

FALL-WINTER HABITAT UTILIZATION OF EURASIAN WIGEON
AND AMERICAN WIGEON WITH NOTES ON MIGRATION AND
HIGHLY PATHOGENIC AVIAN INFLUENZA H5N1 VIRUS

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by

Jeremey Brandon Ashe

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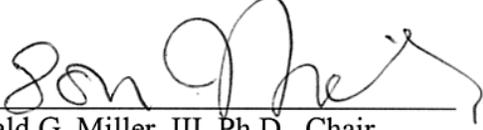
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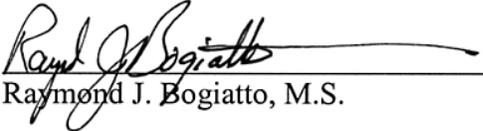
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ABSTRACT

FALL-WINTER HABITAT UTILIZATION OF EURASIAN WIGEON AND AMERICAN WIGEON WITH NOTES ON MIGRATION AND HIGHLY PATHOGENIC AVIAN INFLUENZA H5N1 VIRUS

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I studied fall and winter habitat utilization of Eurasian Wigeon (*Anas penelope*), and American Wigeon (*Anas americana*) using time budgets in the Sacramento Valley, California. Habitat utilization by American and Eurasian Wigeon differed only in the proportion of time spent in locomotion and vigilance. Resting, feeding, and locomotion were the top three behaviors exhibited by wigeon (American and Eurasian Wigeon collectively) during each month and in each pond. Increased feeding by wigeon from November through February suggested an increase in their energetic demands. Seasonally flooded wetlands were determined to be an important habitat for wigeon, as feeding and resting were the most common behaviors each month in these habitats. Asymmetric aggressive behavior patterns of Eurasian Wigeon toward American Wigeon suggested these wigeon species may be competing for resources.

I studied the migration patterns of Eurasian Wigeon and their associations with Highly Pathogenic Avian Influenza Virus H5N1. One Eurasian Wigeon was equipped with a North Star solar-powered 16g platform transmitter terminal (PTT). I followed this bird's two-day migration to Central Washington and, subsequently, its daily movements for the final six months of its life. Using a data base of all banded Eurasian Wigeon from 1929 to 2010, a map was constructed showing migration routes, stopovers, and a pattern of winter philopatry. In addition, oral and cloacal swabs of eight Eurasian Wigeon were taken, with negative results for H5N1.

CHAPTER I

INTRODUCTION

Migration routes of waterfowl in North America are thought to have originated during the glaciations of the Quaternary (Ploeger 1968), resulting in the four North American flyways: Pacific, Central, Mississippi, and Atlantic. Though the migration routes of each waterfowl species may vary, migration flights are generally lengthy, with birds relying upon endogenous fat resources to sustain flight. For example, American Wigeon wintering in California migrating to Canada's Boreal Forest involves a 2200 kilometer flight, whereas Northern Pintail migrating to the Yukon Delta is a 3500 kilometer flight (Bellrose 1980). During the southward migration, birds are migrating to Fall-Wintering habitats, whereas during the northward migration, birds are migrating to breeding habitats. Birds may also stage at traditional stopover areas to rest and forage in order to add endogenous fat resources for their continued migration (Alerstam and Hedenstrom 1998, Miller et al. 2005).

Researchers have tried to elucidate routes, distances, and rates of migration in order to better comprehend North American waterfowl migration routes and philopatry (Bellrose 1980). Philopatry is normally associated with a return to an individual's birthplace but can be generally defined as returning to any particular place (wintering or breeding) every year. Approximately 1.5 million ducks were banded in the United States in the 1930s

and 1940s to determine breeding locations, main wintering sites, and migration routes (Crissey 1955).

During banding, tarsal or foot bands with identification numbers are placed on individuals to track returns from hunter harvest, recapture, or other forms of mortality factors. Essentially two data points, the capture site and the final destination (harvest, mortality, or recapture site) are generated for each individual. With these data, migration maps can be constructed to reconstruct general migration routes of waterfowl. As a result of these early banding efforts, the four flyways were delineated, and the framework for the management of these flyways was designed and put into practice (Crissey 1955).

New technologies have since been developed, which allow for the generation of more fine scale data sets. Satellite telemetry units known as Platform Transmitting Terminals (hereafter PTT) can be used to track individuals anywhere on the globe (Davis and Miller 1992, Petersen and Douglas 1995, Miller et al. 2005). PTT units can be placed internally (sub-cutaneous) or externally (neck collar, back pack, or tail mounted), and each is programmed with an original identification number that can be tracked by polar orbiting satellites that are 850 kilometers above the earth (ARGOS 2007). Unlike tracking techniques employed by banding, PTTs require smaller sample sizes and produce more detailed results. Past studies on an abundant waterfowl species, the Northern Pintail (*Anas acuta*), involved PTTs on 140 birds for four years (Miller et al. 2005), while a study on the Spectacled Eider (*Somateria fischeri*), a threatened species, used PTTs on 12 birds (Peterson and Douglas 1995). Each of these studies produced detailed results on migration routes, distribution, ultimate destinations, and yielded significant management implications.

A species of particular interest is the Eurasian Wigeon (*Anas penelope*). This Palearctic species of dabbling duck (Tribe Anatini: ducks, geese, and swans) overwinters across southern Eurasia, including portions of the Middle East and India; wintering also occurs in areas of northern Africa (Johnsgard 1978). Eurasian Wigeon nest across Eurasia from Great Britain east to the Kamchatka Peninsula, Russia (Edgell 1984, Gardarsson and Einarsson 1997). Through migration, this Palearctic species has reached the Nearctic without the assistance of humans. Published and anecdotal evidence strongly suggests that the wintering population of Eurasian Wigeon is increasing throughout the Pacific Flyway, from the Aleutian Islands, Alaska, south to the Central Valley of California (Edgell 1984, Gibson and Byrd 2007, National Audubon Society 2009). Christmas Bird Counts data suggest that the current Pacific Flyway wintering population is at least 2,000 individuals (Bellrose 1980, Edgell 1984). Edgell (1984) argues that these distributional and population trends in Eurasian Wigeon are accurate and not a result of observer bias. Evidence supporting his conclusion includes Christmas Bird Counts (CBC) showing stable Eurasian Wigeon numbers from the Atlantic flyway while Pacific flyway numbers show a steady increase. The numbers and distribution patterns of other Palearctic waterfowl (e.g., Tufted Duck (*Aythya fuligula*), Eurasian Green-winged Teal (*Anas crecca crecca*), and the less common Smew (*Mergellus albellus*), are also known to immigrate to the Nearctic, although they do not show the same pattern as Eurasian Wigeon. Therefore, the CBC data are strongly supportive of either a range expansion, an unknown breeding population(s) in the Nearctic, or both.

Additionally, the association of Eurasian Wigeon with the Highly Pathogenic Avian Influenza Virus H5N1 (hereafter H5N1) is significant. H5N1 is responsible for the loss of millions of dollars in revenue due to outbreaks and resulting mortality in Palearctic

poultry farms. This disease with its associated mortality has also been recorded in native Eurasian and African bird and mammal populations. For example, approximately 10% of the world's population of Bar-headed Geese (*Anser indicus*) died in 2005 as a result of an H5N1 outbreak at Lake Qinghaihu in Western China (Liu et al. 2005, Olsen et al. 2006). In addition, H5N1 has been known to mutate into strains deadly to humans (Claas et al. 1998). One such example was the 1918 Spanish Flu epidemic that killed more than 50 million people (Johnson and Mueller 2002). As a result, in 2006 a major surveillance effort was undertaken by the U.S. Department of Agriculture, U.S. Department of the Interior, and State and Provincial fish and game agencies, to detect H5N1 in live and hunter-harvested birds in the Pacific Flyway (Duesk et al. 2009). In their study, cloacal samples were collected from birds known to be potential carriers of H5N1 from the Families Anatidae (waterfowl; $n = 18,139$) and Scolopacidae (sandpipers; $n = 2,010$). Of these samples, only 83 birds tested positive for avian influenza, and none were positive for H5N1.

Although H5N1 has not yet been detected in the Nearctic, this does not preclude the trans-hemispheric movement of this virus. Alaska, the northernmost portion of the Pacific Flyway, is the most likely location for an Asia-to-U.S. transfer of H5N1 (Winker et al. 2007). Laboratory and field research support the hypothesis that the spread of H5N1 is due in part to wild bird migration (Perkins and Swayne 2002, Keawcharoen et al. 2008). Controlled studies confirm that wild birds, including Eurasian Wigeon, are susceptible to H5N1 but manifest no clinical signs of the disease (Brown et al. 2006, Keawcharoen et al. 2008). Therefore, a trans-hemispheric spread of the virus through birds that show no clinical signs is clearly possible.

Currently there are no confirmed reports of Eurasian Wigeon nesting in North America, although Eurasian Wigeon have been observed in Northwestern Canada during the nesting season (Fournier and Hines 1996). With perhaps thousands of Eurasian Wigeon wintering throughout the Pacific Flyway, and with no confirmed reports of nesting, most, if not all Eurasian Wigeon are likely migrating to Eurasian nesting grounds in the spring. Therefore, I investigated whether Eurasian Wigeon migrate between Nearctic wintering grounds and Palearctic nesting grounds, and whether they are carriers of the H5N1 virus.

I believe the Eurasian Wigeon is a prime candidate for the transmission of the virus from Eurasia to North America, with the most likely migration routes crossing either the Bering Strait or following the Aleutian Islands. The Bering Strait from Russia to Alaska is only 85 kilometers at its narrowest. Evidence for the use of this migration corridor comes from numerous Alaskan/Bering Sea Island records of Palearctic shorebirds such as Lesser Sand-plover (*Charadrius mongolus*), and Common Greenshank (*Tringa nebularia*), as well as a variety of Eurasian waterfowl such as Eurasian Green-winged Teal (*Anas crecca crecca*), Baikal Teal (*Anas formosa*), and Tufted Duck (*Aythya fuligula*). With over 60% of Pacific Flyway waterfowl (approximately five million birds) wintering in the Central Valley, the potential for Eurasian Wigeon to transmit H5N1 virus throughout this wintering waterfowl community demands attention. To examine the possible transfer of H5N1, I looked at Eurasian Wigeon migration through the use of a PTT.

Wintering numbers of Eurasian Wigeon are sufficiently large within the Sacramento Valley of California to allow for a habitat utilization study. One method that has been used successfully in determining how waterfowl use their habitats is time budget analysis (Paulus 1984, Quinlan and Baldassarre 1984). Past studies quantified behaviors such

as foraging, resting, courtship, aggression, and vigilance, comparing them to factors such as habitat type, nearest neighbor, and responses to weather (Paulus 1983, Hepp and Hair 1984, Miller 1985). Most of these studies concentrate on conspecific interactions (Paulus 1983, Hepp and Hair 1984, Miller 1985, Turnbull and Baldassarre 1987). Using an interspecific approach can provide new ecological and behavioral insights. For example, interspecific differences in the proportion of time spent on various behaviors suggest differences in physiological needs and niches (Turnbull and Baldassarre 1987). Moreover, studies involving sister species and time budgets are few in number if not absent from the waterfowl literature; there have been no habitat utilization studies of American or Eurasian Wigeon in the Pacific Flyway.

An important aspect of wintering ecology for ducks is the formation of pair bonds many months prior to the breeding season (Bellrose 1980). Prior to formation of pair bonds, social courtship groups of multiple males display for a single female during the fall and winter. Males compete through the use of displays directed toward females, with antagonistic displays directed toward rival males. Since these displays occur during the fall and winter, a time when food resources may become limiting, benefits of pair formation must outweigh the energetic costs of courtship (Fretwell 1972, Hepp and Hair 1983). Benefits of pairing include feeding efficiency and dominance over unpaired individuals (Ashcroft 1976, Jorde et al. 1983, Paulus 1983); pairs generally win battles over resources with unpaired birds because of their increased dominance. This is known as the dominance hierarchy hypothesis. I tested the hypothesis that pairs illustrate dominance over unpaired individuals.

Some challenges waterfowl face during the winter include balancing energetic expenditures for courtship and flight. As most waterfowl food in the Sacramento Valley

occurs on managed wetlands and in rice fields (Miller 1987), a large quantity of food can be produced with proper management. Wetland management can best be described as the active manipulation of wetland habitats to produce quality food resources and provide thermal vegetative cover; the management of water regimes influences plant diversity. Strategies include seasonal flooding (flood in fall and drain in spring), semi-permanent flooding (remains flooded in spring and summer but dry for 2-6 months each year), or permanent flooding (year round flooding). Each of these water management strategies results in a unique community of wetland plants and invertebrates, which can influence waterfowl species composition. For example, Northern Pintails prefer open water seasonally flooded wetlands (Miller 1985 and 1987), whereas Mallards (*Anas platyrhynchos*) prefer more closed, heavily vegetated wetlands (Turnbull and Baldassarre 1987). I studied both wigeon species on three different managed wetlands in an attempt to answer the question of whether wigeon behaviors differ by management strategy.

Interspecific competition for resources such as food, space, and other important resources has been documented within many waterfowl species assemblages as well as other wetland taxa (White and James 1978, Nudds 1983, Allouche and Tamisier 1984, McKnight and Hepp 1998). Though competition is difficult to quantify, it is best described based on niche and optimal foraging theory (Schoener 1982, Stephens and Krebs 1986). In general optimal foraging theory predicts that animals will forage optimally by choosing foods that yield the greatest net energy per unit time foraging, while niche theory suggests that a species' spatial occupancy is limited through competition. Consequently, competition is predicted to be highest where niche overlap between species occurs. Arguments over whether resources tend to be more limiting during the breeding (Bethke 1991) or non-

breeding season (DuBowy 1991) are ongoing; the effects of interspecific competition on waterfowl communities have yet to be resolved. Moreover, interspecific competition has never been examined between American and Eurasian Wigeon.

An understanding of nearest neighbor and aggressive patterns is essential to make conclusions of potential interspecific competition between wigeon species. The closest neighboring species (inter or conspecific) to a given individual is its nearest neighbor (Boettcher and Haig 1994). Interspecific aggression in waterfowl suggests competition for food and space in waterfowl communities (Baker and Baker 1973, Wiens 1977, DuBowy 1991). Using both concepts, if aggression is nonselective, then aggression is predicted to be proportional to the time spent near a neighbor. For example, if Eurasian Wigeon are found in association with other Eurasian Wigeon 90% of the time, then 90% of their aggressive behaviors should be directed towards Eurasian Wigeon. However, if aggression is selective, then these aggressive behaviors are not predictable based on proximity. Thus, if aggressive behaviors are selective, then they serve as an indicator of competition. I hypothesized that aggression among American and Eurasian Wigeon is selective, because these sister species are similar in morphology and have been observed using the same habitats.

In summary, ecological and natural history studies of Eurasian Wigeon in the Nearctic are absent from the literature in North America. To help fill this void, I first looked at Eurasian Wigeon migration and possible associations with H5N1. Secondly, I examined American and Eurasian Wigeon habitat utilization through time budget analysis. I investigated whether time budgets of paired birds differed from those of unpaired birds. This study is the first to incorporate satellite tracking of Eurasian Wigeon and compare time budgets of the two wigeon species in the Nearctic.

CHAPTER II

METHODS

Study Area

The study site for the habitat utilization component included wetland units at the Llano Seco Unit of the North Central Valley Wildlife Management Area, Butte County, California. The units consisted of a 37 ha seasonally flooded wetland (Unit 12), a 23 ha permanent to semi-permanent marsh (Unit 13), a 34 ha seasonally flooded wetland (unit 14), and a 47 ha open water seasonally flooded wetland (units 18 and 19). Unit 12 is an open water habitat that is dominated by pricklegrass (*Heleochoa spp.*). Unit 13 is a more closed marsh habitat dominated by hard-stemmed bulrush (*Schoenoplectes acutus*) and cattails (*Typha spp.*). Units 14 and 18/19 are open water habitats dominated by watergrass (*Echinochloa crusgalli*), smartweeds (*Polygonum spp.*) and hard-stemmed bulrush.

All trap efforts for this project were conducted on National Wildlife Refuge (NWR), State Wildlife Area, and private lands throughout the northern Sacramento Valley. Although Eurasian Wigeon were observed at these locations, none were captured. As a result, trap activities shifted to the Klamath Basin NWR Complex near the California-Oregon border in Siskiyou County. The Klamath Basin serves as an important spring migration staging area for wigeon and other waterfowl species (Miller et al. 2005).

Rocket Netting

My trapping effort began in February 2009 and extended into late March 2009. The February starting date was intended to prevent loss of banded birds to hunting-related mortality. Rocket nets were used during my attempt to capture Eurasian Wigeon. I used one to six nets; each net had three attached rockets. Nets were placed on loafing islands (places where birds rest), rice checks (raised land separating rice fields), or roads where high concentrations of birds had been seen. To reduce disturbance, nets were set up at night, and unrefined rice was placed in the water at the edge of the nets in order to concentrate birds. A crew member (see acknowledgments) with a spotting scope sat in an elevated position, usually in the back of a motor vehicle or on a hillside overlooking the nets. Once birds were within range (5m), crews set off the rockets using a hand-held detonator. After detonation all captured birds were placed in poultry crates. Each healthy bird was aged, sexed, weighed, measured for wing cord (length), and banded.

Platform Transmitter Terminal (PTT)

I used a 16-20 gram solar-powered PTT (Northstar Science and Technology, King George, Virginia). The PTT measured 59mm long, 20mm wide, 17mm tall, with a 19.8cm antenna. PTT output power is 200-250 mW, with a transmission frequency of 401.644 Mhz. The unit was equipped with activity and temperature sensors. The activity sensor recorded bird movements, while the temperature sensor recorded an average of ambient and body temperature.

To ensure that PTT + harness mass (18g) would be $\leq 3.5\%$ of body mass, I verified that the captured Eurasian Wigeon weighed at least 850g (Caccamise and Hedin

1985). The age, sex, wing cord (mm), and bill culmen length (mm) of each captured bird were also recorded (Carney 1992). PTT attachment and release were carried out following methods described by Miller et al. (2005). The PTT was placed dorsally on the bird and Teflon ribbon was attached to the posterior end of the PTT (Fig. 1). The ribbon was drawn ventrally and a knot was made over the keel of the bird. The ribbon was moved over the anterior portion of the bird's shoulders and attached to the anterior portion of the PTT. Once the PTT was attached the bird was released at the capture site.



FIGURE 1: PTT attachment on a second year male Eurasian Wigeon.

Screening for H5N1 Virus

The single Eurasian Wigeon with a PTT and seven hunter-harvested Eurasian Wigeon from local wildlife refuges (Little Dry Creek Unit of the Upper Butte Basin Wildlife

Area, Sacramento NWR, and Delevan NWR) were swabbed orally and cloacally for H5N1 virus particles. These swabs were placed in a vial and shipped overnight on ice to UC Davis Wildlife Health Center Laboratory for analysis. Once at the Davis lab, technicians ran real-time reverse transcriptase-polymerase chain reaction (RT-PCR) using the matrix gene RT-PCR assay. Any positive samples would indicate the presence of avian influenza and would then be further characterized by the H5- and H7-specific RT-PCR assays of Spackman et al. (2002). When negative, no additional tests were run.

Computer Tracking

PTT tracking was carried out through CLS America, which uses the ARGOS tracking system. Personal program numbers are assigned to each PTT unit. PTTs then transmitted signals picked up by polar orbiting satellites that are 850Km above the earth. These satellites stored the signals and transmitted them back to earth in real time. Signals are then picked up by one of 40 ground antennas located throughout the world and then sent to one of two global ARGOS processing centers. Once data arrived, they were processed and became directly available to researchers. Available data included GPS coordinates and data accuracy. Each GPS location had a radius of error which was the radius from the GPS location. The error associated with each GPS location was classified into four categories. Location data error was classified as 0 (over 1500m radius error), 1 (less than 1500m radius error), 2 (less than 500m radius error), and 3 (less than 250m radius error). For the purposes of this study, maps were generated using location 2 and 3 data only because the GPS data point given had less than 500m of radius error.

My PTT was set to transmit at 8 hours on and 23 hours off. This transmitting rate allowed for daily movements to be recorded at different times of the day. Location data were delivered through weekly, via electronic email. Location data were then used to construct migratory pathway(s), as well as the bird's location during the breeding season.

Time Budgets

I collected time budget data according to the following protocol for Eurasian and American Wigeon from November 2009 through March 2010. Three Fall-Winter surveys were conducted between the 1st-10th, 11th-21st, and 22nd-31st of each month. Additionally, each survey day was broken into five equal timeslots (time periods) (sunrise, midmorning, midday, afternoon, evening), each ranging from 1.5hr-2.5hr.

At the beginning of each survey day, I selected survey starting points, using dice. Air temperature, wind speed, and general weather conditions were recorded at the start of each timeslot. During each timeslot, Eurasian and American Wigeon were located using a 20-60X spotting scope and binoculars. No predetermined scanning areas of ponds or rice fields were made beforehand. Scanning of ponds began where birds were observed, and to ensure against double counting, ponds were systematically scanned from side to side.

Once a Eurasian Wigeon was located, behavioral observations were recorded for five minutes for that focal individual (Altmann 1974). The activities were scored as loafing, feeding, courtship (aerial, displays, or swim), preening, locomotion (swim, walk, or fly), aggression, vigilance, bathing, mock copulation, and diving.

Behavior Definitions

1) I defined “resting” as a bird being on land or water with its head tucked behind its wing or having its eyes closed and head in a down position.

2) I defined “feeding” as a bird either tipping up, surface feeding, or grazing on land.

3) I defined “locomotion” as a bird either swimming (not associated with courtship), flying (not associated with courtship), or walking on land.

4) I defined “courtship” as a male performing courtship displays to a female, actively following the female in a social group (not associated with locomotion), or actively following a female in flight with more than one male and no more than one female.

5) I defined “aggression” as a bird threatening, biting, or otherwise physically attacking another bird.

6) I defined “vigilance” as a bird having the head and neck extended vertically.

7) I defined “preening” as a bird grooming its feathers with the bill or head, or bathing by flapping its wings on the surface of the water or rolling in the water.

Rather than record total amount of time spent on each behavior, I recorded behaviors every 10 seconds using a stopwatch, on the assumption that spot checks every 10 seconds were representative of time allocations for each behavior. Additionally, I recorded the location (pond units 12, 13, 14, or 18/19) where each bird was observed, its social status (paired or unpaired), and its nearest neighbor (the closest bird to the focal individual). Data were immediately recorded on a data sheet if more than one observer was present. In cases with a single observer, a personal voice recording device was used to record data that were later transferred to data sheets. After or during a five-minute observation, the observer located the nearest American Wigeon of the same sex and pair status and then conducted

observations using the same protocol. This process was repeated until no additional Eurasian Wigeon could be located on a pond.

Occasionally, multiple birds were observed at once; however, data were collected for multiple birds only if individuals could be tracked accurately.

Once all Eurasian Wigeon were located, or if the risk of double counting increased, I moved to the next pond or rice field. This process was repeated until the end of each timeslot. If no Eurasian Wigeon were found in an area during a particular timeslot, my assistants and I then attempted to locate birds on another survey pond before the start of the next timeslot. This ensured that optimal time observing Eurasian and American Wigeon occurred during the observational timeslot.

Upon completion of this study, the activities observed were used to create time budgets for Eurasian and American Wigeon. As each bird was observed for five minutes, with behavior being recorded every 10 seconds, a total of 30 behavioral observations per individual were obtained. Behavioral tallies were then converted into proportions (percentages) by dividing by 30.

Nearest Neighbor and Aggression

In the waterfowl nesting literature, nearest neighbor is often defined as the shortest distance between one nest and another nest (Lokemoen et al. 1983, McLandress 1983, Ackerman et al. 2004). On the other hand, plant literature defines nearest neighbor as the shortest distance between one plant and another, and its application is generally in regards to competition for available light (Clark and Evans 1954). I defined nearest neighbor as the closest waterfowl species to a focal individual whose behaviors were being recorded.

These frequencies were converted into percentages by dividing nearest neighbor totals by total focal birds. For example, a total of 874 focal American Wigeon were observed, and the nearest neighbor was an American Wigeon 602 times. Therefore, the nearest neighbor was an American Wigeon 69% of the time. In addition, when a focal individual engaged in an aggressive behavior towards another individual, the recipient was identified to species. The most parsimonious expectation would be that aggressive behaviors are equal across species. Using this same example, the expected number of aggressive behaviors towards American Wigeon would be 69% of all observed aggressive interactions.

Data Analysis

I used three statistical tests for data analysis. I constructed a general linear model by performing a balanced multivariate analysis of variance (MANOVA). The MANOVA was used to test for differences in the proportion of time spent on each dependent variable within and between independent variables. The proportions of all recorded behaviors served as dependent variables, as they were continuous. Species, social status, month, timeslot, and pond served as independent variables, as they were categorical. I computed when possible two-way interactions between independent variables (e.g., species X month, species X location). Two-way interactions were used to test whether birds spent equal proportions of time on behaviors for each interaction. These interactions were non-additive, but were used to help explain complex relationships between variables. I then used a univariate analysis of variance (ANOVA) for each independent variable to test whether time spent on individual behaviors differed. The independent variables social status, month, timeslot, and pond were analyzed by pooling both species, as species was not a factor in the ANOVA. A Chi-Square

Test was then used to determine if interspecific aggressive behaviors of American and Eurasian Wigeon were proportional to the time spent near their neighbor. I used observed nearest neighbor counts and aggression counts to determine expected aggression (see above *Nearest Neighbor & Aggression* for an example).

CHAPTER III

RESULTS

Habitat Utilization

Upon completion of the study, a total of 146 hours of behavioral observations were made for Eurasian Wigeon and American Wigeon. No Eurasian Wigeon were observed in March or at pond 18/19 on certain dates, the MANOVA interactions could not be computed. Therefore, I did not include March observations or data collected from pond 18/19.

The proportion of time spent on all behaviors differed significantly ($P < .001$) among all independent variables (Table 1). The null hypothesis that birds spend equal proportions of their time engaged in these behaviors can thus be rejected. All two-way interactions that did not contain the “species” variable showed significant differences ($P < .05$) (Table 2). For example, the “location X date” interaction indicated that, at different locations on different dates, proportion of time spent on behaviors differed significantly ($P < .001$). However, interactions containing the “species” variable were not distinct ($P > .05$). For example, the “species X location” interaction suggested location did not affect behavior because species behaviors were not distinct by location. Therefore, there was no interaction between species and location ($P = .09$). The interactions that contained the “species” variable suggested the two wigeon species behaviors were the same when compared to other variables.

TABLE 1. Summary of MANOVA results for species (American and Eurasian Wigeon), social status (pair and unpaired), location (12, 13, and 14), month (Nov-Feb), and timeslot (1-5) comparing the proportion of time on each behavior ($n=842$).

Independent Variable	Df	<i>F</i>	<i>P</i>
Species	1	5.552	<.001
Social Status	1	7.353	<.001
Location	2	8.254	<.001
Month	3	9.511	<.001
Timeslot	4	4.556	<.001

TABLE 2. Summary of all possible interactions of species (American and Eurasian Wigeon), social status (pair and unpaired), location (12, 13, and 14), month (Nov-Feb), and timeslot (1-5) for the GLM ($n=842$).

Interaction	Df	<i>F</i>	<i>P</i>
Species X Location	2	1.589	0.09
Species X Timeslot	4	0.754	0.8
Species X Date	3	1.056	0.39
Species X Status	1	1.278	0.26
Location X Timeslot	6	2.387	<.001
Location X Date	6	3.681	<.001
Timeslot X Date	6	2.336	<.001
Social Status X Location	2	2.115	0.013
Social Status X Timeslot	4	3.957	<.001
Social Status X Date	3	5.361	<.001

Eurasian Wigeon arrived prior to the first survey date, and following a peak in mid-January, numbers decreased until no Eurasian Wigeon could be found by the end of March. A total of 874 focal Eurasian and American Wigeon were observed throughout this

study. The proportion of time spent on different behaviors was similar for American and Eurasian Wigeon ($P > .05$) with the exception of locomotion and vigilance (Table 3).

TABLE 3: Two-way ANOVA comparing all behaviors of American and Eurasian Wigeon ($n=842$ for each species).

Species	Behavior	Mean	P
AMWI	Locomotion	7%	<.001
EUWI	Locomotion	11%	
AMWI	Vigilance	0.80%	0.021
EUWI	Vigilance	1%	
AMWI	Resting	31%	0.21
EUWI	Resting	29%	
AMWI	Feeding	52%	0.21
EUWI	Feeding	50%	
AMWI	Courtship	3%	0.77
EUWI	Courtship	3%	
AMWI	Preening	5%	0.57
EUWI	Preening	5%	
AMWI	Aggression	1%	0.96
EUWI	Aggression	1%	

Eurasian Wigeon spent 4% more time in locomotion ($P < .001$), and 0.2% more time engaged in vigilance ($P = .021$) than American Wigeon. However, notwithstanding the low P value, these differences in percent time between species, for the two behaviors, seemed very slight. All comparisons hereafter are for both wigeon species combined, as the independent variable (species) were not a factor in any other ANOVA's.

A total of 592 paired and 1,156 unpaired wigeon were observed throughout this study (Table 4). Unpaired wigeon spent more time resting ($P < .001$), in locomotion

TABLE 4. Two-way ANOVA comparing percent of time spent on behaviors by social status for wigeon ($n= 592$ paired, $n= 1,156$ unpaired).

Social Status	Behavior	Mean	<i>P</i>
Unpaired	Resting	33%	<.001
Paired	Resting	24%	
Unpaired	Feeding	45%	<.001
Paired	Feeding	64%	
Unpaired	Locomotion	11%	<.001
Paired	Locomotion	6%	
Unpaired	Vigilance	.007%	0.017
Paired	Vigilance	.12%	
Unpaired	Preening	5%	0.74
Paired	Preening	6%	
Unpaired	Aggression	1%	0.26
Paired	Aggression	1%	
Unpaired	Courtship	4%	<.001
Paired	Courtship	0%	

($P < .001$), and engaged in vigilance ($P = .017$); paired wigeon spent more time feeding ($P < .01$). There was not a statistical difference in the time spent in preening or aggressive behavior ($P > .05$).

There was a significant difference in the proportion of time spent for all behaviors except aggression by location (Fig. 2). Wigeon significantly rested for longer periods of time in pond 12, they spent more time feeding and courting in pond 14, and they spent more time preening, in locomotion, and exhibiting vigilance in pond 13 ($P < .05$).

With the exception of feeding, the proportion of time spent on all behaviors differed by timeslot (the time of day) (Fig. 3). The proportion of time spent resting increased as the day progressed, while courtship and locomotion activities decreased.

The proportion of time spent on all behaviors by wigeon was significantly different by month ($P < .05$) (Fig. 4). The top three behaviors performed during each month

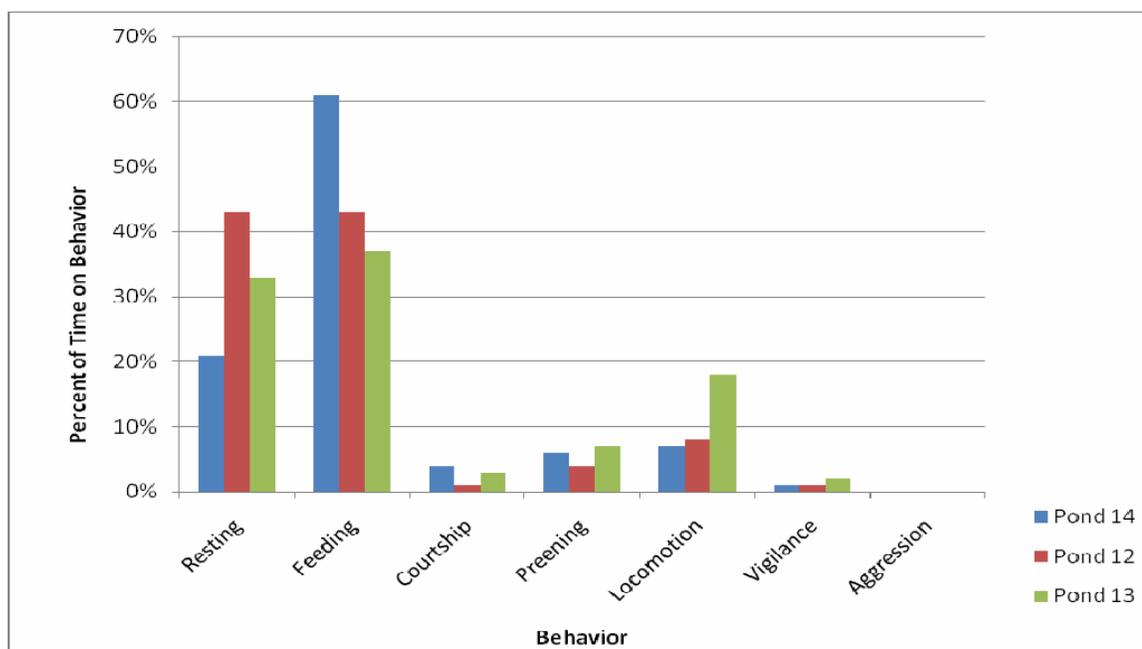


FIGURE 2. Two-way ANOVA results for percent time spent on behaviors by location for wigeon (aggression $P = .11$, all other behaviors $P < .05$). The percent time spent in Aggression for wigeon was $< .01\%$.

were resting, feeding, and locomotion. A clear pattern of decreasing time spent resting, engaged in courtship, and in locomotion activities was observed by wigeon, while the opposite pattern was shown for feeding. Preening, vigilance, and aggression stayed relatively constant.

Both Eurasian and American Wigeon were found to be associated more with members of their own species (Fig. 5 and Fig. 6). American Wigeon were less aggressive toward Eurasian Wigeon than expected, while Eurasian Wigeon were twice as aggressive toward American Wigeon as expected. A Chi-Square Test found patterns of aggression illustrated by American and Eurasian Wigeon to be selective (Fig. 7 and Fig. 8). Expected levels of aggression by both wigeon species differed from observed aggressions (American Wigeon $P < .01$, Eurasian Wigeon $P < .001$).

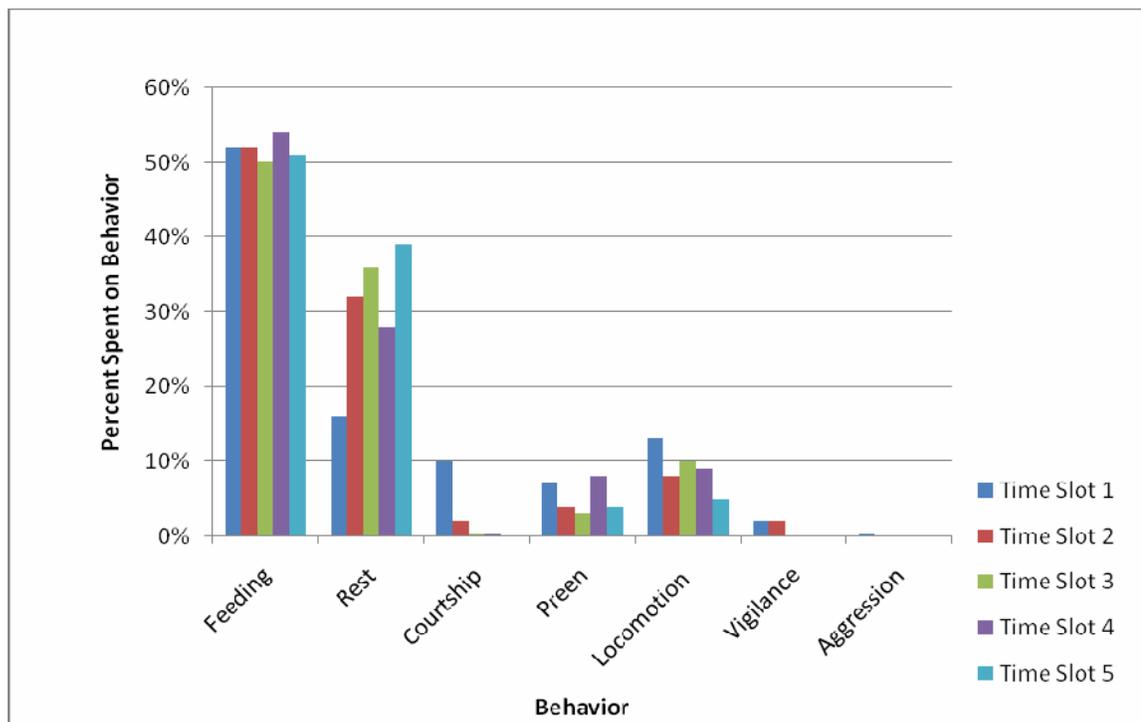


FIGURE 3. Two-way ANOVA results for percent of time spent on behaviors by timeslot for wigeon (feeding $P = .76$, all other behaviors $P < .001$).

Migration and H5N1

A single male Eurasian Wigeon was equipped with a Solar PTT at the Lower Klamath National Wildlife Refuge on March 22, 2009, and released the same day; the bird moved locally until late May. On May 25 the bird began a sudden, 660 Km northward migration, that ended on May 27, at a location near Rock Lake, Whitman County, Washington. There the bird moved locally until June 29 when he flew northwest for 142 Kilometers and stopped near Banks Lake, Grant County, Washington. Local movements continued until October 2, 2009. PTT sensors suggested the bird died near Moses Lake and Potholes Reservoir, Grant County, Washington (Fig. 9).

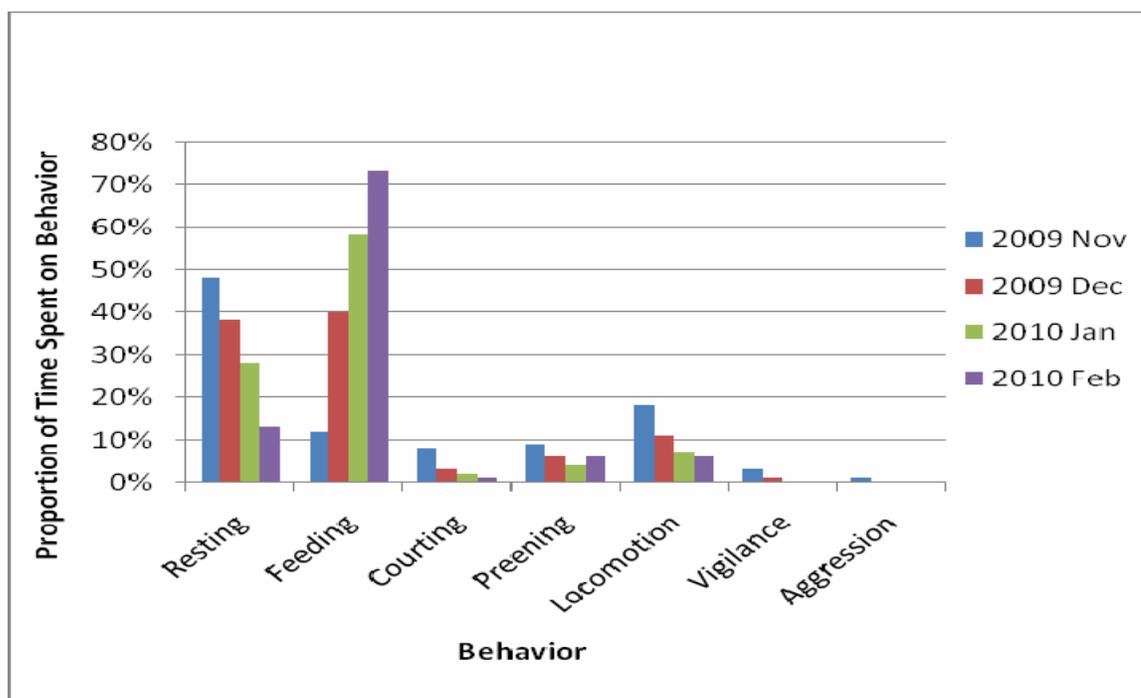


FIGURE 4. Two-way ANOVA results for percent of time spent on behaviors by month for wigeon ($P < .05$).

Eight Eurasian Wigeon were swabbed and tested for H5N1 (Table 5). Of the eight birds, six were adult males, one was an immature male (equipped with the PTT), and one was an immature female. All birds tested negative for the H5 or H7 gene qRT-PCR. However, the female was a carrier for avian influenza, although not the highly pathogenic strain.

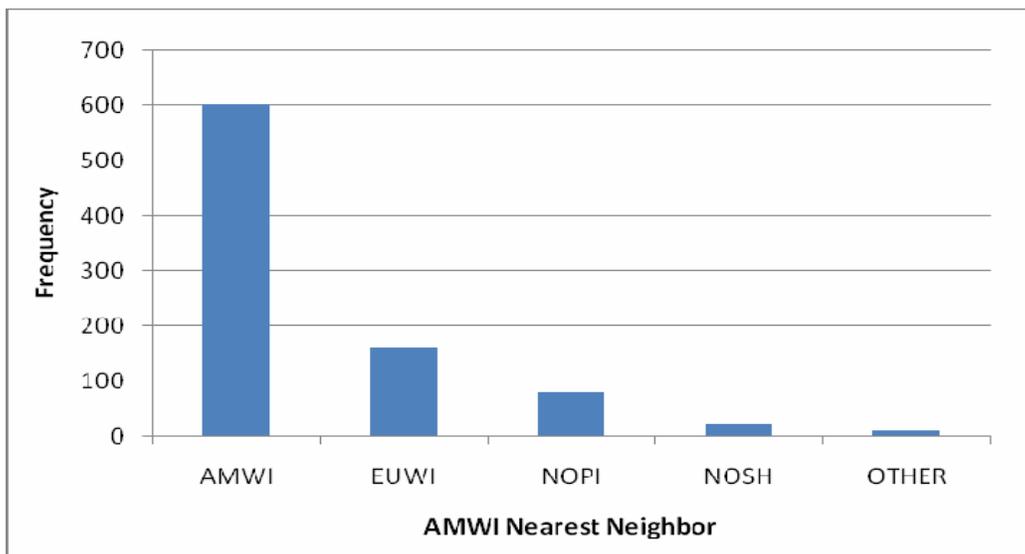


FIGURE 5. Summary data of all the nearest neighbor frequencies and associated species that were nearest to an American Wigeon (AMWI).

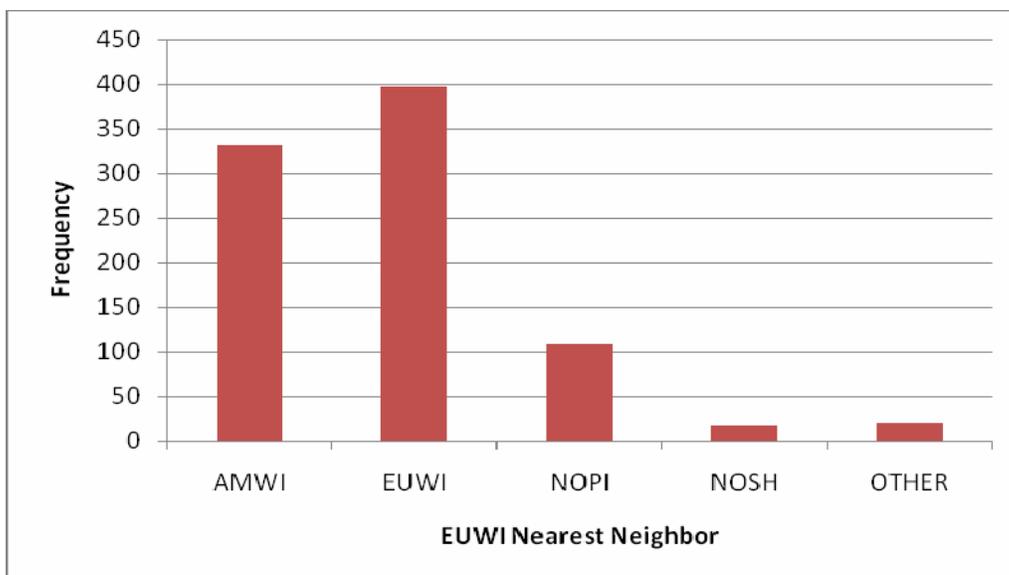


FIGURE 6. Summary data of all the nearest neighbor frequencies and associated species that were nearest to an Eurasian Wigeon (EUWI).

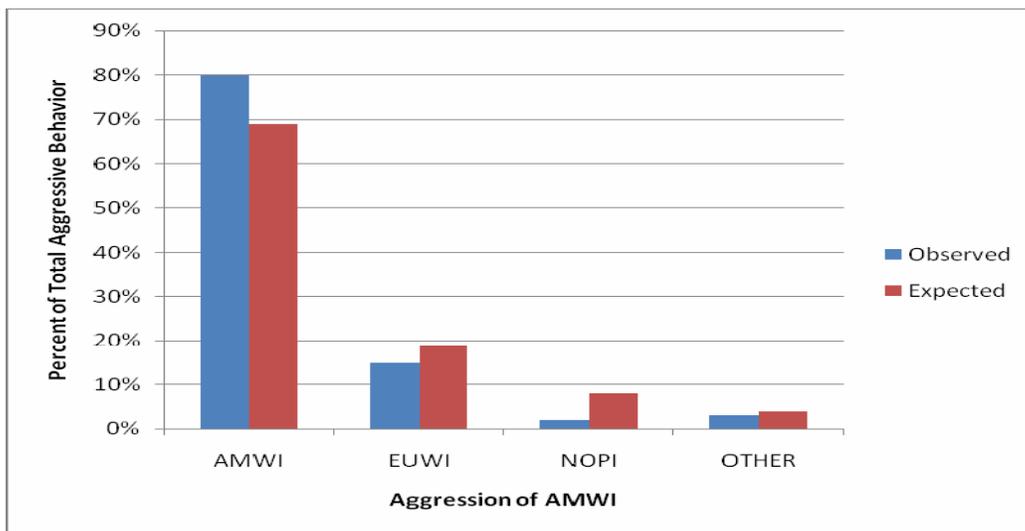


FIGURE 7. Aggression of American Wigeon toward American Wigeon (AMWI), Eurasian Wigeon (EUWI), Northern Pintail (NOPI), and other species ($P < .01$).

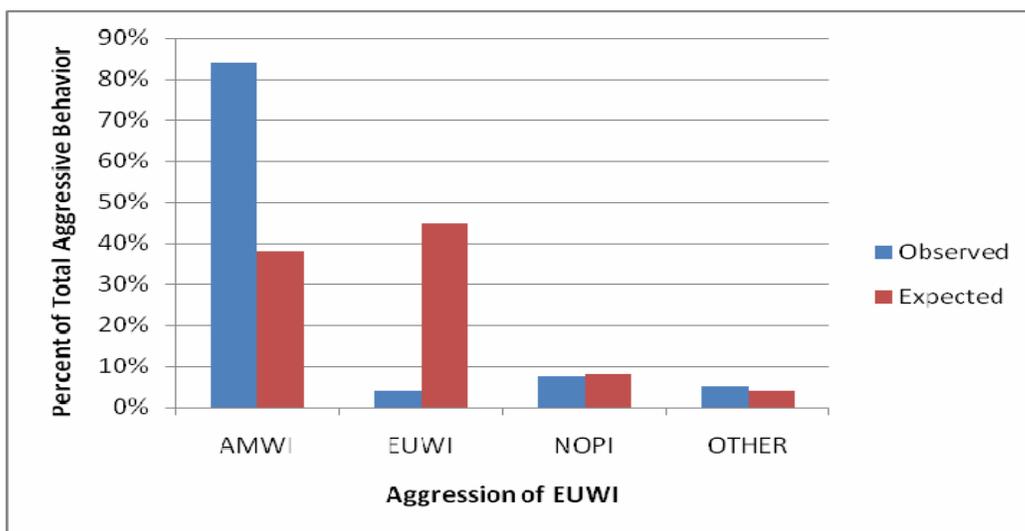


FIGURE 8. Aggression of Eurasian Wigeon toward other American Wigeon (AMWI), other Eurasian Wigeon (EUWI), Northern Pintail (NOPI), and other species ($P < .001$).

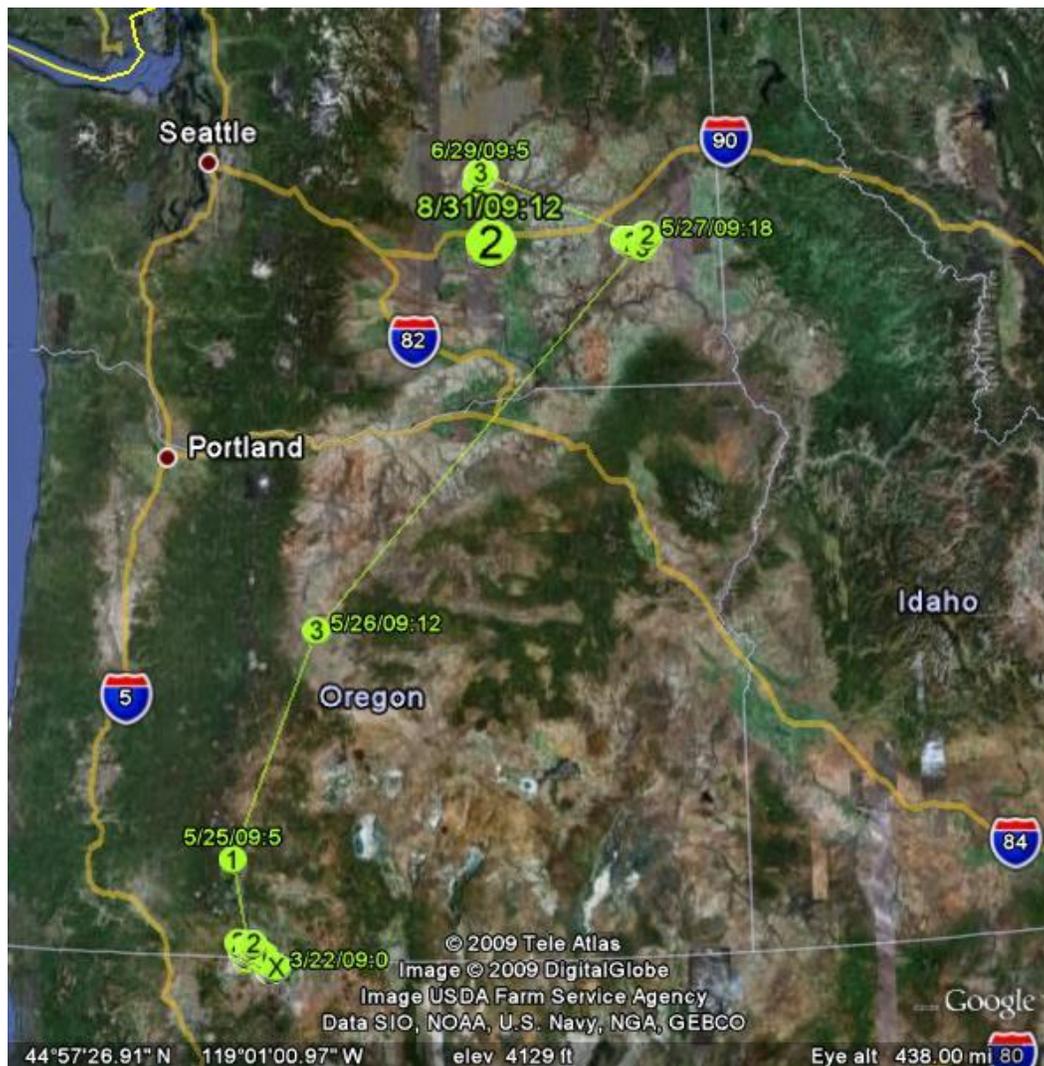


FIGURE 9. The capture site (X), non local migration (dates), and location accuracy 1, 2, and 3 show the overall migration route of a hatch year male Eurasian Wigeon.

TABLE 5. Swab results for the matrix gene qRT-PCR and the H5 gene qRT-PCR for seven males and one female from 2009-2010.

Sex	Age	matrix gene qRT-PCR	H5 or H7 gene qRT-PCR
Male*	HY	Negative	Negative
Female	HY	Present	Negative
Male	ASY	Negative	Negative
Male	ASY	Negative	Negative
Male	ASY	Negative	Negative
Male	ASY	Negative	Negative
Male	ASY	Negative	Negative
Male	ASY	Negative	Negative

* indicates the Eurasian Wigeon equipped with a PTT.

CHAPTER IV

DISCUSSION

Habitat utilization by Eurasian and American Wigeon was essentially the same. Only the percent time spent in locomotion and on vigilance was different between wigeon species. The aggression and nearest neighbor patterns suggested competition between wigeon species; both species showed selective aggressive patterns. Paired wigeon spent more time feeding than unpaired wigeon, adding support for pair dominance in waterfowl. In addition, I tagged male a second year Eurasian Wigeon with a PTT, and it migrated to Central Washington and died. H5N1 was absent from the 8 individual Eurasian Wigeon samples I screened. Banding records of Eurasian Wigeon indicate a pattern of winter philopatry.

Habitat Utilization

For each wigeon species, MANOVA results showed a significant difference in the proportions of time spent on behaviors for each independent variable: species, social status, location, month, and timeslot. There is statistical evidence that the proportion of time spent on behaviors is distinct for all independent variables examined. However, it is important to note that only the general pattern for behaviors was different.

The results from the two-way interactions show that interactions between location, timeslot, month, and social status differed significantly. However, all

interactions that contain the “species” variable were insignificant. Therefore, these results suggest that American and Eurasian Wigeon are for the most part ecologically equivalent. These results also suggest that the two wigeon species are not partitioning niches as would be expected by Gause’s principle of competitive exclusion. This principle predicts that two species occupying the same niche cannot coexist indefinitely; rather, one of the competitors will have a slight advantage over the other which will lead to the extinction or to an evolutionary change by the inferior competitor into a different niche. Currently these wigeon species are coexisting and utilizing the same habitats. The hypothesis that there is a measurable difference in habitat use by the two wigeon species is therefore not supported.

This is not to say that the two wigeon species utilized their habitats in exactly the same manner. Between the wigeon species, only the proportion of time spent in locomotion and vigilance were significantly different from each other. Eurasian Wigeon spent significantly more time in locomotion ($P < .001$) and in vigilance activities ($P = .021$). I attribute the increase in locomotion to unpaired males of Eurasian Wigeon searching for unpaired females. It is difficult to determine why Eurasian Wigeon were more vigilant because the difference between the two species was only 0.2%. Finding such a statistical difference is attributed to the high power that the large sample size gives. Though the difference is significant it appears to be trivial.

Previous studies, although few, have looked at and isolated inter and intraspecific differences in the proportion of time spent on various behaviors. Mallards and American Wigeon spend different amounts of time feeding and resting (Turnbull and Baldassarre 1987). Mallards rest 39-54% of the time, compared to 20-30% for American Wigeon. On the other hand, American Wigeon fed for 45-71% of the time compared to figures of 10-50% for

Mallards. Both feeding and resting accounted for a large proportion of American and Eurasian Wigeon time budgets, but no significant differences in the time allocated for these behaviors were found. This is likely due to their close phylogenetic relationship, and also to their similar morphologies (Bellrose 1980). As a result, they appear to have similar niche space.

Consistent with results showing that the two wigeon species are utilizing their habitats similarly, nearest neighbor and aggression data suggest that they are in competition with one another. Previous studies have examined food availability, foraging strategies, and physical space to demonstrate interspecific competition (White and James 1978, Nudds 1983, McKight and Hepp 1998), whereas I used a nearest neighbor and aggression patterns. It is logical that species aggression patterns should be equal to nearest neighbor patterns if aggression is not discriminative based on species. Therefore, I chose to examine aggression and nearest neighbor patterns to determine whether aggression is asymmetric. I found an asymmetric aggression pattern in both American and Eurasian Wigeon suggesting interspecific competition.

American Wigeon were found to be more aggressive towards other American Wigeon, while their aggression towards Eurasian Wigeon was less than expected ($P = .01$). Aggressive behaviors towards American Wigeon can be explained by conspecific competition. Male to male competition during courtship was observed consistently throughout the study. Courtship and aggression for American Wigeon followed the same general patterns. Aggression and courtship peaked in November with a subsequent decrease by month. When males were competing for females, male to male aggression was observed on a regular basis. Conversely, over twice the expected aggressive behaviors by Eurasian

Wigeon were directed toward American Wigeon. Morphological differences between species do not explain this pattern, as Eurasian Wigeon are slightly smaller. Data suggests that Eurasian Wigeon are highly intolerant of American Wigeon, whereas the reverse does not seem to be the case. These findings hint at a possible mechanism facilitating the biological invasion of Eurasian Wigeon into North America. With instigators of aggressive behaviors often winning fights, Eurasian Wigeon could be gaining access to better resting and feeding areas. This study is the first to quantify behavioral interactions between these two wigeons. In all, these results support a hypothesis of competition between wigeon species.

The proportion of time spent resting, courting, preening, in locomotion, being vigilant, and being aggressive for wigeon changed significantly by month ($P < .001$). The proportions of time spent in locomotion, resting, and courtship decreased from November through February, while foraging time increased during this time period. These data are consistent with previous time budget or energetic studies of waterfowl (Paulus 1984, Miller 1985, Turnbull and Baldassarre 1987, Bergan et al. 1989, Miller and Newton 1999). The energetic demands of waterfowl best explain the decrease in the proportion of time spent in locomotion, resting, and courtship. Energetic demands play a large role in the behaviors of wintering waterfowl. These demands have been shown to affect waterfowl activity patterns based on food availability and temperature (Hickey 1980, Albright 1981). The most energetic costly activities waterfowl perform during the fall-winter are courtship, locomotion, and homeostasis. Courtship is extremely costly, as fighting, courtship flights, and other displays all consume energy yet yield no energetic return (Paulus 1983, Hepp and Hair 1984, Jorde et al. 1984, Miller and Newton 1999). Energetically costly behaviors associated with courtship are outweighed by the benefits of feeding efficiency, dominance

(win fights) over unpaired individuals (Ashcroft 1976, Jorde et al. 1983, Paulus 1983), and ultimately, increased fitness. Conversely, resting is a low energy activity. As temperatures decline, homeostatic maintenance demands more energy (Miller 1986b). This increased energetic demand results in an increase in time allocated to feeding, with a subsequent decrease in time spent in resting, courtship, and engaged in locomotory activities.

A chronological increase in time spent feeding by month has been documented for a number of species including Eurasian Wigeon in Great Britain (Owen and Thomas 1979). Owen and Thomas (1979) found that Eurasian Wigeon increased the percent of their time feeding resulting in a peak in February. Another study comparing Mallards and American Wigeon in Alabama found that although the foraging activities of Mallards increased from November to February, American Wigeon feeding did not increase by month (Turnbull and Baldassarre 1987). These authors suggested wigeon could not meet the metabolic demands of cold wintering months by simply increasing foraging rates; rather, wigeon always incorporated feeding as a large proportion of their time budgets. Turnbull and Baldassarre (1987) suggest that American Wigeon rely upon endogenous fat reserves to use as extra calories during extreme cold much as do other waterfowl (Raveling 1979). My results suggested that wigeon increased feeding rates from December through February, in order to accommodate higher metabolic needs for maintenance. In addition, by increasing feeding rates, the resulting increase in endogenous fat reserves used during migration to nesting areas can increase their overall reproductive fitness.

As suggested by Turnbull and Baldassarre (1987), further examination of lipid content of waterfowl and activity patterns of different waterfowl based on geographic region warrant investigation. The formation of ice over wetland habitats for a long period of time is

rare in the Sacramento Valley, whereas in other parts of North America, food resources might be unavailable for long periods of time (Jorde et al. 1983, Baldassarre and Bolen 1984). In these cases, birds must rely on fat reserves. During my study, some ponds were partially but never entirely frozen. As a result, wigeon were seen foraging each day.

The proportions of time spent on resting, feeding, locomotion, and vigilance activities differed between paired and unpaired wigeon. Unpaired individuals spent significantly more time resting, in locomotion, and in vigilance, while paired individuals spent more time feeding. These results are consistent with the benefits of pairing (Ashcroft 1976, Jorde et al. 1983, Paulus 1983), and are in support of the dominance hierarchy hypothesis.

Populations of wigeon require large quantities of food to support energetic demands of courtship and pair formation (Miller 1986a), body mass gain during the fall and winter (Miller 1986b), and other important activities. Time budgets should reflect the significance of these energetically costly activities. Dominance allows paired individuals to forage for a longer period of time in prime foraging locations. This hierarchy would likely result in unpaired individuals having to spend more time and energy locating food resources through locomotion. In addition, unpaired individuals must actively search in order to find and participate in courtship groups.

The proportion of time spent on behaviors differed by time of day, with the exception of feeding. Resting increased as the day progressed, while courtship and locomotion activities decreased. Courtship activities peaked during the early morning, as wigeon were likely feeding nocturnally in neighboring rice fields. Male wigeon were actively searching for courtship groups by swimming rapidly and calling in the early morning.

Searching for social groups contributed to the increase in locomotion during the early part of the day. As the day progressed, wigeon conserved energy by resting. This explains the decrease in courtship and locomotion.

The hypothesis that different wetland management strategies affect habitat utilization by wigeon was supported ($P < .05$). The three management strategies utilized on survey ponds were a mosaic seasonal wetland (pond 14), an open water seasonal wetland (pond 12), and a semi-permanent to permanent wetland (pond 13). Though no quantitative measurements of food availability were taken, it seems likely that these results reflected differences in habitat preference. I would predict that relative caloric availability would be higher in ponds 14 and 12 because of food availability. These ponds are moist soil plots known to provide quality food resources such as pricklegrasses, watergrass, and smartweeds. These habitats provide ideal feeding depths of 20-25 centimeters. Historically, pond 13 was a permanent marsh, known to provide relatively low quality food resources, with a water depth of 0.6-1.0 meters. Therefore, food availability and accessibility may have been important factors explaining the use of ponds 12 and 14 by wigeon.

In pond 13, wigeon spent twice the time engaged in locomotion than in other ponds. As the time allocated to courtship was nearly the same for all ponds, this increased locomotion in pond 13 was likely related to food searching. Wigeon were regularly seen swimming with their heads looking down and occasionally stopping to dabble or surface feed. The behavior of swimming for a long period of time followed by a short feeding period was only seen in pond 13. In the other ponds, birds were observed feeding in one area for large portions of time. This suggests that these ponds had higher concentrations of food and required less locomotion.

Wintering waterfowl in the Sacramento Valley rely heavily upon rice resources. Each morning, birds were seen flying back to the refuge from flooded rice fields. No Eurasian Wigeon were observed feeding in rice fields; whereas many American Wigeon were observed foraging in these habitats. As it is unlikely that Eurasian Wigeon avoid these habitats, I attribute this to birds avoiding the roads and vehicle traffic, resulting in long distance scanning of fields during low light.

Migration and H5N1

Only limited conclusions can be made from the migration study. The Klamath Basin is a possible staging or wintering area for at least some migrating Eurasian Wigeon. Banding data and personal observations are consistent with this conclusion, as several Eurasian Wigeon were observed during capture attempts in 2009 and 2010; many were banded in this region. These findings are consistent with many bird species that use the SONEC (south-central Oregon, northwestern Nevada, and northeastern California) as a spring migration stopover point (Miller 2005). It is likely that the bird equipped with the PTT was a fall-winter resident of the Central Valley, using the Klamath Basin as a staging area.

Band recovery data provided evidence of winter philopatry in Eurasian Wigeon. Philopatry is generally discussed in terms of females returning to successful natal or breeding grounds, although it has also been documented for wintering waterfowl returning to the same wintering grounds (Greenwood 1980, Robertson and Cooke 1999). Winter philopatry is evidenced by similar capture and recovery sites (Fig. 10). Eurasian Wigeon banded in the Klamath Basin during the spring were recovered in the Sacramento Valley during a subsequent fall-winter.

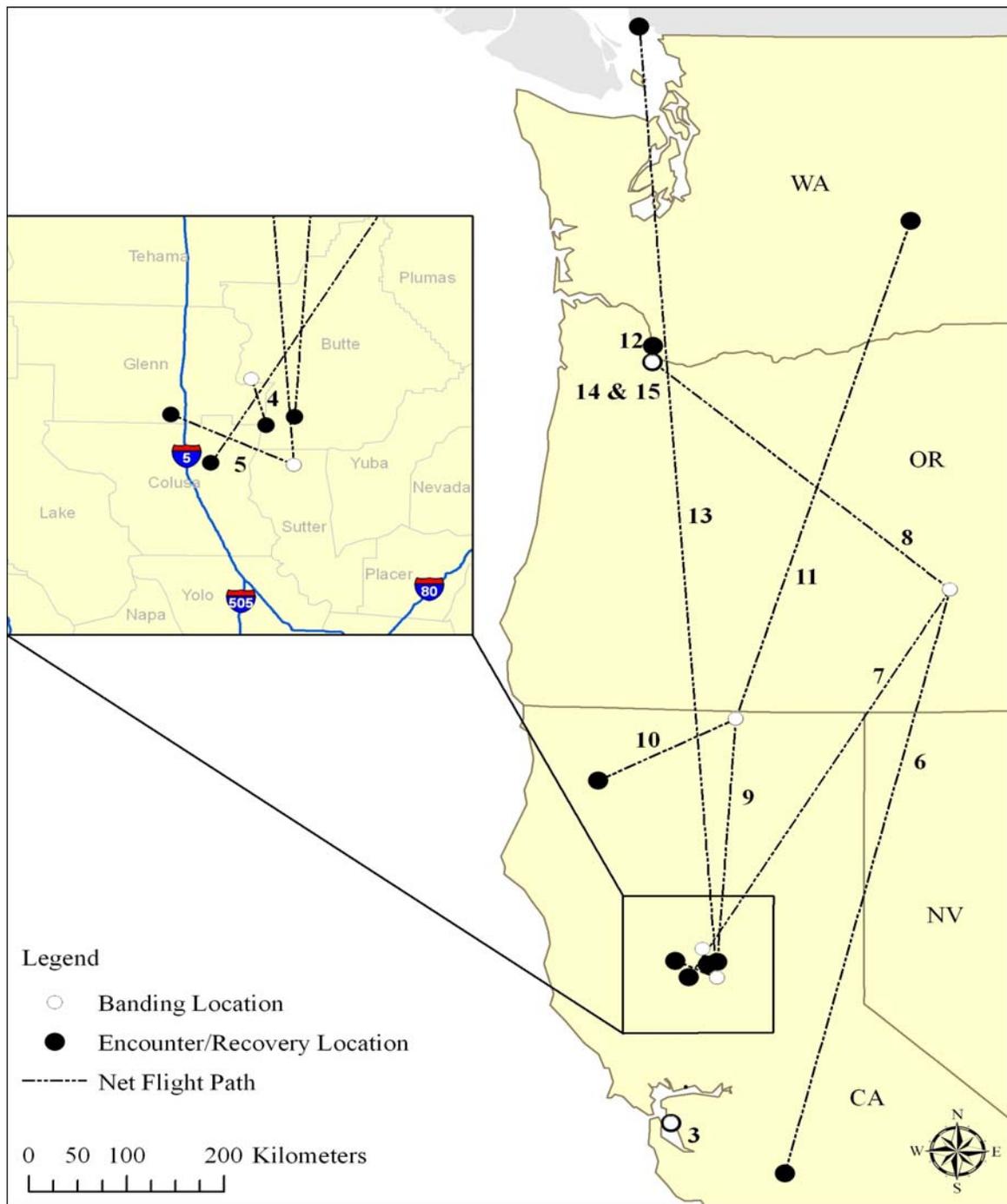


FIGURE 10. Pacific Flyway banding and recovery/encounter locations for all Eurasian Wigeon banded from 1929-2010 (USGS Bird Banding Lab 2010). Bird 11 is the one Eurasian Wigeon I captured and equipped with a PTT.

The tagged bird had a prolonged stay in the SONEC, as aerial surveys at the time estimated wigeon populations to be only about 500 birds. This suggests that most other ducks had already departed for the north. One possible explanation for this prolonged stay could have been this bird's physiological condition. Dugger (1997) suggested that an individual's physiological conditions can affect migration departures, although in his study with radio-tagged mallards, he suggested that migration departures are independent of physiological condition. Also, Miller (2005) found that Northern Pintails of smaller mass tend to migrate later than larger-massed birds. As this male was a low mass immature bird, this could explain the late departure.

The activity count readings in early October remained constant, had low temperatures, and the PTT was still charging. These data are suggestive of mortality. Location data led searchers to a rocky slope adjacent to a wetland, a known area where Peregrine Falcons (*Falco peregrinus*) consume freshly caught ducks. The search effort for the PTT and the bird were ultimately unsuccessful. I concluded that the bird had died.

This study demonstrated the potential value of PTTs for determining migration routes, although having multiple transmitted wigeon should remain a goal for the future. Ideally, future studies would include adult birds, due to their experience in migration and larger body size, enabling them to better deal with stress. Other studies have found that PTTs can present extra stress (capture, handling, extra weight, and bulk of PTT) to an individual, which may lead to a premature death (Miller 1995). In addition to the migration patterns of Eurasian Wigeon, the hypothesis that Eurasian Wigeon are potential carriers of the H5N1 virus was examined. All samples collected were negative for H5N1; there have been no wild wigeon ever found to be positive for H5 or H7 gene qRT-PCR (Pearce et al. 2005). In all,

swabbing produced no evidence that Eurasian Wigeon are serving as carriers of the H5N1 virus. Efforts to continue to swab captured or harvested Eurasian Wigeon should remain a priority, as they have been clearly shown to harbor the virus (Keawcharoen et al. 2008).

Summary

Time budgets of American and Eurasian Wigeon revealed that there were few significant differences between wigeon species, suggesting they are ecologically similar. Nearest neighbor and aggression patterns revealed Eurasian Wigeon are more aggressive towards American Wigeon than the reverse: this indicates asymmetric levels of aggression which is suggestive of interspecific competition. Management strategies for moist soil impoundments and seasonally flooded marshes should continue to be employed in order to promote healthy wintering populations of wigeon, as they promote feeding and resting for wintering birds. Resting was a major component of wigeon time budgets for all months. Resting is clearly an important behavior for wigeon and other waterfowl as illustrated by the overall contribution to time budgets (Jorde et al. 1984, Miller 1985a). Therefore, providing loafing sites in managed wetland is essential.

Despite the limitations of the PTT study, general migration routes were determined for an immature male, and implications of H5N1 were addressed. The PTT study was successful in tracking an individual, but more transmitted birds are needed to investigate the possibility of a trans-hemispheric movement of H5N1, or in order to finding possible Nearctic Eurasian Wigeon nesting sites. In addition, evidence from band and recapture data suggest that at least some Eurasian Wigeon are philopatric and return to the Pacific Flyway.

Future studies of Eurasian Wigeon would include a more detailed and thorough examination of migratory routes for both species using PTTs. Many more transmitted Eurasian Wigeon would be necessary in order to determine migratory routes or possible breeding areas. A larger sample size would ensure a more comprehensive model of migration routes and destinations. Evidence of ecological equivalence among the wigeon and Eurasian Wigeon being overly aggressive towards American Wigeon may be facilitating Eurasian Wigeon in the Nearctic. A better understanding of the importance and extent of interspecific competition between Eurasian and American Wigeon must be addressed. Expanding efforts to swab Eurasian Wigeon at all hunter check stations is important in order to monitor possible H5N1 outbreaks.

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LITERATURE CITED

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