THESIS

ASSESSING BIRD-MEDIATED ECOSYSTEM SERVICES AND DISSERVICES IN COLORADO APPLE ORCHARDS

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ABSTRACT

ASSESSING BIRD-MEDIATED ECOSYSTEM SERVICES AND DISSERVICES IN COLORADO APPLE ORCHARDS

Agriculture provides food, fuel and fiber to our growing human population and as the largest terrestrial biomes, crop and pastureland are major drivers of land use change. Small organic farms have the potential to provide habitat for biodiversity while also contributing to food security. My research examined the characteristics of organic apple orchards associated with habitat use of human-adapted and human-sensitive birds as well as how birds influence fruit production positively through insect pest control and negatively through fruit damage. I used a stratified study design to survey birds, observe bird frugivory, capture birds to collect and analyze avian fecal samples, and assess bird and insect damage with an exclosure experiment in small organic farms in western Colorado. I calculated species richness and community similarity among apple blocks and adjacent habitat and evaluated bird habitat use as a function of orchard characteristics (i.e., location in orchard, size of apple block or edge-to-area ratio). I calculated the proportion of bird observations associated with apple frugivory and the proportion of fecal samples that were positive for codling moth DNA to identify bird species that could affect production. I compared bird damage to apples as a function of orchard characteristics and investigated factors that influenced codling moth damage, including access to fruit and moths by birds. I found that organic apple orchards in this region provided habitat for 42 human-adapted and 27 human-sensitive bird species and the bird community in orchards was relatively similar to shrub/tree habitat adjacent to apple blocks. There was sufficient data to model habitat use by

seven species; however, use did not vary as a function of the orchard characteristics I measured. Similarly, apple damage by birds and codling moths was consistent within and across apple blocks that varied in size and variety. However, codling moth damage was negatively associated with the exclusion of birds. The molecular technique used to detect codling moth DNA in fecal samples was successful and one species (brown-headed cowbird) had fecal samples positive for codling moth DNA. Five species of birds (Bullock's oriole, common raven, house finch, Lewis's woodpecker, and western scrub-jay) were observed foraging on apples. However, the effect of birds as either agents of fruit damage or pest control in this agroecosystem appeared rather minor. These results demonstrate that organic apple orchards have the potential to provide habitat for diverse bird communities, including species typically sensitive to human activities. Further, because rates of bird-induced fruit damage were low and attributed to a small subset of the avian community, these agroecosystems may provide bird habitat without compromising production.

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CHAPTER ONE

WILD BIRD USE OF ORGANIC APPLE ORCHARDS AND THEIR IMPACTS ON PRODUCTION

INTRODUCTION

More than 40% of the land on Earth has been converted to agriculture or urban development (Foley et al. 2005), and much of the undisturbed habitat that remains is fragmented by infrastructure associated with these land uses (Barnosky et al. 2012). Crop and pastureland are the largest terrestrial biomes (Foley et al. 2005), and land use change associated with agriculture is the leading driver of biodiversity loss worldwide (Vitousek et al. 1997). As the demand for food increases with population growth (United Nations et al. 2015) and changing diet preferences (Tilman et al. 2001), sustaining productive agroecosystems that also conserve biodiversity is more important than ever.

The majority of agricultural lands are privately owned and occur disproportionally in biologically productive areas (Tilman et al. 2002). Thus, these lands have the potential to have very large positive or negative effects on biodiversity and human well-being. The direct costs of increased agricultural production and landscape simplification include species extinctions, increased nutrient runoff, water and air pollution, and negative impacts on human health through exposure to pesticides and livestock pathogens (Tilman et al. 2001). Other issues such as the poisoning of non-target arthropods by pesticides can have unintended consequences for agricultural production through the loss or decline of populations of pollinators (Hooven et al. 2013) and the natural enemies of insect pests (Pimentel 2005).

Yet agriculture is critical for global food security (Power 2010), supports the economy of many nations (The World Bank 2016; USDA National Agricultural Statistics Service 2014), and can have demonstrable co-benefits for biodiversity (Altieri 1999; Simon et al. 2010). Agroecosystems contribute to a variety of ecosystem services including carbon sequestration, regulation of soil and water quality and cultural services (Power 2010), and have the potential to provide habitat for diverse plant and animal communities. For example, some agricultural landscapes can provide benefits for even human-sensitive species by buffering patches of intact habitat against the negative effects of urbanization and facilitating animal and plant propagule movement through fragmented landscapes (Daily et al. 2001; Ricketts et al. 2001).

Ecological research in agricultural systems has focused largely on the detrimental impacts of agriculture on biodiversity and the "ecosystem disservices" or negative effects of birds and other animals on crop production (e.g., (Anderson et al. 2013; Cummings et al. 2005; Elser et al. 2016; Gebhardt et al. 2011)). In contrast, the capacity of agroecosystems to support habitat for animal communities and the potential benefits of those animals for food production remain understudied (Peisley et al. 2015), although there are notable exceptions (Garfinkel and Johnson 2015; Kross et al. 2016; Kross et al. 2012; Perfecto et al. 2004; Zhang et al. 2007). Research on this topic suggests birds in particular can fill important, and sometimes irreplaceable, roles in ecosystem function, as well as providing benefits to human communities (Boyd and Banzhaf 2007; Şekercioğlu et al. 2004). Wild birds have the potential to contribute to pest insect, bird and small mammal control (Dale and Polasky 2007), seed dispersal (Greenberg et al. 1995; Hollander et al. 2010; Souza da Mota Gomes et al. 2008), pollination (Nabhan and Buchmann 1997; Şekercioğlu 2011) and decomposition (Bird et al. 2000; Şekercioğlu 2011).

Birds can also act as bio-indicators, providing early warning of environmental change (Naccari et al. 2009; Weber et al. 2008).

Organic fruit orchards are perfect systems for advancing understanding of the services and disservices that birds provide, as well as evaluating the capacity of agroecosystems to provide habitat for diverse animal communities. Fruit damage by wild birds can have serious economic impacts on producers, which have been well documented in some regions (e.g., Washington Honeycrisp apples $7267/ha, New York sweet cherries $5197/ha and Oregon blueberries $4571/ha (Anderson et al. 2013)). Similarly, birds can provide pest control services in orchards making small, yet valuable impacts on both insect numbers and fruit yield (Mols and Visser 2002; Peisley et al. 2016). Additionally, fruit orchards can vary in their capacity to provide quality habitat for bird communities depending on orchard size, plant diversity, management practices such as pest control strategies, and surrounding land cover (Belfrage et al. 2005; Bouvier et al. 2011; Robertson et al. 1990).

In western Colorado (USA), organic apples (*Malus domestica*) are an important cash crop that appear to provide habitat for birds, yet the composition of the bird community and the degree to which individual species cause damage to apples or play an active role in pest mitigation is unknown. Anecdotal observations by farmers suggests that birds are foraging on apples, although similar to other regions, levels of damage are reported to be varied and localized (Tracey et al. 2007). A number of farmers have adopted minimal measures such as visual or auditory deterrents to prevent birds from depredating apples.

Although wild birds are capable of causing fruit damage, the codling moth (*Cydia pomonella*; Lepidoptera: Tortricidae) is considered the most economically important pest for apples in this region. The codling moth is capable of causing extremely high levels of damage,

up to 90% of the fruit crop, if left uncontrolled (Caprile 2011). Adult moths emerge in spring and lay eggs directly on apples and leaves (Agnello and Kain 1996). When the larvae hatch, they cause damage by burrowing into apples where they undergo five larval instar while feeding on the developing fruit and seeds (Cranshaw and Hammon 2013). When fully developed, the larvae leave the fruit for the bark or soil to spin cocoons and pupate. There are typically three generations of codling moth every year in western Colorado, with the last generation overwintering as pupae to reemerge in spring (Cranshaw and Hammon 2013). Organic farmers use an integrated pest management approach including pheromone treatments, organic pesticides, and cultural practices in an attempt to keep damage levels under control. Control methods can be costly (e.g., approximately $99/ha for organic insecticide (Klonsky and Stewart 2014)) and labor intensive (e.g., repeated sprays every 7-14 days). As insectivorous predators, some birds may be able to supplement, or reduce the need for, these practices and provide a valuable service to organic farmers by contributing to the reduction in codling moth populations and damage (Baumgartner 1999; McAtee 1912; Peisley et al. 2016; Solomon et al. 1976). Although it has been suggested that the pest control service provided by birds outweighs the damage they cause (Henderson 1913), few studies have quantified this potential tradeoff while also documenting the extent that agroecosystems provide refuge for birds in an increasingly fragmented and anthropogenic world.

The objectives of this study were to characterize the bird community associated with organic orchards and to quantify the nature and magnitude of services and disservices provided by human-adapted and human-sensitive birds in these agroecosystems. I selected apple orchards as a study system because apples are economically important crops that are commercially grown in Colorado as well as 28 other states, and worldwide more than 63 million tons are produced

annually (USDA National Agricultural Statistics Service 2015; Yara 2016). My specific research questions were: 1) How does bird species richness and community composition differ between apple orchards and adjacent habitat, and what factors influence use by particular species within orchards?; 2) Which bird species depredate fruit?; and 3) What is the magnitude of fruit damage, and pest control in this system? I conducted bird surveys and foraging observations in and adjacent to apple orchards and assessed fruit and codling moth damage using an exclosure experiment to achieve the objectives of this study.

I predicted that apple blocks would have lower species richness than surrounding habitat types and that the bird communities would have little overlap (Tillman et al. 2000; Tracey and Saunders 2010). I also anticipated that habitat use would be greater along the edges of orchards than in the interior (Altieri 1999; Somers and Morris 2002; Tracey et al. 2007), and that these differences would be exacerbated in species known to be sensitive to human land use (Somers and Morris 2002). I expected only a small subset of the bird community would contribute to fruit depredation (Tobin 1989). Finally, I predicted that birds would inflict moderate levels of fruit damage, concentrated on the edges of the apple blocks (Somers and Morris 2002; Tracey et al. 2007), and that insect pest damage would be greater in apples where birds were experimentally excluded (Kellermann et al. 2008; Peisley et al. 2016; Van Bael et al. 2007). Understanding the ecological linkages between bird communities and orchards will help generate strategies for biodiversity conservation that are compatible with agricultural production.

METHODS

Study Region

This study was completed in partnership with three organic farms in Delta County, Colorado (38°51'00"N, 107°45'00"W, Figure 1.1). This area is an ideal location for fruit

production with cool nights, hot days and water from the North Fork of the Gunnison River. Delta County consists of just under 24 000 ha of irrigated agriculture, with more than 750 ha dedicated to orchards growing a variety of fruit crops in patches, or blocks, including apples, peaches, cherries and grapes (USDA 2014). Of these orchards, 91 farms grow a total of 244 ha of apples (USDA 2014). The average farm size in the county is 81 ha (median = 15 ha) (USDA 2014). In addition to agriculture, other major land cover types in this region include shrubland (e.g., Gambel oak (*Quercus gambelii*), serviceberry (*Amelanchier spp.*), greasewood (*Sarcobatus spp.*) and saltbrush (*Atriplex spp.*)) and woodland (e.g., pinyon (*Pinus edulis*)-juniper (*Juniperus osteosperma*), aspen (*Populus tremuloides*), spruce (*Picea spp.*) and fir (*Abies spp.*)) (Figure 1.1).

Study Design

Study sites were located on organic farms in Hotchkiss and Paonia, Colorado that were representative of organic fruit orchards in Delta County in terms of size, crops grown and general management practices. I reached out to all farmers growing apples in the county who had publicly available contact information (n = 16). Farms were selected based on three criteria: 1) informal conversations with farm owners indicating observed damage from bird and insect pests, 2) minimal use of bird control techniques and pesticides (i.e., organic) and 3) farmer willingness to participate. Due to limitations gaining access to operational organic farms, site selection was non-random; however, all farms that met the above criteria were included in the study. The average size of the three farms that met the criteria of the study was 52.86 ha (range 25.04 – 88.70 ha). I surveyed all apple blocks (n = 12) that were large enough to conduct the methods described below, where apple trees were producing fruit and where access was granted on the selected farms. All blocks that met these criteria were included in the study. The average apple

block size was 2.78 ha (range 1.19 – 5.99 ha) and each block contained approximately 2 – 3 apple varieties ($\bar{x}$ = 2.3, range 1 – 6); Gala and Honeycrisp were the dominant varieties. All sampling occurred during June – October 2015, although some data were collected in a subset of apple blocks or months, as described below.

I used a stratified study design to survey birds, observe bird frugivory, and assess bird and insect damage throughout each apple block. I defined edges as the outermost 18 m (i.e., approximately three rows of trees) of an apple block. As the apple blocks were embedded in a diverse landscape of agricultural crops, hedgerows and uncultivated vegetation, the type of habitat directly adjacent to the edges varied. Therefore, sampling within edges was further stratified into three categories of adjacent habitat: crop (i.e., peach and cherry), grass (i.e., irrigated hay and fallow fields) and shrubs/trees (i.e., vertical vegetation such as hedgerows).

Bird Surveys

Bird surveys were conducted in twelve apple blocks on three farms June – September 2015 using line transect surveys (n = 38 transects) (Buckland et al. 2001) to quantify species richness, community composition and habitat use by human-adapted and human-sensitive species. Since this study system is substantially altered by humans, I anticipated that birds more adapted to human-dominated landscapes would occupy and use the area more frequently than those sensitive to anthropogenic land uses. Therefore, I classified species as human-adapted if previous studies reported that occupancy/use, activity or abundance/density stayed the same or increased with urbanization or housing density. Human-sensitive species were defined as those for which occupancy/use, activity or abundance/density declined (see Appendix 1.1 for species classifications and references). If multiple studies reported conflicting findings on species' response to urbanization, the reference that was geographically closer to my study sites was used

(Farr 2015). When information on species' response to urbanization or housing density was not available from previous studies, species were categorized based on information in the Birds of North America species accounts (The Cornell Lab of Ornithology 2016).

Line transects were 50 m or 100 m long depending on the size and shape of the surveyed apple block. Standard protocol (Burnham et al. 1980) was used to survey each transect up to seven times ($\bar{x}$ = 6.3 $\pm$ 0.1). Observers (n = 2) walked each transect slowly and recorded all birds detected aurally or visually. The distance to each bird was estimated with the assistance of a laser rangefinder (Bushnell Sport 850 or Bushnell Yardage Pro 1000). The location where each bird was detected (i.e., interior, edge or adjacent habitat) was recorded, and survey covariate data (i.e., observer, date and time of survey, temperature, noisy or disruptive farm activity, wind and sky cover) and site covariate data (i.e., farm ownership and transect length) were also collected. Surveys were conducted approximately 30 min before sunrise to approximately four hours after sunrise (05:45 – 10:45 h), and were terminated during periods of heavy rain, fog or high winds. Additionally, as all survey sites were on operational farms, surveys were not conducted during application of organic pesticides or during the four-hour re-entry period following application.

Bird Foraging Observations

Behavioral observations were conducted in apple blocks on three farms July – September 2015, in both the interior (n = 8 blocks) and along the edges (n = 10 blocks; cherry n = 3 edges, peach n = 4, grass n = 3, shrubs/trees n = 4) of the blocks. Focal-animal sampling methods described by Altman (1974) and used by Lindell et al. (2012) for the express purpose of identifying the relative importance of frugivorous species, were modified for use in apple orchards in this study. Observers (n = 4) began each observation session in either the interior, or near the edge of an apple block and slowly walked between the rows of trees searching for birds

for 30 min. When a bird was detected in an apple tree, the observer kept the bird in sight for as long as possible and used a handheld digital recorder (Olympus model: V405171SU000) to log the species, number of conspecifics in the same tree, how many apples the bird damaged and the amount of time that individual spent feeding. When foraging events were observed, a handheld GPS (Garmin eTrex 20) was used to record the location of the event. Once a focal bird flew off or was lost from sight, the observation of that individual ended and the observer resumed searching for another bird. Results from pilot observations in 2014 suggested that feeding activity was not limited to a particular time of day, therefore surveys were conducted during the morning (sunrise to 10:30 h; n = 76 surveys), afternoon (approximately 12:00 to 14:00 h; n = 75) and evening (approximately 18:00 to 20:00 h; n = 75) for a total of 113 hours of field observations.

Bird and Codling Moth Damage

To comparatively assess apple damage by birds and damage by codling moths in the presence and absence of birds, netted bird exclosures (n = 55 trees) were installed after fruit set (July 2015) in eight apple blocks on three farms. Exclosures consisted of 19 mm mesh plastic netting (Bird-X, Standard BirdNet) and each enclosed 25 (± 10) apples. Unnetted control trees (n = 55) within 10 m of each paired exclosure tree were selected and 25 (± 10) apples were designated using colored flagging to denote the branch on which they were growing. Depending on the exclosure installation date and apple harvest date, apples in the experiment were assessed for bird and codling moth damage up to five times ($\bar{x}$ = 3.3 ± 0.1) from July – October 2015.

Bird damage was identified by v-shaped peck marks and subsequent scrapes on the skin and flesh of the fruit (Figure 1.2 A). Only unnetted control trees were assessed for bird damage. Codling moth damage was identified by diagnostic markings called stings (i.e., larval entry

points) and frass (i.e., excrement) (Figure 1.2 B). Stings indicate the entry point where larva burrow into the fruit, and frass indicates damage deep within the apple (Cranshaw and Hammon 2013). Both the number of apples damaged and the intensity of the damage, determined by the percent of the fruit pecked or number of stings and frass, were recorded.

Data Analysis

Bird species richness, community similarity, and habitat use – To compare species richness of human-adapted and human-sensitive species in apple blocks and adjacent habitat, I applied the selection framework outlined by Brose et al. (2003) to choose an appropriate species richness estimator based on the mean estimated sample coverage. Uneven detection probabilities between bird species effect estimator performance, therefore, sample coverage, several species richness estimates and confidence intervals were generated with program SimAssem (Reese et al. 2013). The second-order jackknife estimator was determined to be the most appropriate estimator based on the mean estimated sample coverage (range 30.5 – 59.5) (Brose et al. 2003). Jackknife estimators reduce bias due to sampling effort and species' rarity by subsampling from the entire sample to estimate the number of undetected species (Burnham and Overton 1979; Iknayan et al. 2014).

To compare community composition between apple blocks and adjacent habitats, I calculated a Jaccard similarity index for all pairwise combinations of habitat (i.e., apples, adjacent grass and adjacent shrub/tree) for both human-adapted and human-sensitive species. The Jaccard index is defined as the proportion of species that are common to both habitats or $S_j = n_{11}/(n_{11}+n_{10}+n_{01})$, where n_{11} represents the number of species common to both habitats, n_{10} represents the number of species unique to the first habitat and n_{01} represents the number of species unique to the second habitat (Real and Vargas 1996).

To test for differences in use of apple blocks by human-adapted and human-sensitive birds, I used single season, single species occupancy models (MacKenzie 2006). Failing to account for imperfect detectability results in underestimates of occupancy (MacKenzie et al. 2003), therefore I modeled both occupancy, or the probability of a site being occupied by a given species, as well as detection, or the probability of detecting at least one individual of a species, given it is present. Because bird home ranges extend beyond the boundaries of the surveyed apple blocks, the model assumption that a sampling unit is closed to immigration and emigration is not met. Consequently, I redefined the interpretation of bird occupancy to refer to habitat use rather than true occupancy (Bailey and Adams 2005).

In addition to the site covariates collected during the transect surveys discussed above, the size of each apple block where a transect was located and the edge-to-area ratio of each block were calculated using ArcGIS (ESRI 2014) and included in model building. Occupancy models included main predictor variables (i.e., farm ownership, habitat location, block size, and edge-to-area ratio) as well as other site and survey covariates that I predicted would influence detection (Appendix 1.2). Transects in the same habitat location type but less than 200 m apart were pooled in the analysis phase (n = 31). Detected birds were assigned to an appropriate transect (i.e., interior, edge crop, edge grass or edge shrub/tree) which were collapsed into two main categories, interior (n = 15 transects) or edge of apple blocks (n = 16). In order to avoid over parameterization, one of each set of covariates with a correlation value greater than $|0.7|$ was eliminated, or when the covariates represented competing hypotheses (e.g., size and edge-to-area ratio or survey date and time) they were included only in separate models (Anderson 2008). Continuous predictor covariates were all standardized $(x - \bar{x})/\sigma$. All possible combinations of remaining biologically-meaningful models were built, corresponding to hypotheses regarding

detection and habitat use probabilities (Doherty et al. 2012). I ran a preliminary analysis for each species to determine the model complexity that the data would support. When possible, single and additive effects, as well as two-way interactive effects between ownership and size, ownership and habitat location, and habitat location and size were considered to develop a concise model set for each species. Models with variables that did not converge or could not be estimated were eliminated from the model set.

I used package RMark (Laake 2013) in R (R Core Team 2015) to construct and compare competing occupancy models for program MARK (White and Burnham 1999). Model selection was based on Akaike's Information Criterion for small sample size (AICc) which balances model fit and parameter precision to select the most parsimonious model (Hurvich and Tsai 1993). To address potential lack of independence among transects that arose from the small and patchy landscape, only birds that were observed using the apple blocks during transect surveys were included in the analysis of bird use; flyover birds or birds in adjacent habitat that could not be assigned to a designated transect were excluded. To account for any remaining overdispersion that I was not able to eliminate with my study design, model fit for each species was assessed using the most global model that fit the data. I used a parametric bootstrap procedure (MacKenzie 2006; MacKenzie and Bailey 2004) with 10 000 simulated datasets in the unmarked package (Fiske and Chandler 2011) in R. For species that showed overdispersion in the data, the overdispersion correction parameter ($\hat{c}$) was used to adjust the model selection results and calculate QAICc values. The most parsimonious models for each species were determined by comparing the difference in (Q)AICc values (Δ(Q)AICc) and model weights (w) (Anderson 2008). Estimates of use and detection probability were interpreted from the top model. I assessed

the strength and directionality of each occupancy covariate and calculated the cumulative model weights as the sum of *w*'s from all models that included the effect (Anderson 2008).

Bird and codling moth damage – To determine which bird species damage fruit, I identified the species responsible for damage through direct observation of foraging events. Observations of birds foraging on apples were pooled by species to calculate the proportion of observations in which a species was damaging fruit.

To determine the intensity of bird damage to apples, I quantified damage as a function of apple block and apple characteristics. Because data from the apple damage assessments did not meet normality assumptions (Shapiro-Wilk W = 0.66, p = 4.20e-10), I used a Kruskal-Wallis test to compare median bird damage to apples as a function of location within the apple block (i.e., interior vs. edges) and apple variety. Damage was assumed to be cumulative (i.e., the number of bird damaged fruits would only increase on subsequent assessment visits) therefore only the assessment visit with the greatest number of apples damaged was used in the analysis. This selection of data for analysis accounted for the occasional bird-independent loss of fruit from the trees over time. Only the two main varieties of apple trees (i.e., Gala (n = 20 trees) and Honeycrisp (n = 23)) were included in the analysis as other varieties had sparse data ($n \leq 3$). The proportion of bird-damaged apples was arcsine transformed to stabilize the variance and account for the large number of zero values. Additionally, because of the large number of zero values, raw counts of apples in each damage category (i.e., < 1%, 1-10%, 11-50% or > 50% of an individual apple damaged by birds) are reported to describe bird damage intensity.

To investigate the factors that influence apple damage by codling moths, I quantified the damage as a function of bird access (i.e., netted treatment or unnetted control) and other apple block characteristics. I used a binomial logistic regression for small samples, non-normal data

and heteroscedastic variance. Only treatment and control trees, and apples that were well matched in terms of variety, height above ground level (i.e., above or below 2 m) and habitat location within the orchard (i.e., interior (n = 14 pairs) or edge (n = 21)) were included in this analysis. If apples inside exclosures showed signs of birds accessing the fruit (i.e., bird damage to fruit), then it was assumed that birds could access insects within the netting as well, so the pair of treatment and control trees were excluded from the analysis. Additionally, any apples that showed signs of codling moth damage at the time of the exclosure installation were excluded from further assessment. As described above, damage was assumed to be cumulative, therefore only the assessment visit with the greatest number of apples damaged per tree was used in the analysis.

Variables of interest included the netting treatment, habitat location, apple variety, harvest date and farm ownership (Appendix 1.3). Based on variance inflation factor values (VIF), there was evidence of collinearity between the ownership and location covariates (VIF > 10). Although the ownership covariate accounts for unknown or unmeasured elements of the study (e.g., management practices that could not be quantified), it was necessary to remove this covariate as habitat locations were a main effect of consideration. Diagnostics of the most general model also suggested that extra-binomial variation was a problem which was remedied using a quasi-likelihood approach to handle overdispersion with package dispmod (Scrucca 2012) in R. All combinations of singular and additive effects were used in creating a candidate model set. Pretending variables, which added additional parameters to a model yet did not significantly reduce the deviance from the null model, were removed from the candidate model set (i.e., harvest date). Model selection and ranking were based on AICc with small sample size correction (Burnham and Anderson 2002).

RESULTS

Bird Species Richness, Community Similarity, and Habitat Use

A total of 59 bird species were detected during transect surveys and foraging observations including 40 human-adapted species and 19 human-sensitive species (Appendix 1.1). There were apparent differences in species richness estimates for both groups of birds, with the highest estimates in adjacent shrub/tree habitat, followed by apple blocks and the lowest in adjacent grass habitat (Table 1.1). However, the only estimates without overlapping confidence intervals were between the grass and shrub/tree habitats for human-adapted species and between the human-adapted and human-sensitive species within the shrub/tree habitat. The composition of the bird community was most similar between apple blocks and adjacent shrub/tree habitat (Jaccard similarity index (S_j) human-adapted: $S_j = 0.64$, human-sensitive: $S_j = 0.73$), followed by apple and adjacent grass habitat (human-adapted: $S_j = 0.44$, human-sensitive: $S_j = 0.27$) (Figure 1.3 and Appendix 1.4). Adjacent shrub/tree and adjacent grass habitat communities were least similar (human adapted: $S_j = 0.39$, human-sensitive: $S_j = 0.24$).

Of the 37 species detected in the apple blocks during transect surveys, 7 had sufficient detections for occupancy modeling. The American robin (*Turdus migratorius*), Brewer's blackbird (*Euphagus cyanocephalus*), cedar waxwing (*Bombycilla cedrorum*) and house finch (*Haemorhous mexicanus*) are classified as human-adapted while human-sensitive species included blue grosbeak (*Passerina caerulea*), lesser goldfinch (*Spinus psaltria*), and Lewis's woodpecker (*Melanerpes lewis*). The estimates of use (Ψ) for blue grosbeak, cedar waxwing, lesser goldfinch, and Lewis's woodpecker had large 95% confidence intervals and low estimates of detection (p) (Table 1.2). For human-adapted species, the house finch and American robin had high probabilities of use (> 0.70), but the Brewer's blackbird and cedar waxwing had estimates

of use < 0.30. All three of the human-sensitive species modeled had relatively high probabilities of use, > 0.5. Across all visits, detection probability for all species ranged from 0.09 – 0.49 (Table 1.2).

Habitat use was explained best by a constant occupancy structure (no covariates) on Ψ (psi) for six out of the seven species modeled; the edge vs. interior habitat location covariate was in the top model for lesser goldfinch (Table 1.3). Covariates of interest (i.e., location, size of apple block, and edge-to-area ratio of blocks) appeared in model sets with considerable empirical support (i.e., Δ(Q)AICc < 2) (Anderson 2008) for some human-adapted and human-sensitive species. Although these models explained substantial variation in the data, the regression coefficients did not indicate significant effects for any of the modeled species (Appendix 1.5).

Bird and Codling Moth Damage

Of the bird species recorded in the apple blocks during foraging observation surveys (n = 52), 21 were observed in apple trees, and only 5 of those were observed damaging fruit. Two of the species inflicting damage to apples (Bullock's oriole (*Icterus bullockii*) and western scrub-jay (*Aphelocoma californica*)) were observed infrequently (n = 4 and n = 1, respectively) and are therefore excluded from further discussion. The three species with sufficient observations (n > 5) that damaged fruit were common raven (*Corvus corax*) (n = 12), Lewis's woodpecker (n = 35), and house finch (n = 129). The proportion of observations during which these species damaged apples was 0.75, 0.69 and 0.12, respectively.

Very few of the unnetted apples (2.3%, n = 1205) had measurable bird damage. There were no statistically significant differences between apple damage on interior trees or edges adjacent to crops, grass or shrubs/trees (Kruskal-Wallis $\chi^2 = 4.25$, p = 0.24), nor among apple varieties (Kruskal-Wallis $\chi^2 = 3.32$, p = 0.07). Of the fruits with bird damage, moderate levels of

damage (1-10% and 11-50% of the apple surface area) were observed more often across all locations and varieties (n = 24 apples) compared to extreme levels of damage (< 1% or > 50%) which were observed infrequently (n = 4).

Damage from codling moths was recorded on 7.5% (n = 1481) of all paired treatment and control apples assessed for damage. Codling moth damage was greater in unnetted control trees than in treatment trees where birds were excluded (McNemar's $\chi^2 = 5.26$, $p = 0.02$). The treatment effect alone appeared as a strong top model (ΔAICc < 2, $w = 0.999$) (Appendix 1.6) and the regression coefficient indicated a statistically significant negative trend ($\beta = -0.85$ (95% CI = -1.64, -0.05)).

DISCUSSION

This study demonstrates that organic apple orchards in western Colorado provided habitat to a diverse bird community similar to that of adjacent shrub/tree habitat. In return, there was no evidence that birds reduce codling moth damage, but apple damage by birds was also minimal, and restricted to several species. These results suggest it is possible to conserve diverse birds in novel habitats while sustaining organic production.

Contrary to the prediction that apple blocks would support fewer species, species richness estimates in apples and adjacent habitat had overlapping confidence intervals. However, the trends suggest that species richness in apples was lower than that of the adjacent shrub/trees but higher than adjacent grass habitat. The bird communities were also far more similar than predicted in the apples and adjacent shrub/tree habitat, with only a few species restricted to one habitat type or the other. In contrast, there was little overlap in composition observed across apple blocks and adjacent grass habitat. Interestingly, these trends did not differ between human-adapted and human-sensitive species, although the total number of human-adapted birds was

greater and the trends were more pronounced. With just over 70% of human-adapted and human-sensitive species observed in apples, this agroecosystem appears to provide habitat for a large number of species in the study region. These findings, in a system which includes a mosaic of fruit orchards and adjacent strips of uncultivated vegetation, are consistent with recent literature demonstrating that planting hedgerows can enhance avian diversity in field crops (Batáry et al. 2010; Kross et al. 2016). Although orchards are not a substitute for undisturbed natural lands (Round et al. 2006), my results suggest that the benefits of this management practice could be extended to birds in more structurally diverse orchard systems, even for some birds typically sensitive to human activities. For example, woodland birds such as the blue grosbeak (*Passerina caerulea*) or Lewis's woodpecker, a Watch List species (Rosenberg et al. 2014), may benefit from the structure and food resources provided by orchards and adjacent linear patches of shrubs and trees.

Estimates of use for most modeled bird species in this system were relatively high and were not strongly associated with site-level covariates. However, there were several trends worth highlighting. For example, for the three species where apple block size was in the top model set (i.e., Brewer's blackbird, cedar waxwing and blue grosbeak), the regression coefficients showed a greater probability of use in larger sized blocks. Additionally, both the lesser goldfinch and Lewis's woodpecker had lower probabilities of use in the edge compared to the interior of the apple blocks. These trends are in contrast to previous literature that suggests that bird habitat use in orchards is greater in smaller plots (Belfrage et al. 2005) and along edges (Somers and Morris 2002).

Nevertheless, based on the 95% confidence intervals of the modeled regression coefficients, I found no significant relationships between edge/interior locations, apple block

size, or edge-to-area ratio and habitat use by any bird species. There are several possible explanations for this outcome. The species detected frequently enough to meet the requirements of the model had high occupancy estimates and may be using all apple blocks often and indiscriminately. Edge habitat in particular may be utilized more often in a study area with larger apple blocks and a greater contrast between the fruit crop and adjacent habitat. In addition, the apple blocks in this region are relatively similar in size and shape; bird habitat use may vary in response to apple block size or edge-to-area ratio in landscapes with greater heterogeneity in orchard size and configuration.

Levels of fruit damage by birds were low, and in contrast to my predictions, there were no discernible spatial patterns of damage. Farmers used a variety of approaches to deter birds from their crops, which may have helped minimize damage. Previous research has shown that these crop protection techniques have various levels of efficacy depending on the bird species and crop involved (Bomford and O'Brien 1990; Conover 1982; Tracey et al. 2007). However, these deterrent efforts were minimal and sporadic, making them impractical to incorporate into this study; therefore, I used farm ownership as a proxy variable to account for management practices among apple blocks.

Although farmers in the county describe bird damage to apples as moderate, other fruit crops in the region, such as cherries and grapes, experience higher reported levels of fruit depredation. Auditory and visual deterrents were often directed at birds in these adjacent crops and were not applied in a systematic manner, making any effects difficult to quantify. As multiple fruit crops are often grown on the same farm, the variation in damage among fruit crops may affect the willingness of producers to support or encourage avian diversity as a part of their agroecosystem, despite my findings that birds inflict little damage to apples. Although beyond

the scope of this study, it is also conceivable that birds damaging fruit could have been targeting codling moth larvae inside the apples. While in some systems, birds appear not to select for or against insect-infested food (Koenig and Benedict 2002), in other seed-dispersal studies, they appear to avoid it (Traveset et al. 1995) or select for it (Valburg 1992). While no codling moth signs were detected on any of the unnetted control apples with bird damage in this study, controlled feeding choice experiments could be used to more conclusively determine if birds preferentially attack or avoid infested apples.

The foraging observation method I used to identify bird species responsible for damage is valuable as it can provide more accurate information than bird surveys alone and may be useful for informed decision making (Lindell et al. 2012). Because of the conspicuousness of birds and the high variability in damage they cause, objective estimates of damage by producers can be difficult. Bird damage is often attributed to the most abundant or noticeable species (Lindell et al. 2012), and these observations can influence control decisions (Canavelli et al. 2013). Four of the five species depredating fruit in this study were classified as human-adapted; however, the Lewis's woodpecker, a human-sensitive species, also inflicted damage. The subset of birds causing damage was previously unknown in this system, although informal conversations with farmers suggested that house finches were responsible for much of the damage and early natural history literature described Lewis's woodpecker's as occasional orchard visitors (Henderson 1913). Direct observation, although effective for describing bird species depredating fruit, is not an effective method for identifying avian predators of the codling moth (Symondson 2002). Thus, I was unable to compare species damaging fruit and consuming pests directly in this manner.

Apple damage from codling moths was relatively low (7.5%), but could still have important economic consequences for producers; acceptable levels of damage typically range from 1 – 5% (Arthurs et al. 2005; Judd et al. 1997). Contrary to my expectations, I found less codling moth damage on apples protected from birds with netting, providing no evidence that birds were mitigating codling moth damage on apples in this system. Several factors could explain the discrepancy between my results and predictions. First, the plastic mesh netting may have made it more difficult for observers to identify codling moth damage within exclosures and it was not practical to temporarily remove the netting and reinstall it after each assessment. Second, it is possible that the exclosure material (i.e., 19 mm plastic mesh) deterred codling moths. However, adult codling moths are typically 10 – 12 mm in length with a wingspan of 15 – 20 mm (Agnello and Kain 1996), so they should have been able to move through the mesh to access the fruit. Additionally, similar exclosure experiments within apple orchards have used even smaller mesh (i.e., 15 mm) and found significantly more codling moth damage within exclosures (Peisley et al. 2016). Discrepancies between my results and other exclosure experiments may be due to different installation time (before flower vs. after initial fruit development) or differences in avian communities (Mols and Visser 2002; Peisley et al. 2016; Solomon and Glen 1979). Finally, it is conceivable that the mesh netting protected arthropod predators such as lacewings, earwigs, or spiders from birds, resulting in greater predation on codling moths and less fruit damage within exclosures (Karp and Daily 2014). Because it is unclear whether my findings are due to exclosure design or are biologically meaningful, I am cautious in interpreting these results without further experimentation.

Study Limitations and Future Research Priorities

Several limitations of this study warrant further discussion. First, these data were collected over a single season and as such, I was not able to assess temporal variability in bird habitat use or ecosystem services and disservices. There is reason to believe these systems are not static; for example, during pilot observations in 2014, common ravens were not observed damaging fruit, or even in the study area, yet were present and observed consuming apples frequently in 2015. Further, inter-annual variation in climate influences crop production and is likely to have an impact on farm management and wildlife use. The study region experienced a reduced fruit crop in 2015 resulting from a late frost, which may have influenced management practices (e.g., some farmers applied less than normal or almost no organic pesticides), as well as insect and bird abundance and activity.

There may be variables that I did not measure that would have better explained habitat use by birds as well as bird and codling moth damage. Relevant landscape scale variables might include the proportion of undisturbed and human-altered habitat at scales of 500 – 2000 m and the distance to anthropogenic features such as residential or agricultural structures (Garcia and Ortiz-Pulido 2004; Petit et al. 1999). Population parameters such as the density of birds and codling moths could also be considered as densities of prey have been shown to relate to bird presence (Blake and Hoppes 1986) and bird density is positively correlated with avian crop damage (Tracey et al. 2007). Finally, farm scale activities such as the volume and frequency of insecticide application, crop yield and cultural practices including fruit thinning may relate to bird and codling moth presence and damage (Hallmann et al. 2014; Hampe 2008). Because these farm scale practices were impractical to incorporate into this study, I used farm ownership as a proxy variable for accounting for management practices among apple blocks.

Building on the scope and outcomes of this study, I highlight several priorities for future research. Because of the diversity of crops grown in the region and even within the boundaries of a farm, scaling this research up to the farm level could provide more complete information on the services and disservices provided by birds. Furthermore, evaluating the cost/benefit tradeoffs of various control methods would further support the decision making process. However, anecdotal comments from farmers suggests that there may be underlying factors that influence their appreciation of particular species that goes beyond economic or conservation value. For example, the Lewis's woodpecker appears to provide some intrinsic benefit to farmers who may be more willing to tolerate damage attributed to this species, than other, less charismatic birds. Social science methods, such as producer surveys, may help illuminate these non-monetary values and their influence on decision-making.

Landscape scale comparisons of bird habitat use in apple blocks and similarly sized patches of undisturbed natural areas could provide further insight into the relative conservation value of organic apple orchards. Additionally, although use by both human-adapted and human-sensitive species was generally high, presence alone is not necessarily an indication of habitat quality (Daily et al. 2001). Measuring bird survival and fecundity in apple orchards and adjacent habitat types should be a priority for studies assessing the value of orchards for biodiversity. In addition, birds may consume codling moths during life stages when the insects are not on the fruit (i.e., adult moths and pupae). Investigating whether birds consume codling moths at all life stages would provide a more comprehensive assessment of their potential role in pest control and associated ecosystem services (Baumgartner 1999).

This study was focused on organic apple production on Colorado's western slope. The climate and fauna in and around orchards in other regions of the world are likely to vary

substantially. A meta-analysis of the ecological role of animals in orchards from diverse sites could illuminate important variables affecting the nature and magnitude of animal-mediated ecosystem services. Finally, while there is a large body of literature comparing biodiversity in organic and conventional agroecosystems (Hole et al. 2005; Rahmann 2011), future research on birds in apple orchards could specifically assess fruit damage and pest control as it relates to pest management practices. I would predict that bird and codling moth damage would be lower in conventional orchards, but that these orchards would also support fewer bird species than organic farms (Hole et al. 2005).

Summary: Recommendations for Practice

Although several species were observed feeding on apples somewhat frequently, the low level of bird damage measured during this study suggests that wild birds are not a major concern for organic apple producers in this region. Given minimal damage by a small subset of the bird community, I do not recommend changing current management practices to exclude particular species from apple blocks. Additionally, since the majority of the species causing damage were human-adapted, there may be relatively low risk associated with actions designed to attract higher densities of human-sensitive species to orchards.

The moderate level of codling moth damage in this system suggests that this insect is being controlled relatively well by current organic pest management practices; however, there is the potential for pesticide resistance to develop or for outbreaks to occur (Martin and Garczynski 2016; Mota-Sanchez et al. 2008). Although I found no evidence that birds are mitigating codling moth damage, others have suggested that birds can provide additive services to organic farmers by extending the time between insect outbreaks (Mols and Visser 2002) or providing additive pest control during outbreaks in some agroecosystems (Garfinkel and Johnson 2015).

With the global population predicted to exceed 9.7 billion people by 2050 (United Nations et al. 2015), the expansion and intensification of land dedicated to agriculture seems probable (Tilman et al. 2002; Tilman et al. 2001). Regardless of how agricultural systems adapt to meet global demand, balancing food production with other ecosystems services provided by biodiversity in agroecosystems will become increasingly important (Tilman et al. 2002). Organic apple orchards in western Colorado provide habitat for a diversity of bird species, yet during this study, these birds did not appear to play a significant role in ecosystem services or disservices in this agroecosystem. Because levels of bird-induced fruit damage were low and attributed to a small subset of the avian community, organic orchards may provide bird habitat similar to adjacent uncultivated land with complex vegetation structure without compromising production. Further research across a network of study sites is needed to determine whether spatial and temporal variability in land cover, farm management practices, and seasonal weather variation influence bird habitat use and rates of ecosystem services and disservices.

TABLES AND FIGURES

Table 1.1. Second-order jackknife estimates of species richness (95% confidence intervals). Confidence intervals associated with richness estimates in the apple habitat overlapped those of the adjacent habitat types for both human-adapted and human-sensitive groups of birds.

	Species Richness Estimates (95% CI)	
	Human-Adapted	**Human-Sensitive**
Apple	35.79 (29.13, 53.19)	17.10 (13.32, 31.60)
Adjacent Shrub/Tree	47.64 (37.98, 67.71)	17.91 (14.77, 33.93)
Adjacent Grass	14.55 (14.01, 36.32)	14.88 (9.77, 29.29)

Table 1.2. Estimates of use ($\widehat{\Psi}$) and detection (p), and corresponding 95% confidence intervals from the top model for human-adapted and human-sensitive species with sufficient data for occupancy modeling.

Species	$\widehat{\Psi}$	**Lower 95% CI**	**Upper 95% CI**	**p**	**Lower 95% CI**	**Upper 95% CI**
Human-Adapted						
house finch	0.924	0.724	0.983	0.490	0.412	0.567
American robin	0.754	0.518	0.897	0.341	0.240	0.454
cedar waxwing	0.298	0.074	0.694	0.119	0.023	0.298
Brewer's blackbird	0.270	0.106	0.536	0.208	0.074	0.395
Human-Sensitive						
blue grosbeak	0.688	0.130	0.970	0.112	0.042	0.251
lesser goldfinch	0.532	0.148	0.882	0.210	0.112	0.349
Lewis’s woodpecker	0.523	0.174	0.851	0.092	0.010	0.198

Table 1.3. Top model sets (Δ(Q)AICc < 2) of occupancy model selection results for human-adapted and human-sensitive species. AICc values were used in models with $\hat{c}$ values = 1 and QAICc values were used in models with $\hat{c}$ values > 1. Number of parameters (k), model weight (w_i), log likelihood (-2LnL) and overdispersion parameter ($\hat{c}$) values are also reported.

Species **Model**	**k**	**(Q)AICc**	**Δ(Q)AICc**	w_i	**-2LnL**	$\hat{c}$
Human-Adapted						
American robin						
p(Time^2)Ψ(.)	3	97.603	0.000	0.405	190.500	2.1
p(Time^2) Ψ (Edge-to-Area)	4	99.471	1.867	0.159	188.858	2.1
Brewer's blackbird						
p(Time^2) Ψ (.)	3	62.995	0.000	0.191	58.350	1
p(Time^2) Ψ (Edge-to-Area)	4	64.100	1.105	0.110	56.744	1
p(Time^2 + Effort) Ψ (.)	4	64.642	1.647	0.084	57.308	1
p(Time^2) Ψ (Size)	4	64.696	1.701	0.082	57.364	1
cedar waxwing						
p(.)Ψ (.)	2	62.089	0.000	0.084	57.660	1
p(Observer) Ψ (.)	3	62.293	0.204	0.076	55.404	1
p(.)Ψ (Size)	3	62.478	0.390	0.069	55.590	1
p(~Observer) Ψ (Size)	4	62.969	0.881	0.054	53.431	1
p(.)Ψ (Edge-to-Area)	3	63.766	1.677	0.036	56.877	1
p(Effort) Ψ (.)	3	63.892	1.803	0.034	57.003	1
p(Time^2) Ψ (.)	3	64.086	1.997	0.031	57.197	1
house finch						
p(.)Ψ (.)	2	96.848	0.000	0.257	262.471	2.8
Human-Sensitive						
blue grosbeak						
p(Time^2) Ψ (.)	3	52.192	0.000	0.218	92.418	2
p(Observer) Ψ (.)	3	52.415	0.224	0.195	92.874	2
p(.)Ψ (.)	2	53.255	1.063	0.128	99.605	2
p(Time^2) Ψ (Size)	4	53.842	1.651	0.096	90.380	2
lesser goldfinch						
p(Time^2) Ψ (Location)	4	115.066	0.000	0.206	105.528	1
p(Observer) Ψ (Location)	4	115.299	0.233	0.184	105.760	1
p(Observer) Ψ (Ownership + Location)	5	115.407	0.341	0.174	103.007	1
Lewis's woodpecker						
p(Time^2 + Effort) Ψ (.)	4	81.064	0.000	0.252	71.526	1
p(Observer + Effort) Ψ (.)	4	81.742	0.678	0.180	72.204	1

p(Time^2) Ψ (.)	3	82.838	1.773	0.104	75.949	1
p(Time^2 + Effort) Ψ (Location)	5	82.894	1.830	0.101	70.494	1
p(Observer) Ψ (.)	3	82.982	1.918	0.097	76.094	1

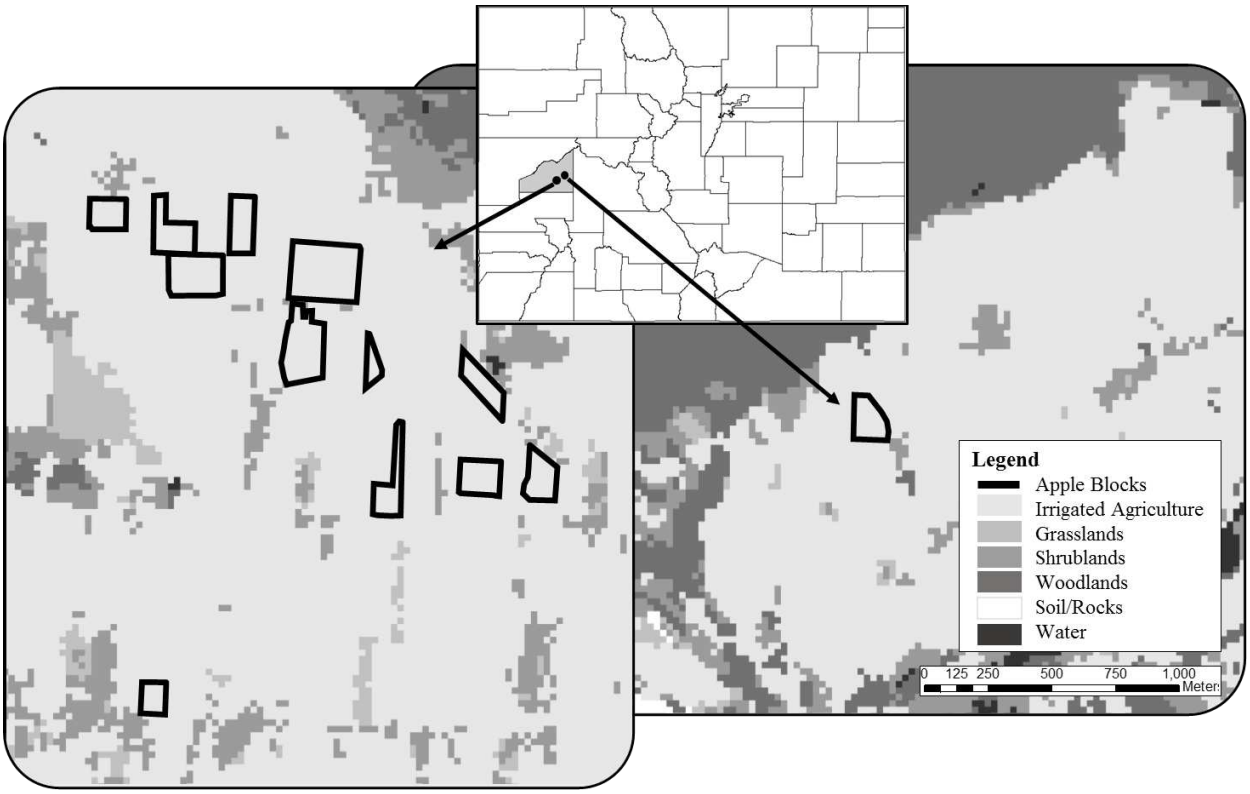

Figure 1.1. Study site locations in Delta County, Colorado (grey-shaded polygon on Colorado map). Black-lined polygons indicate apple blocks studied in Hotchkiss (left) and Paonia (right). Land cover vegetation classes are illustrated in grey scale at a resolution of 25 meters (Simpson et al. 2013). Irrigated agriculture includes fruit orchards, vegetable crops, hops and hay. Roads, property boundaries, etc. are not included to protect the anonymity of collaborating farmers.

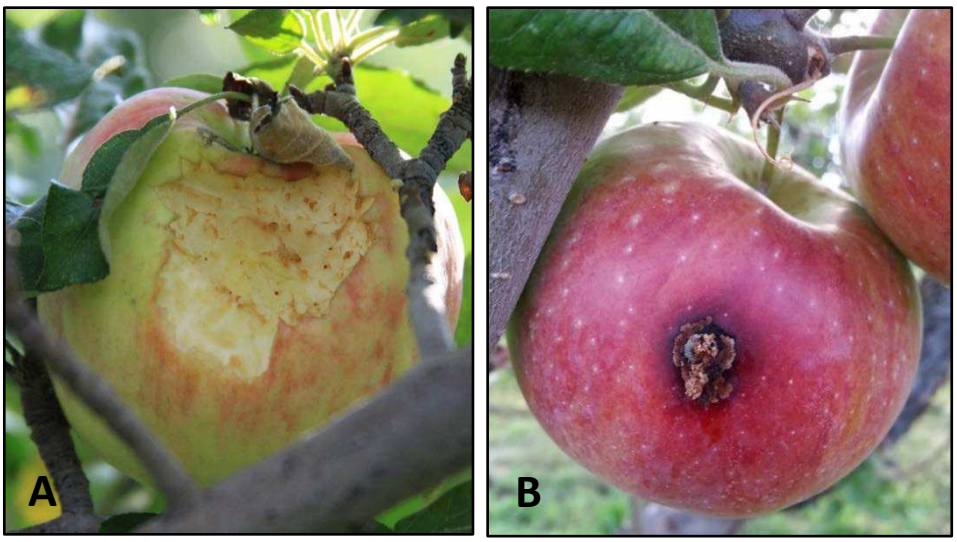

Figure 1.2. Characteristic damage to organic apples in Delta County, Colorado. (A) Bird damage is distinguished by v-shaped peck marks, and (B) codling moth (*Cydia pomonella*) damage is characterized by stings (i.e., larval entry points) and frass (i.e., brownish excrement).

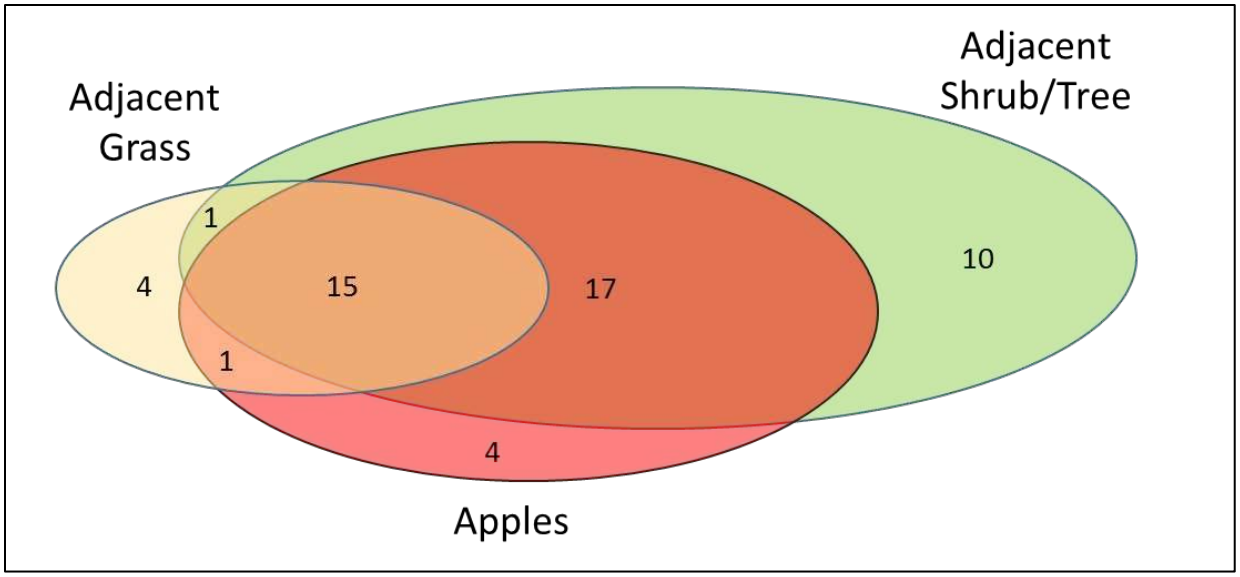

Figure 1.3. Venn diagram representing the raw number of the bird species in the apple blocks and two adjacent habitats (i.e., grass and shrub/tree) as well as the intersections of each. The diagram shows both human-adapted and human-sensitive species as they showed similar trends in composition. Approximately 70% of species (n=37) were detected in apple blocks. See Appendix 1.4 for list of species in each habitat type.

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CHAPTER TWO

A MOLECULAR ANALYSIS TO ASSESS CODLING MOTH (*CYDIA POMONELLA*) PREDATION BY ORCHARD BIRDS

INTRODUCTION

Organic growers have a limited set of tools for managing insect pests (National Organic Program 2011). Their challenge is to satisfy increasing demands for environmentally friendly food, while keeping pests below thresholds required to maintain economic viability (Willer 2011). Research has demonstrated the potential value of birds in controlling pests in specialty crop agroecosystems such as coffee (Perfecto et al. 2004), cocoa (Van Bael et al. 2007) and wine grapes (Jedlicka et al. 2011). In another specialty crop, organic apples, the most damaging pest is the codling moth (*Cydia pomonella*; Lepidoptera: Tortricidae). The cryptic nature of this species makes identifying its natural enemies particularly difficult (Agnello and Kain 1996; Walton and Grieshop 2016), but aerial predators such as birds and bats may help reduce populations of codling moth (Baumgartner 1999; Long et al. 2013). Because of their mobile behavior, birds may be able to track insect outbreaks (Railsback and Johnson 2011) and migrating insectivorous species may feed on pest insects in short bursts as they pass through an area (Ji et al. 2008). Yet despite this potential, our understanding of whether birds provide this ecosystem service in organic apple orchards is incomplete.

Observing predation of codling moth by wild birds in situ is not practical. Not only is direct observation highly labor intensive, but due to the small body size of the prey and the skill required to identify prey items in a bird's bill, more focused techniques such as cameras at nest sites would be necessary for accurate identification (Symondson 2002). Historically, studies on

avian predators of agricultural pests have relied on morphological identification of invertebrates in bird stomach contents, often requiring invasive or destructive techniques such as a stomach pump or lethal collection of birds (Henderson 1913; McAtee 1912; Symondson 2002), which may not be desirable when studying species of conservation concern. Examination of fecal samples has also been used for identifying prey items but has been described as producing "taxonomically crude results" (Jedlicka et al. 2013), partially because digestive processes can reduce prey items to unidentifiable remains and because predation on larvae may not provide any recognizable remains (Burger et al. 1999; Symondson 2002).

Depending on the species being analyzed and the method of sample collection, molecular detection of prey items can be a less invasive, non-destructive alternative that has the potential to provide more accurate and complete results than those described above (Symondson 2002). Additionally, using molecular methods in an ecological context can offer novel insights into species interactions and inform conservation strategies (Karp et al. 2014). Group- and species-specific primers have been utilized as a tool for identifying arthropod (Boreau de Roincé et al. 2012; Chen et al. 2000; Durbin et al. 2012), mammalian (Deagle et al. 2005) and avian (Deagle et al. 2007) predators of prey items of interest. Yet, despite the difficulty in determining if specific agricultural pests have been predated by birds, such approaches have not been used frequently to identify targeted insect pests in avian feces, with few exceptions (Karp et al. 2014).

The codling moth is a major economic pest of apples, severely damaging crops and creating labor and supply costs for farmers to mitigate damage (Caprile 2011; Klonsky and Stewart 2014). Organic farms have restricted options for controlling codling moths, yet must do so, as damaged fruit cannot be sold to traditional markets (e.g., wholesale, Community Supported Agriculture (CSAs), or farmer's markets) and result in decreased profits. Natural

enemies of these insect pests, such as insectivorous birds, may supplement pest management practices (Henderson 1913; Solomon and Glen 1979). A more complete understanding of the predator-prey relationship between birds and codling moths is important for evaluating the ecosystem services provided by birds and the practicality of supporting or encouraging birds in orchard ecosystems in terms of both production and conservation value.

The goal of this study was to use published, species-specific primers to detect codling moth prey in orchard birds' diets using a non-invasive sampling method (i.e., feces). My specific objectives were to: 1) describe the sensitivity of a published primer for codling moths in avian feces and 2) report the presence or absence of codling moths in avian fecal samples collected from organic apple orchards. I identify the strengths and weaknesses of this molecular approach and discuss the implications for sustainable agriculture and avian conservation.

METHODS

Sample Collection

To determine whether birds were consuming codling moths in orchards, I used mist nets set in apple blocks on five organic farms in Delta County, Colorado (Figure 2.1) to capture birds and collect fecal samples (Federal Fish and Wildlife Permit number MB019065-0; NWRC QA 2286). Mist netting occurred May – September in the interior and along the edges of 9 apple blocks in 2014 and 11 blocks in 2015 for a total of 56 mornings. Standard mist netting operating procedures were followed (The North American Banding Council 2001); nets were opened approximately 30 min before sunrise, closed by approximately 10:00 h, and closed promptly in cases of rain, wind or excessively hot or cold temperatures. I used all-purpose mesh sizes of 36 mm or 38 mm. Captured birds were removed from mist nets, placed individually in clean cotton bags, and processed to identify species and record basic measurements. Immediately after processing, birds were released and the cotton bag was checked for fecal material. Using spatulas

cleaned with ethanol, fecal samples were transferred into Eppendorf tubes containing either 99.5% ethanol or 70% isopropyl alcohol and were stored at -20 °C until they could be processed at the National Wildlife Research Center's Wildlife Genetics Laboratory in Fort Collins, CO. All cotton bags were cleaned with a 70% bleach solution, washed and dried to prevent contamination among captured birds. Adult codling moths were collected from pheromone traps in Hotchkiss, CO and stored at -20 °C in Eppendorf tubes containing 99.5% ethanol, for use as positive controls. Individual moths were positively identified with assistance from experts and online resources (Gilligan et al. 2014).

DNA Extraction

Initially, DNeasy Stool Mini Kits (Qiagen) were used for DNA extraction of avian feces because this kit is standard for this type of sample. However, preliminary analysis of this extraction method showed low DNA capture. Zarzoso-Lacoste et al. (2013) demonstrated that an alternative, DNeasy mericon Food Kits (Qiagen), performed similarly to morphological identification of rodent fecal contents. Although morphological identification of the codling moth in my samples was not feasible, this kit had superior performance in a preliminary analysis using known coding moth DNA (Appendix 2.1). Therefore, DNA was extracted from the fecal samples (n = 211) in May – June 2016 using DNeasy mericon Food Kits. The standard protocol was used by first disrupting an approximately 200 mg fecal sample with 1 mL of food lysis buffer and a 5 mm stainless steel bead in a TissueLyser LT (Qiagen) for six minutes at 30 Hz then adding 2.5 µL Proteinase K solution. Manufacturer's standard 200 mg protocol was followed with the modification of automating a portion of the DNA extraction process (QIAcube, Qiagen). Extractions were purified using OneStep™ polymerase chain reaction (PCR) Inhibitor Removal Kits (Zymo Research) prior to PCR to limit inhibition caused by the

uric acid present in avian fecal material (Jedlicka et al. 2013). Whole codling moth extractions were performed using DNeasy Blood and Tissue Kits (Qiagen) by crushing 2 dry codling moth legs or an abdomen segment (Gilligan 2013) and following manufacturer's protocol with the modification of automating a portion of the DNA extraction process (QIAcube, Qiagen). An extraction blank containing only kit reagents was included in all extraction sets to monitor contamination. All laboratory work was conducted at a facility where DNA extractions, PCR and post-PCR procedures were carried out in separate rooms.

Primer Sensitivity

Sensitivity was tested by spiking avian fecal samples with known amounts of codling moth DNA and running serial dilutions to determine where detection was lost. Adult codling moth DNA was extracted as described above and quantified (100 ng/mL) using a Qubit® 2.0 Fluorometer (Invitrogen). Avian feces were obtained from captive birds with no access to codling moths, and extracted and purified as described above. These codling moth-free samples were then spiked with 0.075 ng of codling moth DNA. Spiked samples were diluted using diethylpyrocarbonate (DEPC) treated water (Thermo Fisher Scientific) (0.075 ng, 0.0075 ng, 0.00075 ng, 0.000075 ng, 0.0000075 ng, 0.00000075 ng, and 0.000000075 ng) and detection was assessed through PCR.

PCR Amplification and DNA Sequencing

Using published Tortricidae primers (C.pom-F 5'-AATTTCAAGCAGAATCGTT-3' & C.pom-R 5'-TTAACAGCTCCTAAAATA-3') (Boreau de Roincé et al. 2012), a 153 base pair (bp) segment of mitochondrial cytochrome oxidase I (COI) was amplified. PCR were carried out in 10 μL reactions consisting of 1.7 μL of DEPC-treated water, 5 μL 2x Taq buffer (Qiagen multiplex), 0.5 μL Bovine Serum Albumin (BSA), 0.4 μL of each 10 mM primer, and 2 μL

template DNA. A PCR program consisting of a 15 min denaturing step at 95°C, a cycle of 94°C for 30 sec, 52°C for 30 sec and 72°C for 45 sec was repeated 34 times, and then a last extension period at 72°C for 5 min was performed (Boreau de Roincé et al. 2012) using Eppendorf Mastercycler™ pro S PCR System (Fisher Scientific). Each PCR set included a negative control containing only PCR reagents to monitor contamination as well as a positive control containing codling moth DNA to verify that the reaction was successful. Fragment analysis of PCR products was conducted using a 3500xL Genetic Analyzer (Applied Biosystems) and was visualized using GeneMapper® Software 5 (Applied Biosystems). I identified samples as containing codling moth DNA if the amplified fragments' fluorescence intensities in the electropherogram were sufficiently high (≥ 1000), at the target bp size, and included a peak topology similar to that of the positive control (Figure 2.2). Each sample was amplified in triplicate to account for stochasticity and account for sources of error (Taberlet et al. 1999). I considered a positive PCR in any one of the three replicates to be a detection.

These primers had previously been tested against a closely-related moth species, the oriental fruit moth (*Grapholita molesta*; Lepidoptera: Tortricidae), and had not cross-amplified (Boreau de Roincé et al. 2012). Further, codling moths are the only other known member of the Tortricidae family in my study location so I did not expect problems with cross-amplification of other species. Nevertheless, successfully amplified PCR products (n = 2) from field samples, and a subset of samples without amplification, positive controls, and negative controls (n = 40) were sequenced for confirmation. Amplification products were purified using ExoSAP-IT (USB Corporation, OH) to remove excess primers and unincorporated nucleotides. Cycle sequencing reactions were then performed in 10 μL reactions with 1 μL of purified PCR product, 1 μL primer, 0.25 μL BigDye and 2.275 μL sequencing buffer. Cycle sequencing cleanup was

performed with Sephadex G-50 and PrepEase columns (USB). Sequences were visualized on a Genetic Analyzer 3500/3500xl (Life Technologies) and aligned and edited using Sequencher 5.9. Final species identification was verified using a Basic Local Alignment Search Tool (BLAST) with the National Center for Biotechnology Information website (Benson et al. 2012).

RESULTS AND DISCUSSION

Fecal samples (n = 211) were collected from 31 species (Table 2.1). Interestingly, more than half (n=16) of the captured species were characterized as sensitive to anthropogenic land use, or human-sensitive. Results of serial dilutions indicated that codling moth DNA in avian feces could be detected to 0.000075 ng (Figure 2.3); therefore, codling moth DNA below this amount in field samples would likely not be detected using this method. Two samples (i.e., less than 1% of the 211 collections) had peaks in the fragment analysis (florescence intensity > 3300). Positive detection of codling moth DNA in one of these samples was confirmed by sequencing and BLAST search. Sequences from codling moth positive control samples and the amplified field sample had high identity matches (i.e., ≥ 97%) to GenBank accession number LC031953. While I was unable to successfully sequence the second amplified PCR product, both samples were collected from a single species, the brown-headed cowbird (*Molothrus ater*). Although the sample size was small, extraction blanks and PCR negative controls showed no signs of contamination. Therefore, I am confident that peaks in the fragment analysis in these two field samples were not a result of contamination and conservatively report one positive sample and one putative positive.

I anticipated that at least several species of insectivorous birds would be consuming codling moths (McAtee 1912), thus the very few positive detections from one species was unexpected. However, the percent of analyzed samples that contained codling moth DNA (0.5%)

was consistent with similar research targeting coffee berry borer beetle (*Hypothenemus hampeii*; Coleoptera: Scolytidae) DNA in bird feces (Karp et al. 2014). Although all birds I captured were insectivorous, only the brown-headed cowbird, a brood parasite, provided this pest removal service. As a nest parasite, brown-headed cowbirds can be detrimental to native bird populations including human-sensitive and threatened and endangered species (Lowther 1993). From a conservation standpoint, it would not be beneficial to manage orchards specifically to increase populations of this species.

To my knowledge, this study is the first use of DNeasy mericon Food Kits for successful extraction of DNA from avian feces. Although not the primary purpose of this study, refining DNA extraction methods showed superior results with this kit, which was designed to control inhibitors (Qiagen 2016). All PCR were run with BSA, a known inhibitor remover (Bessetti 2007), yet the serial dilutions performed better when extractions where conducted using the DNeasy mericon Food Kits than with DNeasy Stool Mini kits (Appendix 2.1). This is particularly important when dealing with non-invasive samples known for inhibition such as feces.

There are several challenges to consider when interpreting the results of this non-invasive molecular approach. First, while extraction and PCR methods were optimized, DNA may have continued to degrade over the storage period and with freeze/thaw cycles (Deuter et al. 1995), having the same effect as extreme dilution (Taberlet et al. 1999). Additionally, detection of codling moth DNA may have been affected by the storage solution, as the only two positive samples were stored in 99.5% ethanol (versus 70% isopropyl alcohol; Table 2.1). Second, the inherent low quality/quantity DNA in fecal samples may have contributed to the low number of detections (Taberlet et al. 1999). Third, it is conceivable that some field samples that showed

negative results for codling moth might have had DNA present, yet I was unable to detect it if the amount was below 0.000075 ng, the amount at which detection dropped off in the dilution series test. Feeding trials conducted by Karp et al. (2014) suggest that this method is prone to false negatives, however they and others (Oehm et al. 2011) successfully detected arthropod DNA that passed through the avian gut. Therefore, my results likely represent a conservative characterization of the species consuming codling moths during this study. Fourth, it is also possible that birds may have excreted the remains of the targeted prey prior to fecal sample collection due to short gut retention times (Levey and Karasov 1989). Furthermore, adult codling moths are most active during evening hours (Caprile 2011), therefore, although other life stages (e.g., larvae and pupae) may be available prey sources at all times of day, mist netting focused in the mornings may have missed opportunities to detect birds consuming adult codling moths. Consequently, the probability of codling moth DNA detection may vary by birds' foraging behavior (e.g., gleaning or flycatching) or the timing of mist netting. Finally, passive mist netting did not allow comparisons of the relative importance of all insectivorous species as potential agents of pest control, as I did not capture all of the species detected in the orchards. In the future, targeted sampling during various times of day may provide an opportunity to study the foraging behaviors of particular bird species of interest more thoroughly.

In spite of these challenges, there are many strengths of molecular approaches. Molecular analysis of fecal samples is a powerful tool that is less invasive and less biased than alternative methods of investigating predator diets (Jedlicka et al. 2013). Critically, specific components of a bird's diet can be determined with certainty without lethal collection of the individual, which is particularly beneficial when the avian predators studied are of conservation concern. Although there were very few positive detections, these results demonstrate that a species-specific primer

can be a viable method for positively identifying avian predators' contribution to the control of a pest species of interest in an agricultural landscape.

Other techniques that could be applied to identifying birds providing pest control services could include quantitative PCR (qPCR), metabarcoding, or metagenomics shotgun sequencing which may allow a more detailed and sensitive molecular assessment of predator-prey relationships between birds and pests in agricultural settings (Clare et al. 2009). The benefits of qPCR include speed, reproducibility and quantitative capability in comparison to conventional PCR methods and importantly for this study, qPCR is more sensitive (Paiva-Cavalcanti et al. 2010).

Alternatively, metabarcoding allows for mass-PCR-amplification and high-throughput (next-generation) sequencing of a single target gene and separate sequences are produced for individual DNA molecules from homogenized samples like feces (Yu et al. 2012). This approach can be more informative about the total diet while remaining cost- and time-efficient (Brandon-Mong et al. 2015). For example, while genetic applications are becoming a common method for diet analysis, it can be difficult to collect enough samples to detect a particular prey species in the diet of a generalist feeder. Generalist avian predators using apple orchards may also be foraging in neighboring crops or uncultivated natural areas and it may be of interest to investigate the potential for pest control of multiple insect species realized from mobile species between these novel and undisturbed habitats. An important disadvantage of metabarcoding is that it relies upon sequence databases to accurately interpret the generated sequences and these databases may not house sequences from all species in a target habitat. However, these database are continuously expanding (Pompanon et al. 2012).

Finally, metagenomics shotgun sequencing, while similar to metabarcoding, does not require the selection of amplification targets beforehand (e.g., metabarcoding) and as such allows for a broader study of all genomic material (Srivathsan et al. 2016). However, this approach is more expensive and requires a more comprehensive reference database to appropriately interpret the data (Srivathsan et al. 2016). Depending on the study system and research questions posed, any one of these molecular approaches could be considered for future research to better understand the ecosystem services provided by wild birds in agroecosystems.

This study confirmed the sensitivity of a published primer for codling moths and identified an avian predator of this pest insect in orchards in western Colorado. The development and use of molecular tools to identify predators of agricultural pests is an important mechanism for enhancing understanding of predator-prey interactions in agroecosystems. These tools may be particularly powerful when applied to mobile predators like birds that not only have the potential to remove pest insects, but may provide other ecosystem services such as pollination and seed dispersal over wide geographic areas. This method holds promise for helping farmers make evidence-based decisions on how to harness the valuable services provided by avian species, and to encourage agricultural practices that supports avian biodiversity.

TABLES AND FIGURES

Table 2.1. The proportion of fecal samples with positive detections of codling moth DNA (n = sample size). Fecal samples (n = 211) were collected from 31 bird species in blocks of organic apples. References are listed for classification decisions of human-adapted or human-sensitive species. All species captured are described as insectivorous or omnivorous (The Cornell Lab of Ornithology 2016). Species in bold had positive detections of codling moth DNA. Storage solution was either 99.5% ethanol ([1]) or 70% isopropyl alcohol ([2]).

Species	Latin Name	Reference	Proportion with Codling Moth DNA Detected
Human-Adapted			
black-chinned hummingbird[1,2]	*Archilochus alexandri*	(Rottenborn 1999)	0.0 (n = 7)
red-naped sapsucker[2]	*Sphyrapicus nuchalis*	(Walters et al. 2014)	0.0 (n = 2)
northern flicker[1]	*Colaptes auratus*	(Wiebe et al. 2008)	0.0 (n = 3)
barn swallow[2]	*Hirundo rustica*	(Blair 1996)	0.0 (n = 1)
American robin[1,2]	*Turdus migratorius*	(Odell and Knight 2001)	0.0 (n = 38)
gray catbird[2]	*Dumetella carolinensis*	(Smith et al. 2011)	0.0 (n = 1)
cedar waxwing[1]	*Bombycilla cedrorum*	(Witmer et al. 1997)	0.0 (n = 2)
yellow warbler[1,2]	*Setophaga petechial*	(Rottenborn 1999)	0.0 (n = 9)
white-crowned sparrow[1]	*Zonotrichia leucophrys*	(Chilton et al. 1995)	0.0 (n = 6)
red-winged blackbird[2]	*Agelaius phoeniceus*	(Lenth et al. 2006)	0.0 (n = 1)
Brewer's blackbird[2]	*Euphagus cyanocephalus*	(Maestas et al. 2003)	0.0 (n = 2)
brown-headed cowbird[1,2]	***Molothrus ater***	**(Odell and Knight 2001)**	**0.22 (n = 9)**
Bullock's oriole[1,2]	*Icterus bullockii*	(Maestas et al. 2003)	0.0 (n = 14)
American goldfinch[1,2]	*Spinus tristis*	(Maestas et al. 2003)	0.0 (n = 8)
house finch[1,2]	*Haemorhous mexicanus*	(Bock et al. 1999)	0.0 (n = 33)
Human-Sensitive			
Lewis's woodpecker[1]	*Melanerpes lewis*	(Vierling et al. 2013)	0.0 (n = 2)
western wood-pewee[1]	*Contopus sordidulus*	(Blair 1996)	0.0 (n = 2)
dusky flycatcher[1]	*Empidonax oberholseri*	(Odell and Knight 2001)	0.0 (n = 1)
ash-throated flycatcher[1]	*Myiarchus cinerascens*	(Blair 1996)	0.0 (n = 1)
warbling vireo[1]	*Vireo gilvus*	(Rottenborn 1999)	0.0 (n = 6)
ruby-crowned kinglet[1,2]	*Regulus calendula*	(Ingold and Wallace 1994)	0.0 (n = 2)
Townsend's warbler[1]	*Setophaga townsendi*	(Wright et al. 1998)	0.0 (n = 1)
Wilson's warbler[1]	*Cardellina pusilla*	(Rottenborn 1999)	0.0 (n = 3)
green-tailed towhee[1]	*Pipilo chlorurus*	(Odell and Knight 2001)	0.0 (n = 1)
spotted towhee[1]	*Pipilo maculatus*	(Odell et al. 2003)	0.0 (n = 1)
chipping sparrow[1,2]	*Spizella passerine*	(Crooks et al. 2004)	0.0 (n = 23)
song sparrow[1,2]	*Melospiza melodia*	(Rottenborn 1999)	0.0 (n = 2)

black-headed grosbeak[1]	*Pheucticus melanocephalus*	(Odell and Knight 2001)	0.0 (n = 5)
lazuli bunting[1,2]	*Passerina amoena*	(Maestas et al. 2003)	0.0 (n = 6)
western meadowlark[1]	*Sturnella neglecta*	(Lenth et al. 2006)	0.0 (n = 2)
lesser goldfinch[1,2]	*Spinus psaltria*	(Crooks et al. 2004)	0.0 (n = 16)

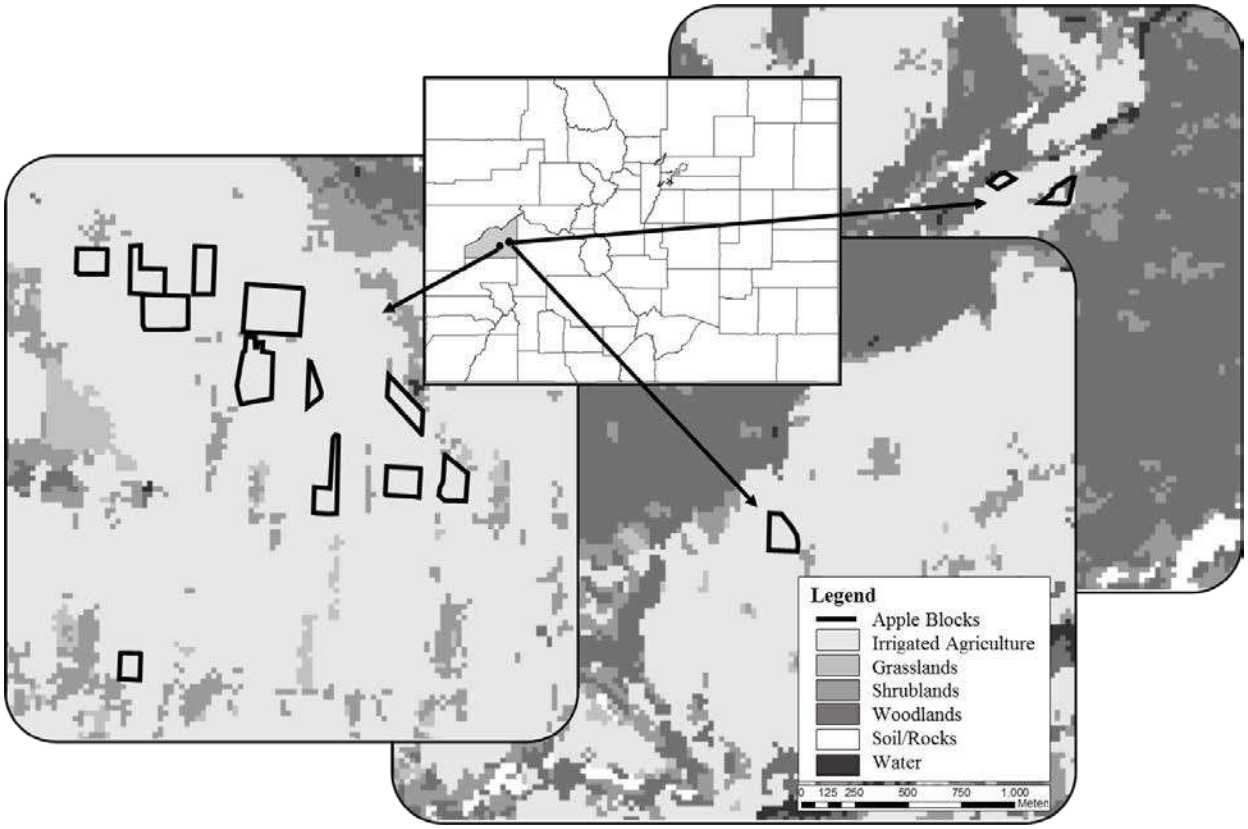

Figure 2.1. Study site locations in Delta County, Colorado (grey-shaded polygon on Colorado map). Black-lined polygons indicate apple blocks studied in Hotchkiss (left) and Paonia (middle and right). Land cover vegetation classes are illustrated in grey scale at a resolution of 25 meters (Simpson et al. 2013). Irrigated agriculture includes fruit orchards, vegetable crops, hops, and hay. Roads, property boundaries, etc. are not included to protect the anonymity of collaborating farmers.

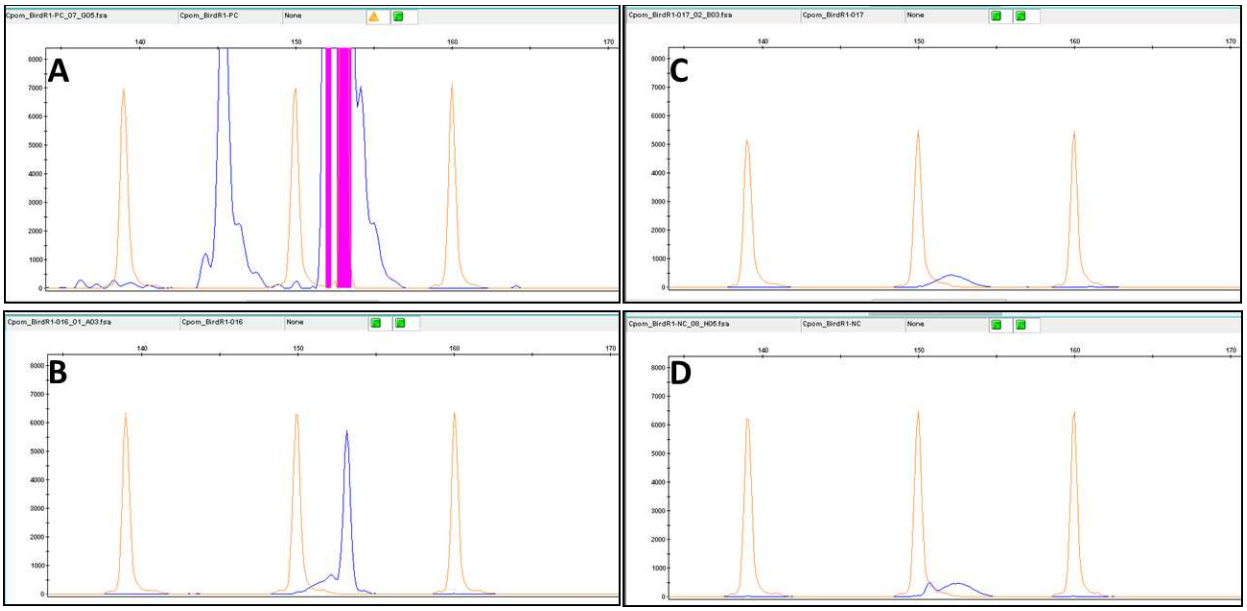

Figure 2.2. Fragment analysis images from GeneMapper software depicting (A) a positive control of codling moth (*Cydia pomonella*) DNA, (B) a positive field sample from a brown-headed cowbird (*Molothrus ater*), (C) a negative field sample from a western meadowlark (*Sturnella neglecta*), and (D) a negative control. The x-axis shows base pairs and florescence intensity is on the y-axis. Blue dye indicates the target DNA, orange dye indicates ladders and pink indicates off-scale display intensity. Inflorescence intensities < 1000 or bp < 152 or > 154 were determined to be negative for codling moth DNA as confirmed by DNA sequencing and BLAST search.

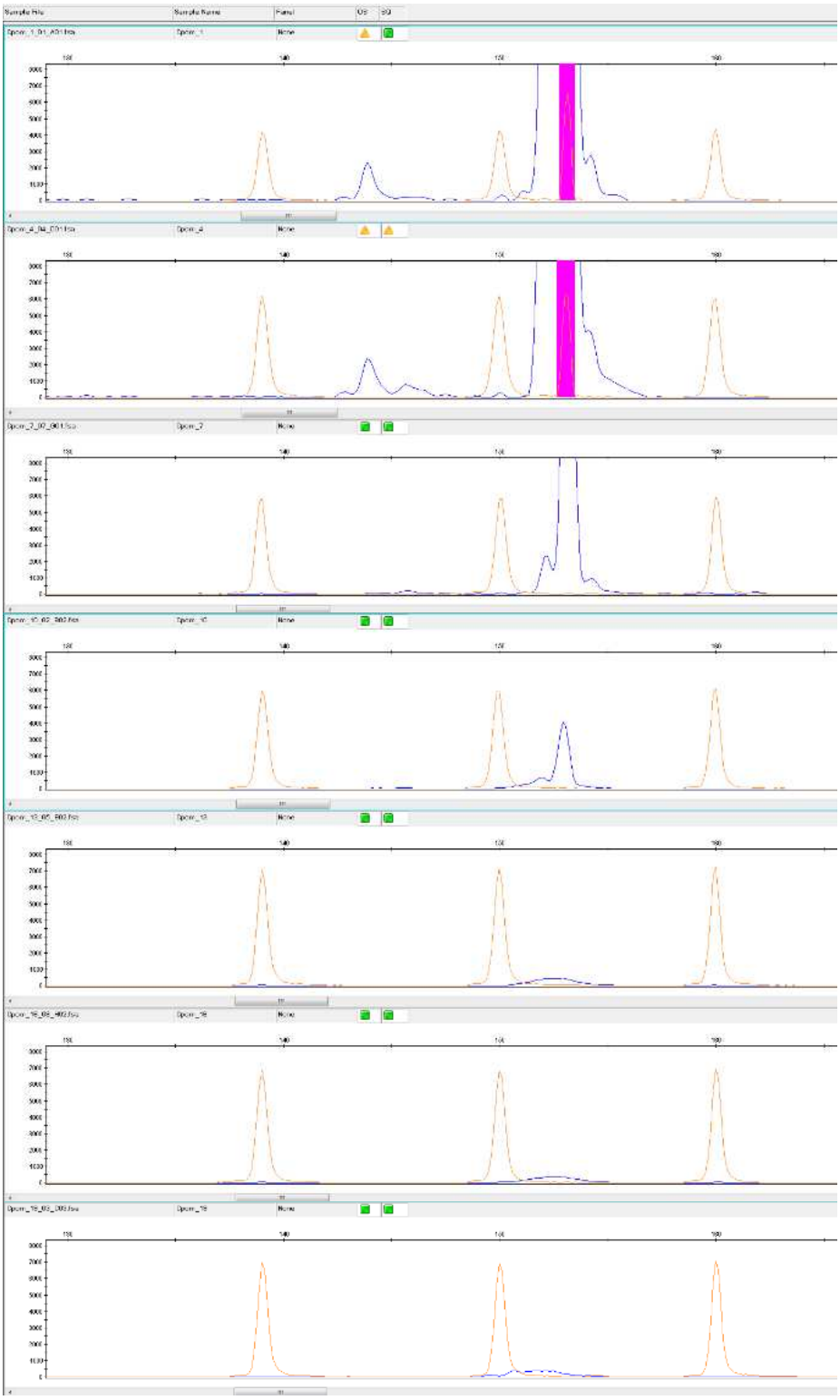

Figure 2.3. Fragment analysis images from GeneMapper software depicting primer sensitivity for avian fecal samples spiked with codling moth DNA – showing detection to 0.000075 ng (i.e., the 4th panel). The x-axis shows base pairs and florescence intensity is on the y-axis. Blue dye indicates the target DNA, orange dye indicates ladders and pink indicates off-scale display.

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APPENDICES

Appendix 1.1: Common and scientific names of 59 species detected during 2015 in organic apple orchards in western Colorado. Species were assigned as human-adapted (n = 40) or human-sensitive (n = 19) based on the corresponding reference. Detections were recorded through the following methods: TS (AB, AH) = transect survey (apple block or adjacent habitat) and FO = foraging observations.

Species Name	Scientific Name	Human-adapted/ sensitive	Reference	Conservation Importance	Detection
mallard	*Anas platyrhynchos*	Adapted	(Blair 1996)	Least Concern	TS (AH)
ring-necked pheasant	*Phasianus colchicus*	Sensitive	(Giudice and Ratti 2001)	Least Concern	TS (AH)
turkey vulture	*Cathartes aura*	Sensitive	(Rottenborn 1999)	Least Concern	TS (AH)
Cooper's hawk	*Accipiter cooperii*	Adapted	(Curtis et al. 2006)	Least Concern	TS (AH)
red-tailed hawk	*Buteo jamaicensis*	Adapted	(Berry et al. 1998)	Least Concern	TS (AH)
American kestrel	*Falco sparverius*	Adapted	(Berry et al. 1998)	Least Concern	TS (AB, AH), FO
killdeer	*Charadrius vociferus*	Adapted	(Lenth et al. 2006)	Least Concern	TS (AH)
rock dove	*Columba livia*	Adapted	(Lenth et al. 2006)	Least Concern	TS (AH)
Eurasian collared dove	*Streptopelia decaocto*	Adapted	(Hansen and Urban 1992)	Least Concern	TS (AB, AH)
white-winged dove	*Zenaida asiatica*	Adapted	(Chace and Walsh 2006)	Least Concern	TS (AH)
mourning dove	*Zenaida macroura*	Adapted	(Lenth et al. 2006)	Least Concern	TS (AB, AH)
common nighthawk	*Chordeiles minor*	Adapted	(Brigham et al. 2011)	Least Concern	TS (AB)
black-chinned hummingbird	*Archilochus alexandri*	Adapted	(Rottenborn 1999)	Least Concern	TS (AB, AH), FO
broad-tailed hummingbird	*Selasphorus platycercus*	Adapted	(Odell et al. 2003)	Least Concern	TS (AB, AH)
belted kingfisher	*Megaceryle alcyon*	Adapted	(Rottenborn 1999)	Least Concern	TS (AH)
Lewis's woodpecker	*Melanerpes lewis*	Sensitive	(Vierling et al. 2013)	Watch List	TS (AB, AH), FO
downy woodpecker	*Picoides pubescens*	Sensitive	(Rottenborn 1999)	Least Concern	TS (AB, AH)
hairy woodpecker	*Leuconotopicus villosus*	Adapted	(Jackson et al. 2002)	Least Concern	TS (AH)
northern flicker	*Colaptes auratus*	Adapted	(Wiebe et al. 2008)	Least Concern	TS (AB, AH), FO

western wood-pewee	*Contopus sordidulus*	Sensitive	(Blair 1996)	Least Concern	TS (AB, AH), FO
least flycatcher	*Empidonax minimus*	Sensitive	(Chace and Walsh 2006)	Least Concern	TS (AH)
Say's phoebe	*Sayornis saya*	Sensitive	(Schukman and Wolf 1998)	Least Concern	TS (AH)
western kingbird	*Tyrannus verticalis*	Sensitive	(Rottenborn 1999)	Least Concern	TS (AH)
western scrub-jay	*Aphelocoma californica*	Adapted	(Rottenborn 1999)	Least Concern	FO
pinyon jay	*Gymnorhinus cyanocephalus*	Adapted	(Balda 2002)	Watch List	TS (AH)
black-billed magpie	*Pica hudsonia*	Adapted	(Odell and Knight 2001)	Least Concern	TS (AB, AH), FO
common raven	*Corvus corax*	Adapted	(Crooks et al. 2004)	Least Concern	TS (AB, AH), FO
violet-green swallow	*Tachycineta thalassina*	Adapted	(Brown et al. 2011)	Least Concern	TS (AB, AH)
cliff swallow	*Petrochelidon pyrrhonota*	Adapted	(Brown and Brown 1995)	Least Concern	TS (AH)
barn swallow	*Hirundo rustica*	Adapted	(Blair 1996)	Least Concern	TS (AB, AH)
black-capped chickadee	*Poecile atricapillus*	Sensitive	(Odell and Knight 2001)	Least Concern	TS (AB, AH)
bushtit	*Psaltriparus minimus*	Adapted	(Blair 1996)	Least Concern	TS (AB, AH), FO
red-breasted nuthatch	*Sitta canadensis*	Adapted	(Ghalambor and Martin 1999)	Least Concern	TS (AB, AH)
house wren	*Troglodytes aedon*	Adapted	(Odell and Knight 2001)	Least Concern	TS (AH), FO
American robin	*Turdus migratorius*	Adapted	(Odell and Knight 2001)	Least Concern	TS (AB, AH), FO
European starling	*Sturnus vulgaris*	Adapted	(Odell and Knight 2001)	Least Concern	TS (AB, AH)
cedar waxwing	*Bombycilla cedrorum*	Adapted	(Witmer et al. 1997)	Least Concern	TS (AB, AH), FO
yellow warbler	*Setophaga petechia*	Sensitive	(Rottenborn 1999)	Least Concern	TS (AB, AH)
yellow-rumped warbler	*Setophaga coronata*	Adapted	(Hunt and Flaspohler 1998)	Least Concern	TS (AH)
Wilson's warbler	*Cardellina pusilla*	Sensitive	(Rottenborn 1999)	Least Concern	TS (AB, AH)
green-tailed towhee	*Pipilo chlorurus*	Sensitive	(Odell and Knight 2001)	Least Concern	FO
chipping sparrow	*Spizella passerina*	Sensitive	(Crooks et al. 2004)	Least Concern	TS (AB, AH), FO
lark sparrow	*Chondestes grammacus*	Sensitive	(Lenth et al. 2006)	Least Concern	TS (AB, AH)
white-crowned sparrow	*Zonotrichia leucophrys*	Adapted	(Chilton et al. 1995)	Least Concern	TS (AB, AH)
dark-eyed junco	*Junco hyemalis*	Adapted	(Nolan et al. 2002)	Least Concern	TS (AB, AH)

blue grosbeak	*Passerina caerulea*	Sensitive	(Lowther and Ingold 2011)	Least Concern	TS (AB, AH), FO
lazuli bunting	*Passerina amoena*	Sensitive	(Maestas et al. 2003)	Least Concern	TS (AB, AH), FO
red-winged blackbird	*Agelaius phoeniceus*	Adapted	(Lenth et al. 2006)	Least Concern	TS (AB, AH), FO
western meadowlark	*Sturnella neglecta*	Sensitive	(Lenth et al. 2006)	Least Concern	TS (AB, AH), FO
Brewer's blackbird	*Euphagus cyanocephalus*	Adapted	(Maestas et al. 2003)	Least Concern	TS (AB, AH)
brown-headed cowbird	*Molothrus ater*	Adapted	(Odell and Knight 2001)	Least Concern	TS (AB, AH)
Bullock's oriole	*Icterus bullockii*	Adapted	(Maestas et al. 2003)	Least Concern	TS (AB, AH), FO
pine siskin	*Carduelis pinus*	Adapted	(Dawson 2014)	Least Concern	TS (AB, AH), FO
lesser goldfinch	*Spinus psaltria*	Sensitive	(Crooks et al. 2004)	Least Concern	TS (AB, AH), FO
American goldfinch	*Spinus tristis*	Adapted	(Maestas et al. 2003)	Least Concern	TS (AB, AH), FO
evening grosbeak	*Coccothraustes vespertinus*	Adapted	(Gillihan and Byers 2001)	Watch List	TS (AH)
house sparrow	*Passer domesticus*	Adapted	(Bock et al. 1999)	Least Concern	TS (AH)
blue-gray gnatcatcher	*Polioptila caerulea*	Sensitive	(Odell and Knight 2001)	Least Concern	FO
house finch	*Haemorhous mexicanus*	Adapted	(Bock et al. 1999)	Least Concern	TS (AB, AH), FO

Appendix 1.2. Predictor variables included as covariates in single season occupancy models for human-adapted and human-sensitive species for Ψ_1 (psi; probability that a unit is occupied/used) and p_j (probability that species is detected in a unit in survey j, given presence).

Covariates used to model Ψ_1				
Predictor Variable	**Description**	**Measurement Method**	**Variable Type/Value**	**General Occupancy Predictions**
Ownership	Ownership/management of each farm; two of the three participating farms had similar management and were combined for this analysis	Farmer contacts	Categorical (Farm A, Farm B)	Vary by management
Habitat Locations	Where on the farm a transect was located	GPS locations and visual inspection of adjacent habitat type	Categorical (edge, interior)	+ along edges; - in interior
Edge-to-Area Ratio	The length (m) of the apple block edge to the area (m^2) of the block containing the transect	ArcGIS edge length:block size area	Continuous (ratio)	+ with increasing edge ratio
Size	The area (m^2) of the apple block containing the transect	ArcGIS field calculation of polygons	Continuous (square meters)	- with increasing block size
Covariates used to model p_j				
Survey Specific				
Predictor Variable	**Description**	**Measurement Method**		**Variable Type/Value**
Observer	Observer who conducted the survey	Recorded by observer		Categorical (0,1)
Wind	Wind speed category	Beaufort scale of wind speed as measured at time of survey		Categorical (0 – 4)
Sky	Sky cover category	Scale of cloud cover and precipitation measured at time of survey		Categorical (0 – 7)
Time	Time of day survey was conducted	Time of day (24 hour clock format) at which the survey was started		Continuous
Temperature	Degrees Fahrenheit	Estimated within 5 degrees by observer assisted by a centrally-based thermometer		Continuous
Date	Date survey was conducted	Recorded as MM/DD/YY by observer and transformed to the Julian day associated with the date the survey was conducted		Continuous
Activity	Noise or activity associated with farm work (e.g., harvesting, thinning, etc.) near the transect	Described by observer and categorized if it was deemed loud enough to interfere with detections		Categorical (0,1)
Site Specific				
Predictor Variable	**Description**	**Measurement Method**		**Variable Type/Value**
Effort	Effort (transect length) - transects were 50 m, 100 m or 200 m (combined transects in analysis)	Determined when transects were established		Categorical (50, 100, 200)

Appendix 1.3. Predictor variables included as covariates in the binomial logistic regression models for comparison of codling moth damage related to bird access, apple block and apple characteristics.

Predictor Variable	**Description**	**Measurement Method**	**Variable Type (Value)**	**General Damage Predictions**
Treatment	Apples enclosed in netting treatment to restrict bird access or unnetted control apples	Installed netting treatments or not	Binary (Treatment, Control)	+ inside exclosure treatments
Habitat Location	Where in the apple block a surveyed tree was located	GPS locations and visual inspection of adjacent habitat type	Categorical (interior, edge crop (combined cherry and peach), edge grass, edge shrub/tree)	- along edges where bird use is predicted to be greater
Apple Variety	The type of apple tree surveyed	Gathered from farmers	Categorical (Gala, Honeycrisp, Other (Akane, Golden Delicious, Granny Smith, Pristine, Rome, Zestar))	Vary by variety
Ownership	Ownership/management of each farm	Farmer contacts	Categorical (Farm A, Farm B, Farm C)	Vary by owner
Harvest Date	Julian day when apples were picked	Gathered from farmers or noted in field observations	Continuous (ordinal day number)	+ with later harvest date

Appendix 1.4. Locations corresponding to where each human-adapted or human-sensitive species was detected (indicated by an X). The adjacent shrub/tree habitat showed the greatest number of species (n = 43) while the adjacent grass habitat had the fewest (n = 21) and apple blocks were intermediate (n = 37); these data were used to estimate species richness using a second-order jackknife estimator and to calculate Jaccard similarity indices.

Species Name	Apple	Adjacent Grass	Adjacent Shrub/Tree
Human-Adapted			
American kestrel	X	X	X
American robin	X	X	X
black-billed magpie	X	X	X
black-chinned hummingbird	X	X	X
Brewer's blackbird	X	X	X
common raven	X	X	X
Eurasian collared dove	X	X	X
European starling	X	X	X
house finch	X	X	X
mourning dove	X	X	X
northern flicker	X	X	X
red-winged blackbird	X	X	X
American goldfinch	X		X
barn swallow	X		X
brown-headed cowbird	X		X
Bullock's oriole	X		X
bushtit	X		X
dark-eyed junco	X		X
pine siskin	X		X
red-breasted nuthatch	X		X
white-crowned sparrow	X		X
belted kingfisher			X
broad-tailed hummingbird	X		
cedar waxwing	X		
common nighthawk	X		
Cooper's hawk			X
evening grosbeak			X
house sparrow		X	
house wren			X
killdeer		X	
mallard			X
pinyon jay			X
violet-green swallow	X		
white-winged dove			X

yellow-rumped warbler			X
Human-Sensitive			
chipping sparrow	X	X	X
western meadowlark	X	X	X
western wood-pewee	X	X	X
black-capped chickadee	X		X
blue grosbeak	X		X
downy woodpecker	X		X
lark sparrow	X	X	
lazuli bunting	X		X
lesser goldfinch	X		X
Lewis's woodpecker	X		X
western kingbird		X	X
Wilson's warbler	X		X
yellow warbler	X		X
least flycatcher			X
ring-necked pheasant		X	
Say's phoebe		X	
turkey vulture			X

Appendix 1.5. Regression coefficients (β) and 95% confidence intervals for covariates in the top model sets (i.e., Δ(Q)AICc < 2). Estimates of the regression coefficients are presented from the top model that included the covariate. Cumulative model weights are the sum of w_i from all models that include the covariate. These estimates of relative variable importance rank the variables by their importance.

Species	Covariate	β value (95% CI)	Σ*wi*
Human-Adapted			
American robin			
	Edge-to-Area	0.597 (-0.343, 1.536)	0.205
Brewer's blackbird			
	Edge-to-Area	-0.667 (-1.772, 0.438)	0.259
	Size	0.456 (-0.450, 1.362)	0.226
cedar waxwing			
	Edge-to-Area	-0.468 (-1.541, 0.604)	0.167
	Size	0.728 (-0.324, 1.779)	0.348
Human-Sensitive			
blue grosbeak			
	Size	4.431 (-2.984, 11.845)	0.249
lesser goldfinch			
	Location	-3.376 (-6.808, 0.056)	0.924
	Ownership	-1.993 (-4.498, 0.511)	0.305
Lewis's woodpecker			
	Location	-1.234 (-3.725, 1.2559)	0.260

Appendix 1.6. AICc model selection results for binomial regression model with small sample size, investigating orchard and landscape characteristics affecting the proportion of codling moth damage as assessed in an exclosure experiment. All models are shown, yet only the bold model with ΔAICc < 2 (Treatment only) is considered supported. A quasi-likelihood approach for handling overdispersion was conducted using package dispmod in R.

Model Names	k	AICc	Δ AICc	Weight	Log Likelihood
Treatment	**2**	**86.83471**	**0**	**0.998821**	**-41.3278**
Apple Variety	3	101.8762	15.04151	0.000541	-47.7563
Treatment + Locations	5	102.85	16.01532	0.000333	-45.9563
Treatment + Apple Variety	4	103.7691	16.93443	0.00021	-47.5769
Locations	4	105.4061	18.57143	9.26E-05	-48.3954
Treatment + Locations + Apple Variety	7	113.4104	26.5757	1.69E-06	-48.802
Locations + Apple Variety	6	115.5233	28.6886	5.89E-07	-51.095

Appendix 2.1. PCR results from serial dilutions of spiked fecal samples using DNeasy Stool Mini Kits and DNeasy mericon Food Kits. Successfully amplified products are denoted with (+). All samples were run with Qiagen Multiplex PCR kit and were run in triplicate.

DNA Amount	DNeasy Stool Mini Kit	DNeasy mericon Food Kit
0.075 ng	+	+
0.0075 ng	+	+
0.00075 ng	-	+
0.000075 ng	-	+
0.0000075 ng	-	-
0.00000075 ng	-	-
0.000000075 ng	-	-

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