INFLUENCES OF DIET, SPATIAL SCALE, AND SOCIALITY ON AVIAN FORAGING BEHAVIOR AND HABITAT USE IN CULTIVATED SWEET CHERRY ORCHARDS AND THE RESULTING IMPLICATIONS FOR MANAGEMENT

By

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A DISSERTATION

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ABSTRACT

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Agricultural crops provide foods that attract a variety of foragers. In particular, fruit crops attract many fruit eating bird species because fruits are densely available, energy-rich, and readily accessible. Agricultural systems have important implications for avian foraging because they manipulate the availability and quality of food. Avian fruit orchard use and crop consumption represent a major conflict between humans and wild birds. Despite nearly a century of attention paid to understanding the nature of this conflict, many inconsistencies and avenues for research remain. In this dissertation, I utilized a variety of techniques including radio tracking, focal observation, and bioenergetic modeling to understand more fully where, how, and to what extent wild fruit eating birds use cultivated fruit resources in northwest Michigan, as well resulting implications for crop producers. Species-specific information on crop damage and habitat use is essential for better-informed pest management programs and damage mitigation.

Bird damage to fruit crops amounts to tens of millions of dollars in losses annually. Yet, the development of successful damage-mitigation strategies for fruits is hindered by a lack of species-specific damage information. In chapter 2, I used bioenergetic modeling that integrated species-specific data on energetic demands and diet to estimate sweet cherry (*Prunus avium*) consumption by American robins (*Turdus migratorius*) and cedar waxwings (*Bombycilla cedrorum*). I then developed economic models to quantify species-specific financial loss due to bird damage. Individual waxwings consumed significantly more sweet cherry and caused seven times the financial loss than robins. I estimated economic losses at \$US1.8 million and \$US147,000 from the waxwing and robin populations, respectively.

Species-specific variation in diet preferences could result in varying use of orchards and impacts on the fruit-producing industry by different bird species. However, species-specific studies of avian orchard use are lacking, particularly throughout the fruit-growing season. Cultivated sweet cherries are high in sugar and low in proteins and lipids; American robins typically prefer lipid-rich fruits, while cedar waxwings choose sugary fruits. Differences in diet preferences may translate into species-specific patterns of habitat use for birds in fruit crops. In chapter three, I used radio telemetry to quantify frequency of daily bird visits to orchards and the amount of time birds spent visiting orchards each day over the fruit-ripening season. I found that waxwings visited orchards a greater percentage of days than robins and spent more time in orchards each day.

Birds forage in habitats where food abundance varies at multiple spatial scales; relative resource abundance between hierarchical spatial scales likely influences within-patch foraging. For frugivorous birds, fruit-growing agricultural regions provide a system of readily available food resources heterogeneously distributed at increasingly broad hierarchical scales. In chapter four, I conducted foraging observations and quantified fruit abundance at three spatial scales to evaluate influences of fruit abundance at multiple spatial scales, and influences of sociality, on avian behavior in sweet cherry orchards. Fruit abundance across multiple scales interacted to influence patch residence time and proportion time spent feeding at sweet cherry trees; these patterns differed between species. In addition, fruit abundance at large spatial scales influenced patch residence time in robins and proportion time feeding by waxwings more strongly for birds in large foraging groups than for those in small groups.

This thesis is dedicated to all the kind people in my life who were willing to put up with me while I completed it. Thank you for everything.

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CHAPTER 1

NEGATIVE AND POSITIVE IMPLICATIONS OF BIRDS IN FRUIT AGRICULTURE

Rachael A. Eaton

Introduction

Bird use of agricultural habitat is long-documented (Beal 1915, McDowell and Pillsbury 1959). Indeed "economic ornithology", the study of bird-agriculture interactions and conflict, began officially within the USDA in 1885 (Henderson and Preble 1935). Many bird species utilize agricultural habitats for food resources, with disparate consequences for crop producers (Drake and Grande 2002, Retamosa et al. 2008). In one regard, avian use of agriculture can be beneficial. Birds can provide ecosystem services, natural processes that provide some benefit to humans (Whelan et al. 2008), in the form of biological control and pest reduction, including both invertebrate and vertebrate crop pests (e.g. Mols and Visser 2002). In contrast, avian use of agriculture can have negative consequences, such as depredation or damage to the crops themselves, that result in financial losses for crop producers (Retamosa et al. 2008, Lindell et al. 2012, Anderson et al. 2013). Thus, avian use of agricultural systems represents a complex interaction between humans and wildlife with both positive and negative implications (Messmer 2009). The negative and positive implications of birds in agriculture have been studied in numerous crops and in growing regions around the world (Dolbeer et al. 1994, Peisley et al. 2015). Yet, much of the research addressing costs or benefits of birds in agriculture has focused on major crops (e.g. corn, grains; Dolbeer et al. 1994), while bird use of less abundant but highvalue crops such as fruits has historically received less attention. In this introductory chapter, my objective was to explore the complex interaction between birds and fruit agriculture by synthesizing existing literature on the negative and positive implications of wild birds in cultivated fruit crops, evaluating our current understanding, and suggesting future directions for fruit crop management and research.

Cultivated fruit crops provide abundant, dense, and readily accessible food resources for many birds (Sallabanks 1993). However, the manner in which wild birds utilize fruit agriculture for food can result in either damage to fruit crops and costs for crop growers, or protection against other crop pests, benefiting crop producers. Historically, attempts to characterize the relationship between birds and fruit agriculture have emphasized the negative consequences of avian use of fruit orchards and potential for crop damage by birds (DeHaven 1974, Gebhardt et al. 2011). Birds consume a wide variety of cultivated fruits (Johnson et al. 1989, Nelms et al. 1990, Somers and Morris 2002, Lindell et al. 2016). In addition to direct fruit consumption, birds cause indirect damage to fruiting plants, such as flower bud damage (Summers and Pollack 1978), affecting fruit production (Wright and Summers 1960). The positive implications of avian fruit orchard use are primarily viewed in the context of ecosystem services birds may provide. The use of non-chemical biological agents to regulate or control pest species abundance, known as biological control, is utilized in a variety of fruit crops both in the U.S. and Europe. In agricultural settings, some birds provide regulating services by consuming other orchards pests such as invertebrate herbivores or crop-damaging small mammals (Whelen et al. 2008, Wenny et al. 2011). The majority of research in this area has assessed the role of birds in controlling herbivorous insects. Considerably less information is available about predatory birds and the beneficial consumption of avian and mammalian pests.

Methods

I searched the Web of Science database with relevant combinations of the keywords: bird, orchard, avian, crop, damage, fruit, and vineyard to generate an initial list of papers for this review. To this list I added any papers I knew of but that had not been produced by the database

search. Last, I added relevant references cited within or by any of these papers. Database searches were conducted between January 28, 2016 and February 8, 2016. From the database results, I included relevant studies that took place in fruit agriculture in

temperate regions of North America and Eurasia. I focused my review on these regions because of their high contribution to global fruit production and their long-standing, but sporadic, history of research into avian use of fruit agriculture. I included only studies that evaluated the role of birds in fruit agriculture and excluded studies that were interested in agriculture's effects on birds or bird communities. I also excluded studies that took place exclusively in laboratory settings and studies that reported on the efficacy of different bird deterrent techniques but provided no data for bird damage in the absence of such techniques.

Negative Implications Of Avian Fruit Orchard Use

Bird damage to fruit by direct consumption

Studies reporting bird damage to fruit via direct consumption of the fruit itself occurred in North America but not Europe, while European studies reported alternative mechanisms of damage such as bud eating (Summers and Pollack 1978) or pollinator consumption (Galeotti and Inglisa 2001). Most of the work in this area has been conducted in the United States, but some studies have taken place in fruit growing regions of Ontario, Quebec, and British Columbia in Canada. This geographic difference in foci could be attributed to long-standing infusion of funding and research effort by national agencies such as the United States Department of Agriculture into studies of bird damage to crops, economic losses, and loss mitigation. Within the United States, research has occurred in major fruit-growing regions like Michigan, California, New York, Washington, and Florida.

Species causing damage

In fruit-growing regions, orchards offer birds rich patches of foraging habitat with numerous, perennial fruit resources (Dolbeer et al. 1994, Simon 2008, Lindell et al. 2012). Cultivated fruits are attractive food resources for many species of birds because fruits are abundant, energy-rich, and easily accessible. A variety of bird species consume and damage cultivated fruit. Such damaging species range from predominantly frugivorous species such as cedar waxwings (*Bombycilla cedrorum*; Stone 1974, Lindell et al. 2012) to omnivorous species such as American robins (*Turdus migratorius*; Lindell et al. 2012) and common starlings (*Sturnus vulgarius*; Stone 1973, Guarino et al. 1974). To a lesser extent, some studies identify birds that are typically insectivores like woodpeckers and flycatchers (Boudreau 1972, DeHaven and Hothem 1981) and granivores like house finches (DeHaven 1974, DeHaven and Hothem 1981, Tobin et al. 1989) as fruit damaging birds.

Among this diversity of avian fruit crop consumers, the most frequently cited fruit crop pests across an array of fruit types are the omnivorous American robin and common starling (Stevenson and Virgo 1971, Stone 1973, Guarino et al. 1974, Anderson et al. 2013) and the frugivorous cedar waxwing. Birds of these species are frequent orchard visitors (Guarino et al. 1974, Lindell et al. 2012, Eaton et al. 2016) and often consume substantial amounts of fruit (Boudreau 1972, Guarino et al. 1974, Lindell et al. 2012). These three species are considered significant fruit pests in wine grapes (*Vitis* spp.; Stevenson and Virgo 1971, Bourdeau 1972), sweet and tart cherries (*Prunus avium* and *Prunus cerasus*; Stone 1973, Guarino et al. 1974, Lindell et al. 2012), and blueberries (*Vaccinium corybosum*; Lareau and Vincent 1985, Nelms et al. 1990, Avery et al. 1991). American robins and common starlings, along with American crows (*Corvus brachyrhynchos*), are significant pests in apples (NASS 1999, Anderson et al. 2013). A

survey of apple growers across the U.S. in 1998 estimated that common starlings and American robins cause 16% and 9% of the damage to apple crops, respectively (NASS 1999). In Ontario, starlings comprised 42% of all birds identified in sweet cherry orchards and caused 60% of observed damaged (Virgo 1971). In Michigan cherry orchards, cedar waxwings were responsible for >60% of all avian sweet cherry consumption, while American robins were responsible for >40% of tart cherry consumption (Lindell et al. 2012). Most recently, apple, grape, blueberry, and cherry growers from New York, Michigan, and the Pacific Northwest identified starlings and robins as two of the most damaging bird species in fruit crops (Anderson et al. 2013).

Several features of American robins, common starlings and cedar waxwings contribute to their role as principle fruit-damaging bird species. All three species frequently live and forage in human-modified environments, including agricultural environments (Homan et al. 2010, Lindell et al. 2012). These species take advantage of readily available fruit food resources; for example, when foraging in high-fruit areas American robins increase the proportion of fruit in their diets (Wheelwright 1986). Cedar waxwings are also highly frugivorous; 84% of their annual diet consists of fruit (Witmer 1996). In addition, cedar waxwings show preferences for sugar-rich fruits, like many cultivated crops, over lipid-rich fruits, like many wild fruits (Witmer and Van Soest 1998). In addition, cedar waxwings and common starlings forage in large groups in orchards and vineyards, which can contribute to the heavy degree of fruit consumption and damage, making them particularly troublesome pests (Stone 1974, Nelms et al. 1990, Lindell et al. 2012).

Much of the data on the identity of avian fruit crop pests comes from fruit grower reports and species surveys of birds in fruit crops. For instance, a survey of >1500 fruit growers in New York, Michigan, and the Pacific Northwest identified American robins and common starlings as

the top species responsible for bird damage to blueberry, wine grape, and cherry crops (Anderson et al. 2013). However, the association between bird species frequently observed in orchards and those that actually cause crop damage is not always clear. Virgo (1971) noted a high density of robins present in Ontario sweet cherry orchards (28% of all birds observed); however, robins were responsible for a relatively small proportion (\sim 5%) of the damage. Critical components of wildlife damage-control programs include understanding the identity and ecology of species causing the damage (Somers and Morris 2002, Tracey et al. 2007). Recent work has emphasized feeding observations of birds actually consuming fruit crops over survey-based studies or grower-identified assessments to evaluate the role of different species in fruit damage (Lindell et al. 2012). In order to understand better the extent of bird damage to fruit crops, more targeted research studies are needed to identify the birds causing crop damage and robustly quantify species-specific damage. Additional research that identifies problem species in particular regions or crops of interest will be important to generate efficient and effective deterrent techniques. Such an approach will be more efficient and economical than attempting to deter all birds since not all birds cause problematic levels of damage. In the third chapter of my dissertation, I explored this by quantifying and comparing the species-specific crop damage of two common fruit-consuming species, American robins and cedar waxwings.

Types of fruit damaged and field-based damage estimates

The majority of research into estimating avian fruit crop consumption took place between the 1970s and early 1990s (e.g. Virgo 1971, Stone 1974, Guarino et al. 1974, DeHaven and Hothem 1981, Nelms et al. 1990, Avery et al. 1993, Vincent and Lareau 1993). Prior to this time, bird consumption of cultivated fruit was noted as a growing concern but relatively little research

had investigated the problem (Virgo 1971). The current body of literature on the extent of bird consumption of fruit crops comes from in-field damage assessments, as well as some direct surveys of fruit growers. These studies reveal that a variety of cultivated tree, vine, and shrub fruits are damaged by birds (Lindell et al. 2016), with most studies focused on North American wine grapes (DeHaven and Hotherm 1981), sweet and tart cherries (e.g. Virgo 1971), and blueberries (e.g. Avery et al. 1992). These fruits are economically valuable and thus there is strong economic motivation to evaluate the extent of avian crop damage. For example, in the United States wine grape production has a value of >2.5 billion dollars annually (NASS 2016), and Canada's wine industry generates 1.1 billion dollars annually (Agriculture and Agri-Food Canada 2016).

Wine grapes, cherries, and blueberries also share several characteristics that make them attractive food resources for fruit-consuming birds (Avery 2002). Grapes, cherries, and blueberries are high in sugar and energy rich. They also have thin skins and soft pulp, enabling easy consumption by birds (Avery 2002). In terms of quantifying bird damage and consumption, other fruit crops have received considerably less attention in the literature than wine grapes, cherries, and blueberries. A limited number of studies reporting bird damage exist for apples (Tobin et al. 1989) and citrus fruit (Johnson et al. 1989). Several major patterns emerge from the studies of avian fruit crop consumption.

The first major patterns is that most studies report low bird damage levels (e.g. <10%), and this is evident across multiple crop types. Bird damage affects a relatively small proportion of the overall fruit crop in apples (*Malus pumila*; Tobin et al. 1989), grapefruit (*Citrus x paradise*; Johnson et al. 1989), wine grapes (DeHaven 1974), and cherries (Stone 1974, Lindell et al. 2016). A recent multi-year field study of damage to Honeycrisp apples in Michigan, New

York, and Washington estimated damage at 2% (Lindell et al. 2016). My literature search revealed one study of grapefruit (Citrus paradisi) damage in Texas (Johnson et al. 1989); estimated damage across 30 grapefruit groves was 8%. In Ontario vineyards Stevenson and Virgo (1971) found that 85% of 108 vineyards had some degree of bird damage, but most (69%) showed damage levels of 10% or less. In Michigan tart cherries, Stone (1974) estimated damage at 7.4% and Lindell et al. (2016) recently found a three-year average for damage was 2.6% (Lindell et al. 2016). Sweet cherry crops tend to incur greater damage than those of tart cherries; however, overall bird damage to sweet cherry is still relatively low (Virgo 1971, Lindell et al. 2016). Virgo (1971) estimated damage to sweet cherries in Ontario as 3%. Lindell et al. (Lindell et al. 2016) generated three-year average estimate of 9% across multiple orchards in New York, Michigan, and Washington. Notably, one study found higher bird damage in tart cherries than in sweet cherries, in contrast to most reports (Guarino et al. 1974). However, this study was limited to four trees in two orchards and may thus reflect local trends rather than large-scale patterns. One important caveat regarding these reports of relatively low levels of bird damage is the existence of considerable year-to-year variation among in-field damage estimates (Lindell et al. 2016). For example, damage is much higher in years of low overall crop yield (i.e. due to poor weather or growing conditions) compared to years when crop yield is high (Lindell et al. 2016).

The relatively low damage in apples and citrus fruits may be explained in part by the presence of a thick, tough outer skin of these fruits. A thicker fruit skin is likely more difficult to break for birds with smaller bills, thus relatively few bird species may be capable of damaging apple and grapefruit crops. Indeed, apple growers report that larger-billed birds like American crows and wild turkeys (*Meleagris gallopavo*) are among the most significant apple pests (Tobin et al. 1989, Anderson et al. 2013), while great-tailed grackles (*Quiscalus mexicanus*) are major

grapefruit consumers (Johnson et al. 1989). With fewer possible apple and grapefruit problem species, overall damage estimates in these crops tend to be low. The reports of low bird damage in wine grapes and cherries are somewhat surprising given the soft-skinned texture and highenergy content that make these fruits attractive to wild foraging birds (Avery 2002). Estimated bird damage could also be low across many studies and crop types because the high density of available fruit in cultivated systems exceeds avian resource demands. In many fruit-growing regions, orchards and vineyards occur in close proximity to other fruit agriculture. Thus, the availability of fruit on a broad scale may be high enough that overall damage is low because fruit resources are broadly available. This phenomenon is already reflected in instances of temporal variation in fruit abundance; bird damage is lower in years with high fruit yield than in years with low fruit yield (Lindell et al. 2016). The effect of fruit resource abundance at broad spatial scales and the interaction between fruit abundance across multiple scales (e.g. an orchard and the surrounding landscape) on avian foraging behavior have not been well explored and I investigated these ideas further in my fourth dissertation chapter.

The second notable pattern among published studies is that damage estimates are highest in blueberries compared to other crops. Damage estimates in blueberries range from of 17% in Florida (Nelms et al. 1990) to as high as 85% in Michigan (Avery et al. 1993). Bird preferences for particular fruit characteristics may explain the substantially high level of damage in blueberry crops. Abundant fruit-consuming birds like American robins have demonstrated preferences for blue fruits over red, green or yellow options (Willson 1994). In addition, highly frugivorous birds like cedar waxwings demonstrate preferences for relatively small fruits that were similar in diameter to ripening blueberries (~7 mm), compared to larger fruits (McPherson 1988, Avery et

al. 1993). Given their small size, blueberries are accessible to a variety of fruit-consuming species of many sizes.

The third major pattern in bird damage to fruit is that early ripening fruit varieties incur greater damage than varieties that ripen later. Early-ripening varieties of sweet cherries (Virgo 1971), blueberries (Nelms et al. 1990), and apples (Tobin et al. 1989) incur more damage than their later-ripening counterparts. Early-ripening blueberry crops in Florida incurred damage as high as 75% (Nelms et al. 1990). Tobin et al. (1989) reported that apple varieties that displayed red coloration early in the season suffered the most damage. Several factors may contribute to high damage among early-ripening fruits. Fruit color in an important factor in the avian fruit selection process (Sallabanks 1993). Early-ripening fruits that turn from colors indicating unripe fruit like green and yellow to "ripe" colors like red and blue likely stand out among other fruit options and catch the attention of foraging birds. This effect is also supported by differences in damage among varieties of different colors. For example, susceptibility to damage is higher among darker varieties of grapes than lighter varieties (Boudreau 1972, DeHaven 1974).

Fruit varieties that ripen before others also represent an attractive but sparse resource in orchards and vineyards. Such varieties likely incur heavy damage because alternative fruit options in the foraging area are low at the time of ripening. Heavy damage to early-ripening fruits can have particularly negative consequences for growers because these fruits are first to hit markets and can have high economic value (Nelms et al. 1990). Patterns of heavy damage in early-ripening varieties suggest that fruit growers could mitigate potential bird damage by avoiding planting some varieties that ripen or color much earlier other varieties in the field.

Spatial patterns of field-based damage estimates

Bird damage to fruit crops shows several interesting spatial patterns. First, damage can be vertically stratified within plants; evidence for this comes from studies of grapes, cherries, and grapefruit. For example, DeHaven (1974) and Somers and Morris (2002) observed greater levels of damage on grape bunches growing high on a vine, further from the ground. Similarly, cherry-consuming birds in Michigan were observed almost exclusively in the top half of trees, suggesting that damage will be heavier in the higher parts of cherry trees than in lower parts (Lindell et al. 2012). However, like many trends in bird damage, there are inconsistencies in the pattern of vertical stratification of damage. Virgo (1971) found no evidence of such stratification in Ontario sweet cherry orchards. The upper parts of plants may incur greater damage because fruit density and nutritional quality is often higher in the upper parts of fruit trees, making those parts more attractive to fruit-eating birds (Houle et al. 2014). Future field assessments of bird damage to fruit should account for this vertical stratification to avoid biased estimates of damage. For example, sampling only in plant areas that are easily accessible to humans could lead to underestimated damage.

Second, habitat features adjacent to fruit crops influence the degree of damage; however, such patterns are inconsistent among studies. Anecdotal reports from fruit producers suggests that orchards that are spatially isolated from other fruit agriculture suffer greater damage than those that are near to other cultivated fruit fields. My literature search generated only two studies to corroborate this point; Johnson et al. (1989) found more damage in isolated grapefruit orchards than in orchards surrounded largely by other orchards. Isolated orchards may be especially attractive because they offer birds a high density of food resources in an area that may otherwise be limited in high-energy fruit resources. Lindell et al. (2016) recently determined that

sweet cherry blocks in Michigan sustained less damage when surrounded to a greater degree (e.g. on 1 or more sides) by other sweet cherry orchards compared to isolated blocks. In contrast, Virgo (1971) found no indication that the habitat surrounding a cherry orchard influenced the amount of bird damage. Some studies report that crops surrounded by a relatively high amount of non-fruit crops, such as forest, tend to have less damage than those with little surrounding forest (Lindell et al. 2016). This pattern may due in part because prominent avian fruit pests, like common starlings are not forest-dwelling species and tend to avoid fruit crops surrounded by forests (Boudreau 1972). Man-made habitat features like power lines can also affect the extent of bird damage because they offer perching places for many birds and draw in large numbers of crop-damaging birds to adjacent fruit crops (Bourdreau 1972). For example, plantings of Honeycrisp apples suffered slightly greater damage if utility wires ran overhead compared to those without overhead wires (Lindell et al. 2016).

Some studies also report the existence of edge effects, wherein plants nearer to the edge of an orchard or vineyard have greater damage than plants nearer to the interior (Somers and Morris 2002). Texas grapefruit orchard edges had higher damage than interior areas (Johnson et al. 1989). However, support for edge effects is not consistent within or among crop types (Lindell et al. 2016). Somers and Morris (2002) found that damage levels in vineyards in Ontario were greater near edges and declined closer to the vineyard interior. In contrast, DeHaven and Hothem (1981) found no evidence of edge effects is consistent with the larger literature on the edge effect phenomenon, which has been difficult to generalize (Ries and Sisk 2004). Given that these few studies in fruit crops suggest higher vulnerability to bird damage along field edges, crop producers may experience more efficient damage mitigation by targeting edge areas. However, it

is clear that additional studies are needed to determine the circumstances under which edge effects occur, and to what extent these effects vary among pest bird species.

These spatial effects contribute to variation in damage incurred by different fruit growers. Situations in which many growers have little or no damage, while few growers have substantial damage, can lead to relatively low costs to the industry overall despite significant challenges to some growers (Virgo 1971). Collectively, these spatial patterns in bird damage suggest that fruit producers may benefit from targeting bird deterrent efforts toward particular edges or growing plots that are more likely to suffer bird damage, how such foci are likely to vary among fruit types and growing locations. Therefore, the variability among studies and the relatively low amount of research into bird damage to fruit crops suggest that further work is needed to elucidate generalizable patterns of bird damage; especially considering most of the published literature is over 20 years old.

Economic damage estimates

Some studies have translated in-field damage estimates into economic consequences for fruit producers; however, such estimates are sparse throughout the past 40 years. The most prominent pattern regarding economic estimates is the high degree of variability in costs incurred by different fruit growers. Despite the generally low levels of bird damage reported in the literature, some individual growers can suffer high financial losses. Johnson et al. (1989) quantified US\$ 2.2 million in damage in Texas grapefruit groves. However, bird damage was highly variable among groves; some growers experienced loss of as little as \$10 per ha, others incurred as much as \$1900 per ha.

The high degree of variability in field-based damage estimates suggests that alternative mechanisms to overcome such variability may be important to generate more broadly applicable damage estimates and resulting values of economic loss. Accurate loss estimates are important for growers to evaluate whether, and to what extent, money and effort should be spent on bird damage mitigation. Bioenergetic-based crop damage estimates that incorporate data on bird diets and energy needs, along with the energy content of crops have gained prominence in the literature in recent decades (e.g. Wiens and Dyer 1975, Peer et al. 2003, and Homan et al. 2011). A bioenergetics method is not based upon damage levels at different orchards or vineyards and is thus subject to less variance. Such an approach has not yet been applied to fruit agriculture. In the second chapter of my dissertation, I utilized a bioenergetics approach to estimate bird damage to Michigan cherry crops.

Indirect damage to fruit crops

There are considerably fewer studies of non-consumptive bird damage to fruit crops and fruit plants compared to studies of avian crop consumption. Beyond direct consumption, negative implications of avian orchard use include increased susceptibility of damaged fruit to other pathogens (e.g. Ioriatti et al. 2015), pollinator consumption (Golawski and Golawska 2013), and bud consumption (Greig-Smith and Wilson 1984).

Bird damage to fruit increases susceptibility to other pests

Birds often damage fruits but do not consume them fully. These injuries to fruit skin provide entry points for invertebrate pests such as fruit flies (Stevenson and Virgo 1971, Ioriatti et al. 2015) or fungal pathogens (Xu et al. 2001, Holb and Sherm 2008). The earliest mention of this damage type comes from Stevenson and Virgo (1971); they posited that bird-damaged grapes attracted fruit flies in Ontario vineyards but provided no data to that effect. Iorriati et al. (2015) tested the likelihood of bird damage to increase spotted wing Drosophila (*Drosophila suzukii*) infestation of wine grapes in Oregon and Italy. *D. suzukii* is a common invertebrate pest that feeds on and lays eggs in cultivated fruits. Iorriati et al. (2015) experimentally incised grapes to mimic bird damage and found a higher incidence of *D. suzukii* in these grapes than in unmanipulated grapes.

Bird damage also invites fungal infestation such as brown rot, *Monilinia fructigena* (van Leeuwen et al. 2000, Xu et al. 2001, Holb and Sherm 2008); studies addressing this type of damage take place primarily in apple crops. Brown rot is the most significant fungal pathogen of stone fruits, fruits with a fleshy outer tissue that surrounds a hard "stone" around the seed, throughout the warm climates of the world (Ritchie 2000). Brown rot caused an 11% loss in yield in Polish apple orchards; bird damage was responsible for 29% of new brown rot inoculations (Xu et al. 2001). In Hungary, brown rot occurred in 94% of all injured apples. However, insects were responsible for much more damage than birds; bird damage comprised only 25% of the fruit injury (Holb and Sherm 2008). In Poland, birds caused more damage to pears than insects or typical growth cracking (Xu et al. 2001); approximately 70% of new *M. fructigena* inoculations stemmed from bird damage (Xu et al. 2001).

Only a few studies have explored the capacity for birds to increase fruit's susceptibility to other pathogens and drawing general patterns is difficult. Overall, such research is recent and agrees that birds contribute to higher incidences of insect and fungal pathogens by damaging fruit crops. There is some disagreement as to whether bird-caused injury in fruits leads to higher pathogen incidence than insect-caused injury. Additional research is necessary to elucidate more

clearly the relative roles of birds and fruit-damaging insects in increased pathogen susceptibility. In addition, no study attempted to quantify the financial consequences of increased pathogens due to bird damage. Doing so would provide fruit producers and managers a more holistic picture of the economic costs of bird damage to fruit.

Birds consume invertebrate crop pollinators

Some insectivorous birds in orchards consume fruit tree pollinators like bees (Bosch and Trostle 2006, Galeotti and Inglisa 2001, Golawski and Golawska 2013). This type of damage could adversely affect crop growth and yield and would be especially problematic for crops that require cross-pollination. However, I found no study that directly quantified the effect of pollinator consumption on crop yield. Among studies, the extent to which birds consume pollinator bees varies. For instance, bees (Apidae) are more important for pollination of fruit trees than other hymenopterans (Galeotti and Inglisa 2001). Galeotti and Inglisa (2001) analyzed stomach contents of European bee-eaters (Merops apiaster) foraging in orchard-rich regions of Italy and found that honeybees comprised up to 63% of the diet. In contrast, bees (Family: Apidae) comprised just 2% of the red-backed shrike diet in Polish apple orchards (Golawski and Golawska 2013). Bosch and Trostle (2006) noted that bluejays and American robins consumed orchard mason bees (Osmia lignaria) emerging from hives in Utah sweet cherry orchards, negatively affecting bee population growth. These varied results and the limited research in this area invite further exploration to understand the extent of avian pollinator consumption and specifically quantify the potential yield losses due to pollinator consumption. If bird consumption of pollinators adversely affects crop yield, then bird damage mitigation strategies should be expanded to protect crops during the flowering period.

Birds consume fruit tree flower buds

A few studies from the 1960s through the 1980s explored the negative consequences of avian consumption of fruit tree buds (Newton 1964, Summers and Pollack 1978, Greig-Smith and Wilson 1984, Greig-Smith 1987). However, research in this area is limited in scope and has looked exclusively at Eurasian bullfinches (*Pyrrhula pyrrhula*) feeding on dormant flower buds in English pear orchards (Summers and Pollack 1978). Wild tree fruit buds are a common foods for Eurasian bullfinches and these birds take advantage of the abundance of buds in cultivated fruits (Newton 1964), which explains why research on bud consumption focuses on this species. Other noted bud-consuming species are tit species (*Parus* spp.) and house sparrows (*Passer domesticus*; Newton 1964).

Eurasian bullfinches consume the center of the bud itself, which is a highly nutritious food item (Summers and Pollock 1978). The type of indirect damage can adversely affect fruit production because when birds consume flower buds, fewer flowers are available for pollination and fruit production, which can lower yields. Yield loss is proportional to the severity of bud loss (Summers and Pollock 1978). Summers and Pollock (1978) experimentally removed >50% of buds from trees in a pear orchard to mimic bird damage and recorded yield losses between 50 and 85%. Bud damage, like direct fruit consumption, displays spatial and temporal patterns (Wright and Summers 1960, Newton 1964, Summers and Pollack 1978). For example, bullfinches removed 100% of buds from one pear variety, but only 12% of another in 1961 (Newton 1964). In contrast, bud removal the following year was less than 2% in both varieties (Newton 1964). The exterior areas of orchards incur greater damage via bud loss than interior areas (Summers and Pollack 1978, Greig-Smith and Wilson 1984). Greig-Smith and Wilson (1984) documented up to 80% bud removal in pear trees near wooded edges. This is likely

because woodland areas are the preferred breeding habitat of Eurasian bullfinches (Newton 1964), making woodland-adjacent orchards particularly vulnerable to bud damage.

Birds consume dormant flower buds in the winter, outside the typical vulnerable period for ripening fruit (Greig-Smith and Wilson 1984). These studies suggest that damage mitigation efforts should not be limited to protecting fruits. Based on the available literature, it is not known whether bud feeding and subsequent yield loss occur outside this system of bullfinches and English fruit orchards. There is no evidence of research in this area after the 1980s. Given the potential for high yield loss due to bud consumption, additional work is needed to determine whether bud consumption is a concern in other crops and growing regions and whether other bird species are causing winter season crop damage via bud consumption.

A significant gap in the literature remains regarding these indirect, non-consumptive mechanisms of bird damage to fruit. Given the relatively limited and situation-specific information in these areas, it is not yet clear how badly these alternative bird damage mechanisms affect crop production. More research is necessary in these areas to determine whether these negative implications of birds in fruit crops 1) are substantial enough to warrant mitigation by crop producers and 2) are occurring on a broad scale across crop types and growing regions.

Positive Implications Of Avian Fruit Orchard Use

Birds consume orchard pests

Invertebrate orchard pests

Insects are becoming increasingly resistant to pesticides and public concern about the use of pesticides due to health concerns have become more widespread. This environment supports

the need for increasing research to understand the potential for biological control of persistent and widespread invertebrate pests. Studies of avian consumption of crop pests are plentiful, but few studies explore the potential for avian predation on crop pests to result in yield benefits due to increased yield with the reduction in pest species (Mooney et al. 2010). Similarly to uneven distribution among crop types in studies quantifying crop damage by birds, studies of potential avian benefits to fruit crops are clustered among a relatively small number of crop types. Research has been conducted primarily in apples (e.g. Mols and Visser 2002), and grapes (e.g. Jedlicka et al. 2011).

A series of studies in apple orchards in the Netherlands have focused caterpillar consumption by on great tits (*Parus major*) and the reduction in leaf damage caused by caterpillars (Mols and Visser 2002, Mols et al. 2005, Mols and Visser 2007). Mols and Visser (2002) demonstrated that bird predation on leaf-damaging caterpillars increases apple yield. When birds were permitted to consume caterpillars, leaf damage decreased from 13.8% to11.2% compared to trees from which birds were excluded (Mols and Visser 2002). Bird consumption of caterpillars resulted in a 3.1 kg increase in crop yield per tree, specifically the production of more apples (Mols and Visser 2002). In contrast, Pinol et al. (2010) found a relatively weak effect of birds on arthropod abundance in citrus groves in Spain. Most of the research in this area comes from apple orchards in the Netherlands. The contrast between those studies and that of Pinol et al. suggests that the potential benefits of avian pest consumption are variable among crop types, farms, or growing regions. This variability illustrates the need for future studies to assess the relationships not only between birds and invertebrate pests but also between avian pest consumption and resultant crop production to understand how crop growers can benefit from and take advantage of avian orchard use.

By installing nest boxes in orchards, fruit growers can exploit bird predation on pest arthropods (Mols et al. 2005, Mols and Visser 2007, Jedlicka et al. 2011). For example, apple orchards with great tit nest boxes installed had half as much caterpillar damage as orchards without nest boxes, resulting in an increased yield of 1200 kilograms per hectare (Mols and Visser 2007). Jedlicka et al. (2011) saw insectivorous bird density increase by nearly four times after installing nest boxes in California vineyards. In addition, Jedlicka et al. (2011) used sentinel prey to determine that prey removal in vineyards with nest boxes was 2.4 times greater than in vineyards without added nest. These studies illustrate not only that insectivorous birds can benefit fruit growers by consuming herbivorous insects and contributing to increased yield, but also that this benefit can be enhanced relatively easily and inexpensively by adding nest sites (Mols and Visser 2002, Jedlicka et al. 2011). However, given that these patterns have been explored in a select few studies and in only two types of fruit crops, more work in this area is needed before making generalized recommendations to growers regarding the value of installing structures to attract insectivores.

Invertebrate pests do not just consume tree leaves; species such as the codling moth (*Cydia pomonella*) and winter moth (*Operophtera brumata*) attach to and build cocoons in bark to overwinter. During the fruiting season, moth larvae are common fruit pests, damaging and consuming the fruit itself. Bird species like great tits (Soloman et al. 1976), pine siskins (Roland et al. 1986), and woodpecker species (MacLellen 1958) benefit fruit growers by uncovering and feeding on these bark pests. The role of birds in controlling moth larval density in fruit orchards was explored several decades ago in both North America (e.g. MacLellan 1958, Roland et al. 1986) and Europe (e.g. Soloman and Glen 1979). Bird consumption of codling moth larvae can be substantial. In Nova Scotia, Canada downy woodpeckers (*Picoides pubescens*) and hairy

woodpeckers (*Leuconotopicus villosus*) took 52% of overwintering codling moth larvae experimentally placed on apple trees (MacLellan 1958). Roland et al. (1986) found that when birds were excluded from foraging in certain trees, codling moth larvae density was three times greater than in trees where birds could freely consume larvae. Soloman and colleagues experimentally added codling moth larvae to apple orchards in the UK to assess moth mortality due to great tits (Soloman et al. 1976, Soloman and Glen 1979). In two successive years, birds depredated approximately 95% of codling moth larvae. Consumption declined when larval density declined, suggesting a density-dependent pattern to codling moth regulation by birds (Soloman et al. 1976, Soloman and Glen 1979).

The extent to which bird predation on overwintering moths benefits crop production has not been explored quantitatively. More research could better elucidate the conditions under which birds regulate moth density most effectively. However, despite substantial avian predation on moth larvae (MacLellan 1956, Roland et al. 1986), moth density often remains high during the fruiting season and considerable moth damage to crop leaves and fruit remains (Roland et al. 1986). This lack of sufficient pest control benefit by birds may explain why research in this area apparently subsided thirty years ago. Therefore, devoting additional energy to such studies may not result in valuable information for fruit producers if avian moth larvae consumption is consistently unable to mitigate moth abundance and subsequent crop damage.

Mammalian orchard pests

Bird predation on mammalian crop pests is another positive implication of avian use of fruit orchards. Mammalian pests like voles (e.g. *Microtus pennsylvanicus*), moles, and gophers (Family: Geomyidae) damage orchards and vineyards by digging burrows throughout fields,

damaging equipment like irrigation systems, or chewing the bark around fruit trees (Ashkam 1990, Moore et al. 1998). Use of rodenticides to regulate these pests is costly and concerns about consequences for food safety have fueled study of biological control mechanisms. Relatively recently, birds of prey have been investigated as means for controlling vertebrate damage in fruit crops (Ashkam 1990, Moore et al. 1998, Paz et al. 2013). However, there is considerably less published research in this area than studies of birds mitigating invertebrate damage. This discrepancy may be due to the considerable challenges of systematically locating and tracking sufficient numbers of wide-ranging predatory birds, quantifying consumption of mammalian pests, and simultaneously assessing effects on pest mammal populations.

Studies of predatory birds and mammalian fruit pests typically explore ways in which crop producers can attract predatory birds and reduce mammalian pest abundance (e.g. Askham 1990, Moore et al. 1998, Merwin et al. 1999, Paz et al. 2013). Askham (1990) installed artificial perches and nest boxes to attract predatory birds to Washington apple orchards. However, no owls occupied owl nest boxes and American kestrels (*Falco sparverius*) occupied only 13% of boxes erected for them. Askham (1990) provided some summary data to suggest that vole activity in the orchards with bird attracting structures was generally lower than in control plots, but did not support these conclusions with robust analyses. Moore et al. (1998) surveyed fruit growers in California to assess the perceived efficacy of owl nest boxes in controlling gophers. While fruit growers saw 40% box occupancy, only 23% believed that barn owls (*Tyto alba*) effectively controlled gophers (Moore et al. 1998); overall this survey revealed a high level of variation among growers in the perceived efficacy of barn owls on gopher pests (Moore et al. 1998). In addition, Merwin et al. (1999), observed raptor species like red-tailed hawk (*Buteo jamaicensis*) and American kestrel hunting around apple orchards with high vole density, but these predators did not control vole abundance or reduce pest damage. The on-going problem of mammalian pests, increasing interest in biological control methods, and dearth of robust data on the capacity of predatory birds to regulate pest mammals suggest that such studies should be an area of active research.

An on-going question about the positive implications of birds in fruit agriculture and the of vertebrates as biological control agents is whether they can demonstrate a sufficient numerical response to abundance of pest organisms to offer some kind of damage-limiting benefit and subsequent increase in crop yield. The literature addressing the positive roles of birds offers mixed messages regarding the capacity for insectivores and birds of prey to control crop pests and positively affect crop production. Studies of insectivorous birds have begun exploring this, but the number of studies remains limited, as does the number of crops in which these studies are conducted. Overall, research energy could be expended on studies of tri-trophic interactions involving predators, prey, and crops are necessary to quantify actual consequences of bird predation of pest organisms on crop yield. Furthermore, I was unable to find published data from North America or Eurasia on whether birds of prey affect fruit consumption by pest bird species; however, such studies have demonstrated this relationship elsewhere in places like New Zealand (e.g. Kross et al. 2012). Given the considerable evidence of birds as fruit pests, the potential for biological control of fruit-consuming birds by raptors could be a valuable area of future research.

Addressing Gaps In Avian Use Of Cultivated Fruit Orchards

My review of the positive and negative implications of avian use of fruit crops revealed several areas that warranted further exploration. First, bird damage to fruit exhibits variation over time and space, but little has been done to evaluate avian orchard use over extended temporal

scales such as throughout the fruit-growing season. Second, estimates of bird damage based upon in-field studies are highly variable and do not typically quantify damage by individual bird species, despite indications that birds vary in fruit consumption within orchards. Third, the availability of fruit at broad spatial scales and the habitat context within and around fruit orchards can influence fruit damage. However, it remains unclear how fruit consumption of individual birds is affected by resource availability at broad spatial scales and across multiple scales.

I investigated these problems in the second, third, and fourth chapters of my dissertation by studying two common fruit consuming species in Michigan sweet cherry orchards. American robins and cedar waxwings are frequently identified crop pests and are responsible for a relatively high proportion of cultivated sweet cherry consumption (Lindell et al. 2012). Cherry orchards are attractive for fruit-eating birds because cherries are brightly colored, densely available, and have easily accessible pulp (Sallabanks 1993). Cherries are also an economically valuable fruit crop; Michigan growers estimate annual losses to birds of over \$US2 million statewide (Anderson et al. 2013). Therefore, sweet cherry orchards provide an ideal system in which to explore questions of avian use of cultivated fruit crops. Below, I introduce and explain the objectives for my second, third, and fourth dissertation chapters.

In my second dissertation chapter, I addressed the problem that, despite numerous studies investigating avian consumption of cultivated sweet cherries (Virgo 1971, Curtis et al. 1994, Lindell et al. 2012), the extent of avian orchard use over the growing season has not been established. Information on the species-specific foraging patterns of fruit-eating birds throughout the fruit growing season orchards can help growers target particular bird species and times when fruit loss is greatest (Dolbeer et al. 1994, Somers and Morris 2002, Tracey et al. 2007).

Omnivorous American robins consume some fruit, as well as a large amount of invertebrates; while cedar waxwings are heavily frugivorous (Witmer 1996). In addition these species differ in fruit preference, which likely influences orchard use. In the second chapter of my dissertation, my objective was to determine whether cedar waxwings exhibited more intense use of sweet cherry orchards than robins based on their differences in diet. To achieve this objective I captured wild birds and used radio-telemetry techniques to assess the frequency of visits to cherry orchards throughout the cherry-growing season, as well as the time birds spent visiting orchards each day.

In my third dissertation chapter, I addressed the problem that estimates of bird damage and resulting financial loss lack a species-specific approach and can be subject to high variability from one site to another. Bioenergetic models of bird damage provide species-specific estimates that are based on avian energy needs, diet composition, and crop energy content (Wiens and Dyer 1975, Peer et al. 2003). A species-specific approach is important because recent work has shown that the degree of avian cherry consumption varies among species (Lindell et al. 2012). In the third chapter of my dissertation, my objective was to provide the first species-specific, region-wide estimates of bird damage and financial loss in sweet cherry crops. To achieve this objective I collected data on avian energy needs, diet composition, and local population sizes to construct bioenergetic and economic models of bird damage.

In my fourth dissertation chapter, I addressed the gap in the literature regarding the influence of resource availability at broad spatial scales and across multiple scales on avian foraging behavior in fruit orchards. Traditional foraging models are difficult to apply to highly mobile animals foraging on broadly distributed resources because resource heterogeneity occurs at multiple spatial scales. The influence of multi-scale resource availability on behavioral
responses is understudied, despite the hierarchical nature of foraging decisions. Fruit-eating birds make foraging decisions at multiple scales (Sallabanks 1993). Thus, fruit resource availability at the scale of the foraging patch, as well as across broader habitat and landscape scales likely affect the behavior of frugivorous birds. In addition, research has not examined how multi-scale resource availability could affect foraging within the context of sociality. In the fourth chapter of my dissertation, my objectives were to 1) evaluate whether avian foraging behaviors depend on relative fruit abundance at hierarchical spatial scales, and 2) determine if fruit abundance at large spatial scales constrains social foragers more than solitary foragers.

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CHAPTER 2

ESTIMATING FRUIT DAMAGE AND ECONOMIC LOSS DUE TO BIRDS WITH A BIOENERGETIC APPROACH

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Abstract

Bird damage and consumption of fruit crops amounts to tens of millions of dollars in losses annually across the United States. Yet, the development of successful damage-mitigation strategies for fruits is often hindered by a lack of species-specific damage information. A bioenergetic model of crop damage integrates species-specific data on energetic demands and diet to estimate crop consumption. Compared to traditional damage surveys, a bioenergetic approach permits a regional quantification of damage. In conjunction with local population sizes and crop economic value, bioenergetic models can be used to develop economic models that quantify financial loss due to bird damage on a species-specific level. We used a bioenergetic approach to quantify damage to sweet cherry crops (Prunus avium) by American robins (Turdus *migratorius*) and cedar waxwings (*Bombycilla cedrorum*) in an important sweet cherry production region of Michigan. Individual waxwings consumed three times as much sweet cherry and caused seven times the financial loss as robins, in large part because of larger local population sizes and greater reliance on fruit in trees by waxwings; robins take over half their fruit from the ground. We estimated that economic losses from this damage in our study area, over 28 days from preharvest to postharvest, were \$US1.8 million and \$US147,000 from the waxwing and robin populations, respectively. Bioenergetic model estimates allow us to contrast damage from multiple pest species and understand pest species ecology, which is essential for better-informed management programs.

Introduction

Human demand for cultivated fruits has increased in recent decades (ERS 2015), due in part to increased attention on the associated health benefits of fruit consumption (e.g., World

Health Organization 2010, Lock et al. 2005, Hjartåker et al. 2014). Fruit production in the United States is substantial; 28.4 million tons in 2014 with a value of more than \$US20 billion (ERS 2015). High-value fruit crops are often subject to extensive depredation by fruit-eating birds (Beal 1915, Dolbeer et al. 1994, Simon 2008); resulting financial losses are of major concern to fruit producers. Growers in Michigan, New York, and the Pacific Northwest recently estimated that bird damage to wine grapes, blueberries, apples, and cherries costs over \$US180 million annually (Anderson et al. 2013). Successful strategies to mitigate bird damage have been hindered by the lack of information regarding 1) how much of the crop different bird species consume and 2) the size of local populations of crop-damaging species (Dolbeer et al. 1994, Somers and Morris 2002). Here, we used bioenergetic modeling to quantify avian consumption of a high-value crop, sweet cherry (*Prunus avium*), by two prominent fruit-consuming species. We provide the first species-specific, region-wide estimates of bird damage for this crop. We then integrated these bioenergetic-based consumption estimates with avian population data and the economic value of sweet cherry to generate models of monetary losses due to bird damage.

A bioenergetic approach provides species-specific quantifications of bird damage that are based on avian energetic needs, diet composition, and energy content of the focal crop (Wiens and Dyer 1975, Peer et al. 2003). This approach overcomes a common challenge in understanding avian crop damage: quantifying the impact of individual pest species (Somers and Morris 2002, Simon 2008). Field-based estimates typically quantify the extent of pest damage by identifying damaged and missing fruits (e.g., Tracey and Saunders 2010, Lindell et al. 2016). Yet, such approaches cannot attribute damage to particular species because doing so would require near-continuous, wide-scale observation of birds feeding in crops. Such efforts are timeand cost-prohibitive. Previous attempts to quantify fruit damage by individual species have relied

upon surveys of birds seen in orchards and attributed crop damage to the most frequently detected species (e.g., Johnson et al. 1989). However, frequently detected species are not necessarily the most important fruit consumers (Virgo 1971, Lindell et al. 2012).

Economic models are typically used to estimate financial loss resulting from avian fruit damage and consumption. Usually economic models are based upon estimates of damage quantified by lost yield estimated by producers or from in-field damage surveys (Drake and Grande 2002). However, these methods can be subject to a high degree of variance and are timeintensive and personnel-intensive (Peer et al. 2003, Saxton 2006, Lindell et al. 2016). Additionally, previous economic models have typically assessed damage at the taxonomic level of class (e.g., Aves) rather than species (Drake and Grande 2002), yet Lindell et al. (2012) have shown that the degree of avian fruit consumption of sweet cherries is species specific. Accurate and species-specific assessments of financial losses due to bird depredation are crucial for the targeted and cost-effective implementation of loss-prevention strategies (Somers and Morris 2002, Tracey et al. 2007).

A bioenergetic approach has been undertaken to quantify damage to crops like corn (Weatherhead et al. 1982) and sunflower (Peer et al. 2003), but not in other valuable crops such as fruits. On a per-block annual basis cherry growers lose 2 - 13% of their crop to bird damage or consumption (Lindell et al. 2016). A block is defined as a contiguous area of crop with boundaries to adjacent land cover types of at least wide meters in width. Michigan growers estimate that bird damage to sweet cherries amounts to annual losses of over \$US2 million statewide (Anderson et al. 2013). American robins (*Turdus migratorius*) and cedar waxwings (*Bombycilla cedrorum*) are frequent visitors to sweet cherries than other fruit-consuming birds

(Lindell et al. 2012). Additionally, fruit producers perceive these species to be problematic, especially robins (Anderson et al. 2013). However, the extent of sweet cherry consumption and resulting economic cost of damage by these particular species over the fruit-ripening season in northwestern Michigan, an important sweet cherry production region, is not known. For this study, we developed species-specific bioenergetic models of American robin and cedar waxwing cherry consumption over the cherry-ripening season. We then incorporated these consumption data, along with population estimates, into economics models to quantify economic losses sustained by growers due to robin and waxwing crop damage.

Methods

We conducted this study in Leelanau County, Michigan, a peninsula (land area = 900 km², water area = 5659 km²) on Lake Michigan and an agricultural region containing many orchards and vineyards (Figure 2.1). We selected as our study area a region of eastern Leelanau County (208 km²) that contains a majority of the county's sweet cherry orchards. We used the USDA NASS CropScape program and the 2014 National Cropland Data Layer (NASS 2014) to calculate how much of this area comprised each of the three habitat types used in our study. Our study area consists of 70.7 km² (33.9%) woodland, 51.8 km² cherry orchard (sweet and tart varieties; 24.9%), and 20.0 km² urban/built space (9.6%). Other land use types in the area include grassland/pasture, fallow or barren land, herbaceous land, and crops like corn and alfalfa (NASS 2014). Sweet cherries make up 43% of the total cherry acreage in Leelanau County and 22% of total cherry acreage in Michigan (NASS 2015a). Given that the majority of cherry orchards in the county are included in our study area, we assumed this ratio of sweet to tart cherries held true

in our study area. Thus we used this ratio to calculate the area of sweet cherries $(22.3 \text{ km}^2, 32\%)$ in our study area from total cherry area.

Mean monthly rainfall and air temperature during the 2015 study period (May – July) were 5.8 cm and 17.4 °C, respectively (NWMHRS 2015). Both robins and waxwings are common in the study region during the summer cherry-growing season. Waxwings arrive in the region by late May and nest between mid-June and August (McPeek 2011a). Robins typically arrive in March, begin nesting in April, and often rear two broods (McPeek 2011b).

Bioenergetic models of avian sweet cherry consumption

We generated species-specific bioenergetic models to estimate daily sweet cherry consumption by robins and waxwings. We first quantified robin and waxwing field metabolic rates (FMR) using a formula for free-living passerines (Nagy et al. 1999):

$$v = 10.4x^{0.68}$$

where *y* is FMR (kJ/day) and *x* is mean bird body mass (grams). This formula is appropriate for estimating metabolic rate of wild birds because it incorporates basal metabolic rate, as well as activities like foraging and digestion, flying, reproduction, growth, and anti-predator behavior (Nagy et al. 1999). We calculated mean body mass from birds captured in mist nets (methods described below) from 30 June – 19 July 2015.

Our species-specific bioenergetic models of cherry consumption during the fruit-ripening period took the following form:

 $Per-bird \ consumption = \frac{DER}{cherry \ energy \ density} \times moisture \times diet \times days$

where DER is daily energy requirements (kJ/day), cherry energy density is the energy content of sweet cherries (14.85 kJ/g dry mass), moisture is a correction for water content of consumed cherry (1.82; USDA Agricultural Research Service 2016), diet is the proportion of sweet cherries in the diet, and days is the number of days in the study region over which cherries are most vulnerable to depredation (28 days).

For both species we quantified daily energy requirements (DER) in kJ/day by dividing FMR by the apparent metabolizable energy coefficient (MEC^{*}) of birds feeding on fruit (Smith et al. 2007). MEC^{*} is defined as: (energy content of ingested food – energy content of excreta) / energy content of ingested food) (Karasov 1990). We used an MEC^{*} value of 0.64 for passerines feeding on fruit pulp and skin (Karasov 1990, Smith et al. 2007). We calculated species-specific daily required dry food intake if birds were feeding solely on sweet cherries (g/ day) by dividing DER by the energy density (kJ/g dry mass) of sweet cherries (USDA Agricultural Research Service 2016). As these values are based on dry mass, we corrected for moisture content of sweet cherries (Peer et al. 2003, Smith et al. 2007) by multiplying by 1.82 (one plus the moisture proportion of raw sweet cherries: 0.82). To estimate the actual daily mass of sweet cherries in the diet of robins and waxwings (Peer et al. 2003, Smith et al. 2007).

We quantified cherry consumption and subsequent economic loss for the period in our study area when sweet cherries are vulnerable to robin and waxwing depredation (Alkio et al. 2014). We defined this as the twenty-eight days between the date on which cherries were first detected in fecal samples (method described in the following section) and the last date of cherry harvest in 2015. We excluded samples (n=11) collected prior to this period because cherries were not yet ripening. We did not distinguish males and females for analyses because sexes were of

similar size, several waxwings could not be reliably sexed, and males and females did not differ in the proportion of cherries in the diet for either species.

Estimating proportion of sweet cherries in diets

We captured birds in mist nets (38-mm and 30-mm) in four sweet cherry orchards from 30 May – 19 July 2015 (Figure 2.1); nets were open for a total of 1255 net-hours.



Figure 2.1 Map of Leelanau County study region with mist netting and point count locations identified. Map of Leelanau County, Michigan with Traverse City, Michigan identified. Shaded region identifies the 208 km² study area. Open triangles identify mist-netting sites (n = 4) for fecal sample collection. Black circles identify point count (n = 22) survey locations.

We extracted and placed each captured robin or waxwing in a paper bag to collect fecal samples. We air-dried samples in bags for at least 24 hours, transferred samples to vials, and froze them until processing. Fecal samples are a non-invasive technique for avian diet analysis and can provide accurate estimates of diet composition without the risks associated with use of emetics or harvest of stomach contents (Ralph et al. 1985, Rosenberg and Cooper 1990, Carlisle and Holberton 2006). Differential digestibility of diet items (e.g., invertebrates versus plant material) can complicate the use of fecal samples to quantify proportions of foods in bird diets. To overcome this, we applied correction factors based on the assimilability of food types (see below).

Under a dissecting microscope, we sorted fecal sample contents into major food types: animal matter, fruit skin, seeds, and fruit pulp. We identified sweet cherries among samples of fruit skin by viewing samples under a compound microscope and comparing these to reference samples and images from the literature (Jordano and Herrera 1981, Martella et al. 1996, Oliveira et al. 2002). For each sample that contained sweet cherry skin, we dried fecal material to constant mass at 60 °C and weighed it to the nearest 0.001 g. We calculated the proportion by dry mass of each food type in these samples (n = 89). To account for differential digestibility of food types, we applied correction factors based on the apparent assimilable mass coefficients (AMC*) of particular food types (Lane et al. 1999). $AMC^* = (Dry mass of food consumed - Dry$ mass of excreta) / Dry mass of food consumed (Karasov 1990, Fassbinder-Orth and Karasov 2006). Following suggestions of Castro et al. (1989) we used published species-specific AMC* values for a given food type, when available, and mean AMC^{*} values for passerines for a given food type when species-specific information was unavailable (Table 2.1). We divided the dry mass of each food type in a sample by (1- AMC^{*}) for that food (Lane et al. 1999). We assumed any pulp and fruit skin in a sample to be from the same fruit type because in no instance did a sample contain more than one type of fruit skin as well as pulp. We then calculated mean corrected proportions of sweet cherries, animal matter, and other fruit in samples (Lane et al. 1999). The final mean proportions of sweet cherries in robin and waxwing diets included

samples with no cherries present. Non-cherry fruit occurred only in waxwing fecal samples, therefore we used an AMC^{*} value from waxwings feeding on a diet of mixed lipid-rich and sugar-rich fruits to correct the proportion of non-cherry fruit in the waxwing diet (Table 2.1).

Table 2.1 Types and sources of AMC values used to calculate proportion of sweet cherries in diet.

| Food type | AMC* | Value based on | Source |
|--------------|-------------------|--|-----------------------------|
| Arthropods | 0.74 ^a | Published studies | Karasov 1990 |
| Sweet cherry | 0.61 ^a | Published studies; fruit pulp and skin | Karasov 1990 |
| Other fruit | 0.34 | Waxwings on mixed whole fruits | Holthuijzen & Adkisson 1984 |

^aCalculated from reported metabolizable energy content (MEC) values using AMC = MEC - 0.03 (Karasov 1990).

Population sizes

To quantify the size of robin and waxwing populations in the study region, we conducted fixed-radius (25 m) point count surveys at 22 randomly selected sites throughout the study area. Sixteen of these sites were at sweet cherry orchards, 3 were in urban/built areas and 3 were in woodland areas. All point count sites were > 1.8 km from one another. We initiated surveys between 0700 and 0930 and between 1700 and 1930 eastern daylight time; each survey was eight minutes in duration. We recorded all visual and aural observations of robins and waxwings detected within the survey radius, including birds flying within 25 m above the survey point. The first author (RAE) conducted surveys between 9 June and 29 July 2015 and surveyed each location five times. Temporal replicates allow for accommodation of imperfect detection of unmarked individuals (Fiske and Chandler 2011). We used counts of robins and waxwings from

each survey to fit N-mixture models of population abundance (Royle 2004), using the R package "unmarked" (Chandler and Fisk 2011). We modeled population abundance as a negative binomial process and extracted the mode and 95% credible intervals for the abundance values at each survey site. We then used these estimates to quantify bird densities in each of the three surveyed land cover types (sweet cherry orchards, developed land, woodland). We multiplied these densities by the total area of each of the three surveyed land cover types of our study area to estimate habitat-specific population sizes. Finally, we summed habitat-specific estimates to quantify the total population sizes of robins and waxwings in our 208-km² study area; we incorporated these population sizes into economic models of avian damage to sweet cherries (see below). We performed analyses in R statistical software (Version 3.0.3; R Core Team 2012).

Economic models of avian damage to sweet cherries

Our bioenergetic models generated a per-bird total mass of cherry skin and pulp consumed because robins and waxwings do not digest and obtain energy from the cherry pit. However, the market price that fruit growers are paid includes the cherry pit mass, and economic models based on per-bird cherry consumption alone would underestimate loss. The proportion of cherry pit mass to total fruit mass comprises a range of 0.07 to 0.11 (Bandi et al. 2010). To account for the mass of the unconsumed pit when calculating financial loss, we multiplied our bioenergetic estimate of consumption by a correction factor of one plus the midpoint of this range (1.09).

We used the average market price for sweet cherries in Michigan over the five-year period of 2010-2014 (\$US0.0011/g; NASS 2015b) to calculate per bird economic loss over the study period. In addition, we multiplied this monetary value by population abundance estimates

for each species to quantify the population-scale economic losses from robin and waxwing damage to sweet cherries. We calculated a range of economic loss estimates based on the 95% credible intervals of the population abundance estimates.

As part of a related study, we conducted 150 man-hours of focal animal observations (Altmann 1974) on robins and waxwings consuming sweet cherries in Michigan orchards over the cherry-ripening period from 4 June 4 - 2 July, 2012 and 1 July - 24 July, 2014. All waxwings observed (n = 43) were consuming cherries directly from the tree, while robins ate cherries both in the tree and on the ground (n = 62; RAE, *unpublished data*). During 41% of these observations, robins ate cherries only in the tree. Given that growers do not harvest cherries that have fallen to the ground, only fruit consumption within trees should result in economic loss for growers. Therefore, in the economic model of loss due to robins we used an additional correction factor of 0.41 to represent the proportion of robin sweet cherry consumption that occurs in trees.

Our species-specific models of economic loss from damage to sweet cherries took the following form:

Per-bird economic losses = per-bird consumption × pit correction × market price

where per-bird consumption is the total per-bird cherry consumption over the study period from our bioenergetics model, pit correction is a correction for the mass of cherry pit that birds do not utilize for energy but for which growers are paid (1.09), and price is the market price of sweet cherry (\$US0.011/g). Robin models included an additional correction (0.41) for birds feeding in cherry trees.

Results

Bioenergetic models of avian sweet cherry consumption

We analyzed 47 American robin fecal samples and 31 cedar waxwing samples. We estimated daily energy requirements of robins and waxwings at 318.8 and 181.3 kJ/day, respectively. After correcting for assimilation efficiency, the proportion of sweet cherries in the robin diet was 10.8% (\pm 24); the waxwing diet contained 51.4% (\pm 46) sweet cherry. For comparison, the uncorrected proportions of sweet cherry in the diet were 13.6% (\pm 27) for robins and 51.3% (\pm 46) for waxwings. Based on these results, individual robins consumed 4.0 g sweet cherry each day, while waxwings consumed 12.0 g sweet cherry each day (Table 2.2).

Economic models of avian damage to sweet cherries

Robins and waxwings have a combined estimated population size of 772,956 individuals in the cherry orchard, woodland, and developed areas of our study region (Table 2.2). These two cherry-eating species caused an estimated \$US1,986,948 in losses to local cherry producers during the 2015 cherry-ripening season. When considering the 95% CI of population estimates, this loss may range from \$US991,609 - \$US3,952,449.

Table 2.2 Estimated sweet cherry consumption by American robins and cedar waxwings in northwest Michigan orchards and resulting economic losses.

| Model Elements | American Robin | Cedar Waxwing |
|---------------------------------|----------------|---------------|
| Body mass (g)* | 79.3 (±3.9) | 34.6 (±4.3) |
| FMR (kJ/day) | 204 | 116 |
| Proportion of cherries in diet | 10.8% (± 24) | 51.4% (±46) |
| Daily per-bird consumption (g) | 4.0 | 12.0 |
| Total per-bird consumption (g)^ | 112.0 | 336.6 |

Table 2.2 (cont'd)

| Population size (95% CI) | 267,563 (151,227 – 618,994) | 455,393 (224,860 - 894,060) | | | |
|---|--------------------------------|--------------------------------|--|--|--|
| Total economic loss (\$US) | | | | | |
| Per bird [^] | 0.55 | 4.04 | | | |
| Per species $(95\% \text{ CI})^{^{\wedge}}$ | 147,160 | 1,839,788 | | | |
| Tel species (3378 CI) | (83,175 - 340,447) | (908,434 - 3,612,002) | | | |
| *Means and standard deviations of field-collected body masses. Values for the entire 28 | | | | | |

day pre-harvest study period.

Discussion

In these first bioenergetic and economic models of avian damage to fruit crops we demonstrate that species differences in proportion of fruit in the diet and local population sizes result in substantial between-species variation in fruit consumption and resulting financial loss.

Our bioenergetic models generated damage estimates based upon species-specific diet and physiology data. Recent field studies of birds in cherry orchards demonstrated that bird species vary in both their reliance on orchard habitat (Eaton et al. 2016) and their cherry consumption (Lindell et al. 2012). Building upon this work, our models showed that a speciesspecific approach uncovers striking differences in the damage attributable to different species. We estimated that an individual cedar waxwing caused a financial loss that was seven times that of an individual robin. This substantial difference between species stems from 1) a five-fold greater proportion of cherries in the waxwing diet, than to robins, and 2) the fact that waxwings consume only saleable cherries that are still on the trees, while robins often forage on the ground.

Despite robins' greater daily energy needs, waxwings had a substantially larger proportion of sweet cherries in the diet. We found that sweet cherries comprised 11% of the robin diet; this is similar to Virgo's (1971) calculation of 12% for robins caught in Ontario sweet cherry orchards. We estimated that sweet cherries made up 51% of the waxwing diet, which corresponds reasonably with Witmer's (1996) estimate that fruit, including non-cherry species, comprises 72% of the waxwing summer diet. Our results suggest that class-based (i.e., all birds) or non-specific quantification of damage misses important patterns that could influence bird management strategies. Assuming that all species detected in orchards have equal potential as fruit consumers could incorrectly characterize the problem. For example, robins and waxwings are both frequently observed in orchards, but our species-specific approach demonstrated that these species vary widely in the extent of damage inflicted. This is consistent with previous studies of robins in sweet cherry orchards that show relatively low cherry consumption by robins, despite their frequent detection (Virgo 1971, Lindell et al. 2012).

Where birds feed in an orchard affects their role as a crop pest. In our system, waxwings eat cherries in trees while robins feed both in trees and on the ground (RAE, *unpublished data*). Virgo (1971) also noted extensive ground foraging by robins in Ontario sweet cherry orchards. Cherry growers only harvest and sell fruit from trees, and our models indicated that robins feeding in trees caused relatively little damage compared to waxwings. However, robins occasionally knock fruit to the ground or descend from a tree carrying a fruit and consume it on the ground (RAE, *personal observation*). We cannot assume all instances of robin ground feeding are completely free of cost to fruit growers. However, waxwings are clearly more problematic to growers than robins, whose ground consumption of fruit may actually be beneficial in removing resources for arthropod or fungal species that damage fruit. Despite growers' frequent reports that robins are pest species in sweet cherry orchards (Anderson et al. 2013), our current study and previous work suggest that bird damage mitigation efforts in

northwest Michigan sweet cherry orchards could be more targeted and efficient if focused on waxwings (Lindell et al. 2012).

Our study is the first bioenergetic approach to quantifying bird damage to fruit. This technique has been used successfully in field crops (e. g., Peer et al. 2003) to provide regional, species-specific estimates of avian crop damage. Previous attempts to attribute damage to various bird species have often relied on surveys of birds flying in orchards or observations of birds consuming crops (e.g., Virgo 1971, Johnson et al. 1989). However, bird species vary in their conspicuousness, and survey or observation-based data alone may provide inaccurate or incomplete information on the level of the damage (Dolbeer et al. 1994). In addition, such approaches typically have not considered population size variation among potential pest species.

Our study demonstrated the added importance of population data to understanding the capacity of certain species for crop damage. For example, individual waxwings caused seven times greater financial loss than robins over the study period. However, when extrapolated to the population scale, waxwings caused 12.5 times greater financial loss to the region than robins. This substantial difference in robin and waxwing estimated population sizes is a largely a result of more widespread waxwing sightings and larger waxwing groups, than robins. We detected waxwings more frequently, at more locations, and in larger groups than robins, leading to our larger population estimates for waxwings than robins.

Our population estimates are reasonable for robins and waxwings in a fruit-growing region. Our estimate of 1878 robins per km² in sweet cherry habitat is similar to Virgo's (1971) average density of 18.53 robins per hectare (or 1853 per km²) of sweet cherry orchards in Ontario, Canada. We estimated that waxwings have a larger population than robins, which is expected given waxwings' smaller size, the great amount of cultivated fruit in the region, and the

waxwings' greater reliance on fruit (Witmer 1996). Fruit comprises the majority of waxwings' diet throughout the year (Witmer 1996). In addition, waxwings are semi-colonial breeders and relatively non-territorial (Lea 1942). Rothstein (1971) reported a density of 14.1 nests per hectare (1410 nests per km²) in a forested area near a field of wild cherry trees in northern Michigan. Waxwings also forage in large groups in orchards away from the nesting site (Lea 1942, Nelms et al. 1990, Lindell et al. 2012). For example, a group of > 500 waxwings consumed blueberries on a 0.024 km² farm in Florida (Nelms et al. 1990). Our own work has shown that waxwings in cherry orchards forage in groups four times larger than groups of robins, a territorial species (Lindell et al. 2012). The gregarious and frugivorous nature of waxwings could allow for a high number of birds during the breeding season, particularly in resource-rich fruit-production regions.

We conducted this study in a major sweet cherry growing area of Michigan. Approximately half of Michigan's total sweet cherry acreage is in Leelanau County (NASS 2015a). We estimated that our 208 km² study area within Leelanau County contained 22.6 km² of sweet cherry (~29% of total Michigan sweet cherry acreage; NASS 2014). Our bioenergetic models of damage suggested robins and waxwings caused at least \$US991,000 in damage in this area and may cause as much as \$US3.9 million. Anderson et al. (2013) used grower-reported damage estimates from 2011 to generate a statewide damage value for Michigan sweet cherries. They calculated that all birds collectively caused \$US2,090,723 in damage to sweet cherries annually (Anderson et al. 2013). Given that robins and waxwings are two significant cherry-consuming species in Michigan (Lindell et al. 2012), our estimate of damage by these two species is reasonable for an area that contains a substantial proportion of all sweet cherry orchards in Michigan.

Provided model inputs are available or obtainable (e.g. proportion of crop in the diet and avian population size) for the area of interest, bioenergetic models of damage are applicable to a variety of crops and to production areas of various sizes. Bioenergetic and economic models of avian crop damage are important prerequisites to comprehensive damage management programs. Sweet cherry growers implement bird damage management strategies in an effort to reduce financial losses. Economic models indicate that these efforts save the United States sweet cherry industry up to \$US238 million in the short run and up to \$US29 million in the long run (Elser et al. 2016). However, evidence suggests that many commonly used management techniques like scare-eye balloons, raptor-resembling kites, and loud audio deterrents have limited or inconsistent success in mitigating bird damage to fruit crops (Eaton 2016). These may be particularly ineffective for species like waxwings that are relatively tolerant of people and have a short fright distance (Eaton 2016). Bird damage mitigation techniques that specifically target problem-species, like waxwings, may permit more efficient management. For example, planting a more-preferred fruit source adjacent to orchards, a decoy crop, could draw waxwings away from cherry crops and reduce damage. Waxwings show size preference when selecting berries and choose fruits that are much smaller (\sim 7.5 mm diameter; Avery et al. 1993) than ripening sweet cherries ($\sim 12 - 23$ mm; NWMHRC 2016). Therefore, luring waxwings away from cherry crops could be an additional management strategy that would increase success more than solely attempting to frighten them away.

Bioenergetic model estimates add to the suite of damage quantification tools including block-based field estimates and crop producer surveys. Our bioenergetic approach to quantifying bird damage to fruit can be used to assess the impact of other potential problem species. For example, cherry, apple, blueberry and grape growers surveyed across the U.S. identified

common starlings (*Sturnus vulgaris*) as important fruit pests (Anderson et al. 2013). A bioenergetic approach would provide a tool to quantify the impact of this and other suspected avian crop pests. In turn, model estimates allow us to contrast damage from multiple pest species and understand pest species ecology, which is essential for more informed pest management programs and damage management (Dolbeer et al. 1994, Somers and Morris 2002).

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LITERATURE CITED

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CHAPTER 3

AMERICAN ROBINS AND CEDAR WAXWINGS VARY IN USE OF CULTIVATED CHERRY ORCHARDS

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Abstract

Some fruit-eating bird species commonly consume cultivated fruit. Species-specific variation in diet preferences could result in varying use of orchards and impacts on the fruitproducing industry by different bird species. However, species-specific studies of avian orchard use are lacking, particularly throughout the fruit-growing season. Our objectives were to quantify the frequency of daily bird visits to orchards and the amount of time birds spent visiting orchards each day over the fruit-ripening season. Birds are well-documented consumers of cultivated sweet cherries (*Prunus avium*), which are relatively high in sugar and low in proteins and lipids. American Robins (Turdus migratorius) and Cedar Waxwings (Bombycilla cedrorum) are common fruit-consumers in sweet cherry orchards. Robins often consume larger proportions of invertebrates and prefer lipid-rich fruits, while waxwings choose sugary fruits. Given these species-specific diet differences, we hypothesized waxwings would spend a greater proportion of days and more time each day in cherry orchards than robins. We used radio telemetry to track the habitat use of 25 American Robins and 17 Cedar Waxwings in Michigan sweet cherry orchards. Over their respective radio-tracking periods, waxwings visited orchards a marginally greater percentage of days than robins (waxwings: mean = 21%, SD = 22; robins: mean = 6%, SD = 4). In addition, waxwings visited orchards for significantly more time each day. Differences in diet preferences and nutritional physiology may translate into species-specific patterns of habitat use for birds in fruit-rich environments.

Introduction

Animals are expected to forage where and when they can obtain sufficient accessible and nutritious foods (Hengeveld et al. 2009). Orchards offer rich patches of foraging habitat with

abundant food resources for birds, which lead to conflicts with orchard growers (Simon 2008). Growers experience lost yields and often implement costly techniques to mitigate bird consumption of crops (USDA 1998, Anderson et al. 2013). Fruit growers in New York, Michigan, and the Pacific Northwest have reported yield losses due to birds of up to 31% in cherries, 18% in blueberries, and 9% in wine grapes; these losses translate to tens of millions of dollars (Anderson et al. 2013). Knowledge of foraging patterns of avian frugivores in and around orchards can thus offer crop producers valuable information for mitigating bird consumption of crops through targeting species and times when fruit loss is greatest (Dolbeer et al. 1994, Somers and Morris 2002, Tracey et al. 2007). For example, bird consumption of blueberries is greater in early ripening varieties; such information could allow growers to identify fruit varieties that ripen later in the season and reduce the potential for avian crop consumption (Tobin et al. 1991).

Birds are well-documented consumers of cultivated sweet cherries (*Prunus avium*) (Curtis et al. 1994, Lindell et al. 2012), but neither the frequency nor length of bird visits to commercial cherry orchards over the growing season have been established. A limited understanding of the orchard use and behavior of cherry-consuming species has hindered our ability to develop effective management programs that minimize costs of bird activity in orchards (Tracey et al. 2007). Cherry orchards are attractive for fruit-eating birds because cherries are brightly colored, densely available, and have easily accessible pulp (Sallabanks 1993). Cherries are relatively sugar-rich fruits; >50% of dry pulp mass comprises sugars (Witmer and Van Soest 1998, USDA 2013b). However, the lipid and protein contents among *Prunus* fruits (including cherries) are relatively low (<2%) compared to the protein content of other fruits (5%) or insects (Stiles 1993, Witmer and Van Soest 1998). Fruit consumption by birds is behaviorally and physiologically complex (Sallabanks 1993, Levey and Martinez del Rio 2001,
Corlett 2011). Birds can discern nutritional differences among food types and make foraging decisions to meet energetic and nutritional needs (Lepczyk et al. 2000, Schaefer et al. 2003, Alan et al. 2013). Therefore, cherries may not appeal equally to all birds.

American Robins (*Turdus migratorius*) and Cedar Waxwings (*Bombycilla cedrorum*) [hereafter robins and waxwings] are highly frugivorous (Wheelwright 1986, Witmer 1996). These species are also responsible for a relatively high proportion of observed avian cherry consumption compared to other species, e.g. American Crow (Corvus brachyrhynchos), Common Grackle (Quiscalus quiscula), European Starling (Sturnus vulgaris; Lindell et al. 2012). Fruit comprises \sim 57% of the annual diet of robins, in addition to large proportions of invertebrates, while waxwings' diet contains ~84% fruit (Witmer 1996). In addition, robins more efficiently assimilate and prefer fruits that are relatively high in proteins and lipids, and low in sugars (Stiles 1993, Willson 1994, Witmer and Van Soest 1998, but see Lepcyzyk et al. 2000). Waxwings more efficiently assimilate and show a preference for high-sugar fruits (Witmer and Van Soest 1998, Witmer 1998). Furthermore, waxwings maintain body mass on fruit alone for extended periods, for example up to 27 days (Holthuijzen and Adkisson 1984), despite fruit's relatively low protein content. In contrast, Levey and Karasov (1989) attempted a 10-day fruitonly feeding trial on captive robins but shortened the trial to four days as birds had already lost 10-14% of initial body mass. In addition, waxwings feed nestlings insects for approximately three days (Putnam 1949), after which fruit comprises 87% of food deliveries (Lea 1942), while robins provision almost exclusively with animal matter (Hamilton 1935), but older nestling robins may also receive fruit (Eaton 1914). Our previous work has revealed relatively little use of cherry orchards by robins and waxwings for invertebrate consumption and nesting activities, therefore we focused this study on fruit consumption.

These species-specific patterns likely influence the frequency and length of foraging visits in orchards during the cherry-growing season. For certain frugivorous birds, orchards may become increasingly attractive as fruits ripen because sugar content increases and bird energy needs may be met more efficiently (Serrano et al. 2005). Furthermore, after harvest, orchards may no longer be viable foraging habitat for avian frugivores, given the near-complete removal of fruit from trees (<10% of cherries remaining, M. Whiting, *Personal communication*).

Here, we used radio-telemetry to evaluate the use of cultivated sweet cherry orchards in Michigan by robins and waxwings. We hypothesized that waxwings would exhibit more intense use of cherry orchards than robins based on their diets. We predicted that waxwings would 1) visit focal orchards on more days throughout the cherry season, and 2) spend more time each day visiting orchards than robins. Further, given that sugar content increases as cherries ripen, we expected that 1) robins and waxwings would increase their use of orchards as harvest approached, and 2) that orchard use by both species would decline abruptly after cherries were harvested and fruit availability declined. For both of these expectations, we predicted a stronger effect for the more fruit-specialized waxwings.

Methods

Study Area & Species

We conducted the study in four sweet cherry orchards in Leelanau County, near Traverse City $(44^{\circ} 46^{\circ} N, 85^{\circ} 37^{\circ} W)$, in northwest Michigan from June - September 2013 (Figure 3.1). Leelanau County is a peninsula (land area = 900 km², water area = 5659 km²) extending into Lake Michigan and an agricultural region comprising many orchards (e.g. sweet and tart cherries, wine grapes, apples). As of 2012, orchards comprised 6% of the county land area, with sweet cherry orchards accounting for 2% of the county land area (USDA 2012). Other major crops and land cover types include alfalfa, mixed forests, and residential or developed areas (Lindell et al. 2012). The average rainfall during the 2013 fruit-growing season (April – October) was 54.9 cm (Northwest Michigan Horticultural Research Station 2013).



Figure 3.1 Map of Leelanau County study region and focal sweet cherry orchards. Map of Michigan with Leelanau County identified (*left*). Leelanau County with Traverse City and the four sweet cherry study orchards identified (*right*).

The mean distance between study sites was 5.1 km (range = 1.4 - 10.4 km). One site was located at the Northwest Michigan Horticultural Research Station (STA) and Cherry Bay (CB) Orchards, Inc. managed three sites (Table 3.1). In the study region, sweet cherry trees typically reach full bloom in early May; small green fruits are evident 20 days later, and cherries begin ripening 50 - 60 days after full bloom. Growers apply a variety of insecticides depending upon the target pest species, fruit growth stage, and product availability (W. Klein, *Personal communication*). Products vary in required application frequency (e.g. from three days up to two weeks). Michigan State University Extension provides recommendations for insecticide use to commercial fruit producers in the region. Orchard managers prune trees and mow grass occasionally throughout the growing period.

In Michigan, robins are abundant during the breeding season and typically arrive in March; most robins do not overwinter (McPeek 2011a). Robins begin nesting in April and May and commonly rear two broods (Howell 1942, McPeek 2011a). Waxwings are common in the study region where they travel and forage in small flocks year-round (McPeek 2011b). Waxwings generally arrive in Michigan by late May (although some overwinter). They are among the latest nesting birds in North America and nest in colonies in trees of various species including maple (*Acer* spp.), oak (*Quercus* spp.), and pine (*Pinus* spp.; Lea 1942, Putnam 1949, Rothstein 1971). The majority of nesting occurs between mid-June and August (McPeek 2011b). Orchard growers in the study region do not remove nests from cherry trees during the growing season (growers may remove old nests during the winter; W. Klein, *Personal communication*).

Capture & Radio Deployment

We captured birds via mist nets in each study orchard and radio-tagged adult robins and waxwings between 1 June and 15 July. We typically opened nets by 0700 and closed them by 1600 EDT. We aged and weighed birds and sexed them using external breeding characteristics (i.e. presence of brood patch or cloacal protuberance; Pyle 1997). Waxwings did not exhibit breeding characteristics and could not be reliably sexed. We fitted a metal band, plastic colored bands, and an A1055 radio transmitter from Advanced Telemetry Systems (Isanti, Minnesota, USA) on 25 robins and 17 waxwings that appeared in good condition and were sufficiently massive to wear the 0.9 g radio transmitter and harness (<3% of bird body mass). We used 1-mm elastic cord and the figure-eight leg-harness method to attach transmitters (Rappole and Tipton 1991). Transmitters broadcasted at a pulse rate of 30-34 pulses per min within a frequency range of 164.00–165.66 MHz. Expected battery life was 50 - 60 days. After radio deployment, we gave

birds a two-day acclimation period to permit a return to normal behavior prior to data collection. Radio-tags from two waxwings were recovered during the study; we suspected both birds were depredated. We had valid orchard use data from both individuals and included these data in analyses.

Data Collection

To track orchard use, we placed one stationary data receiving system in each study orchard, away from objects that could dampen or block incoming signals. We installed receiving systems between 15 June and 20 June 2013 and retrieved them on 11 September 2013. To assemble stationary systems, we encased a programmable, R4550 data-logging signal receiver from Advanced Telemetry Systems (Isanti, Minnesota, USA) powered by a deep-cycle battery in a large plastic container and cabled the receiver to a six-element Yagi antenna bolted to an elevated mount of 3-m height (Homan et al. 2013). Prior to data collection, we time and date synchronized all receivers.

The receivers scanned through a list of all radio frequencies associated with birds, remaining on each frequency for 6 sec, for 24 hr per day throughout the study. If a frequency was detected during these 6 sec, the receiver monitored that frequency for 50 sec and recorded the date, time, and strength of the strongest signal (a function of distance between the receiving antennae and a bird's transmitting antenna) detected for that bird during the 50 sec. The receiver then continued to scan through the list of frequencies. To promote independence among data for a given bird, receiving systems ultimately stored only the data record (if one was made) with the strongest signal detected over every 10-min period throughout the day. This record also included the number of radio pulses recorded for that bird during the 10-min period. The number of radio

pulses reflected the number of times (i.e. for how long) a bird's transmitter emitted the signal during the 10-min period. The strength of a bird's signal did not affect the receiver's ability to detect other birds in the area. If a particular frequency was not detected, the receiver scanned for the next frequency. To ensure that radio-tagged birds were still in the region during the study, we searched the area 5 -7 days per week using a pickup truck with a roof-mounted, rotatable set of dual 6-element Yagi antennae. The tracking periods of individual birds could include days on which birds were not detected using orchards, but were located in the study region during mobile searches.

Data Preparation

Telemetry data receiving systems can detect false signals from objects (e.g. solar flares, power lines, garage door openers) with frequencies similar to those in our study. We used Visual Basic for Applications with Excel to cull false records and extract valid data for analysis. Valid data were those with associated pulse rates of 28–34 pulses per min; this range accounted for fully functioning radio transmitters, as well as slower pulsing radios whose batteries had weakened. We determined a bird was using an orchard if the receiver recorded a signal strength \geq 140 (maximum radio signal strength was 155). We conducted calibrations at each study site prior to deployment and determined that a signal of \geq 140 would only register if a bird were in a study orchard. To calibrate orchard use, we affixed a radio transmitter to a 2 m-long pole, stood with the transmitter extended into a tree to simulate a bird at 4–6 locations in each orchard, and recorded the signal strength detected by the receiving system at each location. The line of sight receiving distance of the stationary systems was \leq 0.05 km (Homan et al. 2103).

Day-to-day & Within-day Orchard Use

We evaluated bird use of cherry orchards in two ways. First, we quantified day-to-day orchard use by calculating the proportion of days a bird was within a focal orchard out of the total number of days in the bird's tracking period (defined as the first day after the bird's acclimation period through the last day a bird was detected in the study region; Equation 1). We defined a day as only the daylight period (one hr before sunrise through one hr after sunset). We calculated one day-to-day orchard use value for each bird. Second, we quantified within-day orchard use to determine the amount of time birds visited focal orchards on a given day (Equation 2). To quantify within-day orchard use, we first identified the length of the daylight period for each day of the study and divided this period into 10-min time blocks. We then quantified the number of 10-min time blocks in which a bird was in an orchard on a given day and divided this by the total number of 10-min blocks of that day (Equation 2). An individual could have multiple within-day orchard use values. We report values for day-to-day and within-day orchard use as percentages.

Equation (1)
$$Day - to - day \text{ orchard } use = \frac{number \text{ of } days \text{ bird } detected \text{ in orchard}}{number \text{ of } bird's \text{ total } tracking \text{ } days}$$

Equation (2) Within - day orchard $use = \frac{number \text{ of } 10-\min \text{ time } blocks \text{ in orchard } on \text{ one } date}{number \text{ of } time \ blocks \text{ in } date's \ daylight \ period}}$

Statistical Analyses

The proportion values for day-to-day orchard use were right-skewed so we applied a logarithmic transformation. We approximated the log-transformed day-to-day orchard use data using a normal distribution with equal variances, which satisfied assumptions for a two-sample Student's *t*-test. We determined if day-to-day orchard use data from male and female robins could be pooled. To account for sample size differences in males (9) and females (3), we used

boot-strapping techniques to select three samples from males at random, with replacement, to compare with females. We ran 1000 iterations of the sampling and *t*-test procedures and applied the false discovery rate approach to correct α for multiple statistical comparisons (Benjamini and Hochberg 1995). We used a two-sample Student's *t*-test to evaluate differences in the day-to-day orchard use of robins and waxwings.

We constructed generalized linear mixed models (GLMM) with a binomial distribution, a logit link function, and bird as a random effect to analyze within-day orchard use. We first used a GLMM with sex as a fixed effect and individual bird as a random effect (to account for some birds having multiple within-day orchard use values) to determine whether male and female within-day orchard use data could be pooled. A binomial distribution was appropriate for the within-day use data because we calculated these values as the proportion of 10-min time blocks in a given day in which a bird was in an orchard. The total number of time blocks in a day served as the number of trials for these models. We constructed 10 GLMMs to assess the effects of species and days-to-harvest on within-day orchard use (Table 3.2). We calculated the variable days-to-harvest for each date by subtracting this date from the harvest date of the relevant orchard. We included the orchard in which a bird was detected by a receiving system as a covariate for which we had no *a priori* expectation but which might have confounded the influence of days-to harvest. We used the Akaike Information Criterion corrected for small sample sizes (AICc) for model selection; we identified the best-fit model as that with ΔAIC value < 2 (Burnham and Anderson 2002). We performed analyses in R statistical software (R Core Team 2012), using 'lme4' (Bates et al. 2014) and 'AICcmodavg' (Mazerolle 2013) packages.

Results

Study Demographics

We outfitted 25 robins (16 males, 9 females) and 17 waxwings (sexes unknown) with

radio transmitters (Table 3.1).

Table 3.1 **Study orchard area, 2013 harvest date, and land cover types adjacent to study orchards**. The number and sexes (M: male, F: female, U: unknown) of American Robins and Cedar Waxwings caught at each sweet cherry orchard. Adjacent land covers (within 25 m of orchard edge) were assessed visually at each site as part of a related study in 2013.

| Orchard | Site Area | Harvest | Adjacent land cover types | Robins | Waxwings |
|---------|--------------|---------|---|----------|-------------|
| STA | 3.84 ha | 19 July | Tart cherry, mowed grass, non-fruit crops, herbaceous (< 1 m tall) | 5 M, 3 F | 8 U |
| CB1 | 2.6 ha | 11 July | Tart cherry, mowed grass, herbaceous (< 1 m tall) | 4 M, 3 F | 3 U |
| CB2 | 11.6 ha | 10 July | Mowed grass, paved road, sweet cherry, non-fruit crops | 2 M | - 11 |
| CB3 | 0.4 ha | 9 July | Tart cherry, paved road, herbaceous | 5 M, 3 F | |
| | | | (< 1 m tall) | | |

Among all radio-tagged birds, we did not detect 19 individuals (six male and seven female robins and six waxwings) in any of our study orchards after initial capture. Our sample population for analyses was comprised of 12 robins and 11 waxwings that used orchards STA, CB1, and CB3 no birds used CB2. Student's *t*-tests with bootstrapping showed no difference between male and female robins for day-to-day orchard use (t = -0.50, P = 0.94). The GLMM with sex as the fixed effect and individual bird as a random effect suggested that within-day orchard use did not differ between male and female robins (z = 0.32, P = 0.75). Therefore, we pooled data for the two sexes.

Day-to-day and Within-day Orchard Use

Among robins and waxwings who used cherry orchards (n = 23), we detected individuals somewhere in the study region for a mean of 40.8 d (SD = 19.5), while birds visited focal orchards for a mean of 3.3 d (SD = 3.0), or 13% (SD = 17). Waxwings visited orchards on a marginally greater percent of days throughout the season (mean = 21%, SD = 22) than robins (mean = 6%, SD = 4; t = -1.97 on log-transformed data, df = 21, P = 0.063; Figure 3.2).



Figure 3.2 Percent of days American robins and cedar waxwings visited cherry orchards relative to their respective tracking periods. Waxwings visited orchards for a greater proportion of their total tracking days than robins. Data represent day-to-day use values (n = 23). Black squares represent sample means. Data are untransformed and are jittered for visual clarity.

The best-fit model of within-day orchard use, according to AICc selection criteria,

included species as the fixed effect and individual bird as a random effect ($R^2 = 0.46$; Table 3.2). Waxwings visited orchards a mean of 5% (SD = 6) of the daylight period in orchards, while robins visited a mean of 2% (SD = 2). Waxwings spent significantly more time visiting orchards per day than robins (species = 0.88, SE = 0.31, P = 0.005; Figure 3.3). Individual variation among birds explained 34% (SD = 0.58) of the variance in within-day orchard use.

Table 3.2 Generalized liner mixed models exploring the relationships between within-day orchard use of American robins and cedar waxwings relative to species, orchard, and days-to-harvest. Parameter numbers (K), deviance (Dev), AICc, Δ AICc, and model weight (w_i) values are also included. All models also included individual bird as a random effect. The star symbol denotes a two-way interaction term between covariates.

| Model | K | Dev | AICc | ΔAICc | Wi |
|---|---|-------|-------|-------|------|
| Within-day orchard use~ | | | | | |
| Species | 3 | 382.7 | 389.9 | 0.0 | 0.64 |
| Days-to-harvest + Species | 4 | 382.3 | 392.6 | 2.6 | 0.17 |
| Orchard + Species | 5 | 380.9 | 394.4 | 4.5 | 0.07 |
| Days-to-harvest | 3 | 387.3 | 394.6 | 4.7 | 0.03 |
| Orchard | 4 | 385.9 | 396.1 | 6.2 | 0.03 |
| Days-to-harvest + Orchard + Species | 6 | 380.8 | 398.1 | 8.2 | 0.01 |
| Days-to-harvest + Orchard | 5 | 385.5 | 399.1 | 9.1 | 0.01 |
| Days-to-harvest + Orchard + Species + | 8 | 374.3 | 400.5 | 10.6 | 0.00 |
| Species*Orchard | | | | | |
| Days-to-harvest + Orchard + Species + | 7 | 380.1 | 401.5 | 11.6 | 0.00 |
| Species*Days-to-harvest | / | | | | |
| Days-to-harvest + Orchard + Species + | 9 | 374.0 | 405.9 | 15.9 | 0.00 |
| Species*Orchard + Species*Days-to-harvest | | | | | |



Figure 3.3 Percent of the daylight period that American robins and cedar waxwings visited cherry orchards on a given day. Waxwings visited orchards for more time each day than robins. Data represent within-day use values (n = 77) from a study population of 23 individual birds. Black squares represent sample means. Data are jittered for visual clarity.

The days-to-harvest and orchard covariates did not appear in the best-fit model of within-day orchard use (Table 3.2). The days-to-harvest covariate was retained in the second best model of within-day orchard use (Δ AIC = 2.6). This model suggested a decreasing trend in within-day orchard use as harvest approached, however this was not significant (days-to-harvest = -0.004, *z* = -0.57, *P* = 0.57). Orchard use at the STA orchard declined slightly up to 20 days before harvest; orchard use then remained constant until after harvest (Figure 3.4). Orchard use at CB1 and CB3 was seemingly constant across the entire study period (Figure 3.4).



Figure 3.4 Percent of the daylight period that American robins and cedar waxwings visited cherry orchards on a given day relative to days-before-harvest. Data are separated by orchard (STA, CB1 and CB3). Data represent within-day use values (n = 77) from a study population of 23 birds. Dashed lines represent the first possible date of valid data collection for birds radio-tagged at each orchard. On the *x*-axis, zero represents the date of harvest for a given site.

Discussion

Robins and waxwings differ in fruit preference, nutritional requirements, and physiology (Levey and Karasov 1989, Witmer and Van Soest 1998). These differences translated into species-specific patterns of orchard use.

Day-to-day Orchard Use

Our metric of day-to-day orchard use showed a marginally significant trend (P = 0.063) suggesting that waxwings visited orchards a higher percentage of days throughout their tracking periods than robins. Fruit comprises a larger proportion of waxwing annual diets (Witmer 1996),

and, thus, waxwings take greater advantage of the abundant supply of cherries over the growing season than robins. Robins, although predominantly frugivorous, typically consume and provision nestlings with large proportions of animal matter during the summer, while fruit consumption is higher in fall and winter (Wheelwright 1986). Therefore, a sweet cherry orchard may not be as valuable of a foraging habitat for robins seeking proteinaceous foods like insects and annelids, compared to waxwings. While it is possible that robins forage for non-cherry foods while visiting cherry orchards, 165 hrs of foraging observations yielded only six instances of robins consuming invertebrates but dozens of instances of cherry consumption (R. Eaton, *Personal observation*). Additionally, growers in focal orchards used insecticides regularly to diminish insect populations, potentially further limiting the value of cherry orchards for foraging robins. However, more study is needed to determine the relative proportions of fruit and invertebrates in the diet of robins in fruit orchards. Individual variation may also be a contributor to the patterns of day-to-day orchard use, as three individual waxwings appear to drive the relatively high day-to-day orchard use of waxwings.

Our hypothesized difference in day-to-day orchard use between robins and waxwings was marginally significant, which could arise if robins used orchards more than expected while waxwings used them less. Robins may have used orchards more than predicted if orchards were near nesting sites, e.g. in windbreaks around orchards (Yahner 1982). In comparison, waxwing use of orchards may not have been particularly high if late-nesting waxwings were not yet tied to a breeding territory (Putnam 1949), and freer to travel among foraging patches than breeding robins. We conducted a preliminary, systematic search for nests in the study region that revealed very few, thus it is unlikely that robins and waxwings used cherry orchards for nesting.

Within-day Orchard Use

Waxwings spent significantly more time visiting focal orchards than robins on a given day. Outside of the cultivated-fruit growing season, robins and waxwings also show differential timing of within-day fruit-foraging behavior (Chavez-Ramirez and Slack 1994). Wintering robins and waxwings in Texas spent 5 h and 8 h per day, respectively, feeding on Juniper berries (*Juniperus ashei*; Chavez-Ramirez and Slack 1994). Furthermore, once nesting is underway, waxwings may spend more time visiting orchards than robins on a given day to gather fruit for nestlings. Waxwings provision chicks primarily with fruit and begin doing so as early as day three after hatching (Putnam 1949), whereas robins do not provision with fruit until chicks are older (Howell 1942 and references therein). Future studies could address the potential influence of nesting phenology on frugivore orchard use by tracking breeding status, nesting, and brood rearing throughout the fruit-growing season.

Unexpectedly, we did not detect an influence of days-to-harvest on the amount of time birds spent visiting orchards. As cherries ripened, we expected birds to spend more time visiting orchards each day. In contrast to expectations, a temporal decline in within-day orchard use as harvest approached was evident for the STA orchard only. STA is a research orchard with dozens of sweet cherry varieties, including some early ripening. Unlike other orchards in the region, multiple trees at STA had red and ripening fruit when our study began. Therefore, STA may have attracted birds early in the fruiting season (Nelms et al. 1990, Tobin et al. 1991). Cultivated orchards may provide fruit-eating birds with the majority of—or only—fruit options during this time. For example, waxwings consumed substantial proportions of early-ripening varieties of cultivated blueberries compared to later-ripening blueberries (Nelms et al. 1990).

Contrary to our expectations, birds used orchards after harvest. After harvest, some fruits remain on the trees (<10% of the pre-harvest amount; M. Whiting, *Personal communication*) and ground. Remaining fruits are still numerous, accessible, and visually appealing, and could attract frugivorous birds (Sallabanks 1993, USDA 2013a). The first author observed robins consuming cherries in trees and on the ground in post-harvest orchards in the study region (R. Eaton, *personal observation*). In addition, as late-season nesters waxwings are likely provisioning offspring around or after cherry harvest. Remaining fruit in post-harvest orchards may continue to serve as important waxwing foraging habitat. If focal orchards were near nesting sites and within the regular foraging ranges of radio-tagged birds, post-harvest orchard use may reflect birds' tendencies to forage close to nests (Swihart and Johnson 1986). Birds may also have continued to use orchards after cherry harvest to forage for food unrelated to harvest (e.g. invertebrates), however most cherry growers apply a post-harvest insecticide spray which may limit insect availability (W. Klein, *Personal communication*).

Nearly half of our radio-tagged birds were detected in the area throughout the study but never used study orchards after the initial capture and acclimation period. Birds may have been captured as they traveled through an otherwise unused orchard. The home range sizes of robins are not well documented (Vanderhoff et al. 2014), although breeding robins have been known to forage up to 300 m from their nests (Knupp et al. 1977). Given the distance among our focal orchards (\geq 1.4 km) and their typical area (mean = 4.6 ha; SD = 4.9), robins captured at one orchard would not likely be detected using another, and robin foraging ranges in our study region do not likely contain more than a couple cherry orchards. To our knowledge, the home range sizes of waxwings are unknown. We did not find any radio-tagged birds using multiple focal orchards. Alternatively, captured birds may have avoided orchards if the capture experience itself

served as a deterrent. For instance, we captured two male robins at CB2, but neither returned to that orchard. However, we later detected both individuals using the nearby STA orchard.

While we documented the frequency and length of visits to focal orchards, the extent to which robins and waxwings used other cherry orchards in our study region is unknown. Given that cherry orchards are widespread in the study region, it is probable that robins and waxwings used non-focal orchards during the study period. However, the number of orchards visited is difficult to estimate given limited of knowledge of robin and waxwing home ranges. If home ranges of robins and waxwings are large relative to orchard size, our study provides a conservative picture of avian use of cherry orchards in an orchard-rich landscape. If home ranges are relatively small, it is possible that birds used non-focal orchards very little. Thus, our results suggest that orchards might not be predominant foraging habitat for frugivorous birds in this region. These uncertainties invite further study, particularly to track and evaluate avian habitat use in orchard landscapes with a more detailed resolution (e.g. GPS-tracking) to determine frequency of use of non-orchard habitat and home ranges of prominent avian frugivores.

Bird use and consumption of agricultural crops is often viewed as problematic (Weatherhead et al. 1982, Anderson et al. 2013). However, avian use of these habitats may also provide ecosystem services to growers (Whelan et al. 2008) both before and after harvest. Before harvest, avian consumption of crop-damaging invertebrates can increase the yield of cultivated crops (Mols and Visser 2002). For example, great tits (*Parus major*) reduced caterpillar consumption on cultivated apples and increased fruit yield (Mols and Visser 2002). After harvest, fruit often remains on the ground and our study showed that birds continue to visit postharvest orchards. Fruit remaining after harvest can serve as vectors for infections such as American brown rot (*Monilinia fructicola*). This fungus can over-winter in fruits that have fallen

to the ground and inoculate infections during the following spring (Bush et al. 2009). Avian postharvest consumption of cherries on the ground could reduce remaining fruits and limit the spread of infection. This and other potential benefits of avian fruit consumption deserve further study. This work demonstrates that two prominent avian fruit-eating species differ in how intensely they use orchards over the fruit-growing season, likely as a result of the differences in their food preferences and reliance on fruit. While waxwings visit orchards on a greater proportion of days and spend more time within orchards each day than robins, waxwings also consume a relatively high proportion of fruit than robins and other fruit eating species e.g. Common Grackles (Quiscalus quiscula) and European Starlings (Sturnus vulgaris; Lindell et al. 2012). In addition, waxwings are more likely to forage in groups than robins (Lindell et al. 2012) and have faster sugary-fruit assimilation rates than thrushes (Witmer and Van Soest 1998). Robins typically eat relatively little fruit during the breeding season than other times of year, yet showed higher fruit consumption when foraging around orchards than in less-fruiting habitats like meadows (Wheelwright 1986). Therefore, cherry orchards may serve as more important foraging habitat for more-frugivorous birds like waxwings than birds requiring proteinaceous resources, like robins. More work is needed to evaluate the extent to which birds foraging in orchards consume fruit versus other food sources like invertebrates.

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CHAPTER 4

FOOD ABUNDANCE AT MULTIPLE SPATIAL SCALES INFLUENCES FORAGING BEHAVIORS

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Abstract

Animals forage in habitats where food abundance varies at multiple spatial scales; relative resource abundance between hierarchical spatial scales likely influences within-patch foraging. We evaluated influences of fruit abundance at multiple spatial scales and sociality on avian behavior in sweet cherry orchards (Prunus avium). We observed omnivorous American robins (Turdus migratorius) and frugivorous cedar waxwings (Bombycilla cedrorum) and quantified cherry abundance at three spatial scales. Fruit abundance across multiple scales interacted to influence patch residence time and proportion time feeding at sweet cherry trees; these patterns differed between species. Fruit abundance at the tree scale relative to that of the orchard did not affect patch residence time; however, waxwings at trees with little food had a greater proportion time feeding within low-fruit orchards than within high-fruit orchards. As fruit abundance increased in an orchard, robins decreased proportion time feeding regardless of fruit abundance at the landscape scale; waxwings decreased proportion time feeding only in high-fruit landscapes. Fruit abundance at large spatial scales influenced robin patch residence time and waxwing proportion time feeding more strongly for birds in large foraging groups than for those in small groups. Differences in robin and waxwing behaviors may be explained, in part, by species differences in the degrees of frugivory and sociality; waxwings are more frugivorous and typically forage in larger groups than robins. Our study is among the first to demonstrate that avian behaviors are influenced by food abundance across multiple spatial scales, including large scales.

Introduction

Animals forage in heterogeneous and spatially complex environments where food abundance and distribution can vary spatially and at multiple spatial scales (MacArthur and Pianka 1966, Levin 1992, Johnson et al. 2001, Garcia and Ortiz-Pulido 2004, Butler et al. 2005). Thirty years ago in their seminal review, Senft et al. (1987) proposed that traditional applications of foraging models prove difficult for animals foraging on broadly distributed resources because heterogeneity in food abundance can occur at scales beyond just the patch itself, defined as a discrete aggregation of resources. For highly mobile species able to forage over large areas, the relative availability of resources at hierarchical spatial scales likely influences foraging behavior (Sallabanks 1993, Ritchie 1998, Searle et al. 2006, Searle et al. 2008). For instance, behavioral decisions may be affected by food abundance at the scale of a tree (patch), a forest of many trees (a habitat area comprised of multiple patches), or a landscape (a region of non-contiguous foraging habitats). Understanding and accounting for this spatial hierarchy in resource distribution when investigating foraging behaviors remains a key challenge in ecology (Senft et al. 1987, Kotliar and Wiens 1990, Thompson et al. 2001, Searle et al. 2005, Searle et al. 2006).

Although ecologists are aware of the influence of resource availability at multiple spatial scales on animals (Wiens 1989, Kotliar and Wiens 1990, Caro and Sherman 2011), research has typically focused on demography (Richmond et al. 2012), reproduction (Cornell and Donovan 2010), and population-level responses such as abundance and distribution (Lima and Zollner 1996, Olsson et al. 2000, Moegenburg and Levey 2003, Withey and Marzluff 2008, Pickett and Sirwardena 2011). The influence of multi-scale resource availability on behavioral responses is much less studied. Searle et al. (2006) studied captive mammalian herbivores in an experimental system with heterogeneous resource distribution at hierarchical scales. They demonstrated that

patch residence time was influenced by heterogeneity in resource abundance at multiple spatial scales. However, the effect of food availability across spatial scales on the behavior of other highly mobile foragers in a non-captive setting has not been assessed. In order to understand the effects of resource heterogeneity across multiple spatial scales on wild foragers, we studied the behavior of fruit-eating birds foraging in an agricultural environment.

Our current understanding of the relationship between wild foraging birds and food availability is generally limited to the positive correlations between bird abundance and food availability measured at different spatial scales (Withey and Marzluff 2008, Moorman and Bowen 2012). These relationships can vary with spatial scale (Garcia and Ortiz-Pulido 2004). Yet, studies of the relationships between food abundance and avian foraging behaviors are typically approached from a single spatial scale (e.g. Goss-Custard et al. 2006), despite the hierarchical nature of foraging decisions (Stephens 2008). Fruit-eating birds forage in particular patches (e.g. a tree) but travel widely throughout foraging habitats and regions (Price 2006). Compared to birds in other foraging guilds (e.g. insectivores), fruit-eating birds have relatively high movement activity (Neuschulz et al. 2012) and make foraging decisions at multiple scales (Sallabanks 1993). Thus, fruit resource availability at the scale of the foraging patch, as well as across broader habitat and landscape scales likely affect the behavior of frugivorous birds.

For frugivorous birds, fruit-growing agricultural regions provide a system of readily available food resources heterogeneously distributed at increasingly broad hierarchical spatial scales. Birds forage at individual fruit trees (a patch), within an orchard containing many fruit trees (a habitat), and within a broader landscape that may contain multiple fruit orchard habitats. Trees and orchards vary in fruit abundance because heterogeneity in tree health, age, and pollination success influence a tree's fruit yield. This heterogeneity leads to variation in fruit

abundance between the tree and orchard spatial scales. In addition, fruit orchards vary in the extent to which they are isolated from other orchards of the same type in the surrounding landscape. Thus, fruit abundance at a landscape scale (i.e. a particular orchard and the surrounding matrix of land covers) varies among orchards. Sweet cherry (*Prunus avium*) production regions of Michigan display this hierarchical nature of fruit abundance and permit us to assess the extent to which variation in food abundance among spatial scales (e.g. between tree and orchard and between orchard and landscape) influences avian foraging behaviors. Fruit orchards are an ideal system in which to study multi-scale influences of resource availability on foraging behavior because 1) orchards provide abundant resources for avian frugivores (Pimentel et al. 1992), 2) fruit consumption is easily observed, and 3) fruit availability can be quantified at the tree, orchard, and landscape spatial scales.

In addition, we wanted to explore the idea that variation in resource abundance across spatial scales has different effects on the decisions made by social and solitary foragers (Galef and Giraldeau 2001, Sernland et al. 2003, Fernandez-Juricic et al. 2004, Jedlicka et al. 2006). Unlike solitary feeders, social foragers may be more sensitive to variation in resource availability because of potential intra-group food competition (Rieucau and Giraldeau 2009). The potential for resource competition can influence a forager's use of a particular foraging patch or habitat (Symington 1988, Giraldeau and Dubois 2008, Rieucau and Giraldeau 2009). For instance, larger foraging groups require more resources in a given patch than smaller foraging groups; foraging patches with sufficient food to support multiple foragers are likely more limited than patches for solitary individuals (Livoreil and Giraldeau 1997). Thus, food abundance and distribution at larger spatial scales may exert a stronger influence on the behavior of socially foraging birds than solitary birds. However, research has not examined how multi-scale resource availability affects foraging within the context of sociality. This knowledge gap limits our ability to predict and analyze consequences of environmental heterogeneity on behavior.

In this study, we evaluated the effects of hierarchical variation in resource abundance and foraging sociality on the amount of time fruit-eating birds spent in and feeding at sweet cherry trees. The amount of time animals spend at a particular foraging patch or site is influenced by food abundance (Charnov 1976) and can be used to assess how resource abundance across spatial scales influences the likelihood of staying in the patch (Searle et al. 2006). While spending time in a patch, birds forage but also engage in behaviors such as grooming, vigilance, calling, and perching. Therefore, a measure of the time animals spend actually feeding at a patch (proportion time feeding) is an important behavioral variable for evaluating the effects of food abundance on foraging behavior (Searle et al. 2006). For this study, we define the tree-scale (patch) as focal cherry trees in or under which a bird is observed foraging (Figure 4.1). We define the orchard-scale as areas of multiple contiguous rows of evenly spaced cherry trees. We define the landscape-scale as a circular area (500-m radius) extending from the center of each orchard.



Figure 4.1 Schematic of the tree, orchard, and landscape spatial scales. Scales increase in size from left to right. Dark green parcels in the landscape represent other potential sweet cherry orchards in the landscape surrounding a study orchard.

Within the context of this framework we developed the following hypotheses:

Hypothesis 1: Highly mobile fruit-eating birds use their environments at multiple spatial scales; therefore patch residence time and proportion time feeding behaviors should depend on relative fruit abundance at hierarchical spatial scales. We predicted that the interactions between fruit abundance of 1) trees within orchards and 2) orchards within landscapes would significantly affect avian patch residence time and proportion time feeding.

Hypothesis 2: Birds foraging in groups are more constrained by fruit abundance at relatively large spatial scales (e.g. orchard and landscape) than solitary foragers. We predicted that fruit abundance at the relatively large scales of orchard and landscape would exert a stronger influence on birds foraging in groups than on solitary birds.

Methods

We conducted this study in northwest Michigan sweet cherry orchards in eastern Leelanau County, near Traverse City (44° 46' N, 85° 37' W) from June - July in 2012 and 2014. Leelanau County is primarily a peninsula (area = 804 km²) surrounded by Lake Michigan and an agricultural area with many orchards (e.g. sweet and tart cherries and apples) and vineyards. As of 2011, fruit orchards comprised 7% of the peninsula land area; sweet cherry orchards accounted for 26% of the total orchard acreage (USDA 2012). Other prominent land cover types include non-fruit agriculture (e.g. corn), forests, and open fields. We conducted this study in 12 sweet cherry orchards in 2012 and 10 in 2014, totaling 14 distinct orchards.

To address our objectives, we observed American robins (*Turdus migratorius*) and cedar waxwings (*Bombycilla cedrorum*), two key cherry-consuming species (Lindell et al. 2012). Robins and waxwings are common in the study region and breed during the summer cherrygrowing season. Waxwings arrive by late May (although some overwinter) and nest semicolonially, primarily between mid-June and August (McPeek 2011a). Robins typically arrive in March, begin nesting in April, and rear two broods (McPeek 2011b). Robins and waxwings vary in their degree of foraging sociality (Lindell et al. 2012). In cherry orchards, robins typically forage alone or in small groups with a mean group size of 1.2 ± 0.5 SD (Lindell et al. 2012). Waxwings travel and forage in flocks throughout the year (McPeek 2011b) and the mean group size of waxwings feeding in cherry orchards during summer is 4.2 ± 3.8 SD (Lindell et al. 2012).

Behavioral Observations

We conducted observations over the cherry-ripening period from 04-Jun-2012 – 02-Jul-2012 and 01-Jul-2014 – 24-Jul-2014. We walked systematically through orchards and conducted focal-animal sampling (Altmann 1974). When we detected a bird, we followed it until the bird left the orchard or was lost from sight and recorded all behaviors (e.g. eating, perched, calling, grooming, walking) into a digital voice recorder (Sony ICD-BX800). In some instances, it was possible to follow a bird from the initial tree to another. If birds traveled to subsequent trees but no additional eating was observed, for the purpose of analyses, we considered the observation to end when a bird left the initial tree. If birds were observed in an initial tree but only ate cherries in the second tree, we considered the observation to begin when the bird flew to the tree in which it was actually observed eating. If a bird was observed eating in multiple trees, we randomly selected one tree from the observation and used the corresponding behavioral data from that tree in analyses. We considered these periods in which a bird was seen foraging and consuming cherries to be "observed foraging bouts." We set a minimum observation length of 20 seconds for inclusion in analyses (Morrison et al. 2010), and in doing so omitted three observations. After

observations ended we flagged focal trees for quantification of tree-scale cherry abundance. Upon preparation of data for analysis, we excluded any observations for which corresponding tree data or group sizes were missing. Four observers performed foraging observations, with the first author (RAE) conducting >78% of the observations.

We quantified two foraging response variables for each observation: 1) "patch residence time" and 2) "proportion time feeding". We defined patch residence time as the total amount of time (in seconds) that a bird spent in or under the focal tree. We defined proportion time feeding as the proportion of the patch residence time in which a bird was actually consuming cherries. This was calculated as the total duration of all feeding activity divided by the patch residence time. We adjusted the denominator in the proportion time feeding calculation to omit any time where the bird was out of the observer's sight and thus feeding could not be confirmed. We defined group size as the number of conspecific birds in or under the same tree as the focal bird during the observation (Chavez-Ramirez and Slack 1994). To insure independence among observations, we did not observe additional individuals from a foraging group after observing one member.

Fruit Abundance

We calculated cherry abundance at three spatial scales: individual cherry trees, cherry orchards comprised of multiple trees, and landscapes around cherry orchards (500-m-radius buffer area surrounding orchards; Fig. 1).

Tree-scale fruit abundance

We sampled two branches on each focal tree. We randomly selected a horizontal sector of the tree (north-northeast, east-northeast, etc.) for each branch to be sampled. Next, we measured the tree's height with a laser range finder (Nikon Forester model) and randomly selected a height, in 0.5-m intervals, from the base of a tree's foliage (roughly 0.5 m above the ground) to the tree's height. We identified the closest branch to the chosen sector at the chosen height and counted all cherries on the branch from the terminal end of woody growth on the tip of the branch inward, up to 1 m. If the branch was less than 1 m, we measured the branch length. We calculated the number of cherries per meter of branch length for each sample and averaged the two samples to generate our metric of tree-scale cherry abundance. Cherries were ripening and no longer green during the observation and cherry sampling periods.

Orchard-scale fruit abundance

To conduct orchard-wide cherry sampling, we first divided each orchard spatially into five strata (north, east, south, west, and interior). The two outermost rows of trees on any edge were assigned to the respective edge stratum; all other trees were considered part of the interior (after Tracey and Saunders 2010). To identify sample trees in each stratum, we randomly selected a starting tree and systematically identified up to 11 additional trees for sampling, for a maximum of 60 trees per orchard. If a stratum had fewer than 12 trees, we sampled as many as trees as possible. Branch selection procedures were the same as for tree-scale cherry quantification; however, we used only one branch per tree during orchard-scale sampling (Lindell et al. 2016).

To quantify orchard-scale fruit abundance, we calculated a value of cherries per meter of branch for each sampled tree and averaged these values across all trees sampled in an orchard. Because orchards varied in tree number, we incorporated the total number of trees in an orchard (which included both sampled and un-sampled trees) into our variable of orchard-scale fruit abundance. To estimate the number of trees in each study orchard, we counted the number of rows of trees within an orchard and the number of trees in the outermost rows. We multiplied these two numbers to estimate the maximum number of trees in the orchard. This method may slightly overestimate the number of trees because orchards sometimes have gaps where a tree would otherwise be planted within a row. We then multiplied the orchard-level average of cherries per meter of branch length by the number of trees in the orchard. Thus, our final metric of orchard-scale fruit abundance is presented as cherries per meter of branch length, scaled to the size of each orchard. One study orchard was harvested in 2014 before orchard-wide fruit sampling could be conducted. For the two observations that occurred there, we assigned the 2014 mean orchard abundance value among all study orchards as the orchard abundance value for that site. Preliminary analyses indicated no difference in cherries per meter between trees in edge or interior strata within an orchard, and we made no distinction between these in further analyses.

Landscape-scale fruit abundance

We conducted geographic analyses in ArcGIS 10.0 (ESRI). We digitized study orchards using 2012 National Agricultural Imagery Program (NAIP) orthoimages. We then calculated the geographic centroid of each study orchard and delineated a 500-m-radius buffer around this point. We used NAIP orthoimagery to digitize and classify land cover parcels within each buffer. Using NAIP land cover classifications, we could not distinguish between orchards of different

tree fruits; therefore, we conducted ground-truthing surveys in 2013 to verify which parcels were sweet cherry orchards. We calculated the area of each polygon comprising sweet cherry orchards and summed these areas (Figure 4.1). We defined the landscape scale metric of cherry abundance for each study orchard as the percent of the total buffer area consisting of sweet cherry orchards. This technique included the area of the study orchard itself in the landscape-scale metric of cherry abundance. Therefore, for parsimony and to prevent collinearity between orchard- and landscape-scale fruit abundance, we did not include orchard area as a separate covariate during analyses.

Statistical Analyses

We performed all analyses in R statistical software (Version 3.0.3; R Core Team 2012), using the 'lme4' (Bates et al. 2014) and 'lmerTest' (Kuznetsova et al. 2015) packages. We square root transformed fruit abundance data at all three scales to reduce skew. We then *Z*-transformed these values to allow for comparisons of effect sizes among variables with differing units of measure (Gelman et al. 2013). We *Z*-transformed group size within each species, in order to correct for differences in foraging sociality (Gelman et al. 2013). We *Z*-transformed, without centering, patch residence time in order to improve model convergence. We constructed species-specific generalized linear mixed models (GLMMs) to compare influences of cherry abundance at the three scales and group size on patch residence time and proportion time feeding. To address Hypothesis 1, we included the interactions between tree-scale and orchard-scale fruit abundance and between orchard-scale and landscape-scale fruit abundance. To address Hypothesis 2, we included three additional interaction terms: foraging group size and fruit abundance at each of the three scales. We treated patch residence time as a gamma distributed

variable with an inverse link function and proportion time feeding as a binomial distributed variable with a logit link function. The total number of seconds a bird was observed (excluding any time the bird was out of sight) served as the number of trials for the binomial distribution in this model. Orchard identity and study year were included as random effects. "Time of day" (before or after 1200) and "bird position" covariates (e.g. in tree, on ground, both) were initially included in models, but we removed them after preliminary analyses indicated no influence on response variables. We make the simplifying assumption that model predictor variables are measured without error, which means that all effect size estimates are optimistic. We conducted variance inflation factor (VIF) tests to assess collinearity among predictor variables (VIFs < 8.8; Neter et al. 1996). We calculated R^2 values as one minus the ratio of the residual sum of squares and the total sum of squares.

Results

In total, we have data from 105 observations of birds consuming cherries (62 robins, 43 waxwings). Patch residence time was explained, in part, by interactions among cherry abundance at multiple spatial scales and group size ($R^2 = 38\%$ and 16% for robins and waxwings, respectively). These factors also explained some of the variation in proportion time feeding ($R^2 = 19\%$ and 30% for robins and waxwings, respectively). The random effects of "orchard identity" and "study year" explained low amounts of variation in patch residence time ($R^2 = 0\%$ for both effects for waxwings; $R^2 = 5\%$ and 0%, for "orchard identity" and "study year", respectively for robins). Random effects explained <4% of the variance in proportion time feeding for both species.
Fruit abundance at the tree scale and orchard scale interacted to affect proportion time feeding but not patch residence time

Fruit abundance at the tree scale relative to that of the entire orchard did not affect robin (Figure 4.2A) or waxwing (Figure 4.3A) patch residence time. Fruit abundance at the tree scale relative to that of the entire orchard significantly affected proportion time feeding for waxwings (Figure 4.3C), but not for robins (Figure 4.2C). In particular, robin proportion time feeding declined with increasing fruit abundance at the tree scale regardless of orchard-scale fruit abundance (Figure 4.2C). Waxwings at a tree with low fruit abundance had a greater proportion time feeding when the tree was within an orchard also with low fruit abundance, than when the tree was within an orchard with high fruit abundance; the opposite pattern was observed for waxwings in trees with high fruit abundance (Figure 4.3C).

Fruit abundance at the orchard scale and landscape scale interacted to affect proportion time feeding, but not patch residence time

Fruit abundance at the orchard scale relative to that of the landscape scale did not affect waxwing patch residence time (Figure 4.3B). Neither fruit abundance at the orchard nor landscape scale affected robin patch residence time (Table 4.2), despite a small but significant interaction effect between these two predictor variables (Table 4.2, Figure 4.3B). As cherry orchards increased in fruit abundance, robins stayed longer at a cherry tree (patch) when an orchard was within a high-fruit-abundance landscape. In contrast, robins left a tree sooner when in a high-fruit-abundance orchard within a low-fruit landscape (Figure 4.2B). In addition, fruit abundance at the orchard scale relative to that of the landscape scale significantly affected proportion time feeding of both robins (Figure 4.2D) and waxwings (Figure 4.3D). As fruit

abundance increased at the orchard scale, robins decreased proportion time feeding, with a stronger effect for robins in fruit-rich landscapes than robins in fruit-poor landscapes (Figure 4.2D). As fruit abundance increased at the orchard scale, waxwings in high-fruit landscapes similarly decreased proportion time feeding (Figure 4.3D).



Figure 4.2 The effects of fruit abundance across multiple spatial scales on American robin foraging behavior. The interaction between fruit abundance at the tree scale and orchard scale on American robin patch residence time (A) and proportion time feeding (C). The interaction between fruit abundance at the orchard scale and three levels of landscape-scale fruit abundance on robin patch residence time (B) and proportion time feeding (D). Solid line represents low fruit abundance value (1st quantile), Dashed line represents median abundance value, Dotted line represents high fruit abundance value (3^{rd} quantile). Cherry abundance data are square root and Z-transformed.



Figure 4.3 The effects of fruit abundance between spatial scales on cedar waxwing foraging behavior. The interaction between fruit abundance at the tree scale and orchard scale on cedar waxwing patch residence time (A) and proportion time feeding (C). The interaction between fruit abundance at the orchard scale and three levels of landscape-scale fruit abundance on robin patch residence time (B) and proportion time feeding (D). Solid line = low fruit abundance value (1st quantile), Dashed line = median abundance value, Dotted line = high fruit abundance value (3rd quantile). Cherry abundance data are square root and Z-transformed.

Sociality altered the influence of fruit abundance at large spatial scales on foraging behavior

Waxwing foraging group size ranged from one to six birds with a mean of 2.2; no

waxwing groups of four were observed (Table 4.1). Robin foraging group size ranged from one

to four with a mean of 1.5 (Table 4.1). To clarify, we did not assess between-scale interactions in

the context of foraging sociality in these analyses, but rather the interaction between fruit

abundance at a single scale and foraging group size (Table 4.2). For both robins and waxwings,

fruit abundance at large spatial scales (e.g. orchard and landscape) interacted with foraging group size to affect behavior (Table 4.2). Fruit abundance at large spatial scales did not affect patch residence time differently for solitary waxwings than group-foraging waxwings (Table 4.2). Fruit abundance at large spatial scales scale affected patch residence time of robins in groups differently and more strongly than solitary robins (Table 4.2).

Foraging group size interacted significantly with fruit abundance at large spatial scales to affect waxwing proportion time feeding (Table 4.2). The effect of fruit abundance at large spatial scales on proportion time feeding was stronger for waxwings in relatively large foraging groups than solitary or paired waxwings (Table 4.2). In contrast, fruit abundance at large spatial scales did not affect proportion time feeding differently for solitary robins compared to group-foraging robins (Table 4.2).

Table 4.1 **Group sizes, patch residence times, and proportions time feeding for American robins and cedar waxwings.** Mean, standard deviation, and maximum values of group size. Mean and standard deviation for response variables: patch residence time and proportion time feeding. Mean, standard deviation, and range of tree-, orchard-, and landscape-scale cherry abundance.

| Species | Group size | Patch residence time | Proportion time feeding | | |
|----------------|--|-----------------------|-------------------------|--|--|
| American robin | 1.5 ± 0.9 ; max: 4 | 132 ± 115 seconds | 48 % ± 28 % | | |
| Cedar waxwing | 2.2 ± 1.2 ; max: 6 | 183 ± 145 seconds | 44 % ± 27% | | |
| Spatial scale | Cherry abundance | | | | |
| Tree | 44. 8 ± 46.1 ; range: 0 – 194.6 cherries/m of branch length | | | | |
| Orchard | $17,665 \pm 51,172$; range: $642 - 166,509$ (cherries/m * # trees in orchard) | | | | |
| Landscape | $11\% \pm 6.5$; range: $1.1 - 24.1\%$ of 500-m radius buffer | | | | |

Table 4.2 **Outcomes of species-specific generalized linear mixed models of patch residence time and proportion time feeding**. Model-generated parameter estimates, standard errors (SE), *t- z-*, and *P*-values of covariates and interaction terms from cedar waxwing-specific (unshaded rows) and American robin-specific (shaded rows) GLMMs for dependent variables patch residence time and proportion time feeding. Statistically significant values are bolded.

| Covariate | Estimate | SE | t | Р |
|---|----------|-------|--------|---------|
| Response Variable: Patch residence time | | | | |
| Lutonomt | 1.05 | 0.199 | 5.27 | < 0.001 |
| Intercept | 1.93 | 0.34 | 5.68 | < 0.001 |
| | -0.122 | 0.357 | -0.492 | 0.62 |
| Tree-scale cherry abundance | -0.048 | 0.233 | -0.204 | 0.84 |
| Orchard cools sharry shundance | -0.236 | 0.357 | 0.662 | 0.51 |
| Orchard-scale cherry abundance | 0.167 | 0.281 | 0.593 | 0.55 |
| | 0.385 | 0.259 | 1.49 | 0.14 |
| Landscape-scale cherry abundance | -0.100 | 0.281 | -0.356 | 0.72 |
| | -0.044 | 0.136 | -0.323 | 0.75 |
| Group size | 0.161 | 0.182 | 0.889 | 0.37 |
| Tree y orchand | -0.252 | 0.323 | -0.781 | 0.44 |
| Thee x orenard | 0.365 | 0.208 | 1.76 | 0.08 |
| Orchard v landsoono | 0.35 | 0.28 | 1.26 | 0.21 |
| Ofenard x landscape | -0.377 | 0.189 | -2.00 | 0.045 |
| | -0.076 | 0.165 | -0.458 | 0.65 |
| Tree x group size | 0.592 | 0.285 | 2.08 | 0.038 |
| | 0.186 | 0.222 | 0.838 | 0.40 |
| Orchard x group size | -0.180 | 0.262 | -0.69 | 0.49 |
| Landscape y group size | -0.002 | 0.138 | -0.016 | 0.99 |
| Lanuscape x group size | -0.605 | 0.302 | -2.00 | 0.045 |

Table 4.2 (cont'd)

| Response variable: Proportion time feeding | Estimate | SE | z | Р |
|--|----------|-------|--------|--------|
| Intercent | -0.187 | 0.449 | -0.416 | 0.68 |
| intercept | -0.727 | 1.36 | -0.53 | 0.59 |
| | 0.603 | 0.068 | 8.848 | <0.001 |
| Tree-scale cherry abundance | -0.373 | 0.06 | -6.61 | <0.001 |
| Orchard socia charry shundance | 0.015 | 0.098 | 0.1550 | 0.88 |
| Orenard-scale energy abundance | -2.32 | 0.193 | -12.1 | <0.001 |
| Landscane-scale cherry abundance | -0.993 | 0.403 | -2.47 | 0.014 |
| Landscape-scale enerry abundance | 1.16 | 0.33 | 3.49 | <0.001 |
| Crown size | 0.411 | 0.048 | 8.53 | <0.001 |
| Group size | 0.292 | 0.036 | 7.99 | <0.001 |
| Tree y orchard | 0.184 | 0.089 | 2.07 | 0.038 |
| Thee x orenard | 0.082 | 0.060 | 1.37 | 0.17 |
| Orchard x landscape | -0.589 | 0.099 | -5.94 | <0.001 |
| Orenard x landscape | 0.198 | 0.077 | 2.55 | 0.011 |
| T. · | -0.261 | 0.051 | -5.17 | <0.001 |
| I ree x group size | 0.114 | 0.062 | 1.86 | 0.06 |
| | -0.674 | 0.081 | -8.35 | <0.001 |
| Orchard x group size | -0.048 | 0.065 | -0.741 | 0.46 |
| T 1 . | 0.834 | 0.075 | 11.06 | <0.001 |
| Landscape x group size | -0.053 | 0.065 | 0.813 | 0.42 |

Discussion

We hypothesized that fruit abundance at multiple spatial scales in a fruit-growing region would interact to affect the foraging behavior of fruit-eating birds. We found support for Hypothesis 1 in that relative fruit abundance between the tree and orchard scales and between the orchard and landscape spatial scales interacted to influence American robin and cedar waxwing proportion time feeding. However, we found no indication that fruit abundance at multiple spatial scales affected patch residence time. In addition, we found that fruit abundance at multiple spatial scales interacted in a complex manner with foraging group size to influence proportion time feeding and patch residence time. We discuss these principle findings in detail below.

Fruit abundance at the tree scale and orchard scale interacted to affect proportion time feeding but not patch residence time

We expected that the heterogeneity in fruit abundance between cherry trees and cherry orchards would interact to influence robin and waxwing patch residence time and proportion time feeding. Unexpectedly, the relative fruit abundance between the tree and orchard spatial scales did not affect patch residence time of either species. Similarly, Palacio et al. (2015) found no correlation between fruit crop size at a single spatial scale and the amount of time wild fruit-eating birds spent at trees. Searle et al. (2006) considered multi-scale effects using a controlled experiment and found that the food availability and spatial arrangement of patches within larger-scale areas affected patch residence time in captive grizzly bears and mule deer, in contrast to our findings. Unlike Searle et al. (2006), we conducted our study with wild birds in a non-captive setting. The amount of time pulp-consuming birds like robins and waxwings spend at fruit trees may be affected by fruit handling time, rather than fruit abundance alone (Palacio et al. 2015). Fruit handling time, such as the time required to bite, consume, and digest fruit pulp, could require a minimum amount of patch residence time (Foster 1987).

In addition, robins and waxwings nest during the cherry-growing season in Michigan (McPeek 2011a, McPeek 2011b). The need to leave a particular tree and return to feed offspring at necessary time intervals likely influences robin and waxwing patch residence time

(Kacelnik 1984). Furthermore, while at cherry trees, many birds displayed non-feeding behaviors in addition to actual cherry consumption. For example, birds spent time perching, calling, or grooming. Our findings suggest that patch residence time of fruit-eating birds is not influenced simply by heterogeneity in fruit abundance between hierarchical spatial scales, but is likely affected by additional complexities for animals in the wild.

Heterogeneity in fruit abundance between a cherry tree and the orchard did influence proportion time feeding, however this effect was small and evident only in waxwings. This result likely arises because waxwings exhibit greater frugivory during summer than robins (Witmer 1996), and thus variation in fruit abundance affected our response variable that specifically measured fruit consumption behavior, proportion time feeding, for the highly frugivorous focal species but not the more omnivorous species. The effect of fruit abundance at a particular cherry tree on waxwing proportion time feeding varied with fruit abundance at the orchard scale. When fruit was locally sparse at a tree, waxwings in low-fruit orchards devoted more time to feeding compared to waxwings in high-fruit orchards. The opposite pattern was observed for birds in high-fruit trees. When fruit is sparse at both the tree and orchard scales, birds may need to devote a lot of time to consuming cherries in order to meet fruit resources needs, since these resources are relatively hard to come by at a particular tree and throughout the orchard (Olsson et al. 2000). These findings indicate that the influence of resource abundance at a small spatial scale (e.g. a particular tree) on avian foraging behavior can be contingent upon fruit abundance across a somewhat broad foraging area, such as an orchard.

Fruit abundance at the orchard scale and landscape scale interact to affect proportion time feeding but not patch residence time

We found no clear evidence that relative fruit abundance between the orchard and landscape scales affected robins and waxwing patch residence time. Similar to our discussion of the tree-scale and orchard-scale interaction above, this result is likely due to fact that while at cherry trees, robins and waxwings engaged in behaviors unrelated to fruit abundance such as grooming and communicating.

Cherry abundance at the orchard and landscape scales interacted to affect proportion time feeding of both robins and waxwings. Robins decreased proportion time feeding as fruit became more abundant across the orchard, and this effect was slightly greater for robins in high-fruit landscapes than those in low-fruit landscapes. Waxwings in fruit-rich landscapes showed a similar pattern. Birds make fruit selection decisions hierarchically, with abundance being one of the initial determinants of selection (Sallabanks 1993). If birds are feeding in fruit-rich orchards (habitats) and landscapes, they may be able to spend a smaller proportion of time eating and more time searching for, or selecting among, fruit options and still meet their energy needs. Indeed, theoretical foraging models suggest selectivity among food options should increase with food abundance (Emlen 1966), and selectivity in birds foraging among fruits of a single type may also increase with abundance, especially given the multi-step nature of avian fruit selection (Sallabanks 1993).

In contrast, waxwings in relatively low-fruit landscapes actually devoted more time to consuming cherries, as orchards became more fruit rich. Waxwings feed preferentially on abundant fruits over rare fruits (McPherson 1987) and likely seek out foraging areas (e.g. landscapes with an abundance of fruiting cherry orchards) with widely available fruit. Therefore,

foraging decisions for waxwings and other fruit-specialized species may occur at scales larger than that of a particular fruit orchard. These species should devote more time to feeding at a given tree if alternative fruit-rich orchards are sparse in the landscape and will require considerable search time and energy to locate (Charnov 1976). These interactions between fruit abundance at the orchard and landscape scales suggest that small-scale, observable foraging behaviors are affected by the relative abundance of fruit across multiple, relatively large spatial scales, such as the landscape surrounding a particular foraging habitat (Searle et al. 2006). Furthermore, these multi-scale interactions can significantly influence not only highly frugivorous birds (e.g. waxwings), but more omnivorous species (e.g. robins) as well.

Sociality altered the influence of fruit abundance at large spatial scales on foraging behavior

We hypothesized that fruit abundance at the relatively large orchard and landscape scales would have a greater effect on birds foraging in groups than on solitary foragers. As expected, the degree of foraging sociality interacted with fruit abundance at the orchard and landscape scales and affected the foraging behaviors of robins and waxwings differently (Table 4.2). Interactions between waxwing foraging group size and fruit abundance affected only proportion time feeding, while these interactions affected only the patch residence time for robins.

For the highly frugivorous and group-foraging waxwings, birds in small groups (i.e. solitary or paired birds) exhibited weaker behavioral responses to increases in fruit abundance at large spatial scales, compared to waxwings in large groups (e.g. three or more birds). In addition, waxwings in small groups showed opposite responses to changes in fruit abundance at large spatial scales compared to waxwings in large groups. These results supported our expectation that fruit abundance at scales larger than the patch (e.g. the orchard or surrounding landscape)

would exert a stronger influence on birds in large groups compared to solitary birds or those in small groups. As group size increases, the potential for resource competition and intra-group aggression also increases, which can reduce resource intake (Rutten et al. 2010). The effects of resource competition on the behavior of group-foraging birds can be mitigated if groups feed in areas with more widely available resources (Caraco 1979). Thus, resource availability at the relatively large orchard and landscape scales and the availability of suitable foraging areas to support the needs of a foraging group are important considerations for group-foraging birds (as reviewed in Marshall et al. 2012).

Conclusion

It is important to consider multiple spatial scales in evaluating relatively large-scale ecological patterns (e.g. population abundance, distribution, and species diversity; Wiens 1989, Levin 1992, Cornell and Donovan 2010, Caro and Sherman 2011). The hierarchical nature of resource availability for animals in natural and semi-natural systems affects foraging behavior in a manner that cannot be fully understood via traditional single-scale approaches. Our study is among the first to demonstrate that avian behaviors are influenced by food abundance across between spatial scales, including relatively large scales. In order to understand avian behavior in complex and heterogeneous resource environments more accurately and completely, we must take into account multiple scales (Senft et al. 1987, Pinaud and Weimerskirch 2006, Searle et al. 2006). Furthermore, cross-scale influences of resource abundance should be evaluated within the context of other important influences like foraging sociality and species-specific feeding preferences.

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