

Spatial Use by Wintering Greater White-Fronted Geese Relative to a Decade of Habitat Change in California's Central Valley

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Abstract

We investigated the effect of recent habitat changes in California's Central Valley on wintering Pacific greater white-fronted geese (*Anser albifrons frontalis*) by comparing roost-to-feed distances, distributions, population range sizes, and habitat use during 1987–1990 and 1998–2000. These habitat changes included wetland restoration and agricultural land enhancement due to the 1990 implementation of the Central Valley Joint Venture, increased land area used for rice (*Oryza sativa*) production, and the practice of flooding, rather than burning, rice straw residues for decomposition because of burning restrictions enacted in 1991. Using radiotelemetry, we tracked 192 female geese and recorded 4,516 locations. Geese traveled shorter distances between roosting and feeding sites during 1998–2000 (24.2 ± 2.2 km) than during 1987–1990 (32.5 ± 3.4 km); distance traveled tended to decline throughout winter during both decades and varied among watershed basins. Population range size was smaller during 1998–2000 (3,367 km²) than during 1987–1990 (5,145 km²), despite a 2.2-fold increase in the size of the Pacific Flyway population of white-fronted geese during the same time period. The population range size also tended to increase throughout winter during both decades. Feeding and roosting distributions of geese also differed between decades; geese shifted into basins that had the greatest increases in the amount of area in rice production (i.e., American Basin) and out of other basins (i.e., Delta Basin). The use of rice habitat for roosting (1987–1990: 40%, 1998–2000: 54%) and feeding (1987–1990: 57%, 1998–2000: 72%) increased between decades, whereas use of wetlands declined for roosting (1987–1990: 36%, 1998–2000: 31%) and feeding (1987–1990: 22%, 1998–2000: 12%). Within postharvested rice habitats, geese roosted and fed primarily in burned rice fields during 1987–1990 (roost: 43%, feed: 34%), whereas they used flooded rice fields during 1998–2000 (roost: 78%, feed: 64%). Our results suggest that white-fronted geese have altered their spatial use of California's Central Valley during the past decade in response to changing agricultural practices and the implementation of the Central Valley Joint Venture. (JOURNAL OF WILDLIFE MANAGEMENT 70(4):965–976; 2006)

Key words

agriculture, Anser albifrons, California, Central Valley Joint Venture, flooded rice, greater white-fronted geese, habitat use, landscape change, radiotelemetry, wetland management.

Historically, the Central Valley of California, USA, contained 1.6–2.0 million ha of wetland habitat (U.S. Fish and Wildlife Service 1978). However, more than 90% of these wetlands have been lost, mainly to agriculture and urban expansion, and less than 121,000 ha of wetlands remain (U.S. Fish and Wildlife Service 1978, Gilmer et al. 1982, Frayer et al. 1989, Dahl 1990). Despite this large decline in waterfowl habitat, the Central Valley of California, USA, provides wintering habitat for 60% of the migratory waterfowl in the Pacific Flyway and 20% of all waterfowl in North America (U.S. Fish and Wildlife Service 1978, Gilmer et al. 1982). Adequate wintering habitat in the Central Valley is important for maintaining waterfowl populations because poor habitat or crowded conditions can increase mortality rates due to density-dependent factors (e.g., disease and predation) and

because geese use nutrient reserves acquired on wintering areas, in part, for reproduction (Heitmeyer and Frederickson 1981, Krapu 1981, Gilmer et al. 1982, Raveling and Heitmeyer 1989, Ankney et al. 1991, Gauthier et al. 2003).

During the past decade, changing agricultural practices and conservation programs have altered the landscape in the Central Valley of California, USA. Three of the most important habitat changes for wintering waterfowl were the implementation of the Central Valley Habitat Joint Venture (CVHJV, renamed Central Valley Joint Venture [CVJV]), increased land area planted in rice (*Oryza sativa*) production, and the widespread agricultural practice of flooding, rather than burning, rice straw residues for decomposition. The CVJV was formed in 1988 under the auspices of the North American Waterfowl Management Plan (Canadian Wildlife Service and U.S. Fish and Wildlife Service 1986) with the goal of protecting, maintaining, and restoring wetland habitats, increasing carrying capacity, and maintaining traditional distributions of waterfowl in the Central Valley. In 1990, the CVJV developed an implementation plan with the goal of enhancing or

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restoring 380,000 ha of wetlands and agricultural lands at a capital cost of more than \$528 million and an annual cost of about \$29 million (CVHJV Implementation Board 1990). Habitat improvements included establishment of new state Wildlife Areas and National Wildlife Refuges, restoration of private wetlands, and enhancement of agricultural lands for wildlife.

In addition to the CVJV, restrictions placed on burning rice straw residues (California Rice Straw Burning Reduction Act of 1991; AB-1378) led to the increased practice of flooding rice fields after harvest to speed straw decomposition as farmers sought alternatives to burning (Brouder and Hill 1995, Wrynski et al. 1995, Elphick and Oring 1998, Bird et al. 2000). At the same time, the amount of land area in rice production increased by 23% in the northern Central Valley (Fleskes et al. 2005) because of improved rice prices and subsidies (Childs 1997). Rice fields flooded after harvest increased from 24,000 ha in 1985 to 61,000 ha in 1995, with about 2,400 ha serving as waterfowl sanctuaries in 1985 because of no or light hunting pressure compared with 16,200 ha serving as sanctuary in 1995 (CVHJV Technical Committee 1996). Flooding of harvested rice fields increases use by waterfowl and provides foraging habitat, thereby partially alleviating the loss of historic wetlands (Day and Colwell 1998, Elphick and Oring 1998, Elphick 2000, Czech and Parsons 2002). In contrast, other farming practices (e.g., use of the more efficient stripper-header rice harvester and the recent expansion of cotton farming into the Sacramento Valley) may have reduced the potential foraging quality of agricultural habitats to waterfowl (Miller and Wylie 1996). Overall, wetland habitat has increased by 67% (J. P. Fleskes, U.S. Geological Survey, unpublished data), and flooded rice habitat has increased by 47% in the northern Central Valley from 1989 to 1999 (Fleskes et al. 2005), increasing the availability of waterfowl sanctuaries and feeding sites.

Although these habitat changes presumably have benefited wintering waterfowl, it is unknown whether waterfowl altered their distribution, movements, and use of habitats in response to these landscape changes. We compared the wintering ecology of Pacific greater white-fronted geese (*Anser albifrons frontalis*, hereafter white-fronted geese) before these major habitat changes occurred (1987–1990) and after a decade of habitat change in the Central Valley (1998–2000). Specifically, we used radiotelemetry to examine the distance traveled from roosting to feeding sites, population range size, distribution among basins, and habitat used by white-fronted geese.

Study Area

The Central Valley of California, USA, is composed of 9 basins (U.S. Fish and Wildlife Service 1978, CVHJV Implementation Board 1990) with 95% of California's rice area in the Butte, Colusa, American, Sutter, Yolo, and Delta Basins (Fig. 1) in the northern Central Valley (Tippet and Hettinger 1986). Rice production in the Central Valley ranges annually from 140,000–180,000 ha (Hill et al. 1992) and has some of the highest yields in the world (Miller et al. 1989, Brouder and Hill 1995). In addition to rice habitats, there are numerous federal and state waterfowl refuges and private reserves (Fig. 1) in the Central Valley that comprise about 191,000 ha (J. P. Fleskes, U.S. Geological Survey, unpublished data).

Methods

Capture and Radiomarking

We captured geese in Alaska, USA, during late summer and in the Upper Klamath Basin (1987–1990 only) in northeastern California, USA, during early fall before their arrival in the Central Valley. In Alaska, USA, we herded molting geese into corral traps (Cooch 1953) with aircraft near the Kashunuk and Manokinak rivers on the central Yukon–Kuskokwim Delta (YKD; 61°20'N, 165°20'W) on 23–25 June 1987, on 29 July in 1988, from 26 July 1989 to 9 August 1989, from 21 June 1998 to 31 July 1998, and from 8 July 1999 to 5 August 1999. In the Klamath Basin, we captured geese using rocket nets (Winn-Star Inc., Marion, Illinois; Dill and Thornsberry 1950) at the Tule Lake National Wildlife Refuge from 27 September 1987 to 17 October 1987, from 22 March 1988 to 1 November 1988, and from 19 March 1989 to 31 October 1989. We determined the age and sex of all captured geese, and we weighed and measured most adults (Orthmeyer et al. 1995) and radiomarked adult females. We marked geese with United States Fish and Wildlife Service leg bands and either a 45-g radiotransmitter attached to a backpack harness (1987 and 1988; Advanced Telemetry Systems Inc., Isanti, Minnesota) or a 30-g solar radiotransmitter (Advanced Telemetry Systems) glued to a yellow plastic neck collar (Spinners Plastics, Springfield, Illinois) individually identified with black digits (1989, 1999, and 2000; see Ely 1993, Ely and Takekawa 1996). Transmitter life was about 14 months for backpack radiotransmitters and 24 months for solar-powered radiotransmitters. We released geese at the capture site.

Radiotelemetry

We tracked geese when they arrived in the Central Valley of California, USA, from trucks and fixed-wing aircraft equipped with dual 4-element Yagi antenna systems (Advanced Telemetry Systems); trucks had null-peak systems (AVM Instrument Company, Livermore, California) to accurately determine bearings, whereas aircraft had left–right systems (Advanced Telemetry Systems) to circle and pinpoint signals on either side of the plane (Gilmer et al. 1981). We located geese daily by truck from 1 November through 15 March and monthly by aircraft from 1 November to 15 April of each year (Ely and Takekawa 1996). For each location by truck, we obtained 2 bearings within several minutes to minimize movement error. We did not use >2 bearings because our initial tests indicated doing so did not increase location accuracy in our flat and open study areas. Warnock and Takekawa (1995) reported average error rates of 1.5 degrees for bearings, 58 ± 35 (SE) m for distances between true and calculated locations, and 1.1 ha for error–polygon size with similar truck systems and location distances (e.g., <3 km). We used a modified version of XYLOG and UTMTEL triangulation programs (Dodge and Steiner 1986, Dodge et al. 1986) to calculate Universal Transverse Mercator coordinates for each location. White-fronted geese generally fly from roosting to feeding sites each morning and evening to feed in agricultural fields (Ely 1990, 1992, Krapu et al. 1995), and based on our field observations, we classified locations collected during morning (0531–1030 hours) and evening (1531–2230 hours) as feeding sites and midday (1031–1530 hours) and night-time (2231–0530 hours) as roosting sites. We verified feeding and roosting locations with direct observations whenever possible, or we recorded the

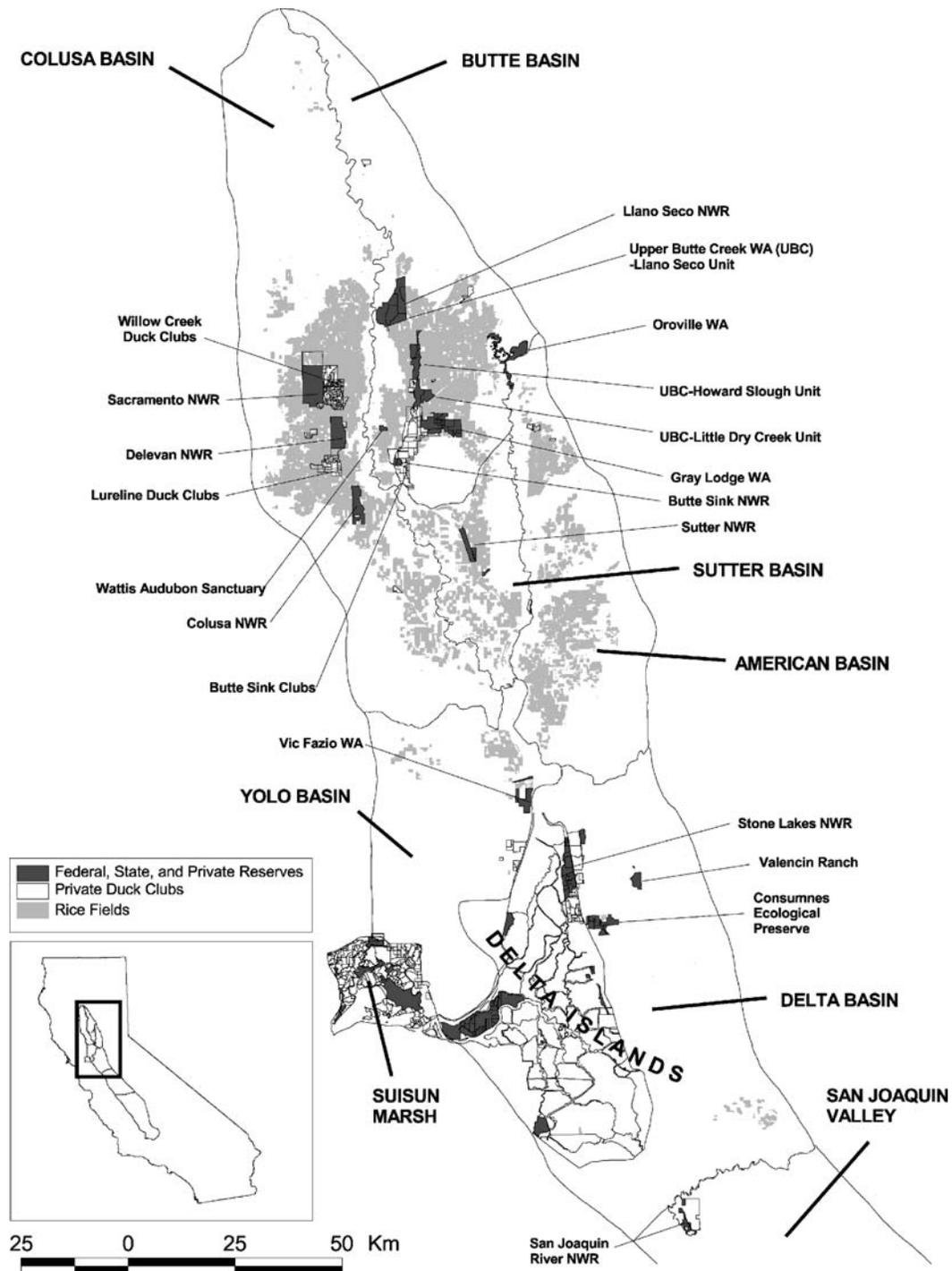


Figure 1. Study area map showing current watershed basins, National Wildlife Refuges (NWR; dark shading), State Wildlife Areas (WA; dark shading), nongovernmental ecological preserves (dark shading), and associated wetland habitats (not shaded) within the Central Valley of California, USA. Areas in rice production during the 1999–2000 winter are in light shading. Wetlands added or enhanced since 1987–1990 in the northern Central Valley focus area include Wattis Audubon Sanctuary, Vic Fazio WA, Llanos Seco NWR, Upper Butte Creek WAs (Llanos Seco Unit, Howard Slough Unit, and Little Dry Creek Unit), Stone Lakes NWR, Valencin Ranch, and Consumnes Ecological Preserve. The Suisun Marsh includes numerous (nonlabeled) duck hunting clubs, Grizzly Island WA, Joice Island WA, Hill Slough WA, Island Slough WA, Grey Goose WA, Gold Hills WA, Cordelia Slough WA, West Family WA, and Goodyear Slough WA. The Sacramento–San Joaquin River Delta islands mainly include rice fields flooded after harvest, corn fields unflooded after harvest, and some wetlands.

main behavior associated with a time period when we could not observe the goose during triangulation. Rather than visually identifying the radiomarked individual within a large flock located at the point of triangulation, we assumed that the behavior of the radiomarked goose was similar to the main behavior of the flock.

Waterfowl hunting seasons were ongoing during the start of our study and ended in the third or fourth week of January each year; therefore, November, December, and January data mostly represent hunting conditions, whereas February and March data represent posthunting conditions.

Habitat Types

We intersected radiotelemetry locations in 1998–2000 with digitized habitat maps (Landsat imagery) and conducted direct observations of habitat use in 1987–1990 to obtain habitat-use data for each bird location. Habitat patch sizes (generally large continuous fields of rice or managed wetlands) were much larger than triangulation error reported using similar systems (Warnock and Takekawa 1995). To facilitate interpretation of habitat types, we grouped similar habitats into 4 categories: wetland, upland, rice, and other crops. Wetland habitat category included open marsh, hemi-marsh, and emergent marsh subcategories. Upland habitat category included grassland, irrigated pasture, and woodland subcategories. Rice habitat category included all types of agricultural rice habitats, including burned, postharvest; flooded, postharvest; puddled, postharvest (postharvested fields that were ponded from rainfall); and dry, postharvest subcategories. We determined puddled, postharvest fields using visual observations during tracking. The “other crop” category included winter wheat, corn, milo, onion, sunflower, black dirt (postharvested fields that were disked), fallow bare, and fallow weeds subcategories. We excluded other habitats (including lake, reservoir, and sewage pond subcategories) from our habitat analysis because they were used infrequently by geese (<1% of locations). We did not determine the availability of different habitat types throughout the Central Valley; rather, we examined goose habitat use.

Statistical Analyses

To determine whether white-fronted geese changed their wintering ecology from 1987–1990 to 1998–2000, we used Akaike's Information Criterion (AIC) to select the best models of distance traveled from roosting to feeding sites, population range, distribution among basins, and habitats used by geese. This approach often performs better than restricting the selected model to those variables with statistically significant effects in hypothesis-based tests, especially for observational data (Burnham and Anderson 1998, Anderson et al. 2000). We used a second-order AIC for small sample sizes: $AIC_c = -2(\log\text{-likelihood}) + 2K(N/N - K - 1)$, where K is the number of fitted parameters including variance, and N is the sample size (Burnham and Anderson 1998, Anderson et al. 2000). We considered the model with the smallest AIC_c to be the most parsimonious (Burnham and Anderson 1998, Anderson et al. 2000). We used the AIC_c differences between the best model and the other candidate models ($\Delta_i = AIC_{c_i} - \text{minimum } AIC_c$) to determine the relative ranking of each model. For biological importance, we considered models for which $\Delta_i \leq 2$ (Burnham and Anderson 1998, Anderson et al. 2000, 2001). Additionally, we calculated Akaike weights ($w_i = \exp[-\Delta_i/2] / \sum \exp[-\Delta_i/2]$) to assess the weight of evidence that the selected model was the actual Kullback–Leibler best model in the set of models considered (Burnham and Anderson 1998, Anderson et al. 2000). We also calculated hypothesis weights by summing Akaike weights across models that incorporated the same set of variables to help assess the relative importance of variables. For all analyses, we used telemetry locations of female geese from 1 November to 15 March of each year. We conducted statistical analyses with SAS (SAS Institute Inc. 1999).

Distance traveled between roosting and feeding sites.—To reduce the likelihood of autocorrelation among locations, we

treated the locations of separate birds, or the same birds in separate months or roosting basins, as independent replicates of distance behavior. For each combination of bird, month, and roosting basin, we calculated roost-to-feed distances by averaging the straight-line distances for all possible roosting and feeding location pairings. For example, we calculated and averaged 6 distances if a bird had 2 roosting and 3 feeding locations. To avoid potential biases associated with differential sampling intensity across time, we used the first feeding and roosting location collected for each bird and week combination.

We calculated and compared AIC_c values for 18 candidate models consisting of linear mixed models incorporating variables selected from decade, month, roost basin, and all 2-way interactions, including a model with no effects. We included a random year effect in all models without a decade term, and we included a random year effect nested within the decade effect in all models that included a decade term.

Population range.—We defined population range size as the size of the overall distribution of radiomarked geese. We used only the first location per bird each month in the population range analyses to eliminate any potential biases associated with differential sampling intensity among individuals. We determined the size of radiomarked geese's population range using a 95% fixed-kernel estimator for ArcView (ESRI Inc., Redlands, California; Hooge and Eichenlaub 1997).

We calculated and compared AIC_c values for 5 candidate models consisting of linear mixed models incorporating variables including decade, month, and the 2-way interaction, including a model with no effects. We included a random year effect in all models without a decade term, and we included a random year nested within the decade effect in all models that included a decade term.

Distribution among Central Valley basins.—We used only the first location per bird each month in distributional analyses to reduce any potential biases associated with sampling intensity of individuals. Very few geese (<1%) were located in the northern and southern (Tulare Lake) San Joaquin Valley Basins, so we excluded these from analysis. We used log-linear mixed models to analyze the relative frequency of goose locations across basins. We further modeled the frequency of goose locations in relation to decade, month, roost or feed behavior effects, and random year effects (Wolfinger and O'Connell 1993, Littell et al. 1996). Any interaction effect involving basin with another variable represents an effect by this variable on the relative frequency of goose locations distributed across basins (Agresti 2002). Therefore, we considered 18 hypothesized models incorporating variables interacting with the basin effect, using variables selected from decade, month, roost or feed behavior, and 3-way interactions containing basin including a model with no interactions with basin. Each of the hypothesized models could be structured in 18 variations based on 9 variations of possible additional interactions among the variables decade, month, and roost or feed behavior (but not involving basin), and 2 variations based on whether there was a random-year interaction with basin. Because we were not certain which variation would best describe the hypothesized models, we ran 18 variations of 18 hypothesized models for a total of 324 candidate models. We calculated the total AIC weight of

Table 1. Ranking of candidate models describing white-fronted goose distributions and habitat use between 1987–1990 and 1998–2000 in the Central Valley of California, USA. All candidate models with Akaike weights ≥ 0.05 are shown.

Model type/structure ^a	Log-likelihood	N	k ^b	AICc	Δ AICc ^c	Akaike weight ^d	GOF ^e
Roost-to-feed distance traveled ^f							
m rb m d, random y(d)	-1,197.16	750	16	2,427.07	0.0	0.81	0.12
m rb m d rb d, random y(d)	-1,193.44	750	21	2,430.15	3.1	0.17	0.13
Population range size ^f							
m, random y	-232.13	25	4	474.26	0.0	0.55	0.60
m d, random y(d)	-229.63	25	6	475.93	1.7	0.23	0.67
m d, random y(d)	-231.53	25	5	476.22	2.0	0.20	0.60
Basin distribution ^f							
m d rf, b d b m, random y(d) b \times y(d)	-252.40	250	38	594.84	0.0	0.67	1.08
m d rf d, b d b m, random y(d) b \times y(d)	-252.38	250	39	597.61	2.8	0.17	1.08
m d rf, b d b m, random y(d)	-255.47	250	37	598.20	3.4	0.12	1.18
Habitat use ^f							
m d rf d, h d h m h rf, random y(d)	-188.75	200	35	462.87	0.0	0.36	3.79
m d rf d, h m h rf, random y(d) h \times y(d)	-192.32	200	33	464.15	1.3	0.19	3.56
m d rf d, h d h m h rf, random y(d) h \times y(d)	-188.17	200	36	464.68	1.8	0.15	3.64
m d rf, h m h d rf, random y(d)	-185.78	200	38	465.97	3.1	0.08	3.62
m d rf d, h m h d rf, random y(d)	-185.78	200	38	465.97	3.1	0.08	3.62
Rice habitat use ^f							
m d rf d, h d h m h rf, random y(d) h \times y(d)	-186.76	160	31	451.02	0.0	0.30	3.53
m d rf d, h m h rf, random y(d) h \times y(d)	-192.79	160	27	451.03	0.0	0.30	3.43
m d rf, h d h m h rf, random y(d) h \times y(d)	-189.08	160	30	452.58	1.6	0.14	3.62
m d rf, h m h rf, random y(d) h \times y(d)	-195.43	160	26	453.42	2.4	0.09	3.52
m d rf d, h m, random y(d) h \times y(d)	-198.85	160	24	454.60	3.6	0.05	3.93

^a Abbreviations: d = decade, m = month, b = basin, rb = roost basin, h = habitat type, rf = roosting or feeding behavior, y = year. “d|m” represents d, m, and d \times m interaction, whereas “d m” represents d and m.

^b The number of estimated parameters in the model including the variance.

^c The difference in the value between AICc of the current model and the value for the most parsimonious model.

^d The likelihood of the model given the data, relative to other models in the candidate set (model weights sum to 1.0).

^e Goodness-of-fit measured as R^2 for the distance and range size models, and as deviance of overdispersion for the distribution and habitat use models.

^f The number of candidate models for each model type were 18 for roost to feed distance traveled, 5 for population range size, 180 for basin distribution, 180 for habitat use, and 180 for rice habitat use.

each hypothesized model by summing the AIC weights across the 18 variations.

Habitat use.—We used every location recorded for the habitat analyses. We assumed that our observations of use-of-habitat types were not biased by any differences in sampling intensity and detection probability. Sampling methodologies were similar between decades, so if any sampling biases did exist, they would not have affected our main results: assessing changes in habitat use between decades (i.e., they would be consistent biases). We analyzed habitat use among the 4 major categories and among the 4 rice subcategories by repeating the same analysis used for basin distribution, except we replaced the basin variable with the habitat category variable and the rice subcategory variable, respectively. For the rice habitat subcategory analysis, we combined data from February and March because our models did not converge due to low sample sizes in March when we treated it as a separate month.

Basin use related to habitat change between decades.—For each basin, we calculated the proportional change between decades in distances traveled by geese from roosting to feeding sites, roosting basin use, and feeding basin use and compared this with the proportional change between decades in rice production, postharvested flooded rice during midwinter, and wetland habitats. Rice production and postharvested flooded rice data were summarized by Fleskes et al. (2005), and wetland habitat data were summarized by J. P. Fleskes (unpublished data) using data provided by the CVJV.

For each of the 3 dependent variables describing changes in

goose behavior, we compared simple univariate regressions, excluding the intercept term, for each of the 3 predictor variables and the first principal component of the 3 variables. Finally we compared these 4 models with the null model that included only the intercept, for a total of 5 candidate models.

Goodness-of-fit.—We assessed goodness-of-fit in linear models for the analysis of roost-to-feed distance and population range size by calculating the r -square (i.e., the coefficient of determination), based on all fixed effects. We assessed goodness-of-fit in log-linear models for the analysis of distribution and habitat use by estimating the overdispersion scale, calculated as deviance divided by degrees of freedom. Overdispersion scales much larger than 1 can indicate either lack of fit or overdispersion (Christensen 1990). We adjusted all AIC statistics to reflect any overdispersion in the log-linear models (Littell et al. 1996; O. Schabenberger, SAS, personal communication).

Results

We tracked 100 adult female white-fronted geese during winters of 1987–1990 and 92 adult female geese during winters of 1998–2000 in the Central Valley of California, USA. We recorded 2,907 goose locations during 1987–1990 and 1,609 goose locations during 1998–2000. We first conducted the basin-distribution analysis on data collected from 1987–1990, and we replaced the decade effect with the capture location to examine whether differences in marking locations interacted with relative basin use because we captured and marked most radiotracked geese in 1987–

Table 2. Distances (km) radiomarked white-fronted geese traveled from roosting locations to foraging sites during 1987–1990 and 1998–2000 in each basin throughout the Central Valley of California, USA.

Basin	Distance traveled				Change
	1987–1989		1998–1999		
	Mean	SE	Mean	SE	
American	30.5	4.1	22.5	3.6	–26%
Butte	23	3.1	18.6	3.1	–19%
Colusa	25.7	4.3	23.5	2.9	–9%
Delta	69.9	17.2	39.1	14.6	–44%
Sutter	20.4	4.1	18.6	2.4	–9%
Yolo	41.1	6.1	37.8	6.4	–8%
Total	32.5	3.5	24.2	2.3	–26%

1990 in the Klamath Basin on their southern migration toward the Central Valley (87 of 100), and all geese (92) in 1998–2000 were marked at YKD in Alaska before the start of their southern migration. The most parsimonious model contained month and year but not capture location ($w_i = 0.66$). Models that contained a capture location effect had a combined AIC weight of only 26%, compared with 74% without these effects, indicating that capture location did not have a large effect on goose distribution among basins. Hereafter, we pool all data from the two capture sites.

Distance Traveled Between Roosting and Feeding Sites

Using AIC model-selection criteria, the most parsimonious model explaining the distance traveled between roosting and feeding sites included decade, month, roost basin, and decade \times month and month \times roost basin interaction effects. The same model with the additional decade \times roost basin interaction also had some support (Table 1). Overall, models that contained decade had the most support, with a combined AIC weight of >99%, compared with <1% weight for models that did not contain a decade effect. The R^2 values for the top models were not high (12–13%; Table 1), indicating that our best models did not predict roost-to-feed distances accurately.

White-fronted geese traveled shorter distances between roosting and feeding sites during 1998–2000 (24.2 ± 2.2 km) than during 1987–1990 (32.5 ± 3.4 km), and distance traveled during February was less than during December and January (Fig. 2A) and varied among basins (Table 2). White-fronted geese traveled the shortest distances from roosting to feeding sites in Butte and Sutter Basins, whereas they traveled farthest in the Delta and Yolo Basins during both decades.

Population Range

The most parsimonious model explaining the population range size of radiomarked white-fronted geese contained only month, but models containing decade and month also provided good fits to the data (Table 1). The model that contained only month had the most support, with an AIC weight of 55%, compared with 23% for the model containing decade, month, and decade \times month interaction, and compared with 20% for the model containing decade, month, and no interactions. The R^2 values for the top models were high (60–67%; Table 1), indicating a good fit to the data. The population range of white-fronted geese was smaller during 1998–2000 (average of months: $3,367$ km²) than

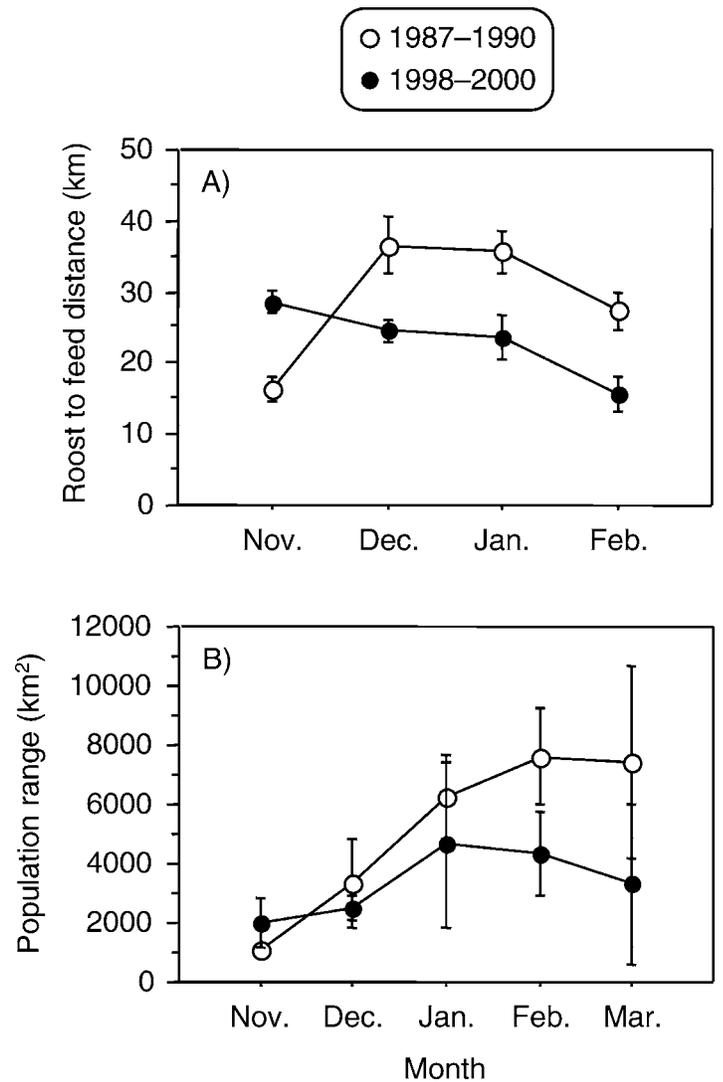


Figure 2. (A) Distance traveled from roosting to feeding sites (mean \pm SE) by radiomarked white-fronted geese during the winters of 1987–1990 (open) and 1998–2000 (filled) in the Central Valley of California, USA. (B) Population range size (mean \pm SE) of radiomarked white-fronted geese during the winters of 1987–1990 (open) and 1998–2000 (filled) in the Central Valley of California, USA.

during 1987–1990 (average of months: $5,145$ km²) and tended to increase throughout winter during both decades (Fig. 2B). The population range size was relatively small during November (1987–1990: $1,113$ km²; 1998–2000: $2,015$ km²) and tended to increase throughout winter until March (1987–1990: $7,390$ km²; 1998–2000: $3,322$ km²; Fig. 2B).

Distribution among Central Valley Basins

Sparse use by geese in some basins caused all models with a month \times basin interaction in our distributional analyses to fail to converge, making it impossible to evaluate month effects on basin distribution. We, therefore, combined Yolo and Sutter Basins to increase statistical convergence for all subsequent distributional analyses. Geese used Yolo Basin infrequently during both decades, and most locations in Yolo Basin were concentrated in one area just south of the Sutter Basin (Fig. 3). Eight out of the 18 hypothesized models that contained a 3-way interaction involving basin, month,

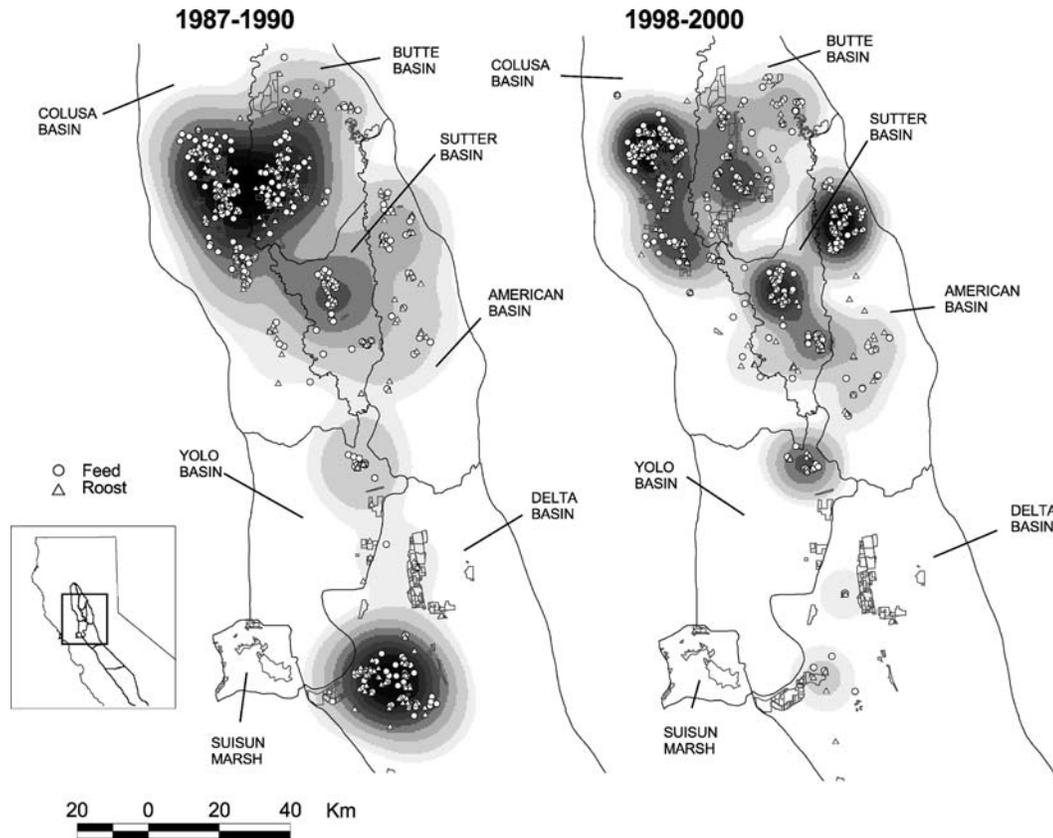


Figure 3. Distribution of radiomarked white-fronted geese during 1987–1990 ($n = 561$) and 1998–2000 ($n = 536$) in the northern Central Valley of California, USA. For each goose, only the first roosting and feeding location per month was used in distributional analyses to eliminate any potential bias in sampling effort among individuals. Fixed-kernel contours indicate use distributions by feeding (circles) and roosting (triangles) geese. Thick lines are basin boundaries, and thin lines delineate wetland habitats and state and federal waterfowl refuges (refer to Fig. 1 for details).

and a third variable failed to converge, even after we combined Yolo and Sutter. We assumed the 10 remaining hypothesized models were sufficient to identify a month effect and did not combine any further basins. Therefore, we calculated Akaike weights for 18 variations of only 10 models for 180 weights.

The 3 most parsimonious models explaining distribution of white-fronted geese among basins included the basin \times decade and basin \times month interactions (Table 1). Overall, models that contained basin \times decade and basin \times month interactions had the most support, with a combined AIC weight of 99%. The overdispersion scales for model fit were close to 1 (1.1–1.2; Table 1), indicating that our models fit the data reasonably well. During 1987–1990, white-fronted geese primarily used the Colusa, Butte, and Delta Basins, whereas during 1998–2000 geese were located

mainly within the Colusa, American, Butte, and Sutter Basins (Table 3). The relative distribution of geese shifted out of the Delta Basin in 1987–1990 and into the American Basin in 1998–2000 (Fig. 3). Most geese used the Sacramento Valley in early winter, and a portion of geese moved south into the Delta Basin as winter progressed during 1987–1990. Goose use of the Colusa Basin tended to decline throughout winter during both decades.

Habitat Use

Main habitat types.—We found strong evidence that goose habitat use varied with decade and even stronger evidence that habitat use varied with month and roosting or feeding behavior. The most parsimonious model explaining habitat use included the habitat type \times decade, habitat type \times month, and habitat type \times roosting or feeding behavior interactions (Table 1). Models

Table 3. Roosting and feeding distributions (percentage of locations) of radiomarked white-fronted geese among basins during 1987–1990 and 1998–2000 in the Central Valley of California, USA.

Basin	Roosting basin			Feeding basin		
	1987–1990	1998–2000	Difference	1987–1990	1998–2000	Difference
American	10	22	12	8	19	11
Butte	24	20	–4	22	21	–1
Colusa	28	34	6	34	34	0
Delta	23	4	–19	23	3	–20
Sutter	11	16	5	10	16	6
Yolo	5	5	0	5	7	2

Table 4. Habitat used (percentage of locations) by radiomarked white-fronted geese for feeding and roosting during the 1987–1990 and 1998–2000 winters in the Central Valley of California, USA.

Behavior/ habitat type	1987–1990	1998–2000	Difference
Roosting locations ^a			
Rice	40	54	14
Wetland	36	31	–5
Upland	2	5	3
Other crop	23	10	–13
Feeding locations ^a			
Rice	57	72	15
Wetland	22	12	–10
Upland	2	3	1
Other crop	19	13	–6

^a Sample size was 2,044 for roosting locations and 2,505 for feeding locations.

including these 3 interactions had the most support, with a combined AIC weight of 56%; compared with 23% for models containing habitat type × decade × roost or feed behavior interaction and habitat type × month interaction; and compared with 21% for models containing habitat type × month interaction and habitat type × roosting or feeding behavior interaction. The overdispersion scales for model fit were >1 (3.6–3.8; Table 1), indicating that our best models might be missing other factors that were predictive of habitat use.

Among the 4 main habitat type categories (rice, wetland, upland, and other crops), white-fronted geese roosted primarily within rice habitat (1987–1990: 40%, and 1998–2000: 54%) and also fed within rice habitat (1987–1990: 57%, and 1998–2000: 72%; Table 4). Use of rice habitat increased between decades, whereas use of wetlands and other crops declined for both roosting and feeding sites (Table 4). Within each decade, a higher proportion of feeding sites were in rice habitat compared with roosting sites, whereas a higher proportion of roosting sites were in wetlands compared with feeding sites (Table 4).

Rice habitat subcategories.—We found strong evidence that goose use of rice habitat subcategories (burned, postharvest; dry, postharvest; flooded, postharvest; and puddled, postharvest) varied with month and roosting or feeding behavior, and we found some support that rice habitat use varied among decades. The 2 best models explaining the use of rice habitat by geese were equally supported by the data. One model included rice habitat type × month and rice habitat type × roosting or feeding behavior interactions, and the second model included these interactions and the rice habitat type × decade interaction (Table 1). A second variation of these hypothesized models ranked third and fourth and also provided good fits to the data (Table 1). Models that contained rice habitat type × decade, rice habitat type × month, and rice habitat type × roosting or feeding behavior interactions had the most support, with a combined AIC weight of 47%, compared with 42% for models containing rice habitat type × month and rice habitat type × roost or feed behavior interactions, and compared with 6% for models containing only rice habitat type × month interaction. The overdispersion scales for model fit were >1 (3.4–3.9; Table 1), indicating that our best models were missing factors predictive of habitat use.

Table 5. Rice habitat used (percentage of locations) by radiomarked white-fronted geese for feeding and roosting during the 1987–1990 and 1998–2000 winters in the Central Valley of California, USA.

Behavior/ habitat type	1987–1990	1998–2000	Difference
Roosting locations ^a			
Burned	43	3	–40
Dry postharvest	14	9	–5
Flooded postharvest	25	78	53
Puddled postharvest	19	11	–8
Feeding locations ^a			
Burned	34	6	–28
Dry postharvest	32	18	–14
Flooded postharvest	10	64	54
Puddled postharvest	24	12	–12

^a Sample size was 681 for roosting locations and 1,186 for feeding locations.

Within rice habitats, geese roosted primarily within rice burned after harvest during 1987–1990 (43%), whereas they roosted in rice flooded after harvest during 1998–2000 (78%; Table 5). Similarly, geese fed mainly within rice burned after harvest during 1987–1990 (34%) and rice flooded after harvest during 1998–2000 (64%; Table 5). Use of rice burned after harvest decreased by 40% for roosting and 28% for feeding sites between decades, whereas use of rice flooded after harvest increased by 53% for roosting and 54% for feeding sites (Table 5). Roosting and feeding use of dry and puddled postharvested rice habitats also declined between 1987–1990 and 1998–2000 and could have contributed to the increased use of flooded rice between decades (Table 5).

Basin Use Related to Habitat Change between Decades

The most parsimonious models explaining decadal changes in both roosting and feeding distributions among basins contained the change in total basin area in rice production (Table 6). The next-best model contained the first principal component of changes in total rice area, flooded rice area, and wetland area within basins (Table 6). This indicates that feeding and roosting distributions of geese shifted between decades into basins that had the greatest increases in the amount of area in rice production, but changes in the amount of flooded rice and wetland habitat also influenced changes in goose distributions to a lesser extent (Table 7). For example, the greatest percentage increase in basin area in rice production was American Basin (40% [11,290 ha]), and the greatest percentage decline in rice production was in the Delta Basin (–70% [–3,306 ha]). Correspondingly, geese increased their use of the American Basin for roosting by 128% and for feeding by 129%, whereas they decreased their use of the Delta Basin for roosting by 82% and for feeding by 88% (Table 7).

In contrast, the most parsimonious model explaining decadal changes in distances traveled between roosting and feeding sites among basins contained the change in wetland habitat (Table 6). This indicates that declines in roost-to-feed distances between decades were greater in those basins with the largest increases in wetland area. For example, the Delta Basin had one of the greatest relative increases (129% [4,186 ha]) in wetland habitat between decades and also the largest decline (–44%) in the distance traveled from roosting to feeding sites by geese. Similarly, the

Table 6. Ranking of candidate models describing the response of white-fronted geese to changes in habitat within basins between 1987–1990 and 1998–2000 in the Central Valley of California, USA. All candidate models with Akaike weights ≥ 0.05 are shown.

Model type/structure ^a	Log-likelihood	N	K ^b	AICc	$\Delta AICc^c$	Akaike weight ^d
Change in roosting basins ^e						
Total rice change	-2.98	6	2	13.95	0.0	0.68
Prin1	-4.24	6	2	16.47	2.5	0.20
Flooded rice change	-5.60	6	2	19.21	5.3	0.05
Change in feeding basins ^e						
Total rice change	-4.43	6	2	16.85	0.0	0.59
Prin1	-5.61	6	2	19.21	2.4	0.18
Intercept	-6.21	6	2	20.41	3.6	0.10
Flooded rice change	-6.45	6	2	20.90	4.0	0.08
Wetland change	-6.66	6	2	21.32	4.5	0.06
Change in distance traveled from feed to roost sites ^e						
Wetland change	5.18	6	2	-3.37	0.0	0.59
Intercept	4.77	6	2	-2.54	0.8	0.40

^a Total rice change = change in the total rice area in production within a basin between decades; prin1 = first principal component of total rice change, flooded rice change, and wetland change; flooded rice change = change in the flooded rice area within a basin between decades; and wetland change = change in the wetland area within a basin between decades. All models have the intercept excluded, except for the intercept model that has the intercept and no covariates.

^b The number of estimated parameters in the model including the variance.

^c The difference in the value between AICc of the current model and the value for the most parsimonious model.

^d The likelihood of the model given the data, relative to other models in the candidate set (model weights sum to 1.0).

^e The number of candidate models for each model type were 5 for change in roosting basins, 5 for change in feeding basins, and 5 for change in distance traveled from feed to roost sites.

Colusa Basin had the smallest relative increase (20% [4,121 ha]) in wetland habitat and one of the smallest declines between decades in roost-to-feed distances (-9%; Table 7). However, the intercept model containing none of the habitat variables also fit the data well (Table 6), indicating that the relationship between the change in distance traveled from roosting to feeding sites and changes in wetland habitat was weak.

Discussion

During the past decade, changing agricultural practices and wetland conservation programs have altered the landscape in the Central Valley of California, USA. As a result, availability of waterfowl habitat in the northern Central Valley has increased by

38,000 ha of rice lands (23%), 25,000 ha of rice flooded after harvest (47%), and 29,000 ha of wetlands (67%) between 1989 and 1999 (Fleskes et al. 2005; J. P. Fleskes, unpublished data). In response to these habitat changes, we found that white-fronted geese altered their spatial use of the Central Valley by decreasing distances traveled between roosting and feeding sites, reducing their range, and changing their distribution and habitat use between 1987–1990 and 1998–2000.

Our methodology between decades was similar, but we used different radioattachments as methodologies improved over the years. Backpack radios (45 g; 1987 and 1988) may have been more energetically costly to geese than neck-collar radios (30 g; 1989, 1999, and 2000) because geese marked at the YKD with backpack

Table 7. Percentage change in habitat availability, white-fronted goose behavior, and hunter effort by basin between 1987–1990 and 1998–2000 in the Central Valley of California, USA.

Basin	Change between decades									
	Habitat type			Goose behavior			Hunter effort ^c			
	Total rice ^a	Flooded rice ^a	Wetlands ^b	Roost-to-feed distance	Roosting basin use	Feeding basin use	Hunter numbers	Days hunted	Geese bagged	Hunter success ^d
American	40	14	40	-26	128	129	26	23	58	7
Butte	20	62	156	-19	-17	-4	35	65	55	-2
Colusa	30	108	20	-9	18	3	30	26	36	3
Delta	-70	-82	129	-44	-82	-88	-10	-44	-28	7
Sutter	14	4	48	-9	48	70	22	17	27	3
Yolo	-10	-37	62	-8	11	56	24	90	69	-4
Total	23	47	67	-26	na	na	25	24	36	3

^a Fleskes et al. 2005.

^b J. P. Fleskes, U.S. Geological Survey, unpublished data.

^c Data from California Department of Fish and Game (1987, 1988, 1989, 1998, 1999; D. Yparraguirre, California Department of Fish and Game, personal communication). Data for all geese (white and dark) were averaged for 1987, 1988, and 1989 and separately for 1998 and 1999. Data were summarized among all counties occurring within a basin's boundary.

^d Difference between 1987–1990 and 1998–2000 in numbers of white and dark geese bagged per days hunted.

radios arrived in the Upper Klamath Basin later and departed later than geese wearing neck-collar radios (Ely and Takekawa 1996). This type of radioeffect probably did not influence our results pertaining to distribution and habitat use, although energetic constraints imposed by backpack radios could limit the distances traveled between roosting and feeding sites. However, in all basins, geese traveled longer distances in 1987 and 1988 than in 1998–2000 (Table 2), indicating that any limitations imposed by backpack radios were minimal when compared with decade effects.

Distance Traveled between Roosting and Feeding Sites

White-fronted geese traveled shorter distances between roosting and feeding sites during 1998–2000 than during 1987–1990 in all basins. Presumably this decline was due to an increased availability of both feeding and roosting sites. Distances traveled also varied among basins, with geese traveling the farthest in the Delta and Yolo Basins and the shortest distances in Butte and Sutter Basins, during both decades. Basin-specific declines in the distance traveled between decades were weakly related to positive changes in wetland habitat within basins.

Distance traveled tended to decline throughout winter during 1998–2000 and declined after December in 1987–1990. The winter decline was mostly due to short roost-to-feed distances occurring after the hunting season during February when more safe habitats were available, and geese, presumably, could roost closer to preferred foraging areas. It also is possible that more suitable roosting habitat became available as the winter progressed and more rice fields became flooded, providing roosting sites that were closer to preferred foraging areas. Geese may have reduced traveling distances in late winter to conserve energy (see Hill and Frederick 1997) and slow their winter decline in bodyweight (Ely and Raveling 1989). Conversely, Hobbs (1999) found that the distance traveled between roosting and feeding sites increased throughout winter in the Sacramento Valley, California, USA, for tule greater white-fronted geese (*Anser albifrons elgasi*); tule geese traveled 3.6 km in October and 5.9 km in January. Austin (1989) found that the distance traveled between roosting and feeding sites increased during winter for Canada geese (*Branta canadensis*) in Missouri, USA, from 2.5 km in late fall to 10.2 km in the spring. Hill and Frederick (1997) also found that the distance traveled from roosting to feeding sites by greater snow geese (*Chen caerulescens atlantica*) in Delaware, USA, increased from 5.3 km in early winter to 11.8 km in midwinter and then declined to 4.3 km in late winter. Presumably the increase in distance traveled between roosting and feeding sites found in these other studies (Austin 1989, Hill and Frederick 1997, Hobbs 1999) was due to the depletion of local food resources and static roosting sites (Harmon et al. 1960, Frederick and Klaas 1982, Hobaugh 1984, Hill and Frederick 1997).

Population Range

During our study, the Pacific white-fronted goose population increased 2.2-fold, from 174,900 to 390,700 (average of fall population indices from 1987–1989 and 1998–1999; Pacific Flyway Council 2003 Pacific Flyway Management Plan for the Greater White-fronted Goose, Greater White-fronted Goose Subcommittee, Pacific Flyway Study Committee [c/o United

States Fish and Wildlife Service], unpublished data). Despite this increase, the wintering population range size of radiomarked geese decreased from an average of 5,145 km² in 1987–1990 to 3,367 km² in 1998–2000. This indicates geese were able to concentrate their use of habitats to smaller areas, possibly due to increases in rice production within several basins. The population range also increased throughout winter during both decades, from 1,113 km² in November to 7,390 km² in March during 1987–1990 and from 2,015 km² in November to 3,322 km² in March during 1998–2000 (Fig. 2B). This indicates food resources became depleted as winter progressed and geese dispersed to find food, but resources became depleted to a lesser extent during 1998–2000 when more rice habitat was available. The decline in roost-to-feed distances between decades also supports this view, and it suggests that currently geese do not have to travel as far to find food. Increased land area used in rice production likely provided geese more food resources closer to preferred roosting sites, and increases in rice flooded after harvest and other wetland habitats likely provided geese additional roosting sites. The combination of these habitat changes apparently has allowed the larger goose population to concentrate their habitat use, thus reducing the population range and roost-to-feed distances between decades.

Distribution among Central Valley Basins

We found strong evidence that basin use varied with decade and month. White-fronted geese primarily used Colusa, Butte, and Delta Basins during 1987–1990 and Colusa, American, Butte, and Sutter Basins during 1998–2000. During 1987–1990, geese were mainly concentrated at the Sacramento and Delevan National Wildlife Refuges in the Colusa Basin, Gray Lodge, and Upper Butte Creek Wildlife Areas in the Butte Basin, and the Sacramento-San Joaquin River Delta in the Delta Basin. During 1998–2000, geese continued to be concentrated around the Sacramento and Delevan National Wildlife Refuges in the Colusa Basin, but they used the Butte Basin less frequently and rarely used the Delta Basin. Instead, geese increased their use of rice habitats within the American Basin and, to a lesser extent, the Sutter National Wildlife Refuge within the Sutter Basin. In general, the relative distribution of geese shifted out of the Delta Basin in 1987–1990 and into the American Basin in 1998–2000 (Fig. 3).

These distributional shifts corresponded to changes in habitat at the landscape level. Roosting and feeding distributions of geese shifted between decades into basins that had the greatest increases in the amount of area in rice production and out of basins with the largest declines (Table 7). For example, geese increased their use of the American Basin for roosting by 128% and for feeding by 129%, likely because of a 40% increase in the amount of basin area used for rice production, whereas geese decreased their use of the Delta Basin for roosting by 82% and for feeding by 88%, when rice production declined by 70% between decades. Geese may have fed mainly on corn in the Delta Basin because <5,000 ha of rice was produced in 1989 (of 164,000 ha total in the northern Central Valley) and declined to only 1,500 ha in 1999 (Fleskes et al. 2005). Changes in the amount of rice flooded after harvest and wetland habitat also may have influenced these changes in distribution but to a much lesser extent.

Habitat Use

Wintering white-fronted geese are highly dependent on agricultural habitats, and they feed heavily on waste grain, especially rice and corn (*Zea mays*; Glazener 1946, Leslie and Chabreck 1984, Ely and Dzubin 1994, Ballard and Tacha 1995, Krapu et al. 1995, Anderson et al. 1999). We also found that white-fronted geese used agricultural fields extensively during both decades but that their specific use of habitats differed between decades. White-fronted geese roosted primarily within rice and wetland habitats during both decades, but roosting geese increased their use of rice habitats and decreased their use of other wetlands between decades. Within rice habitats, geese roosted primarily within rice fields burned after harvest during 1987–1990, whereas they roosted predominantly within flooded rice fields after harvest during 1998–2000.

We found similar changes between decades in goose use of feeding habitats. Geese fed primarily in rice fields during both decades, and their use of rice fields for feeding sites increased between decades. Conversely, use of wetlands for feeding sites decreased between decades. Within rice habitats, geese fed mainly within rice fields burned after harvest in 1987–1990, whereas they fed mainly within flooded rice fields after harvest in 1998–2000. Within each decade, a higher proportion of feeding sites were in rice habitat compared with roosting sites, whereas a higher proportion of roosting sites were in wetlands compared with feeding sites. Time activity budgets of tule greater white-fronted geese in the Sacramento Valley of California, USA, also indicate that rice is the preferred feeding habitat; tule geese spent 55% of their time in rice habitats feeding, whereas they spent only 11% of their time in wetlands feeding (Hobbs 1999). Leslie and Chabreck (1984) also found that harvested rice fields were the major feeding habitat used by white-fronted geese in Louisiana, USA, and that geese preferred feeding in wet, and avoided dry, postharvested rice fields.

We did not measure the availability of different habitat types, so we cannot assess habitat selection. However, the large decline in the use of rice burned after harvest and increase in the use of flooded rice by geese was probably due to burning restrictions enacted in 1991 and farmer's subsequent shift to flooding rice fields after harvest as an alternative way of decomposing rice straw residues. In addition, the amount of land used in rice production has increased by 23% in the northern Central Valley, probably because of improved rice prices and subsidies (Childs 1997). As a result, the amount of flooded rice has increased by 47% in the

northern Central Valley, and some of these areas act as waterfowl sanctuaries because of little or no hunting pressure (CVHJV Technical Committee 1996).

Management Implications

The CVJV, together with recent increases in rice production and flooding, has likely contributed to the observed changes in spatial and habitat use by white-fronted geese during the past decade. To ensure that these habitat gains are sustained into the future, the challenge for the CVJV and other habitat program managers will be to meet the long-term habitat needs of waterfowl and to maintain the distribution of geese throughout the valley. The dependence of white-fronted geese on agriculture for feeding and roosting sites might give the false impression that natural wetland habitats are not necessary for maintaining wintering geese populations. However, the current level of rice flooded after harvest may not be sustainable given the increasing demands on water in California, USA, new uses for rice-straw residues, mosquito control, and changing agricultural practices (Gilmer et al. 1982, Wrynski 1995). Therefore, managers should continue to plan for the amount of wetland habitat that is necessary to maintain the distribution and abundance of geese in the future (CVHJV Implementation Board 1990).

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