Bird Health in California's Central Coast: Using Immunological Parameters to Understand the Impact of Land Use and Life History on Avian Communities

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ABSTRACT

The Central Coast of California has implemented bare-ground buffers to deter the presence of food-borne pathogens in produce. Besides being ineffective, the destruction of natural habitat may also place avian communities at risk as they decrease critical resources for wildlife. To ascertain how rapid land use changes in the Central Coast are impacting surrounding biotic communities, I mist-netted birds on organic strawberry farms in Monterey and Santa Cruz counties during July and August 2018. I sampled passerine and near passerine birds as they are commonly used as indicators of environmental health. For each sampled bird, a blood smear was made and stained with Giemsa-Wright stain for the quantification of white blood cells. The ratio of two white blood cells, heterophils and lymphocytes, (H:L ratio) served as a proxy for bird health. Mixed-effects modelling revealed that song sparrow health slightly increased on farms with high proportions of agriculture; this trend was marginally significant at $p = 0.08$. High levels of reproductive readiness were also linked to improved song sparrow health, with this trend being statistically significant at $p = 0.007$. Foraging and habitat resources created by agriculturalists and fledging survivorship may be impacting bird health in the Central Coast. This preliminary work calls for a re-evaluation of human-wildlife relationships as agricultural spaces may be safeguarding avian communities. Providing farmers with incentives and resources to foment bird-friendly crop production may be critical in balancing wildlife and human concerns in rapidly changing agricultural regions.

KEYWORDS

Passerine and near passerine birds, organic strawberry farms, H:L ratio, mixed-effects models, ArcGIS

INTRODUCTION

Avian communities near agricultural fields impact both human health and surrounding ecological communities. Birds provide critical ecosystem services to farmers by predating on crop pests in a variety of agroecological systems including coffee, cacao, and palm oil farms (Railsback and Johnson 2014, Maas et al. 2013, Koh 2008). However, birds also pose challenges to agricultural production because they eat crops and their feces can be found in adjacent waterways and on produce (Karp et al. 2015a, Westerlund et al.1999, Bihn and Gravani 2006, Clark and Hall 2006). As birds are vectors for food-borne pathogens such as *E. coli*, *Salmonella* spp. and *Campylobacter* spp., destroying natural habitat near farms potentially deters the spread of infectious agents (Wetzel and LeJeune 2006, Park et al. 2013, Karp et al. 2015a, Karp et al. 2015b, Wild Farm Alliance 2016). Bare ground buffers, swaths of unvegetated land adjacent to farmland, destroy critical resources for wildlife cohabiting with agro-ecological systems and disrupt ecosystem services. These landscape changes are linked to decreases in bird biodiversity in the surrounding landscape (Hallman et al. 2017, Inger et al. 2015). Consequently, the study of birds in agricultural areas has been centered on human concerns; nonetheless anthropogenic actions may likewise affect avian communities.

To shift the focus from humans to wildlife in agricultural systems, the landscape matrix approach allows for discerning at multiple scales the complex interplay between an organism's health and its surroundings. This approach envisions a collection of natural habitat patches coalescing to form the landscape at large, referred to as the matrix (Fahrig 2001, Perfecto and Vandermeer 2009). Carving out portions of the natural environment for agricultural purposes potentially disturbs the overall matrix (Lindenmayer et al. 2008). Thus, areas with more connected natural habitat patches are preferred. Adopting the established landscape matrix approach provides a more robust theoretical foundation for the idea of a "quality" landscape. Wildlife health studies have widely implemented this framework to discuss how landscape changes impact wildlife health in terms of: species composition, abundance and richness, gene flow, and parasitism (Buskirk 2012, Brady et al. 2011, Häkkilä et al. 2017, Laurance et al. 2013). Yet few molecular and cellular–level techniques have been implemented at the landscape scale to discuss community well-being.

Immunology can assess how wildlife health is being impacted by varying landscape matrix compositions. The ratio of two white blood cell types, heterophils and lymphocytes (H:L ratio), has been used to infer a bird's future and present state of health in a variety of contexts, from confined feeding operations to national reserves (Kilgas et. al 2006, Al-Murrani 2007, Bienzle et. al 1997, Lobato et. al 2005). Although the H:L ratio is a high fidelity marker of bird health, it has not been used to quantify how bird health is impacted by changing landscapes. By linking the H:L ratio to landscape quality, specific landscape configurations can be discerned as detrimental to birds in agro-ecological systems.

Using the H:L ratio as a measure of bird health within a landscape matrix framework can determine how bird health is impacted by landscape composition in agricultural areas. This study asks if certain agricultural land use types are more critical to avian health in comparison to others. We also consider if particular species are more vulnerable to certain landscape configurations. In addition, birds of different reproductive states are examined to ascertain whether this factor impacts overall health in the face of variable environmental conditions. By understanding how changing agricultural landscapes are impacting avian communities, farmers and food regulators will be able to balance human and wildlife concerns more equitably.

METHODS

Study sites

During July and August of 2018, as part of the Kremen Lab at UC Berkeley and the Karp Lab at UC Davis, I mist-netted for passerine and near-passerine (tree perching and dwelling) birds on 20 organic strawberry farms in Monterey and Santa Cruz Counties (Figure 1). These 20 farms were selected to capture a spectrum of agricultural and landscape conditions. Farm sizes ranged from 0.04 to 9 km^2, with production models greatly differing. Some sites were monocultures, while others contained over 60 crops. These farms are also located along a land-use gradient, where the density of natural landscapes was 53% in some areas while in others 87% of the area corresponded to agriculture.

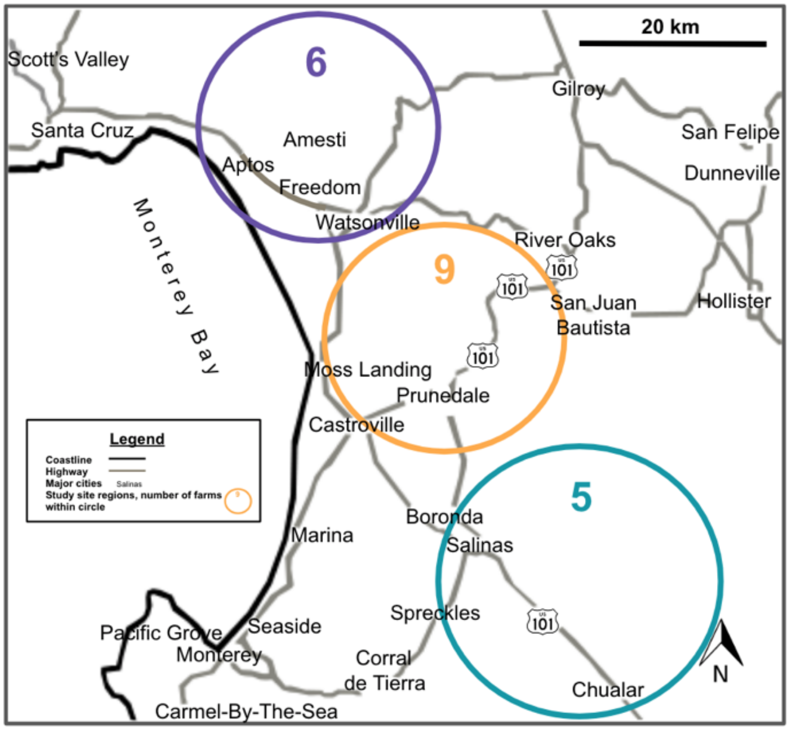


Figure 1. **Spatial distribution of the 20 sampled farms in Monterey and Santa Cruz Counties.** Each circle encloses a region of sampled farms. The number of farms found within each circle is denoted at the top of each region. The base map was created using National Agricultural Imagery Project (NAIP) photographs (United States Department of Agriculture Farm Service Agency 2018).

Landscape diversity

To determine each site's landscape diversity, I digitized land use types on and surrounding each farm. I downloaded National Agricultural Imagery Project (NAIP) photographs corresponding to Santa Cruz and Monterey Counties and imported them into ArcGIS (United States Department of Agriculture Farm Service Agency 2018, ESRI 2018). I overlaid GPS waypoints of each farm onto NAIP imagery to locate the sites within the larger landscape matrix. A one kilometer buffer circle was drawn around each farm and all land uses within this region were digitized. Using the Gonthier Lab's landscape digitization protocol (K. Garcia, *personal communication*), land uses were categorized into the following types: forest and woodlands, shrublands, herbaceous vegetation, low to no vegetative cover, agriculture, urban or built environment, exurban, suburban, and water features (Figure 2). Google Maps was also used to confirm land use categorizations (Google Maps 2018). Based on the focal bird species' life histories, I used the proportion of agriculture and natural habitats (oak woodlands and shrublands combined) in the final mixed-effects model (Table 1). For instance, when considering breeding habitat (Table 1), the focal species require forested areas, brushland, or thickets, which roughly corresponded to the oak woodlands and shrubland vegetation types I digitized.

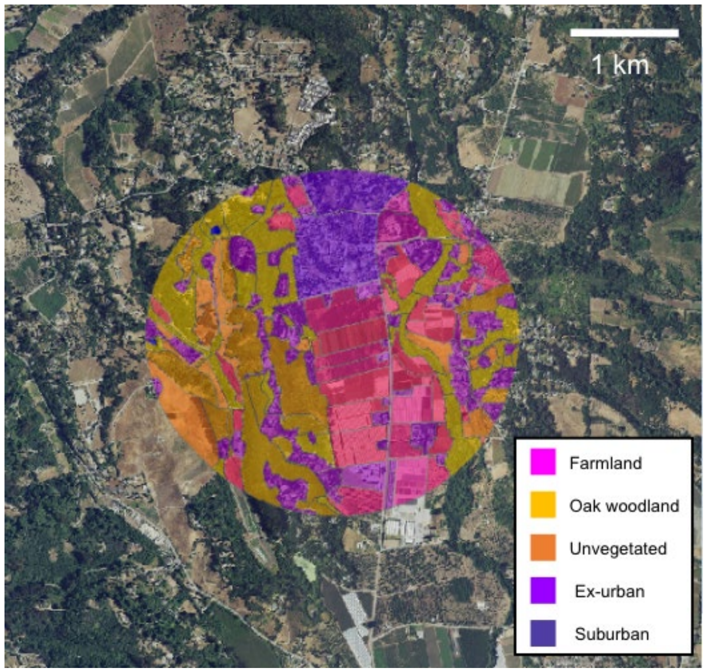


Figure 2. Digitization of land uses within an example farm in ArcGIS (ESRI 2018). Each color within the one-kilometer buffer corresponds to a different land use type.

Study organisms

Although California's Central Coast has diverse flora and fauna, I focused on passerine and near passerine birds as these taxa often serve as indicators of environmental health, and more specifically landscape changes in agricultural areas (Ormerod and Watkinson 2000). Of the captured birds, I selected a subset representing the 4 most common agricultural species: song sparrows (*Melospiza melodia*), house finches (*Haemorhous mexicanus*), Oregon juncos (*Junco hyemalis*), and spotted towhees (*Pipilo maculatus*). Each bird species' banding alpha code is: house finches (HOFI), Oregon juncos (ORJU), song sparrows (SOSP), and spotted towhees (SPTO). The subset selected amounted to 200 birds, approximately 15% of the entire mist-netted sample of 1303 birds. These 200 birds represented 13 of the 20 sampled farms. Each bird species has different foraging, nesting, and breeding habits (Table 1). The differences in biological functional traits are expected to be predictive of certain bird species being more vulnerable to changes in the natural landscape.

Table 1. Summary of song sparrows, house finches, Oregon juncos, and spotted towhees' life histories. All taxa are from the family passerellidae, order *passeriformes* (Dobkin 1990, Granholm 1990a, Audubon 2019, Granholm 1990b, Green 1990). Each bird species' banding alpha code is included (i.e. house finches as HOFI).

Species	Food Guild	Cover	Nestling	Clutch Size	Start of Breeding Season	Breeding Habitat
House finch (*Haemorhous mexicanus*) **HOFI**	Fructivore and granivore	Trees, tall shrubs, and buildings	Trees, abandoned nests, and human-made structures	Lay 2-6 eggs, 2-3 broods per year	March or April	Varied; conifers, cacti, man-made structures, and old bird nests
Oregon junco (*Junco hyemalis*) **ORJU**	Insectivore and granivore	Trees, shrubs, and ground herbage	On ground, small tree or shrub near water	Lay 3-5 eggs, 2-3 broods per year	April into August, peaking in May and June	Forests, woodlands, and forest edges
Song sparrow (*Melospiza melodia*) **SOSP**	Omnivore, eats litter	Low dense vegetation near moist areas	On ground, small trees and shrubs	Lay 3-6 eggs, 2-3 broods per year	April	Dense riparian thickets and wetlands
Spotted towhees (*Pipilo maculatus*) **SPTO**	Omnivore, eats litter	Shrubs, ground herbage, and thickets with abundante leaf litter	On ground, in slash pile, dense shrub, or vine tangle.	Lay 2-6 eggs, 2 broods per year	Late April to late August, peaking in May and June	Dense brush or thickets with substantial accumulation of litter

Mist-netting

To representatively sample avian communities surrounding farms, we implemented the standard mist-netting protocol. Mist-netting uses nets to capture and sample avian communities in a given area (Figure 3). We set up 10 mist nets per site along field edges, bordering strawberry fields, other crops, and natural areas alike. A diversity of mist-net locations ensured that we captured birds that were using various land use types. We recorded GPS waypoints for each net to later locate them on satellite imagery. Following standard protocol, all nets were opened at sunrise (around 5 AM) and left open for 5-6 hours (Ralph et al. 2004). Nets were checked at 20 minute intervals and all birds caught were brought back to the banding station for data collection. We worked on each farm for three continuous days to reach sample saturation. Doing so ensured that most, if not all, birds surrounding the farms were sampled.

Figure 3. Chipping sparrow (*Spizella passerina*) caught inside a mist-net. Mist-netting, when done properly, does not place the bird at risk.

Sample collection

To collect data on each captured bird, we transported specimens from the nets to the on-site station for banding and morphometric calculations. Each bird was banded with a metal ring, imprinted with a unique serial number provided by the United States Geological Service (USGS). Banding prevented a bird from being counted as a unique observation after the initial collection. The band also allows future researchers to access the data we collected. Mist-netting data must be provided to the USGS, which is then made publically available via the Bird Banding Laboratory website (https://www.usgs.gov/centers/pwrc/science/bird-banding-laboratory; United States Geological Survey 2018). Each captured bird was sexed based on its plumage and/or visible reproductive organs. Birds were aged via the level of skull ossification and/or plumage (Pyle 1997). An individual's beak length, beak width, tail length, and tarsus length were also measured (Ralph et al. 2004). Lastly, we noted the presence of strawberry residue on a bird's beak, and any evidence of ectoparasites such as wing lice and head ticks.

To determine a bird's state of reproduction, we calculated a "reproductive readiness" index. Reproductive readiness was determined by examining a bird's cloacal protuberance or brood patch, for males and females respectively (Figure 4). The cloacal protuberance and brood patches' size, color, and texture indicate a bird's breeding preparation (Pyle 1997). These organs were assigned a score ranging from 0-4, where larger numbers designate a bird is more prepared for reproduction. Using cloacal protuberance and brood patch scores as proxies for "reproductive readiness," I calculated z-scores for both male and female breeding parameters and combined them into a single metric called "reproductive readiness." Standardizing the scores via a z-score calculation allowed for models that included a single term to describe a bird's current or potential sexual activity.

Figure 4. A female house finches' (*Haemorhous mexicanus*) brood patch. Brood patch and cloacal protuberance scores, for female and male birds respectively, served as a proxy for a bird's level of breeding preparation (Pyle 1997).

White blood cell differential

Collecting avian blood samples

To determine avian community health, we collected a blood sample from each captured individual to create blood smears. Using a 27-gauge needle, we extracted approximately 50 µL of blood from a bird's brachial vein (Morishita et al. 1999, Valera et al. 2006). The blood was then placed in a heparinized tube to prevent coagulation. With the heparinized blood, we made a blood smear for each sampled bird, following Owen's suggested protocol (2011). Blood smears were then placed in a slide box to dry and relocate to the laboratory.

Staining blood smears

To determine the white blood cell composition of each bird, I stained the blood smears with Giemsa-Wright stain. Giemsa-Wright staining was selected because it causes different blood elements to acquire characteristic colors (Figure 5), resulting in the precise quantification of white blood cell types. Giemsa-Wright staining is a routine procedure in wildlife health studies, however there are no published protocols in the peer-reviewed literature (Owen 2011, Eberhard & Lammie 1991). As I result, I developed a protocol for staining. First, I fixed each blood smear with 100% methanol to prevent the stain from washing away the blood sample. To stain the samples, I used phosphate buffer pH 7.2 (Sigma Aldrich, P3288) and modified Giemsa stain (Sigma Aldrich, GS500). I placed 4 mL of the stain and 20 mL of the buffer inside a coplin jar. Next, I placed ten slides back to back inside the jar and let them stain undisturbed for 50 minutes. Once 50 minutes had passed, I removed the slides from the jar with forceps. I rinsed the smears with distilled water (Arrowhead) to allow any stain that did not bind with the blood to wash off. Removing residual stain and buffer increased image resolution under the microscope. I was able to reuse the staining solution for a total of 5 dips (= 50 slides). Slides placed into the solution past this point resulted in faintly stained samples, making blood element identification difficult. After staining the slides, I laid them out to dry for an hour by placing them against plastic bins lined with paper towels.

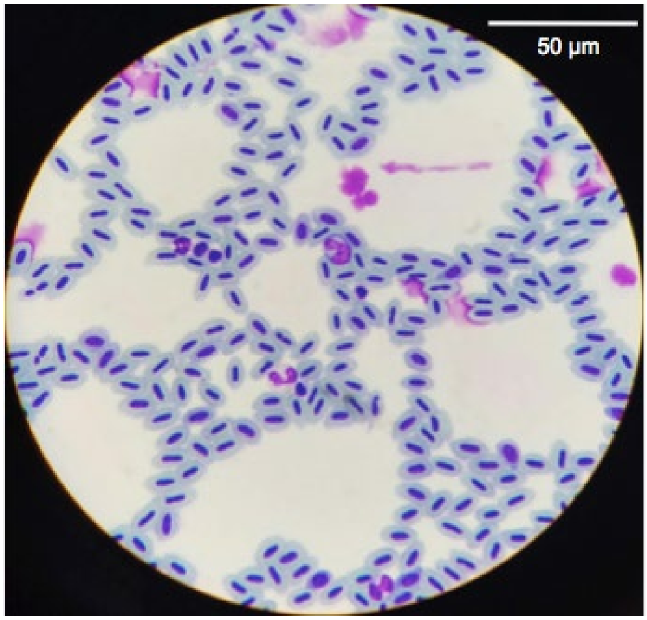


Figure 5. Blood smear viewed at the 100x oil immersion objective. Note the differential staining of the white and red blood cells due to the Giemsa-Wright stain.

Identifying and quantifying white blood cell types

To perform a white blood cell differential for each smear, I observed the stained samples under a microscope. I used a Zeiss Primo Star iLED Fluorescence Microscope for all the differentials. I placed each smear under the lowest power objective (10x) and searched for a field of view that did not have overlapping cells nor cells sparsely distributed (R. Bandivadekar, *personal communication*). A distribution of cells within these extremes is called the monolayer. Once the monolayer was identified, I placed a single drop of oil immersion fluid onto the slide. I moved up to the 100x oil immersion objective and scanned the smear until 200 white blood cells were counted (Ciesla 2007). To avoid double counting, I followed a snaking pattern from head to tail of the smear (Figure 6; Godfrey et al. 1987, Merino et al. 1997). I tracked the observed white blood cells with a cell counter. White blood cell types were categorized into one of the following types: lymphocytes, heterophils, basophils, monocytes, and eosinophils. Separately, I made note of any parasites I identified, particularly *Haemoproteus* spp. and microfilariae given they greatly place bird health at risk (Atkinson 1991, Bartlett 2008). Once a smear had been fully analyzed, I calculated its H:L ratio by dividing a sample's heterophil count by its lymphocyte count. High

H:L ratios are associated with birds in poor health (Kilgas et. al 2006, Al-Murrani 2007, Lobato et. al 2005).

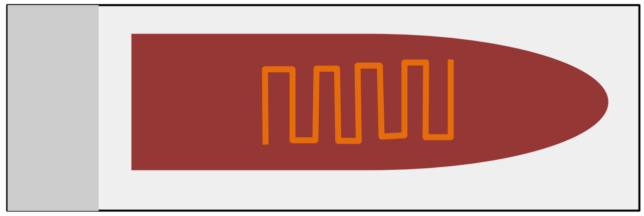


Figure 6. The snaking pattern, from head to tail of the smear, followed when systematically counting blood elements.

Mixed-effects model

To distill the relationship between landscape composition and bird health, I created and ran linear mixed-effects models (LMEs). For modeling, I used the statistical program R version 3.6.1 (R Core Team 2018) with the *lme4* (Bates et al. 2015), *lmtest* (Zeileis and Hothorn 2002), and *stargazer* (Hlavac 2015) packages. Visualizations were created using the *ggplot2* package (Wickham 2016). As the H:L ratio was not normally distributed based on the QQ-plot, I first log-transformed the H:L ratio so that it could be used in parametric tests (Appendix Figure A1-2). The model's syntax was determined based on the experimental design and hypotheses as: $Bird\ Health\ \sim Reproductive\ Readiness * Species + Natural\ Habitat * Species + Agriculture * Species + (1\mid Farm)$. The "Bird Health" variable is the log transformed H:L ratio. Farm is the random effect and there are three interaction effects with species and: the proportion of agriculture, proportion of natural habitat, and reproductive readiness standardized score respectively. As the research question is focused on how bird health is being modulated by changes in the landscape, "Bird Health" is the response variable. The random effect of farm assumes that birds sampled from the same location, regardless of their intrinsic characteristics, will have similar H:L ratios given the shared context. Most importantly, by setting each variable (reproductive readiness, natural habitat, agriculture) in interaction with bird species, the model may reveal if in fact some bird species are inherently more sensitive to certain land use types and how different levels of reproductive readiness are impacting bird health.

RESULTS

Farm landscape characteristics

The thirteen farms in the study varied greatly in terms of the proportion of agricultural fields, shrublands, and oak woodlands present (Table 2). Farm 11 had the largest proportion of land dedicated to agriculture, followed by farm 1, with values of 0.87 and 0.73 respectively. Farm 6 had the least amount of agriculture present at 0.02. Shrublands were the land use type least represented in the sample, with the highest proportion corresponding to farm 7 at 0.18 (Table 2). Although the median proportion of shrublands was 0.02, some locations, such as farms 1 and 10, did not have shrublands represented (Table 2). Conversely, the proportion of oak woodlands fluctuated between farms. Farm 10 did not have any oak woodlands, while farm 6 had over a third of its area comprised of this land use type (Table 2).

Table 2. **Proportion of agriculture, shrublands, and oak woodlands on each farm.** Dominant land use types (proportions above 0.5) are bolded. Note that the proportions do not add up to 1 as there were additional land use types not considered in this study, such as suburban and urban land uses.

Farm	Proportion of Land as Agriculture	Proportion of Land as Shrubland	Proportion of Land as Oak Woodlands
1	**0.73**	0	0.02
2	0.29	0.09	0.19
3	0.36	0.08	0.23
4	0.34	0.01	0.27
5	0.24	0.003	0.09
6	0.02	0.16	0.37
7	0.15	0.18	0.002
8	**0.68**	0.002	0.14
9	0.14	0.1	0.21
10	**0.82**	0	0
11	**0.87**	0.00007	0.03
12	0.32	0.09	0.15
13	0.32	0.02	0.30

Bird community composition

Each farm had a distinct bird community composition in terms of the richness and abundance of the four focal species (Figure 7). The highest bird count occurred in farm 6, while the lowest count occurred in farm 10. On each of these farms, 27 versus 4 birds were sampled respectively. Only farm 6 had all four species of interest present; most farms had only three out of the four study species present. Within the entire sample, song sparrows were the most represented (69 birds, 35% of sample), while spotted towhees were the least sampled (31 birds, 16% of the sample) (Figure 7). Each farm also represented different age and sex demographics (Appendix Table B1-2).

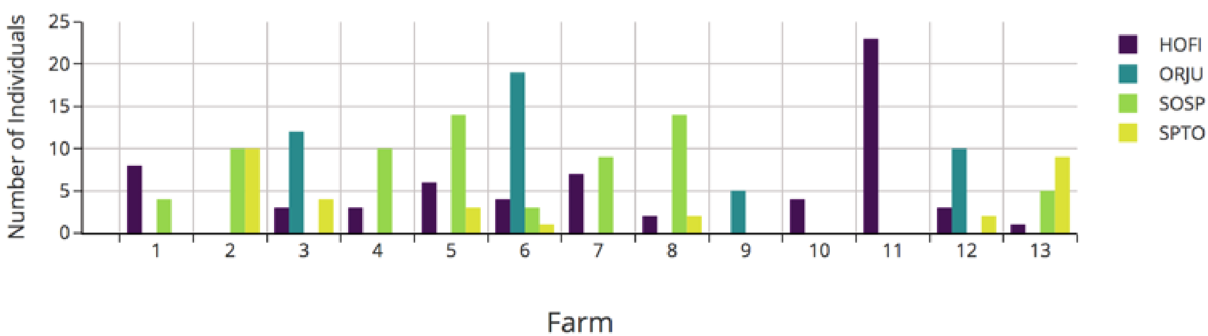


Figure 7. Bird species counts by farm. Each bird species is referred to by its bird banding alpha code: House finches (HOFI), Oregon juncos (ORJU), song sparrows (SOSP), and spotted towhees (SPTO). Each bird species has its own bar and is shown in a different color. Bars are grouped by farms.

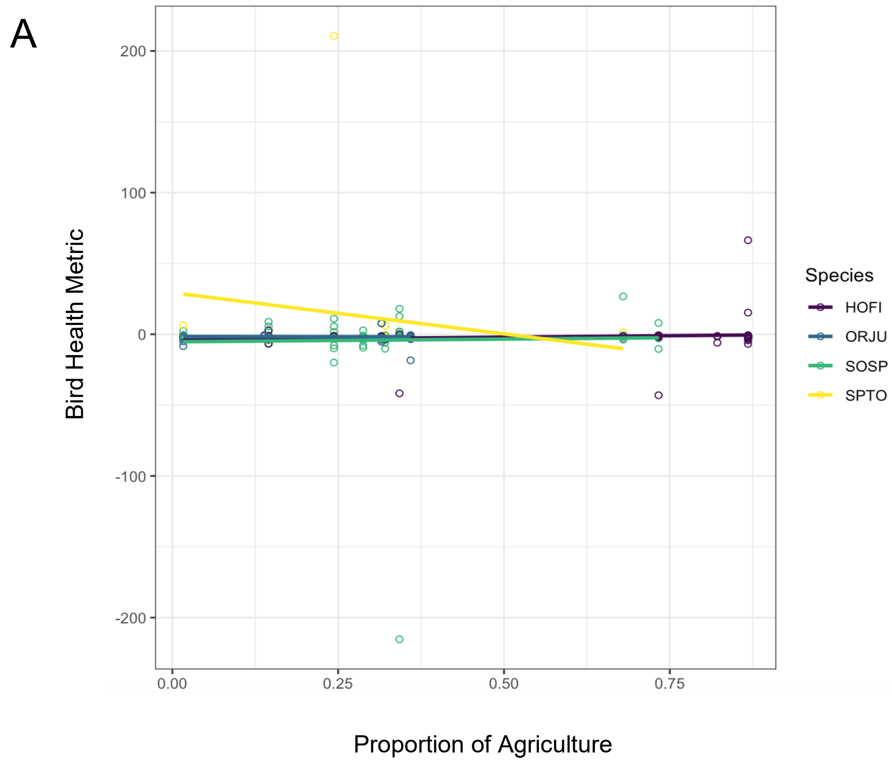
Modeling bird health and landscape quality

In the mixed-effects model, only two terms emerged as significant: the interaction effect between song sparrows and the proportion of agriculture on farms, and the interaction effect between song sparrows and reproductive readiness (Table 3). The interaction effect involving agriculture was marginally significant at $p = 0.08$, while the interaction effect with reproductive readiness was highly statistically significant at $p = 0.007$ (Table 3). When comparing the effect sizes of the two significant effects, the interaction effect with reproductive readiness emerged as greater than the interaction effect with agriculture, 6.13 and 5.46 respectively (Table 3).

Table 3. Relationship between bird health, proportion of natural habitat and agriculture on farms, and reproductive readiness. The final model was as follows: Bird Health ~ Reproductive Readiness * Species + Natural Habitat * Species + Agriculture * Species + (1 | Farm). In the output table, one asterisk denote $p < 0.01$ and bolded terms denote $p < 0.1$. House finches were the reference group. The degrees of freedom associated with each factor was 98. The effect size reported is a standardized effect size, where each predictor variable was subtracted by its mean and divided by two standard deviations. Each bird species is referred to by its bird banding alpha code.

Factor	**Effect Size**	**Standard Error**	**T-Value**	**P-value**
Null	-1.90	1.04	-1.83	**0.07**
ORJU	1.40	2.02	0.70	0.49
SOSP	1.30	1.32	0.98	0.33
SPTO	2.82	2.27	1.24	0.22
Natural Habitat	0.5	2.91	0.17	0.86
Agriculture	1.53	2.08	0.74	0.46
Reproductive Readiness	-2.18	1.77	-1.23	0.22
Natural Habitat*ORJU	-6.68	7.28	-0.92	0.36
Natural Habitat*SOSP	4.84	3.70	1.31	0.19
Natural Habitat*SPTO	4.32	7.10	0.68	0.54
Agriculture*ORJU	-8.21	8.87	-0.93	0.36
Agriculture*SOSP	5.46	3.12	1.75	**0.08**
Agriculture*SPTO	2.12	8.72	0.24	0.8
Reproductive Readiness*ORJU	-2.89	3.18	-0.91	0.37
Reproductive Readiness*SOSP	6.13	2.24	2.74	0.007*
Reproductive Readiness*SPTO	-3.07	3.95	-0.78	0.44

The positive effect sizes for the significant and marginally significant interaction effects indicate that, compared to house finches (the reference group), song sparrows experienced a steeper increase in health with: increasing proportions of agriculture on farms and higher levels of reproductive readiness (Figure 8, Figure 9). As there is a less statistically significant relationship between song sparrow health and the proportion of agriculture, this relationship is less marked on the scatterplot as compared to the relationship between reproductive readiness and bird health (Figure 8, Figure 9).



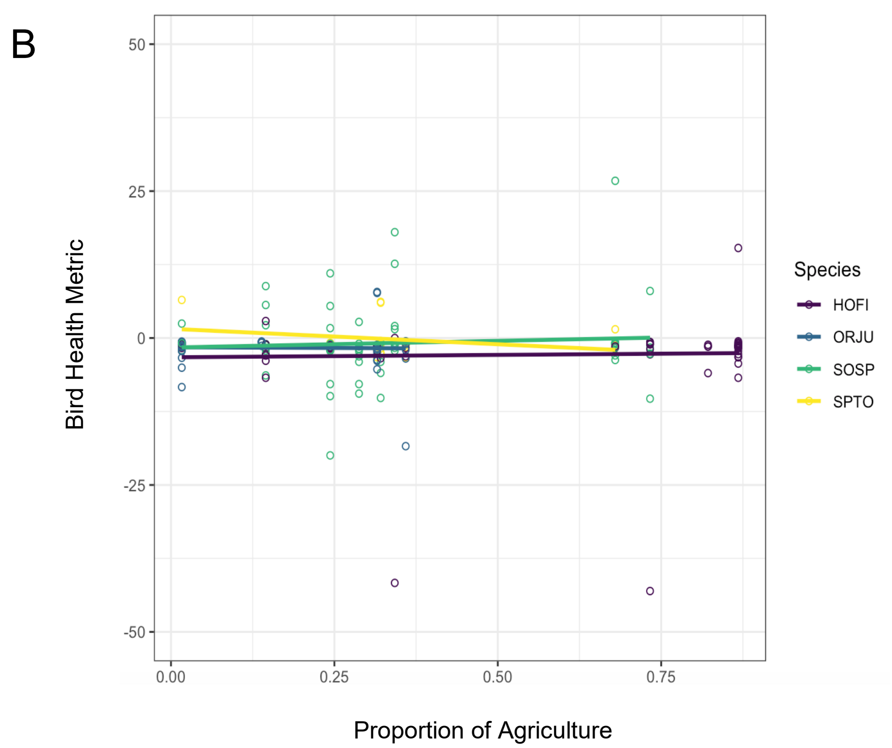


Figure 8. Relationship between the proportion of land devoted to agriculture and bird health. The "bird health metric" is the log-transformed H:L ratio that has been inverted, such that higher values indicate better health. Each bird species is referred to by its bird banding alpha code; each bird is shown in its own color on the plot. (A) The scatterplot depicting the trends between bird health and the proportion of agriculture on farms, with all points in the data set included. (B) The same scatterplot as (A) but zoomed in to better visualize individual species' trends.

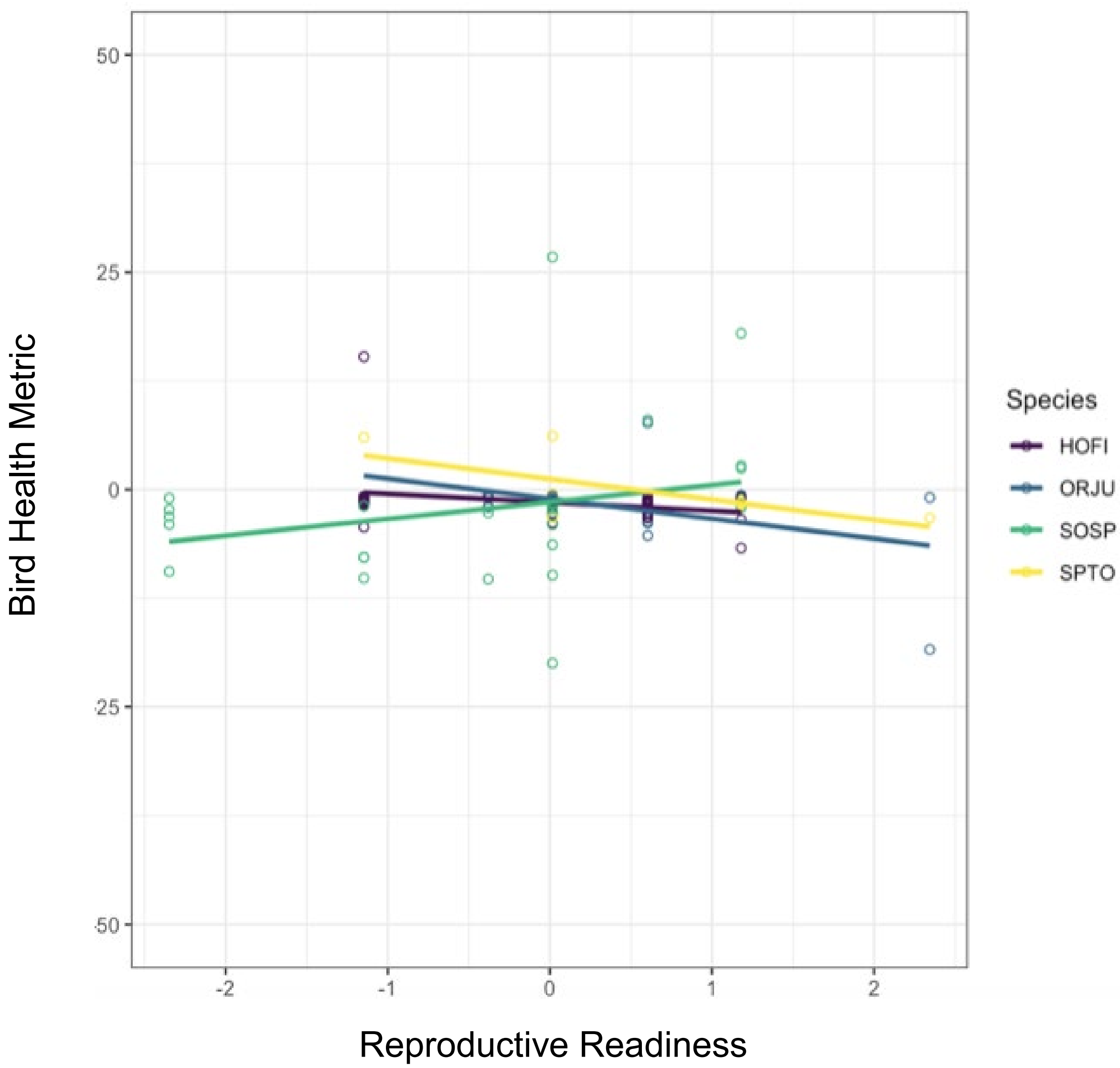


Figure 9. Relationship between reproductive readiness and bird health. The "bird health metric" is the log-transformed H:L ratio that has been inverted, such that higher values indicate better health. "Reproductive readiness" is the standardized cloacal protuberance and brood patch scores for male and female birds respectively. Each bird species is referred to by its bird banding alpha code; each bird is shown in its own color on the plot.

DISCUSSION

The proportion of agriculture on farms and bird's reproductive readiness were the two factors that most influenced song sparrow health. Compared to house finches, song sparrows were in marginally improved health on farms with higher proportions of agriculture. Similarly, song sparrows were the healthiest at higher levels of reproductive readiness as compared to the reference species. In considering food guilds and the resources present on anthropogenic landscapes, our findings imply that birds may obtain critical resources from agricultural spaces in the form of habitat and forage. Trends in reproductive readiness can be interpreted through the lens of survivorship: birds that survived the breeding season had more robust immune systems. By means of the H:L ratio, we can begin to uncover how changes in the landscape matrix are impacting avian community health in the Central Coast of California.

Foraging and habitat resources on farmland

During statistical modeling, song sparrows were in marginally better health as compared to the reference species as the proportion of agriculture on farms increased (Figure 8). This trend can initially appear counterintuitive, as human intervention in the landscape has historically negatively impacted wildlife (c.f. Laurance et al. 2013, Hallman et al. 2017, Inger et al. 2015). Irrespective of the statistical significance of the modeling results, historical land use trends purport that agricultural land may not be the paramount stressor to avian communities. The proportion of agricultural lands in California has remained relatively stable, with the state only losing only 1% of this land type between 1973 and 2000 (Sleeter et al. 2011). Instead there has been a greater landscape pressure from suburban and exurban development; agricultural intensification may be a more critical factor when discussing wildlife health (Sleeter et al. 2011, Donald et al. 2006, Jerrentrup et al. 2017). Even if the amount of agricultural land has remained relatively stable, the percentage of active farmland in Mediterranean climates favors passerine species richness prior to the breeding season (Moreira et al. 2005, Civantos et al. 2018). This is because Mediterranean farmlands provide a variety of foraging and habitat resources to wildlife through fallow fields, cereal crops, and soil-living invertebrates, among others (Moreira et al. 2005, Civantos et al. 2018). In this Central Coast study system, it may be that the marginal trend between agriculture and bird health points to the potential benefits associated with agricultural landscapes. However, study limitations require caution in ascribing anthropogenic land uses as positive to wildlife health.

Food guilds in changing agricultural landscapes

For song sparrows, food guilds may elucidate why there was a positive association between health and the proportion of agricultural land. Disturbances within the landscape promote the presence of specialist species, while heterogeneous landscapes promote generalists (Jeliazkov et al. 2016). Song sparrows are generalists and reproduce and survive well on varying amounts of natural habitat (Table 1; Granholm 1990b, Marzluff et al. 2016). Such findings imply that song sparrows are a resilient species, as they can persist in changing land use configurations and efficiently use the resources present (Marzluff et al. 2016). Song sparrows' generalist nature may contribute to the modelling results that indicate this species was less severely impacted by increases in agriculture (Table 3). By comparison, house finches and Oregon juncos have more restricted diets as they are fructivore and insectivores respectively (Table 1). Their more restricted feeding habits may not have been met on the studied farms, potentially contributing to non-significant interactions between their health and the proportion of agriculture on farms (Table 3; Figure 8). Spotted towhees are omnivorous birds like song sparrows, however they are also terrestrial birds. This taxa nests on the ground within slash piles and often breeds in thickets (Table 1; Dobkin 1990). Terrestrial birds can thus experience higher levels of pathogenic infection as they are more exposed to the warm and humid forest understory. Similarly, they are highly mobile hosts, and so their migration patterns can expose them to a plethora of pathogens (Laurance et al. 2013, Gronesova et al. 2008, Swetnam et al. 2018). Thus for spotted towhees, pathogenic infection may diametrically oppose the benefits garnered from the resources on farmland. Overall, considering food guilds provides a more holistic and species-centered perspective on how birds interact in complex landscape mosaics, and yet a bird's reproductive readiness presents an added stressor that may compound the impacts of changing landscapes.

Reproductive readiness and bird health

Reproductive readiness was the variable that most strongly modulated song sparrows' state of health (Table 3, Figure 9). The relationship between these two variables was positive, such that higher levels of readiness were vinculated to improved health. These findings strongly contrast with others. Although bird species have different baseline levels of stress (Valkiūnas

1997, Hawkey et. al 1984, Maxwell and Robertson 1998), higher levels of reproductive stress correlate with lower reproductive success and fledgling survival rates (Bienzle et. al 1997, Lobato et. al 2005, Kilgas et. al 2006, Al-Murrani et al. 2007, Gustafsson et. al 1994). In taking a survivorship perspective, our findings would suggest that only the fittest birds survived the breeding season (Song et al. 2016, Paxton et al. 2017, Guindre-Parker and Rubenstein 2018). Parents often bear the costs of anthropogenic landscape change in order to supply for their young, and thus ensure their offsprings' health (Kight and Swaddle 2007).

For species besides song sparrows, the scatterplot depicts that higher levels of reproductive readiness predict impaired health; nonetheless these associations were non-significant (Figure 9). These divergent trends posit that different dynamics are at play for song sparrows and the other three bird species in the sample. Breeding seasons are loosely defined, so even when attempting to standardize and account for different levels of reproduction, the z-score reproductive readiness index may not holistically capture varying levels of sexual activity. It may be that song sparrows were the only species that had finished their reproductive cycle, while spotted towhees, Oregon juncos, and house finches had just begun brooding when the sampling period was conducted. The reproductive readiness index may not have a high enough granularity to distinguish these two life stages.

Anthropogenic landscapes and avian reproduction

Mixed-effects models revealed that high proportions of agriculture and high levels of reproductive readiness led to improved song sparrow health within the study system. Our results highlight that humans can provide critical resources to birds through agricultural landscapes in the form of foraging and habitat resources (Hardman et al. 2015, Mendenhall et al. 2013, Civantos et al. 2018). Although the models did not provide any information on species' vulnerabilities to land use changes, we infer that song sparrows were the most resilient species in the sample given that their generalist nature would allow them to exploit a variety of resources, including those on farmland (Granholm 1990b). We expected sexual maturity to detrimentally impact bird health based on past research (Bienzle et. al 1997, Lobato et. al 2005, Kilgas et. al 2006, Al-Murrani et al. 2007, Gustafsson et. al 1994), and yet song sparrows were in improved health at higher levels of reproductive readiness. In taking a life-history approach, this finding implies that song sparrows were the only species that had completed their breeding period during our fieldwork. Thus we would have mostly sampled birds that survived the brooding and rearing life stages – these organisms would inherently be the most fit taxa (Song et al. 2016, Paxton et al. 2017, Guindre-Parker and Rubenstein 2018). Within the study system, bird health was impacted both by landscape composition and life history traits, where reproduction was most the critical factor in accounting for changes in health.

Limitations and future directions

H:L ratio as a health metric

Although the H:L ratio is the most commonly used health index in veterinary medicine, debate surrounds what the ratio exactly denotes. Does a higher H:L ratio indicate a bird is stressed and ill, or does it indicate that it requires fewer leukocytes to safeguard itself from infection (Davis et al. 2008)? Or does a high H:L ratio indicate the lack or presence of parasites (Davis et al. 2008)? Besides ambiguous interpretations, relative and absolute heterophil counts are affected by co-variables that are often not controlled nor accounted for such as: age, sex, environment, hormonal and cytokine status, disease, stress, and diet at the time of collection (Maxwell and Robertson 1998). Even when considering these limitations, the H:L ratio is still the most widely used metric to infer bird health and is still widely implemented in avian research (Carleton et al. 2012, Taves et al. 2017, Younjung et al. 2018). We took steps to control for co-variables but it is not feasible to fully account for all the factors that may be affecting the H:L ratio. Other metrics of bird health could be implemented to circumvent the uncertainty surrounding the H:L ratio, such as determining at blood parasite loads via PCR (Valkiūnas et al. 2008, Coker et al. 2017). In future studies, using genetic methods to infer bird health may result in higher-fidelity analyses but these methods come at higher costs.

Sample characteristics and spatiotemporal replication

The level of spatiotemporal replication, alongside the species represented, limit the level of generalizability of the study. We can only discuss trends for the four focal species, restricted to the study region in the Central Coast of California. Bird-landscape studies tend to implement larger spatial scales, often comprising over 40 sampled plots or 1000 km^2 of land (c.f. Moreira et al. 2005, Laurance et al. 2013, Dayananda et al. 2016). Our sample represented 13 farms no larger than 9 km^2. Furthermore, the Central Coast of California's cultural and environmental history, with Native American fire regimes and food-borne pathogen outbreaks, may lead to site-specific trends between bird health and landscape composition (Gifford-Gonzalez et al. 2013, Cuthrell 2013, Karp et al. 2015a, b). Further site sampling within the Central Coast would allow for more cogent discussions on the large-scale trends of bird health on agricultural lands in the region. It may also be useful to sample over larger spans of time, both during and outside the summer growing season. This wider sampling period would not only allow for more data to be modeled, but could also more rigorously account for differences in the reproductive cycles of species; our data was collected over the span of two months. Limitations in spatiotemporal reproducibility and the nature of the H:L ratio require caution when discussing larger agricultural trends but also foment further research on bird-agriculture interactions.

Broader implications

The Central Coast of California is facing rapid agricultural change that must be quantified to assess its impacts on wildlife (Wild Farm Alliance 2016). Within this study, bird health was marginally impacted by landscape quality in an unexpected fashion. Higher proportions of agriculture resulted in better "quality" landscapes in terms of improved bird health for one species, song sparrows. Conversely, reproductive readiness most strongly drove bird health, where higher levels of readiness were associated with improved health for song sparrows. Our preliminary findings suggest that agriculturalists may be providing foraging and habitat resources to song sparrow communities, linked to marginally improved health for this species (Moreira et al. 2005, Civantos et al. 2018). This finding is not to ignore the deleterious impacts humans have had on their surroundings, such as rapid deforestation and pollution of the biosphere. Nonetheless, our work encourages us to more critically assess and describe humans' impacts on their surroundings. Instead of demonizing birds or agriculturalists, our results propose that we need to recognize humans as a keystone species in agricultural landscapes. We must redefine the role of farmers in agricultural spaces as wildlife stewards. We also need to provide incentives for farmers to create multi-use spaces that both provide critical resources for birds and maintain productivity. Thresholds for particular crops or land cover types may be a tactic to foment multi-use landscapes. (Jerrentrup et al. 2017). Similarly, it may be necessary to provide additional safeguards for birds at the peak of their reproductive cycle, for instance moving mowing and pesticide application dates, but further research is required to substantiate such policy prescriptions (Grice et al. 2004). A larger sample size, other bird species, and additional metrics of bird health should be considered to ascertain at a larger spatiotemporal scale how agricultural land use changes in the Central Coast are impacting avian community health. Farmers are not destined to desecrate the environment – they should be supported in becoming active ecosystem managers that improve landscape heterogeneity and avian health.

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APPENDIX A: Normalizing the H:L Ratio

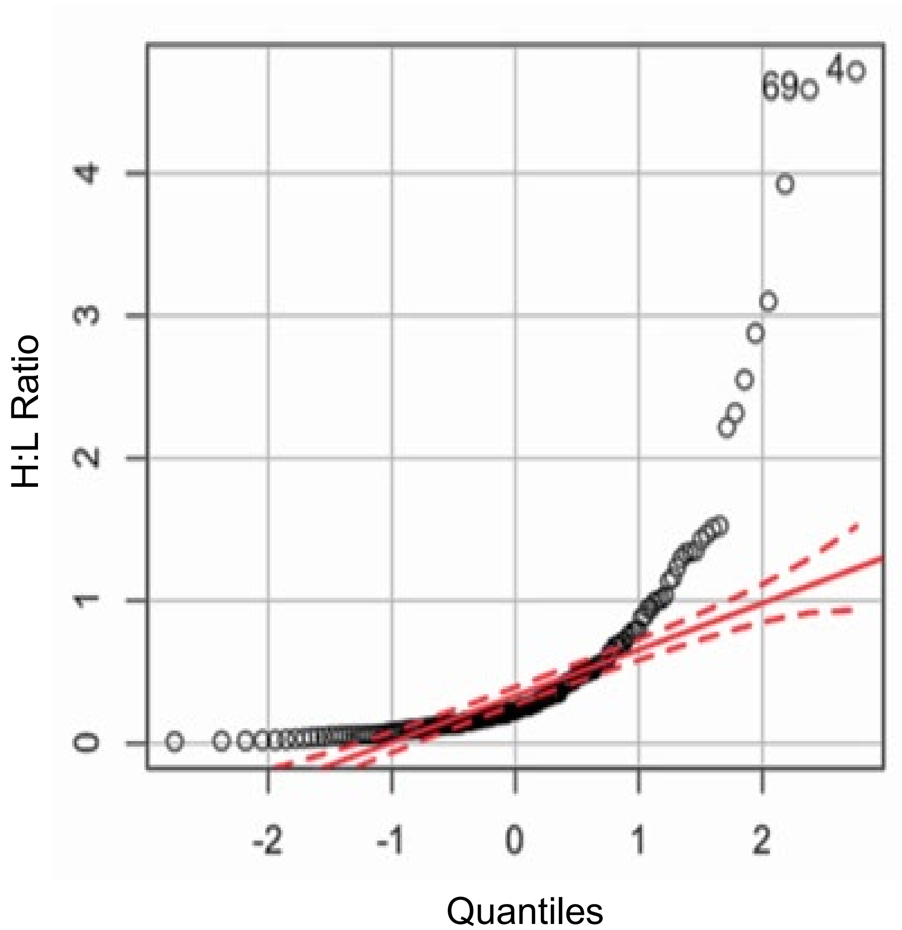

Figure A1. QQ-plot testing for the H:L ratio's normal distribution. Note that the ratio has an extremely curved distribution, greatly deviating from the red-lined boundary demarcating a normal spread.

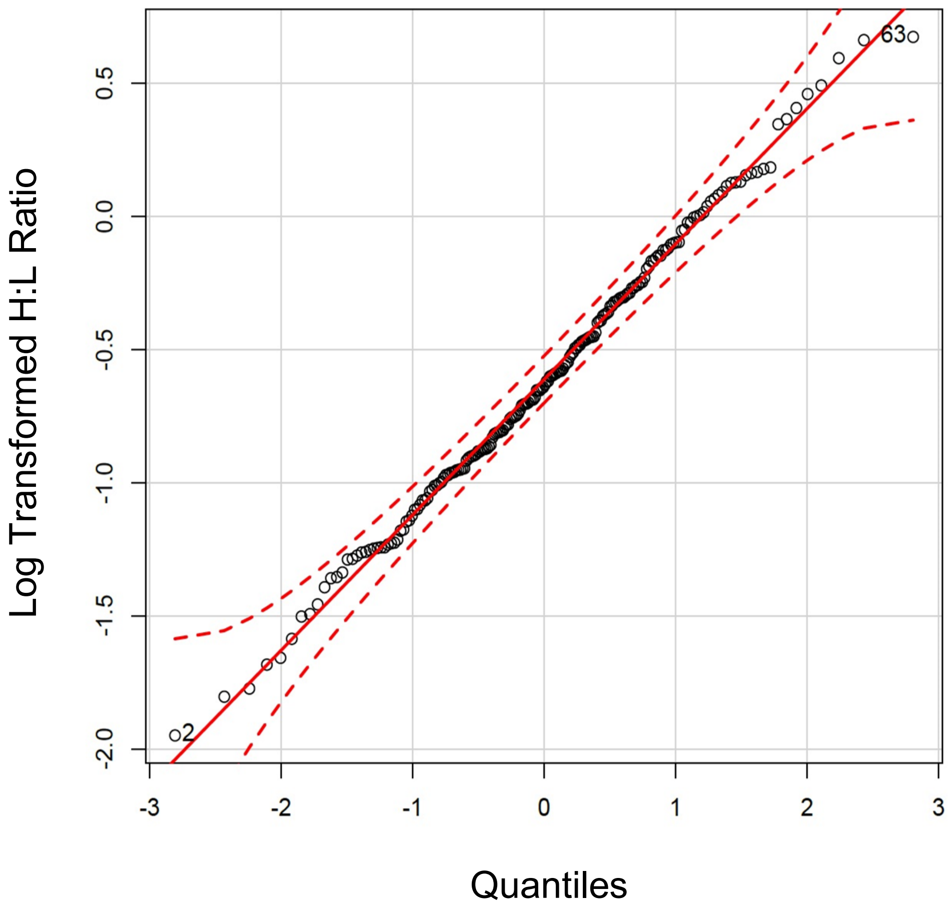

Figure A2. QQ-plot testing for the log transformed H:L ratio.'s normal distribution Notice that this plot is more normally distributed than the plot with the raw H:L ratios (Figure A1) as the transformed ratio now lies between the red-lined boundaries demarcating a normal spread.

APPENDIX B: Bird Age and Sex Demographics

Table B1. Bird age distribution by farm. Each bird was assigned an age based on the following categories: after hatch year (AHY), after second year (ASY), hatch year (HY), and second year (SY). Birds that could not be aged were given the code N/A.

	Age				
Farm	**AHY**	**ASY**	**HY**	**SY**	**N/A**
1	4	0	8	0	0
2	4	0	5	1	0
3	14	0	4	1	0
4	13	0	0	0	0
5	12	1	5	4	1
6	8	1	18	0	0
7	14	0	2	0	0
8	9	2	7	0	0
9	2	0	3	0	0
10	4	0	0	0	0
11	11	0	12	0	0
12	4	0	10	1	0
13	15	0	0	0	0
Total	**114**	**4**	**74**	**7**	**1**

Table B2. Bird sex distribution by farm. Birds were categorized as either being male or female. There was a large proportion of birds that could not be sexed (denoted as N/A) due to their immature sexual organs.

	Sex		
Farm	**Female**	**Male**	**N/A**
1	1	3	8
2	1	4	5
3	8	7	4
4	2	7	4
5	6	11	6
6	3	6	18
7	5	8	3
8	3	8	7
9	1	1	3
10	1	3	0

11	4	7	12
12	2	3	10
13	7	8	0
Total	**44**	**76**	**80**

APPENDIX C: Reproductive Readiness Across Bird Species

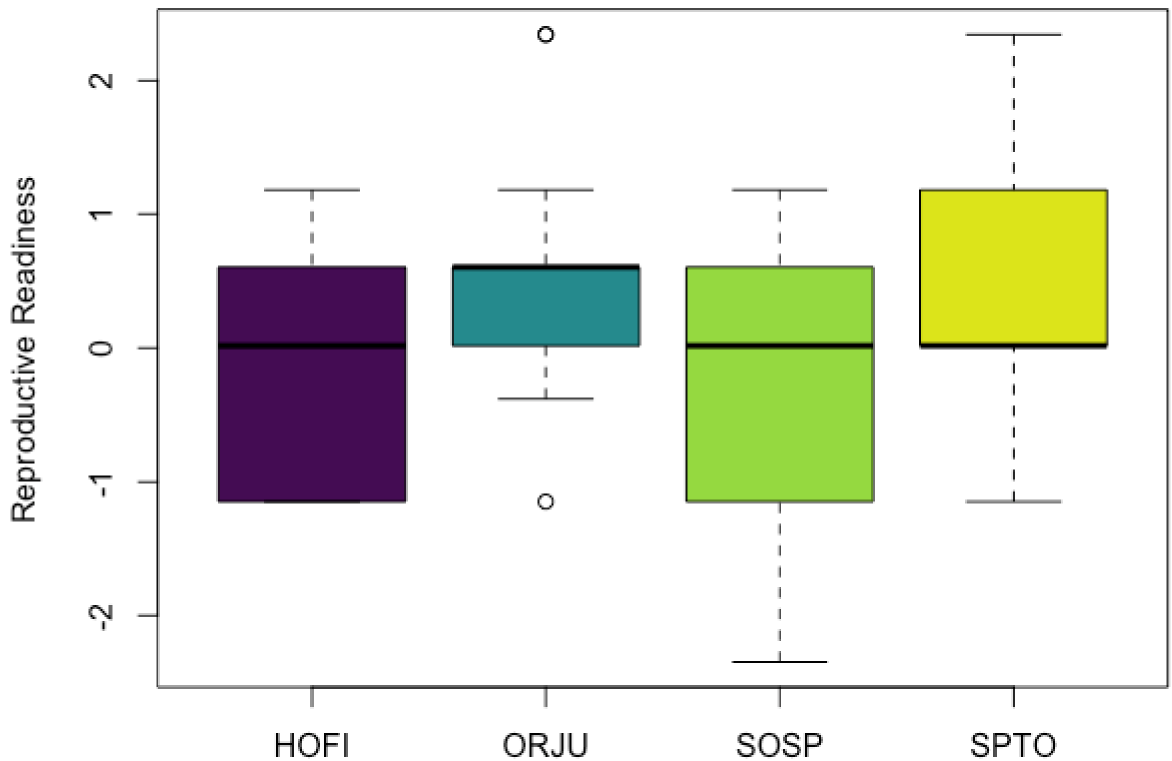

Figure C1. Differences in reproductive readiness between bird species. Each bird species is shown in its own color, referred to by its bird banding alpha code (United States Geological Survey 2018).