). Another approach for attracting pest-eating birds is installing artificial nest boxes around farms (Jedlicka et al., 2011). Our model predictions suggest that some species most commonly occupying nest boxes tend to have low *Campylobacter* spp. prevalence (e.g., Western Bluebirds [*Sialia Mexicana*] and Tree Swallows [*Tachycineta bicolor*]; Smith et al., 2021). However, caution is warranted as nonnative European Starlings and House Sparrows regularly evict native species from nest boxes (Weitzel, 1988). Although nonnative status was less important in predicting *Campylobacter* spp. than other traits, nonnative species in our study still had higher prevalence than native birds (OR $= 3.36$; $\beta = 1.21$, $P = 0.027$). Thus, growers should monitor nest boxes and evict nonnative birds when possible.

Caveats and limitations

A few caveats and limitations must be noted. First, although our study covers many bird species and a wide area along the West Coast, trends from our study may not extend into other regions (e.g., other temperate areas or the tropics); other production systems (e.g., orchard or vineyard monocultures); or conventional, large-scale agriculture. Indeed, our analyses focus on farms that largely grow row crops, with much of the data derived from small, organic operations. Crop contact rates, in particular, may be elevated on the relatively diversified farms included in our study (Smith et al., 2020b). Additionally, some bird species may have regional and context-specific differences in crop contact rates that could cause them to move into the high-prevalence–high-contact quadrant in specific settings and/or regions. For example, Wild Turkeys (*Meleagris gallopavo*) were predicted to have overall low crop contact rates in our study, likely because their range does not extend into a large portion of the farms surveyed. However, they may constitute significant food safety risks where they do occur because they have been found to carry STEC and intrude into agriculture in other settings (Jones et al., 2015).

Second, it should be noted that birds may contaminate crops via indirect routes not studied here, including mechanically vectoring pathogens on feathers or through defecation in irrigation water (Navarro-Gonzalez et al., 2020; Smith et al., 2020c). Third, the duration of bacterial survival in bird feces is a key variable in the probability that foodborne pathogens will spillover from wild birds to humans (Smith et al., 2020c). However, no studies to date that we know of inoculate songbird feces with *Campylobacter* spp., the most common foodborne pathogen found in songbirds, and monitor *Campylobacter* spp. survival. One study that examined *Campylobacter* spp. survival in Canada Goose feces suggests bacteria may become unviable rapidly (2 d) in summer (Moriarty et al., 2012), but we were unable to examine this important aspect of the spillover cycle. Current evidence suggests that *Salmonella* spp. and *E. coli*, which were rarely found in bird feces in our study, may survive over longer time periods in bird feces (Feare et al., 1999; Fonseca et al., 2020; Kauffman & Lejeune, 2011; Moriarty et al., 2012).

Finally, we note that our study provides evidence regarding the gradient of risk that bird species pose to food safety, when considering crop contact and pathogen prevalence. Although foodborne pathogens may be rare in birds, in some instances, pathogens could enter a field via birds and amplify when conditions for pathogenic bacteria are favorable (Gardner et al., 2011). Although we conclude that many bird species can be managed in agroecosystems with low risks to food safety, we note that when bird species are present in and around crop fields and are capable of carrying foodborne pathogens, the risk to food safety is non-zero. The amount of risk that is tolerable will likely vary by stakeholder group (e.g., food safety certifiers, conservationists, etc.) and is beyond the scope of our study.

CONCLUSIONS

Although birds do harbor foodborne pathogens, their prevalence in birds is generally quite low. Still, we found that species traits mediate food safety risks and can be used to extrapolate risks to understudied species. In particular, species associated with feedlots are both more likely to carry pathogens and to defecate in farm fields than species that avoid feedlots. Fortunately, we suggest that growers can still harness ecosystem services from insectivorous birds and promote conservation without greatly compromising food safety, either by installing nest boxes or by maintaining non-crop vegetation (Jedlicka et al., 2011; Karp et al., 2015; Smith et al., 2020a). Efforts to deter species that are more problematic and "tip the scales" towards those that are less harmful may facilitate a "win-win-win" for human health, biodiversity, and crop production.

ACKNOWLEDGMENTS

We thank the many growers who provided us access to their farms and participated in our individual studies. This work was funded by the United States Department of Agriculture (USDA-NIFA-OREI grant 2015-51300-24155 and USDA-NIFA-BcENRE grant 2017-67019-26293) and the National Science Foundation (grant CNH-1824871). Any opinions, findings, conclusions, or recommendations expressed in this publication are those of the authors and do not necessarily reflect the view of the U.S. Department of Agriculture. M. Jay-Russell and E. S. Pro provided assistance with project development. We thank L. Michelotti, A. Tormanen, S. Knutie (master banding permit that was essential to parts of the data collection), and the many others who assisted with lab and field work for individual studies.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Olivia M. Smith, Elissa M. Olimpi, and Daniel S. Karp. designed the research with input from Nora Navarro-Gonzalez, Luke O. Frishkoff, Tobin D. Northfield, and William E. Snyder; Olivia M. Smith, Kevin A. Cornell, Luke O. Frishkoff, Johnna Eilers, Karina Garcia, and Daniel S. Karp collected traits data; Olivia M. Smith, Elissa M. Olimpi, Max Edworthy, Karina Garcia, David J.

Gonthier, Zhen Fu, Joseph M. Taylor, Erin E. Wilson-Rankin. and Daniel S. Karp. collected pathogen and contact data; Olivia M. Smith. meta-analyzed the data and created figures; Olivia M. Smith. and Daniel S. Karp. led the writing of the manuscript; Luke O. Frishkoff, Tobin D. Northfield, Timothy M. Bowles, Max Edworthy, David J. Gonthier, Christina M. Kennedy, Christopher E. Latimer, Jeb P. Owen, and William E. Snyder. provided comments on the manuscript, with large contribution from Elissa M. Olimpi, Nora Navarro-Gonzalez; all authors made substantial contributions to studies included in the meta-analysis and approved manuscript submission.

DATA AVAILABILITY STATEMENT

Data (Smith et al. 2021) are available in Dryad: https://doi.org/10.5061/dryad.m63xsj42m.

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How to cite this article: Smith, Olivia M., Elissa M. Olimpi, Nora Navarro-Gonzalez, Kevin A. Cornell, Luke O. Frishkoff, Tobin D. Northfield, Timothy M. Bowles, et al. 2022. "A Trait-Based Framework for Predicting Foodborne Pathogen Risk from Wild Birds." *Ecological Applications* 32(2): e2523. https://doi.org/10.1002/eap.2523