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Habitat Use and Distribution Implications of Four Goose Species Wintering in California's Sacramento Valley

By

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ABSTRACT

Competition is one of the most important biotic interactions influencing animal communities and species distributions. In the Central Valley of California, several species of waterfowl compete for space and food during winter. Goose populations are increasing in California and the Pacific Flyway and are now at levels well above population targets. The growing numbers of geese may have negative impacts on smaller-bodied members of the *Anatidae* family. To evaluate the potential of this growing conflict, we used high frequency GPS-GSM telemetry to track 211 individuals of four species of geese: the Lesser Snow goose (*Anser caerulescens caerulescens*), Ross's goose (*Anser rossii*), Pacific White-fronted goose (*Anser albifrons sponsa*), and Tule White-fronted Goose (*Anser albifrons elgasi; hereafter referred to as Tule goose*) across the Sacramento Valley (the northern portion of the Central Valley) of California. Using step selection analyses, we modeled how field type, photo period (day or night), habitat condition (wet or dry) and age of those habitat conditions impact goose use and habitat selection. All species showed a strong preference for wet rice habitat at night, but daytime preferences varied. Lesser Snow and Pacific White-fronted geese were most similar, selecting wet fallow and dry rice habitats over wet rice and dry fallow during the day. Conversely, California species of concern, Tule geese, strongly preferred wetlands while Ross's geese preferred dry rice, followed by wet and dry fallow habitats. Habitat age was important and the preference for wet rice and wetlands decreased over time, while selection of dry rice and wet fallow generally increased with age. Due to agricultural flood regimes, wet rice habitats likely offer substantial quantities of nutrient dense food resources to arriving migratory birds. However, over time, heavy consumption and decomposition caused by water cover reduces the

attractiveness of this habitat, coinciding with the period which birds often switch to green browsing in other habitats.

INTRODUCTION

Competition is one of the most important biotic interactions that influences communities and species distributions. Species typically occupy specific ecological niches (Bethke, 1991; Gause, 1934) and when communities of animals co-occur within an ecosystem, species (or taxa) often partition resources to reduce competition*,* a process called niche differentiation or partitioning, which allows species to coexist through differential exploitation of environmental resources (Cloyed & Eason, 2017). Millions of ducks and geese arrive in the Sacramento Valley of California in the fall (late August through November; Gilmer et al., 1982), after a lengthy migration from distant breeding grounds in Alaska, Canada, and Russia (Pacific Flyway Council, 2006, 2013; USFWS, 2019). Brought to the Valley for the intrinsic value of the landscape, the different waterfowl species often face the challenge of biotic interaction adding competitive pressure, for the same resource.

The Central Valley is one of the most productive agricultural regions in the USA with the Sacramento Valley (the northern portion of the Central Valley) responsible for some of the highest rice yields in the world (van Groenigen et al., 2003). With its Mediterranean climate that is arid in summer and most precipitation falling during winter (Polade et al., 2017), conditions are beneficial to waterfowl, offering substantial habitat and food resources. As a result, the region also supports one of the largest concentrations of wintering waterfowl in the world (Petrie et al., 2016). Over the last century, important natural wetlands have been

impacted by expansion of agricultural and other human development. It is estimated that only 10% of the historic wetlands in the Central Valley now remain (Fleskes et al., 2018; Gilmer et al., 1982). Privately owned land comprises approximately two-thirds of the suitable waterfowl habitat in the Central Valley (Central Valley Joint Venture, 2006) with rice crops accounting for a large percent of the valley's agricultural land use (Fleskes et al., 2018). While agricultural development has replaced vast amounts of natural habitat (including wetlands, riparian, and grassland habitat), the waste grain left behind after rice fields have been harvested (typically September to October; Halstead et al., 2011), has become an important food source for waterfowl (Gilmer et al., 1982). Traditionally, burning was the primary method to remove the remaining rice stubble post-harvest. However, burn restrictions implemented in 1991 (taking effect in 1992), radically shifted post-harvest treatments away from rice stubble burning, to flooding, to enhance straw decomposition, and field plowing (Miller et al., 2010). Miller (2010) reported 40% of 888 surveyed plots were burned in a 1986 assessment of post-harvest field treatments; this number was reduced to just 1% by 2007. Conversely, flooding and plowing post-harvest treatments increased from 16% and 22% respectively in 1986 and 43% and 42% by 2007 (Miller et al., 2010). The augmented flooded rice fields provided beneficial habitat for wintering waterfowl, with significantly greater use by waterfowl when compared to nonflooded fields (Elphick & Oring, 1998). While this shift in post-harvest treatment of rice has supported waterfowl in lieu of historic natural habitat, many duck populations remain below the long-term average (USFWS, 2019).

The Sacramento Valley harbors the largest goose populations in the Pacific flyway, dominated by Lesser Snow geese (*Anser caerulescens caerulescens*) and Ross's geese (*Anser*

rossii) (hereafter collectively referred to as white geese) and Pacific White-fronted geese (*Anser albifrons sponsa*), a subspecies of Greater White-fronted Geese (*A. albifrons*). White goose populations in particular have demonstrated prolific population increases, and California wintering populations are estimated to have more than doubled since 1977 (Pacific Flyway Council, 2013, 2019, 2020, 2021). This explosive population growth is likely to have implications for food availability for other waterfowl that share the same wintering habitat in the Sacramento Valley because white geese consume more food per individual than any of the duck species (Central Valley Joint Venture, 2006). Geese exploit both flooded and non-flooded habitats for food resources (Skalos et al., 2021). Although some researchers note greater utilization of dry fields (Elphick & Oring, 1998), if geese fulfill their food requirements from flooded habitats, this may put them in direct competition with dabbling ducks that preferentially select flooded habitat (Central Valley Joint Venture, 2006; Petrie et al., 2016). With drought frequency and severity increasing and water, as a result, becoming scarcer (Diffenbaugh et al., 2015), some rice fields now remain dry the entire winter. Without the intentional application of water on rice fields, these fields remain unavailable for ducks until winter rains provide enough water accumulation (Fig. 1). These seasonal rains often do not occur with any significance until later in the winter (December – February; www.cnrfc.noaa.gov). However, by that point, geese have likely foraged those fields, resulting in less available food for ducks.

Figure 1: Average proportion of rice fields remaining dry, without flooding due to agricultural treatments or rainfall, beginning September 1 and assessed 2018-2021 (USGS, unpub. data).

Many biotic and abiotic variables can influence waterfowl habitat selection. In a dynamic environment, the landscape changes in response to urbanization, increased establishment of high-value agriculture types (e.g., nut and fruit orchards, which replace waterfowl-friendly crops such as rice) and extreme drought conditions, which have affected California for more than a decade (Mann & Gleick, 2015; Sleeter, 2008; Soulard & Wilson, 2015). Habitat fragmentation and increasing water scarcity are causing the contraction of habitat (Saunders et al., 1999; Soulard & Wilson, 2015) with smaller habitat areas that often offer little to no value for waterfowl (Xu et al., 2019). When competing taxa are forced to

occupy the same habitat niche and resources are limited, one taxon would ultimately be driven to extinction or at least local extirpation (Hardin, 1960). Waterfowl management aims to ensure the provision of sufficient food resources for all waterfowl species over the wintering months. Therefore, as environment resources become increasingly depleted, it is important to understand the spatio-temporal habitat use patterns of different species and the factors that influence habitat preferences, which can be determined by habitat type, food and water availability, and proximity to disturbance and various other factors (Kahara et al., 2022).

The objective of this study was to obtain a better understanding of the distributions of geese throughout the Sacramento Valley and assess habitat-use by geese in this important wintering area. Using high resolution GPS tracking data and satellite imagery, we aimed to identify the habitats most frequently exploited by four different species of geese and to identify specific biotic and abiotic factors that influence habitat selection. Finally, since waterfowl are known to undertake different activities at night and during the day, we also wanted to understand if and how habitat use varied between day and night, which may offer further insight into whether and how frequently geese and ducks are in direct competition for food resources.

METHODS

Study Area

Migratory geese cover large expanses of area annually between their breeding and wintering grounds. For this study, we focused on the main wintering area in California: the Sacramento Valley. We focus on the Sacramento Valley to examine the distribution and habitat

use of the increasing goose populations and to determine how these changes may affect resource competition with other waterfowl in this high-density wintering area. The boundary of our study area was defined by the Central Valley Joint Venture's watershed basin planning subregions (Central Valley Joint Venture, 2006) including: American, Butte, Colusa, Suisun, Sutter, and Yolo basins (Fig. 2). We captured individuals of four species of goose: Lesser Snow geese, Ross's geese, and two subspecies of Greater White-fronted geese: Pacific White-fronted geese and Tule White-fronted geese *(A.a. elgasi*), which are a California species of special concern. We captured birds between February 2018 and February 2021 on wintering grounds, a stopover site, and summer Arctic breeding grounds. Winter capture locations include Sacramento National Wildlife Refuge Complex, CA (39°23' N, 122° 9' W); Upper Butte Basin Wildlife Area (39°28' N, 121°53'W) and Gray Lodge Wildlife Area, CA (39°18' N, 121°49' W). The Tule goose was the only species captured at a stopover site: Summer Lake Wildlife Area, OR (42° 57' N, 120° 45' W). Arctic breeding ground capture locations included Snow geese only and occurred at Colville River Delta, AK (70° 23' N, 150° 50' W); Ikpikpuk River Delta, AK (70° 48' N, 154° 24' W); Banks Island, Canada (72° N, 123° W); and Wrangel Island, Russia (71° 2' N, 179° 48' E).

Figure 2: Study area of the Sacramento Valley of California defined by CVJV watershed basins including prominent wildlife refuges and habitat type distribution based on USDA's CropScape cropland data layer condensed into fallow, rice, wetlands, and other.

Capture and Transmitter Attachment

Geese were captured during fall and winter in California and Oregon with rocket nets, while Arctic geese were captured on breeding grounds during molt drives using a helicopter to herd the flightless birds into a catch pen. In any given capture event, we only marked adult males or adult females with GPS transmitters to avoid marking a bonded pair. Geese were collared with solar-powered Ornitela® (Ornitela, Vilnius, Lithuania) GPS-GSM neck collars (~5m accuracy) appropriate to body size. Larger Snow geese and male Tule geese were marked with Ornitrack-N38 collars (inner diameter 38 mm, outer measurements 46-61 mm, height 47 mm; 3 solar panels) while smaller Snow geese, Pacific White-fronted geese, female Tule geese, and Ross's geese received Ornitrack-N35 collars (inner diameter 35 mm, outer measurements 41-56 mm, height 46 mm; 2 solar panels). Transmitters were programmed to acquire GPS fixes every 15-minutes and transmit location (latitude/longitude) and date-time data via the cellular network every 24-hours when in range. When out of cellular range, GPS collars stored data onboard and backfilled to servers when back in range. We recorded the age and sex of every captured individual and measured culmen length (mm), short tarsus length (mm), flattened wing length (mm), and mass (g). To differentiate between the closely related Tule and Pacific White-fronted goose subspecies, we also measured bill width (mm) and bill height (mm) which we referenced against a discriminant function described by Orthmeyer et al., (1995) that distinguishes between Tule and Pacific White-fronted geese.

Each bird was banded with an individually numbered aluminum leg band issued by the U.S Geological Survey Bird Banding Lab. All banding operations, handling, and transmitter placement were performed under federal banding permit # 21142, and California state permit

#SC-8090. All research was approved by the U.S. Geological Survey Western Ecological Research Center Animal Care and Use Committee.

Data attributes and Identification of Habitat Choice

The goal of this study was to assess habitat use on the wintering grounds in the Sacramento Valley of California. We restricted all data spatially to the study area described in figure 2, and temporally between September to April, spanning 3 "winter seasons" to reflect the timeframe that the geese occupied the region. These winter seasons began September 1 and ended on April 1 of the following year during 2018-2021. We attributed each GPS location with local time and time of sunrise and sunset to determine whether it occurred during day or night. We also identified the individual field containing each point using a parcel boundary layer derived from LandIQ and Department of Water Resources, 2014 in ArcGIS® 10.5 for desktop, ArcMap™ software (Esri, Redlands, CA, USA). We supplemented this layer with refined fieldlevel maps for public wildlife areas including Sacramento, Sacramento River, Delevan, Colusa (National Wildlife Refuge) and Upper Butte Basin Wildlife Area. Additional areas were manually digitized to include unmapped regions containing concentrations of bird locations.

We nearly eliminated spatial and temporal autocorrelation among analyzed data by focusing on demonstrated selection of habitats, when birds moved among patches. Intrinsically, geese do not spend equal amounts of time doing different behaviors (e.g., roosting and foraging). Since we know that waterfowl behavior is strongly influenced by daily activity patterns and movements, we expect to see disproportionate amounts of time and consequently a more disproportionate number of locations in certain habitats (Paulus, 1988).

Thus, we were able to eliminate these discrepancies associated with a time-based approach by using models that provide equal choice of all available habitats and found an event-based selection approach to be more appropriate to evaluate the importance of habitats in the Sacramento Valley. This removes serial dependence resulting from behaviors that do not reflect the process of 'selecting' habitat patches such as resting for intra-patch foraging or movements. To accomplish this, we removed any GPS locations where the bird occupied a parcel for <1 hour to account for any movements that may have been disturbance or active flight related, rather than a selection of habitat (McDuie et al., 2021). Selection events were identified by any movement of >500m or movement into a parcel that was non-adjacent to the parcel at the origin of the movement. The stipulation that shorter movements had to be into non-adjacent parcels is because birds often roost on levees that serve as the boundaries between two parcels resulting in locations that frequently switched among adjacent parcels despite typically low GPS error (~5m). This also helped to remove almost all autocorrelation of our dataset as it determined the selection of any new habitat patch and not the probability of being in any given habitat.

Habitat Type and Water Availability

Land cover was evaluated using the USDA National Agricultural Statistic Service's CropScape cropland data layer (https://nassgeodata.gmu.edu/CropScape). A raster of crop types was downloaded for 2018, 2019, and 2020 and overlaid on the parcel boundary layer to then classify each pixel (30m2) within a parcel as a specific crop type, using the '*exactextractr'* and '*sf*' packages (Baston et al., 2021; Pebesma et al., 2022) in R (V3.5.1, R Core Team, 2021). We determined land cover by applying a majority filter described by Kim (1996) to the NASS

CropScape data for each parcel. This indicates the most common land cover present within the boundary which we interpreted as the land cover or crop type. Each parcel was classified according to the dominant crop type. Parcels in CropScape were categorized into 75 specific crop types found within our study area. For the purpose of our study, we condensed these crop types into four broader categories based on their ecological significance to waterfowl: rice, wetland, fallow, and "other" (SI Table 1, 2). The "fallow" category described any parcel that was bare soil, low grass (pasture) or cover crops including alfalfa, clover, and vetch due to their likeness to pasture. The "other" category spanned a wide range of crop classifications, that comprised 32% (Fig. 3) of total land in the valley but <1% of use by our geese (SI Table 5).

Figure 3: Proportion of California's Sacramento Valley study area covered by six different habitat types, assessed in a GPS tracking study of four species of geese, conducted between September 1 and April 2018-21. Use by geese of the first 5 habitats (wet rice, dry rice, wetlands, wet fallow, and dry fallow) was assessed with step selection function models. The 'other' habitat had very little use and was excluded from models.

Shallow flooded habitats are highly important to waterfowl, providing both food resources and secure roosting sites. We determined habitat flooding on parcels using satellite imagery processed through Google Earth Engine's data analysis platform (Gorelick et al., 2017) to classify each parcel as wet or dry. Satellite data combined surface reflectance corrected images from Sentiel-2, Landsat 7 and Landsat 8 with clouds masked out from Landsat images and clouds, cloud shadow, and saturated pixels masked out from Sentinel images (Principe (undated) geetools GitHub Repository v 0.2.0, https://github.com/fitoprincipe/ geetools-codeeditor). The modified normalized difference water index (MNDWI) was calculated from each pixel within each cloud-masked satellite image. MNDWI was summarized for each parcel to produce an object-based classification for entire parcels rather than a pixel-based classification of raw satellite imagery. MNDWI values greater than 0 indicated water was visible for a pixel while values less than 0 indicate the pixel was dry or obscured (e.g., by vegetation). Since emergent vegetation can conceal large extents of some habitat types, "flooded" conditions were indicated when 10% or more of a parcel indicated visible water (USGS, *Unpub. data*). This resulted in accurate classification of both wetland and agricultural field winter flooding condition despite each habitat type having different vegetation structure and composition (USGS, *Unpub. data*). Sequences of images allowed us to identify specific dates when the status changed from wet to dry, or vice versa, to quantify the duration ('habitat age') of a parcel's wet or dry status. The Sentinel satellite captures imagery of our study area every 5 days. Each Landsat satellite provides data every 16 days. Combined, cloud-masked images from all three satellites provided a habitat assessment for each parcel every 3.8 days between 2018 and 2021. We also evaluated whether dynamic habitat condition was more accurately assigned using a

rolling median of image conditions which could reduce errors associated with individual images that may have poorly resolved cloud cover conditions or other atmospheric interference such as dense smoke. To do this, we surveyed 107 randomly selected fields within the project area along a route that included both wetland and agricultural habitats. To ensure accuracy of these data, we ground-truthed moisture and crop classifications with physical surveys throughout the winter of 2020-2021 (October – February) on the same days that the satellite was scheduled to capture imagery. We compared these physical field data to the satellite imagery to validate the output accuracy of our wet/dry classifications (Fig. 4). We used the rolling median to compare outputs as it produced greater accuracy (98%) than by individual images (94.7%; USGS, *Unpub*

Figure 4: Map of Sacramento Valley, California showing the average flood conditions over the duration of a GPS tracking study of four species of geese throughout the winter months September 1 to April 1 2018-21.

data).

Step-selection Models

For each relocation event (step) an individual made into a new habitat patch, 100 randomly oriented replicate locations were generated from the same origin. The distances of replicates from each actual GPS location (hereafter referred to as "used"), were randomly sampled from the step lengths produced by every individual's movement into new patches that we observed in this study. These reflected available habitat and were annotated with the same information as the observed movements including land cover type and flooded status of the parcel in which the location fell.

We created our step-selection using the conditional Poisson methods of Muff et al., (2020) which allow incorporation of random individual effects to obtain population-level inference of habitat selection patterns. Models were run using *the 'glmmTMB'* package (Brooks et al., 2017), running all analyses in R (Version 3.6.0, R Core Team, 2021). Packages used for data wrangling, interpreting results and producing summary tables included*: dplyr, lubdridate, ggplot2, sf, geosphere, readr, data.table, sjPlot, multcomp*. (Dowle et al., 2021; Hijmans et al., 2021; Hothorn et al., 2022; Lüdecke et al., 2021; Pebesma et al., 2022; Spinu et al., 2021; Wickham et al., 2021; Wickham, François, et al., 2022; Wickham, Hester, et al., 2022). The stepselection models evaluate use of categorical habitats relative to a reference level that is omitted from the model statements and produce parameter estimates for habitat types that are present in the model which reflect the logarithm of the ratio of selection for the relevant habitat and the reference class(es). These parameters are described as reflecting the "Relative Strength of Selection" (RSS) for the modelled habitat relative to the reference habitat(s) (Avgar et al., 2017; Fieberg et al., 2021). Generally, a single habitat class is chosen as a reference level,

for all models; we chose what we anticipated to be the most commonly selected habitat, – wet rice, as our reference habitat with an exception where the most general model used, which did not include flooding dynamics, used rice (both wet and dry combined) as the reference level. However, the computational difficulties of calculating both fixed and random effects occasionally resulted in non-convergence during modelling. In each case where nonconvergence resulted for models with wet rice as the reference level, the same model converged using an alternate habitat type as the reference level (SI Table 5). In these cases, we were able to use custom contrast statements and general linear hypothesis test (`*ghlt*` function from the package "*multcomp*" in R) to recalculate parameters equivalent to use of wet rice as the reference level. This enabled straightforward comparison of model results despite computational difficulties.

We developed a set of models (Table 1) for each species that was run separately for day and night to evaluate the preferences, in more detail. "Other" habitats were infrequently or never used by most individuals (SI Table 5). These habitat types are widely considered unsuitable for waterfowl, such as orchards and urban areas, or land covers with very low resource values such as deep open water habitats or row crops. Because this land cover was rarely used, parameter estimates could not be reliably calculated. Therefore, we proceeded with all modelling after excluding all used and available locations classified as "other" from the dataset and interpret the resource value for other habitats to be zero.

Our most basic "null" model included only the two remaining land cover classes relative to the reference habitat (rice) (Table 1). Our second model, "dynamic habitat model", included flooding condition for rice and fallow ground treated as a categorical habitat, resulting in four

modelled habitat classes relative to the reference habitat (wet rice: Table 1). Four models each added a linear effect to the dynamic habitat model, three assessed the proximity of a patch to a particular habitat type (orchard, urban, or known sanctuary areas occurring on public lands) as a factor affecting selection (Kahara et al., 2022; Mackell et al., 2021; McDuie et al., 2021; Newbold & Eadie, 2004). The fourth linear covariate assessed parcel size as a factor influencing habitat selection. All linear covariates were assessed additively within the dynamic habitat model (Table 1). The last set of models incorporated specific influences of the "age" of a habitat patch on selection of each habitat type (Table 1). Habitat age was modelled as an interaction with habitat type since habitats expected to provide forage resources, are often expected to provide the majority of their resource value when they are new (e.g., newly flooded rice fields) before decomposition and competition reduce the amount of food. Other habitats such as those used for roosting, are expected to be less influenced by habitat age. Since we do not know the functional relationship between the age of a habitat patch and selection patterns, we investigated linear, quadratic, and logarithmic relationships with habitat age, 2 categorical groupings of younger vs older (>30 or >60 day old) habitat patches, and linear and quadratic relationships with habitat age right truncated at 1 year (365 days) old (Table 1). This resulted in seven functional relationships of habitat age being assessed. Relative performance of each model was assessed using AIC values for each species x photo period (Burnham et al., 2011).

Table 1: Model parameters and interactions run with all 4 species x photo period (day/night) variations to calculate the AIC score for each model to determine which model best fits the data. Land cover included rice, fallow, and wetland. In models 2-13, rice and fallow were split into flooding condition (wet or dry) and termed dynamic habitat. Wetland remained wet and dry combined. Wet rice was used as the reference level (unless otherwise stated; SI Table 4).

RESULTS

Throughout the capturing and transmitter deployment portion of this study, 111 Snow geese, 40 Ross's geese, 44 Pacific White-fronted geese, and 20 Tule geese were marked between 2018 and 2021, resulting in a total of 1,936,767 GPS points within that time frame (Fig. 5, Table 2). Our cleaned dataset provided 1,798,971 GPS locations at 15-minute intervals for the four goose species. Using these points, we identified a total of 42,474 individual selection events occurred in five habitat types during our three "winter seasons".

Figure 5: Map of Sacramento Valley, California (with National Wildlife Refuges and State Wildlife Areas indicated), showing movements of four species of geese from all GPS locations acquired between September 1 and April 1 from the three years of the study (2018-21).

Table 2: data summary of the total GPS locations acquired between September 1 and April 1 (2018-21) and points we used to analyze our data and determine selection events during September 1 and April 1 (2018-21) for the 4 goose species used during our study.

	Snow	Ross's	Pacific White-	Tule
	goose	goose	fronted goose	goose
No. individuals	111	40	44	20
No. locations	951937	53520	659043	272267
No. locations analyzed	873236	49766	620197	255772
No. selection events	15908	796	21237	4533
Total points	1936767			
Total points analyzed	1798971			

Figure 6: Total number of selection events (each instance between two flights when a goose remained in a habitat for ≥ 1 hour) by hour of the day from a GPS tracking study of 4 species of geese. The study was conducted in California's Sacramento Valley between 2018-21.

Figure 7: Number of selection events (each instance between two flights when a goose remained in a habitat for ≥ 1 hour) by month from a GPS tracking study of four species of geese. The study was conducted in California's Sacramento Valley between 2018-21.

Figure 8: Number of selection events (each instance between two flights when a goose remained in a habitat for ≥ 1 hour) by day or night from a GPS tracking study of four species of geese. The study was conducted in California's Sacramento Valley between 2018-21 and, from 1,048,576 GPS locations between September 1 and April 1 each year we identified 42,474 selection events that occurred in wet rice, dry rice, wetlands, wet fallow, and dry fallow.

At night, the wet rice habitat was strongly selected, and all other habitat types were avoided by all species (Table 3, Fig. 9). By contrast, during the day, geese either demonstrated significantly weaker selection of wet rice habitats or strongly avoided them compared with nighttime selection (Table 3, Fig. 9). Moreover, daytime patterns of relative habitat selection differed among species. Pacific White-fronts and Snow geese selected wet fallow (39.3% and 36.1%, respectively), Ross's geese preferred dry rice (34.5%) and Tule geese showed a strong preference for wetlands (43.4%). The white geese (Ross's and Snow) demonstrated strong

avoidance of wet rice during the day while White-fronts (Pacific and Tule) strongly avoided dry

fallow habitat during both day and night (Table 3, Fig. 9).

Table 3: Expected relative distribution of use among equally available habitat classes during day and night by four species of geese in the Sacramento Valley of California 2018-2021.

Table 4-7: Model 7 statistical results showing just the habitat type effects at mean parcel age of four species of geese in California's Sacramento, from GPS tracking conducted 2018-21. Additional information provided by model 7 also provided an estimate of the quadratic relationship between habitat age and habitat type.

Table 4: Model 7 statistical results for Pacific White-fronted geese during the Table 5: Model 7 statistical results for Snow geese during the day & night day & night

Table 6: Model 7 statistical results for Tule geese during the day & night Table 7: Model 7 statistical results for Ross's geese during the day & night ²⁴

Dry rice was significantly selected for by Snow geese (Table 3; Table 5a), Pacific White-fronted geese (Table 3; Table 4a), and Ross's geese (Table 3; Table 7a) during the day and avoided by Tule geese (Table 3; Table 3a) while all species avoided this habitat during the night (Table 3; Table 4b-7b). All four species exhibited selection for wetland during the day (Table 3; Table 4a-7a), although only the Pacific White-fronted geese and Ross's geese did so significantly (Table 3; Table 4a, 7a). Wet rice was strongly selected by all species at night (Table 3; Table 4b-7b) while all other habitats were significantly avoided (Table 3; Table 4b-7b), except for Tule geese and Ross's geese showing non-significant avoidance of wet fallow (Table 3; Table 6b) and wetlands (Table 3; Table 7b).

Habitat Age

All species' habitat preferences were influenced by the age of the habitat, with strong overall preference for newly flooded rice. A consistently and strongly negative relationship between time and relative strength of habitat selection was evident in wet rice fields during both day and night for all species (Table 3, Fig. 9). One exception was Ross's geese which showed the weakest preference for wet rice overall, regardless of age. While this species selected wet rice more than other habitats at night, the relative strength of selection was comparatively weak (Fig. 9). During the day Ross's geese also varied from the other species, demonstrating a stronger relative selection of all habitats other than wet rice and with a substantially stronger preference for dry fallow than the other species which avoided it. Nevertheless, this relationship illustrated their similar preference for younger over older wet rice habitats (Table 3, Fig. 9). Tule geese's daytime preference for wetland habitats showed a

similar relationship to age of the habitat, with their preference weakening with time since flooding.

By contrast, preferential selection of dry rice fields during the day increased with the age of those habitats, a pattern seen across all species even though Tule geese tended to avoid this habitat. Similarly, the relative selective preference for wet fallow habitats by Snow and Pacific White-fronted geese also increased with habitat age while Ross's geese exhibited a negative relationship between selection of this habitat and time and Tule geese's weak preference did not vary with time.

Figure 9: Relative selection of five habitat types by four species of geese in California's Sacramento Valley from a GPS tracking study conducted between September 1 and April 1 from the three years of the study (2018-21). GPS data (from selection events only) were modeled with step selection function models which modeled species, habitat and habitat age for wet rice, dry rice, wetlands, wet fallow and dry fallow and the best model results (Model 7) are presented.

DISCUSSION

Understanding habitat use and selection by goose populations in California's Sacramento Valley will contribute toward improving land management and conservation strategies across this large and important wintering habitat for Pacific Flyway waterfowl. Patterns of habitat use varied significantly between day and night for all goose species, varied according to habitat age and demonstrated some interspecific divergence. All four species exhibited strong selective preference for wet rice at night (though not all RSS values were significant; Table 4-7), avoiding all other habitats, while daytime habitat preferences differed more among the species, with relative selection favoring other habitats such as wetlands, dry rice, and wet and dry fallow.

The importance of wet rice habitats for geese at night has several possible explanations. First, geese generally feed during the day, making crepuscular foraging flights before and after roosting for the night (Ackerman et al., 2010; Ely, 1990, 1992; Krapu et al., 1995). The strong selection of wet rice at night is likely explained by this crepuscular foraging activity, leading into a period of rest in the same or similar area. However, foraging may not be exclusively tied to these periods and geese could also take advantage of additional foraging opportunities during the night to supplement their energetic needs (Lameris et al., 2021; McNeil et al., 1992). Geese may be utilizing wet habitats that provide advantageous roosting situations, offering greater protection from predators at night (McNeil et al., 1992; McWilliams et al., 1994). Another possibility is, this pattern may be partially attributable to disturbance from hunting pressure. During winter, the commencement of the annual waterfowl hunting season coincides with the arrival of many of the migratory geese and continues until early February. Although we were

not able to directly quantify these effects in our study, hunting activity during daylight hours substantially disturbs ducks causing changes to movement and habitat use (Elphick & Taft, 2010; Madsen & Fox, 1995; McDuie et al., 2021). Disturbance from preferred habitats may drive geese to delay roost-forage movements until hunting activity has ceased and may also have contributed to the wider variation in daytime selected habitats for all species (McDuie et al., 2021).

The preference revealed for other habitats (wet fallow, dry rice and dry fallow) during the day likely reflects changes in water cover across the landscape, as winter progresses (added flooding and rainfall), that drives geese to switch resources during the season and highlights different periods in the winter life cycle of geese. For example, as residual seeds begin to sprout green shoots in fallow fields later in the winter after seasonal rains, geese frequently switch to "green browsing" - consuming green vegetation rather than cereal grains to supplement energetic needs (Hill & Frederick, 1997; Skalos et al., 2021). Additionally, the decomposition of rice due to winter flooding, eventually degrades and decomposes the waste rice grain such that it no longer holds value as a food resource (Greer et al., 2009). Post-harvest flooding of rice fields occurs across large spatial extents throughout the Sacramento Valley to decompose postharvest rice stubble without burning (Miller et al., 2010). Post-harvest flooding treatment occurs between October and December and produces wet rice habitat beneficial for waterfowl, while beginning the decomposition of post-harvest rice waste (Elphick & Oring, 1998). These processes could explain the strong daytime preference across all species for wet fallow habitats, most particularly Pacific white-fronted geese and snow geese, for which it was the most strongly selected diurnal habitat, closely followed by dry rice.

Large expanses of dry rice habitat are created when the rice is harvested in September (www.ers.usda.gov) producing waste rice – rice left behind by the mechanical harvesting process (Gilmer et al., 1982; Halstead et al., 2011; Naylor et al., 2005). This timing coincides with the arrival of populations from their lengthy fall migrations (Pacific White-fronted geese – beginning early to mid-September; Snow, Ross's and Tule geese – October-November) and dry rice provides a beneficial food resource that offers immediate, high nutritional value to replenish the energy used from migration (Fleskes et al., 2018; Gilmer et al., 1982; Miller et al., 2010). Geese are known to exploit dry rice fields for food (Elphick & Oring, 1998; Skalos et al., 2021). Therefore, dry rice fields likely provide the most important post-migration food resource for geese populations (Central Valley Joint Venture, 2006, 2020; Ely, 1992), prior to postharvest field flooding.

Tule geese by contrast, exhibited a clear preference for wetlands during the day and Ross's geese favored dry rice, followed by wet and dry fallow. Tule geese, a California species of special concern (Deuel & Takekawa, 2008), potentially prefer this habitat because, unlike the other species that are adapted to graze, Tule geese have long necks and bills that aid them in feeding in deeper wetland settings on the tubers of emergent vegetation (Deuel & Takekawa, 2008; Wege, 1984). However, the sharp decline in wetland over the last century has since caused them to supplement their diet with waste grains (Deuel & Takekawa, 2008; Gilmer et al., 1982). Ross's geese also differed from the other geese with a daytime habitat preferential selection that moderately favored dry rice over wet and dry fallow habitats.

Additionally, their nocturnal habitat selection also differed from the other species, with a lower relative selection of wet rice than the other geese. These results likely reflect the fact

that the majority of our Ross's geese data were collected in the spring when much of the forage available in rice fields had either been depleted or decomposed (Greer et al., 2009) and "green browse" became available. At this time of year, after other food resources (rice) have been depleted through intensive foraging, by early season migrant arrivals (Greer et al., 2009; Petrie et al., 2016), the green shoots sprouted from residual fallowed seeds offer an alternative food source. Moreover, Ross's geese were primarily observed in the Llano Seco unit, which primarily consists of wetlands, vernal pools, and pasture, which the CropScape satellite imagery reads as fallow or wetland land covers. Furthermore, management actions in Llano Seco have focused on grass seed planting (CALFED & River Partners, 2004). "Dry fallow" areas that have grass growth, while containing less digestible energy than rice, offer higher nutritional value than the exposed dirt fallow fields more common on agricultural lands (McDonald et al., 2010).

Habitat selection preferences also varied with the amount of time the habitat had been in its wet or dry condition. Recent flooding was highly important, and geese's consistent preference of younger wet rice habitats may be driven by several factors. The practice of flooding rice fields not only serves to reduce rice stubble burning and thus, air pollution, but also produces beneficial habitat and food resources for waterfowl that would otherwise not be in burnt fields (Fleskes et al., 2016; Hill et al., 2006; Miller et al., 2010). However, flooding not only decomposes post-harvest rice stubble, but also ultimately decomposes the energy rich rice grains, reducing desirability and availability of food in flooded fields (Greer et al., 2009).

The use of non-flooded habitats by geese in the day may allow dabbling ducks to take advantage of wetland habitats and flooded fields to meet their own resource needs in the absence of direct competition from geese. However, coincident use of these habitats by ducks

and geese is likely to be detrimental to the smaller duck species which may be out competed by larger geese that consume more food (Central Valley Joint Venture, 2006; Petrie et al., 2016). Although the exponential increase of white geese will eventually become self-limiting (Massé et al., 2001), replacement of rice fields with crops of greater economic value such as nut orchards, further reduces this important waterfowl food resource in the Central Valley (Sleeter, 2008; Soulard & Wilson, 2015) resulting in a cascading effect of increasing interspecific competition. If the presence of geese in these habitats reduce the ability of ducks to meet their resource requirements, and if ducks are unable to supplement their diet elsewhere due to habitat loss, it will undoubtedly impact duck populations negatively through increased competitive exclusion. This is a serious concern for waterfowl managers when two species occupy identical niches, competition will inevitably drive the other to local exclusion, if not extinction (Hardin, 1960).

Considerations and Future Research

While we examined several variables to quantify spatial habitat-use patterns and selection of geese, a number of other variables beyond the scope of this study could potentially influence habitat use. For example, proximity to (and thus, disturbance effects of) hunting activity, the quantity of food available in each parcel, predator abundance, strength of philopatry, conspecific and allospecific interactions, and intrinsic and extrinsic behaviors could all further affect how geese choose to use the landscape. Furthermore, we were unable to incorporate or assess bioenergetic factors such as calories consumed, or amount of time spent eating. This would require assessment of seed density and decomposition rates of various wetsoil seed types as well as detailed time budget analyses. Finally, a similar analysis on dabbling ducks would provide valuable information regarding the occurrence and impacts of direct

interspecific competition, niche partitioning or differentiation and competitive exclusion, and how these factors impact Pacific Flyway waterfowl so that management and conservation actions could be developed to the benefit of all species.

Conservation and Management Implications:

Duck populations continue to decline in California as populations of white geese and, to a lesser extent White-fronted geese, consistently increase (Central Valley Joint Venture, 2006, 2020; USFWS, 2019). While the management implications extend far beyond the scope of this study, the methods described, coupled with high-frequency locational data, are tools we could use to obtain ongoing insights on waterfowl habitat-use patterns, which is particularly important in a changing landscape. With detailed GPS data, we can continue to identify areas of importance at a much larger scale, than more limited, labor-intensive tracking methods (VHF telemetry) and during times when visual surveys are not possible (e.g., night). Unsurprisingly, we found that geese avoided orchards and urban areas, and instead selected rice, fallow, and wetland habitats. Geese exploit both wet and dry rice fields, where ducks almost exclusively utilize wet rice (Central Valley Joint Venture, 2006; Petrie et al., 2016). While there currently is no shortage of rice available for both ducks and geese, accessibility of these habitats favors geese. With water becoming less abundant, more harvested rice fields are remaining dry for longer periods, providing the abundant, larger bodied geese more time to reduce the amount of available post-harvest rice accessible to ducks once water is applied. In light of this, a staggered flooding approach, starting as early as September, when ducks begin to arrive back in the Sacramento Valley, would expand the wet rice habitat available to ducks, increasing available and beneficial food resources, aiding their post-migratory recovery.

Management strategies similar to The Nature Conservancy's 'Bird Returns', a dynamic conservation incentive program that provides temporary habitat for migrating shorebirds in the Pacific Flyway (Golet et al., 2018), could accomplish this by providing incentives for land managers. For example, funding farmers for water purchases would enable them to amend their water regimes to apply water to habitat parcels earlier in the year, which would benefit the different phenological timing of ducks' and geese's returns from migration. By using similarly detailed duck GPS locations we could begin to evaluate areas in the valley, of high habitat-use overlap with geese (e.g., Fig. 10) and identify those which would most benefit from these types of programs to minimize or abate spatial competition. We could also use this information to identify duck "strongholds." Of our four tracked goose species, the Tule goose is the only species that utilizes the Suisun Marsh (Fig. 10). With ducks regularly using the Suisun Marsh, and infrequent use by individuals of the small Tule goose population (estimated ~6000 individuals total; CDFW *pers. com*, 2020), we observed limited interference between the taxa (Fig. 10). This exemplifies the importance of the conservation of Suisun Marsh and any other habitats where competition may be minimal, and thereby preventing further duck population declines.

Figure 10: Map of Sacramento Valley, California (with National Wildlife Refuges and State Wildlife Areas indicated), showing the overlap of geese and ducks from all GPS locations acquired from an expansive tracking study of four species of geese (shades of pink) and nine species of ducks (shades of blue) conducted over 7+ years (2015-22). The lighter the colors represent the fewer locations in any given area and darker shades indicate the areas of heaviest use. When goose and duck locations overlap the colors mix, forming shades of purple, the darker of which indicate heavier overlap.

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Supplemental Information

SI Table 1: USDA National Agricultural Statistic Service's CropScape cropland data layer classifications condensed into broader categories based on their ecological significance to our study.

SI Table 2: USDA National Agricultural Statistic Service's CropScape cropland data layer classifications condensed into "Other". The "other" category is also sorted into subcategories: orchard, grain, row crops, urban, and water.

SI Table 3: ΔAIC values for 13 models with 8 variations (4 species x photo period).

 SI Table 4: Models with different reference levels other than the standard "wet rice" reference level. The models indicated by the colors below, were unable to converge with "wet rice" as its reference level when the models were run.

Species Category

 SI Table 5: Frequency of observed (used) points from each species during the day or night in each of the 6 categories.

SI Table 6: Frequency of randomly generated points within an empirical step length from any given selection event (available points) in each habitat category. The numbers in parenthesis and in bold are the number of observed selection event points (used) in each habitat category.

